

A TAXONOMICAL STUDY  
OF THE GENUS *APISTOGRAMMA* REGAN,  
WITH A REVISION  
OF BRAZILIAN AND PERUVIAN SPECIES  
(TELEOSTEI: PERCOIDEI: CICHLIDAE)

by

SVEN O. KULLANDER

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## 1. INTRODUCTION

The genus *Apistogramma* Regan, 1913, is a well-defined group of more than 40 species of small South American cichlid species. It has been known since 1906 as related to the genus *Geophagus* Heckel, 1840, but differing in smaller size, in having the lateral line running closer to the dorsal fin, slightly fewer dorsal fin rays, and narrower preorbital depth. The systematic work during the last 70 years has chiefly consisted in the descriptions of new species of which there has seemed to be an inexhaustible supply. New species are presented also in this contribution, but a large part of the paper is devoted to the summing-up of the history, taxonomy and geographical distribution of the genus, that I hope shall provide a basis for these additions, and also the long desired basis for further work with fishes of this group.

For loan of specimens I am much indebted to Dr. Jean-Pierre Gosse (IRSNB), Dr. Peter H. Greenwood and Mr. Gordon J. Howes (BMNH), Dr. Wolfgang Klausewitz (SMF), Prof. Horst Wilkens (ZIMH), Prof. K. Deckert (ZMB), Dr. Paul Kähsbauer (NHMW), Dr. Karl Heinz Lüling (ZFMK), Dr. Charles Roux (MNHN), Dr. Han Nijssen (ZMA), Dr. Bo Fernholm and Mr. Erik Åhlander (NRM), Dr. Ernst A. Lachner and Ms. Susan J. Karnella (USNM), Dr. William N. Eschmeyer (CAS) and Mrs. Carol Hutchings (AMNH), Dr. William L. Fink and Messrs. Robert Schoknecht and Karsten E. Hartel (MCZ), Dr. Loren P. Woods and Mr. Garrett S. Glodek (FMNH), Dr. James E. Böhlke and Mr. William G. Saul (ANSP), and Dr. Jørgen Nielsen (ZMK).

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I am much obliged to Dr. Gunnar Bertmar for promoting my interest in a revisionary study of *Apistogramma* by placing facilities and working space at my disposal at the University of Umeå, Umeå (Department of Biology, Section of Ecological Zoology) (1974-1976), and to Prof. Alf G. Johnels who provided working space at the NRM (Spring 1977). A large part of the present paper is a revised version of a thesis submitted to the University of Umeå in 1976.

I am also very grateful to my parents, Mr. and Mrs. Sven J. Kullander, for the financial support.

## 2. HISTORICAL REVIEW

### The 19th century

The first Caucasian to collect a specimen of *Apistogramma* was probably the British naturalist, Henry W. Bates, who found the type-specimen of *A. taeniata* in the rio Cupari, Brazil, in 1852. This species was technically described 10 years later by Albert C. L. G. Günther in the fourth volume of his catalogue of the fishes in the British Museum (1862: 312).

Günther erected a new genus, *Mesops*, for the new species and *Geophagus cupido* Heckel, 1840. Of *M. taeniatus* he had only the 42.7 mm long holotype, and of *G. cupido* obviously only Heckel's rather complicated description, so insufficient material may account for some of the currently recognized artificiality in the classification (*G. cupido* is the type-species of *Biotodoma* Eigenmann & Kennedy, 1903, regarded as closely related to *Geophagus* Heckel, but very distinct from *Apistogramma*). The new genus was intended for *Geophagus*-like fishes, i.e. with a lobe on the first gill-arch, but with the "eye in, or in advance of, the middle of the length of the head", as stated in Günther's key (p.265), and "preorbital not elevated", as indicated in the generic diagnosis (p. 311). In *Geophagus* [= *G. surinamensis* (Bloch, 1792)], and *Satanoperca* Günther, 1862 [= virtually, *Geophagus*] of Günther, the eye is situated behind the middle of the length of the head, and the preorbital is deep. No type-species was designated for *Mesops*.

During the Thayer Expedition (1865—1866) in Amazônia, J. Louis R. Agassiz noted "a great variety of small types [of Chromides = essentially, Cichlidae], no doubt hitherto overlooked by naturalists travelling in this region, simply under the impression that they must be the young of larger species" (Agassiz & Agassiz, 1969: 184). More than 600 specimens of *Apistogramma* taken by the expedition were labelled *Cotinhoa* sp. by Agassiz, but this material was never reported (W. L. Fink, in litt. 1977), and rediscovered too late for inclusion in this study. Another large portion of the Thayer material was described by Steindachner (1875).

In a report upon two collections of fishes from the Marañon (= R. Amazonas), Edward D. Cope, noted the presence of several specimens of *Mesops taeniatus* in a collection made by John Hauxwell "near Pebas, Ecuador" (= Pebas, Departamento Loreto, Peru), but gave no description (Cope, 1870: 570).

In his subsequent study of Amazonian fishes, Cope (1872: 250) described briefly as new species *Geophagus amoenus* from "River Ambyiacu" (= R. Ampiyacú, Departamento Loreto, Peru; cf. Lüling in Meinken, 1969a). It is said to be allied to Günther's *M. taeniatus*, and has, since Steindachner (1875), been regarded as either a synonym of that species or as a closely related valid species. The type-specimen is now lost (W. G. Saul, in litt. 1977), and new material seems not to have been collected. The characters used by Günther to split *Geophagus* into *Geophagus*, *Mesops*, and *Satanoperca*, principally the eye position in the head length, are not discrete, and Cope could not see the "necessity" of the subdivision. Consequently he referred his *amoenus* to *Geophagus*, but the second of his

new "*Geophagus*" species, *G. badiipinnis* (p.251), is demonstrably a specimen of *Chaetobranchius flavescens* Heckel, and his criticism of Günther's classification is thus made on questionable grounds.

Franz Steindachner was the first to synonymize *G. amoenus* with *M. taeniatus* (1875). He described at length "*Geophagus (Mesops) taeniatus*" from "Obidos, Teffé, Tabatinga und aus dem Flusse Tapajos", collected by the Thayer Expedition. I have examined part of his material and find at least three species (two from Codajás, one from Tefé, Estado do Amazonas, Brazil), none of which is Günther's species.

Steindachner reclassified *Mesops* as a subgenus of *Geophagus* and included in it besides *taeniatus* also *G. cupido*, and the new species *G. (M.) Thayeri* [= *Acarichthys heckelii* (Müller & Troschel, 1848)], and *G. (M.) Agassizii*. The latter is an *Apistogramma* species, and was based on specimens from "...Curupira..., Cudajas..., Rio Puty..., Lago Maximo..., See Manacapuru..." (in the type-series are also specimens from Lago Saraca), all collected by the Thayer Expedition. The localities are situated along the mainstream of the R. Amazonas in Brazil, except for the R. Puty (= R. Potí, Estado do Piauí, Brazil). In the lengthy description is noted sexual dimorphism in the shape of the fins (dorsal, anal, ventral and caudal), in the body depth, and in the colouration, and a large male in lateral aspect, the dorsal aspect of a head, and a scale are figured.

Cope (1878: 697) recorded two specimens of *Geophagus taeniatus* from Pebas or Nauta (Departamento Loreto, Peru). At least one of them may be an *Apistogramma*, since it had "... a deep brown band along the middle of the abdomen . . ." (probably a midventral stripe).

In a list of the freshwater fishes of South America, Carl H. Eigenmann and Rosa Eigenmann (1891: 70) retained *Mesops* as a subgenus of *Geophagus*, including *thayeri*, *cupido*, *taeniatus* (syn.: *amoenus*), *agassizii*, and *badiipinnis*.

With William L. Bray, Eigenmann revised the American cichlids, and they also considered *Mesops* a subgenus of *Geophagus*. *G. cupido* was designated as type-species. (Eigenmann & Bray, 1894: 621.)

George A. Boulenger produced the sixth description of an *Apistogramma* species, identified as "*Mesops taeniatus*", from Colonia Risso in Paraguay, collected by Alfredo Borelli (1895a: 1). This series was later found to be a composite of *A. borellii*, *A. trifasciata*, and *A. commbrae* (Regan, 1906a). Borelli collected more "*Mesops taeniatus*" in the Corumbá area (Estado do Mato Grosso, Brazil), reported again by Boulenger (1900: 1). These are *A. borellii* and *A. commbrae* (Regan, 1906a).

## 1902—1913

At the turn of the century had been described three *Apistogramma* species, generally classified as *Geophagus (Mesops)*, together with species of the genera

*Acarichthys*, *Biotodoma*, and, in one case, *Chaetobranchus*. The known range of the genus (sensu stricto) included the mainstream R. Amazonas from the mouth to the Peruvian Amazonas, and the upper course of the R. Paraguay.

Already in 1903 a new species was added, viz. *Biotodoma trifasciatus*, described by Eigenmann and Clarence H. Kennedy on a specimen collected by J. Daniel Anisits in Paraguay. *Biotodoma* was proposed as a substitute name for *Mesops* which had been found preoccupied. Interestingly, Eigenmann and Kennedy indicated in their key (p. 533) that the cichlid genera with a gill-arch lobe are mouth-brooders, and the name *Biotodoma* was given "in allusion to their habit of carrying the young in the gills" (*biotos*, Greek, living; *domos*, Greek, a home). That seems to be a too far going assumption based on observations on a few true *Geophagus* species (cf. Agassiz & Agassiz, 1869: 282; Agassiz, 1865: 282). Cichocki (1977a) has shown that the type-species of *Biotodoma*, *B. cupido*, is a substrate brooder.

The year before Jacques Pellegrin had published a list of the cichlids collected by Jobert in Brazil in 1878 (Pellegrin, 1902a). Of the *Geophagus* (*Mesops*) *taeniatus* listed from Tefé, Tonnantins, and Tabatinga, only the three Tefé specimens were included in his monograph of the cichlids that appeared two years later (Pellegrin, 1904: 187). One specimen from Manaus, and another from French Guyana were added, however. Although Pellegrin had reexamined the holotype of *M. taeniatus*, his redescription of the species is not very useful since it includes data from Boulenger (1895a), and Steindachner (1875). *Geophagus amoenus* is regarded as a synonym. The other species considered are *agassizii* (including doubtfully syntypes of *Acara punctulata* Günther, 1863, later described as *Nannacara anomala* Regan, 1905), the description copied from Steindachner (1875), only a specimen from "Amazoné" listed, and *trifasciatus*, the description copied from Eigenmann & Kennedy (1903).

Pellegrin's paper is important because he was the first to view the minute, lobe-bearing South American cichlids as a separate genus, including *agassizii*, *taeniatus* (incl. *amoenus*), and *trifasciatus*. However, he used the name *Biotodoma*, being of the opinion that *Geophagus cupido* was really a *Geophagus* species, and that Günther had meant the genus *Mesops* rather for *M. taeniatus*. The generic diagnosis was extended to include "Branchiospines rudimentaires ou absentes. Ecaillés cténoïdes, grandes (22—24). 2 lignes latérales, la supérieure extrêmement rapprochée de la dorsale surtout en arrière ou plus ou moins rudimentaire." (p. 187). Pellegrin also considered the eye position, previously used to characterize the *Geophagus*-like genera, as of lesser importance than the low gill-raker number, and the lateral line position (p. 186). The statement "Se rapproche du genre africain *Nanochromis*" (p. 187), probably refers to similarity rather than expresses an opinion on relationships.

In a series of papers published 1905—1906, Charles Tate Regan presented a revision of the American cichlids of much greater precision than achieved by Pellegrin. Regan (1906a: 60) did not accept Pellegrin's opinion on the name of the genus containing *Mesops taeniatus*, but followed Pellegrin in considering it and its allies generically distinct from *Geophagus cupido*, and proposed the name

*Heterogramma* without designating a type-species. The genus was characterized as having fewer dorsal fin rays (5–7) than *Geophagus* (9–14), and the upper lateral line running closer to the dorsal fin (not more than one scale between for most of its course). The diagnosis is fairly like that of Pellegrin (1904). Regan described five *Heterogramma* spp., viz. *H. taeniatum*, *H. agassizii*, *H. trifasciatum*, and the new *H. commbrae* and *H. borellii*, but obviously he also considered *G. amoenus* a member of this genus. In *H. taeniatum* he included Steindachner's (1875), and Pellegrin's (1904) material, but the description is essentially of the holotype.

Two nomenclatural problems take their dates from Regan's paper. The first concerns the correct spelling of *commbrae*, emended to *commbae* in the index to the volume of the *Annals and Magazine of Natural History* in which *commbrae* was published (Regan, 1906c), but actually the result of a misinterpretation of Eigenmann's hand-written "*corumbae*", the name Eigenmann had intended for the species and communicated to Regan by letter. The other is the gender of the name *Heterogramma* (and *Apistogramma*), treated as neuter by Regan (see p. 22, this paper).

Regan's next paper (1906b) concerning reference to *Heterogramma*, dealt with the evolution of the genera of Neotropical cichlids and their distribution. He attempted to show the phylogeny in a dendrogram in which the position of *Heterogramma* may be interpreted as if it was considered evolved from *Acara* Heckel, 1840 [= *Aequidens* Eigenmann & Bray, 1894], along a line giving off branches leading to *Retroculus* Eigenmann & Bray, 1894, *Geophagus*, and *Biotocetus* Eigenmann & Kennedy, 1903 (see Fig. 8, this paper).

Eigenmann, Waldo L. Mc Atee, and David P. Ward (1907) redescribed *trifasciata* as a member of Regan's genus, but ignorant of Regan on this point, Eigenmann and Ward described as a new species *H. corumbae*, which is obviously the same as was called *commbrae* and *commbae* by Regan. The two species are illustrated on photographs.

Rodolpho T. G. W. von Ihering's survey of Brazilian freshwater fishes (1907) may, as far as this family is concerned, be regarded as an abridged version of Regan's revisions (1905–1906), restricted to the Brazilian species.

Pellegrin (1908), in a popular review of the fishes of French Guyana, remarked that "*Biotodoma* ou *Heterogramma*" grow to 4 or 5 cm (p. 587), although actual presence in French Guyana was not indicated (but cf. Pellegrin, 1904).

In 1908 also appeared the fourth published figure of an *Apistogramma* species, this time of *steindachneri*, accompanying the protolog (Regan, 1908). This was the first record of *Apistogramma* in Guyana.

On a single specimen sent by the German aquarist Johann P. Arnold, labelled "La Plata", Regan (1909) described *Heterogramma pleurotaenia*. The holotype is the second reported specimen of this genus with four anal fin spines. The first was a *H. commbrae* reported by Regan (1906a), and as *Mesops taeniatum* by Boulenger (1895a).

Eigenmann (1910: 478) designated *Mesops taeniatus* as the type-species of *Heterogramma*, and listed the 7 species described up till then (*G. amoenus* as questionable synonym of *H. taeniatus*).

In a well-illustrated paper, John D. Haseman (1911c) recognized 9 taxa of *Heterogramma* in material collected by himself in the Paraguay and Amazonas basins during the one-man "Expedition of the Carnegie Museum to Central South America, 1907—1910". That collection, now in the Field Museum of Natural History, and the California Academy of Sciences, contains 108, mostly small and poor specimens of *Apistogramma*. Haseman's determinations leave something to desire on the point of accuracy, particularly as concerns his "*H. taeniatum*". 8 of the 9 taxa are figured on retouched photographs. *H. ritense*, *H. taeniatum pertense*, and *H. trifasciatum maciliense* are described as new species or subspecies. The name *H. ortmanni* is given to specimens from Manaus and the R. Guaporé, but it is evidently a nomen nudum (see p. 70, this paper).

Haseman continued his career with an extensive discussion on the South American ichthyofauna (1912). It contains a statement that "*Heterogramma taeniatum* can easily give rise to all of the species of this genus. In fact, I have reasons to doubt the reality of all of these species, because they may be nothing more than fluctuating variations, principally in color, or somatic changes which may or may not be inherited. At any rate, there is an almost complete intergradation of all of the species of the genus. Hence experimental work is needed before this genus can be properly classified."

Eigenmann (1912) described, and figured on retouched photographs *H. steindachneri*, and the new species *H. ortmanni*. His *steindachneri* in part had extensions of marginal caudal fin rays, and this is the first report on that type of caudal fin shape for this genus.

Regan eventually (1913) discovered that *Heterogramma* was preoccupied, and in his last paper in which the genus is treated, he proposed the new name *Apistogramma*, listed the known species, and described what he thought was *amoenus* on specimens from the R. Ucayali, Peru.

#### 1914—1977

With the coining of the name *Apistogramma*, 12 taxa had been described that were referable to this genus. *Mesops taeniatus* had been designated type-species, although still only one specimen was known of this species. Pellegrin and Regan had given a good characterization of the genus, and the latter also discussed its relationships. The known range included Guyana, French Guyana, and the Amazonas and Paraguay basins.

In 1914, Henry W. Fowler described *A. ortmanni rupununi*, from the Rupununi district of Guyana. It was based on two females of *A. steindachneri*.

In his great work on the fishes of Brazil (curiously often overlooked by later authors), Alipio de Miranda Ribeiro (1915) repeated descriptions of the Brazilian species, except for the description of an *Heterogramma taeniatum* of unknown locality. In 1918 he described and figured (monochrome photographs) *H. rondoni*. It is an *A. borellii*-like species known still only from the not reexamined six syntypes from Cáceres, Brazil (upper R. Paraguai).

David S. Jordan (1919: 520) designated *H. borellii* as the "ortho-type" of *Heterogramma*.

Eigenmann's (1922a: 196; 1922b: 239) records of *A. taeniatum* from the upper R. Meta system in Colombia, actually concern a new species, *A. macmasteri* (Kullander, in prep. a). His *A. corumbae* from the same region (1922a: 196; 1922b: 240) are probably misidentified, but have not been available for checking. These were, however, the first *Apistogramma* recorded from Colombia.

Nathan E. Pearson (1925: 53) recorded *A. taeniatum* and *A. taeniatum pertense* collected in the Departamento Beni, Bolivia, by the Mulford Expedition (1920–1921). The determinations are probably not correct, but the material has not been reexamined.

In the 1930's Ernst Ahl produced descriptions of several new *Apistogramma* species, based on single individuals, chiefly received from aquarium fish importers: *A. parva* (1931; Estado do Pará, Brazil), *A. ornatipinnis* (1936b; = *A. steindachneri*), *A. weisei* (1936a; = *Taeniacara candidi* Myers, 1935), *A. aequipinnis* (1938; vermutlich Argentinien), and *A. reitzigi* (1939; = *A. borellii*). *A. weisei* and *A. ornatipinnis* were figured by Arnold & Ahl (1936: 470, 566).

The Matto Grosso Expedition of the Academy of Natural Sciences of Philadelphia (1931) collected *A. commbrae* and *A. borellii* at Descalvados (R. Paraguai, Brazil), described and figured by Fowler (1932: 373–374).

In 1935 George S. Myers described, without figure, *Taeniacara candidi*, new genus and new species, from, possibly, the mouth of rio Negro, Brazil. In the habitus, sexual dimorphism, and small size, this species resembles *Apistogramma*, but it lacks the epibranchial lobe, and, curiously, a lateral line. Myers considered it close to *Nannacara*, another genus of minute Neotropical cichlids.

The double-banded *A. bitaeniata* was described from aquarium material (imports) by Pellegrin (1936) as a variety (subspecies) of *A. pertensis*. The type-locality, R. Madeira, Brazil, is probably wrong (p. 102, this paper).

Repeating in a rather striking manner the mistake Cope (1872) made with *G. badiipinnis*, his successor at the Academy of Natural Sciences of Philadelphia, Fowler (1940a), described and figured an *Acaronia* species as *Apistogramma ambloplitoides* (p. 142, this paper).

Fowler (1943: 265) reported a specimen of *A. corumbae* from Villavicencio (Departamento Meta, Colombia), but it is probably the case with it as with Eigenmann's (1922a, b).

The first Venezuelan species to be reported was discovered in 1947 by aquarium fish collectors, and described by Myers and Robert R. Harry (1948) as *A. ramirezi*. This species was later placed in a new genus, *Papiliochromis* (Kullander, 1977).

J. J. Hoedeman (1951) described and figured *A. cacatuoides*, stating his material to come from Surinam, but it is probably a Peruvian Amazonas species (p. 87, this paper). The occurrence of *Apistogramma* in Surinam was reliably reported first by M. Boeseman (1952, 1956) who recorded *A. steindachneri*.

Fowler (1954) in his magnificent reference collection of Brazilian freshwater fishes, overlooked *A. parva* (and *A. weisei* and *Taeniacara candidi* as well), and his bibliographies are somewhat too uncritically compiled to be of any greater use. However, he erected a new genus for *A. trifasciata*, viz. the monotypic *Pintoichthys*, distinguished by a serrate preoperculum (pp. 316, 386). The type-species was, however, still listed as an *Apistogramma* species (p. 278), and *Pintoichthys* is probably not maintainable (p. 33, this paper). Other papers by Fowler including references to *Apistogramma*, are his lists of Bolivian (1940b), Colombian (1942), and Peruvian (1944a) fishes.

Wolfgang Wickler (1956) studied the attachment apparatus of cichlid eggs and found it of taxonomical use as shown in his discussion of the systematic position of *A. ramirezi* (1960). In the latter paper the typical *Apistogramma* eggs are described as being of "p-Typ", i.e. the attaching spot is limited to one pole, and the adhesive threads are wound together in a corkscrew fashion and embedded in a jelly-like substance.

The reproductive behaviour of *A. reitzigi* [= *A. borellii* ?] was studied by Eva Butz and Peter Kuenzer (1957), who found that, although it was generally assumed for Dwarf Cichlids that the female alone takes care of the brood, their *A. reitzigi* male was fully capable of performing female brood-care activities, but no pair-bond could be demonstrated. Kuenzer (1962a, b) studied the parent-brood communications in "*A. reitzigi*", and "*A. borellii*" [= *A. cacatuoides*].

The German aquarist and amateur fish taxonomist Hermann Meinken published more than 60 pp. on *Apistogramma* between 1960 and 1971. He introduced the arrangement of the lateral line pores on the head as a taxonomic character and also (1962) attempted to distinguish groups of species within the genus. Most of his papers contain a discussion of the geographical distribution of the genus. Unfortunately, several of his new species are based on material in very poor condition, rotten or malformed, with obscure or no locality data; his scheme for groups of species is based on characters of dubious relevance (eye diameter

relative snout length; fin shape of males); in the discussions are frequently given new data without mention from where it is; and he was not always careful in the examination of critical characters such as the lateralis pores.

In his 1962 survey of the genus Meinken recognized 25 taxa, overlooking *A. bitaeniata*. Of these he had himself described *A. wickleri* [= *A. steindachneri*], and *A. trifasciatum haraldschultzi* [= *A. trifasciata*] in 1960 (a, b), *A. sweglesi* in 1961 (a), and *A. klausewitzii* [= *A. bitaeniata*] in 1962. He had then also described *A. cacatuoides* as *A. borellii* in 1961(b). In 1964 appeared the description of *A. kleei* [= *A. bitaeniata*], in 1965(b) the description of the first true *Apistogramma* species to be recorded from Venezuela, viz *A. hoignei*. *A. gibbiceps* (1969) was the first, and still only, species described in this genus having an occipital protuberance, not uncommon in other genera of cichlids, but the type-series included also *A. agassizii* and a not described species without that characteristic. The last paper on the fishes of the genus (1971) presented the description of *A. geisleri* from Óbidos, and *A. borellii* [= *A. regani*] from near Manaus. Besides these papers, Meinken wrote several shorter, and mentioned the genus in papers on other fishes. He is also the author of the *Apistogramma* descriptions in Holly et al.

*Apistogrammoides pucallpaensis* Meinken (1965a) was described as *Apistogramma*-like, but without epibranchial lobe and with 8 anal fin spines. Re-examination of the poor material in the type-series shows that there is indeed a lobe, and the anal spine number is 7 in three specimens and 8 only in one. Nevertheless, the genus appears to be valid. The type-material was collected by Albert J. Klee, who described their natural habitat and that of *A. borellii* [= *A. cacatuoides*] near Pucallpa, Peru (Klee, 1965).

John E. Burchard Jr. (1965) presented a rather detailed study of family behaviour in *A. trifasciata*. He concluded that the sexual dimorphism in species of this genus arose chiefly from intraspecific selection for territory size in males, and labelled the pair-bond structure polygamous. Wickler (1966) classified a number of *Apistogramma* species as polygamous (= polygynous), dimorphic, and concealment brooders (Versteckbrüter).

Georges Marlier collected *A. agassizii*, *A. gephyra*, *A. pertensis*, and *A. regani* when studying lakes in the Amazonas basin in 1963 and 1964. Ecological data for his localities were given in his papers of 1965 and 1967.

Michael M. Ovchynnyk (1967: 42; 1968: 263) studied the fish fauna of Ecuador, and recorded *A. amoenus* [= ?] from headwaters of the R. Amazonas.

Rosemary H. Lowe-McConnell studied the ecology of fishes in Guyana and treated the cichlids at length without more than mentioning the existence of *Apistogramma* spp. (1969).

Karl Heinz Lüling collected *A. luelingi* in the Todos Santos area in Bolivia, and reported on the habitats in which it was found (1969a, b; 1973b), although he used the name *A. borelli*.

In a stomach content analysis of a large series of Amazonian fishes, Hans-Armin Knöppel (1970) noted in *A. agassizii* an appetite for Hydracarina.

During the 1970's Pierre Vandewalle (1973) published a paper on caudal osteology in cichlids with reference to *A. agassizii* and *A. ortmanni* [= *A. sp. nov.* from French Guyana], Kullander (1976) described *A. luelingi* from the Mamoré drainage in Bolivia, the first known *Apistogramma* species with normally 4 anal fin spines, and Kullander (1977), describing a new genus, *Papiliochromis*, for *A. ramirezi*, gave some new diagnostic characters for *Apistogramma* (more anterior dorsal fin origin; cycloid predorsal and preventral scales; gill-rakers on the lower pharyngeal tooth-plate).

By 1977 thus had been described 31 species and subspecies of *Apistogramma*, but the number of valid species was only 20. The known range of the genus included the Amazonas basin from Santarem to Pucallpa, R. Capim, the Bolivian Amazonas, R. Portuguesa in Venezuela, R. Meta headwaters in Colombia, Ecuadorian Amazonas headwaters, Guyana, French Guyana, Surinam, and the R. Paraguay in Paraguay and Brazil. The genus was known to consist of small species, often, if not always, sexually dimorphic, and with a specialised reproductive behaviour including polygyny and concealment of the egg-spot. Little was known about the ecology, although a few habitats had been described. Systematically, the genus was known as close to *Geophagus*, but very little else.

Table 1. Records or descriptions of *Apistogramma* specimens in chronological order, with redeterminations. Unless otherwise stated the material has been reexamined. Protologs are marked with an asterisk (\*).

Original determination	Author	Locality	Redetermination
<i>Mesops taeniatus</i>	* Günther, 1862: 312	River Cupai	<i>Apistogramma taeniata</i>
<i>Mesops taeniatus</i>	Cope, 1870: 570	Pebas, Ecuador	Not reexamined
<i>Geophagus amoenus</i>	* Cope 1872: 250	Ambyiacu River	Lost
<i>Geophagus (Mesops) Agassizii</i>	* Steindachner, 1875: 111	Curupira; Cudajas; Rio Puty; Lago Maximo; See Manacapuru	<i>Apistogramma agassizii</i> ; A. sp. Part examined
<i>Geophagus (Mesops) taeniatus</i>	Steindachner, 1875: 115	Obidos; Teffé; Tabatinga; Tapajos	<i>Apistogramma</i> spp. Part examined
<i>Geophagus taeniatus</i>	Cope, 1878: 697	Pebas or Nauta	Not reexamined
<i>Mesops taeniatus</i>	Boulenger, 1895a: 1	Colonia Risso	<i>Apistogramma borellii</i> ; A. <i>commbrae</i> ; A. <i>trifasciata</i>
<i>Mesops taeniatus</i> <sup>1</sup>	Boulenger, 1900: 1	Carandasinho; Urucum	A. <i>borellii</i> ; A. <i>commbrae</i>
<i>Geophagus (Mesops) taeniatus</i>	Pellegrin, 1902a: 183	Teffé; Tonnantins; Tabatinga	Not reexamined
<i>Biotodoma trifasciatus</i>	* Eigenmann & Kennedy, 1903: 536	Arroyo Chagalalina	<i>Apistogramma trifasciata</i>
<i>Biotodoma taeniatum</i>	Pellegrin, 1904: 187	Guyane française; Manaos; Teffé	Not reexamined
<i>Biotodoma Agassizi</i>	Pellegrin, 1904: 187	Amazone	Not reexamined (? syntype)
<i>Heterogramma Borellii</i>	* Regan, 1906a: 63	Carandasinho, Matto Grosso; Colonia Risso	<i>Apistogramma borellii</i>

Original determination	Author	Locality	Redetermination
<i>Heterogramma commbrae</i>	* Regan, 1906a: 64	Carandasimho, Matto Grosso; Colonia Risso	<i>Apistogramma commbrae</i>
<i>Heterogramma trifasciatum</i>	Regan, 1906a: 65	Colonia Risso	<i>Apistogramma trifasciata</i>
<i>Heterogramma trifasciatum</i>	Eigenmann et al., 1907: 145	Corumba	Not reexamined
<i>Heterogramma corumbae</i>	* Eigenmann et al., 1907: 146	Corumba; Puerto Max	Part of Corumbá material reexamined: <i>Apistogramma combrae</i>
<i>Heterogramma borelli</i>	Eigenmann et al., 1907: 146	Corumba	Not reexamined
<i>Heterogramma steindachneri</i>	* Regan, 1908: 370	Georgetown, Demerara	<i>Apistogramma steindachneri</i>
<i>Heterogramma pleurotaenia</i>	* Regan, 1909: 270	La Plata	<i>Apistogramma pleurotaenia</i>
<i>Heterogramma</i> spp.	Haseman, 1911: vide Tab. 2		
<i>Heterogramma ortmanni</i>	* Eigenmann, 1912: 506	Erukun, etc.	<i>Apistogramma ortmanni</i> , Part reexamined
<i>Heterogramma steindachneri</i>	Eigenmann, 1912: 508	Guyana localities	<i>Apistogramma steindachneri</i> Part reexamined
<i>Apistogramma amoens</i>	Regan, 1913: 283	R. Ucayali	<i>Apistogramma</i> sp.
<i>Apistogramma ortmanni rupununi</i>	* Fowler, 1914: 277	Guyana, 2-3°N, 50°20'W	<i>Apistogramma steindachneri</i> Holotype reexamined
<i>Heterogramma taeniatum</i>	A. de Miranda Ribeiro, 1915: 45	---	Not reexamined
<i>Heterogramma rondoni</i>	* A. de Miranda Ribeiro, 1918: 16	Caceres, na Caicara (Campina)	Not reexamined

Original determination	Author	Locality	Redetermination
<i>Heterogramma taeniatum</i>	A. de Miranda Ribeiro, 1918: 17	Manáos	Not reexamined
<i>Apistogramma taeniatum</i>	Eigenmann, 1922a: 196; 1922b: 239	Rio Negro, Villavicencio	<i>Apistogramma macmasteri</i>
<i>Apistogramma corumbae</i>	Eigenmann, 1922a: 196; 1922b: 240	Barrigón	Not reexamined
<i>Apistogramma taeniatum</i>	Pearson, 1925: 53	Reyes; Lago Rogoagua; Ivon	Not reexamined
<i>Apistogramma taeniatum pertense</i>	Pearson, 1925: 53	Lago Rogoagua	Not reexamined
<i>Apistogramma parva</i>	* Ahl, 1931: 210	Rio Capim	<i>Apistogramma parva</i>
<i>Heterogramma corumbae</i>	Fowler, 1932: 373	Descalvados	<i>Apistogramma corumbae</i>
<i>Heterogramma borellii</i>	Fowler, 1932: 373	Descalvados	<i>Apistogramma borellii</i>
<i>Heterogramma ortmanni</i>	di Caporiacco, 1935: 70	Demerara	Not reexamined
<i>Apistogramma pertense</i> var. <i>bitaeniala</i>	* Pellegrin, 1936: 56	Rio Madeira, Brésil	<i>Apistogramma bitaeniala</i>
<i>Apistogramma weisei</i>	* Ahl, 1936a: 268	Santarem	Not reexamined
<i>Apistogramma ornatipinnis</i>	* Ahl, 1936b: 141	Britisch-Guiana	<i>Apistogramma steindachneri</i>
<i>Apistogramma aequipinnis</i>	* Ahl, 1938: 246	vermutlich Argentinien	<i>Apistogramma aequipinnis</i>
<i>Apistogramma reitzigi</i>	* Ahl, 1939: 81	wahrscheinlich Brasilien, Amazonasstromgebiet	<i>Apistogramma borellii</i>
<i>Apistogramma ambloplitoides</i>	Fowler, 1940a: 281	Contamana, Peru	<i>Acartonia nassa</i>

Original determination	Author	Locality	Redetermination
<i>Apistogramma corumbae</i>	Fowler, 1943: 265	Villavicencio; five miles from Villavicencio	Not reexamined
<i>Apistogramma ramirezi</i>	* Myers & Harry, 1948: 1	Venezuela	<i>Papiliochromis ramirezi</i>
<i>Apistogramma cacatuoides</i>	* Hoedeman, 1951: 1	near Paramaribo, Dutch Guiana	<i>Apistogramma cacatuoides</i>
<i>Apistogramma steindachneri</i>	Boeseman, 1952: 198	Lucie River; Upper Corantyne River?	Not reexamined
<i>Apistogramma steindachneri</i>	Boeseman, 1956: 196	Surinam	Not reexamined
<i>Apistogramma wickleri</i>	* Meinken, 1960a: 655	---	<i>Apistogramma steindachneri</i>
<i>Apistogramma trifasciatum haraldi schulzi</i>	* Meinken, 1960b: 291	Oberer Guaporé	<i>Apistogramma trifasciata</i> (incl. holotype); <i>A. sp.</i>
<i>Apistogramma sweglesi</i>	* Meinken, 1961a: 136	Letitia in Peru	Not reexamined
<i>Apistogramma taeniatum longirostris</i>	* Meinken, 1961a: 138	Letitia in Peru	Not reexamined
<i>Apistogramma borellii</i>	Meinken, 1961b: 166	---	Not reexamined
<i>Apistogramma kausewitzi</i>	* Meinken, 1962: 138	Brasilien, Oberer Solimões, Igarapé Preto	<i>Apistogramma bitaeniata</i>
<i>Apistogramma kleei</i>	* Meinken, 1964: 293	---	<i>Apistogramma bitaeniata</i>
<i>Apistogramma hoignei</i>	* Meinken, 1965b: 257	Camaguan swamps, R. Portuguesa, Venezuela	<i>Apistogramma hoignei</i>
<i>Apistogramma borellii</i>	Klee, 1965: 424	between the Pachitea River and Tournavista	<i>Apistogramma cacatuoides</i> ; <i>Crenicara punctulata</i> ; <i>Geophagus jurupari</i>
<i>Apistogramma amoenus</i>	Ovchynnyk, 1967: 42	Rio Lagortacocha, ..., Prov. Napo-Pastaza	Not reexamined

Original determination	Author	Locality	Redetermination
<i>Apistogramma amoenus</i>	Ovchynnyk, 1968: 263	Rio Pana Yacu, ..., Prov. Napo-Pastaza	Not reexamined
<i>Apistogramma laeniatum</i>	Marlier, 1967: 103	Lago Redondo	<i>Apistogramma regani</i>
<i>Apistogramma gibbiceps</i>	* Meinken, 1969: 91	Rio Negro-Gebiet	<i>Apistogramma gibbiceps</i> (incl. holotype); <i>A. agassizii</i> ; <i>A. sp.</i>
<i>Apistogramma ortmanni</i> <i>rupununi</i>	Lowe-McConnell, 1969: 299	Rupununi district	<i>Apistogramma steindachneri</i> Part examined
<i>Apistogramma borelli</i>	Lüling, 1969b: 72	"Hoffmann Lagune" (Todos Santos)	<i>Apistogramma luelingi</i>
<i>Apistogramma amoenum</i>	Lüling, 1969b: 76	Rio Chipiriri	Not reexamined
<i>Apistogramma agassizii</i>	Knöppel, 1970: 309	Lago Calado	Not reexamined
<i>Apistogramma geisleri</i>	* Meinken, 1971: 35	Rio Curuçamba bei Obidos	<i>Apistogramma geisleri</i>
<i>Apistogramma borellii</i>	Meinken, 1971: 38	Igarape, S. Jorge, bei Manaos	<i>Apistogramma regani</i>
<i>Apistogramma agassizi</i>	Vandewalle, 1973: 280	---	<i>Apistogramma agassizii</i>
<i>Apistogramma ortmanni</i>	Vandewalle, 1973: 280	---	<i>Apistogramma sp. nov.</i> (Oyapock)
<i>Apistogramma luelingi</i>	* Kullander, 1976: 259	Todos Santos area, Bolivia	<i>Apistogramma luelingi</i>

Table 2. The *Apistogramma* specimens collected and reported by Haseman (1911c), with his determinations, CM and present registration numbers, localities, and my redeterminations.

Haseman's determination	CM No.	Present reg. No.	Locality	Redetermination
<i>H. agassizi</i>	2729	FMNH 54161	Manaus	<i>A. agassizii</i>
<i>H. agassizi</i>	2730a—b	FMNH 54162	Santarem	<i>A. agassizii</i>
<i>H. agassizi</i>	2731a—c	FMNH 54163	San Joaquín	<i>A. sp. (new)</i>
<i>H. taeniatum</i>	2732a—c	FMNH 54164	Bragança	<i>A. caetei</i>
<i>H. taeniatum</i>	2733a—c	FMNH 54165pt ?	São Antônio de Guaporé	<i>A. sp. (new)</i>
<i>H. taeniatum</i>	2734a—d	FMNH 54165pt ?	São Antônio de Guaporé	<i>A. sp. (new)</i>
<i>H. taeniatum</i>	2735	FMNH 54166	Santarem	<i>A. sp. (new)</i>
<i>H. taeniatum</i>	2736	FMNH 54167	Santarem	<i>A. sp. (new)</i>
<i>H. taeniatum</i>	2737	FMNH 54168	Cáceres	<i>A. sp. (new)</i>
<i>H. taeniatum</i>	2738a—e	FMNH 54165pt ?	São Antônio de Guaporé	<i>A. sp. (new)</i>
<i>H. taeniatum</i>	2739	FMNH 54169	Manaus	<i>A. pertense</i>
<i>H. taeniatum</i>	2740a—b	FMNH 54170	Posada	<i>A. sp. (new)</i>
<i>H. t. pertense</i>	2741	FMNH 54171	Manaus	Holotype; not reexamined
<i>H. t. pertense</i>	2742	Unknown	Santarem	Not reexamined
<i>H. corumbae</i>	2752	FMNH 54178pt	Cáceres	<i>A. sp. (new)</i>
<i>H. corumbae</i>	2753	FMNH 54179	Corumbá	? <i>A. commbrae</i>
<i>H. corumbae</i>	2754	FMNH 54180	Villa Hayes	<i>A. commbrae</i>
<i>H. corumbae</i>	2755	FMNH 54178pt	Cáceres	<i>A. sp. (new)</i>
<i>H. ortmanni</i>	2757a—k	pt: CAS 14774	Bastos	Not reexamined
<i>H. ortmanni</i>	2756	Unknown	Manaus	Not reexamined
<i>H. trifasciatum</i>	2743	FMNH 54172pt	Cáceres	<i>A. trifasciata</i>
<i>H. trifasciatum</i>	2744a—b	FMNH 54173	Villa Hayes	<i>A. trifasciata</i>
<i>H. trifasciatum</i>	2745a—e	FMNH 54172pt	Cáceres	<i>A. trifasciata</i>
<i>H. trifasciatum</i>	2746a—b	FMNH 54174pt	Campos Alegre	<i>A. trifasciata</i>
<i>H. trifasciatum</i>	2748a—j	pt: FMNH 54175	Bastos	<i>A. trifasciata</i>
<i>H. trifasciatum</i>	2750a—i	FMNH 54176	São Antônio de Guaporé	<i>A. trifasciata</i>
<i>H. trifasciatum</i>	2758a—b	FMNH 54174pt	Campos Alegre	<i>A. trifasciata</i>
<i>H. trifasciatum</i>	2759	FMNH 54183	Cáceres	<i>A. trifasciata</i>
<i>H. t. maciliense</i>	2751a—d	pt: CAS 33722	São Antônio de Guaporé	Holotype
<i>H. borellii</i>	2760a—c	FMNH 54184	Villa Hayes	<i>A. borellii</i>
<i>H. borellii</i>	2761	FMNH 54185pt	Corumbá	<i>A. borellii</i>
<i>H. borellii</i>	2762	FMNH 54185pt	Corumbá	<i>A. borellii</i>
<i>H. borellii</i>	2763a—e	Unknown	Puerto Suarez	Not reexamined
<i>H. borellii</i>	2764a—h	FMNH 54186	Puerto Suarez	<i>A. borellii</i>
<i>H. ritense</i>	2765a—d	pt: FMNH 54187	Santa Rita	Not reexamined

### 3. THE GENUS *APISTOGRAMMA* REGAN, 1913

#### Type-species

*Mesops taeniatus* Günther, 1862, by subsequent designation (Eigenmann, 1910: 478).

#### Bibliography

- Mesops* (pt) Günther, 1862: 311 (protolog, diagnosis; spp.: *Geophagus cupido* Heckel, *M. taeniatus* Günther; no type-species), 265 (in key to cichlid genera).
- Geophagus* (pt) Cope, 1872: 251 (*Mesops* Günther included in *Geophagus* Heckel).
- Geophagus* (*Mesops*) (pt) Steindachner, 1875: 107 (*Mesops* Günther regarded as subgenus of *Geophagus* Heckel; spp.: *G. cupido* Heckel, *G. (M.) thayeri* Steindachner, *G. (M.) agassizii* Steindachner, *M. taeniatus* Günther).
- Geophagus* (*Mesops*) (pt) Eigenmann & Eigenmann, 1891: 70 (in list of taxa of South American freshwater fishes; name; spp.: as of Steindachner, 1875, and *G. badiipinnis* Cope).
- Geophagus* (*Mesops*) (pt) Eigenmann & Bray, 1894: 621 (bibliography; discussion of generic characters; *Geophagus cupido* Heckel designated as type-species).
- Biotodoma* (pt) Eigenmann & Kennedy, 1903: 533 (in key to American cichlid genera; nom. nov. subst. *Mesops* Günther, preocc.).
- Biotodoma*, Pellegrin, 1904: 186 (bibliography; diagnosis; indicated *Mesops taeniatus* Günther type-species of *Mesops* Günther = *Biotodoma* Eigenmann & Kennedy; spp.: *M. taeniatus*, *G. (M.) agassizii* Steindachner, *B. trifasciatus* Eigenmann & Kennedy).
- Heterogramma* Regan, 1906a: 60 (protolog; bibliography; diagnosis; key to spp.: *Mesops taeniatus* Günther [indicated as type-species], *Geophagus (Mesops) agassizii* Steindachner, *H. borellii* Regan, *H. commbrae* Eigenmann, *Biotodoma trifasciatus* Eigenmann & Kennedy).
- Heterogramma* von Ihering, 1907: 321 (bibliography; diagnosis; based on Regan, 1906a).
- Heterogramma* Eigenmann, 1910: 478 (in list of tropical and temperate South American freshwater fishes; name, distr.; *Mesops taeniatus* Günther designated as type-species; 7 spp.).
- Heterogramma* Eigenmann, 1912: 506 (bibliography; diagnosis).
- Apistogramma* Regan, 1913: 282 (nom. nov. subst. *Heterogramma* Regan, preocc.; 10 spp.).
- Heterogramma* Jordan, 1919: 520 (in list of fish genera; *H. borellii* Regan designated as type-species).
- Apistogramma* Eigenmann & Allen, 1942: 400 (bibliography; distr.; diagnosis).
- Apistogramma* (pt) Fowler, 1954: 273 (bibliography).
- Pintoichthys* Fowler, 1954: 316, 386 (protolog; diagnosis; type-species by original designation *Biotodoma trifasciatus* Eigenmann & Kennedy).
- Apistogramma* (pt) Meinken, 1962: 141 (key-like list of spp.; 23 spp., 2 ssp.).

#### Etymology

*Heterogramma* from *heteros* (Greek), different, and *gramma* (Greek), line, i.e. with different (from *Geophagus*) lateral line. Gender feminine.

*Apistogramma* from *apistos* (Greek), unreliable, and *gramma* (Greek), line, i.e. with unreliable (often rudimentary) lateral line. Gender feminine.

Neither name explained by Regan.

*Pintoichthys*, "em atenção ao Dr. Oliveira Mario de Oliveira Pinto, graças ao seu interesse em tornar possível a publicação do presente trabalho [Fowler, 1954]" (Fowler, 1954). Gender masculine.

## Remarks

As pointed out on p. 8, Pellegrin (1904) guessed that Günther (1862) intended the genus *Mesops* primarily for *M. taeniatus* rather than for *Geophagus cupido*. In a way, Pellegrin's statement is a type-designation, but his use of the name *Biotodoma* for the genus invalidates the fixation, since the type-species of *Mesops* = *Biotodoma* was already given as *G. cupido* by Eigenmann & Bray (1894). Regan's (1906a) statement: "I am quite in agreement with Pellegrin in regarding *M. cupido* as a *Geophagus* and *M. taeniatus* and its allies as generically distinct; but the name *Biotodoma* cannot be applied to the latter.", together with the nomenclatural establishment of *Heterogramma*, may as well be interpreted as an indication of type-species, but this time with a genus for it. A definite type-fixation appeared first in Eigenmann (1910), and it definitely designates *M. taeniatus* as type-species. Jordan (1919) designated *H. borellii* as "orthotype" of the genus *Heterogramma*, but only Allen (in Eigenmann & Allen, 1942) has accepted this superfluosity.

Regan (1906a) used first neuter adjectival endings in connection with *Heterogramma*, viz. *taeniatum* and *trifasciatum*. Later he spelled adjectival names *amoenum* (1908), *trifasciatum* (1909), and *trifasciatum, ritense, amoenus, taeniatum, pertense* (1913). Most other authors have considered *Apistogramma* and *Heterogramma* as being neuter, only Ahl employing both feminine and neuter endings (1931: *parva* and *trifasciatum*). Myers & Harry (1948) definitely meant that *Apistogramma* is neuter, in their changing of *ornatipinnis* to *ornatipinne*.

In not explaining explicitly the meaning of his names, Regan left us with a problem. There are two Greek words that can be latinized into *gramma*, viz. *γράμμα* and *γραμμή*. The first is neuter and means letter, something written, or basic knowledge (cf. English words grammar, program), the second is feminine and means stripe or line. If the meaning is considered, there can be no doubt about which word Regan had in mind. Meinken (in Holly et al.) explains *Apistogramma* as meaning "mit unzuverlässiger Seitenlinie", i.e. the feminine word is the one sought, and it retains its gender after latinization. *-a* is also the common Latin feminine ending. The "gender problem" was first observed by Schmettkamp (1976), who noted that neuter endings to specific names were commonest in literature, but that also masculine (*amoenus*), and, mistakingly, feminine (*pleurotaenia*) occurred.

The genus *Pintoichthys* is the only junior subjective synonym of *Apistogramma*. Reason for invalidating it is presented on p. 33.

## Diagnosis

- Gill-rakers on the sides of the lower pharyngeal tooth-plate
- Compressed lobe on the first epibranchial, with gill-rakers on the margin
- 3, rarely 4 or 6 anal fin spines
- 14–18 dorsal fin spines

These characters separate the genus *Apistogramma* from:

- *Apistogrammoides* Meinken, the only species of which has 7–9 anal fin spines, but also a different upper lateral line course, different colour pattern, etc.
- *Geophagus* Heckel, the 10 species of which have no tooth-plate gill-rakers, but also a different colour pattern, much deeper preorbital bone (lacrimal), toothed 4th ceratobranchial, more gill-rakers, different upper lateral line course, etc.
- *Biotodoma* Eigenmann & Kennedy, the 2 species of which have no tooth-plate gill-rakers, but also a different colour-pattern, deeper preorbital, 2 instead of 1 supraneural, etc.
- *Gymnogeophagus* A. de Miranda Ribeiro, the 4 species of which have no tooth-plate gill-rakers, but also a different colour pattern, no supraneurals, etc.
- *Papiliochromis* Kullander, the only species of which has no tooth-plate gill-rakers, but also a different colour pattern, lateral line branched on caudal fin, different jaw dentition, rather few dorsal fin spines, etc.
- *Acarichthys* Eigenmann, the 2 species of which have no tooth-plate gill-rakers, only one of them an epibranchial lobe, but also a different colour pattern, different lateral line course, etc.
- "*Crenicara*" *altispinosa* Haseman, which obviously has no epibranchial lobe, but also a different colour pattern, many dorsal fin rays, etc. (This species is known only from data on outer morphology given by Haseman, 1911c.)
- *Biotocus* Eigenmann & Kennedy, the only species of which has only 7–8 dorsal fin spines.
- *Taeniacara* Myers, the only species of which has no epibranchial lobe, and also lacks a lateral line.

These 8 genera and 1 species, with *Apistogramma* form the group provisionally called Geophagines (p. 45), and may be regarded as the closest relatives of *Apistogramma*. From all other cichlid genera *Apistogramma* is separated by the epibranchial lobe, usually one or more of the other characters listed above as well.

The following characteristics also have to be regarded as more or less diagnostic for the genus, and are offered as a summary of the subsequent description: Parasphenoid articulation of the upper pharyngeal tooth plates; 5 branchiostegal rays; pseudobranch present, embedded; a single supraneural (predorsal bone); 22–24 vertebrae; spicular ossified; first hyobranchial straight, narrowest on middle; 5 hypurals, a parhypural spine (Vandewalle, 1973); no teeth on the 4th ceratobranchial; number of outer first ceratobranchial rakers reduced (0–5, usually less than 4); tip of maxilla usually exposed; maxilla at more than 45° angle to the horizontal (except in *A. taeniata*); vertical free edge of preoperculum serrated or entire (less than 42 denticuli); lower pharyngeal tooth-plate teeth unmodified; mouth terminal (subterminal in *A. taeniata*); jaws equal anteriorly; jaw teeth conical, apically recurved, in 2–4 series, not more than 60 in outer series; fold of lower lip continuous; orbit in anterior half of head length; orbit diameter greater than snout length (usually) and preorbital depth; dorsal fin

origin in advance of vertical from distal margin of gill-cover; dorsal fin base length more than 50 % of SL; 14–18 dorsal fin spines, 5–8 rays,  $D_{\text{tot}}$  20–25; ratio dorsal fin spines to rays usually more than 2:1; 3 (rarely 4 or 6) anal fin spines, 7–11 rays; 11–12 (rarely 10 or 13) pectoral fin rays; pectoral fin rounded, to vent or anal fin spinous base; 16 principal caudal fin rays; caudal fin shape basically rounded; flanc scales large, ctenoid, not different in size from lateral line scales; squ. long 20–24; squ. tr.  $7 + 1 + 1/2 - 1 1/2$ ; predorsal and preventral scales cycloid; cheek and opercular bones, except preoperculum, scaled; dorsal and anal fins scaleless; caudal fin scaled basally; 16 circumpeduncular scales; upper lateral line separated from dorsal fin by  $1/2$  scale for most of its course, posterior part commonly of pored scales, not overlapping lower; lower lateral line anteriorly or entirely of pored scales usually, of not more than 10 scales, at most 8 canals; lateral line on caudal fin of 1–2 scales, immediately behind lower lateral line of body; colour pattern of 7 transverse bars, first above operculum, last on caudal peduncle, a spot in 3rd bar, caudal fin base spot on middle rays, a band from gill-cover to caudal fin base, a stripe from orbit to occiput, another to mouth, a third posteriorwards to gill-cleft, a fourth to join of sub- and interoperculum, dark anterior 2–3 dorsal fin membranes, but all markings not exclusive and not present all in every species; no ocellus-like spot; sexual dimorphism: males larger, with additional life colours, longer ventral fin, longer soft dorsal and anal fins, in some species with produced anterior dorsal fin lappets and/or caudal fin rays forming one or two streamers, females with contrasting colour pattern when brooding; maximum size 63 mm SL; eggs of p-type (Wickler, 1960).

## Species

Below are listed the previously described species of *Apistogramma* considered valid (24), and 14 new species, data from which are included in the diagnosis and the subsequent description. 12 of the latter are described later in this paper.

In the list appear in all 36 nominal species, and 2 undescribed. 3 of these are doubtful, viz. *A. amoena*, *A. parva*, and *A. sweglesi* (see p. 142). The status of 4 more species is not clear, viz. *A. taeniata* (p. 142), *A. pleurotaenia*, *A. rondoni*, and *A. aequipinnis*. The genus contains at least 10 more species from the Amazonas and Orinoco basins, of which adequate material is not yet available.

Names not appearing in the list are considered junior synonyms on basis of studies on type-material:

- Heterogramma corumbae* Eigenmann & Ward = *A. commbrae*  
*Heterogramma trifasciatum maciliense* Haseman = *A. trifasciata*  
*Apistogramma ortmanni rupununi* Fowler = *A. steindachneri*  
*Apistogramma ornatipinnis* Ahl = *A. steindachneri*  
*Apistogramma reitzigi* Ahl = *A. borellii*  
*Apistogramma ambloplitoides* Fowler = *Acaronia nassa* (p. 144)  
*Apistogramma wickleri* Meinken = *A. steindachneri*  
*Apistogramma trifasciatum harald schultzi* Meinken = *A. trifasciata*  
*Apistogramma klausewitzi* Meinken = *A. bitaeniata* (p. 97)  
*Apistogramma kleei* Meinken = *A. bitaeniata* (p. 97)

or considered synonyms on basis of careful consideration of the original descriptions:

*Heterogramma ritense* Haseman = *A. borellii*  
*Apistogramma weisei* Ahl = *Taeniacara candidi*

or considered unavailable:

*Heterogramma ortmanni* Eigenmann in Haseman  
*Apistogramma taeniatum longirostris* Meinken

or placed in a separate genus:

*Apistogramma ramirezi* Myers & Harry = *Papiliochromis ramirezi*.

I have examined at least one specimen of each of 35 species listed (not of: *A. amoena*, type lost; *A. rondoni*, no response to loan request; *A. sweglesi*, type-series dislocated?). Besides, the holotypes of *A. pertensis* and *A. ortmanni* (but several paratypes), could not be reexamined, no museum admitting having them.

It may be pertinent to remark here that with at least 38 species (and probably more than 50), *Apistogramma* is the largest genus of South American cichlids. The only Neotropical genus with more species is *Cichlasoma* with more than 100 spp., the majority in Central America, only about 20 species in South America.

List of valid and to be described *Apistogramma* spp., with distribution, number of wild specimens examined, and maximum SL in mm recorded for each sex (in paranthesis of not wild).

Species	Distribution	n	♂	♀
<i>A. taeniata</i> (Günther, 1862)	R. Cupari, Brazil	1	42	—
<i>A. amoena</i> (Cope, 1872)	R. Ampí-yacú, Peru	0		
<i>A. agassizii</i> (Steindachner, 1875)	Along R. Amazonas and R. Solimões	226	42	32
<i>A. irifasciata</i> (Eigenmann & Kennedy, 1903)	R. Paraguay and R. Guaporé	48	38	24
<i>A. commbrae</i> (Eigenmann in Regan, 1906)	R. Paraguay	16	23	28
<i>A. borellii</i> (Regan, 1906)	R. Paraguay	26	36	25
<i>A. steindachneri</i> (Regan, 1908)	Guyana, Surinam	106	63	38
<i>A. pleurotaenia</i> (Regan, 1909)	R. Paraguay	(1)	—	(28)
<i>A. pertensis</i> (Haseman, 1911)	Manacapuru to Santarem	62	39	30
<i>A. ortmanni</i> (Eigenmann, 1912)	Guyana	8	36	28
<i>A. rondoni</i> (A. de Miranda Ribeiro, 1918)	R. Paraguai	0		
<i>A. parva</i> Ahl, 1931	R. Capim, Brazil	1		16
<i>A. bitaeniata</i> Pellegrin, 1936	Upper R. Solimões, R. Amazonas in Peru	22	33	25
<i>A. aequipinnis</i> Ahl, 1938	R. Paraguay (?)	(1)	(35)	—
<i>A. cacatuoides</i> Hoedeman, 1951	Upper R. Solimões, R. Amazonas and Ucayali in Peru	23	41	31
<i>A. sweglesi</i> Meinken, 1961	Leticia region, Peru	0		
<i>A. hoignei</i> Meinken, 1965	R. Portuguesa, Venezuela	(2)	—	(32)
<i>A. gibbiceps</i> Meinken, 1969	? R. Negro, Brazil	(7)	(45)	—
<i>A. geisleri</i> Meinken, 1971	Óbidos	3	25	28
<i>A. luelingi</i> Kullander, 1976	Todos Santos, Bolivia	15	26	29
<i>A. macmasteri</i> Kullander, in prep.	R. Meta, Colombia	14	55	34
<i>A. hongloi</i> Kullander, in prep.	R. Guarrojo, Caño Perro, Colombia	14	34	30

<i>A. viejita</i> Kullander, in prep.	R. Yucao, Colombia	3	30	20
<i>A. iniridae</i> Kullander, in prep.	R. Inirida, Colombia	29	36	29
<i>A. moae</i> sp. nov.	R. Moá, Brazil	2	50	—
<i>A. regani</i> sp. nov.	near Manaus	40	49	29
<i>A. caetei</i> sp. nov.	R. Caeté, R. Apeu, Brazil	4	36	—
<i>A. piuiensis</i> sp. nov.	R. Parnaíba, Brazil	3	—	23
<i>A. elizabethae</i> sp. nov.	R. Uaupés, Brazil	11	40	24
<i>A. brevis</i> sp. nov.	R. Uaupés, R. Tiquié, Brazil	114	39	27
<i>A. personata</i> sp. nov.	R. Uaupés, Brazil	23	49	33
<i>A. meinkenii</i> sp. nov.	R. Uaupés, Brazil	35	35	32
<i>A. uaupesi</i> sp. nov.	R. Uaupés, Brazil	48	28	26
<i>A. gephyra</i> sp. nov.	mouth of R. Negro to Santarem	18	33	27
<i>A. pulchra</i> sp. nov.	R. Candeias, Brazil	9	32	19
<i>A. roraimae</i> sp. nov.	Boa Vista, Roraima, Brazil	5	23	20
<i>A.</i> sp. nov.	R. Oyapock, Fr. Guyana	6	41	27
<i>A.</i> sp. nov.	Cáceres, Brazil	3	37	24

### Comparative material

For the description below was used all wild specimens listed in the table above, and the following material: *Apistogramma agassizii*, 1 specimen, pers. coll. unreg., alizarin (import); *A. borellii*, 1 specimen, pers. coll. unreg., alizarin (aquarium); *A. cacatuoides*, 1 specimen, pers. coll. unreg., head sectioned and stained (import?); *A. bitaeniata*, 1 specimen, pers. coll. unreg., dissected (import?); *A. steindachneri*, 1 specimen, pers. coll. unreg., alizarin, 1 specimen pers. coll. unreg., dissected (both aquarium); *Apistogrammoides pucallpaensis*, SMF 7565 (holotype), SMF 7566-7568 (3 paratypes), 1 specimen, SMF 12635 pt (import?), 4 specimens, pers. coll. unreg. (aquarium); *Acarichthys heckelii*, 1 specimen, pers. coll. unreg. (import); *A. geayi*, 1 specimen, pers. coll. unreg. (aquarium?); *Aequidens curviceps*, 2 specimens, pers. coll. unreg. (import?); *Crenicara filamentosa*, ZIMH 343 (lectotype), ZIMH 343 (paralectotype), 3 specimens NRM 11245, 2 specimens NRM 11246, 17 specimens 11247, 5 specimens NRM 11248, 1 specimen 11249, 2 specimens, pers. coll. unreg., alizarin (aquarium); *Nannacara* sp., 3 specimens, pers. coll. 43-0001, 1 specimen, pers. coll. 43-0002, 1 specimen pers. coll. 43-0003, alizarin (all aquarium); *Cichlasoma bimaculatum*, 6 specimens, pers. coll. unreg. (import; one alizarin); *Papiliochromis ramirezi*, 9 specimens, NRM 11250, 7 specimens, NRM 11251, 21 specimens, NRM 11252; *Pelvicachromis taeniatus*, 1 specimen, pers. coll. unreg. (aquarium); *Geophagus surinamensis*, 1 specimen, pers. coll. unreg. (aquarium?); *Pterophyllum scalare*, 1 specimen, pers. coll. unreg. (import).

### Body shape

The body shape is of fairly regular cichlid fashion, i.e. for a percoid moderately elongate or elongate, laterally moderately compressed, deepest just in advance of the ventral fin insertions and tapering by the slopes of the anal and dorsal fin bases. Within the genus may be distinguished deep (depth up to about 40 % of SL) and elongate species (to just below 30 % of SL), and all intermediate forms. The depth generally increases with increasing SL.

The caudal peduncle length occupies 7.8–18.3 %, generally 10–15 % of the SL; its depth decreases caudad, the ventral edge being longer than the dorsal and oblique; on the middle of the peduncle the depth is 11.6–20.7 % of the SL. Specimens with a longer than deep caudal peduncle are not uncommon among Amazonian species, but generally the length is only from little more than 50 % to about 90 % of the depth, total range 42.9–123.5 %.

The head shape varies, but the profile may generally be described as bluntly pointed. The predorsal contour may be straight or arched within a species, in one species only do we find an occipital hump developed, viz. in male *A. gibbiceps*. The preventral head contour also varies slightly in convexity; especially in dehydrated specimens the lower jaw end projects somewhat, forming an angle in the profile below the orbit. Generally, deep species have short heads, and elongate species long heads, but not always, and the head length generally decreases with increasing SL (total range 27.9–41.7 % of SL). The depth (22.0–35.7 % of SL) is always greater than the width (12.0–20.9), and lesser than the length, dependent to some degree on the body depth.

The snout is usually shorter than the orbit diameter and in shape more or less bluntly pointed. It occupies 3.6–12.5 % of the SL, generally less than 10 %, and becomes longer with increasing SL. The mean length in Amazonian species will probably be found to be close to 6 % of the SL in most species.

The orbit is situated in the anterior half of the head length, usually slightly below the forehead contour. Its shape is approximately circular. In small specimens its lower rim is at the horizontal level of the lower lip, but more dorsal in larger specimens, to slightly above the level of the upper lip. The diameter occupies 9.4–16.1 % of the SL (generally 10–15 %), proportionally larger in smaller specimens.

The lacrimal bone is longer than deep, the depth always distinctly less than the orbital diameter, down to 1/7 or 1/8 in small specimens, greater in adults (total range 0.8–4.9 % of SL).

The mouth is terminal in position except in *A. taeniata* in which the lower jaw is an insignificant part of the snout. In comparison with other cichlids, the mouth size is rather moderate, only *A. cacatuoides* has a rather large mouth. The lips are moderately thick, the fold of the lower continuous. The premaxillary processes are short, but protractile. The maxilla is at more than 45° (c. 60°) angle to the horizontal, except in *A. taeniata* in which it is less. The tip is usually exposed, but most of the bone is covered by the lacrimal. It reaches to about the margin of the orbit, at most to its centre.

## Size

The list on p. 25 summarizes maximum length data for 35 species. The largest specimen recorded is a male *A. steindachneri*, 62.8 mm SL, 84.6 mm TL. The largest female recorded is of the same species, and is 38.3 mm SL, 51.8 mm TL. Specimens of more than 39 mm SL are known from 10 of 31 species, and all are males. Of 27 species females of more than 29 mm SL are known from 8 species. In some species of which only individuals less than 30 mm SL are known, females larger than the largest male are known (*A. commbrae*, *A. luelingi*), but as a rule the maximum length of males is greater than that of females of the same species. In species of which a larger material is available the maximum size difference

between the sexes is 2 (*A. uaupesi*), 3 (*A. meinkenii*), 10 (*A. agassizii*), 12 (*A. brevis*), 20 (*A. regani*), or 25 (*A. steindachneri*) mm. One may expect that in all species males grow larger than females, but that the size difference varies between species. Adult size appears to be reached at between 20–30 mm SL.

In aquarium literature the sexual size dimorphism is usually exaggeratedly emphasized. In aquarium small fishes grow much larger than they would do in nature, and this effect is especially upon males who are relieved from the constant brooding stress on females. The largest not wild specimen that I have examined is the holotype of *A. wickleri* [= *A. steindachneri*], 75.8 mm SL, 98.8 mm TL.

Data from aquarium literature (Holly et al.; Pinter, 1951 a, b; and others) indicate that in the aquarium *Apistogramma* specimens are sexually mature in about 4 months, and are 12–15 mm long after 5–6 weeks from egg-laying. In estimating the reproductive periods (in the Ecology sections of the species descriptions), 10–15 mm specimens are thus assumed to be about 1–2 months old. Growth rate may be different in aquarium than in the natural habitat, however.

## Fins

The dorsal fin is rather long, its base length more than one-half of the SL (52.1–66.4 %), generally increasing with increasing SL. It commences with a frequently minute spine in advance of a vertical from the distal margin of the gill-cover. The spines increase gradually in length to the last, but except for the anteriormost three to four, they are usually of almost the same length. The number of spines varies from 14 through 18, 15–16 being the commonly encountered counts. There is usually less than one-half as many rays as spines, 4 (rarely) – 8, commonly 6 or 7. The anterior rays are always longer than the last dorsal spine, the ultimate often very short and unbranched. The middle rays are longest and form usually a point, frequently continued by a filament in males. Counts encountered are: XIV. 6–8, XV. 3. i<sup>v</sup>, XV. 4. ii, XV. 5–8, XVI. 4.i–8, XVII.4.i–8, XVIII.4.i (the last in one specimen of *A. commbrae*). The total number of spines and rays varies between 20 and 25, i.e. there are about as many dorsal radii as scales in a longitudinal series and vertebrae.

In several species the anterior dorsal lappets of males are much prolonged, the longest (the 3rd or 4th usually) considerably longer than the spine before it. The lappets may also be long and pointed anteriorly in the fin or long and united beyond spine tips. "Normally" as in females and young, they are pointed or truncate, and reach little beyond spine tips.

The anal fin is symmetrical with the dorsal fin, i.e. the soft part begins opposite the beginning of the soft dorsal fin, but since the slope of the anal fin base is greater than that of the dorsal fin base it ends slightly before the end of the dorsal soft fin base, even if equal in length. The length of the anal fin base is 14.8–26.6 % of the SL, commonly less than 20 %. The regular number of spines is 3, but one indi-

vidual of *A. agassizii* examined has only 2 (probably abnormal), one species has usually 4 spines (*A. luelingi*), and 4 spines are found in individuals of 4 other species (*A. agassizii*, 1 specimen; *A. cacatuoides*, 1 specimen; *A. commbrae*, 2 specimens; *A. pleurotaenia*, only known specimen). The single known specimen of an undescribed species from the R. Guaporé (ZIMH 1210A; paratype of *A. trifasciata haraldschultzi*) has 6 anal spines (*A. VI.5.i*). It is generally believed that Neotropical cichlid species have either invariably 3 anal spines or a variable number greater than 3, and that the anal spine number is a reliable generic character. The above noted 4-spined individuals are surely exceptional, but the *A. luelingi* indicate that 4 spines may be an advanced character state that may occur within natural taxa normally characterized by 3 anal spines, and that a division based on anal spine number is of limited value. There are 4–8, regularly 6–7 anal fin rays, and a total of 7–11, commonly 9–10 anal fin radii, i.e. less than one-half as many as in the dorsal fin. The spines increase in length to the last which is longer than the last dorsal spine except in large individuals. The soft fin shape is similar to that of the soft dorsal fin. Counts encountered are: III.3.iii, III.4, III.4.ii, III.5–8, IV.4.i–6.

The caudal fin shape is basically rounded or subtruncate, never emarginate or truncate as in other Geophagines, but rather of the type found in *Aequidens* and *Cichlasoma*. The number of principal rays in each lobe is 16 (8 + 8), one or two of the marginal rays in each lobe unbranched. In males of many species the shape is modified as the result of certain rays being prolonged. In *A. agassizii* the middle rays are much prolonged, gradually shorter to the marginal rays. In *A. bitaeniata*, *A. steindachneri* and others, the middle rays in each lobe are prolonged. Young males have female (basic) caudal fin shape. The caudal and dorsal fin modifications often occur in the same species (*A. bitaeniata*, *A. cacatuoides*, etc.), or only the dorsal lappets (*A. trifasciata*, *A. macmasteri* group), or only the caudal fin rays (*A. agassizii*, *A. steindachneri*, etc.) are prolonged.

The pectoral fin is rounded and asymmetrical. It has 11 or 12 rays (rarely 10 or 13), and a supporting ray that is not separated from the superior principal ray. The marginal rays are unbranched. The base is a short axilla, and laid backwards the fin tip is above the vent or the base of the spinous anal fin.

The ventral fins originate close together below or slightly behind a vertical from the pectoral axilla insertion. The count is I. 5 or, rarely, I. 4.i. The spine reaches halfway to vent or anal fin origin, rarely is it shorter. The first ray is the longest, produced by a more or less long filament in males of several species, the inner rays gradually shorter.

### Scales

With the following exceptions the scales are ctenoid: before the dorsal fin and in various degrees towards the flanks, exceptionally a short distance behind the dorsal fin origin above the upper lateral line; before the ventral fins and also usually between their bases; with exceptions on cheek, operculum and suboperculum; with rare exceptions on interoperculum; with many exceptions distally on

the caudal fin. On the pectoral axilla the type of scales varies. The midventral scales do not have ctenii along the median line.

The predorsal squamation ends just above the median frontal lateralis pore. Usually the preventral squamation proceeds forwards of the free edge of the branchiostegal membrane, but in several species (*pertensis* group) the throat is naked. The preoperculum is naked, in some species also the lower part of the cheek.

On the cheek the scales are arranged in series (1–6; usually 3), on operculum (6–17 scales) more irregular. On suboperculum are 1–2 series parallel with the border to the operculum, 2–9 scales in total. The interopercular scales are in one series, of 1–4 scales. Usually the cheek and gill-cover scales are fairly deeply embedded, and particularly the interopercular scales difficult to observe without manipulation. Embedment characterizes also the predorsal and preventral scales. The predorsal scales are irregularly arranged along the midline, the preventral anteriorly, where they are also quite small.

The squ.tr. count commonly obtained is 7+1+1, in very elongate species/specimens 7+1+1<sup>1/2</sup>, in very deep species/specimens 7+1+1<sup>1/2</sup>. The squ. long. count varies from 20 through 24, but not by more than 3 scales within the same species. There are 16 circumpeduncular scales (7 between the lateral line scales). Between the origins of the soft dorsal and anal fins are 7 horizontal scale series. There are 2 scales between the pectoral axilla and the ventral fin base.

The largest scales are those of the anterior flanks, size reduction proceeding towards edges. The lateral line scales are not different in size from adjacent scales.

The fins are, with two individual exceptions (probably abnormal), naked except for the caudal fin. The body scales next to dorsal and anal fin bases do not cover these, but in a specimen of *A. hoignei* and one of an undescribed species (ZIMH 1210A) are minute scales on the soft dorsal fin base. The caudal fin squamation consists in a proximal part of rather large, ctenoid scales, about 3 scales long, and distalwards smaller scales, between the rays, distally very elongate and frequently non-denticulate. The squ. caud. count generally increases with increasing SL, from 3 to around 15 in large males. Up to one-half of the length of the fin may be scaled but usually only 1/4 to 1/3.

The upper lateral line proceeds rapidly upwards to run at only one, posteriorly 1/2 scale distance from the dorsal fin for most of the length. It is separated from the lower lateral line by two horizontal scale series.

In small specimens the lateral lines are chiefly pored. The canals form from minute conical projections formed above and below each pore. These unite over the pore and grow into a tube along the exposed portion of each scale. Thus, small specimens have fewer canals than larger specimens of the same species. But exceptions exist, and in some species canals are rarely or never developed in the

lower lateral line and the number of canals reduced in the upper lateral line (Paraguay basin spp.). The pores are normally found posteriorly in the upper lateral line and anteriorly in the lower.

The upper lateral line reaches to below the end of the spinous dorsal fin but is frequently continued by very few (1–2 usually) pores or canals on the next scale series below (subserial). In some species occur pored scales also on the next scale series (subsubserial). The total number of upper lateral line scales oscillates around 15 usually; recorded variation 0–18 canals, 0–19 canals + pores. There is no overlap of the lateral lines. The lower comprises at most 10 scales, 0–8 of which may have canals, very rarely no scale is modified. In several species the lower line is continued by 1, rarely 2 canals or pores on the caudal fin. The lateral line is continued on the head by pores, arranged as shown in Fig. 2.

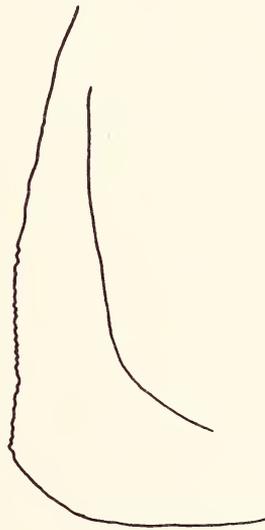


Fig. 1. Serrated preoperculum in a specimen of *Apistogramma steindachneri* (FMNH 75164, 23.6 mm), c. 15 x.

### Preoperculum serrations

Although projections of various kinds on opercular bones are not uncommon among perciform fishes, other than even-edged (entire) opercularia are known only from a few South American species within the family Cichlidae, viz. those of the genera *Batrachops*, *Crenicichla*, and *Crenicara*, and the species *Papiliochromis ramirezi*, *Crenicara altispinosa* Haseman, and *Pintoichthys trifasciatus* (Eigenmann & Kennedy). In these, the preoperculum is always or individually serrated along the free vertical edge and corner, and this condition has been regarded as of systematic importance.

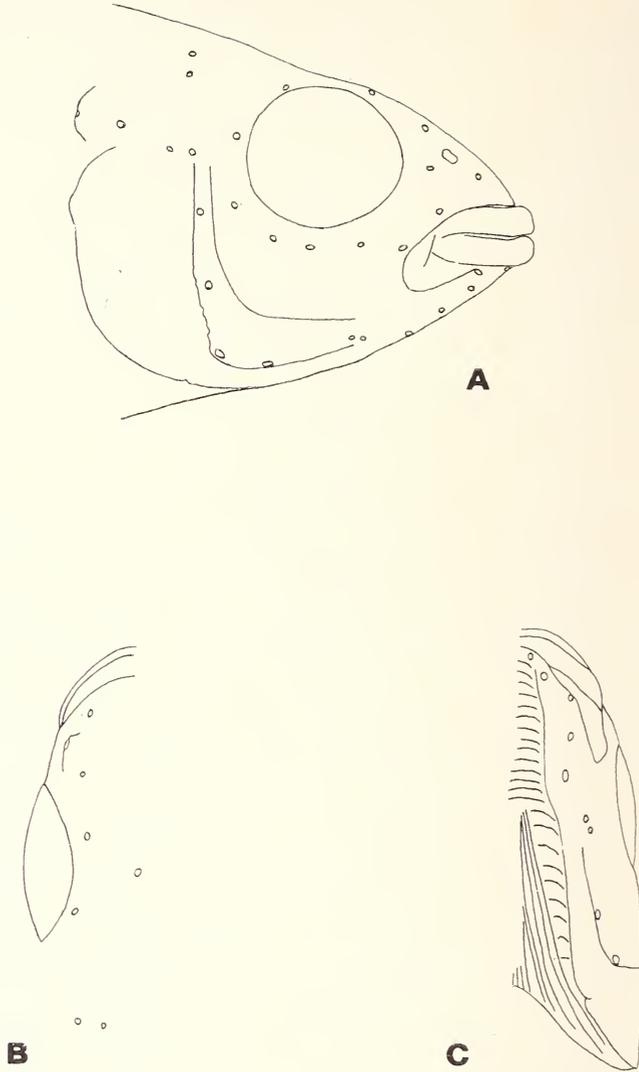


Fig. 2. Sketch of head of *Apistogramma* specimen showing lateral pores. A lateral aspect, B dorsal aspect (left side), C ventral aspect (left side).

The genus *Pintoichthys* was established for *Apistogramma trifasciata* on basis of the serrated preoperculum (Fowler, 1954). I have not seen the character in that species, but I have found it in the following species: *A. agassizii*, *A. bitaeniata*, *A. brevis*, *A. cacatuoides*, *A. pertensis*, *A. regani*, *A. steindachneri*, and *A. uaupesii*. This list suggests to me rather that Fowler's genus is invalidated, than that the listed species should also be included in it.

As apparent from the species descriptions given below, the frequency of individuals with serrations may be very low, and is never a species character. In *A. steindachneri* and *A. regani* serrations are found only in individuals from certain populations. The number of denticuli may be as high as 41 (*A. pertensis*), but usually there are less. The projections are commonly irregularly distributed along the preoperculum edge, and quite small. In *Crenicara* they are distinct, numerous, and regularly arranged, the number up to 100 in *C. punctulata*, up to 42 in *C. filamentosa* (Kullander, in prep. b). In *Papiliochromis* they are much like in *Apistogramma*, but more frequent, usually less than 20 (Kullander, in prep. c). *Crenicichla* and *Batrachops* have rather a jagged preoperculum edge, but there appears to be quite a variation between the many species. The table should give an idea of the variation between the genera.

Genus	No. spp.	w. serrations	frequency	developm.	max. no.
<i>Crenicara</i>	3	all	all indiv.	regular	100
<i>C. altispinosa</i>	1	all	?	?	?
<i>Crenicichla</i>	c. 26	all	most ind.	varying	?
<i>Batrachops</i>	c. 6	all	most ind.	varying	?
<i>Papiliochromis</i>	1	all	+ 50 %	irregular	40
<i>Apistogramma</i>	38	9	few	irregular	41

### Jaw teeth

The jaw dentition is made up of relatively strong, pointed, apically recurved teeth, in an anteriorly broadening band in each jaw. The outer series extends along the entire rim of each jaw. The inner (1–3 series) are commonly confined to the anteriormost part of the jaw, but may be longer, and of different lengths in each jaw.

The number of teeth in the outer series increases with increasing SL. The largest specimens of a species may have as many as 60 teeth in this series. The development of the inner series is more irregular. One of these may, in adults at least, be as long as the outer, but if more than two, one is commonly restricted to the symphyseal part of the jaw (commonly the inner). A lateral inner series is found in *A. macmasteri*, *A. borellii*, *A. regani*, *A. ortmanni*, *A. cacatuoides*, *A. agassizii*, *A. bitaeniata*, *A. elizabethae*, *A. gibbiceps*, *A. personata*, *A. trifasciata*, *A. brevis*, *A. gephyra*, *A. pertensis*, *A. iniridae*, *A. uaupesii*, and *A. taeniata*. 3–4 series of teeth in both jaws are found in the *macmasteri* and *regani* group species, *A. sp. nov.* (Oyapock), the Paraguay basin species, *A. luelingi*, *A. steindachneri*, *A. agassizii* and *A. bitaeniata*. *A. gibbiceps* and *A. gephyra* have 3 lower jaw series, and 2 upper jaw series, the remainder 2, *A. trifasciata*, *A. brevis*, and *A. meinkenii* intermediate (3rd series not always developed).

The outer teeth are larger than the inner, and anterior stronger than posterior. In large specimens of *A. agassizii*, *A. trifasciata*, *A. cacatuoides*, *A. bitaeniata*, and *A. pertensis*, the anteriormost teeth are commonly enlarged, subcaniniform.

In general, the shape of the tooth-band and the teeth is similar to that of *Aequidens*, *Nannacara*, or South American *Cichlasoma* species, and may be regarded as relatively unspecialised. *Crenicara filamentosa* Ladiges, has very strong anterior teeth (Kullander, in prep. b), and *Papiliochromis ramirezi* reduced number of teeth (Kullander, in prep. c).

The dentition needs deeper study, but it may be conjectured that many series is ancestral to few, and that a laterally extended inner series is a derived character.

### Gill-rakers and tooth-plates

The gill-rakers of all available Neotropical cichlids are of the dimorph-monacanth type (sensu Zander, 1906, who did not study cichlids). The rakers of the external surface of the first ceratobranchial (C1) are often reduced in size and number, but in some genera very long and numerous (e.g. *Chaetobranchius* Heckel). Of the other rakers those of the fourth ceratobranchial (C4) differ from the rest in being more teeth-like. In but few genera occur rakers along the lower pharyngeal tooth-plate opposite the C4 rakers.

In a generalised Neotropical cichlid, *Cichlasoma bimaculatum* (Linnaeus, 1758), all ceratobranchials carry rakers, but not the lower pharyngeal tooth-plate. The superior ridge between the series of rakers on each arch is moderately developed. The external C1 rakers are simple, and in preserved specimens they lie with their apices rostrally. The size of a raker decreases the more rostral its position, but each raker is connected with a non-osseous elevation between it and the median ridge, and it becomes larger near the rostral end of the arch. In the most rostral part, these "soft rakers" (SRs) gain contact with the corresponding SR on the internal side of the arch. In *C. bimaculatum* the SRs are very moderately developed on the external C1, but on the inner side of it and on C2 and C3 they are dominant. The rakers of the internal C1, of C2 and C3, and external C4 form knobs which constitute the interlocking mechanism of the arches. On C4 the SRs become smaller rostrally, being largest medially on the arch. There are no distinct SRs on the internal C4 and the internal C4 rakers are small, not knob-like, but finger-like. On the C4 there is also a distinct rather median tooth-patch on the internal surface (a single small dental plate with two teeth in an alizarin specimen).

*Aequidens curviceps* Ahl, 1924, and a *Nannacara* species are essentially similar, but the shape of the outer C1 rakers differs and there is no tooth-patch on the C4.

In *Geophagus surinamensis* the picture is very different. The rakers and the SRs appear to form bifurcate rakers which join above a high soft median ridge. The upper C1 rakers tend to become long and slender, as they are on E1 and the edge

of the lobe. They become smaller and separate from the SRs rostrad. The rakers form the interlock structure on the inner side of C1, on C2 and C3, and the outer side of C4. On C4 the median ridge is considerably reduced and there is a tooth-patch, obviously of four close dental plates, mediorostrally on the inner surface. There are no SRs on the internal side, but the rakers are developed into long finger-like structures. The lower pharyngeal tooth-plate lacks rakers.

In *Apistogramma*, studied particularly on *A. steindachneri*, there is considerable reduction in the number of outer C1 rakers. In some species there are no ceratobranchial rakers at all. Reduction in size and number proceeds caudally. In *A. steindachneri* there may be as many as 7 external C1 rakers, and that number approaches the common in South American cichlids. The number and size of the inner rakers appears not to be reduced, but the SRs are inconspicuous on all arches. The inner C4 rakers are as described for *C. bimaculatum*, but in *Apistogramma* they have an interlocking counterpart in a series of rakers along the side of the lower pharyngeal tooth-plate. These appear on alizarin-stained material to be osseous only in the form of a basal plate. There is no trace of a dental plate on C4. The lower pharyngeal tooth-plate is made up of bilateral elements forming a unit, but the anterior processes are not quite fused rostrally. The upper pharyngeal tooth-plates are separated from each other. All bear pointed teeth, stronger in the upper tooth-plate.

*Apistogrammoides* has short, but many (up to 7) C1 rakers. It is otherwise like *Apistogramma*, also in the pharyngeal rakers.

*Acarichthys heckelii* is characterized by a much reduced or feebly developed lobe on the first epibranchial. It is otherwise similar to *Geophagus*, but the SR and raker development is not so marked. It has also a C4 dental plate. A C4 plate is present also in an *Aequidens* species of geophagine habitus, *Ae. gayi* (Pellegrin, 1902). I suggest that it be removed from *Aequidens*, and, provisionally, be placed with *Acarichthys heckelii*, which it resembles most. It has no epibranchial lobe, but small preventral scales, deep preorbital, truncate or emarginate caudal fin, many cheek scale series (4–5) and pectoral rays (15), D. XIV–XV.9–11, A. III.8 (Pellegrin, 1902b; pers. obs.).

The apophysis of the upper pharyngeals is in *Apistogramma* from the parasphenoid, without incorporation of basioccipitals or prootics. This condition is found also in *Cichlasoma bimaculatum*, *Nannacara* sp.; and *Crenicara filamentosa*. According to Regan (1920), the basioccipitals contribute in but one Neotropical cichlid genus, *Cichla* Schneider, 1801.

### The epibranchial lobe

The most important character defining the geophagines is the flattened lobe on the first epibranchial, first described by Heckel (1840). It has been discussed from various aspects by Agassiz & Agassiz (1969), Pellegrin (1904), Haseman (1911b), and Trewavas (1974). Its structure and function has yet to be explained.

Macroscopically, three types of lobes can be distinguished: (1) In *Retroculus* and *Acarichthys heckelii* there are no rakers along the edge, but basally on the epibranchial proper, (2) in *Geophagus* it is hyperdeveloped and carries long rakers along the free edge, (3) in *Apistogramma*, *Apistogrammoides*, and *Papiliochromis* it is smaller than in *Geophagus*, and the rakers along the edge are short. The differences between the latter two groups are probably due to differences in feeding, since the lobe has probably some function in the feeding mechanism. The lobes of *Gymnogeophagus*, *Biotodoma*, and *Biotocetus* have still to be described in more detail.

Trewavas (1974) confused the lobe in *Geophagus* with a downhanging pharyngeal roof pad found in various Afrotropical cichlids. This pad is a modification of the histologically specialised epithelium anterior to the upper pharyngeal tooth-plates (cf. Trewavas, 1974) found in all cichlids available to me. The hanging pad and its unmodified counterpart was described in detail by Trewavas (1974). She called the latter "sessile pad".

I have studied the epibranchial lobe chiefly on *Apistogramma steindachneri* and *A. cacatuoides*. For comparison were examined macroscopically the pharynx of *Cichlasoma bimaculatum* (unmodified), and *Pelvicachromis taeniatus* (Boulenger) (African, with hanging pad). Comparison with these and with Trewavas (1974) shows that the lobe is structurally, but perhaps not so much functionally, unrelated to the hanging pad, and seems to confirm Trewavas' observation that the latter is a hyperdevelopment of the sessile pad.

In *Apistogramma* (Fig. 3) the roof of the oropharynx can be divided into three regions. Anteriorly is a strongly folded epithelium forming a groove medially, "unfolding" to some extent posterolaterally as the buccal cavity becomes wider before this epithel abruptly terminates. Behind it, the roof of the pharynx commences with a translateral narrow isthmus of seemingly unspecialised epithel which may be strongly pigmented. Posteriorly, anterior and lateral to the upper pharyngeal tooth-plates, are bilaterally symmetrical areas of highly tuberculate, seemingly mucous epithel, somewhat elevated particularly medially. This epithel extends onto the tooth-plates.

The first epibranchial is attached under the unspecialized epithel and from it extends transversely a narrow ridge which reaches a flattened ventral swelling (the lobe) of the epibranchial. There is no mucous epithel over the second epibranchial. The mucous areas are sharply pinched off from the rest of the pharynx by a distinct groove.

The lobe has a bony skeleton, a compressed broad osseous extension of the epibranchial. Such a structure characterizes also the second epibranchial, but in a more rostral direction. On the sectioned example of an *A. cacatuoides*, the lobe skeleton is essentially of bone, with a superior flange of hyaline cartilage (Fig. 6). The epiosseous epithel is not different from that otherwise characterizing the pharynx, except that it is somewhat thin and has no tubular secretory cells.

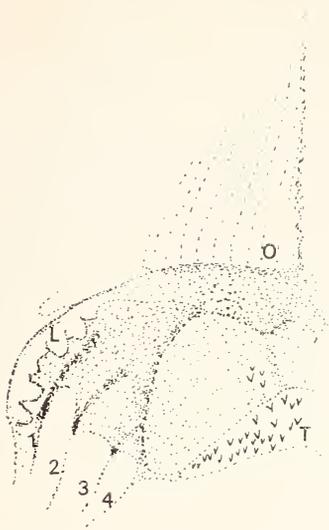


Fig. 3. The roof of the pharynx in a specimen of *Apistogramma steindachneri*, 35.5 mm SL (right side, c. 9x). 1-4 = epibranchials 1-4; L = lobe; O = oral epithel; T = upper pharyngeal tooth-plate.

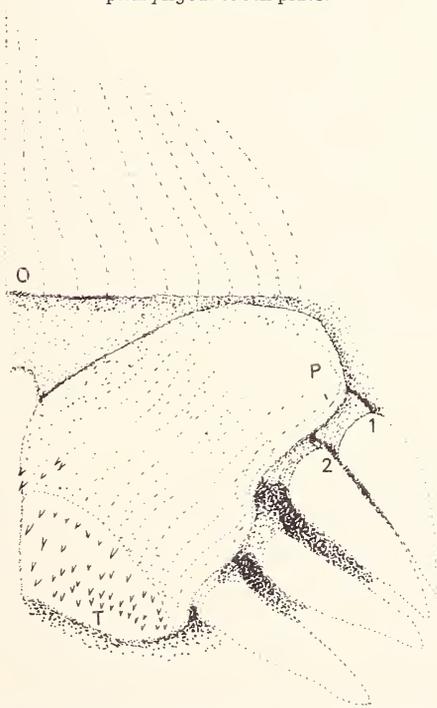


Fig. 4. The roof of the pharynx in a specimen of *Pelvicachromis taeniatus*, 49.5 mm (left side, c. 9x). 1-2 = epibranchials 1-2; P = hanging pad; O = oral epithel; T = upper pharyngeal tooth-plate.

Generally, the pharynx is rich in taste buds, and the mucous dorsal epithel contains secretory cells (hardly staining in Masson's trichrome) (Fig. 5).



Fig. 5. *Apistogramma cactuoides*, 23.7 mm. Lateral view of sagittal section of head, showing lobe (Masson's Trichrome, 10  $\mu$ ).

In *Pelvicachromis taeniatus* (Fig. 4) there is no middle region of unspecialized epithel, but the mucous epithel extends anteriorly to the margin of the folded buccal epithel. However, over the attachment of the second gill-arch the mucous epithel area is considerably thickened to form a somewhat flattened hanging pad which for some bit follows the course of the second epibranchial.

*Cichlasoma bimaculatum* is similar to *Apistogramma* in having a middle isthmus of unspecialized epithel, but there is no lobe on the first epibranchial. Instead, I notice that the mucous area extends onto part of the epithel covering the horizontal part of the second epibranchial, and thus, because of the slight elevation due to the underlying bone there forms a very little pad. The skeletal



Fig. 6. Same specimen as in Fig. 5. Sagittal section of head, near median, showing lobe (L) and pseudobranch (P). E = eye; arrow indicating oralward direction. (Masson's Trichrome, 10  $\mu$ .)

structure is a short, compressed osseous flange of the second epibranchial, present also in *Nannacara* sp., and in *Crenicichla multispinosa* (Vandewalle, 1971: Fig. 19). The first epibranchial skeleton is unmodified in the non-geophagine taxa (and in *Acarichthys geayi*?).

Conclusively, the sessile pad is a basic structure in cichlids, and may be enlarged to form a hanging pad. It is associated with the second epibranchial, which by a flattened extension forms its skeletal basis (cf. Trewavas, 1974). The lobe is formed independent of the pad in *Apistogramma*, and forms by the skeletal support of the first epibranchial.

#### Other anatomical characters

Gosse (1976) found the number of supraneurals useful for distinguishing *Bioto-doma* (2 supraneurals), *Geophagus* (1) and *Gymnogeophagus* (0), and considered an evolutionary series from 2 to 0. Data on supraneural number in other cichlids (Vandewalle, 1971; Gosse, 1976), support the hypothesis that higher numbers are more plesiomorph. *Apistogramma steindachneri*, *A. macmasteri*, *A. hongsloui*, *A. viejita*, *A. iniridae*, *A. regani*, *A. agassizii*, and *A. borellii* have one supraneural, like *Apistogrammoides pucallpaensis*.

Radiographed specimens have 22–24 vertebrae: *A. borellii* (22); *A. macmasteri*, *A. hongsloui*, *A. viejita*, *A. cactuoides*, *A. regani*, *A. steindachneri*, *A. agassizii* (24); *A. iniridae* (23–24). These numbers are very low for cichlids. *Papiliochromis*

*ramirezi* has 25–27 vertebrae (Kullander, in prep. c), other large geophagines 27–34 (Gosse, 1971, 1976), *Apistogrammoides pucallpaensis* 24. The vertebrae number is probably related to the maximum size of the species.

A large embedded pseudobranch is present in both *Apistogramma* and *Apistogrammoides*, and probably all other cichlids. Diagnoses of the family commonly note its absence (e.g. Günther, 1862). The cichlid pseudobranch was discovered and described in detail for *Sarotherodon mossambicus* (Peters) by Menon (1966).

The first hyobranchial in *A. steindachneri* and *A. agassizii* is long, straight, narrowest on middle, and at 90° angle to the basihyal, not short and angled as in *Crenicichla multispinosa* Pellegrin, 1903 (Vandewalle, 1971: Fig. 19), or short and broad as in *Cichlasoma bimaculatum* and *Nannacara* sp.

Günther (1862) gives a variation of four to five branchiostegal rays in cichlids; in *Apistogramma* and all other available cichlids there are five.

### Colour pattern

The genus might be recognized on the structure of the colour pattern alone, and it is very important in species level taxonomy. The ground colour of preserved specimens is usually more or less yellowish, the pattern made up of brownish to black markings, in live specimens the ground colour is whitish to yellowish, the markings predominantly brownish or black, but in part also iridescent, red, blue, yellow or maroon at least in males. Only preserved material will be considered here though. There is obviously always a sexual dimorphism in colouration in live specimens, but such is not always found in preserved material. Below is given a description of the dark markings. Terms italicized are nominal definitions, and used in the species descriptions for brevity. All markings listed are not found all together in any species, and there are markings typical to particular species.

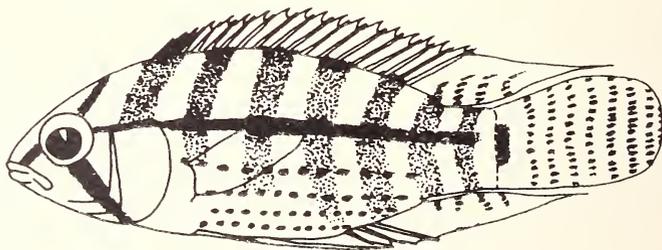


Fig. 7. Dark markings in colour pattern of *Apistogramma*. Shown is a lateral band, crossed by 7 fainter bars, a lateral spot, a rectangular caudal spot, 4 dotted abdominal stripes, a pectoral spot, pre-, super-, and suborbital stripes, dark anterior dorsal fin membranes, caudal fin stripes, and 4 terminal spot-stripes in the dorsal and anal fins.

The *bars* occur chiefly in deep-bodied species, and are usually faint, restricted to the dorsum or lateral band pigment intensifications. In many elongate species the adults do not show the bars, but they are present in the young of all species. The bars number seven, and extend from the dorsal contour of the flanks (Bars 1—6) or across the caudal peduncle (Bar 7). Numbering proceeds caudally from the first bar above the operculum (superopercular bar). The position is shown in Fig. 7. The anterior five bars run obliquely forwards to about the body axis or below, the two posteriormost are usually relatively vertical. As a rule the bars are not contrasting, and the edges are never sharp. Very often they are vague, particularly the two anteriormost. Intensification of the pigmentation occurs close to the dorsal fin base, along the lateral line, or, less commonly, below the lateral band. This intensification may assume the shape of more or less well-defined spots. The dark contrasting back of many elongate species, like *A. agassizii* and *A. trifasciata*, probably developed from bar spots confluency.

Continuing the postorbital stripe to the caudal fin base or before, is a *lateral band* of no greater width than  $1\frac{1}{2}$  scale. It usually ends above the lower lateral line. In the *borellii* group species it is reduced to the posterior part of the body. When bars are present, the band may be spotty, is at least not as contrasting and prominent as it is in not barred specimens/species.

The *lateral spot* is formed by an intensification of the middle portion, on the lateral band, of the third bar. It may be rounded, rectangular, deeper than the band, extended to the dorsal fin, or absent. It is sometimes preceded by a smaller spot in Bar 2.

The head stripes are: (1) a *superorbital stripe* which may be absent or reduced to a spot, when complete extended from the orbit to the occiput, (2) a *suborbital stripe*, which continues the superorbital stripe below the orbit to at most the borders of sub- and interoperculum, (3) a *preorbital stripe* between the anterior orbital rim and the upper lip, never wanting, (4) a *postorbital stripe* which continues the preorbital stripe behind the orbit, across the superiormost edge of the gill-cover, absent at least in the *borellii* group species.

The *pectoral spot* is a small spot superiorly on the unexposed side of the pectoral axilla, part of which can be observed on the superior edge close to the base. In few species there is a corresponding spot basally on the inferior edge. Often absent.

The *abdominal (side) stripes* are composed of more or less confluent scale dots on varying numbers of horizontal scale series below the lateral band, from about the pectoral axilla to the caudal or anal fin base. In *A. cacatuoides* males they are, characteristically, zigzag-lines.

The *midventral stripe* is in many species present only in the females, or is at least best developed in females. It runs along the middle of the abdomen from the vent or anal fin origin to the ventral fin bases or is shorter. In the *macmasteri* group it is continued in advance of the ventral fins in the shape of a *chest blotch*.

Other, more species characteristic markings include interorbital frontal stripe in *A. personata*, the oblique abdominal stripe in *A. trifasciata*, and the abdominal side blotches in *A. personata*.

The fins also have their characteristic markings, but as in the case of the fin shapes, they are much more varied. The *caudal spot* is a generally roundish to quadratic spot on the bases of the middle caudal fin rays (scaled part). In a few species it is extended narrowly upwards and downwards. When absent, the caudal spot is generally replaced by a continuation of the lateral band, not so strongly pigmented, and this is probably a secondary development of the spot. The caudal spot is not ocellated; the only ocellus-like spot encountered is a very small pale spot in the upper caudal fin lobe in males of *A. cacatuoides*. In many species the caudal fin is spotted and usually vertical caudal stripes are formed. The caudal fin in young of these species may be immaculate though. In adult *A. agassizii* males a very special marking is formed out of the spotting, and no species have identical type of caudal striping. Dark anterior two dorsal fin inter-radial membranes is a characteristic of many species. *Terminal spot-stripes* in the dorsal and anal fins are one to four (rarely more) stripes formed by interradiial spots on the terminal part of the soft dorsal and anal fins. Absent in some species. In several species the bars are set off as spots basally on the dorsal fin. Frequently is encountered also basal interradiial dots continued as streaks along the dorsal spines. This pattern does not show in poorly preserved or only slightly discolored specimens. The darkening of the ventral fin spine and the outer ventral fin membranes is frequently limited to females, should at least be expected to be more intensely pigmented in females.

Brooding females generally have a rather uniform yellow colour and contrasting black markings, not necessarily all those present in the non-brooding fish. *A. "reizigi"* young identify their mother as a yellow fish, but *A. cacatuoides* young are attracted by the black/yellow contrast (Kuenzer, 1962 a, b).

Characteristic of the genus are above all the 7 bars and their positions, and the midventral stripe, to a great extent also the lateral band position, and the abdominal stripes, to some extent the head stripes, the position of the caudal spot, the absence of an ocellus, and the lateral spot and its position.

### **Distribution, ecology, ethology**

Precise localities are not yet known for all species, but those of more or less unknown distribution at least can be expected to be found in certain drainage basins (*A. gibbiceps* Amazonian; *A. pleurotaenia* and *A. aequipinnis* Paraguayan). More of an obstacle to a serious discussion of geographical distribution is the very few localities known for many species, making them seem more restricted than they may be. But a few have been collected twice in the same area; no less than 18 species are known from one lot or specimen only.

The genus is strictly South American, restricted to the tropical regions, and only east of the Andes and the Colombian Cordillera, but not south of the Río Paraguay or in eastern Brazil. Comparing with *Geophagus*, one finds in this genus endemic species west of the Colombian Cordillera and a SE Brazilian species (Gosse, 1976); *Crenicichla* also has expanded its range eastwards, and southwards to the Río Negro (Argentina) (Pozzi, 1945), northwards to Trinidad (Boeseman, 1960); *Aequidens* is probably a composite, but as it is presently viewed it has a wide range covering southern Central America (Miller, 1976), the pacific slope of South America to about Lima (Peru) (Lüling, 1973a), the Amazonas, Orinoco, Paraguay-Paraná basins, Guyana, and probably parts of eastern Brazil; *Cichlasoma* is found everywhere where South American cichlids are found, but not so far south as *Crenicichla*, and reaches Texas by Central America, and also has endemic species on Cuba and Haïti; *Chaetobranchius* is found in the Guyanas, the Amazonas basin, and the upper R. Paraguay basin. These are the genera that have a wide distribution. The others are restricted to the northern parts of South America, or to the Paraguay-Paraná basin (*Gymnogeophagus*; Gosse, 1976), none west of the Orinoco basin or in eastern Brazil. If *Batrachops* be considered a separate genus it has nevertheless about the same distribution as *Crenicichla*.

*Apistogramma* are recorded from the following river systems: Ucayali, Napo, Amazonas (Peru and Brazil), Içá, Javari (Yavari), Solimões, Juruá, Purus, Madeira, Mamoré, Guaporé (Itenez), Negro, Branco, Tapajós, Capim, Caeté, Apeu, Parnaíba, Meta, Portuguesa, Vichada, Inirida, Paraguai (Paraguay), Essequibo, Coppename, Gran Rio, Oyapock.

They are not (yet) collected in the Marañon, Huallaga, Tigre, Pastaza, Caquetá (Japura), Ortón, Tambopata, San Miguel, Beni, Aripuana, Xingú, Araguaia, Tocantins, Paraná, rivers east of R. Parnaíba south to R. Paraná, Pilcomayo, Maroni, Itany, Camopi, and Courantyne (Corantijn) systems.

The greater number of species (23) is found in the Amazonas basin, but there is a marked endemism within and outside this basin. All Orinoco species are endemic as well as most Paraguayan and all Atlantic coast species. Within the Amazonas basin, R. Uaupés, R. Branco, R. Madeira, and the upper R. Juruá have species not yet found elsewhere. There appears also to be a shift of species in the upper R. Solimões, *A. agassizii* leaving, and at least *A. cacatuoides* and *A. bitaeniata* replacing upstreams.

Endemism is found where it should be expected, and wide distribution as well. Only one species, *A. trifasciata*, is found in two separate river systems (R. Paraguay and R. Guaporé). The most widely distributed species is otherwise *A. agassizii* (from about Santarem to about Leticia, on both sides near the R. Amazonas). Three other species are found on both sides of the R. Amazonas, all near the mainstream: *A. regani* (near Manaus), *A. pertensis* (Manacapuru to Santarem), and *A. geophya* (Arquipélago das Anavilhanas and Santarem area).

Species groups are not all endemic, but the distribution of each is chiefly in a particular basin. There are three cases of vicariance pattern. *A. iniridae* of the

*pertensis* group is found so far in the Orinoco basin (R. Inirida system). *A. ortmani* of the *regani* group is endemic to the Essequibo system (Guyana). *A. luelingi* of the R. Chapare (Bolivian Amazonas) is of the Paraguayan *commbrae* group. *A. caetei* and *A. piauiensis* of the *regani* group are found in Atlantic coast rivers only.

Very little is known about the ecology of *Apistogramma* species. The scant data may be found in Klee (1965), Knöppel (1970), Kullander (1976; in prep. a), Lüling (1969a, b; 1973b), and Marlier (1965, 1967).

The fish communities in which *Apistogramma* species occur are quite varied, and their role cannot be unambiguously interpreted. Principally they appear to be carnivorous, feeding on small invertebrates (cf. Knöppel, 1970; Marlier, 1967; pers. obs.), but probably there is variation between the species. There are no profound differences in mouth shape or jaw dentition between sympatric species. Principally also, they are inhabitants of creeks and small pools, often temporary; only *A. regani* may be a lacustrine species in Lago Redondo, where it may be an element in the floating meadow fauna, as appear to be *Apistogramma* spp. in the Venezuelan Llanos (Mago, 1970). Possibly they are adapted to oxygen depletion (cf. Klee, 1965). Most species are found in rain forest regions, but several also in savannah (the Llanos, Guyana), perhaps in swamps (Paraguay basin), one even in a relatively arid region (R. Parnaíba). The water conditions at most places of collecting are unknown, but data available is from white, clear and black water. The breeding season appears to cover the dry periods and possibly part of the rainy, but this conjecture is based almost solely on estimates of the ages of juveniles, and breeding specimens or eggs have never been observed in nature.

Through aquarium literature and scant ethological studies (Burchard, 1965; Butz & Kuenzer, 1957; Kuenzer, 1962a, b; Wickler, 1966; Meinken, 1960a), we know a little, but far from sufficiently about the reproductive behaviour of some *Apistogramma* species.

In summary, it seems that *Apistogramma* species are rather more sex dimorphic than most other South American cichlids. Males generally have larger fins, more colours and greater size; females are quite small, and rather inconspicuously coloured. The male characters obviously are important in the intraspecific territorial aggression, for imposing on other males (cf. Burchard, 1965). The female colouration and size seems adapted to cryptic behaviour, and may have been developed in response to predation. It appears as if generally the female alone cares for eggs and young, but there are aquarium observations of biparental brooding. Nevertheless a definite pair-bond seems never to have been established, and male brooding appears rather to be female behaviour than a normal male activity. It has been suggested many times that these fishes are polygamous (polygynous), but never clearly demonstrated. The eggs (up to c. 200), are laid on a substrate, usually in some concealed place. The small size of the female allows the hiding-place to be quite small, and since it probably makes the brood protection easier, her size is compensated for in the defence against brood predators (it is nevertheless well known that a brooding female is capable of chasing away fishes of much

larger size than herself). Hiding away means less foraging time though, and there must be an evolution towards smaller sizes, unless there has been an improvement in the ability to capture and digest food. There are large gaps in our knowledge about behaviour and life-histories of *Apistogramma* species, and these subjects should prove most rewarding fields for deeper study, important also to the explanation of the evolution of the genus.

## Relationships

For two reasons particularly, this is not the time and place to discuss at length the relationships and the evolution of the genus *Apistogramma*. (1) Our knowledge of the osteology, general morphology, and adaptations of American cichlids is still much too incomplete, and although much taxonomical work has been done in later years large groups are still very unsatisfactorily known in this respect. (2) The data available on *Apistogramma* is of a rather taxonomical nature, and the characters studied are for the most part not very helpful in a study of phylogeny. Nevertheless it should be possible to point out probable closely related genera, to give a sketch of the intrageneric relationships, and to discuss probable evolutionary tendencies.

*Apistogramma* is no doubt related to *Geophagus* and similar genera of Neotropical cichlids. The particular relationships within this group of genera (the geophagines), characterized best by the epibranchial lobe, cannot in most instances be clearly demonstrated at present. Of several genera our knowledge is too incomplete even to permit conjectures. It cannot be explained yet either the relationships of the geophagines with other cichlids. The genera concerned are:

*Geophagus*, with 10 species, *Biotodoma*, with two species, *Gymnogeophagus*, with four species, all three genera revised by Gosse (1976), *Retroculus*, with three species, revised by Gosse (1971), *Papiliochromis*, with one species, *P. ramirezi*, described by Kullander (1977; in prep. c), and two less well known groups of species: *Acarichthys* with two species, of which *A. heckelii* was described by Eigenmann (1912), and as *Acara subocularis* by Regan (1905b), and as *Geophagus thayeri* by Steindachner (1875), *A. geayi* by Pellegrin (1902b; 1904) and Regan (1905a). "*Crenicara*" *altispinosa* Haseman (1911c) was placed with the geophagines by Kullander (in prep. b). Knowledge of this species is limited to data given by Haseman. It probably represents a new genus.

These 6 genera may be referred to as larger geophagines. By this term is implied a moderate to large size, but they should also be known by a higher number of vertebrae, pectoral fin rays, and gill-rakers, generally present C4 teeth, and absence of rakers on the lower pharyngeal tooth-plate. Some species are mouth-brooders, but all appear to spawn rather openly, and with the exception of the maternal mouthbrooder *Geophagus steindachneri* Eigenmann & Hildebrand, 1910, they are as far as known biparental and relatively isomorph.

*Apistogrammoides* comprises only the small *A. pucallpaensis* from the Peruvian Amazonas. The original description (Meinken, 1965a) contains several errors. There is in fact an epibranchial lobe, and the anal fin spine number varies from 7 to 8 in wild material. The colour pattern is slightly different from that of *Apistogramma*, the scales closest to the dorsal and anal fins cover the fin bases, the scales between the principal lateral lines in the caudal peduncle region are pored, and the ceratobranchial rakers not so reduced as in *Apistogramma*. Obviously closer to *Apistogramma* than any other genus.

*Biotocus opercularis* (Steindachner, 1875) has not been redescribed since the original description on specimens from the central Amazonas basin in Brazil, but at least a similar species was figured from the R. Negro drainage by Axelrod (1976), and Central Venezuela by Fernández-Yépez (1969: "*Taeniacara* sp."). *Taeniacara candidi* is known from the original description (Myers, 1935), and that of *Apistogramma weisei* (Ahl, 1936a). The males of the latter type-series is said to have produced dorsal fin lappets. Myers associated the type-species with *Nannacara*.

*Apistogramma*, *Apistogrammoides*, *Biotocus*, and *Taeniacara* form a possibly heterogeneous group of rather small fishes, difficult to delimit because of insufficient data for the latter two genera. *Apistogramma* and *Apistogrammoides*, however, have pharyngeal tooth-plate rakers and lack C4 teeth. They are maternal concealment brooders, and sexually dimorphic (reproductive behaviour of *Apistogrammoides pucallpaensis* described by Schmettkamp, 1977). The best character may be the more or less rounded primary caudal fin shape. In larger geophagines the caudal fin is truncate or slightly emarginate.

It is difficult to find more characters than the lobe uniting the geophagine genera; 2, maybe 3 species are aberrant also in this respect. A black spot anteriorly in the dorsal fin is found in *Apistogramma*, *Acarichthys*, *Papiliochromis*, *Biotocus*, and *Apistogrammoides*. A black stripe through the eye (sub- and superorbital stripes) is more common, but is also found in non-geophagine genera. Most species have three anal spines, only *Apistogrammoides* having 7–9, *Apistogramma luelingi* normally four, individuals of *Apistogramma* spp. four, six, or even two, and individuals of *Papiliochromis ramirezi* four (D.C. Hicks, pers. comm.). Except for the smaller geophagines, the caudal fin is truncate to emarginate, and in at least *Apistogramma*, *Papiliochromis*, and *Geophagus* the lateral line is continued on the caudal fin. *Papiliochromis* and *Apistogramma*, probably also "*Crenicara*" *altispinosa* have serrated preoperculum. No species is known to be a piscivore.

Haseman (1911b) separated the lobed genera of cichlids and called the group the Geophaginae. Considering them a subfamily we would have a very heterogeneous "*Cichlinae*" besides, and I believe there is no gain in attempting to distinguish subfamilies among cichlids with present knowledge only. Cichocki (1977a) considered a subtribe Geophagi including at least *Biotodoma*, *Apistogramma* and *Geophagus*, but gave no details. He also considered (1977b) *Biotocus*, *Acaronia*, and *Chaetobranchius* to represent the sister group of other American cichlids, excluding *Crenicichla* and *Cichla*, but used evidently numerical taxonomy.

Regan (1906b) tried to show the evolution of the Neotropical cichlids with a dendrogram (Fig. 8, this paper), the interpretation of which is not unambiguous. A similar, but less precise and less intelligible was submitted by A. de Miranda Ribeiro (1915). A failure of both of these dendrograms is that the American cichlids are viewed as having a common ancestor. It appears more likely that there are distinct lineages.

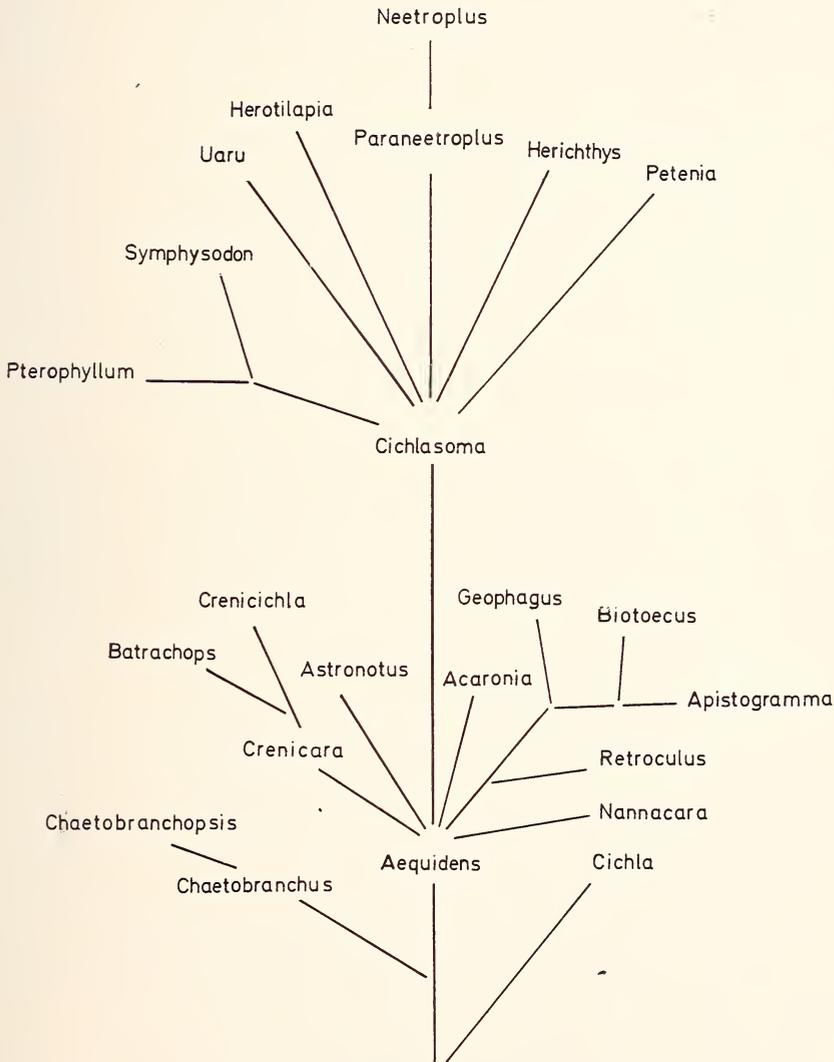


Fig. 8. The evolution of the American cichlids. From Regan (1906b); redrawn, slightly modified, modern names employed.

*Nannacara* Regan, 1905, with four nominal species is a non-geophagine genus very similar to *Apistogramma* in several respects. A *Nannacara* species examined (called *N. anomala* by aquarists) is a sexually dimorphic, small, maternal concealment substrate brooder. The type-species of the genus, *N. anomala* Regan, 1905, is known from Guyana (Regan, 1905a; Eigenmann, 1912), and Surinam (Boeseman, 1952; 1954; 1956). *N. taenia* Regan, 1912, from Manaus is probably a junior synonym and the locality incorrect. *N. bimaculata* Eigenmann, 1912, from Guyana is obviously a distinct species, but never redescribed. *N. hoehnei* A. de Miranda Ribeiro, 1918, from the R. Araguaia system is probably rather an *Aequidens* species.

Examination of aquarium material of the species called *N. anomala* by aquarists suggests that the similarity with *Apistogramma* is rather superficial, and that *Nannacara* may rather be related to *Aequidens*, as suggested by Regan (1906b), in particular then with *Ae. curviceps* Ahl, 1924 and *Ae. dorsiger* (Heckel, 1840). The *Nannacara* sp. has one supraneural, three anal fin spines, no rakers on the lower pharyngeal tooth-plate, no C4 teeth, short and broad first hyobranchial, maxilla concealed, small terminal mouth, scales next to posterior half of spinous dorsal fin, anal fin and soft dorsal fin covering fin bases with their distal parts, 14 principal caudal rays, scaled preoperculum, entire preoperculum edge, cycloid or weakly ctenoid predorsal and preventral scales, 5–7 ceratobranchial rakers, and no epibranchial lobe.

The only character linking *Nannacara* especially with *Aequidens* may be the scaled preoperculum, found also in *Ae. dorsiger*-like species and in *Ae. maronii* (Steindachner, 1882). However, the preoperculum is scaled also in *Pterophyllum scalare* (Lichtenstein, 1823), and this character may be unreliable. A definitive autapomorphy of *Nannacara* is the caudal fin ray number, lower than in any other cichlid known to me. Whatever the relationships of *Nannacara* may be, they appear definitely not to be with *Apistogramma*.

Within the genus *Apistogramma* may be distinguished a few groups of species more similar to each other than to other species, but the relationships of several species are still obscure. Meinken (1962) attempted to distinguish groups of species characterized by different eye diameter /snout length proportions and various shapes of dorsal and anal fins in males. Goldstein (1970) believed the system to be artificial, but it is apparent from Meinken's other papers that he considered his species groups to be natural. The very artificial character states he uses, and the absence of any considerations about the evolution, make the groups recognized appear rather arbitrary, however, and the different characters used here do not produce the same result. It should also be noted that Meinken attributes several species with characters that they certainly do not have. Species groups here recognized are:

The *regani* group: Possibly heterogeneous (symplesiomorph characters). Bars, lateral band, head stripes, anterior dorsal fin spot present, but no chest blotch or lateral spot. 3–4 series of jaw teeth. No dorsal or caudal fin sex dimorphism. Lower

lateral line with canals. Comparatively deep body. 1–4 gill-rakers generally. Species: *A. moae*, *A. regani*, *A. geisleri*, *A. caetei*, *A. ortmanni*, probably *A. piuiensis*.

The *macmasteri* group: Perhaps the most homogeneous group. All species in the Orinoco basin. An exclusive character is the dark blotch on the chest in females. Moderately deep body. Bars present; usually lateral band of spots; head stripes and dark anterior dorsal fin. 3 series of jaw teeth. Dorsal fin with produced lappets in males, but caudal fin rounded. Lower lateral line with canals. 1–4 gill-rakers. Species: *A. macmasteri*, *A. viejita*, *A. hongsloui*, probably *A. hoignei* (males unknown).

The *commbrae* group: The Paraguayan counterpart to the *regani* group. These species do not have as few ceratobranchial rakers as the *borellii* group species, but the lateral line is typically without canals. Moderately deep body. Bars and lateral band present, but lateral spot only in *A. luelingi*; head striping reduced in *A. pleurotaenia*; dorsal fin anterior membranes dark, no chest blotch. No dorsal or caudal fin sex dimorphism known. Lower lateral line without or with few canals. 1–3 gill-rakers. Species: *A. commbrae*, *A. pleurotaenia*, *A. sp. nov.* (Cáceres), probably *A. luelingi*.

The *borellii* group: These species appear to have virtually identical colour pattern, and differ but slightly. Wild material is available only of *A. borellii*. The absence of gill-rakers and the reduced lateral band are typical characteristics. The body is rather deep. Bars present in *A. borellii* at least, lateral band only posteriorly on flank (complete in *A. rondoni*?), lateral spot only in females, postorbital head stripe absent, dorsal fin dark anteriorly, no chest blotch. 3 series of jaw teeth. Unpaired fins larger in males. Lower lateral line typically without canals. No gill-rakers. Species: *A. borellii*, *A. rondoni*, *A. aequipinnis*.

The *agassizii* group: Elongate species without or with very faint bars, lateral band, and lateral spot. More or less complete head stripes. Dorsal fin dark anteriorly. Chest blotch not present. 3 series of jaw teeth. Dorsal fin with or without produced lappets in males; caudal fin with a middle prolongation or a streamer in each lobe. Lower lateral line with canals. Up to 4 gill-rakers. Species: *A. agassizii*, *A. bitaeniata*, *A. elizabethae*.

The *gibbiceps* group: Moderately elongate. Bars principally expressed in ventral flank spots. Lateral band present, lateral spot present or absent, head striping reduced, dorsal fin anterior membranes not distinctly darkened, no chest blotch. 2–3 series of jaw teeth. Dorsal fin with or without produced lappets, caudal fin with a prolongation in each lobe in males. Lower lateral line with canals. 1–3 gill-rakers. Species: *A. personata*, *A. gibbiceps*.

The *pertensis* group: Of the elongate species perhaps the best defined group. Males of three species have at least posterior dorsal fin lappets united beyond spine tips, and the preventral scaling is more or less reduced anteriorly. Caudal fin shape rounded to lanceolate in males. Bars may be traced but are not part of the colour pattern. Lateral band and lateral spot present, head striping incomplete,

no dark spot anteriorly in the dorsal fin, and no chest blotch. 2, rarely 3 jaw teeth series. Lower lateral line with canals. 1–5 gill-rakers. Species: *A. pertensis*, *A. iniridae*, *A. meinkenii*, *A. uaupesi*, *A. gephyra*, *A. pulchra*.

Of the remainder at least two species are very distinct, *A. cacatuoides*, and *A. steindachneri*, the latter with a complete set of the markings listed above, but no chest blotch, 2–3 jaw teeth series, two caudal fin elongations in males, lower lateral line canals, 1–5 gill-rakers, and relatively deep body shape. Each may be regarded as a monospecific species group. *A. taeniata* has its typical body shape, and thus seems also quite distinct. The undescribed Oyapock species resembles the *regani* group species, but may prove to be distinct. Of *A. parva*, *A. amoena*, and *A. sweglesi* nothing can be said about relationships for the moment. *A. trifasciata* and *A. roraimae* may possibly prove to be related in some way to the *pertensis* group. The relationships of *A. brevis* are very obscure.

Bars are found in young of species in which adults lack them, and the presence in adults seems also to be correlated with more teeth-series, deep body, and unmodified fin shape, to some extent at least. The evolution appears to be towards a loss of the bars, more elongate body shape and increased sexual dimorphism. The head stripes are reduced in number and intensity in several species and that character state is probably secondary, like the loss of the dark pigmentation of the anteriormost dorsal fin membranes. A lateral spot on the other hand seems to be a derived character. The produced dorsal fin lappets in males of many species have probably been evolved several times, and are also found in two other genera of cichlids, viz. *Taeniacara* (males) and *Papiliochromis* (both sexes). Caudal fin streamers are more common in the family, found also in African cichlids, and probably also not necessary indicating relationship. It appears natural, however, to regard fin shape modifications as derived character states. The teeth series tend to become fewer, but the dentition is probably correlated with feeding and the change would then reflect a change in diet. Gill-raker number and lateral line development may rather be a subject to latitudinal variation, being more reduced in southern regions. The naked throat is obviously a secondary condition.

#### 4. SPECIES DESCRIPTIONS

##### Methods

##### Selection of species

The 18 species described below represent the *Apistogramma* species of the Amazonas basin in Peru and Brazil, with the addition of two species from the R. Apeu, Caeté, and Parnaíba, draining into the Atlantic south of the R. Amazonas. With descriptions of *A. amoena*, *A. taeniata*, *A. sweglesi*, *A. parva*, *A. luelingi*, and *A. trifasciata*, a revision of the Amazon basin species would have been complete, but since *A. luelingi* was so recently described, and material is insufficient or lacking of the remainder, their exclusion is motivated, unfortunately. Notes

on the four first mentioned are given in the section "Supplementary descriptions", however. A revision of the Orinocoan species has already been prepared, and one on the Guyanas species is planned, appearing elsewhere.

### Measurements and counts

The methods employed in this study in general do not depart from those already in use for cichlids (described by Hubbs & Lagler, 1949; Thys, 1964; Gosse, 1976; and others), but it appears desirable to give as precise descriptions as possible, and in this connection also to comment upon some of the methods of other students of *Apistogramma* and cichlids in general, as far as these are known. The survey of methods is not, and is not intended to be a complete inventory, but should provide a general survey of the subject matter.

Although traditionally of great importance in cichlid taxonomy, clarification of the methods employed for obtaining counts and measurements has never been the subject of deeper attention of students of Neotropical cichlids. But a few have published unambiguous explanations of their methods, mostly as remarks in descriptions of specimens. It is obvious, however, that different methods have been in use, or rather several variants of the same methods, despite the fact that most workers freely compare their data with those of others. Aside from these differences, there is some variation in accuracy, partly due to discrepancy between method indicated or intended, and actual practice. An example is the standard length measurement, taken by some workers to the end of the caudal fin scaling. In this section will be discussed only different methods, however, and only those kinds of measurements and counts that have been used in the present study.

Besides those mentioned above, the following papers contain descriptions of particular measurements or counts that are of value to the understanding of previously employed methods on *Apistogramma* and related genera: Pellegrin (1904), Regan (1905c: *Cichlasoma*), Fowler (1913, 1944b: *Crenicara*, *Geophagus*), Myers (1935: *Taeniacara*), Trewavas (1935, 1964, 1974: Afrotropical cichlids), Myers & Harry (1948: *Papiliochromis*), Fryer (1956: Afrotropical cichlids), Mattes & Trewavas (1960: *Petrochromis*, Afrotropical), Ovchynnyk (1971: Ecuadorian fishes), Eccles (1973: Afrotropical cichlids), Miller (1974: *Cichlasoma*), Busing & Martin (1975: *Cichlasoma*), and Kullander (1976: *Apistogramma*). Some of the papers by Meinken give indications about the methods he used, but comments on them should be looked for in the redescriptions of his species.

### M e a s u r e m e n t s

Measurements were obtained with a vernier calliper reading to 0.1 mm. Perfect bilateral symmetry was assumed, but as far as possible measurements were made on the right side. That is contrary to the common. To avoid errors caused by fluid between specimen and calliper tip, the specimen was allowed a minimum of superficial dryness. Otherwise no particular precaution against errors was taken, except that good lighting was always present.

*SL (Standard length).* The length of the specimen from the caudal fin base (end of hypural plate) on vertical level of the lower lateral line to the tip of the snout including the upper lip.

Remarks: The posterior point, between the articulations of the middle caudal rays, may be determined by bending the fin towards one. The crease representing the caudal fin base may be obscured by the last body scales. The line measured is usually not parallel with the body axis. Different instruments give about identical measurements. The definition given here agrees with that of Hubbs & Lagler (1949), but Thys (1964) included the lower jaw. Some workers include the proximal or all caudal scales in their "standard length", but not consistently. Other terms in use are "skeletal length", "body length" ("Körperlänge"), and "sine caudale" ("s.c.", e.g. in Rendahl, 1937), none of which has advantage over the term here, and usually, employed. The abbreviation SL should be generally recognized, although it is often written "S.L."

*TL (Total length).* The length of the specimen from the tip of the longer middle caudal ray (8th or 9th) to the tip of the snout including the upper lip.

Remarks: This TL equals "Fork length" of fishery biologists, except that a projecting lower jaw is not included. This standard for total length measurements in cichlids was explicitly introduced by Pellegrin (1904) in a somewhat different form, but obviously not invented by him (cf. Boulenger, 1895b). Thys (1964), and probably others, measure the total length of fishery biologists, i.e. from the tip of the snout to the end of the folded caudal fin. The "length" stated by earlier authors, frequently refers to total length, but not always. The abbreviation TL is suggested as a convenient analogue of "SL", but is not extensively used in this paper. The TL is of doubtful value for calculations as the caudal fin is frequently injured or bent in museum specimens, and it may be difficult to establish when it is intact. Record of TL maxima may be of some interest though.

*Head length.* The linear length of the head from a vertical through the posteriormost point of the osseous gill-cover to a vertical through the tip of the snout including the upper lip, on level of the posterior point.

Remarks: The line measured is parallel with the body axis. The measurement is obtained by use of a small measuring board: the head of the specimen is touched against the block which provides the "snout tip point". A similar method was described by Eccles (1973) for some African cichlids, but it seems that the "head length" is usually taken as the greatest length of the head, i.e. the distance between the anteriormost point of the upper lip and the posterodorsal point of the gill-cover. Some workers obviously included the opercular membrane (cf. Hubbs & Lagler, 1949).

*Head depth.* The depth of the head behind the orbit, measured between the ventral and dorsal median lines.

Remarks: This is no very precise measurement, lowered branchiostegal membrane and/or raised gill-cover contributing to variation. The description given here agrees with that of Hubbs & Lagler (1949), except that they take the dorsal point "at the occiput". Thys (1964) measured "entre le point le plus bas du bord operculaire et le bord supérieur de la tête à ce niveau".

*Head width.* The width of the head just behind the orbit on level of its center.

Remark: The repeatability is relatively good, what cannot be said of the measurement described by Hubbs & Lagler (1949) that includes the gill-cover. That of Thys (1964) is obviously similar, aimed at the maximum width on the standard length line.

*Body depth.* The depth of the specimen measured from the ventral median line just anterior to the ventral fins, vertically to approximately the dorsal median line (as close as possible to the dorsal fin base).

Remark: In *Apistogramma* this measurement gives the "greatest depth" implied in the descriptions given by other workers (e.g. Hubbs & Lagler, 1949; Gosse, 1976).

*Orbit diameter.* The diameter of the orbit, parallel to the longitudinal body axis.

Remark: This measurement is obtained by pressing the calliper tips against the orbital rim. There is some uncertainty whether or not earlier workers on Neotropical cichlids measured between the skinny rims of the orbit. The common denotations for this measurement are "diameter of eye" or "eye diameter". The term used here was chosen as the most appropriate, although the measurement is probably not different. I have been unsuccessful in measuring the ocular diameter.

*Snout length.* The linear length of the snout from a vertical through the anteriormost point of the orbital rim to a vertical through the tip of the snout including the upper lip.

Remarks: In practice this measurement is obtained with the use of a block, as in the head length measurement. Methods previously used on *Apistogramma* are unknown to me. Probably this measurement was taken as the direct distance between the tip (anteromedian point) of the upper lip and the orbital rim. For Lake Malawi (Africa) cichlids Trewavas (1935) defined "Snout length" as "... from the vertical from the anterior edge of the eye to the *level* of the tip of the snout, along a line parallel to the longitudinal axis of the body." This measurement is obviously equivalent to that used here. Fryer (1956), working with the same group of cichlids, measured "the shortest distance between the anterior margin of the eye and the tip of the snout", and stated that "Such a measurement is more accurate and more repeatable than that obtained by the method formerly used by Dr. Trewavas and is indeed the method employed by her at present". Besides finding Fryer's description inexact, I disagree on the point of inaccuracy, because a measurement is not accurate only if the stated method is not employed, or the

instrument is not accurate or is misread. In my experience with small specimens, I find Fryer's method less satisfactory as to repeatability, but it certainly permits more rapid mensuration. Whichever method used, variation in the thickness of the snout is reflected in the variation of the snout length, but in opposite directions.

*Cheek depth.* The depth of the cheek along a line continuing the vertical diameter of the orbit, including the infraorbital, to the superior edge of the inferior limb of the preoperculum.

Remark: The cheek is here considered as the soft tissue between the orbit and preoperculum; the infraorbital is included merely for convenience in mensuration. Thys (1964) measured only the depth of the scaled part. The lower point may be difficult to locate in small specimens.

*Interorbital width.* The least distance between the bony orbital rims across the forehead.

Remark: Trewavas (1974) defined this measurement for African cichlids: "... the callipers are pressed against the skin so that this measurement is virtually that of the bony interorbital part of the roof of the skull." Other workers may have included the skinny rim of the orbit unmanipulated (cf. Matthes & Trewavas, 1960).

*Preorbital depth.* "The depth of the preorbital or lacrimal bone measured from the middle of its orbital edge along a line continuing the radius of the eye." (Trewavas, 1974: 333.)

Remarks. Trewavas' definition is precise and is accepted by most workers on cichlids that have published their methods (but cf. Matthes & Trewavas, 1960; Thys, 1964). Gosse's (1976) description of this measurement is only a shorter, less precise one. It is anticipated that "only" the bony part of the preorbital is measured (lacrimal bone + depressed skin). The traditional term has been preserved here, although "lacrimal depth" was used by Kullander (1976), reserving "lacrimal" for osteological terminology.

*Dorsal base.* The distance between the rostral base of the first dorsal fin spine, and the caudal base of the last dorsal fin ray.

Remark: Museum specimens are rarely perfectly straight and no attempt was made to straighten a "normal", less conspicuously curved, specimen. Strongly curved specimens were not used for this measurement.

*Anal base.* Analogous to the preceding measurement.

Remark: The repeatability was not found to be as good as could be desired, because both the anterior and the posterior points may be difficult to find.

*CP depth (Caudal peduncle depth)*. The depth of the caudal peduncle measured over its approximate middle as decided from the dorsal edge, between opposite ventral and dorsal median edge points.

Remarks: Gosse (1976) defined his measurement as "hauteur minimum de ce pédoncule", and that is what is commonly measured on cichlids as well as other fishes. Actually, in many cichlids the peduncle is narrowest on the middle, in *Apistogramma* however, feebly decreasing in depth posteriorwards. This means that, employed on *Apistogramma* specimens, the regular method would equal "depth of caudal fin base". In measuring the middle depth one gains a "mean depth" that better describes the peduncle properties when length and depth are compared, and a measurement at the same longitudinal level as in other cichlids. The abbreviation "CP depth" is here introduced as time and space saving, relatively safe for misinterpretations.

Table 3. Variation in 30 morphometric and meristic characters. Data from wild material listed on p. 25. Measurements are per cent of SL, except "CP/CP" which is CP length as per cent of CP depth.

#### M e a s u r e m e n t s

Head length	27.9— 41.7
Head depth	22.0— 35.7
Head width	12.0— 20.9
Body depth	26.0— 43.5
Orbit diameter	9.4— 16.1
Snout length	3.6— 12.5
Cheek depth	3.0— 9.8
Interorbital width	4.8— 11.4
Preorbital depth	0.8— 4.9
Dorsal base	52.1— 66.4
Anal base	14.8— 26.6
CP depth	11.6— 20.7
CP length	7.8— 18.3
Last D spine	10.1— 24.1
Last A spine	11.5— 19.8
CP/CP	42.9—123.5

#### C o u n t s

Squ. long.	20—24
L <sub>1</sub> (c)	0—18
L <sub>1</sub> (cp)	0—19
L <sub>2</sub> (c)	0— 8
L <sub>2</sub> (cp)	0—10
Cheek scales	1— 6
Squ. op.	6—17
Squ. sop.	2— 9
Squ. iop.	1— 4
D spines	14—18
D <sub>tot</sub>	20—25
A <sub>tot</sub>	7—11
P	10—13
Rakers	0— 5

*CP length (Caudal peduncle length).* The distance between the last anal ray and the end of the caudal peduncle ventrally.

Remarks: The caudal peduncle of *Apistogramma* is characteristically narrowing posteriorwards, and its ventral edge longer than the dorsal. That means that the definitions of the caudal peduncle measurements have to be more precise than is customary. As regards the length, Gosse (1976) and Thys (1964) indicated that they measured the longest edge, what of course improves repeatability, and the longest edge is also the choice here. It is not known, however, if all authors have been aware of the differences in length between the dorsal and ventral edges, although it may not be as apparent in other cichlid genera as it is in *Apistogramma*. Regan (1905c) measured "from the level of the base of the last anal ray to the actual base of the middle caudal rays". Myers (1935) and Myers & Harry (1948) measured from the base of the last dorsal fin ray to the middle of the caudal fin base, Ovchynnyk (1971) similarly, but from the anal fin base, as also described by Hubbs & Lagler (1949).

*Last D spine.* The length of the last dorsal spine along its rostral edge.

*Last A spine.* Analogous to the preceding.

Remarks: Particularly in larger specimens, the last anal and dorsal spines may be curved apically, but this curvature was ignored. A fourth anal spine was considered to be no less the last than a last third. Eccles (1973) measured along the posterior border of a spine.

## C o u n t s

Counts were obtained under a binocular microscope (magnification 6–50 x). The right side was preferred, but due to loss of scales or damaged pectoral fin, counting frequently had to be made on the left side. Lateral line counts were always made on both sides if possible, although only either is used in the tables, preferably the right side count.

The terminology of cichlid meristics is somewhat confused in the literature. The terms chosen were adopted as being brief or more accurately describing the very method. Some terms were invented in analogy with already existing abbreviations (e.g. "squ. caud.").

Not all counts were made on all specimens. Caudal peduncle scales, scales in a transverse series, and ventral fin rays were counted on arbitrarily selected sets of specimens in larger series, but on every individual in smaller series of specimens.

*Squ. long.* The number of scales in a longitudinal series from the last body scale forwards in the series above that including the lower lateral line.

Remarks: The last scale may cover the caudal fin base crease, but was included if judged to be chiefly a body scale. There is indeed a variety of modes in counting the "scales in a longitudinal series", or perhaps are the methods on this important count better documented than those on others. During the first part of the present study, several methods were tried simultaneously, but the one chosen was eventually found to give the least variation. In an earlier paper (Kullander, 1976), I presented the result of a method that is more restrictive in including ultimate anterior and posterior scales, but the one subsequently used alone has the advantage of giving less variation, is more direct than Trewavas' second alternative (below), and does not give rise to confusion about the last scale as Ahl's method does (below).

Pellegrin (1904) counted a series from the operculum to the caudal fin origin. That definition rather embraces the idea of the "squ. long." count as being a record of the number of scale series crossing the flanks. Regan (1905c) defined his count as being of the scales "from above the origin of the lateral line to the case of the caudal fin". Such a count is not possible on *Apistogramma*, but Bussing & Martin (1975) described a count that is, and is probably also that intended by Regan: from "first scale of row immediately below upper lateral line" to "end of hypural plate". Trewavas (1935; 1964) described two methods: (1) the scales "of the upper lateral line and backwards from its posterior end", and (2) the scales of the upper lateral line plus the scales of the lower lateral line from "the scale of the lower lateral line next behind the transverse row that includes the last scale of the upper lateral line and slopes downwards and forwards from it". The two methods obviously give the same count. The latter is that used by Regan, Steindachner, and Boulenger, according to Trewavas (1964), and has been adopted by Thys (1964), Miller (1974), and Gosse (1976). Ahl, according to Trewavas (1935), counted a longitudinal series including the lower lateral line. That is virtually the same method as that described by Myers (1935) and Hubbs & Lagler (1949). Myers & Harry (1948) counted "from the upper edge of the operculum to the base of the caudal". That method is obviously identical with that used for this study.

*Scales in a transverse series.* The number of scales in a series across the side from above the first anal fin spine forwards and upwards to the dorsal fin, the lateral line scale counted as separate.

Remarks: This count is fairly constant in the genus, and is not presented in tables or descriptions (see p. 30). The method was first described by Myers & Harry (1948). Pellegrin (1904) counted from the origin of the dorsal fin to the lateral line and from the lateral line in the same series to the abdomen. Regan (1905c), Thys (1964), and Miller (1974) employed Pellegrin's method. Hubbs & Lagler (1949) modified the count below the lateral line, counting from the origin of the anal fin upwards and forwards. Fowler (1913) counted the scales "between spinous dorsal origin and l.l.", "between rayed dorsal origin and l.l." and "obliquely back from anal origin to beginning of lower branch of l.l.". Later (1944b) he used a different method for the series above the upper lateral line: "below last dorsal spine base and upper section of lateral line". Myers (1935) counted "from anus to dorsal",

hardly different a method from that used in 1948. Gosse (1976) counted the series below the lateral line from before the anus upwards and backwards.

*Ll* (*lateral line scales*).  $Ll_1(c)$  is the number of the canals in the upper lateral line;  $Ll_1(cp)$  is the number of canals and pores in the upper lateral line;  $Ll_2(c)$  is the number of canals in the lower lateral line;  $Ll_2(cp)$  is the number of canals and pores in the lower lateral line.

Remarks: The lower line count does not include scales on the caudal fin, and subserial canals and pores are not included in the counts of the upper lateral line scales. Canals and pores are distinguished as different structures here, but not necessarily by other authors, or they may have included only canals, like Thys (1964).

*Cheek scales*. The number of longitudinal scale series crossing the cheek below the pupil.

Remark: This definition is virtually the same as that of Thys (1964), and Gosse (1976). A count of the entire set of cheek scale series may give a higher figure.

*Squ. op.* (*Operculum scales*). The total number of scales on operculum.

*Squ. sop.* (*Suboperculum scales*). The total number of scales on suboperculum.

*Squ. iop.* (*Interoperculum scales*). The total number of scales on interoperculum.

*Squ. prd.* (*Predorsal scales*). The approximate number of scales along the dorsal midline before the dorsal fin.

*Squ. prv.* (*Preventral scales*). The approximate number of scales along the ventral midline before the ventral fins.

Remarks: The irregularity of the predorsal scale arrangement, and the minuteness and deep embedment of the anteriormost preventral scales, make it difficult to obtain precise counts of the scales in these regions. Results are presented only in the descriptions.

*Squ. caud.* (*Caudal fin scales*). The number of scales in a longitudinal series behind the last scale in the lower lateral line on the body.

Remark: The series counted continues the lower lateral line series on the caudal fin. The counts are presented in the descriptions only.

*Scales around the caudal peduncle*. The number of longitudinal scale series on the caudal peduncle.

Remarks: There is no variation in this count in *Apistogramma*, and the results (16 scales) are not presented in descriptions or tables. The method described by

Hubbs & Lagler (1949), a count of the scales around the narrowest part of the peduncle, appears to be the commonly employed method, and it may, depending on the size of the specimen, give a count of one or two scales less than obtained by my method.

*D.* The number of spines (in capital roman numerals), and rays (in arabic numerals), of the dorsal fin, an ultimate unbranched ray counted as separate from the preceding (in small roman numerals).

*D* spines. The number of spines in the dorsal fin, in arabic numerals.

*D*<sub>tot</sub>. The added numbers of spines and rays in the dorsal fin.

*A.* As for "D", but for the anal fin.

*A*<sub>tot</sub>. As "D<sub>tot</sub>", but for the anal fin.

Remarks: Unbranched rays in the beginning of soft dorsal and anal fins are treated as branched. "D.", "A.", and total counts are given in the descriptions, "D spines", and total counts in the tables. An unbranched ultimate ray is often considered as a part of the preceding ray by other authors.

*P.* The number of pectoral fin rays, not including the dorsal supporting ray.

*Rakers.* The number of gill-rakers on the external side of the first ceratobranchial.

Remarks: Pellegrin (1904) and Regan (according to Trewavas, 1935) counted the number of gill-rakers on the outer side of the inferior branch of the first gill-arch. As appearing from Trewavas' description of this count, Regan included in it the raker on the angle between the epi- and ceratobranchiale. Trewavas' (1935) method, excluding the angular raker unless definitely belonging to the lower limb, is widely accepted by cichlid taxonomists, and that raker, if present, is in *Apistogramma* specimens almost always to be considered as epibranchial and therefore not included in the counts given here.

*Serrations.* The maximum distinguishable number of projections (denticuli) along the free edge of the preoperculum.

### Explanation of descriptions

**Bibliography.** The term bibliography is preferred before synonymy or chresonymy (as recommended by Rentz, 1973). When the material has not been reexamined and doubts exist as to its identity, an interrogation mark (?) precedes the reference. Misidentifications are indicated by a comma after the scientific name. "(pt)" means that the material reported contains other species. Aquarium literature has been avoided, but references of special interest or to photographs of live specimens may be found in the "Remarks".

**M a t e r i a l l i s t s.** The material listed is that used for the descriptions. It should include wild specimens only (killed during capture or shortly afterwards, taken in their natural habitat). Import (taken from a natural habitat and kept and fed in aquarium) or aquarium specimens (raised from eggs in aquarium) studied, may be recorded after the principal material, for the record. Only of *A. gibbiceps*, no wild material has been available.

First is given the registration number of the lot, or specimen (in paranthesis a previous number if of interest), then for each sex (or sex indeterminable; distinguished by the shape of the genital papilla), the number of specimens and the SL for each. "Specimens" are non-typical specimens. The type locality initially given is quoted as appearing on the label or in the protolog, but in the material lists the localities are given in a condensed form: Country (Estado, Território, Departamento), the name of a city or recipient river, the actual place of collecting. Coordinates are either from map measurements, various sources (usually), or from Dr. J.-P. Gosse (IRSNB material). They are all approximate. After the name(s) of the collector(s) follow station or collection numbers (ECMCSA = Expedition of the Carnegie Museum to Central South America, 1907–1910; IMA 1962 or 1967 = IRSNB Mission Amazonie 1962 or 1967; VIT = Leg. T. Hongslo 1971; WLF = Leg. W. L. Fink 1976; only Sta. no. = Leg. G. Marlier 1963–1964).

Most of the material studied is preserved in ethanol, only the NRM material when studied preserved in phenoxetol.

**M o r p h o l o g i c a l d e s c r i p t i o n s.** 64 specific characters were examined on all specimens available or at least a representative series from each lot. Many of these were found to be in the same staté in all species and are described in the genus description, the remainder below. In addition was examined the oral dentition of a number of specimens of different sizes of each species. These data, with colouration and some counts form the descriptions, in which at first are given a subjective impression of the body and head shapes (elongate to deep). The predorsal contour is the profile outline of the head between dorsal fin and the upper lip; the preventral contour is the profile outline between the lower lip and the throat. Relative steepness and form of these contours are noted as well as those of the snout. The orbit position is noted in reference to the predorsal contour, the extension of the maxilla to a line downwards from the anterior rim of the orbit. The pectoral fin extension is noted as the position of the tip when the fin is adpressed to the side, parallel to the body axis, relative a vertical from the vent or an anal fin spine base. Unless otherwise stated, the teeth of the outer series are stronger than the adjacent inner; the size of the teeth in the outer series increases anteriorwards, and the length of this series is always extended to the jaw ends; the teeth recurvature is moderate. By "adult males" is meant males with developed secondary sexual characteristics; by "young" specimens of sizes below that at which differentiation occurs. Figures in parenthesis after fin counts give the number of specimens with the count immediately preceding.

**T a b l e s.** Morphometric and meristic data are given for each species in Tabs. 3–21. They give all measurements except SL and TL, expressed as per cent of SL, CP length also as per cent of CP depth (CP/CP).

**C o l o u r a t i o n.** The colouration was examined on specimens in a petri dish, filled with preservation fluid covering the fish, exposed to direct sunlight. It was noted the ground colour (usually some shade of yellowish), the colour and presence or absence, pigment intensity, and width, size or extension of the markings. The preorbital stripe is present in all species, and is not mentioned in the descriptions.

**S i z e.** The SL/TL for the largest specimen of each sex is given.

### Abbreviations

AMNH	American Museum of Natural History, New York
ANSP	Academy of Natural Sciences of Philadelphia, Philadelphia
BMNH	British Museum (Natural History), London
CAS	California Academy of Sciences, San Francisco
CM	Carnegie Museum, Pittsburgh
ECMCSA	Expedition of the Carnegie Museum to Central South America, 1907–1910
FMNH	Field Museum of Natural History, Chicago
IMA	IRSNB Mission Amazonie
IRSNB	Institut Royal des Sciences Naturelles de Belgique, Bruxelles
MCZ	Museum of Comparative Zoology, Cambridge (USA)
MNHN	Muséum National d'Histoire Naturelle, Paris
NHMW	Naturhistorisches Museum, Wien
NRM	Naturhistoriska Riksmuséet, Stockholm
SMF	Senckenberg Museum, Frankfurt am Main
USNM	United States National Museum, Washington
WLF	leg. W. L. Fink
ZFMK	Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn
ZIMH	Zoologisches Institut und Museum, Universität Hamburg, Hamburg
ZMA	Zoölogisch Museum, Amsterdam
ZMB	Zoologisches Museum, Humboldt-Universität, Berlin
ZMK	Zoologisk Museum, København

*Apistogramma moae* **sp.nov.**

(Fig. 9)

**Holotype.** IRSNB (Types) 586 — ♂, 49.9 mm SL.

**Type-locality.** Igarapé São Salvador, affluent rive gauche du Rio Moa, Cruzeiro-do-Sul. État de Acre. Brésil. (7°38'S 72°36'W.)

**Diagnosis.** Head length 32.3–33.1 %, body depth 37.0–39.1 % of SL. CP length 72.0–72.2 % of CP depth. D. XV.7. A. III.7. Squ. long. 23. Rakers 2. Preoperculum entire. Dorsal fin without produced lappets. Caudal fin rounded. No true

lateral spot, no pectoral spot, abdominal stripes, or midventral stripe. Caudal spot present. Bars developed, not contrasting. No chest blotch. Dorsal fin dark anteriorly. Caudal fin almost immaculate, a few spots posterodorsally. (2 males, 46.5 and 49.9 mm SL.)

**Etymology.** *moae* for the rio Moá.



Fig. 9. Holotype of *Apistogramma moae*.

### Material

**Holotype.** IRSNB (Types) 586 — ♂, 49.9 mm. Brasil (Acre), Cruzeiro do Sul, R. Moá left bank, Igarapé São Salvador (7°38'S 72°36'W). 1967.11.30. Leg. S.M. le roi Léopold de Belgique & J.-P. Gosse (IMA 1967: Sta. 187).

**Paratype.** IRSNB (Types) 587 — ♂, 46.5 mm. Same data as holotype.

### Description

The material is in very fine condition.

Body moderately deep, rather heavy. Head moderately deep. Predorsal contour arched on occiput, about straight descending from above middle of orbit. Preventral contour somewhat less steep, almost straight. Snout broad, rounded, dorsal profile slightly steeper. Orbit subtangential. Tip of maxilla exposed, to anterior margin of orbit. Preoperculum entire.

Predorsal scales cycloid, laterally posteriorwards to vertical from vertical limb of preoperculum. Posterior cheek and opercular scales ctenoid. Squ. prd. 10; squ. prv. 12, 13. Upper lateral line with 2 terminal pores on both sides in holotype; 0—2 anterior pores in lower line; a caudal canal on both sides of both specimens. About 1/3 of caudal fin scaled; squ. caud. 7; a few outer scales cycloid.

Dorsal spines increasing in length to last. Lappets long, pointed, but not produced. Soft part long, pointed, filamentous extension to end of caudal fin. Soft anal fin similar, slightly shorter. D. XV.7(2), A. III.7(2). Pectoral fin to anal fin origin. Ventral fin pointed; first ray slightly produced, to middle of soft anal fin base. Caudal fin rounded.

Table 4. Morphometry and meristics of *Apistogramma moae*. HT = Holotype; PT = Paratype; further explanations in Tab. 5.

	HT	PT
<b>M e a s u r e m e n t s</b>		
Head length	32.3	33.1
Head depth	30.1	29.9
Head width	15.4	16.1
Body depth	39.1	37.0
Orbit diameter	11.6	11.8
Snout length	8.2	7.7
Cheek depth	8.6	8.0
Interorbital width	8.6	8.2
Preorbital depth	3.6	3.4
Dorsal base	58.1	58.5
Anal base	18.4	19.8
CP depth	18.0	17.6
CP length	13.0	12.7
Last D spine	19.0	17.4
Last A spine	17.2	16.1
CP/CP	72.2	72.0
<b>C o u n t s</b>		
Squ. long.	23	23
L <sub>1</sub> (c)	11	15
L <sub>1</sub> (cp)	14	15
L <sub>2</sub> (c)	6	6
L <sub>2</sub> (cp)	7	6
Cheek scales	4	4
Squ. op.	9	10
Squ. sop.	5	6
Squ. iop.	3	3
D spines	15	15
D <sub>tot</sub>	22	22
A <sub>tot</sub>	10	10
P	12	12
Rakers	2	2
Serrations	0	0

Dentition unusually irregular. Outer series of 50–55 teeth in upper jaw, 48 in lower jaw. Anteriorly in both jaws irregular short sequences of teeth, 2–4 series distinguishable. In upper jaw of holotype innermost series continued more or less interrupted as far as the outer series. In lower jaw of paratype a short sequence of postsymphyseal inner teeth. Posterior teeth well spaced, partly with large gaps between them. Some relatively strongly recurved, but most only moderately.

Colouration: Yellowish, somewhat darker dorsally on sides. Markings unusually washed-out, pale brownish. Bars all present, faint. Bars 2–5 to level of lower edge of pectoral axilla or shorter, 6–7 to level of lower edge of caudal peduncle. Indistinct spots along dorsal fin base, faintly extended into basal dorsal fin. Lateral band from narrow postorbital stripe, maculate where crossing anterior bars, rather narrow (1 scale deep) to Bar 6. Spots in Bars 2 and 3 strongest, but no true lateral spot developed.

Suborbital stripe broad; superorbital moderately wide, to occiput. No pectoral spot, abdominal stripes or midventral stripe. Caudal spot faint, obscure, ovate.

Fins whitish to clear. Dorsal fin anterior two spines and membranes black; lappet tips dusky; 0–2 obscure terminal spot-stripes. 2–3 terminal spot-stripes in the anal fin. Caudal fin appearing immaculate, but traces of 2–5 vertical spot-stripes posterodorsally.

### Size

Only two adult males are known, the largest of which is 49.9/68.8 mm long.

### Geographical distribution

Known only from the type-locality. The R. Moá is a tributary of the R. Juruá near the Peruvian border.

### Remarks

*A. moae* may be recognized on its washed-out colour pattern, the least contrasting in the genus, but it does not seem impossible that young specimens and females may be more intensely pigmented. It differs further from other described deep-bodied species of which adult males are known in the principally immaculate caudal fin. From undescribed deep-bodied species of the R. Içá and R. Javari, which are close geographically, it differs in lacking abdominal stripes. The two specimens from the R. Ucayali, reported as *A. amoenus* by Regan (1913), are the most similar in my material. They are 2 probable males, 35.8 and 39.8 mm, loc. R. Ucayali, leg. Mounsey, BMNH 1913.7.30:56–57, in poor condition. The body shape, colour pattern and meristics agree reasonably well. They differ in the

depth of the cheek relative the interorbital width (cheek depth 86.2–88.6 % of the interorbital width; in *A. moae* 97.4–100.0 %), a smaller orbit (10.8–10.9 % of SL), and a broader head (head width 16.2–17.1 % of SL).

It seems probable that the Ucayali specimens represent a close relative of the R. Moá material, if not the same species. The presence of these forms in different river systems (the R. Juruá empties in the middle R. Solimões, the R. Ucayali unites with the R. Marañon near Nauta, Peru, to form the R. Amazonas) may then indicate a historical or contemporary connection between the upper tributaries of the R. Juruá and tributaries of the R. Ucayali (e.g. R. Shehua, R. Tahuania, R. Tamaya), permitting the dispersal of fishes from one system to the other. It remains to see, however, if the Ucayali form is really so close to *A. moae* as the poor material suggests, and whether the distribution of *A. moae* is really restricted to the upper part of the R. Juruá.

It may be noted that *A. moae* is the first species of this genus to be recorded from the Juruá system, but this river is also very incompletely known ichthyologically.

*Apistogramma regani* sp. nov.

(Fig. 10)

**Holotype.** IRSNB (Types) 577 —♂, 37.8 mm SL.

**Type-locality.** Igarapé affluent de la rive gauche du Rio Negro, dans l'Archipel das Anavilhanas, État d'Amazonas, Brésil. (3°00'S 60°45'W.)

**Diagnosis.** Head length 29.1–38.7 %, body depth 32.2–41.0 % of SL. CP length 74.2–105.9 % of CP depth. D. XIV. 8, XV. 6–7, XVI.6.i–7. A.III.5.i–7. Squ. long. 22–23. Rakers 1–3. Preoperculum occasionally serrate. Dorsal fin without produced lappets. Caudal fin rounded. No lateral spot. Caudal spot, pectoral spot, abdominal stripes and midventral stripe present. Bars prominent. No chest blotch. A spot may be present above vent. Dorsal fin dark anteriorly. Caudal fin with 4–9 vertical stripes of spots. (39 specimens of both sexes, 11.7–49.4 mm SL.)

## Bibliography

- ? *Heterogramma ortmanni*, (pt) Haseman, 1911c: 359 (nom. nud.; only specimen from Manaus; short descr.).  
 ? *Heterogramma taeniatum*, (pt) A. de Miranda Ribeiro, 1918: 17 (not Haseman's [1911] material; descr. specimen from Manaus).  
*Apistogramma taeniatum*, Marlier, 1967: 103 (Lago Redondo; listed as stenophagous, carnivorous, not specialized, with regard to feeding habits [IRSNB 15.795, 15.802, 15.803]).  
*Apistogramma borellii*, Meinken, 1971: 38, Tab. 4 (pt, new material from Igarape, S. Jorge, bei Manaus [SMF 10620]; brief descr.).  
*Apistogramma taeniatum*, Lowe-McConnell, 1975: 80 (Tab. 3.3; cop. Marlier [1968], in table illustrating trophic categories of Amazon fishes from Lake Redondo).

**Etymology.** *regani* for Charles Tate Regan (1878–1943) in recognition of his eminent revisions of the American cichlids, 1905–1906.

## Material

- Holotype.** IRSNB (Types) 577 — ♂, 37.8 mm. Brasil (Amazonas), Arquipélago das Anavilhanas, R. Negro left bank, Igarapé (3°00'S 60°45'W). 1967.11.19. Leg. S.M. le roi Léopold de Belgique & J.-P. Gosse (IMA 1967: Sta. 180).
- Paratypes.** BMNH 1939.7.19: 1 — ♂, 49.4 mm. Brasil (Amazonas), Manaus (3°06'S 60°00'W). No date. Leg. J. McCormick.  
IRSNB (Types) 578 — 5♂, 29.7, 29.8, 33.5, 33.8, 34.5 mm; 8♀, 23.4, 23.9, 24.4, 24.8, 26.2, 27.3, 27.5, 28.7 mm. Same data as holotype.  
IRSNB (Types) 579 — 4♂, 26.9, 29.4, 29.5, 33.5 mm. Brasil (Amazonas), Arquipélago das Anavilhanas, R. Negro left bank, Igarapé (3°00'S 60°45'W). 1967.11.18. Leg. S. M. le roi Léopold de Belgique & J.-P. Gosse (IMA 1967: Sta. 179).  
IRSNB (Types) 580 — ♀, 22.6 mm. Same data as holotype.
- Specimens.** IRSNB 15.795 — 5♀, 20.5, 21.6, 25.6, 26.2, 26.2 mm; sex indet., 26.2 mm. Brasil (Amazonas), Lago Redondo, furo (3°10'S 59°44'W). 1964.04.07. Leg. G. Marlier (Sta. 235).  
IRSNB 15.801 — ♂, 26.3 mm. Brasil (Amazonas), near Manaus, Igarapé Mestrinho (3°08'S 60°01'W). 1963.07.19. Leg. G. Marlier (Sta. 35).  
IRSNB 15.802 — 2♀?, 14.3, 15.7 mm; 2 sex indet., 11.7, 15.5 mm. Brasil (Amazonas), Lago Redondo (3°10'S 59°44'W). 1963.10.06. Leg. G. Marlier (Sta. 93).  
IRSNB 15.803 — ♂, 19.1 mm; ♀, 16.7 mm. Brasil (Amazonas), Lago Redondo (3°10'S 59°44'W). 1964.01.04. Leg. G. Marlier (Sta. 138).  
NHMW 17763 — sex indet., 29.2 mm. "Rio Negro". 1913. Leg. J. D. Haseman.  
SMF 10620 — ♂, 28.2 mm; 4♀, 23.4, 25.3, 25.4, 25.8 mm. Brasil (Amazonas), near Manaus, Igarapé São Jorge (appr. 3°06'S 60°00'W = Manaus). 1967.09.15. Leg. R. Geisler.

I have also examined two females, BMNH 1975.7.31: 1–2 (previously 1912.3.2: 6, pt.), "Manaus", Ded. J. P. Arnold, 30.0 and 32.0 mm. These are probably either import or aquarium specimens, and excluded from the following description.



Fig. 10. Holotype of *Apistogramma regani*.

## Description

The type-series, the Igarapé Mestrinho, and the SMF specimens are in fine condition. The Lago Redondo specimens are mostly smaller (11.7–26.2 mm, compared to 22.6–49.4 mm), and also in less satisfactory condition, above all faded and curved. The NHMW specimen is poor, slightly dehydrated and miscolored.

Body moderately deep. Head moderately deep or elongate. Predorsal contour in adults straight descending from occiput, little convex on snout or with minor interorbital notch, more evenly curved in smaller specimens. Preventral head contour little arched, about as steep as predorsal contour. Snout rounded, profiles usually equal, straight, or dorsal convex. Orbit usually tangential. Tip of maxilla exposed, to well behind anterior margin of orbit. Preoperculum serrate in four Lago Redondo specimens (6, 10, 12, or 13 denticuli).

Predorsal scales cycloid, laterally typically posteriorwards only to little behind orbit, at most to a line from little behind dorsal fin origin to orbital rim above longitudinal diameter of orbit. Dorsal, most, or all opercular scales ctenoid; at least anterior cheek scales cycloid; upper subopercular and interopercular scales typically cycloid, occasionally ctenoid. Squ. prd. 8–11; squ. prv. 8–13. Upper lateral line with 0–15 terminal pores, usually 1–4, number decreasing with increasing SL; 1–4 subserial pores in 32 lines, absent from 34 lines; without canals in some small specimens. Lower lateral line usually with pores, 1–7; in some small specimens no canals; 1 pore or canal on caudal fin uni- or bilaterally in 19 instances.  $1/5 - 1/3$  of caudal fin scaled; squ. caud. 3 (small) – 9 (large specimens); all ctenoid or outer cycloid.

Dorsal spines subequal in length from 4th–7th, last longest. Lappets moderately long, rounded (young) or pointed (adults), none produced. Soft part rounded in smallest, in others pointed, produced in large males, at most to end of caudal fin. Soft anal fin similar, but shorter. D. XIV.8(1), XV.6(6), XV.6.i.(8), XV.7(21), XVI.6.i.(1), XVI.7(2).  $D_{tot}$  21(6), 22(30), 23(3). A.III.5.i.(3), III.6(30), III.7(4), III.?(2).  $A_{tot}$  9(33), 10(4). Pectoral fin to vent or (usually) anal fin origin, in juveniles to soft anal fin origin. Ventral fin pointed, to about anal fin origin in females and young males; outer ray slightly produced, to end of anal fin base in adult males. Caudal fin rounded.

Oral dentition in adults triserial, shape of tooth-band similar in both jaws. Outer series of about 45–55 teeth, middle series short, of 20–30 teeth, inner symphyseal or as long as middle series, of 10–30 teeth.

Colouration: Yellowish, counter-shaded, darker dorsally. Markings brown, no conspicuous dark-edging of scales. Bars prominent, but paler than lateral band, in which they may be intensified (spotted band effect) or not; reaching to level of lower edge of pectoral axilla or to anal fin base; broader than interspaces; narrowly darkened near dorsal fin base. Narrow lateral band from narrow postorbital stripe,  $1/2$  to 1 scale wide, to Bar 7, above lower lateral line. Lateral spot small, rounded, not outside band, in Bar 2.

Suborbital stripe moderately wide or broad; superorbital moderately wide, to occiput. Pectoral spot inconspicuous. Abdominal stripes of dark scale edges well-developed: one from upper edge of pectoral axilla vanishing about above anal fin base (not into lateral band), second from lower edge of pectoral axilla to ventral edge of caudal peduncle, third from just below pectoral axilla to middle of soft anal fin base, fourth from origin of ventral fin to middle of spinous anal fin base. Midventral stripe prominent, to almost ventral fin bases. Caudal spot extended vertically, intensely pigmented. Bar 4 frequently forms a spot above vent.

Table 5. Morphometry and meristics of *Apistogramma regani*. n = number of specimens,  $\bar{x}$  = mean,  $s(\bar{x})$  = standard error of the mean,  $s^2$  = variance. Range gives minimum-maximum value in sample; measurements as per cent of SL, except "CP/CP" which is CP length as per cent of CP depth.

	n	Range	$\bar{x}$	$s(\bar{x})$	$s^2$
<b>M e a s u r e m e n t s</b>					
Head length	39	29.1— 38.7	33.6	0.28	3.14
Head depth	39	25.1— 30.7	28.0	0.19	1.35
Head width	38	14.4— 17.9	16.1	0.11	0.46
Body depth	39	32.2— 41.0	36.3	0.26	2.74
Orbit diameter	39	10.3— 14.6	13.3	0.14	0.72
Snout length	38	3.6— 7.4	6.0	0.12	0.51
Cheek depth	38	3.5— 8.2	6.4	0.16	0.92
Interorbital width	39	6.0— 9.0	7.7	0.11	0.48
Preorbital depth	34	1.3— 3.2	2.6	0.07	0.17
Dorsal base	38	52.1— 62.9	59.4	0.36	4.81
Anal base	32	17.2— 22.0	19.5	0.19	1.21
CP depth	39	14.5— 17.2	16.0	0.12	0.53
CP length	38	11.2— 15.4	13.5	0.14	0.73
Last D spine	31	14.4— 21.2	17.6	0.30	2.41
Last A spine	35	14.4— 20.2	18.2	0.18	1.16
CP/CP	38	74.2—105.9	84.6	0.94	33.49
<b>C o u n t s</b>					
Squ. long.	35	22—23	22.6	0.08	0.25
Ll <sub>1</sub> (c)	39	0—14	10.8	0.49	9.50
Ll <sub>1</sub> (cp)	38	13—17	14.4	0.15	0.83
Ll <sub>2</sub> (c)	33	0— 7	3.2	0.33	3.48
Ll <sub>2</sub> (cp)	30	5— 8	6.9	0.14	0.58
Cheek scales	39	1— 3	2.9	0.07	0.17
Squ. op.	23	8—12	9.7	0.22	1.15
Squ. sop.	30	3— 5	4.0	0.13	0.52
Squ. iop.	39	2— 3	2.7	0.07	0.20
D spines	39	14—16	15.1	0.05	0.10
D <sub>tot</sub>	39	21—23	21.9	0.08	0.23
A <sub>tot</sub>	37	9—10	9.1	0.05	0.10
P	38	11—13	11.9	0.06	0.15
Rakers	38	1— 3	1.9	0.09	0.28
Serrations	39	0—13	1.1	0.52	10.68

Dorsal fin clear to dusky, lappets not differentiated in colour. Anterior two membranes black, basal part narrowly dark where bars end; about 2–3 terminal spot-stripes. Anal fin similar in ground-colour, with about 2–3 terminal spot-stripes. Caudal fin clear, with 4–9 very distinct margin-to-margin stripes of spots. The development proceeds from rather medial stripes in young; the last on distal edge of fin. Ventral fin basally dusky, outwards white, spine dusky.

There is noticeable variation in colouration between specimens from different collections (= localities). Young fishes tend to be more yellowish in ground-colour, and the bars may be quite faint, the band and the caudal spot more prominent. The abdominal stripes may be very weakly developed, and the midventral stripe absent. The caudal spot is also more ovate.

### Size

The largest male (BMNH 1939.7.19:1) is 49.4/66.8 mm long, but is then much larger than the next largest (holotype) which is 37.8/51.4 mm. The largest female (IRSNB 578) is 28.7/38.7 mm in length.

### Geographical distribution

The localities at which the species has been collected are all near Manaus: from the Arquipélago das Anavilhanas, little upstreams the R. Negro, to Lago Redondo, a small white water várzea lake on the R. Solimões right bank, some 25 km SW of Manaus.

### Ecology

Marlier (1965, 1967) gave an extensive limnological description of Lago Redondo, and also listed *A. regani* (1967, as *A. taeniatum*) as a stenophagous, not specialized carnivore, together with *Serrasalmus nattereri* Kner, *S. elongatus* (Kner) (Characidae), *Colomesus psittacus* (Schneider) (Tetraodontidae), *Eigenmannia virescens* (Valenciennes) (Rhamphichthyidae), *Pimelodella cristata* (Müller & Troschel) (Pimelodidae), *Plagioscion squamosissimus* (Heckel) (Sciaenidae), ?*Geophagus surinamensis* (Bloch) (Cichlidae). Specialized carnivores distinguished by Marlier included fish-, insect-, and zooplankton-eaters. *A. regani* was the only *Apistogramma* species found in Lago Redondo, and the only small species of the carnivores reported.

Marlier collected in October 1963 (4 specimens, 11.7–15.7 mm; from under a floating meadow), January 1964 (2, 16.7–19.1 mm), and April 1964 (6, 20.5–26.2 mm). Breeding during at least August or September is thus indicated.

*A. pertensis* and *A. gephyra* were sympatric in the igarapé in the Arquipélago das Anavilhanas (IMA 1967: Stas. 179 and 180).

## Remarks

Although nomenclaturally new, this species has a long, and in part complicated, taxonomic history which commences with Haseman's (1911 c: 359) description of *Heterogramma ortmanni* Eigenmann. Haseman listed under that name a series of specimens from "Bastos, Rio Alegre of the Guaporé" (Brazil, Estado de Mato Grosso) (CM 2757 a–k, now in part CAS 14774, 2 specimens), and one specimen from "Manaos" (CM 2756, now possibly FMNH).

No description was given of the Bastos specimens, but for the 3.1 cm long Manaus specimen is stated: "A. III.5; D. XV.6; depth 2.5; head 3; interorbital space 3.33 in the head; last dorsal spine little more than half the length of the head; otherwise like the typical form." Haseman ends the entry with the remark that "This species, from the Amazon basin and Guiana, differs but little from the Paraguayan *H. corumbae*." The last sentence in the description is puzzling if typical form means population of the type-locality, type specimen(s) or average morphology, since that was the first time the name was published. It is also curious that the range is given as "the Amazon basin and Guiana", but no reference to specimens from Guyana.

Evidently, Haseman had, or had had, access to a manuscript or specimens from Guyana labelled *H. ortmanni* by Eigenmann. The name was published as new by Eigenmann (1912: 506) with a diagnosis and a material list including a "Type" and many "Co-types", all from Guyana. Since, Eigenmann's description has become uniformly accepted as the protolog and original description of the Guyana species, and the name is always connected with it.

I have examined several of Eigenmann's *ortmanni* from Guyana, where this species is found within a restricted area. This species is readily separated from *A. regani*, but superficially similar in the basic colour pattern, including abdominal stripes. Since no other species with which *A. ortmanni* from Guyana may be confused is known to occur in the Manaus area, it appears very probable that Haseman's *ortmanni* from Manaus is the same species as that called *regani* here. Unfortunately, it has been impossible to locate Haseman's specimen.

The advance publication of the name *ortmanni* by Haseman, raises the question whether not Haseman's specimens are the real syntypes of *ortmanni*? I believe it would be a mistake to consider them that, because it is clearly stated in the description of the Manaus specimen that the data given are not as in "the typical form". That is, only aberrations from something are described, and thus Haseman does not make the name available. In my opinion therefore, *Heterogramma ortmanni* Eigenmann in Haseman (1911 c) is a nomen nudum. The name *ortmanni* is available only for the species described in 1912 by Eigenmann.

A. de Miranda Ribeiro (1918) probably described the second specimen of this species, as *H. taeniatum*. His text, in Portuguese, may be quoted in full in translation: "One specimen, 55 mm, from Manaus. It shows the band on the three first dorsal spines very conspicuously and the other characteristics in Günther's de-

scription. In addition it has seven black transverse bands on the caudal fin, a character present also on the specimen figured by Hasemann. / That author gave as variety of this species the pl. 46 and the description 59 on p. 359 in his survey of the cichlids of the Carnegie Expedition. / I do not accept his conclusion. / It is sufficient to compare the plates to confirm that they are two distinct species. / The specimen of *H. taeniatum* collected by me has the lateral band characteristically in zig-zag."

The *H. taeniatum* sensu A. de Miranda Ribeiro, figured by Haseman, is *A. caetei* (Haseman, 1911 c: pl. 65). The variety referred to is Haseman's *A. pertensis*. Aside from the zig-zag band, the description may, given the locality, be of *A. regani*.

The Lago Redondo material was reported as *A. taeniatum* by Marlier (1965, 1967, 1968).

The material on which was based the fourth determination of *A. regani*, has also been available for redetermination. Meinken (1971) described the SMF 10620 specimens as *A. borellii*. The finding of *A. borellii* in the Amazônia was said by Meinken (1971) to be remarkable and that seems to have been his justification for the report. Actually, it is the third species he identified as *A. borellii*, and all are Amazonian (cf. Kullander, 1976). The mistake probably has to do with the presence of abdominal stripes in all these species (but not in *A. borellii*), and that character is very evident in *A. cacatuoides*, which Meinken first identified as *A. borellii*.

The diagnosis given here fails somewhat for the not very well preserved Lago Redondo material. These specimens are for the most part faded, curved and soft. When compared directly with specimens from the typical series, the only differences appearing are explained by the state of preservation and the different size ranges (11.7–26.2 mm; 22.6–37.8 mm for the IRSNB type-series). Slight differences in morphometry appear to reflect only size differences, specimens of same size very similar in proportions. Curiously, preoperculum serrations occur only in the Lago Redondo material. Meristically, the left and right bank samples are insignificantly different in the pectoral fin count ( $\bar{x}$  = 11.6 for Lago Redondo material;  $\bar{x}$  = 12.0 for left bank specimens), and dorsal fin total count ( $\bar{x}$  = 21.8, and  $\bar{x}$  = 22.0 respectively).

The R. Amazonas may be an effective barrier to the dispersal of small, small-water species, and it would be interesting to study better series from both sides of the river for an estimate of the degree of geographical separation. Unlike the other species of this genus found on both sides of the R. Amazonas, *A. regani* appears to have a very restricted distribution.

*A. regani* is distinct from all other *Apistogramma* spp. in the colour pattern. Differences from *A. geisleri* in meristics or morphometry do not appear clearly in the available material, but the colour pattern differences readily separate the two. *A. caetei* also has a shorter head and deeper body; *A. piuiensis* has more gill-rakers

(range 2–4; range 0–3, mode 2 in *A. regani*), and a higher mode of dorsal spines (16, range 15–16). It is not easily separated from undescribed material from the R. Javari, R. Içá, R. Guaporé, R. Autaz, and Codajás, except in details of the colour-pattern. The most similar Amazonian species, except for *A. geisleri*, appears to be an undescribed form of which I have examined but a single specimen (SMF unreg., ♂, 42.3 mm, "Brasilien, unterer Amazonas", leg. H. Schultz, ded. 1964.09.10, in fine condition). This specimen, however, has no abdominal stripes, and the 8 stripes on the caudal fin are perfectly straight, not slightly curved as in *A. regani* and other *Apistogramma* spp. with striped caudal fins.

*A. ortmanni* from Guyana may be very closely related. It is not so deep (depth 31.5–35.5 % of SL), has more gill-rakers (range 2–5, mode 3), less conspicuous bars, and no vent spot, instead a spot at the base of the ventral fin.

*A. commbrae* from the R. Paraguay has more dorsal spines (range 16–18, mode 16), fewer lower lateral line canals (0–2, mode 0; mode 4 in *A. regani*), fewer gill-rakers (1–3, mode 1), and a different colouration.

### *Apistogramma geisleri*

*Apistogramma geisleri* Meinken, 1971. Senckenberg. biol. 52: 35.

**Holotype.** SMF 10617 — ♀, 28.2 mm SL.

**Type-locality.** Amazonas-Gebiet, Rio Curuçamba bei Obidos (appr. 1°52'S 55°30'W = Óbidos).

**Diagnosis (revised).** Head length 34.0–36.8 %, body depth 34.0–37.8 % of SL. CP length 87.2–88.9 % of CP depth. D. XV.6.i. A.III.6–7. Squ. long. 22–23. Rakers 1–2. Preoperculum entire. Dorsal fin without produced lappets. Caudal fin rounded. No lateral spot or abdominal stripes. Caudal spot and small pectoral spot present. Females with or without midventral stripe. Bars faint. No chest blotch. Dorsal fin dark anteriorly. Caudal fin with 5 vertical stripes of spots on middle rays. (1 male, 25.3 mm, 2 females, 20.9–28.2 mm SL.)

### Bibliography

*Apistogramma geisleri* Meinken, 1971: 35, Tabs. 1–3 (protolog; detailed descr.; loc.: Rio Curuçamba bei Obidos; Holotype SMF 10617, paratypes SMF 10618–10619), Fig. 1 (monochrome photo of holotype, lateral aspect).

**Etymology.** *geisleri* for the collector of the type-series, the German biologist, Dr. Rolf Geisler.

## Material

**Holotype.** SMF 10617 — ♀, 28.2 mm. Brasil (Pará), Óbidos, R. Curuçamba (appr. 1°52'S 55°30'W = Óbidos). 1967.12.09. Leg. R. Geisler.

**Paratypes.** SMF 10618–10619 — ♂, 25.3 mm; ♀, 20.9 mm. Same data as holotype.

## Description

The specimens are in acceptable condition, the fins more or less folded, and in the holotype the last dorsal spines and the soft dorsal fin deformed.

Body moderately deep. Head moderately deep. Predorsal contour slightly arched. Preventral head contour straight, less steep. Snout rounded, dorsal profile curved, ventral straight and less steep. Orbit tangential. Tip of maxilla exposed, to anterior margin of orbit or slightly beyond. Preoperculum entire.

Predorsal scales cycloid, laterally halfway to operculum. Dorsal opercular and posteriormost cheek scales ctenoid. Squ. prd. 8–9; squ. prv. 8–9. Lateral lines with terminal pores, but no subserial pores in the upper; lower not continued on caudal fin. Right side lateral line in holotype probably atypical:  $7/4 +$  pore; left side line with several unmodified scales: 3 + unmodified + 3 + unmodified + 2 + unmodified + 2 pores/2 pores + 5.  $1/4 - 1/3$  of caudal fin scaled; squ. caud. 4–7; outer cycloid.

Dorsal spines increasing in length to last, but nearly equal from 5th. Lappets short. Soft part pointed, without prolongation, to at most  $1/4$  of caudal fin. Soft anal fin similar, but shorter. D.XV.6.i.(3). A. III.6 (1), III.6.i(2). Pectoral fin to anal fin origin. Ventral fin pointed, not produced, to at most middle of anal fin base. Caudal fin rounded.

Dentition in holotype principally biserial, but a symphyseal irregularity in the arrangement in lower jaw. Outer series of about 60 teeth, middle series one-half the length of the outer (upper jaw) or little extended laterally (lower jaw), inner series symphyseal.

Colouration: Yellowish, shading to brownish dorsally, markings brown. Bars, including superopercular, faint, ventrally reaching to level of pectoral axilla (2–4) or anal fin base (5–6), somewhat intensified in lateral band or not. Darkest along dorsal fin base and extending narrowly into the base of that fin. Lateral band from narrow postorbital stripe, irregular or even, to Bar 7, above and on lower lateral line. No lateral spot.

Suborbital stripe wide, prominent; superorbital stripe wide, to occiput. Pectoral spot small or absent. Two hardly perceptible lines of dots from dorsal and ventral edges of pectoral axilla caudad. A short midventral stripe in the smaller paratype. Caudal spot ovate.

Dorsal fin colourless, anterior two membranes black or brown, 2 terminal spot-stripes. Anal fin colourless, with 2 terminal spot-stripes. Caudal fin colourless, with 5 vertical stripes of dots across middle rays, the last on distal edge of fin. Ventral fin colourless, spine and adjacent part black.

Table 6. Morphometry and meristics of *Apistogramma geisleri*. For explanation, see Tab. 5.

	n	Range	$\bar{x}$	$s_{(\bar{x})}$	$s^2$
<b>M e a s u r e m e n t s</b>					
Head length	3	34.0–36.8	35.1	0.87	2.29
Head depth	3	27.7–30.6	28.9	0.87	2.29
Head width	3	16.2–18.7	17.1	0.82	2.00
Body depth	3	34.0–37.8	36.2	1.15	3.94
Orbit diameter	3	13.5–14.4	13.9	0.26	0.21
Snout length	3	6.4– 8.6	7.5	0.64	1.21
Cheek depth	3	5.7– 7.1	6.2	0.44	0.57
Interorbital width	3	6.7– 7.5	7.1	0.23	0.16
Preorbital depth	3	2.8– 3.3	3.1	0.15	0.07
Dorsal base	3	57.3–58.5	57.7	0.38	0.44
Anal base	3	18.2–19.0	18.5	0.24	0.17
CP depth	3	15.4–16.0	15.7	0.18	0.09
CP length	3	13.4–14.2	13.8	0.23	0.16
Last D spine	2	13.9–17.4	15.7	1.75	6.13
Last A spine	3	17.0–19.8	18.0	0.90	2.44
CP/CP	3	87.2–88.9	88.0	0.49	0.73
<b>C o u n t s</b>					
Squ. long.	3	22–23	22.7	0.33	0.33
L <sub>1</sub> (c)	3	7–10	9.0	1.00	3.00
L <sub>1</sub> (cp)	3	7–15	11.7	2.40	17.33
L <sub>2</sub> (c)	3	4	4.0		
L <sub>2</sub> (cp)	3	5– 7	6.0	0.58	1.00
Cheek scales	3	3	3.0		
Squ. op.	2	8– 9	8.5	0.50	0.50
Squ. sop.	3	4	4.0		
Squ. iop.	3	2– 3	2.3	0.33	0.33
D spines	3	15	15.0		
D <sub>tot</sub>	3	22	22.0		
A <sub>tot</sub>	3	9–10	9.7	0.33	0.33
P	3	12	12.0		
Rakers	3	1– 2	1.7	0.33	0.33
Serrations	3	0	0.0		

### Size

The largest specimen at hand is a female, 28.2/38.3 mm (holotype); the largest male is 25.3/+33.8 mm long.

## Geographical distribution

Known only from the type-series, from the R. Curuçamba at Óbidos (Estado do Pará, Brazil).

## Remarks

The above description agrees reasonably well with Meinken's (1971), but he omitted the colour description (colour similarity with *A. taeniata* listed in the diagnosis though), and included the caudal spot in the standard length and the caudal peduncle length measurements. The ventral fin count (I.6) cannot be repeated; all cichlids have V. I.5, rarely I.4.i. There are no scales on the preoperculum. The longitudinal scale series count includes basal caudal fin scales. The gill-arches are very papillose, but gill-rakers are clearly discernible. The holotype is evidently a female, not a male.

Meinken expressed the opinion that *A. geisleri* would be similar and closely related to *A. taeniata* and compared his data with data on *A. taeniata* from Guiana and Ostperu. The Peruvian material is probably identical with that described by Meinken (1961 a) from Leticia; the "Guiana" data is probably taken from Regan (1906 a: description of *H. taeniatum*). The meristic characters shown in Meinken's table 3 are not well selected (3 preopercular scale series = cheek scales, preoperculum naked; no gill-rakers, but I find 1–2; 25 scales in a longitudinal series, but I count only 22–23; transverse scale series 1 1/2, 1, 8, method of counting unknown), and the morphometric data partly inaccurate as well. The depth: standard length, head: standard length and caudal peduncle ratios are incorrect because the caudal spot was included in the standard length and caudal peduncle length measurements. The preorbital depth is definitely not equal to the diameter of the orbit. The eye: head length ratio is rather an expression of the head length: eye ratio and is probably correct then (I have 2.49–2.57, but measure differently); the interorbital width is listed as contained 4.2–4.5 times in the head length (I have 4.58–5.10), and that may be a real difference from *A. taeniata*, the holotype of which has a broader interorbital width (3.6 times in the head length). The lateral line length is that observed on the holotype and is probably atypical. Meinken thus fails to show convincingly differences between *A. taeniata* and *A. geisleri*. These species are, however, well separated by the different snout shapes (p. 142), and I see no reason to speculate in close relationship.

*A. geisleri* is similar to *A. regani* in many ways, but distinguished above all in the colour pattern.

Only one other *Apistogramma* species is recorded from Óbidos, viz *A. agassizii* (MCZ 16029, p. 89, this paper).

*Apistogramma caetei* sp. nov.

**Holotype.** FMNH 54164A (CM 2732 pt.) — ♂, 35.6 mm SL.

**Type-locality.** Igarapé in Bragança (Estado do Pará, Brazil; 1°45'S 46°47'W).

**Diagnosis.** Head length 27.9–33.7 %, body depth 34.9–39.9 % of SL. CP length 64.6–77.1 % of CP depth. D. XV.6–7. A. III.6–7. Squ. long. 23. Rakers 1–3. Preoperculum entire. Dorsal fin without produced lappets. Caudal fin rounded. No lateral spot, pectoral spot or abdominal stripes. Caudal spot, occasionally a midventral stripe present. Bars developed, but not prominent. No chest blotch. Dorsal fin dark anteriorly. Caudal fin with 5–8 vertical stripes of spots. (4 males, 21.5–35.6 mm SL.)

**Bibliography**

*Heterogramma taeniatum* (pt), Haseman, 1911 c : 357 (brief descr.; specimens from Bragança [FMNH 54164A–C, as CM 2732 a–c]), pl. 65 (retouched monochrome photo [FMNH 54164A, lateral aspect]).

**Etymology.** *caetei* for the rio Caeté, the major river in the type-locality area, probable recipient of the igarapé in which the type-series was collected.

**Material**

**Holotype.** FMNH 54164A (CM 2732 pt.) — ♂, 35.6 mm. Brasil (Pará), Bragança, igarapé (1°45'S 46°47'W). 1909.12.29. Leg. J. D. Haseman (ECMCSA 3352–3365).

**Paratypes.** FMNH 54164B–C (CM 2732 pt.) — 2 ♂, 21.5, 30.9 mm. Same data as holotype.

**Specimen.** MCZ 46090 — ♂, 29.1 mm. Brasil (Pará), Castanhal, Município Boa Vista, R. Apeu (1°21'S 47°55'W). 1965.07. Leg. N. Menezes.

**Description**

The material is in fine condition, also the old specimens in the type-series.

Body deep. Head rather short, more elongate in the smallest specimens. Predorsal contour gently arched to between orbits, straight or with another curvature on snout. Preventral head contour straight or gently arched, less steep. Snout rounded or rather blunt, profiles about straight, dorsal steeper or equal. Orbit subtangential or tangential. Tip of maxilla exposed, to anterior margin of orbit. Preoperculum entire.

Predorsal scales cycloid, laterally posteriorwards to vertical from preoperculum vertical limb, and halfway to operculum. Dorsal or all opercular, and, not al-

ways, posteriormost cheek scales ctenoid. Squ. prd. 8–10; squ. prv. 9–10. Upper lateral line with 1–5 terminal pores, 3 of 8 lines with 1–2 subserial pores; lower with 1–4 anterior pores, not continued on caudal fin.  $1/4 - 1/3$  of caudal fin scaled; squ. caud. 4–6; outer cycloid or all ctenoid.

Dorsal spines subequal in length from 6th, last longest. Lappets short, pointed, none produced. Soft part pointed, to  $1/4$  or  $1/3$  of caudal fin; with filamentous elongation in holotype, to near end of caudal fin. Soft anal fin similar, but shorter. D. XV.6(2), XV.7(2). A. III.6(3), III.7(1). Pectoral fin to anal fin origin. Ventral fin pointed, to anal fin origin, produced in the 3 larger specimens, to base of 2nd or last anal spine. Caudal fin rounded.

Table 7. Morphometry and meristics of *Apistogramma caetei*. For explanation, see Tab. 5.

	n	Range	$\bar{x}$	S(x)	s <sup>2</sup>
<b>Measurements</b>					
Head length	4	27.9–33.7	31.7	1.28	6.58
Head depth	4	28.5–32.0	29.7	0.78	2.42
Head width	4	15.5–17.7	16.7	0.46	0.83
Body depth	4	34.9–39.9	37.7	1.09	4.71
Orbit diameter	4	12.0–14.0	12.8	0.47	0.89
Snout length	4	6.5–7.9	7.2	0.30	0.35
Cheek depth	4	7.2–8.8	8.1	0.34	0.46
Interorbital width	4	7.6–8.4	8.1	0.21	0.17
Preorbital depth	4	2.1–3.7	3.0	0.34	0.46
Dorsal base	4	56.7–60.7	58.5	0.84	2.84
Anal base	4	20.1–22.8	21.4	0.69	1.89
CP depth	4	15.3–18.3	16.8	0.63	1.58
CP length	4	11.6–12.9	12.3	0.32	0.42
Last D spine	3	15.5–17.2	16.2	0.52	0.82
Last A spine	4	14.9–16.9	16.3	0.46	0.84
CP/CP	4	64.6–77.1	73.3	2.90	33.74
<b>Counts</b>					
Squ. long.	4	23	23.0		
Ll <sub>1</sub> (c)	4	11–13	12.5	0.48	0.92
Ll <sub>1</sub> (cp)	4	14–15	14.5	0.29	0.33
Ll <sub>2</sub> (c)	4	4–5	4.5	0.29	0.33
Ll <sub>2</sub> (cp)	4	8–9	8.3	0.25	0.25
Cheek scales	4	3	3.0		
Squ. op.	3	8–9	8.3	0.33	0.33
Squ. sop.	3	3–4	3.3	0.33	0.33
Squ. iop.	3	3	3.0		
D spines	4	15	15.0		
D <sub>tot</sub>	4	21–22	21.5	0.28	0.33
A <sub>tot</sub>	4	9–10	9.3	0.25	0.25
P	4	12	12.0		
Rakers	4	1–3	1.5	0.50	1.00
Serrations	4	0	0.0		

Jaw dentition triserial in both jaws. Outer series of 45–55 teeth, middle series symphyseal, inner little longer than middle series.

Colouration: Yellowish (MCZ specimen) or olivaceous–brownish (FMNH specimens), markings brown. No prominent dark scale-rims. Bars variously developed. In holotype no distinct superopercular bar, in the MCZ specimen a faint, in the others a slightly more intense bar. Similarly with the other bars. Bars 2–6 distinct only close to dorsal fin base in holotype, and then still faint; in the others to ventral body edge or shorter, more prominent. In one paratype and the MCZ specimen also slightly intensified on abdominal sides. Bars 1–6 form spots along the dorsal fin base in the MCZ specimen. Bar 7 in the holotype next below the lateral band as strongly pigmented as the band. Lateral band from moderately wide or narrow postorbital stripe, anteriorly 1 scale deep, posteriorwards broadening, to Bar 7, above lower lateral line. Edges not even, but distinct. Rather as a series of confluent spots in the MCZ specimen. No lateral spot.

Suborbital stripe moderately wide, prominent, slightly recurved; superorbital stripe to occiput, more or less apparent. No pectoral spot or abdominal stripes. A very weak, short midventral stripe in the holotype. No chest blotch. Caudal spot ovate or quadratic.

Dorsal fin almost colourless, anterior two membranes black, bars extended faintly into base, 2–4 terminal spot-stripes. Anal fin ground-colour similar, membranes dark basally or not, 2–4 terminal spot-stripes. Caudal fin almost colourless, with 5–8 stripes of dots vertically from margin to margin, about width of interspaces, the last on distal edge of the fin. Ventral fin white or almost colourless, spine and first membrane dark.

### Size

The largest specimen (holotype) is a male, 35.6/48.6 mm long.

### Geographical distribution

Known only from the R. Apeu and R. Caeté drainages in the Estado do Pará, Brazil, E of the Baía de Marajó.

### Remarks

The only label that I have of the type-series states "Brazil: Pará" for locality. There can be no doubt, however, that this is the series reported as CM 2732 a–c by Haseman (1911 c: 357). The holotype agrees in every detail with the fish figured on his pl. 65, except that the colouration is more uniform now.

Haseman believed his Bragança specimens to represent *A. taeniata*, and so did A. de Miranda Ribeiro (1918: 17). Haseman, however, reported several species under that name, none of which is *A. taeniata* (cf. Tab. 2, this paper). *A. caetei* rather appears close to *A. piauiensis*, and is also similar to the Amazonian species *A. regani* and *A. geisleri*. A comparison with *A. piauiensis* is complicated, since the material available of *A. caetei* consists only of males, and that of *A. piauiensis* of a female and two juveniles. *A. piauiensis* seems to have more gill-rakers (2–4; 1–3, mode 1, in *A. caetei*), and a longer caudal peduncle (CP length 77.3–81.1 % of CP depth; 64.6–77.1 % in *A. caetei*). More material is needed before colour differences can be established. *A. regani* is more elongate, and has a longer head, besides a different colour-pattern. *A. geisleri* has a longer caudal peduncle (87.2–88.9 % of CP depth), and corresponding shorter anal fin base (18.2–19.0 % of SL; 20.1–22.8 % in *A. caetei*).

*A. caetei* is the only *Apistogramma* species recorded from the R. Caeté and the R. Apeu systems. Closest geographically is *A. parva* from the R. Capim, which, on a juvenile (15.8 mm), appears to be an elongate species with a lateral spot.

*Apistogramma piauiensis* sp. nov.

(Fig. 11)

**Holotype.** MCZ 46831 — ♀, 22.7 mm SL.

**Type-locality.** Brazil: 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.)

**Diagnosis.** Head length 32.2–34.6 %, body depth 34.2–35.7 % of SL. CP length 77.3–81.1 % of CP depth. D. XV.7, XVI.5.i–6. A. III.5.i–6. Squ. long. 23. Rakers 2–4. Preoperculum entire. No lateral spot, pectoral spot or abdominal stripes. Caudal spot and narrow midventral stripe present. Bars only traced. No chest blotch. Dorsal fin dark anteriorly. Caudal fin faintly spotted. (Colouration from female, 22.7 mm; otherwise also from 2 juveniles, 11.7–13.3 mm SL.)

**Etymology.** *piauiensis*, from the Estado do Piauí.

**Material**

**Holotype.** MCZ 46831 — ♀, 22.7 mm. Brasil (Piauí), Lagoa Seca (3°08'S 41°54'W). 1968.08.29. Leg. T. R. Roberts.

**Specimens.** MCZ 46830 — sex indet., 11.7 mm. Brasil (Piauí), Barra do Longa, R. Parnaíba (3°08'S 41°54'W). 1968.08.27 — 09.04. Leg. T. R. Roberts.  
MCZ 52212 — sex indet., 13.3 mm. Same data as holotype.

**Description**

The holotype is a fine female with swollen genital papilla and rather contrasting colouration, probably a reproducing adult. The juveniles are less fine; particular-



Fig. 11. Holotype of *Apistogramma piauiensis*.

ly the smaller one has lost many of its scales. The description is essentially of the holotype.

Body moderately elongate. Head moderately elongate. Predorsal contour about straight descending, with ignorable curvatures above orbit and on snout. Preventral head contour gently arched, about as steep as predorsal. Snout rounded, dorsal profile curved, steeper, ventral straight. Orbit tangential. Tip of maxilla exposed, to anterior margin of orbit. Preoperculum entire.

Predorsal scales cycloid, laterally posteriorwards to vertical from preoperculum vertical limb. Dorsal opercular and, on one side only, one postorbital cheek scale ctenoid. Squ. prd. 10 (juv.: 9); squ. prv. 10 (juv.: 8). Lateral lines with terminal pores, unilaterally 2 subserial pores in upper, and one caudal pore (juv.: posterior one-half of upper pored; lower without canals). Less than 1/4 of caudal fin scaled; squ. caud. 3 (juv.: 3); all ctenoid.

Dorsal spines subequal in length from 4th or 5th, last longest. Lappets short, rounded. Soft part pointed, without extension, to 1/3 of caudal fin. Soft anal fin similar, but shorter. D. XV.7 (juv.: XVI.5.i, XVI.6). A. III.5.i (juvs.: III.6). Pectoral fin to vent. Ventral fin pointed, not produced, to middle of spinous anal fin base. Caudal fin rounded.

Oral epithelium with numerous papillae complicating examination of dentition. Apparently 3 series of teeth in each jaw. Outer series of about 40 teeth, middle series symphyseal, inner series one-half the length of the outer.

Table 8. Morphometry and meristics of *Apistogramma piagaiensis*. For explanation, see Tab. 3.

MCZ No.	46831	52212	46830
<b>M e a s u r e m e n t s</b>			
Head length	32.2	34.6	34.2
Head depth	27.3	28.6	24.8
Head width	15.0	18.0	19.7
Body depth	35.7	35.3	34.2
Orbit diameter	13.2	14.3	—
Snout length	6.2	6.0	—
Cheek depth	6.2	5.3	—
Interorbital width	7.5	7.5	6.8
Preorbital depth	2.6	—	—
Dorsal base	57.3	55.6	—
Anal base	18.5	18.8	—
CP depth	16.3	16.5	15.4
CP length	13.2	12.8	—
Last D spine	15.0	—	—
Last A spine	16.3	15.0	—
CP/CP	81.1	77.3	—
<b>C o u n t s</b>			
Squ. long.	23	23	—
LI <sub>1</sub> (c)	10	7	—
LI <sub>1</sub> (cp)	14	13	—
LI <sub>2</sub> (c)	4	0	—
LI <sub>2</sub> (cp)	8	7	—
Cheek scales	3	2	—
Squ. op.	8	8	—
Squ. sop.	4	4	—
Squ. iop.	3	1	—
D spines	15	16	16
D <sub>tot</sub>	22	22	22
A <sub>tot</sub>	9	9	9
P	12	12	—
Rakers	4	3	2
Serrations	0	0	0

Colouration: Pale greyish, markings brown. Bars not apparent, visible as traces; Bar 7 medially as intense as lateral band, extended little above and below it. Confluent, inconspicuous spots along dorsal fin base. Lateral band from narrow post-orbital stripe, contrasting, even-edged, about 1 scale wide, to Bar 7, above lower lateral line. No lateral spot.

Suborbital stripe moderately wide; superorbital stripe prominent, to occiput. No pectoral spot or abdominal stripes. Midventral stripe narrow, prominent, forwards to almost ventral fin bases. Caudal spot ovate.

Dorsal fin dusky, anterior two membranes black; dots on bases of membranes; no terminal spot-stripes. Anal fin dusky, immaculate. Caudal fin smoky, immaculate, but with indications of dots on middle membranes. Ventral fin whitish, spine and adjacent membranes black.

Juveniles greyish, with brown, not contrasting markings. Rather like the adult, but bars distinct though weak.

### Size

The holotype (female) is 22.7/30.6 mm in length.

### Geographical distribution

Known only from two localities near the mouth of the R. Longa, in the Estado do Piauí, Brazil.

### Ecology

The Lagoa Seca (Dry Lake) is situated one or two km from the R. Parnaíba main-stem and Barra do Longa, and is in the flooding area of the R. Parnaíba. At the time of collecting it was about 200–400 m wide and one km long, with a maximum depth of 1 m. The bottom was mostly muddy, with rocks in some places. There was almost no macrophyte vegetation. At higher water levels there would be drowned aquatic vegetation, including grasses and bushes, and connections to swampy areas with aquatic vegetation. With *A. piauiensis* about 20–30 species of fish, including many typical of the mainstream habitat, were found here (T.R. Roberts, in litt.).

The juveniles suggest that the species reproduces at least in late July or early August; the appearance of the female holotype that it is a breeding individual, extending the conjectured breeding season to late August.

At Barra do Longa it was associated with a *Cichlasoma* species (MCZ 46827, 1 specimen, 11.4 mm).

### Remarks

*A. piauiensis* has the easternmost range of the species in the genus. The R. Parnaíba forms from main headwaters on the Chapada das Mangareiras, and may have received part of its fauna from eastern tributaries of the R. Tocantins, but the closest relative of *A. piauiensis* may be *A. caetei* from the R. Caeté and R. Apeu, south of the Ilha de Marajó. A discussion of the extralimital distribution of

*A. piauiensis* must await more collecting in the R. Tocantins as well as in the rivers flowing into the Atlantic ocean south of the R. Amazonas. More material is also desirable for any serious comparison with *A. caetei*.

*A. piauiensis* differs from the similar *A. caetei*, *A. regani*, and *A. geisleri* in morphology, meristics and colouration (see pp. 71 and 79).

### *Apistogramma cacatuoides*

*Apistogramma cacatuoides* Hoedeman, 1951. Beaufortia No. 4: 1.

**Holotype.** ZMA 100.033A — ♂, 38.5 mm SL.

**Type-locality.** R. Amazonas basin, between 69° and 71°W (restricted and emended; see p. 87).

**Diagnosis (revised).** Head length 30.9–36.5 %, body depth 33.1–39.4 % of SL. CP length 60.0–105.0 % of CP depth. D. XIV.7, XV.6–7, XVI.5–7, XVII.7.i. A. III.6–7. Squ. long. 22–23. Rakers 1–2. Preoperculum rarely serrate. Dorsal fin anterior lappets produced in males. Caudal fin with dorsal and ventral streamers in males. Lateral spot present. No pectoral spot. Abdominal stripes as lines of spots in young and females, as v-lines in males. Midventral stripes in females. No caudal spot. Bars developed. No chest blotch. Dorsal fin dark anteriorly. Caudal fin immaculate or, in males, spot-stripes in lower lobe, occasionally 2 ocelli in upper lobe. (23 specimens of both sexes, 12.6–41.1 mm SL.)

### Bibliography

- Apistogramma cacatuoides* Hoedeman, 1951: 1 (protolog, detailed descr. of holotype and paratype, both ZMA 100.033; loc.: near Paramaribo, Dutch Guiana), fig. p. 3 (sketch of holotype, lateral aspect).
- Apistogramma cacatuoides* Meinken, 1960 a: 655 (belongs to group of spp. incl. *A. ornativipinis* Ahl, *A. steindachneri* (Regan), *A. wickleri* Meinken).
- Apistogramma borellii*, Meinken, 1961 b: 167 (detailed descr. of aquarium or import specimens; no loc.; sketch of head showing cephalic lateralis pores; 4 monochrome photos; disc. of relationships).
- Apistogramma cacatuoides* Meinken, 1962: 141 (in key-like list of *Apistogramma* spp.; distr.; no ref.).
- Apistogramma borellii*, Meinken, 1962: 142 (pt; in key-like list of *Apistogramma* spp.; distr.; no ref.).
- Apistogramma borellii*, Kuenzer, 1962 b: 362 (brooding and fry behaviour), Figs. 1–3 (monochrome photos of normal colouration and brooding behaviour), Figs. 4–6 (sketches of dummies).
- Apistogramma borellii*, (pt) Klee, 1965: 424 (habitat description: pool situated alongside of a logging road connecting the Pachitea river and Tournavista [Peru]; no descr.; [ZIMH 3239A, D]; incl. *Geophagus jurupari* Heckel, *Crenicara punctulata* (Günther)).
- ?*Apistogramma borellii*, Burchard, 1965: 155, 156, 157 (notes on behaviour).
- Apistogramma cacatuoides* Meinken, 1969 b: 93 (nuchal hump may be indicated).
- Apistogramma cacatuoides* Kullander, 1976: 264 (*A. borellii* in Meinken, 1961 b = *A. cacatuoides*; differences from *A. luelingi* Kullander), 265 (individuals known with 4 anal spines; no ref.; no specimens).

**Etymology.** *cacatuoides* from *Cacatua* (Kakatoe) (Aves: Psittacidae), and *-eidos* (Greek, suffix), -like; probably expressing the similarity in the produced dorsal lappets of the fish with the produced head feathers of the bird. Not explained by Hoedeman.

## Material

- Holotype.** ZMA 100.033A — ♂, 38.5 mm. "Amazone". Import 1950.04. [Ded. J. J. Hoedeman.] (Not included in the description.)
- Paratype.** ZMA 100.033B — ♀, 32.6 mm. Same data as holotype. (Not included in the description.)
- Specimens.** MCZ 51721 — sex indet., 14.7 mm. Colombia (Amazonas), Isla Santa Sofia, isolated pool (3°58'S, 70°10'W). 1972.07. Leg. R. A. Mittermeier.  
MCZ 51748 — 8 ♂, 15.4, 20.8, 23.6, 26.4, 27.2, 31.1, 33.7, 41.1 mm; 6 ♀, 14.7, 15.8, 16.2, 20.5, 29.8, 31.1 mm; 2 sex indet., 12.6, 14.2 mm. Colombia (Amazonas), Isla Santa Sofia, isolated pool (3°58'S 70°10'W). 1972.07. Leg. R. A. Mittermeier.  
NRM 11281 — 2 ♂, 32.3, 32.8 mm. Perú (Loreto), R. Yavari, Lago Matamata, caño (4°12'S 70°17'W). 1971.09.11. Leg. T. Hongslo (VIT 7)  
NRM 11282 — 2 ♀, 23.2, 26.5 mm. Perú (Loreto), R. Yavari, Caño Piraña (? 4°12'S 70°17'W). 1971.09.06. Leg. T. Hongslo (VIT 3 B)  
ZIMH 3239A, D — 2 ♂, 34.2, 40.9 mm. Perú (Huánuco), logging road R. Pachitea — Tournavista, pool (c. 8°50'S 74°36'W). 1964.08.20 or 25. Leg. A. J. Klee.

## Description

The material is for the most part in very fine condition.

Body moderately deep. Head moderately deep. Predorsal contour about straight descending from dorsal fin origin, may be a little arched on occiput. Pre-ventral head contour as steep or steeper, little arched or straight, lower jaw end projecting. Mouth rather large. Snout rounded, profiles straight, equal. Orbit tangential or subtangential. Tip of maxilla exposed, to anterior margin or 1/3 of orbit. Preoperculum with 16 denticles in one MCZ 51748 specimen.

Predorsal scales cycloid along midline and between orbits. Posterior cheek and dorsal opercular, in adults all opercular and also dorsal subopercular scales ctenoid. Squ. prd. 7—11; squ. prv. 9—13. Upper lateral line with terminal pores; 1—2 subserial pores in 17 of 40 lines; lower line without canals in juveniles; a caudal pore in 11 of 43 lines. 1/6 — 1/2 of caudal fin scaled; squ. caud. 3 (small) — 10 (large specimens); outer cycloid or all ctenoid.

Dorsal spines subequal in length from about 4th, last longest. Lappets in young and females pointed, moderately long; in males from 23.6 mm anterior produced: 2nd—6th, 3rd or 4th longest, spine length or longer, in largest male 2nd—5th, from 6th onwards produced but not so long, 4th and 5th longest, to end of dorsal fin base. Soft part pointed in females and young, to at most middle of caudal fin;

produced in males, to at most end of caudal fin. Soft anal fin similar. D. XIV.7(1), XV.6(3), XV.6.i(1), XV.7(2), XVI.5(1), XVI.6(9), XVI.6.i(2), XVI.7(3), XVII.7.i(1).  $D_{tot}$  21(5), 22(12), 23(5), 25(1). A. III.6(15), III.6.i(3), III.7(5).  $A_{tot}$  9(15), 10(8). Pectoral fin to vent or anal fin origin. Ventral fin in young pointed, to vent; in large females with short extension of first ray, to last anal spine; in large males first ray produced, at most to middle of caudal peduncle. Caudal fin in females and young rounded; in males from 23.6 mm with dorsal and ventral extensions, truncate between: dorsal elongation slightly longer than ventral, of rays 4 and 5, ventral of rays 12 and 13.

In medium-sized individuals 3 series of teeth in both jaws: 40–60 in the outer series of the upper jaw, the innermost as long, the middle series symphyseal, 50–60 teeth in the outer series of the upper jaw, the middle symphyseal, the inner little longer. Anteriorly series difficult to discern, teeth rather crowded. Especially in males outer teeth large, wide-spaced, strongest anteriorly. In the largest male in the upper jaw anteriorly scattered very strong, strongly recurved teeth, no serial arrangement; posteriorly 3 series, the outer of about 55 teeth; in lower jaw only one lateral series, of about 40 teeth, anteriorly much as in upper jaw but an innermost, short series, discernible.

Colouration: Yellowish, markings brown. Scales not dark-edged. Bars, most prominent in juveniles, but present also in adults, wider than interspaces, conspicuously oblique; usually only above lateral band, very little into dorsal fin base. Lateral band from moderately wide postorbital stripe, even, ventrally sharp-edged, about 1 scale deep, to caudal fin, on and above lower lateral line. Lateral spot roundish, deeper than band.

Superorbital stripe moderately wide, to occiput; suborbital moderately wide, slightly recurved. No pectoral spot. Abdominal stripes of spots in juveniles: one from upper edge, another from lower edge of pectoral axilla, a third below; in large males v-stripes (zig-zag-stripes) (upper and lower 1/3 of scales of ventral flanks dark-edged); in adult females only two of the juvenile stripes (the upper) remaining, as more or less interrupted narrow streaks. Very short, narrow mid-ventral stripe in females. A dark spot on chin just below lower lip. Branchiostegal membrane in the largest male dusky ventrally. No caudal spot, but lateral band obscurely continued proximally on middle caudal fin rays; in young usually a vertical stripe over caudal fin base.

Dorsal fin in largest male dusky, anterior two membranes black, with clear produced lappets. Anal fin dusky. Caudal fin yellowish, with 5 obscure vertical stripes of spots on basal half of lower lobe. Ventral fin principal part dusky, elongation white. In the others the fins clear; dorsal fin more or less dusky; anal fin with some dark pigment marginally; no terminal spot-stripes in either fin; anterior two dorsal membranes black. Caudal fin immaculate except in one male with two small ocelli on middle of upper lobe. Ventral fin in males and young white, in adult females spine and outer membrane black.

Table 9. Morphometry and meristics of *Apistogramma cacatuoides*. For explanation, see Tab. 5.

	n	Range	$\bar{x}$	$s(\bar{x})$	$s^2$
<b>M e a s u r e m e n t s</b>					
Head length	23	30.9— 36.5	33.5	0.32	2.32
Head depth	23	24.6— 31.3	27.4	0.39	3.59
Head width	23	15.5— 18.8	17.0	0.19	0.82
Body depth	23	33.1— 39.4	35.8	0.37	3.23
Orbit diameter	23	9.5— 13.6	12.0	0.16	0.63
Snout length	21	4.1— 7.5	5.6	0.19	0.74
Cheek depth	23	4.5— 9.2	6.7	0.24	1.36
Interorbital width	22	6.8— 10.7	8.5	0.20	0.88
Preorbital depth	20	2.0— 3.2	2.5	0.07	0.11
Dorsal base	23	52.8— 61.9	58.7	0.49	5.45
Anal base	23	15.5— 22.0	18.7	0.40	3.68
CP depth	23	14.1— 16.9	15.4	0.18	0.75
CP length	22	10.2— 14.8	12.0	0.25	1.35
Last D spine	19	10.7— 17.0	14.2	0.45	3.84
Last A spine	23	11.6— 17.8	15.6	0.37	3.22
CP/CP	22	60.0—105.0	78.1	2.07	94.36
<b>C o u n t s</b>					
Squ. long.	23	22—23	22.6	0.10	0.25
Ll <sub>1</sub> (c)	21	2—13	9.2	0.55	6.26
Ll <sub>1</sub> (cp)	21	9—16	13.6	0.39	3.15
Ll <sub>2</sub> (c)	22	0— 5	2.0	0.38	3.14
Ll <sub>2</sub> (cp)	23	4— 8	6.7	0.22	1.11
Cheek scales	23	2— 6	3.2	0.16	0.60
Squ. op.	19	10—16	13.7	0.38	2.67
Squ. sop.	23	3— 9	5.4	0.34	2.62
Squ. iop.	23	2— 4	2.7	0.15	0.49
D spines	23	14—17	15.7	0.40	0.63
D <sub>tot</sub>	23	21—25	22.1	0.19	0.86
A <sub>tot</sub>	23	9—10	9.3	0.10	0.24
P	23	11—13	12.0	0.14	0.45
Rakers	23	1— 2	1.2	0.08	0.15
Serrations	23	16 in one specimen only			

**Size**

The largest male (MCZ 51748) is 41.1/55.9 mm long, the largest female (same lot) 31.1/41.6 mm.

**Geographical distribution**

Collected near Tournavista, Peru (R. Pachitea), close to R. Yavari on its lower course, and on Isla Santa Sofia in the R. Amazonas little upstream Leticia, Colombia.

## Ecology

Some exological data relating to the ZIMH specimens were given by Klee (1965: 423). These specimens were collected in a pool the size of a bathtub, with clear, slightly yellow water, after a heavy rain dark brown water. The pH was quite high: 6.8 before, 6.5 after the rain; as was the iron content: 2.0 ppm and 2.5 ppm. Before the rain the pool water contained 3.5 ppm dissolved oxygen, after only 0.5 ppm. Other fishes caught here included *Hoplosternum thoracatum* (Valenciennes) (Callichthyidae), *Pimelodella peruana* Eigenmann & Myers (Pimelodidae), *Erythrinus erythrinus* (Schneider), *Hoplias malabaricus* (Bloch) (Erythrinidae), *Pyrhulina melanostoma* (Cope) (Lebiasinidae), *Carnegiella strigata* (Günther) (Gasteropelecidae), *Hyphessobrycon peruvianus* Ladiges (Characidae), listed by Klee, and also one *Geophagus jurupari* Heckel (34.0 mm) and three *Crenicara punctulata* (Günther) (30.5–32.4 mm) of the family Cichlidae.

The MCZ 51748 series was taken with one *Apistogrammoides pucallpaensis* (20.0 mm), known also from the R. Ucayali near Pucallpa.

The NRM 11282 specimens were taken together with a male *A. agassizii* (31.1 mm).

The smallest Isla Santa Sofia specimens (down to 12.6 mm) suggest that the species reproduces there in June or July.

## Remarks

The type-specimens, being imports, are excluded from the description given above, although they conform rather well to it. The holotype is in poor condition, curved, with first and second right side gill-arches removed (preserved separately), gill-cover scales in part lost, as well as some body scales (a few preserved separately), and many caudal fin scales. The caudal fin shape is indeterminate, and some soft fin ray tips lost. The colour is very dark all over, with scattered black specks that are not part of the colouration. It is 38.5 mm long and has 3 series of cheek scales, squ. long. 22, L<sub>1</sub> 8+2 missing+2 undifferentiated+1, L<sub>2</sub> 2 pores+1+2 pores+1+2 pores, D. XV.6, A. III.6.i, P. 11, 3 rakers. The paratype is as poor, with obvious signs of disease (eyes protruding). It is 32.6 mm long, has 3 cheek scale series, squ. long. 23, L<sub>1</sub> 10+4 pores+4 subserial pores, L<sub>2</sub> 6 pores+1, D. XVI.5.i, A. IV.6, P. 11, 1 raker, caudal fin abnormal (ii.4.3.i).

The type-locality was given by Hoedeman (1951) as near Paramaribo, Dutch Guiana (= Surinam), and he also stated that the type-specimens had been imported alive by a sailor and had been kept in an aquarium for several months. The date of collecting is given as March 1949. The sailor's collection of fishes from near Paramaribo appears to be a reality (cf. Hoedeman, 1952), but it appears beyond doubt that the *A. cacatuoides* were not in it. The original label reads "Aquarium import, April 1950, Amazone, specimens died in October 1950", but

it was later exchanged to one reading "Suriname, Paramaribo" (H. Nijssen, in litt.).

Surinam is well-known ichthyologically, but no *A. cacatuoides* have been found in that country. The lower R. Amazonas in Peru is a center for aquarium fish collecting and it appears very probable that Hoedeman's specimens came from that area, from which also most of the available museum material comes. In connection with the emendation of the type-locality, I therefore also suggest the restriction: between 69° and 71° W.

*A. cacatuoides* is by colouration alone readily separated from all known congeners. Its relationships are uncertain: it combines characters of both the *regani* group and the elongate species, and may represent a distinct line of evolution. The rather large mouth, and strong jaw dentition also places it apart. An undescribed species, represented by a single individual (SMF unreg., 22.6 mm, Brasil (Amazonas), Igarapé Preto [1960.12], leg. H. Schultz) appears superficially similar, but has no abdominal stripes. It has weak bars, a lateral band faintly continued on the scaled part of the caudal fin, but no lateral spot. It has also 4 cheek scale series, squ. long. 23, D. XV.6, A. III.6 and 4 rakers.

I am unable to understand Meinken's (1961 b) determination of some *A. cacatuoides* specimens as *A. borellii*, a Paraguay basin species with incomplete lateral band, no abdominal stripes, no produced dorsal fin lappets, rounded caudal fin etc. His arguments for a two-pointed caudal fin in *A. borellii* are basically unsound, because Regan (1906 a) used the same words to describe the caudal fin shapes of both *A. borellii* and *A. agassizii* (with only one point in adult males), viz. "rounded or pointed", and one would expect Regan then to have been more careful in his choice of expression if the fin shapes were as drastically different as Meinken thought. Unfortunately, one of the syntypes of *A. borellii* is now lost, and the rest of Regan's material of that species is in such a poor condition that the caudal shape cannot be determined.

Later "*A. borellii*" determined by Meinken include *A. luelingi* specimens (Kullander, 1976), *A. regani* specimens (p. 71, this paper), and the *A. borelli* reported by Klee (1965), which all have abdominal stripes, except for the *Geophagus* and *Crenicara* spp. in Klee's lot. *A. borellii* in the aquarium literature are usually *A. cacatuoides*.

In 1973 I reported on the examination of an aquarium specimen of *A. cacatuoides*, and concluded that it was not *A. borellii*, the name by which the species was commonly handled by aquarists, but neither *A. cacatuoides* which would have 24–27 scales in a longitudinal series, and 13 gill-rakers, as stated by Hoedeman (1951). That neither Meinken nor I were able to identify our material as *A. cacatuoides* is at least to some extent a result of the many errors in Hoedeman's description of the type-material. For instance, the longitudinal scale count obviously includes caudal fin scales, and the very high gill-raker count is obviously for the series on the inner side of the arch removed from the holotype.

*A. cacatuoides* is a relatively common aquarium fish and is frequently described and figured in the aquarium literature (e.g. by Goldstein [1973: 104, 124, 125 upper photo only]; Staeck [1974: 191, Fig. 134; 1977: Fig. 49]).

*Apistogramma agassizii*

*Geophagus (Mesops) Agassizii* (pt) Steindachner, 1875. Sber. K. Akad. Wiss. Wien 71: 111.

**Lectotype.** NHMW 23484 — ♂, 39.3 mm SL. (By present designation.)

**Type-locality.** Manacapuru (Estado do Amazonas, Brazil; 3°16'S 60°37'W).

**Diagnosis (revised).** Length of head 29.5–38.4 %, body depth 26.8–35.5 % of SL. CP length 71.7–111.1 % of CP depth. D. XV.6–8, XVI.5–7.i, XVII.6–7, A. (II.6), III.5–7, IV.—. Squ. long. 22–24. Rakers 0–4: Preoperculum occasionally serrate (2–33 denticuli). Dorsal fin without produced lappets. Caudal fin with a median streamer in adult males, rounded in females and young. Lateral spot occasionally absent in adult males. Abdominal stripes in at least upper Solimões and Lago Tefé populations, in females and young males. Pectoral spot small. No caudal blotch. Midventral stripe occasionally present. Bars only in juveniles. No chest blotch. Dorsal fin dark anteriorly. Caudal fin with extension of lateral band along middle; in females and young males usually spotted on middle rays; in adult males a broad dark distal seam. (226 specimens of both sexes, 11.5–41.9 mm SL).

### Bibliography

- Geophagus (Mesops) Agassizii* (pt) Steindachner, 1875: 111 (protolog, detailed descr., no types des.; locs.: Curupira; Cudajas [NHMW 23519–23529 = *A. sp.*]; Rio Puty [? NHMW 17761]; Lago Maximo; See Manacapuru [? NHMW 23478–23484]), pl. 8, figs. 2, 2 a, 2 b (sketches of male in lateral aspect, outline of head in dorsal aspect, and a scale).
- Geophagus (Mesops) agassizii* Eigenmann & Eigenmann, 1891: 70 (in list of taxa of South American freshwater fishes; name, distr.; ref. Steindachner [1875]).
- Biotodoma Agassizii* Pellegrin, 1904: 187 (brief descr., pt. cop. Steindachner [1875]; specimen from "Amazone" [syntype?]; *Acara punctulata* Günther, in part doubtful synonym; new comb.).
- Heterogramma Agassizii* Regan, 1906 a: 62 (brief descr.; no specimens; cop. Steindachner [1875]; new comb.).
- Heterogramma agassizii* von Ihering, 1907: 323 (brief descr.; no specimens; cop. Regan [1906 a]).
- Heterogramma agassizii* Regan, 1908: 371 (relationship to *H. steindachneri* Regan, noted).
- Heterogramma agassizii* Eigenmann, 1910: 478 (in list of taxa of tropical and south temperate American freshwater fishes; name, distr.; ref. Pellegrin [1904]).
- Heterogramma agassizi* (pt) Haseman, 1911 b: 357 (brief descr.; locs.: Manaus [FMNH 54161]; Santarem [FMNH 54162]), pl. 64 (retouched monochrome photo of Manaus specimen in lateral aspect).
- Apistogramma agassizii* Regan, 1913: 282 (in list of species in the genus; name, distr.; new comb.), 283 (difference from *A. pertense* (Haseman)).
- Heterogramma agassizi* A. de Miranda Ribeiro, 1915: 46 (brief descr., abstracted from Steindachner [1875]).

- Apistogramma Agassizi* Pellegrin, 1936: 56 (example of *A. spp.* kept in aquarium in Europe, cit. Rachow, 1928: Handbuch der Zierfischkunde, Stuttgart, p. 170).  
*Apistogramma agassizi* Ahl, 1939: 82 (related to *A. reitzigi* Ahl; list of dissimilarities).  
*Apistogramma agassizii* Fowler, 1954: 273 (bibliography), Fig. 860 (sketch of male in lateral aspect, based on pl. 8, fig. 2 in Steindachner [1875]).  
*Apistogramma agassizi* Meinken, 1961 a: 135 (presence in Letitia [= Leticia, Colombia] area indicated).  
*Apistogramma agassizi* Meinken, 1962 b: 142 (in key-like list of *Apistogramma spp.*; distr.; no ref.).  
*Apistogramma gibbiceps* (pt), Meinken, 1969 b: 91 (protolog, detailed descr.; loc.: Brasilien, wahrscheinlich Gebiet des Rio Negro; two of the paratypes: SMF 9447–9448), Abb. 2 (monochrome photo of female [= male], in lateral aspect [SMF 9448]).  
*Apistogramma agassizi* Meinken, 1969 c: 166 (note on geogr. distr.).  
*Apistogramma agassizii* Knöppel, 1970: 309 (specimens from Lago Calado; brief descr.; stomach contents).  
*Apistogramma agassizi* Vandewalle, 1973: 280 (in tab.; caudal osteology, [IRSNB 15.788 pt]).  
*Apistogramma agassizii* Gosse, 1976: 23 (in synonymy).

**Etymology.** *agassizii* for Prof. Jean Louis Rodolphe Agassiz (1807–1873), scientific leader of the Thayer Expedition which collected the type-series. Not explained explicitly by Steindachner.

## Material

- Lectotype.** NHMW 23484 — ♂, 39.3 mm. Brasil (Amazonas), Manacapuru (3°16'S 60°37'W). [1865–1866. Leg. Thayer Expedition.]
- Paralectotypes.** ? MCZ 16029 — 3 ♀, 14.0, 18.6, 19.2 mm. Brasil (Pará), Óbidos (1°52'S 55°30'W). [1865–1866.] Leg. Thayer Expedition.  
 NHMW 23446–23448 — 3 ♂, 30.7, 32.4, 34.7 mm. Brasil (Amazonas), Silves, Lago Saraca (2°48'S 58°08'W). [1865–1866. Leg. Thayer Expedition.]  
 NHMW 23478–23483 — 6 ♂, 32.8, 32.9, 33.5, 33.5, 34.3, 35.8 mm. Same data as lectotype.  
 ZMK 130 — ♂, 28.9 mm. "Amazonfloden". Rec. 1875.05.01. Ded. NHMW. [1865–1866. Leg. Thayer Expedition.]
- Specimens.** FMNH 54161 (CM 2729) — ♂, 34.4 mm. Brasil (Amazonas), near Manaus, Igarapé de Cachoeira Grande (appr. 3°06'S 60°00'W = Manaus). 1909.11.30. Leg. J. D. Haseman (ECMCSA 3156–3158).  
 FMNH 54162 (CM 2730 a–b) — 2 ♂, 20.5, 23.9 mm; ♀, 22.3 mm; 3 sex indet., 12.3, 13.0, 13.1 mm. Brasil (Pará), R. Tapajós, Igarapé de Jaura (appr. 2°26'S 54°41'W = Santarem). 1909.12.11. Leg. J. D. Haseman (ECMCSA 3256–3271).  
 IRSNB 15.788 — 40 ♂, 21.5, 24.3, 25.2, 26.4, 27.0, 27.2, 27.5, 27.8, 27.8, 27.9, 28.2, 28.3, 28.4, 28.4, 28.5, 28.6, 28.7, 28.7, 28.8, 29.0, 29.0, 29.3, 29.4, 29.6, 29.7, 29.8, 29.8, 30.2, 30.5, 30.6, 31.2, 31.9, 32.2, 32.4, 32.5, 32.9, 33.6, 33.8, 34.3, 34.7 mm; 25 ♀, 16.8, 17.6, 18.6, 19.2, 20.1, 20.3, 20.6, 20.7, 21.5, 22.4, 23.7, 24.1, 25.4, 25.4, 26.3, 26.6, 27.1, 27.5, 28.0, 28.8, 29.5, 29.8, 29.9, 29.9, 31.7 mm; 32 sex indet., 17.0, 17.7, 18.3, 18.5, 19.6, 19.7, 19.8, 21.1, 21.9, 22.0, 22.1, 22.3, 22.3, 22.4, 22.4, 22.5, 22.7, 23.4, 23.6, 23.7, 24.7, 25.0, 25.4, 27.1, 28.0, 28.5, 28.7, 29.0, 29.0, 30.1, 30.5, 34.9 mm. Brasil (Amazonas), R. Jacitara, Igarapé (3°14'S 60°44'W). 1962.11.12. Leg. S. M. le roi Léopold de Belgique & J.-P. Gosse (IMA 1962: Sta. 9).

- IRSNB 15.789 — 15 ♂, 15.9, 21.3, 22.0, 24.6, 24.6, 27.0, 27.2, 28.9, 29.4, 29.5, 30.8, 31.7, 32.1, 32.4, 34.4 mm; 6 ♀, 18.3, 18.5, 19.3, 23.4, 23.5, 28.8 mm; sex indet., 29.9 mm. Brasil (Amazonas), Lago Tefé, Igarapé do Ananas (3°27'S 64°47'W). 1962.11.19. Leg. S. M. le roi Léopold de Belgique & J.-P. Gosse (IMA 1962: Sta. 13).
- IRSNB 15.790 — ♂, 20.8 mm. Brasil (Pará), Santarem, Igarapé Mapiiri (2°26'S 54°42'W). 1963.11.20. Leg. G. Marlier (Sta. 145).
- IRSNB 15792 — ♂, 31.0 mm. Brasil (Amazonas), R. Preto da Eva, Igarapé Tapaiuna, igapo (3°08'S 59°18'W). 1964.01.28. Leg. G. Marlier (Sta. 186).
- IRSNB 15.793 — ♂, 23.6 mm. Brasil (Amazonas), alto R. Preto da Eva (3°08'S 59°18'W). 1964.02.28. Leg. G. Marlier (Sta. 196).
- IRSNB 15.794 — sex indet., 19.2 mm. Brasil (Amazonas), Lago Jari (5°07'S 62°21'W). 1964.03.26. Leg. G. Marlier (Sta. 217).
- MCZ 52159 — 2 ♂, 21.5, 24.7 mm; ♀, 20.7 mm. Colombia (Amazonas), R. Pichuna (appr. 4°S 70°W [label]). 1976.12.02. Leg. W. L. Fink (WLF 76—9).
- NHMW 17762 — ♂, 28.3 mm. Brasil (Pará), Santarem (2°26'S 54°41'W). 1913. Leg. J. D. Haseman.
- NHMW 17765—17773 — 8 ♂, 25.5, 26.2, 28.4, 29.3, 29.8, 31.1, 31.3, 41.9 mm; 4 ♀, 21.8, 24.9, 26.3, 28.2 mm; 3 sex indet., 11.5, 13.2, 18.8 mm. Brasil (Pará), Santarem (2°26'S 54°41'W). 1913. Leg. J. D. Haseman.
- NRM 11274 — ♂, 31.1 mm. Perú (Loreto), R. Yavari, Caño Piraña (? 4°12'S 70°17'W). 1971.09.06. Leg. T. Hongslo (VIT 3B).
- NRM 11275 — 9 ♂, 22.0, 22.0, 22.3, 23.0, 23.5, 24.5, 25.0, 26.5, 29.8 mm; 7 ♀, 15.8, 16.7, 19.2, 21.3, 21.6, 21.9, 22.3 mm; sex indet., 18.0 mm. Perú (Loreto), R. Yavari, Lago Matamata, caño estero (4°12'S 70°17'W). 1971.09.04. Leg. T. Hongslo (VIT 3A).
- NRM 11276 — 2 ♂, 31.2, 31.5 mm; 2 ♀, 24.7, 28.2 mm. Perú (Loreto), Pau-Mari, Caño "Buraco da Lucia" (4°12'S 70°17'W). 1971.09.14. Leg. T. Hongslo (VIT 6).
- NRM 11277 — ♂, 27.7 mm; ♀, 26.7 mm; sex indet., 21.6 mm. Perú (Loreto), Pau-Mari, Lago Guariba, caño (4°12'S 70°17'W). 1971.09.13. Leg. T. Hongslo (VIT 8).
- NRM 11278 — ♂, 35.6 mm. Brasil (Amazonas), Coiava, Igarapé (2°57'S 68°14'W). 1971.10.05. Leg. T. Hongslo (VIT 25).
- NRM 11279 — ♂, 21.0 mm; ♀, 20.4 mm. Brasil (Amazonas), Coiava, Cotje Comprido (2°57'S 68°14'W). 1971.12.10. Leg. T. Hongslo (VIT 35).
- NRM 11280 — ♂, 33.6 mm. Brasil (Amazonas), Coiava, Cotje Simpatia (2°57'S 68°14'W). 1971.12.21. Leg. T. Hongslo (VIT 38).
- SMF unreg. — 16 ♂, 22.5, 22.5, 22.6, 23.0, 25.3, 25.4, 26.0, 26.9, 27.6, 27.9, 29.2, 29.3, 30.7, 31.4, 32.1, 35.2 mm; 11 ♀, 19.2, 19.2, 19.8, 20.0, 20.4, 20.8, 20.9, 21.4, 23.0, 23.6, 23.7 mm. Brasil (Amazonas), Igarapé Preto (mouth appr. 3°54'S 69°23'W). [1960.12.] Leg. H. Schultz.
- SMF unreg. — ♂, 22.1 mm; 4 ♀, 17.7, 20.8, 22.2, 22.3 mm; 2 sex indet., 18.7, 22.4 mm. Brasil (Amazonas), Manacapuru (3°16'S 60°37'W). 1925.07. Leg. W. Ehrhardt.

Material not used in the following description includes BMNH 1925.10.28: 414—419 (6 specimens, Manacapuru, Leg. W. Ehrhardt, 1924), BMNH 1926.10.27: 470—475 (7 specimens, Monte Alegre [Brazil, Estado do Pará], Leg. C. Ternetz, 1925), NHMW 17761 (1 specimen, "Rio Puty", origin uncertain, see Remarks), SMF 9447—9448 (2 specimens, "Brasilien", Ded. W. Schwartz, paratypes of *A. gibbiceps* Meinken), and numerous aquarium specimens (pers. coll., SMF, AMNH, BMNH, MNHN).

Paralectotypes include also the following: NHMW 23519—23529 (9 ♀, 17.2, 19.2, 21.5, 21.8, 22.3, 23.3, 24.7, 28.8, 30.2 mm. Brasil (Amazonas), Codajás. [1865—1866. Leg. Thayer

Expedition.] An underscribed, slender species.) and NHMW 23552 (♂, 34.8 mm; ♀, 22.1 mm. Brasil (Pará), Villa Bella. [1865—1866. Leg. Thayer Expedition.] Another slender, undescribed species.).

Only part of the syntype-material has been reexamined. More paralectotypes are at the NHMW and, probably, at several other museums.

## Description

Body elongate. Head moderately elongate. Predorsal contour gently arched or arched to between orbits, straight rostrally. Preventral head contour about as steep, nearly straight or gently arched. Snout shape varying, from rounded to nearly pointed, profiles about equal or dorsal steeper, arched or straight. Orbit tangential or subtangential. Tip of maxilla exposed, to anterior margin of orbit or slightly behind. Preoperculum serrate in 30 specimens: 6 (IRSNB 15.792), 2—33 (11 specimens, IRSNB 15.788), 3—12 (5 specimens, SMF unreg., Manacapuru), 8 and 28 (2 specimens, MCZ 16029), 3, 5, and 22 (3 specimens, SMF unreg., Igarapé Preto), 8 (1 specimen, NRM 11276), 3—23 (6 specimens, NRM 11275), and 5 denticuli (1 specimen, NRM 11279).

Predorsal scales cycloid, laterally to line between dorsal fin origin and dorsal tip of preoperculum vertical limb, or margin of orbit superoposteriorly. Posterior cheek and dorsal opercular scales ctenoid. Squ. prd. (8) 9—12; squ. prv. (7) 8—12(13). Upper lateral line usually with terminal pores, frequently 1—3 subserial pores or a subserial canal. Lower line usually with anterior pores; a pore or canal on caudal fin in 93 of 290 lines. 1/5 to more than 1/3 of caudal fin scaled; squ. caud. 3—9; outer cycloid or all ctenoid.

Dorsal spines increasing in length to last. Lappets moderately long, pointed, none produced. Soft part pointed, in large males produced, filamentous extension to at most end of caudal fin, in females shorter, at most to middle of caudal fin; differentiation of dorsal fin shape at about 23 mm SL. Soft anal fin similar, but usually shorter. D. XV.6(12), XV.6.i(13), XV.7(44) XV.7.i(2), XV.8(1), XVI.5(1), XVI.5.i(4), XVI.6(44), XVI.6.i(27), XVI.7(64), XVI.7.i(1), XVII.6(5), XVII.6.i(1), XVII.7(1), XV.?(2), XVI.?(1), ?.7(1), ?.?(2). D<sub>tot</sub> 21 (13), 22 (105), 23 (99), 24 (3). A. II.6(1), III.5(7), III.5.i(4), III.6(172), III.6.i(23), III.7(13), III.?(4), IV.?(1), ?.?(1). A<sub>tot</sub> 8(8), 9(176), 10(36). Pectoral fin to vent. Ventral fin pointed, in large males produced, filamentous elongation of first ray to at most end of anal fin base, in females and young first ray somewhat extended, to about anal fin origin at most. Caudal fin in males from about 25 mm SL with elongated middle rays: rays gradually longer from the marginal to the middle which produced, both or either in large males filamentous. The pear-shaped portion occupies in adult males 1/2 or more of the total fin length, and the length of the fin may be 2/3 of the total length of the fish. In females and young males caudal fin rounded.

Dentition biserial in juveniles, outer series of about 40 teeth (upper jaw) or 45 teeth (lower jaw), inner short, in lower jaw symphyseal, in upper not as long as outer. In adults triserial dentition, but middle series in both jaws very short.

Outer series of 40–65 teeth in upper jaw, about 50–55 in lower jaw; innermost series in upper jaw of length of outer, in lower jaw usually much shorter, occasionally approaching length of outer. In large specimens the anteriormost teeth in both jaws may be considerably stronger than the rest and are also wide-spaced, appearing canine-like.

Colouration: Yellowish to brownish yellow, with brown markings. Not conspicuously countershaded, but paler ventrally; no pattern of dark scale-edges.

Juvenile (about 12–15 mm SL) pattern somewhat subdued. Bars rather broad, to ventral body edge, not forming spots on back. There is a lateral spot, and may be present also a spot in Bar 2. The lateral band is expressed chiefly where crossing the bars. Head stripes all present and well-developed. No caudal or pectoral spot, or midventral stripe. Two stripes of dots from each edge of the base of the pectoral axilla to caudal peduncle. Fins colourless, except dark anterior dorsal membranes and a black line along dorsal fin base.

Larger specimens lose the bars on the flanks, and the nape and back close to dorsal fin becomes more or less uniformly dark with sharp lower limit.

Lateral band from moderately wide postorbital stripe; even-edged, about  $1\frac{1}{2}$ –2 scales wide, to caudal fin base, above and on lower lateral line; may be fainter in males than in females of same lot. Lateral spot very intensely pigmented in females, may even be absent (faded) in males; round, not outside band.

Superorbital stripe often absent, at least faint; suborbital stripe moderately wide, short. Pectoral spot small. No abdominal stripes generally, but in many females and young males (less than 25 mm SL) from Lago Tefé and the upper Solimões area with weak narrow lines on ventral flanks: one from upper edge of pectoral axilla to caudal peduncle (wider than those below), second from about lower edge of axilla, third on a scale-series distance below, and fourth from origin of ventral fin to middle of spinous anal fin base. Midventral stripe not always present in females, occasionally in males, narrow, at most to ventral fin bases. No caudal spot, but lateral band continued on caudal fin.

Dorsal fin in males dusky, basally dark, edge white, soft part darker, 0 (–3) terminal spot-stripes. In females dark close to base, rest dusky to almost colourless, lappets basally dark, distally colourless. Anterior two membranes dark in both sexes. Anal fin whitish or clear, with broad dark seam, more intensely pigmented in males. Ventral fin in males white; in females also, but not always, a black spot near base, or first ray and membrane black. Caudal fin in males from about 22 mm SL: The lateral band continues along the middle portion, narrowing to tip, darker than on body. The edge formed by the ray tips has a broad dark seam. Generally the rest of the fin is colourless, whitish or yellowish, but, especially in younger males, an oblique intermediate band or traces of spotting may be present. Caudal fin in females more or less colourless to whitish, band continued on scaled part or little farther, not always spotted along middle for about  $\frac{2}{3}$  of fin length (3–4 indistinct cross-stripes), margin usually with narrow dark seam. Young males like females.

Table 10. Morphometry and meristics of *Apistogramma agassizii*. For explanation, see Tab. 5.

	n	Range	$\bar{x}$	$s(\bar{x})$	$s^2$
<b>M e a s u r e m e n t s</b>					
Head length	218	29.5— 38.4	32.7	0.09	1.83
Head depth	218	22.8— 28.8	25.1	0.07	1.14
Head width	218	13.3— 17.7	15.5	0.05	0.58
Body depth	218	26.8— 35.5	30.9	0.10	2.09
Orbit diameter	219	10.5— 15.1	12.5	0.06	0.73
Snout length	218	4.2— 7.6	5.8	0.04	0.39
Cheek depth	216	3.0— 8.4	5.7	0.05	0.52
Interorbital width	218	5.3— 8.9	7.0	0.03	0.26
Preorbital depth	210	1.3— 3.0	2.2	0.02	0.08
Dorsal base	212	53.5— 65.1	59.3	0.14	4.33
Anal base	209	16.6— 23.8	19.0	0.09	1.63
CP depth	217	12.3— 17.9	14.7	0.06	0.70
CP length	217	10.8— 16.0	13.1	0.06	0.78
Last D spine	206	12.0— 22.1	16.2	0.12	2.76
Last A spine	216	12.4— 19.4	16.5	0.08	1.39
CP/CP	216	71.7—111.1	89.9	0.53	60.72
<b>C o u n t s</b>					
Squ. long.	187	22—24	23.3	0.04	0.35
L <sub>1</sub> (c)	204	0—18	12.3	0.13	3.42
L <sub>1</sub> (cp)	200	8—19	15.1	0.08	1.15
L <sub>2</sub> (c)	169	0— 8	4.0	0.11	2.22
L <sub>2</sub> (cp)	166	4— 9	6.8	0.06	0.68
Cheek scales	223	1— 3	2.3	0.04	0.29
Squ. op.	90	9—17	13.1	0.19	3.11
Squ. sop.	135	3— 9	5.3	0.08	0.83
Squ. iop.	218	1— 4	2.9	0.03	0.15
D spines	223	15—17	15.7	0.04	0.27
D <sub>tot</sub>	220	21—24	22.4	0.04	0.39
A <sub>tot</sub>	220	8—10	9.1	0.03	0.18
P	224	10—12	11.4	0.03	0.25
Rakers	221	0— 4	1.6	0.05	0.48
Serrations	224	0—33	1.2	0.28	17.13

**Size**

The largest male is 41.9/64.4 mm (NHMW 17765—17773), the largest female 31.7/about 40 mm (IRSNB 15.788).

**Geographical distribution**

*A. agassizii* has the greatest range of the species in this genus, besides *A. trifasciata* (R. Paraguay + R. Guaporé). It is found only near the mainstream R. Ama-

zonas, however, eastwards to Santarem on the right bank, Monte Alegre on the left bank (to c.54°W), westwards to R. Pichuna and the lower course of the R. Yavari (to little beyond 70°W). It appears to be absent from the R. Negro and the R. Madeira, but is present in the lower reaches of the R. Yavari, R. Içá, and R. Tapajós systems.

## Ecology

Marlier (1965, 1967) gave some data on the limnology of the black water Terra firme lakes Lago Rio Preto da Eva and Lago Jari. The former makes up the middle part of the R. Preto da Eva, which is an affluent of the R. Amazonas little downstream Manaus. The Lago Jari is on the lower R. Purus.

Geisler (1967) described Igarapé Preto water, but it is not known in which habitat the *A. agassizii* from this brook were collected (see also p. 00, this paper).

Knöppel (1970) examined the stomach contents of 12 specimens from Lago Calado, a várzea lake near Manacapuru (fish from clear water). He found Hydracarina, insect larvae, copepods, and fruits, but predominantly plant matter and detritus.

Hongslo gives the following habitat information: VIT 8: slow-flowing brook, surrounded by high-grown forest. Turbid water (beige). Air temperature c. 31°C; VIT 6: brook with slow-flowing turbid water. Rain-forest; VIT 8: brook with clear, colourless water, relatively strong current (*Paracheirodon innesi* (Myers)[Characidae] was also caught here); VIT 25: brook with clear, tea-brown water, surrounded by high-grown forest. Current very slow.

*A. agassizii* thus appears to be an inhabitant of smaller lakes and brooks of both clear and darker water types.

A 12.3 mm specimen collected near Santarem in December (FMNH 54162) suggests that the species breeds there in November. The 15.9 mm Tefé specimen (IRSNB 15.789) from November places breeding in September or October in that area. The 15.8 mm R. Yavari specimen (NRM 11275) from early September suggests reproduction in July or August. It appears possible that the species breeds from May/June to November, i.e. during the dry season.

Sympatric *Apistogramma* spp. include *A. pertensis* (Igarapé Mapiri, R. Preto da Eva, Manacapuru), *A. cacatuoides* (Caño Piraña), *A. bitaeniata* (? Igarapé Preto, Lago Tefé), *A. sp.* (Igarapé Preto), *A. sp.* (Cotje Simpatia), *A. sp.* (Pau-Mari), and another *A. sp.* (Cotje Comprido). *A. pertensis* and *A. bitaeniata* juveniles are very similar to *A. agassizii* juveniles, the other species quite different at all ages.

## Remarks

The specimen from "Rio Puty" (NHMW 17761) is possibly a specimen referred to by Steindachner (1875), leg. O. St. John. It would then originate from the R. Poti (Estado do Piauí, Brazil). It is 46.6 mm SL, and not well preserved. It agrees rather well with the other *A. agassizii* examined. I have excluded this specimen from the description because of doubts about the origin (zoogeographical considerations, and a *Corydoras* specimen [Callichthyidae] with the same registration number, possibly being *C. agassizii*, anyway labelled *Heterogramma agassizii*), and because if it is a very similar species actually from the R. Poti the remains do not suffice to separate it from *A. agassizii* of the R. Amazonas. I am also doubtful whether it is a syntype, the number suggesting rather that it is from Haseman's collection (R. Amazonas, R. Negro, R. Branco, 1913).

Although the geographical distribution covers a rather large area, and the distance between the easternmost and westernmost populations is considerable for a species of this genus, there appear to be no significant differences between the populations. It may be noted only that abdominal stripes are present above all in the upper Solimões specimens, but absent in the lower Amazonas material.

Meinken (1969) has the most recent opinion on the relationships of *A. agassizii*, and considers it close to *A. gibbiceps*. However, none of the characters listed by him as uniting the two seems to be of any relevance (general body shape, scale counts, well-developed lateral line, proximity of lateral line to dorsal fin, single-pointed caudal fin). *A. gibbiceps* is quite different in finnage, body shape, colour pattern, number of operculum scales (8–9; in *A. agassizii* 9–17), fewer dorsal spines (14–15,  $\bar{x}$  = 14.9; in *A. agassizii* 15–17,  $\bar{x}$  = 15.7). It has also, as pointed out by Meinken, a longer snout (5.9–8.6 % of SL,  $\bar{x}$  = 7.6; in *A. agassizii* 4.2–7.6,  $\bar{x}$  = 5.8 %). On the whole, it appears difficult to confuse the two species, although Meinken did that anyway, and since *A. gibbiceps* males do not have the same caudal fin shape as *A. agassizii* males, the only strong argument for relationship is eliminated. *A. gibbiceps* seems rather to be a relative of *A. personata*.

The species closest to *A. agassizii* appears to be *A. bitaeniata*. Meristically and morphometrically it is hardly different, differing, however, slightly in caudal peduncle proportions (85.0–114.3 %,  $\bar{x}$  = 96.0 %; in *A. agassizii* 71.7–111.1 %,  $\bar{x}$  = 89.9 %), and in the generally fewer cheek scale series ( $\bar{x}$  = 1.9; in *A. agassizii*  $\bar{x}$  = 2.3). The main difference is in the colouration of the lower flanks and the fins, as well as in the adult male finnage.

From *A. pertensis*, *A. agassizii* may be distinguished by the colour-pattern, and more pre-ventral scales (usually), from *A. gephyra* and *A. pulchra* by the different caudal fin pattern. From *A. elizabethae* it is readily separated by the colour-pattern.

*A. agassizii* was imported to Germany as aquarium fish already in 1909 (Holly et al.: 76/77), and is often described and figured in aquarium literature (e.g. by Goldstein [1973: 120, 127 lower photo], and Staeck [1974: 190, Fig. 133]).

The lectotype is a large male in rather good condition considering its age. It is soft and somewhat faded, but very much resembling the specimen figured by Steindachner (1875). The label gives "Manacapourou" for locality. Steindachner (1875) did not mention Manacapuru among his localities, but the See Manacapuru is listed, and this may be the true type-locality.

*Apistogramma bitaeniata*

*Apistogramma pertense* var. *bitaeniata* Pellegrin, 1936. Bull. Soc. natn. Acclimat. Prot. Nat. Paris 83: 56.

**Lectotype.** MNHN 35-34 — ♂, 36.7 mm SL. (By present designation.)

**Type-locality.** Colombia (Amazonas), environments of Leticia (emended; see p. 102).

**Diagnosis (revised).** Head length 32.8–36.8 %, body depth 27.6–34.2 % of SL. CP length 85.0–114.3 % of CP depth. D. XV.6–7, XVI.6–7. A. III.5–6.i. Squ. long. 23–24. Rakers 1–3. Preoperculum rarely serrate. Dorsal fin with produced anterior lappets in adult males. Caudal fin with dorsal and ventral extensions in adult males, rounded in females and young. Lateral spot and pectoral spot present. Abdominal stripes form a band. No caudal spot. Midventral stripe in females. Bars faint. No chest blotch. Dorsal fin dark anteriorly. Caudal fin with or without small spots, or with 4–5 vertical spot-stripes. (22 specimens of both sexes, 13.8–32.5 mm SL.)

**Bibliography**

- Apistogramma pertense* var. *bitaeniata* Pellegrin, 1936:56 (protolog, descr.; syntypes MNHN 35-34 and 35-35, from Rio Madeira [Brésil]).
- Apistogramma pertense bitaeniata* Blanc, 1962: 203 (lists type-specimens).
- Apistogramma klausewitzi* Meinken, 1962: 138 (protolog, descr.; holotype SMF 5526, 5 paratypes SMF 5527–5531, from Brasilien, oberer Rio Solimões, Igarapé Preto), Figs. 1–2 (habitus sketches of holotype and female paratype in lateral aspect), 141 (in key-like list of *Apistogramma* spp.).
- Apistogramma kleei* Meinken, 1964: 293 (protolog, descr.; holotype [USNM 199593], 2 paratypes [USNM 199594], no loc.), 3 figs. p. 295 (habitus sketches of male and female in lateral aspect, head showing lateralis pores).

**Etymology.** *bitaeniata* from *bi-* (Lat. prefix, two-, and *taeniatus*, (Lat. adj. of *taenia*), banded, i.e. with two bands, referring to the lateral band and the band below it. Not explained by Pellegrin.

*klausewitzi*: "zu Ehren von Herrn Dr. Wolfgang Klausewitz, Ichthyologe am Senckenberg-Museum, der mir das Untersuchungsmaterial freundlichst zur Verfügung stellte." (Meinken, 1962).

*kleei* for Dr. Albert J. Klee (Cincinnati, Ohio, USA), biologist and aquarist, donor of the type-specimens.

## Material

- Lectotype.** MNHN 35-34 — ♂, 36.7 mm. "Rio Madeira (Brésil)". [1934.] Leg. Rabot [= A. Rabaut]. Ded. Fumerand. (Not included in the description.)
- Paralectotype.** MNHN 35-35 — ♂, 32.2 mm. Same data as lectotype. (Not included in the description.)
- Specimens.** IRSNB 18.597 — 9 ♂, 14.8, 17.3, 18.8, 21.2, 25.3, 27.9, 28.3, 29.0, 31.6 mm; 5 ♀, 14.5, 17.3, 18.5, 20.0, 24.0 mm; 2 sex indet., 13.8, 14.9 mm. Brasil (Amazonas), Lago Tefé, Igarapé do Ananas (3°27'S 64°47'W). 1962.11.19. Leg. S. M. le roi Léopold de Belgique & J.-P. Gosse (IMA 1962: Sta. 13).  
SMF 5526 — ♂, 32.5 mm. Brasil (Amazonas), Igarapé Preto (mouth appr. 3°54'S 69°23'W). [1960.12.]. Leg. H. Schultz. — Holotype of *A. klausewitzi* Meinken.  
SMF 5527—5531 — 2 ♂, 26.7, 28.5 mm; 3 ♀, 24.4, 24.8, 25.3 mm. Same data as SMF 5526 — Paratypes of *A. klausewitzi* Meinken.  
USNM 199594 — ♂, 44.5 mm; ♀, 30.2 mm. No locality. [Ded. A. J. Klee.] — Paratypes of *A. kleei* Meinken. (Not included in the description.)

In addition I have examined two specimens MNHN 35-293 and 35-294, 41.1 and 42.4 mm, from "Brésil", leg. (ded.?) J. Marnier, probably of the same origin as the type-specimens and determined by Pellegrin. I have also seen several aquarium specimens, usually called *A. kleei* (SMF, pers. coll.). The holotype of *A. kleei* (USNM 199593) was not reexamined; it is figured by Meinken (1964), and is most probably of the same species as the paratypes. The types of *A. bitaeniata* and *A. kleei* appear to be import or aquarium specimens, and are therefore excluded from the principal description.

## Description

The *A. klausewitzi* type-series is in excellent condition, the IRSNB material less good, the flanc and gill-cover scaling only more or less complete (too many specimens packed too tightly?).

Body elongate. Head elongate. Predorsal contour gently arched or straight descending, a moderate curvature on snout. Preventral head contour gently arched or almost straight, about as steep as predorsal. Snout roundish, contours convex, equal. Orbit tangential. Tip of maxilla exposed, to little behind anterior margin of orbit. Preoperculum serrate in four Lago Tefé specimens (7, 13, 14, 16 denticuli).

Predorsal scales cycloid laterally to line from dorsal fin origin to dorsal tip of preoperculum or orbital rim little above horizontal orbit diameter. Dorsal opercular, with exceptions dorsal subopercular, and posterior cheek scales ctenoid. Squ. prd. 8–10; squ. prv. 8–13. Upper lateral line with 0–5 terminal pores and frequently 1–3 subserial pores; lower with 0–6 pores; in 8 specimens a caudal canal or pore on both or one side. 1/4 to 1/3 of caudal fin scaled; squ. caud. 3–7; outer scales cycloid or ctenoid.

Dorsal spines subequal in length from 4th, 5th, or 6th, slightly increasing to last. Lappets in adult males (21 mm and larger) modified: 3rd, 4th (longest), and 5th prolonged, twice spine lengths, the rest moderately long, pointed; modifica-

tion stronger in holotype of *A. klausewitzii* in which all lappets prolonged from 2nd (twice spine length), 3rd three times spine length, 4th through 6th longest, from 9th prolongation moderate. In females moderately long lappets, pointed. Soft fin in males pointed, produced to at most end of principal caudal fin. In females soft fin bluntly pointed, to about 1/4 of caudal fin. Soft anal fin similar. D. XV.6(1), XV.6.i(4), XV.7(2), XVI.6(4), XVI.6.i(2), XVI.7(9).  $D_{tot}$ 21(1), 22(10), 23(11). A. III.5(2), III.5.i(2), III.6(17), III.6.i(1).  $A_{tot}$ 8(2), 9(19), 10(1). Pectoral fin to about vent. Ventral fin pointed; in adult males longer, with extended first ray to at most 1/3 of caudal fin; in females with but short extension, to end of spinous anal fin base. Caudal fin in adult males truncate with rounded corners, ray 5, supported by ray 4, and ray 12, supported by ray 13, extended, extensions up to as long as 1/2 of length of principal fin. Caudal fin rounded-subtruncate in females.

Table 11. Morphometry and meristics of *Apistogramma bitaeniata*. For explanation, see Tab. 5.

	n	Range	$\bar{x}$	$s(\bar{x})$	$s^2$
<b>Measurements</b>					
Head length	22	32.8— 36.8	34.5	0.25	1.39
Head depth	22	22.5— 26.5	24.4	0.24	1.26
Head width	22	14.2— 17.4	15.9	0.21	0.97
Body depth	22	27.6— 34.2	30.5	0.35	2.68
Orbit diameter	22	12.0— 14.9	13.4	0.17	0.64
Snout length	21	4.3— 7.4	5.8	0.15	0.48
Cheek depth	22	3.4— 7.1	4.8	0.19	0.82
Interorbital width	22	6.3— 8.3	7.0	0.10	0.20
Preorbital depth	18	1.9— 2.8	2.2	0.06	0.05
Dorsal base	21	53.2— 61.0	57.5	0.49	5.09
Anal base	20	16.9— 20.1	18.7	0.19	0.69
CP depth	22	12.3— 15.0	13.8	0.17	0.61
CP length	22	11.6— 15.5	13.3	0.20	0.92
Last D spine	21	13.4— 20.3	15.5	0.36	2.67
Last A spine	22	14.5— 18.9	17.0	0.24	1.30
CP/CP	22	85.0—114.3	96.0	1.63	58.38
<b>Counts</b>					
Squ. long.	14	23—24	23.6	0.13	0.25
Ll <sub>1</sub> (c)	18	8—15	12.3	0.39	2.68
Ll <sub>1</sub> (cp)	20	14—17	15.1	0.16	0.52
Ll <sub>2</sub> (c)	13	1— 5	3.8	0.39	2.03
Ll <sub>2</sub> (cp)	11	6— 8	6.8	0.18	0.36
Cheek scales	22	1— 3	1.9	0.09	0.18
Squ. op.	7	12—16	13.7	0.47	0.57
Squ. sop.	16	4— 6	4.9	0.18	0.52
Squ. iop.	22	3	3.0		
D spines	22	15—16	15.8	0.09	0.18
$D_{tot}$	22	21—23	22.5	0.13	0.36
$A_{tot}$	22	8—10	9.0	0.08	0.14
P	22	11—12	11.5	0.11	0.26
Rakers	22	1— 3	1.8	0.15	0.47
Serrations	22	0—16	2.3	1.10	26.49

Dentition triserial in both jaws, sometimes serial arrangement confused anteriorly. Outer series of 40–60 teeth in upper jaw, about 45–50 in lower jaw. Inner series of lower jaw both short, in upper jaw innermost series of larger males almost as long as outermost. In large males a tendency for the outer teeth to become canine-like anteriorly.

Colouration: Pale yellowish to whitish, young specimens uniformly pale brownish with bar interspace spotting. Markings brown. Bars indicated, especially as light interspaces along lateral band, not apparent dorsally except as spots which more or less confluent, along and into dorsal fin base. In large specimens the back spots, extended to the nape, form an uninterrupted dark band along the dorsal fin base. Lateral band from narrow postorbital stripe;  $1-1\frac{1}{2}$  scale deep, uneven, to just before caudal fin base, above and on lower lateral line. Lateral spot roundish or elongated, extending little outside band.

Suborbital stripe moderately wide, faint; superorbital stripe to occiput, sometimes indistinct. Pectoral spot present. Females with narrow midventral stripe. Abdominal striping may be absent in the very smallest specimens, fainter than lateral band, when best developed forming an even band, 1 scale deep, from pectoral fin base to caudal fin base. Caudal spot a continuation of lateral band along scaled caudal fin and as streaks along rays of middle of caudal fin (especially in large males), or roundish, extended somewhat distally (small specimens and females).

Dorsal fin clear or dusky, lappets basally dusky, distally clear; anterior 2 membranes black; 0–2 terminal spot-stripes. Anal fin basally clear, distally dusky-seamed; 0–3 terminal spot-stripes. Caudal fin clear, with or without minute spots (adult males) or 4–5 vertical spot-stripes on the middle part (young and females). Ventral fin white or clear in males, spine and adjacent membrane dark in females.

### Size

The male holotype of *A. klausewitzi* is 32.5/45.3 mm, the largest Tefé male 31.6/43.0 mm. The largest *A. klausewitzi* paratype female is 25.3/33.6 mm, the largest Tefé female 24.0/31.7 mm. Aquarium specimens, such as the paratypes of *A. kleei* (44.5/60.4 and 30.2/40.6 mm), are commonly larger than these wild specimens. Meinken (1964) gives the lengths 50.5/71.25 mm for the holotype of *A. kleei*, but then his "Körperlänge" probably includes part of the caudal fin, and the "Gesamtlänge" the caudal fin extensions.

### Geographical distribution

Known localities include only an igarapé affluent of Lago Tefé, on the upper R. Solimões, and the Igarapé Preto, which empties in the R. Solimões, little downstream the Peruvian border.

## Ecology

The chemical characteristics of some parts of the Igarapé Preto were described by Geisler (1967). Water samples from different places showed differences in the chemical properties, at least partially corresponding to the different biotopes recognized by Géry (1965 a, b), in a study of the characoid fauna. Unfortunately it is not known in which particular biotope the *A. bitaeniata* were taken. Geisler classified the water of the drainage as of the clear-black water type, and although in the Amazonian tertiary region it is considerably richer in minerals than similar rivers in Central or Lower Amazônia, owing to the location near the Andes, *Para-cheirodon innesi* (Myers) (Characidae) is found in some parts of the Igarapé Preto system (Géry, 1965 a), and that is relevant to the below expressed doubts about the original type-locality.

Sympatric *Apistogramma* spp. in the Igarapé Preto include *A. agassizii*, and a more deep-bodied species (see p. 88). If these were actually taken with the *A. bitaeniata* I do not know. The Igarapé do Ananas series was taken with 22 *A. agassizii*.

The sympatry of *A. agassizii* and *A. bitaeniata* is interesting since these species are probably closely related. *A. agassizii* grows larger, the male finnage is quite different, and the colour pattern different at least in details, otherwise I find no obvious differences that may suggest, at best, ecological separation. *A. agassizii* has a wide distribution along the mainstream R. Amazonas, whilst *A. bitaeniata* appears confined to the upper Solimões and the Peruvian Amazonas. This distribution suggests that *A. bitaeniata* may be more specialized in environment requirements, and in its optimal habitats more successful than the purportedly more generalized *A. agassizii*.

## Remarks

The syntypes of *A. bitaeniata* are in poor condition, more or less faded, with damaged fins. In general they agree with the wild material, although they are very large. The lectotype here selected (slightly better than the second specimen), has 3 cheek scale series, squ. long 24, L<sub>1</sub> 8 + 1 pore + 2 + 1 pore + 1 on left side, L<sub>2</sub> 3 pores + 4 on right side, D. XVI.7, A. III.5.i, P. 12, rakers 2. The dorsal fin lappets are not conspicuously produced, the 8th longest, nearly as long as the spine; caudal fin shape indeterminable. The paralectotype has 2 cheek scale series, squ. long. 24, L<sub>1</sub> 16, L<sub>2</sub> 1 pore + 5 + 1 caudal canal, D. XVI.5.i, A. III.5, P. 12, 1 raker. Produced dorsal fin lappets are not apparent, the caudal shape indeterminable.

The *A. kleei* male paratype is in very fine condition. It is 48.5 mm long to end of caudal fin scaling (Meinken's SL), and has 2 cheek scale series, squ. long. 24, L<sub>1</sub> 14 + 1 unmodified + 2 subserial canals, L<sub>2</sub> 7 + 1 caudal canal, D. XVI.7, A. III.7, P. 11, rakers 3. Dorsal and caudal fins as in wild material; longest dorsal lappet the

4th. The female paratype is also very fine. It has 2 cheek scale series, squ. long 24, L<sub>1</sub> 15, L<sub>2</sub> 6?, D. XVI.6.i, A. III.5.i, P. 11, rakers 3. The caudal fin shape is as figured by Meinken (1964).

The USNM and MNHN series are probably both import or aquarium material. The type-series of *A. bitaeniata* was collected by Auguste Rabaut and shipped to a French importer of aquarium fishes in 1934 (Pellegrin, 1936). It is indicated, but not stated clearly, by Meinken (1964) that the *A. kleei* type-series is from an aquarium stock. The history of the *A. klausewitzi* is unknown to me, but although surprisingly fine for wild material, there are no indications that these specimens would have been kept in aquarium.

The syntypes very probably did not come from the R. Madeira, the locality given by Pellegrin (1936). Rabaut collected in the Leticia area (Comisaria Amazonas, Colombia), where he found the Neon tetra (*Paracheirodon innesi* (Myers)), which seems to be restricted to the R. Amazonas in Peru and upper R. Solimões afluent. The collecting sites of this species were long kept secret by the first commercial fish collectors that exploited it to prevent competition. If *A. bitaeniata* was collected in the same region, it then seems natural that neither it was labelled with the correct locality. The rediscovery of the species in the upper Solimões adds support to the theory that the syntypes also came from that area, but of course the R. Madeira is insufficiently investigated ichthyologically, and the occurrence of *A. bitaeniata* also in that system is not entirely impossible, only very unlikely. The suggested emendation of the type-locality is equivalent to a description of the area explored by Rabaut.

*A. bitaeniata* differs from all other described *Apistogramma* spp. in the band on the ventral flanks, is otherwise superficially most similar to *A. agassizii*. Tentatively I consider these two species closely related. They differ from the *pertensis* group in the dark spot anteriorly in the dorsal fin, more complete pre-ventral scaling, and stronger sexual dimorphism in the fin shape.

*A. sweglesi* Meinken, from the Leticia region is a potential synonym of *A. bitaeniata*. It is, however, very difficult to judge from Meinken's description how they may differ. (See further p. 144). Meinken's creation of two junior synonyms is remarkable, but it should be recalled that a) he obviously was totally unaware of Pellegrin's paper (*A. bitaeniata* not included in the 1962 check-list, neither mentioned in later papers), and b) *A. kleei* is based on aquarium material, which, in part due to the larger size, differs especially in habitus from wild fishes.

This species appears to be identical with the *Apistogramma* "U2", thought to be *A. cacatuoides* by Hoedeman (1951), and Meinken (1961 b; as *A. borellii*). Pellegrin (1936), referring to a photograph that I have not seen (Aquarium Philadelphia 2 (1):11, 1933), considered the "U2" as being a different species. The retouched photograph in Innes (1966) shows a male and a female that I do not hesitate to assign to *A. bitaeniata*. The "*A. steindachneri*" described and figured by Arnold (1939), thought by Meinken (1961 a) to represent *A. sweglesi*, also

seem to represent *A. bitaeniata*, but if they do, the figure is far from representative of the species.

*A. bitaeniata* is a relatively common aquarium fish, and is now and then described in aquarium literature, e.g. by Goldstein (1973: 48, 128 lower photo [129 upper photo = *A. trifasciata*]), and Staeck (1974: 192, Fig. 130, 131; 1977: Fig. 50).

*Apistogramma elizabethae* sp. nov.

(Fig. 12)

**Holotype.** IRSNB (Types) 596 — ♂, 39.8 mm SL.

**Type-locality.** Igarapé affluent de la rive droite du Uaupés à Trovao (environ 20 km en amont de l'embouchure de Uaupés), État d'Amazonas. Brésil. (0°02'N 67°26'W.)



Fig. 12. Holotype of *Apistogramma elizabethae*.

**Diagnosis.** Head length 30.9–36.8 %, body depth 28.4–34.0 % of SL. CP length 81.6–105.3 % of CP depth. D. XIV.6.i–7.i, XV.5.i–7. A. III.5.i–7. Squ. long. 22–23. Rakers 1–2. Preoperculum entire. Dorsal fin 2nd–6th lappets produced in adult males. Caudal fin roundish in females and young, middle rays produced in adult males. Lateral spot, a spot in Bar 2, and pectoral spot present. No abdominal stripes, caudal spot, or midventral stripe. Bars as most as traces. No chest blotch. Dorsal fin not dark anteriorly. Caudal fin with vertical spot-stripes in young females, longitudinal streaks in adults. (11 specimens of both sexes, 12.5–39.8 mm SL.)

**Etymology.** *elizabehiae* for Mrs. Elizabeth Cabot Cary Agassiz (1822–1907), second wife of J. L. R. Agassiz, participant of the Thayer Expedition (1865–1866), and principal author of a book on that journey (Agassiz & Agassiz, 1969). The name reflects also the similarity to the *A. agassizii* of the R. Amazonas.

## Material

**Holotype.** IRSNB (Types) 596 — ♂, 39.8 mm. Brasil (Amazonas), Trovao, R. Uaupés right bank, igarapé (0°02'N 67°26'W). 1967.12.09. Leg. S. M. le roi Léopold de Belgique & J.-P. Gosse (IMA 1967: Sta. 193).

**Paratypes.** IRSNB (Types) 597 — ♂, 26.2 mm; 3 ♀, 16.2, 16.7, 23.8 mm; 5 sex indet., 12.5, 13.7, 14.8, 15.0, 15.1 mm. Same data as holotype.  
IRSNB (Types) 598 — ♂, 26.7 mm. Brasil (Amazonas), Lago Peneira, small igarapé (0°01'N 67°21'W). 1967.12.09. Leg. S. M. le roi Léopold de Belgique & J.-P. Gosse (IMA 1967: Sta. 192).

## Description

Most specimens are in acceptable or good condition, but the following description is chiefly from the holotype.

Body elongate. Head elongate. Predorsal contour slightly arched, almost straight descending. Preventral head contour about as steep as predorsal, about straight. Snout rather elongate, rounded, profiles about straight, equal. Orbit sub-tangential. Tip of maxilla exposed, to little behind anterior margin of orbit. Preoperculum entire.

Predorsal scales cycloid, laterally posteriorwards to line from dorsal fin origin to dorsal tip of preoperculum. Posterior cheek and dorsal opercular scales ctenoid. Squ. prd. 8–9; squ. prv. 6–10. Upper lateral line with 3–6 terminal pores in the smaller specimens, 1–2 in the largest; 1–2 subserial pores in 7 of 15 lines; lower line with 0–3 pores; a caudal pore on one side in 2 specimens, a canal on one side in one specimen. About 1/3 of caudal fin scaled in holotype, less in smaller specimens; squ. caud. 4–11 (3 specimens); outer cycloid.

Dorsal spines subequal in length from 4th or 5th, increasing to last. Lappets produced from 2nd to 6th, 4th longest, about 3 times spine length, from 7th nearly moderately long, pointed. In females and young moderately long, more or less truncate lappets. Soft part pointed, but tip broken, to beyond middle of caudal fin; to about middle of caudal fin in the largest female. Soft anal fin similar, about as long. D. XIV.6.i(1), XIV.7(1), XIV.7.i(1), XV.5.i(1), XV.6.i(5), XV.7(1).  $D_{tot}$  21 (3), 22 (8). A. III.5.i(1), III.6(9), III.7(1).  $A_{tot}$  9 (10), 10 (1). Pectoral fin not reaching vent. Ventral fin pointed, first ray long, to almost end of anal fin base; in largest female to anal fin origin. Caudal fin pointed, corners rounded, rays gradually longer to middle pair of rays which longest; in smaller males and females roundish.

Dentition biserial. Outer series comprising about 50–60 teeth in both jaws, inner series of lower jaw short, inner series of upper jaw nearly as long as outer.

Colouration: Yellowish, rather evenly into pale brownish dorsally. Markings brown. Bars not apparent, as traces below lateral band. Darker on back above lateral line and on nape, as in *A. bitaeniata*. Lateral band from broad postorbital stripe, about 1 1/2 scale deep, even-edged, fading on caudal fin scales, above and on lower lateral line. Spots in Bars 2 and 3, roundish, little outside band.

No apparent superorbital stripe; suborbital stripe moderately wide. Pectoral spot present. No distinct abdominal stripes, but indistinct spotting from dark scale-edges on ventral flanks in some specimens. No midventral stripe. No caudal spot — replaced by obscure band continuation.

Dorsal fin in holotype dusky, lappets basally somewhat dusker, outwards paler. A dark edge along base; not dark on anterior membranes; tips of soft part darkened; 2–3 terminal spot-stripes. Similar in the others, but soft part paler or clear. Anal fin dusky, not distinctly dark-edged; 0–3 terminal spot-stripes. Caudal fin in young females with 4 irregular transverse spot-stripes. In adults with longitudinal brownish streaks along membranes, and no apparent spotting. Pectoral fin dusky. Ventral fin inwards clear, outer ray dark.

### Size

The largest male is 39.8/56.7 mm (holotype), the largest female 23.8/31.9 mm long (IRSNB 597).

### Geographical distribution

Known only from the R. Uaupés: an igarapé at Trovao, and another at Lago Peñera.

### Ecology

Sympatric with *A. brevis* at both localities, at the type-locality also with *A. meinkenii* and *A. uaupesi*.

The smallest specimens suggest reproduction in October or early November.

### Remarks

The caudal fin shape in large males of this species suggests relationship with *A. agassizii*, and the colour pattern (dark back, lateral band, etc.), and general body shape also indicate more than casual similarity. However, the anterior dorsal fin membranes are not particularly darkened, and as in *A. brevis*, *A. meinkenii*, and *A. uaupesi*, from the same region, there is a spot in Bar 2.

Table 12. Morphometry and meristics of *Apistogramma elizabethae*. For explanation, see Tab. 5.

	n	Range	$\bar{x}$	$s_{(\bar{x})}$	$s^2$
<b>M e a s u r e m e n t s</b>					
Head length	11	30.9– 36.8	34.3	0.56	3.48
Head depth	11	23.8– 26.7	25.2	0.23	0.59
Head width	11	13.3– 16.1	15.2	0.25	0.70
Body depth	11	28.4– 34.0	31.6	0.49	2.60
Orbit diameter	11	11.3– 16.1	13.9	0.41	1.89
Snout length	11	4.7– 7.4	5.7	0.26	0.77
Cheek depth	11	4.0– 6.5	5.2	0.28	0.88
Interorbital width	11	4.8– 6.7	6.0	0.17	0.30
Preorbital depth	11	1.5– 2.6	2.0	0.10	0.12
Dorsal base	11	53.1– 59.8	55.8	0.76	6.32
Anal base	9	16.8– 19.6	18.7	0.27	0.63
CP depth	11	11.7– 14.3	13.4	0.26	0.72
CP length	11	11.5– 14.6	12.5	0.27	0.79
Last D spine	10	11.3– 18.0	15.3	0.74	5.52
Last A spine	11	15.3– 17.9	16.7	0.24	0.65
CP/CP	11	81.6–105.3	93.8	2.52	69.71
<b>C o u n t s</b>					
Squ. long.	11	22–23	22.6	0.15	0.25
L <sub>1</sub> (c)	9	7–14	10.3	0.83	6.25
L <sub>1</sub> (cp)	10	12–15	14.1	0.31	0.99
L <sub>2</sub> (c)	4	3– 7	4.8	0.85	2.92
L <sub>2</sub> (cp)	4	6– 7	6.8	0.25	0.25
Cheek scales	11	2– 3	2.9	0.09	0.09
Squ. op.	3	9–10	9.7	0.33	0.33
Squ. sop.	7	3– 5	4.1	0.26	0.48
Squ. iop.	11	2– 3	2.9	0.09	0.09
D spines	11	14–15	14.7	0.14	0.22
D <sub>tot</sub>	11	21–22	21.7	0.14	0.22
A <sub>tot</sub>	11	9–10	9.2	0.12	0.16
P	11	11–12	11.5	0.16	0.27
Rakers	10	1– 2	1.6	0.16	0.27
Serrations	11	0	0.0		

From the other Uaupés species, *A. elizabethae* is distinguished by the colour-pattern. Young *A. brevis* are similar to young *A. elizabethae*, but have a caudal spot.

*Apistogramma brevis* sp. nov.

(Fig. 13)

**Holotype.** IRSNB (Types) 570 — ♂, 29.0 mm SL.

**Type-locality.** Petit igarapé du Lago Penera, rive droite du Uaupés, État d'Amazonas, Brésil. (0°01'N 67°21'W.)

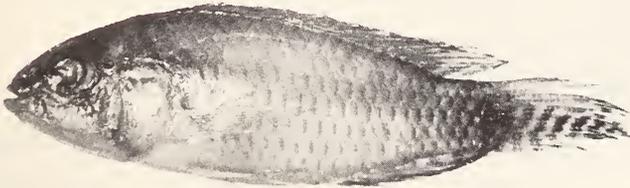


Fig. 13. Holotype of *Apistogramma brevis*.

**Diagnosis.** Head length 30.7–36.3 % of SL, body depth 28.8–36.5 % of SL. CP length 76.7–111.1 % of CP depth. D. XV.6–7.i, XVI.6.i–7. A. III.5.i–7. Squ. long. 22–23. Rakers 1–3. Preoperculum frequently serrate (3–25 denticuli). Dorsal fin without produced lappets. Caudal fin rounded in females and young, with dorsal and ventral prolongations in adult males. Lateral spot, in males also a Bar 2 spot, pectoral spot, abdominal stripes, in females also midventral stripe present. Caudal spot in females and young. Bars faint. No chest blotch. Dorsal fin not clearly darkened anteriorly. Caudal fin with cross-stripes at least dorsally. (114 specimens of both sexes, 13.3–38.7 mm SL.)

**Etymology.** *brevis* (Lat. adj.), short (compared to other Uaupés species of this genus).

**Material**

**Holotype.** IRSNB (Types) 570 — ♂, 29.0 mm. Brasil (Amazonas), Lago Penera, small igarapé (0°01'N 67°21'W). 1967.12.09. Leg. S. M. le roi Léopold de Belgique & J.-P. Gosse (IMA 1967: Sta. 192).

**Paratypes.** IRSNB (Types) 571 — 7 ♂, 19.4, 21.4, 22.9, 24.4, 25.2, 25.2, 38.7 mm; 10 ♀ 16.8, 18.5, 20.2, 20.3, 20.3, 21.0, 23.0, 23.9, 24.0, 27.1 mm. Same data as holotype. IRSNB (Types) 572 — 38 ♂, 13.5, 13.8, 14.6, 14.7, 14.7, 15.2, 15.5, 15.6, 15.7, 15.9, 16.2, 16.3, 16.4, 16.6, 16.9, 17.2, 17.5, 17.6, 17.9, 18.2, 18.4, 18.4, 19.1, 19.8, 20.3, 21.0, 21.2, 21.5, 21.9, 22.3, 23.4, 23.6, 24.5, 24.6, 25.2, 28.7, 28.9, 33.4 mm; 53 ♀, 13.3, 13.9, 14.1, 14.2, 14.6, 14.7, 14.8, 15.1, 15.3, 15.4, 15.6, 15.6, 15.7, 15.9, 16.1, 16.2, 16.4, 16.4, 16.5, 16.6, 16.7, 16.8, 17.0, 17.8, 17.9, 17.9, 17.9, 18.4, 18.5, 18.5, 18.5, 18.7, 18.8, 19.5, 19.8, 20.0, 20.0, 20.2, 20.4, 20.5, 20.6, 20.7, 20.8, 21.0, 21.9, 22.0, 22.3, 22.8, 22.9, 23.9, 27.0, 27.0 mm; 3 sex indet., 16.3, 19.8, 20.2 mm. Brasil (Amazonas), R. Tiquié right bank, Igarapé Acaraposo (0°00'N 68°30'W). 1967.12.07. Leg. S. M. le roi Léopold de Belgique & J.-P. Gosse (IMA 1967: Sta. 193). IRSNB (Types) 574 — ♂, 28.0 mm. Brasil (Amazonas), Assai, R. Uaupés (0°02'N 67°27'W). 1967.12.08. Leg. S. M. le roi Léopold de Belgique & J.-P. Gosse (IMA 1967: Sta. 191 bis).

## Description

The material is in fine condition.

Body moderately elongate. Head moderately elongate. Predorsal contour rather straight from dorsal fin origin, decurved on snout. Preventral head contour little arched, about as steep as predorsal. Snout rounded, dorsal profile more or less convex, steeper, ventral straight. Orbit tangential. Tip of maxilla exposed, to well behind anterior margin of orbit. Preoperculum serrate in 45 specimens (3–25 denticuli).

Predorsal scales cycloid, laterally posteriorwards to vertical from preoperculum vertical limb. Dorsal or all opercular, posterior cheek, not always dorsal subopercular scales, ctenoid. Squ. prd. 9–10; squ. prv. 9–12. Upper lateral line with 1–7 terminal pores; 1–3 subserial pores or one subserial canal in 36 of 106 lines. Lower with 1–6 anterior pores; a caudal canal or pore in 24 of 91 lines. 1/3 to 1/2 of caudal fin scaled; squ. caud. 3–5; outer cycloid.

Dorsal spines subequal in length from about 5th or 6th, last longest. Lappets anteriorly rather long, posteriorly moderate, pointed, none produced. Soft part pointed, a short filament in males, to at most middle of caudal fin. Soft anal fin similar, unextended, to 1/4 or 1/3 of caudal fin. D. XV.6(4), XV.6.i(53), XV.7(51), XV.7.i(1), XV.?(2), XVI.6(1), XVI.7(1), XVI.?(1). D<sub>tot</sub>21(4), 22(104), 23(3). A. III.5.i(8), III.6(93), III.6.i(10), III.7(3). A<sub>tot</sub>9(101), 10(13). Pectoral fin to about anal fin origin. Ventral fin acuminate, with short extension in males, to at most middle of spinous anal fin base. Caudal fin shape variable: In females and young, except in one IRSNB 571 female in which truncate, upper lobe longer. In males differentiation at about 25 mm SL; truncate with dorsal and ventral, usually short, prolongations, of ray 5 supported by ray 4 (and ray 6), ray 11 or 12 supported by ray 10 or 13, at most the dorsal point about as long as principal fin, ventral usually shorter.

Dentition principally biserial in both jaws; outer series of 40–60 teeth in upper jaw, inner one-half to as long; outer series in lower jaw of 45–60 teeth, inner se-

Table 13. Morphometry and meristics of *Apistogamma brevis*. For explanation, see Tab. 5.

	n	Range	$\bar{x}$	$s(\bar{x})$	$s^2$
<b>M e a s u r e m e n t s</b>					
Head length	113	30.7— 36.3	33.2	0.12	1.54
Head depth	113	23.2— 27.4	25.2	0.09	0.95
Head width	113	13.2— 17.6	15.7	0.08	0.80
Body depth	113	28.8— 36.5	31.7	0.12	1.65
Orbit diameter	113	12.1— 16.0	14.3	0.07	0.57
Snout length	111	2.3— 6.7	5.1	0.09	0.82
Cheek depth	113	3.2— 7.2	4.8	0.08	0.74
Interorbital width	113	5.2— 7.0	6.2	0.03	0.11
Preorbital depth	113	0.8— 3.1	2.0	0.04	0.17
Dorsal base	109	53.7— 61.5	57.0	0.16	2.74
Anal base	110	14.8— 20.4	18.0	0.12	1.54
CP depth	112	12.2— 15.9	14.2	0.07	0.56
CP length	112	11.2— 14.5	13.0	0.07	0.52
Last D spine	105	10.3— 19.3	14.9	0.18	3.23
Last A spine	112	14.0— 18.8	16.8	0.11	1.25
CP/CP	112	76.7—111.1	92.1	0.69	53.39
<b>C o u n t s</b>					
Squ. long.	52	22—23	22.8	0.06	0.18
Ll <sub>1</sub> (c)	82	7—14	11.6	0.17	2.37
Ll <sub>1</sub> (cp)	78	13—16	14.8	0.09	0.57
Ll <sub>2</sub> (c)	58	0— 6	3.5	0.18	1.90
Ll <sub>2</sub> (cp)	46	4— 8	7.0	0.15	1.07
Cheek scales	112	3— 4	3.1	0.02	0.07
Squ. op.	16	8—14	11.3	0.43	2.90
Squ. sop.	64	3— 6	4.0	0.08	0.36
Squ. iop.	113	3	3.0		
D spines	114	15—16	15.0	0.01	0.03
D <sub>tot</sub>	111	21—23	21.9	0.02	0.06
A <sub>tot</sub>	114	9—10	9.1	0.03	0.10
P	112	11—13	11.8	0.04	0.17
Rakers	113	1— 3	1.7	0.05	0.30
Serrations	113	0—25	3.7	0.52	30.84

ries very short, little more than symphyseal. In the largest male a symphyseal middle series in lower jaw and scattered teeth anteriorly in upper jaw.

Colouration: Yellowish, with brown, not particularly contrasting markings. Bars more or less developed, most prominent, but still faint, in medium-size individuals. Superopercular bar not well-defined. Bars broader than interspaces, darkening dorsally, ventrally reaching lower edge of pectoral axilla (2—4) or ventral body edge (4—7). Light-spotting along lateral band not conspicuous, interspaces dorsally subdued; not into dorsal fin. Lateral band from narrow postorbital stripe;

1—1<sup>1</sup>/<sub>2</sub> scale wide; more prominent in young; well-defined, but edges not sharp; to Bar 7, above lower lateral line. Lateral spot roundish, little deeper than band; in adult males especially, another spot in Bar 2.

Suborbital stripe moderately wide; superorbital to occiput. Occasionally chin, close to lower lip, darkened. Pectoral spot present. Abdominal striping variously developed, of restricted dark scale-rims, to about beginning of caudal peduncle: one from upper edge of pectoral axilla, a second from lower edge of pectoral axilla, a third below pectoral axilla to middle of soft anal fin, a fourth from origin of ventral fin to middle of spinous anal fin. Males may have a faint spot before or behind vent; adult females dark around vent and with a short midventral stripe forwards. Caudal spot quadratic or longer than deep in young and females; with faint dorsal and ventral extensions close to the fin base; in adult males an obscure base pigmentation.

Dorsal fin dusky, basally narrowly darker; lappets clear; anterior membranes slightly darker but not black; 1—3 terminal spot-stripes. Anal fin basally clear; lappets dark; margin of soft fin dark-seamed; 0—3 terminal spot-stripes. Caudal fin clear; 3—5 very irregular vertical spot-stripes on outer 2/3; in large males dusky, stripes confined to upper lobe. Ventral fin clear to whitish; outwards more or less dusky in adult females.

### Size

The largest male is 38.7/55.4 mm long (IRSNB 571), the largest female 27.1/c. 36 mm (same lot).

### Geographical distribution

Known from the R. Tiquié, in the Igarapé Acaraposo, and the R. Uaupés, at Trovao, Assai, and Lago Penera.

### Ecology

*A. brevis* is found at all four localities in the Uaupés system where *Apistogramma* spp. have been collected; only species in Igarapé Acaraposo, with *A. elizabethae* at the type-locality, with *A. elizabethae*, *A. meinkenii*, and *A. uaupesi* at Trovao, and *A. personata* at Assai.

Small specimens (to 13.3 mm) from early December indicate reproduction in October/November, but the largest females (about 27 mm) appear gravid.

## Remarks

The relationships are obscure. *A. brevis* differs from most other *Apistogramma* species in having caudal fin streamers but not also produced dorsal fin lappets. Very probably it is distinct from all other congeners. It shares with the other Uaupés species the development of a Bar 2 spot, but is distinguished by the not so slender body shape, a relatively short snout, slightly more lateral line scales, frequently serrated preoperculum, etc.

*Apistogramma personata* sp. nov.  
(Fig. 14)

**Holotype.** IRSNB (Types) 575 — ♂, 49.2 mm SL.

**Type-locality.** Rio Uaupés à Assai, État d'Amazonas, Brésil (0°02'N 67°27'W).

**Diagnosis.** Head length 31.5–36.0 %, body depth 31.0–35.6 % of SL. CP length 73.9–91.2 % of CP depth. D. XV.6–8. A. III.5–6.i. Squ. long. 22–24. Rakers 1–3. Preoperculum entire. Males from 32 mm SL with produced anterior dorsal fin lappets and dorsal and ventral caudal fin streamers. No lateral spot or abdominal stripes. A band between orbits and blotches on ventral flanks. Pectoral spot, midventral stripe in females (occasionally in males), and caudal spot present. Bars faint. Dorsal fin anteriorly more or less dark. Caudal fin with up to 7 vertical stripes of spots. (23 specimens of both sexes, 19.7–49.2 mm SL.)

**Etymology.** *personata* (Lat. adj.), masked, with reference to the band between the eyes, across the forehead.

## Material

**Holotype.** IRSNB (Types) 575 — ♂, 49.2 mm. Brasil (Amazonas), Assai, R. Uaupés (0°02'N 67°27'W). 1967.12.08. Leg. S. M. le roi Léopold de Belgique & J.-P. Gosse (IMA 1967: Sta. 191bis).

**Paratypes.** IRSNB (Types) 576 — 15 ♂, 19.8, 22.0, 30.5, 32.1, 33.6, 34.7, 35.1, 36.0, 37.5, 37.6, 38.0, 38.1, 39.4, 39.8, 41.2 mm; 7 ♀, 19.7, 22.5, 29.2, 30.9, 32.6, 32.7, 33.1 mm. Same data as holotype.

## Description

The material is in fine condition.

Body moderately elongate. Head moderately elongate. Predorsal contour about straight or arched, steeper on snout. Preventral head contour little arched, less steep. Snout rounded, broad, profiles arched, dorsal steeper. Orbit subtangential or tangential. Tip of maxilla exposed, to slightly behind anterior margin of orbit. Preoperculum entire.



Fig. 14. Holotype of *Apistogramma personata*.

Predorsal scales cycloid, laterally posteriorwards to preoperculum or even not so far. Posterior cheek and dorsal opercular scales ctenoid. Squ. prd. 9–11; squ. prv. 9–11. Upper lateral line with 0 (largest) to 3 (smallest) terminal pores; 1–2 subserial pores or canals in 18 of 41 lines. Lower line with 1–5 pores; a caudal canal or pore in 17 of 35 lines. Dorsal and anal fins naked.  $1/3$  or less of caudal fin scaled; squ. caud. 3–7; outer cycloid.

Dorsal spines subequal in length from 4th, 5th, or 6th, last longest. Lappets in males moderately long to long, pointed; in holotype 3rd–8th prolonged, 5th longest, about twice spine lengths; in other males (from 32.1 mm SL) only 3rd–5th lappets distinctly prolonged; in females and young males moderately long, bluntly pointed. Soft fin pointed, filamentous elongation of 2nd and 3rd ray to past principal caudal fin in large males, to at most middle of caudal fin in females. Soft anal fin similar, but shorter, only to middle of caudal fin in males, little behind caudal fin base in females. D. XV.6(1), XV.7(18), XV.8(4).  $D_{\text{tot}}$  21(1), 22(18), 23(4). A. III.5(1), III.5.i(1), III.6(19), III.6.i(2).  $A_{\text{tot}}$  8(1), 9(20), 10(2). Pectoral fin to vent. Ventral fin pointed, first ray elongated in males, at most to middle of soft anal fin, not much shorter in the largest females. Caudal fin truncate with rounded corners in females and young males; in males from 32.1 mm SL truncate with produced 5th and 11th or 12th rays, single or supported basally by 4th and 12th or 13th, streamers distally filamentous.

Dentition biserial. Outer series in upper jaw of 40–55 teeth, in lower jaw 40–50; inner series in upper jaw about as long as outer in adults, in lower jaw quite short. Outer anterior teeth wide-spaced, strengthened.

Colouration: Yellowish, or brownish dorsally, yellowish ventrally. Bar 1 indistinct, others apparent, not contrasting dorsally, below lateral band the anterior as intense as the band; ventrally from more or less broad dark scale edges. In younger narrower than interspaces, as broad as or broader than interspaces in the largest specimens; abdominally to level of anal fin origin, dorsally very little into dorsal fin base. Lateral band from moderately wide postorbital stripe; 1 scale deep anteriorly, 1 1/2 scale posteriorly; sharp-edged; to last bar, above lower lateral line. No lateral spot, but band in young slightly intensified where crossed by bars.

Table 14. Morphometry and meristics of *Apistogramma personata*. For explanation, see Tab. 5.

	n	Range	$\bar{x}$	$s_{(\bar{x})}$	$s^2$
<b>M e a s u r e m e n t s</b>					
Head length	23	31.5–36.0	33.3	0.22	1.07
Head depth	23	25.4–31.4	27.1	0.26	1.57
Head width	23	13.6–17.2	15.4	0.18	0.71
Body depth	23	31.0–35.6	33.5	0.25	1.49
Orbit diameter	23	10.6–14.6	12.4	0.21	1.03
Snout length	23	5.1– 8.1	6.5	0.17	0.63
Cheek depth	23	5.9– 8.3	7.3	0.14	0.48
Interorbital width	23	6.6– 8.0	7.2	0.08	0.14
Preorbital depth	23	2.3– 3.3	2.9	0.05	0.06
Dorsal base	23	56.0–61.9	59.4	0.30	2.13
Anal base	23	16.6–19.7	18.3	0.14	0.48
CP depth	23	15.1–17.1	16.0	0.12	0.31
CP length	23	11.3–14.5	13.1	0.16	0.58
Last D spine	23	13.1–18.9	16.1	0.34	2.73
Last A spine	23	14.8–17.3	16.0	0.16	0.59
CP/CP	23	73.9–91.2	81.9	1.01	23.56
<b>C o u n t s</b>					
Squ. long.	22	22–24	22.7	0.12	0.32
L <sub>1</sub> (c)	22	11–14	13.1	0.25	1.36
L <sub>1</sub> (cp)	22	13–16	14.0	0.19	0.76
L <sub>2</sub> (c)	18	3– 7	5.3	0.27	1.29
L <sub>2</sub> (cp)	18	7– 9	7.4	0.15	0.38
Cheek scales	23	3– 5	3.7	0.12	0.33
Squ. op.	14	10–14	12.4	0.36	1.80
Squ. sop.	21	4– 6	4.5	0.13	0.36
Squ. iop.	23	3	3.0		
D spines	23	15	15.0		
D <sub>tot</sub>	23	21–23	22.1	0.10	0.21
A <sub>tot</sub>	23	8–10	9.0	0.08	0.13
P	23	11–12	11.9	0.06	0.08
Rakers	23	1– 3	2.0	0.10	0.23
Serrations	23	0	0.0		

Suborbital stripe broad, superorbital indistinct. A dark band or broad inverted triangle between eyes across forehead. Pectoral spot present. No true abdominal stripes, but bars intensified on ventral flanks (see above). Midventral stripe in females, to ventral fin bases, and, shorter, in some males. A dark spot just below lower lip in both sexes, but not in all specimens. Caudal spot quadratic or rounded.

Dorsal fin not quite colourless, slightly dusky; lappets dark, except elongations, which clear; more or less darkened anteriormost membranes; dark-edged in females; 3 terminal spot-stripes. Anal fin basally whitish, distalwards dusky; dark-seamed in females; 4 terminal spot-stripes. Caudal fin clear; in males up to 7 more or less slanting spot-stripes, absent from dorsalmost part of fin, in females up to 5, fainter. Ventral fin white in males; spine and outer membrane black in females.

### Size

The largest male (holotype) is 49.2/65.3 mm long, the largest female 33.1/44.2 mm.

### Geographical distribution

Known only from the type-locality, R. Uaupés at Assai.

### Ecology

The only other *Apistogramma* collected with the type-series is a specimen of *A. brevis* (28.0 mm).

### Remarks

*A. personata* is distinguished by the band between the orbits, but also by the blotchy bars on the flanks. Unlike most other slender, banded species, it also has a caudal spot, but no lateral spot.

It may be related to *A. gibbiceps*, with similar fin shape and lower flank markings. Among the "slender" species these are the deepest (depth:  $\bar{x}$  = 33.5 % of SL in *A. personata*; 34.8 % in *A. gibbiceps*; in other "slender" species 29.8-32.0 %). They have also a deep head ( $\bar{x}$  = 27.1 and 29.3 % of SL), relatively long snout ( $\bar{x}$  = 6.5 and 7.6 % of SL), deep cheek ( $\bar{x}$  = 7.3 and 9.1 % of SL), etc. Aside from colour pattern differences, *A. gibbiceps* differs in a slightly longer dorsal fin base (60.0—64.5 % of SL,  $\bar{x}$  = 61.7 %; in *A. personata* 56.0—61.9 %,  $\bar{x}$  = 59.4 %), and longer anal fin base (20.0—21.6 % of SL; in *A. personata* 16.6—19.7 %), fewer operculum scales (8—9; in *A. personata* 10—14), etc. It must be kept in mind, however, that the *A. gibbiceps* known are probably import specimens (p. 115).

*Apistogramma gibbiceps*

*Apistogramma gibbiceps* (pt) Meinken, 1969. Senckenberg. biol. 50: 91.

**Holotype.** SMF 9441 — ♂, 44.5 mm SL.

**Type-locality.** Brasilien, wahrscheinlich Gebiet des Rio Negro.

**Diagnosis.** Head length 31.2–33.3 %, body depth 32.2–37.7 % of SL. CP length 74.3–83.3 % of CP depth. D. XIV.6, XV.5.i–7. A. III.6–7. Squ. long. 23. Rakers 1–2. Preoperculum entire. Dorsal fin without produced lappets. Caudal fin with a streamer in each lobe near middle rays. Lateral spot present. No pectoral spot, abdominal stripes, midventral stripes or caudal spot. Bars as faint traces at most, but expressed as spots below lateral band. No chest blotch. Dorsal fin dusky anteriorly (no distinct spot). Caudal fin immaculate, upper lobe more or less clear, lower lobe dark. (7 males, 32.0–44.5 mm SL.)

**Bibliography**

*Apistogramma gibbiceps* (pt) Meinken, 1969 b: 91 (protolog, detailed descr.; loc.: Brasilien, wahrscheinlich Gebiet des Rio Negro; holotype SMF 9441, 6 paratypes SMF 9442–9446, 9449, 2 paratypes 9447–9448 [= *A. agassizii*], 1 paratype 9450 [= *A. sp.*]), Figs. 1 (re-touched monochrome photo of holotype in lateral aspect), 3 (sketch of head); Meinken, 1970: 7 (not seen; from Goldstein [1973]; translation of Meinken [1969 b]).

**Etymology.** *gibbiceps*, noun from *gibbus* (Lat.), a hump, and *caput* (Lat.), head, in allusion to the elevation of the nape. Not explained by Meinken.

**Material**

**Holotype.** SMF 9441 — ♂, 44.5 mm. "Brasilien, wahrscheinlich Gebiet des Rio Negro." Ded. W. Schwartz, 1967.

**Paratypes.** SMF 9442–9446, 9449 — 6 ♂, 32.0, 33.4, 38.1, 38.1, 44.2, 43.0 mm. Same data as holotype.

Other paratypes of this species are SMF 9447–9448 (2 ♂, 36.9 and 37.7 mm = *A. agassizii*), and SMF 9450 (♀, 26.2 mm = *A. sp.*), all with same data as holotype.

**Description**

Only the smallest paratype (SMF 9449, 32.0 mm) in good condition, the holotype in acceptable shape, the rest more or less soft, macerated, SMF 9443 (44.2 mm) in critical condition. Swelling from maceration (before preservation?) has probably increased the size of the gibbosity on the nape. Probably import specimens.

Body elongate, the larger specimens robust. Head short, deep. Predorsal contour characterized by a moderate protuberance of the nape, i.e. very feebly descending from dorsal fin origin to little behind anterior margin of orbit, then steeply descending; straight, moderately sloping rostrally. Preventral head contour gently arched, less steep. Snout short, broad, rounded, dorsal profile steeper. Orbit subtangential. Tip of maxilla exposed, to anterior margin of orbit or slightly behind. Preoperculum entire.

Predorsal scales cycloid, laterally posteriorwards at most including 4 vertical scale series above upper lateral line behind dorsal fin origin. Dorsal opercular and posterior cheek scales or only a dorsal opercular scale ctenoid. Squ. prd. 9–10; squ. prv. 7–9. Upper lateral line with 1–2 pores terminally in 5 of 11 lines; a subserial canal and pore in 1 line, 2 subserial pores in another. An anterior pore in 2 of 10 lower lines; a caudal in 4 of 10. 1/4 of caudal fin scaled; squ. caud. 4–10; outer cycloid.

Dorsal spines increasing in length to last. Lappets rather long, pointed, but none produced. Soft part pointed, tip to about middle of caudal fin; soft anal fin may be longer. D. XIV.6(1), XV.5.i(1), XV.6(1), XV.7(4).  $D_{\text{tot}}$  20(1), 21(1), 22(5). A. III.6(5), III.6.i(1), III.7(1).  $A_{\text{tot}}$  9(5), 10(2). Pectoral fin to vent. Ventral fin acuminate, first ray to end of anal fin base. Caudal fin probably with two streamers, but, whether the natural condition or due to damage, only one streamer in all but SMF 9445 (38.1 mm): the corners are rounded, the 12th ray, supported by the 13th, produced, in SMF 9445 also the corresponding rays of the upper lobe, otherwise appearing rounded.

Dentition biserial in upper jaw, about 50–55 teeth in outer series, inner series as long in the larger, little more than symphyseal in SMF 9449. 2 (9449) or 3 (larger) series in lower jaw, outer comprising at least 40 teeth, inner short.

Colouration: Yellowish, with brown to blackish markings. Bars at most as traces, and, variously developed, 2nd–5th, 3rd–7th, or 4th–5th as blotches of dark scale-edges below lateral band. Dusky on nape and back along dorsal fin base. Lateral band from broad postorbital stripe, very faint before lateral spot, still faint behind, about 1½ scale deep, to caudal fin above and on lower lateral line; lower limit sharp, upper more gradual. Lateral spot roundish, more or less apparent, in band or slightly extended upwards.

Superorbital stripe absent or a faint spot; suborbital stripe faint, moderately wide, across cheek. No pectoral spot, abdominal stripes or caudal spot. No midventral stripe, but a dark line midventrally in the two largest, probably not part of the colour pattern.

Dorsal fin dusky to blackish on spinous part; soft part more or less clear; immaculate. Anal fin spinous and distal soft parts dark. Dorsal caudal fin lobe more or less clear, ventral lobe more or less dark (dusky to blackish). Ventral fin dusky, produced ray part white.

Table 15. Morphometry and meristics of *Apistogramma gibbiceps*. For explanation, see Tab. 5.

	n	Range	$\bar{x}$	$s(\bar{x})$	$s^2$
<b>M e a s u r e m e n t s</b>					
Head length	7	31.2–33.3	32.5	0.28	0.56
Head depth	7	26.9–31.4	29.3	0.61	2.60
Head width	7	15.0–16.5	15.9	0.23	0.36
Body depth	7	32.2–37.7	34.8	0.71	3.57
Orbit diameter	7	10.4–11.4	10.8	0.15	0.15
Snout length	7	5.9– 8.6	7.6	0.37	0.95
Cheek depth	7	7.5–10.0	9.1	0.31	0.67
Interorbital width	7	7.6– 9.4	8.6	0.28	0.56
Preorbital depth	7	2.5– 3.8	3.5	0.18	0.22
Dorsal base	7	60.0–64.5	61.7	0.55	2.12
Anal base	7	20.0–21.6	20.9	0.21	0.30
CP depth	7	14.7–16.9	15.9	0.25	0.43
CP length	7	11.8–13.5	12.6	0.26	0.49
Last D spine	7	16.9–20.7	18.9	0.52	1.89
Last A spine	7	16.3–18.0	17.1	0.26	0.46
CP/CP	7	74.3–83.3	79.2	1.10	8.53
<b>C o u n t s</b>					
Squ. long.	7	23	23.0		
Ll <sub>1</sub> (c)	7	13–14	13.4	0.20	0.29
Ll <sub>1</sub> (cp)	7	13–15	13.9	0.34	0.81
Ll <sub>2</sub> (c)	6	4– 7	5.0	0.45	1.20
Ll <sub>2</sub> (cp)	6	4– 7	5.7	0.49	1.47
Cheek scales	7	3– 4	3.1	0.14	0.14
Squ. op.	5	8– 9	8.4	0.24	0.30
Squ. sop.	7	3– 5	4.0	0.22	0.33
Squ. iop.	7	3– 4	3.1	0.14	0.14
D spines	7	14–15	14.9	0.14	0.14
D <sub>tot</sub>	7	20–22	21.6	0.30	0.62
A <sub>tot</sub>	7	9–10	9.3	0.18	0.24
P	7	12	12.0		
Rakers	7	1– 2	1.6	0.20	0.29
Serrations	7	0	0.0		

### Size

Only males known, the largest (holotype) 44.5/67.0 mm, but probably an import specimen.

### Geographical distribution

Meinken (1969b) believed his fish to originate from the R. Negro region, and since the exporter of the specimens, Mr. Willi Schwartz, has an export firm in

Manaus, and collects, among other areas, the R. Negro, that appears very probable. The conjectured close relationship with *A. personata*, from the R. Uaupés, supports Meinken's guess.

### Remarks

Meinken (1969b) emphasized "a deep interorbital notch, the gibbosity of the forehead, and the conical shape of the caudal fin", and believed these characters in combination to distinguish *A. gibbiceps* from all other *Apistogramma* spp. However, the interorbital notch is a result of the elevation of the nape, the impression of the elevated nape is influenced by the swelling of improperly preserved tissue, and the caudal fin is apparently not "conical". Some other remarks may be made on Meinken's description: a) the morphometrical data for paratype males in the upper table on p. 92, includes the holotype (first figure), b) there is no distinct band before the lateral spot in the holotype, but it has been added on the photo, Abb. 1, and c) the sketch of the head lateralis pores is largely incorrect, pores omitted (near orbit), and added (on suboperculum), and preoperculum not correctly drawn.

The female paratype figured (Abb. 2), and one other female, are two rotten male *A. agassizii*. The third female is correctly sexed, but of a third species, not yet described. It is quite different though, but obviously an aquarium (import) specimen.

*A. gibbiceps* is similar and probably related to *A. personata*, but these species are readily distinguished (p. 114). From all other *Apistogramma* spp., *A. gibbiceps* is separated by the blackened immaculate fins, and the frontal gibbosity, which, however, is probably not so impressive in well-preserved material. For relationship with *A. agassizii*, see p. 96.

### *Apistogramma meinkeni* sp. nov.

(Fig. 15)

**Holotype.** IRSNB (Types) 567 — ♂, 33.1 mm SL.

**Type-locality.** 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.)

**Diagnosis.** Head length 31.9–36.7 %, body depth 30.2–33.5 % of SL. CP length 83.3–104.3 % of CP depth. D. XIV.7–8, XV.6.i–8. A.III.6–7. Squ. long. 22–24. Rakers 1–3. Preoperculum entire. Dorsal fin without produced free lappets, but in males from 33 mm SL united beyond spine tips from 5th posteriorwards. Caudal fin rounded, in large males upper lobe longer. Lateral spot, and Bar 2 spot. Pectoral spot, midventral stripe and caudal spot present. No abdominal stripes. Bars

present at most as traces. No chest blotch. Dorsal fin not dark anteriorly. Caudal fin with up to 10 vertical stripes of spots. (35 specimens of both sexes, 17.3–34.8 mm SL.)

**Etymology.** *meinkeni* for Dr. Hermann Meinken (1896–1976), German amateur fish taxonomist and aquarist, who had a special interest in the genus *Apistogramma*, and published several papers on the taxonomy and geographical distribution of these fishes.

### Material

**Holotype.** IRSNB (Types) 567 — ♂, 33.1 mm. Brasil (Amazonas), Trovao, R. Uaupés right bank, Igarapé (0°02'N 67°26'W). 1967.12.09. Leg. S. M. le roi Léopold de Belgique & J.-P. Gosse (IMA 1967: Sta. 193).

**Paratypes.** IRSNB (Types) 568 — 17♂, 21.6, 21.6, 24.4, 24.8, 24.8, 25.2, 25.9, 26.4, 26.7, 27.2, 27.8, 27.8, 28.2, 30.5, 34.2, 34.2, 34.8 mm; 15♀, 17.3, 17.7, 19.9, 20.5, 21.2, 21.4, 21.7, 21.8, 22.0, 22.2, 24.3, 29.9, 31.4, 31.8, 32.4 mm. Same data as holotype.  
IRSNB (Types) 569 — 2♂, 18.9, 21.8 mm. Same data as holotype.

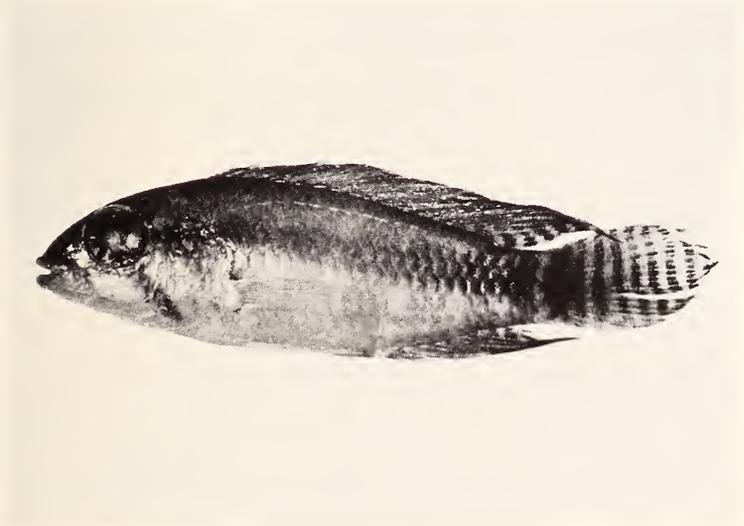


Fig. 15. Holotype of *Apistogramma meinkeni*.

### Description

The material is in fine condition, although it is not possible to obtain complete scale counts on all specimens.

Body moderately elongate. Head moderately elongate. Predorsal contour gently and evenly arched, steeper rostrally, may be more straight in females. Preventral head contour about equal, or less steep, about straight, or (usually) slightly arched. Snout rounded, dorsal profile steeper, arched, ventral profile straight. Orbit tangential, or even supratangential occasionally. Tip of maxilla exposed, to anterior margin of orbit or slightly beyond. Preoperculum entire.

Predorsal scales cycloid, laterally posteriorwards to line anterodorsally curved between dorsal fin origin and preoperculum dorsal tip. Posterior cheek and dorsal opercular scales ctenoid. Squ. prd. 8–11; squ. prv. 8–11. Upper lateral line with (0) 1–5 (10) terminal pores, commonly one or two subserial pores. Lower line with 1–6 anterior pores; a caudal canal or pore in 26 of 51 lines.  $1/4$  to almost  $1/2$  (males) of caudal fin scaled; squ. caud. 3 (smallest) – 9 (largest males); outer cycloid.

Dorsal spines subequal in length from 5th, 6th, 7th, or 8th, little increasing to last. Lappets moderately long, in the four largest males united from the 5th posteriorwards; soft part pointed, without or with short elongation, to little beyond middle of caudal fin in adult males, to  $1/3$  of caudal fin or shorter in females and young. Soft anal fin similar, but shorter. D. XIV.7(1), XIV.7.i(1), XIV.8(1), XV.6.i(6), XV.7(23), XV.7.i(1), XV.8(2).  $D_{tot}$  21(1), 22(31), 23(3). A. III.6(20), III.6.i(7), III.7(8).  $A_{tot}$  9(20), 10(15). Pectoral fin to anal fin origin in young, to vent in the largest. Ventral fin pointed, with filamentous prolongation of first ray to soft anal fin (largest females), or behind anal fin base (largest males). Caudal fin rounded, asymmetrical in large males (upper lobe longer), symmetrical in females and young.

Dentition triserial only in the largest specimens, and then usually only in lower jaw. The outer series comprises 50 (young) to 60 (holotype) teeth; the inner 10 (young) to 30 (adults) in lower jaw, 20 (young) to 45 (adults) in upper jaw, length about half that of the outer or shorter. Third series strictly symphyseal, a few teeth between principal series.

Colouration: Pale brownish, yellowish ventrally. Markings brown. Bars not present, or as traces including superopercular bar, leaving light spots along lateral band, not as conspicuous as in *A. bitaeniata*; to level of lower edge of pectoral axilla (Bars 2–3), or ventral body edge (4–7). No spotting on back. Lateral band from broad postorbital stripe,  $1-1\frac{1}{2}$  scale deep, about same depth along its course, edges not perfectly sharp, to level of last Bar, above and including lower lateral line. Spot in Bars 2 and 3, not outside band; occasionally the other bars are intensified on the band, but not producing a spotted band effect.

Superorbital stripe absent; suborbital stripe moderately wide. Pectoral spot small. Midventral stripe in both sexes, very thin, faint, to ventral fin bases. A dark spot between vent and anal fin origin. No abdominal stripes. Caudal spot roundish.

Dorsal fin clear, lappets dusky; not black anteriorly; up to 7 terminal spot-stripes. Anal fin clear, duskiest towards margin; about 4 terminal spot-stripes. Caudal fin clear, with up to 8–10 interspace-wide stripes of spots across entire depth and length of fin. Ventral fin white, outer ray faintly dusky.

Table 16. Morphometry and meristics of *Apistogramma meinkeni*. For explanation, see Tab. 5.

	n	Range	$\bar{x}$	$s_{(\bar{x})}$	$s^2$
<b>M e a s u r e m e n t s</b>					
Head length	35	31.9– 36.7	34.0	0.22	1.67
Head depth	35	23.3– 26.6	25.5	0.13	0.60
Head width	35	14.0– 17.1	15.2	0.12	0.53
Body depth	35	30.2– 33.5	32.0	0.15	0.79
Orbit diameter	35	12.5– 15.6	13.6	0.14	0.72
Snout length	35	4.9– 7.3	6.1	0.84	0.25
Cheek depth	35	4.6– 6.6	5.8	0.08	0.22
Interorbital width	35	5.4– 6.7	6.1	0.05	0.08
Preorbital depth	35	2.0– 3.1	2.5	0.05	0.08
Dorsal base	35	54.8– 60.6	57.9	0.25	2.17
Anal base	34	17.5– 21.4	19.2	0.15	0.76
CP depth	35	12.2– 14.7	13.8	0.09	0.29
CP length	35	11.4– 14.7	13.4	0.13	0.57
Last D spine	34	14.5– 19.1	16.6	0.20	1.39
Last A spine	35	15.5– 19.8	17.5	0.19	1.25
CP/CP	35	83.3–104.3	97.0	0.79	21.78
<b>C o u n t s</b>					
Squ. long.	34	22–24	23.0	0.05	0.09
Ll <sub>1</sub> (c)	35	1–15	11.9	0.38	5.11
Ll <sub>1</sub> (cp)	35	14–16	15.1	0.07	0.18
Ll <sub>2</sub> (c)	28	2– 6	3.8	0.21	1.21
Ll <sub>2</sub> (cp)	27	5– 8	6.9	0.15	0.59
Cheek scales	35	2– 3	2.9	0.55	0.10
Squ. op.	18	9–13	10.3	0.28	1.41
Squ. sop.	32	1– 5	3.8	0.13	0.52
Squ. iop.	35	2– 4	3.0	0.05	0.09
D spines	35	14–15	14.9	0.05	0.08
D <sub>tot</sub>	35	21–23	22.1	0.06	0.11
A <sub>tot</sub>	35	9–10	9.4	0.08	0.25
P	35	11–12	11.5	0.09	0.26
Rakers	35	1– 3	2.1	0.09	0.26
Serrations	35	0	0.0		

### Size

The largest male (IRSNB 568) is 34.8/47.0 mm long, the largest female (same lot) 32.4/42.5 mm.

### Geographical distribution

Known only from the type-locality, an igarapé in the R. Uaupés system, at Trovao.

### Ecology

Sympatric species at the type-locality include *A. elizabethae*, *A. brevis*, and *A. uaupesi*.

### Remarks

The most similar species appears to be *A. iniridae* in the R. Inirida system, a headwater of the R. Orinoco. There is general agreement in colour-pattern, dorsal and caudal fin shape of males, proportions and meristics, but also differences: *A. iniridae* is more slender (depth 27.0–34.2 % of SL,  $\bar{x}$  = 30.5 %; in *A. meinkeni* 30.2–33.5 %,  $\bar{x}$  = 32.0 %), lacks the caudal spot and Bar 2 spot, has fewer preventral scales (4–8; 8–11 in *A. meinkeni*) (*A. iniridae* data from Kullander, in prep. a). These species may be closely related, though.

The most similar R. Uaupés species is *A. uaupesi*, with about the same body shape, but different colouration, no united dorsal fin lappets, slightly more gillrakers ( $\bar{x}$  = 3.1;  $\bar{x}$  = 2.1 in *A. meinkeni*), lesser variation in the  $A_{tot}$  count (45 of 48 specimens with  $A_{tot}$  = 9; 20 with 9, 15 with 10 in *A. meinkeni*), etc. From other species of the *pertensis* group *A. meinkeni* is easily distinguished by the colour pattern. It is also the most deep-bodied species in this group.

### *Apistogramma uaupesi* sp. nov.

(Fig. 16)

**Holotype.** IRSNB (Types) 594 — ♂, 27.1 mm SL.

**Type-locality.** 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.)

**Diagnosis.** Head length 32.1–36.6 %, body depth 27.2–33.2 % of SL. CP length 81.8–104.3 % of CP depth. D. XV.6–7. A. (III.4), III.5.i–6.i. Squ. long. 22–24. Rakers 1–5. Preoperculum rarely serrate (1 of 48 specimens). Dorsal fin without produced lappets. Caudal fin rounded in females and young, roundish lanceolate in adult males. Lateral spot, frequently Bar 2 spot present. Pectoral spot present. No abdominal stripes, midventral stripe, or caudal spot. Bars nearly vanished or faint. No chest blotch. Dorsal fin not dark anteriorly. Caudal fin with colourless stripes distally. (48 specimens of both sexes, 15.4–28.0 mm.)

**Etymology.** *uaupesi* for the rio Uaupés, in the drainage system of which is the type-locality.

### Material

**Holotype.** IRSNB (Types) 594 — ♂, 27.1 mm. Brasil (Amazonas), Trovao, R. Uaupés right bank, Igarapé (0°02'N 67°26'W). 1967.12.09. Leg. S. M. le roi Léopold de Belgique & J.-P. Gosse (IMA 1967: Sta. 193).

**Paratypes.** IRSNB (Types) 595 — 28 ♂, 17.0, 17.6, 19.2, 19.4, 19.7, 20.0, 20.7, 21.2, 21.3, 21.5, 21.7, 21.8, 22.4, 22.7, 22.9, 23.2, 23.4, 24.0, 24.2, 24.2, 24.3, 24.8, 25.2, 25.8, 26.2, 27.1, 27.2, 28.0 mm; 15 ♀, 19.5, 19.7, 19.7, 19.9, 19.9, 20.3, 20.5, 20.5, 20.8, 20.9, 21.0, 22.4, 22.7, 25.6, 25.9 mm; 4 sex indet., 15.4, 16.1, 17.2, 17.2 mm. Same data as holotype.

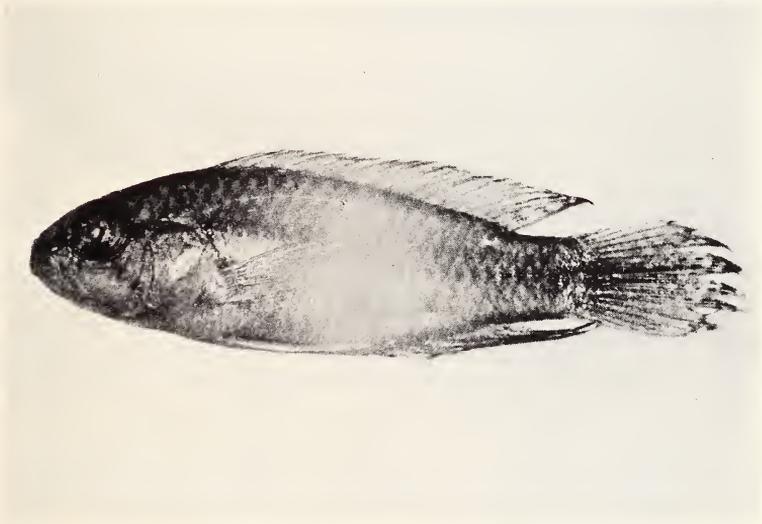


Fig. 16. Holotype of *Apistogramma uaupesi*.

### Description

The material is in fine condition.

Body elongate. Head moderately elongate. Predorsal contour gently arched, descending from dorsal fin origin. Preventral head contour gently arched to almost straight, as steep as predorsal contour. Orbit tangential. Tip of maxilla exposed, to little behind anterior margin of orbit. Preoperculum with 5 denticuli in one specimen.

Predorsal scales cycloid, laterally posteriorwards to line between dorsal fin origin and orbit margin posterodorsally. Posterior cheek and dorsal opercular scales ctenoid. Squ. prd. 8–10; squ. prv. 6–9 (10 in 2 specimens). Upper lateral line with 2–5 terminal pores, only one without pores, 14 of 84 lines with 1 or 3 subserial pores, one with a subserial canal. Lower line with anterior pores, or of only pores; 3 of 62 with a caudal pore.  $1/4$  to  $1/3$  of caudal fin scaled; squ. caud. 3–7; outer cycloid or all scales ctenoid.

Dorsal spines increasing in length to last, the first rather long. Lappets moderately long, pointed, none produced. Soft part pointed, without prolongation; to at most middle of caudal fin in males, to caudal fin base in females. Soft anal fin similar. D. XV.6(7), XV.6.i(5), XV.7(36).  $D_{tot}$  21(7), 22(41). A. III.4(1; obviously atypical), III.5.i(2), III.6(43), III.6.i(2).  $A_{tot}$  7(1), 9(45), 10(2). Pectoral fin to vent or anal fin origin. Ventral fin acuminate, first ray in males long, to beyond spinous anal fin base at most, not prolonged in females, to vent. Caudal fin roundish to lanceolate in males, roundish in females and young.

Dentition biserial. Outer series in upper jaw of 45–60 teeth, inner short, little more than symphyseal. Outer series in lower jaw of about 45–50 teeth, inner symphyseal.

Colouration: Yellowish, markings brown. Bars present, but never prominent, may be next to vanished; to lower edge of pectoral axilla or anal fin base; more apparent in females and young, than in adult males; broader than interspaces; more intense near dorsal fin, as spots, not into dorsal fin. Lateral band from moderately wide postorbital stripe; very even-edged in the holotype, more spotty in the smaller specimens; about  $1\frac{1}{2}$  scale deep; to caudal fin base, on and above lower lateral line. Lateral spot roundish, little or not deeper than band. Frequently a prominent spot in band on Bar 2.

Superorbital stripe distinct in young only; suborbital stripe narrow, reaching hardly more than across cheek. Pectoral spot present. No abdominal or midventral stripes, or caudal spot.

Dorsal fin dusky, darker close to lappets, which clear; not black anteriorly; 2–3 terminal spot-stripes. Anal fin dusky or colourless; holotype with darker marginal seam; 2–3 terminal spot-stripes. Caudal fin dusky; clear vertical spot-stripes on distal half; lateral band faintly continued on scaled part. Ventral fin white.

### Size

The largest male is 28.0/c. 37 mm long, the largest female 25.9/c. 34 mm in length.

Table 17. Morphometry and meristics of *Apistogramma uaupesi*. For explanation, see Tab. 5.

	n	Range	$\bar{x}$	$S(\bar{x})$	$s^2$
<b>M e a s u r e m e n t s</b>					
Head length	48	32.1— 36.6	33.8	0.13	0.80
Head depth	48	24.6— 27.6	26.1	0.09	0.40
Head width	48	14.3— 17.4	15.5	0.10	0.45
Body depth	48	27.2— 33.2	31.1	0.15	1.13
Orbit diameter	48	12.9— 15.5	14.3	0.09	0.37
Snout length	47	4.5— 7.9	6.4	0.09	0.37
Cheek depth	48	3.9— 6.2	5.5	0.06	0.19
Interorbital width	48	5.2— 7.1	6.6	0.05	0.13
Preorbital depth	44	1.7— 3.0	2.5	0.04	0.08
Dorsal base	44	53.5— 60.8	56.6	0.20	1.90
Anal base	44	16.9— 20.7	19.2	0.13	0.70
CP depth	48	13.0— 15.2	14.1	0.08	0.30
CP length	47	11.2— 14.0	12.9	0.08	0.28
Last D spine	47	13.1— 16.6	14.9	0.13	0.80
Last A spine	48	14.8— 18.3	16.4	0.13	0.72
CP/CP	47	81.8—104.3	92.1	0.77	27.55
<b>C o u n t s</b>					
Squ. long.	45	22—24	23.0	0.03	0.05
Ll <sub>1</sub> (c)	46	9—14	11.5	0.18	1.50
Ll <sub>1</sub> (cp)	47	13—16	14.6	0.10	0.51
Ll <sub>2</sub> (c)	35	0— 6	3.4	0.21	1.60
Ll <sub>2</sub> (cp)	35	4— 8	6.5	0.12	0.49
Cheek scales	48	3	3.0		
Squ. op.	18	8—10	8.8	0.17	0.54
Squ. sop.	41	2— 5	3.2	0.10	0.39
Squ. iop.	48	3	3.0		
D spines	48	15	15.0		
D <sub>tot</sub>	48	21—22	21.9	0.05	0.13
A <sub>tot</sub>	48	7—10	9.0	0.05	0.13
P	48	11—12	11.9	0.04	0.08
Rakers	48	1— 5	3.1	0.10	0.50
Serrations	48	5 in one specimen only			

### Geographical distribution

Known only from the type-locality, a creek at Trovao, on the right bank of the R. Uaupés.

### Ecology.

Sympatric species at the type-locality: *A. elizabethae*, *A. brevis*, and *A. meinkei*. A 15.4 mm specimen may be estimated to be 1—2 months old, i.e. from October–November.

## Remarks

The clear instead of dark spot-stripes in the caudal fin is the foremost characteristic of this species, which by the other characters may be placed in the *pertensis* group. It shows no clear affinity or similarity with any particular other species. The most similar species in the R. Uaupés is the sympatric *A. meinkeni*, but they are easily told apart (see p. 122).

### *Apistogramma pertensis*

*Heterogramma taeniatum pertense* Haseman, 1911. Ann. Carnegie Mus. 7: 359.

**Holotype.** FMNH 54171 — ♂?, 26.4 mm SL.

**Type-locality.** Manaos. (= Manaus, Estado do Amazonas, Brazil, 3°06'S 60°00'W.)

**Diagnosis (revised).** Head length 29.6–37.2 %, body depth 26.0–32.3 % of SL. CP length 77.8–123.5 % of CP depth. D. XIV.7–8, XV.6–7, XVI.6. A. III.4–7. Squ. long. 22–24. Rakers 1–3. Preoperculum usually serrate (2–41 denticuli). Dorsal fin without produced lappets, occasionally united posteriorly in adult males. Caudal fin rounded (females) to almost lanceolate (adult males). Lateral spot, small pectoral spot, occasionally a midventral stripe in females, and caudal spot present. No abdominal stripes. Bars as traces in females and young, occasionally in adult males. No chest blotch. Dorsal fin not dark anteriorly. Caudal fin with up to 6 vertical stripes of spots, faint in males, prominent in females and young. (62 specimens of both sexes, 14.5–38.8 mm SL.)

## Bibliography

- Heterogramma taeniatum* (pt), Haseman, 1911c: 359 (no descr.; loc.: Manaos, in a creek [FMNH 54169]).
- Heterogramma taeniatum pertense* Haseman, 1911c: 359 (protolog, brief descr.; locs.: Manaos [holotype FMNH 54171]; Santarem, Rio Tapajos; as "var." of *H. taeniatum* (Günther)).
- Heterogramma taeniatum* var. *pertense* Haseman, 1911c: pl. 66 (retouched monochrome photo of holotype in lateral aspect).
- Apistogramma pertense* Regan, 1913: 282 (in list of species in the genus; no specimens; name, distr.; new comb., new rank), 283 ("...is the species usually known as *H. [eterogramma] taeniatum* [(Günther)]."; close to *A. amoenus* [(Cope)]; differences from *A. amoenus* and *A. agassizii* [(Steindachner)]; no specimens).
- [*Heterogramma pertense*] A. de Miranda Ribeiro, 1918: 17 (elevated to species rank; no specimens; ref. Haseman [1911c]).
- Heterogramma taeniatum pertense* Henn, 1928: 96 (in list of CM type-specimens; lists "Type").
- Apistogramma pertense* Pellegrin, 1936: 57 (close relative of *A. p.* var. *bitaeniata* Pellegrin; no specimens; ref. Haseman [1911c], Regan [1913]; differences from *A. p.* var. *bitaeniata*).
- Apistogramma taeniatum pertense* Fowler, 1954: 276 (incomplete bibliography), Fig. 865 (sketch, based on pl. 66 in Haseman [1911c]).
- ?*Apistogramma pertense* Meinken, 1961a: 135 (presence in Letitia [= Leticia, Colombia] area indicated; no specimens; no ref.).

*Apistogramma pertense* Meinken, 1962: 141 (in key-like list of *Apistogramma* spp.; name, distr.; no specimens, no ref.).

?*Apistogramma pertense* Meinken, 1969c: 166 (note on distr.; no specimens; no ref.).

**Etymology.** *pertense* (Lat., adj.), from *pertinare*, to belong [as variety to *A. taeniata* (Günther)]. Not explained by Haseman.

## Material

**Specimens.** FMNH 54169 (CM 2739) — ♂, 14.5 mm. Brasil (Amazonas), Manaus, "creek" (3°06'S 60°00'W). 1909.11.29. Leg. J. D. Haseman (ECMCSA 3036–3155).  
 IRSNB 18.598 — 5 ♂, 16.3, 16.8, 21.8, 24.3, 26.2 mm; 11 ♀, 14.5, 15.8, 20.0, 20.6, 20.7, 21.1, 21.3, 21.4, 21.6, 22.7, 25.3 mm; 2 sex indet., 20.9, 24.0 mm. Brasil (Pará), Santarem, Igarapé Mapiri (2°26'S 54°42'W). 1963.11.30. Leg. G. Marlier (Sta. 145).  
 IRSNB 18.599 — 8 ♂, 24.7, 25.2, 25.9, 26.6, 28.2, 30.0, 30.1, 32.2 mm; 4 ♀, 22.3, 23.0, 23.2, 23.3 mm. Brasil (Amazonas), Arquipélago das Anavilhanas, R. Negro left bank, igarapé (3°00'S 60°45'W). 1967.11.18. Leg. S. M. le roi Léopold de Belgique & J.-P. Gosse (IMA 1967: Sta. 179).  
 IRSNB 18.600 — 11 ♂, 23.0, 23.5, 27.2, 28.3, 28.7, 29.3, 30.9, 31.0, 31.3, 31.4, 31.7 mm; 8 ♀, 22.0, 24.0, 24.0, 24.9, 25.0, 25.1, 25.3, 26.8 mm. Brasil (Amazonas), Arquipélago das Anavilhanas, R. Negro left bank, igarapé (3°00'S 60°45'W). 1967.11.19. Leg. S. M. le roi Léopold de Belgique & J.-P. Gosse (IMA 1967: Sta. 180).  
 IRSNB 18.601 — 4 ♂, 24.0, 35.7, 37.1, 38.8 mm; ♀, 29.9 mm. Brasil (Amazonas), R. Preto da Eva, Igarapé Tapaiuna, igapo (3°08'S 59°18'W). 1964.01.28. Leg. G. Marlier (Sta. 186).  
 IRSNB 18.602 — 4 ♂, 29.7, 31.7, 35.5, 36.5 mm; 2 ♀, 26.1, 27.1 mm. Brasil (Amazonas), alto R. Preto da Eva (3°08'S 59°18'W). 1964.02.28. Leg. G. Marlier (Sta. 196).  
 SMF unreg. — ♀, 19.8 mm. Brasil (Amazonas), Manacapuru (3°16'S 60°37'W). 1925.07. Leg. W. Ehrhardt.

Specimens not included in the following description are: BMNH 1925.10.28: 404–410 (8 specimens, 22.1–25.0 mm, Lake at Manacapuru, Leg. W. Ehrhardt), BMNH 1925.10.28: 411–413 (4, 22.3–24.5, data as preceding), BMNH 1926.10.27: 476 (1, 31.1 mm, Monte Alegre, Leg. C. Ternetz), BMNH 1926.10.27: 478–487 (18, 23.3–33.8 mm, data as preceding), and a lesser number of aquarium specimens (BMNH, SMF, coll. Erik Åhlander, coll. Mark McMaster, pers. coll.).

## Description

Fresh material fine, older specimens rather poor.

Body elongate. Head elongate. Predorsal contour about straight, descending from between dorsal fin origin and middle of spinous dorsal fin base, very little arched. Preventral head contour about as steep, little curved. Snout short, rounded; dorsal profile slightly steeper, or profiles equal, convex, ventral concave or straight. Orbit tangential. Tip of maxilla exposed, to anterior margin of orbit or slightly behind. Preoperculum with 3–41 denticuli in 48 of 62 specimens.

Predorsal scales cycloid between orbits and along median to dorsal fin, sometimes a slightly broader band of cycloid predorsal scales. Posterior cheek and dorsal opercular, occasionally dorsal subopercular scales ctenoid. Squ. prd. 7–10; squ. prv. 6–8. No terminal pores in 3 upper lateral lines, 1–7 in the rest; 1–4 subserial pores in 86 of 106 lines. Lower line with anterior pores except in one line; only pores in some smaller specimens; 10 of 96 lines continued by one pore or canal on caudal fin. About 1/4 of caudal fin scaled; squ. caud. 4–9; outer cycloid.

Dorsal spines increasing in length to last. Lappets in adult males rather long, less than or about 1/2 spine lengths, but no individual lappets produced; in the largest IRSNB 18.601 males the posterior dorsal lappets united beyond spine tips; in females and young short, rounded. Soft part in adult males pointed, a short extension to beyond middle of caudal fin; in females and young pointed, to behind caudal fin base. Soft anal fin similar, slightly shorter. D. XIV.7(4), XIV.8(1), XV.6(5), XV.6.i(2), XV.7(44), XVI.6(5), XV.?(1).  $D_{tot}$  21(9), 22(52). A.III.4(1), III.5.i(5), III.6(47), III.6.i(6), III.7(2), III.?(1).  $A_{tot}$  7(1), 9(52), 10(8). Pectoral fin to vent. Ventral fin pointed, with much prolonged first ray in large males, to at most end of anal fin base, unextended in females and young, to about anal fin origin at most. Caudal fin in adult males roundish to almost lanceolate, ray 8 commonly longest, but no streamer; in females and young rounded.

Dentition biserial. In upper jaw an outer series of 40–50 teeth, and an inner nearly as long or half as long. In lower jaw an outer series of 40–55 teeth, an inner short, or, by scattered teeth, as long as outer; in some large specimens a few symphyseal teeth behind the inner series. In large individuals a notable strengthening of the anteriormost at least in upper jaw.

Colouration: Yellowish, paler ventrally. Markings brown. Back scales faintly dark-edged, more evident in large specimens. No traces of bars in adult males. Females with faint, dorsally and ventrally confluent Bars 2-7, broader than interspaces, which appear as pale spots above and below lateral band, particularly after Bars 2, 3, and 4. Slightly darker narrowly on back, close to dorsal fin base. Some IRSNB 18.600 males with female body colour pattern. Lateral band from moderately wide postorbital stripes, rather narrow, about 1 scale deep, to Bar 7, above lower lateral line. Lateral spot oblong, extended little above band.

Suborbital and superorbital stripes very faint. Pectoral spot small. No abdominal stripes. Occasionally a short midventral stripe in females. Caudal spot median, roundish (adult males) or vertically extended along fin base (females and young).

Dorsal fin not quite colourless, lappets brownish, an oblong dot near base of each membrane; up to 6 terminal spot-stripes in males, up to 4 in females. Not black anteriorly. Anal fin not quite colourless, basally whitish in males, 0–3 terminal spot-stripes. Caudal fin clear, in adult males up to 6 very weak vertical stripes of dots from margin to margin from base to distal end; in females and young up to 4 prominent stripes. Ventral fin white.

Table 18. Morphometry and meristics of *Apistogramma pertensis*. For explanation, see Tab. 5.

	n	Range	$\bar{x}$	$s(\bar{x})$	$s^2$
<b>M e a s u r e m e n t s</b>					
Head length	61	29.6— 37.2	32.8	0.16	1.48
Head depth	61	22.0— 26.8	24.3	0.12	0.85
Head width	60	12.6— 16.3	14.7	0.11	0.72
Body depth	61	26.0— 32.3	29.8	0.19	2.20
Orbit diameter	61	10.8— 15.2	12.9	0.10	0.57
Snout length	60	4.1— 7.6	6.4	0.09	0.46
Cheek depth	61	4.5— 6.8	5.5	0.07	0.31
Interorbital width	61	5.6— 7.0	6.3	0.04	0.09
Preorbital depth	56	1.9— 3.4	2.5	0.04	0.09
Dorsal base	59	54.8— 61.6	58.4	0.21	2.61
Anal base	57	15.9— 21.6	19.4	0.15	1.21
CP depth	61	11.7— 14.8	13.7	0.08	0.39
CP length	61	10.9— 14.7	12.9	0.09	0.53
Last D spine	54	11.7— 19.3	16.3	0.27	4.05
Last A spine	61	14.1— 19.6	16.7	0.18	2.04
CP/CP	61	77.8—123.5	94.6	0.86	44.80
<b>C o u n t s</b>					
Squ. long.	60	22—24	22.8	0.07	0.28
LI <sub>1</sub> (c)	58	7—14	11.6	0.16	1.55
LI <sub>1</sub> (cp)	58	11—16	14.4	0.12	0.81
LI <sub>2</sub> (c)	53	1— 7	3.7	0.18	1.69
LI <sub>2</sub> (cp)	55	6— 9	6.8	0.10	0.57
Cheek scales	61	1— 3	2.1	0.07	0.26
Squ. op.	32	9—14	11.3	0.21	1.42
Squ. sop.	48	3— 5	4.2	0.10	0.44
Squ. iop.	62	1— 3	2.5	0.08	0.38
D spines	62	14—16	15.0	0.05	0.16
D <sub>tot</sub>	61	21—22	21.9	0.05	0.13
A <sub>tot</sub>	61	7—10	9.1	0.06	0.19
P	62	11—12	11.8	0.05	0.19
Rakers	62	1— 3	1.9	0.08	0.38
Serrations	62	0—41	14.9	1.43	125.93

**Size**

The largest male is 38.8/53.0 mm, the largest female 29.9/39.7 mm long (both IRSNB 18.601).

**Geographical distribution**

Found on the left bank of the R. Amazonas and lower R. Negro near Manaus, Manacapuru, and Monte Alegre, and near Santarem on the right bank.

## Ecology

Limnological data for the Lago R. Preto da Eva were given by Marlier (1965, 1967), but *A. pertensis*, like most other *Apistogramma* spp., appears to prefer running water, and was not found by Marlier in the lake proper.

In the Anavilhanas igarapé it was found with *A. regani*, and the similar *A. gephyra*, at Manacapuru, in R. Preto da Eva creeks, and in Igarapé Mapiri with *A. agassizii*.

Small specimens from late November (14.5 mm; IRSNB 18.598, and FMNH 54169) may indicate reproduction in October near Manaus and Santarem.

## Remarks

Haseman (1911c) described this species as a variety (equivalent to subspecies in modern taxonomy) of *A. taeniata*. He was corrected by Regan (1913), and A. de Miranda Ribeiro (1918), who raised the variety to species rank. Neither Haseman nor A. de Miranda Ribeiro knew the true *A. taeniata* though. Fowler (1954) listed *pertensis* as a subspecies of *A. taeniata*. Regan (1913) considered *A. pertensis* close to *A. amoena*, but his specimens of the latter are the Ucayali specimens possibly close to *A. moae* (see p. 64, this paper). I see no reason at all to consider *A. pertensis* close to *A. taeniata* or to the *regani* group (including *A. taeniata* of Haseman and A. de Miranda Ribeiro). It is also clearly distinct from *A. bitaeniata*, once described as a variety of *A. pertensis*.

The recently discovered *A. iniridae*, *A. gephyra*, *A. pulchra*, *A. meinkenii*, and *A. uaupesi* instead appear to be its closest relatives. With these it has in common united posterior dorsal fin lappets, rounded caudal fin in males, naked throat, no black spot anteriorly in the dorsal fin, very elongate body shape, etc. (characters listed not found all in all species, though).

*A. pertensis* differs from *A. gephyra* in the unusually serrate preoperculum, fewer preventral scales (6–8 vs. 8–10), more  $L_2$  scales (6–9 vs. 2–6), colouration, etc. It differs very much from *A. pulchra* in colouration, but also in the narrower caudal peduncle (11.7–14.8 % of SL; 14.2–15.6 % in *A. pulchra*), etc. *A. meinkenii* and *A. uaupesi* are two deeper species, both with Bar 2 spot, the latter also without caudal spot. *A. iniridae* has a different colour pattern, is otherwise very similar, differing only insignificantly in meristics.

Unfortunately, it has been impossible to reexamine the holotype, but the species is easily recognized on Haseman's (1911c) plate.

*A. pertensis* is now and then described in aquarium literature, but I have seen no description or figure that is of the species here described. It has been imported as aquarium fish, however, as evidenced by specimens in the BMNH (1909.12.4:6, 1913.7.25:23, both ded. J. P. Arnold), SMF (unreg. ded. Troparium Frankfurt,

1956), and private collections listed above (U. S. and European imports). Goldstein's (1973) figure, p. 127, seems to show this species, but is apparently not of a captivated fish.

Meinken (1961a) indicated that this species is found in the Leticia region, but I strongly doubt that it is distributed so far upstream the R. Solimões.

*Apistogramma gephyra* sp. nov.

(Fig. 17)

**Holotype.** IRSNB (Types) 581 — ♂, 32.5 mm SL.

**Type-locality.** Igarapé affluent de la rive gauche du Rio Negro, dans l'Archipel das Anavilhanas, État d'Amazonas, Brésil. (3°00'S 60°45'W.)

**Diagnosis.** Head length 30.4–35.9 %, body depth 28.9–33.0 % of SL. CP length 77.8–95.0 % of CP depth. D. XV.6.i–8, XVI.6. A. III.6–7. Squ. long. 22–24. Rakers 1–2. Preoperculum entire. Dorsal fin without produced lappets. Caudal fin rounded (females) to slightly lanceolate (adult males). Lateral spot, occasionally small pectoral spot, occasionally midventral stripe present. No abdominal stripes or caudal spot. Bars at most as traces, in females. No chest blotch. Dorsal fin not dark anteriorly. Caudal fin with a stripe along middle rays, interrupted in females; dark distal margin in males. (18 specimens of both sexes, 17.5–32.5 mm SL).

**Etymology.** *gephyra* (Greek noun), a bridge, with reference to the superficial morphological intermediacy between *A. agassizii* and *A. pertensis*, belonging to different groups of species.

**Material**

**Holotype.** IRSNB (Types) 581 — ♂, 32.5 mm. Brasil (Amazonas), Arquipélago das Anavilhanas, R. Negro left bank, igarapé (3°00'S 60°45'W). 1967.11.18. Leg. S. M. le roi Léopold de Belgique & J.-P. Gosse (IMA 1967: Sta. 179).

**Paratypes.** IRSNB (Types) 582 — 3 ♂, 27.0, 28.4, 29.3 mm; 3 ♀, 17.5, 26.2, 27.4 mm. Same data as holotype.  
IRSNB (Types) 583 — 4 ♂, 25.6, 26.0, 28.5, 29.1 mm; 4 ♀, 18.9, 19.7, 22.7, 24.0 mm. Brasil (Amazonas), Arquipélago das Anavilhanas, R. Negro left bank, igarapé (3°00'S 60°45'W). 1967.11.19. Leg. S. M. le roi Léopold de Belgique & J.-P. Gosse (IMA 1967: Sta. 180).

**Specimens.** IRSNB 15.791 — ♂, 25.2 mm; 2 ♀, 18.7, 19.8 mm. Brasil (Pará), Lago Jurucuí, Igarapé Grande (2°30'S 54°56'W). 1963.12.06. Leg. G. Marlier (Sta. 147).

**Description**

The type-series is in fine condition, the small Igarapé Grande specimens acceptable.



Fig. 17. Holotype of *Apistogramma gephyra*.

Body moderately elongate. Head moderately elongate. Predorsal contour almost straight descending from dorsal fin origin. Preventral head contour less or as steep as predorsal contour. Snout rounded, profiles equal, convex, or ventral concave. Orbit subtangential. Tip of maxilla exposed, to slightly behind anterior margin of orbit. Preoperculum entire.

Predorsal scales cycloid laterally posteriorwards to line between dorsal fin origin and about preoperculum dorsal tip. Dorsal or most opercular, posterior cheek, occasionally dorsal subopercular scales ctenoid. Squ. prd. 9–10; squ. prv. 8–10. Upper lateral line with terminal pores except in 6 lines, 1–3 subserial pores in 9, a subsubserial in 1, of 34 lines. Anterior pores in lower lateral line except in 2 lines; a caudal canal or pore in 5 of 30 lines.  $1/4$  to more than  $1/3$  of caudal fin scaled; squ. caud. 3–9; outer cycloid or all ctenoid.

Dorsal spines increasing in length to last. Lappets moderate, pointed, none produced. Soft part pointed, without extension to  $1/3$  of caudal fin (females); little produced, to at most middle of caudal fin (males). Soft anal fin similar, to  $1/3$  of caudal fin. D. XV.6.i(1), XV.7(11), XV.7.i(1), XV.8(2), XVI.6(3; IRSNB 15.791).  $D_{\text{tot}}$  22(15), 23 (3). A. III.6(12), III.6.i(1), III.7(4), III.?(1).  $A_{\text{tot}}$  9(12), 10(5). Pectoral fin to vent. Ventral fin pointed, unextended in females, in males first ray slightly produced, to at most soft anal fin origin. Caudal fin rounded in young and females; in large males middle rays slightly prolonged (gives lanceolate fin shape), but by far not so much as in *A. agassizii*.

Dentition in upper jaw biserial: an outer series of about 50–60 teeth, an inner of varying lengths, at most nearly as long as the outer. Triserial dentition in lower

jaw: an outer series of 40–60 teeth, an inner little more than symphyseal, a middle very short, symphyseal.

Colouration: Yellowish brown, with brown markings. No conspicuous dark-edging of scales. Bars absent in males, in females very faint, apparent only from inconspicuous pale spots above and below lateral band. Nape, back close to dorsal fin, and basal dorsal fin, dark. Lateral band in males from moderately wide postorbital stripe,  $1-1\frac{1}{2}$  scale wide, broadening to lateral spot, posteriorly uniformly wide, more intense anteriorly, to middle of caudal peduncle, above and on lower lateral line. In females postorbital stripe inconspicuous, lateral band somewhat narrower than in males, not more intensely pigmented before lateral spot. Lateral spot roundish, in females little extended above band, not in males.

Table 19. Morphometry and meristics of *Apistogramma gephyra*. For explanation, see Tab. 5.

	n	Range	$\bar{x}$	$s(\bar{x})$	$s^2$
<b>M e a s u r e m e n t s</b>					
Head length	18	30.4–35.9	32.3	0.36	2.30
Head depth	18	23.2–26.3	24.4	0.19	0.67
Head width	18	14.3–16.2	15.2	0.12	0.27
Body depth	18	28.9–33.0	31.0	0.28	1.38
Orbit diameter	18	11.6–13.4	12.3	0.12	0.25
Snout length	18	5.1– 7.0	6.1	0.11	0.22
Cheek depth	18	4.2– 6.8	5.6	0.15	0.43
Interorbital width	18	6.0– 8.0	6.8	0.12	0.27
Preorbital depth	18	1.7– 2.4	2.1	0.04	0.02
Dorsal base	18	56.3–61.8	59.3	0.36	2.39
Anal base	17	17.6–21.5	19.4	0.22	0.82
CP depth	18	13.6–15.8	14.6	0.14	0.38
CP length	18	11.1–14.6	12.9	0.16	0.47
Last D spine	15	13.7–17.9	15.7	0.29	1.30
Last A spine	18	15.1–17.9	16.3	0.16	0.48
CP/CP	18	77.8–95.0	88.1	1.00	18.17
<b>C o u n t s</b>					
Squ. long.	17	22–24	22.9	0.10	0.18
L <sub>1</sub> (c)	17	10–16	12.8	0.39	2.57
L <sub>1</sub> (cp)	18	13–16	14.6	0.20	0.73
L <sub>2</sub> (c)	17	2– 6	4.2	0.31	1.65
L <sub>2</sub> (cp)	17	6– 7	6.5	0.12	0.26
Cheek scales	18	1– 3	2.3	0.16	0.45
Squ. op.	10	11–12	11.5	0.16	0.28
Squ. s <sub>op</sub> .	15	3– 6	4.5	0.19	0.55
Squ. i <sub>op</sub> .	18	2– 3	2.9	0.06	0.06
D spines	18	15–16	15.2	0.09	0.15
D <sub>tot</sub>	18	22–23	22.2	0.09	0.15
A <sub>tot</sub>	17	9–10	9.3	0.11	0.22
P	18	11–12	11.5	0.12	0.26
Rakers	18	1– 2	1.2	0.09	0.15
Serrations	18	0	0.0		

Suborbital stripe across cheek, rather faint; superorbital as trace. Pectoral spot small, faint, not in all specimens. No abdominal stripes and no caudal spot. A faint narrow midventral stripe in some specimens.

Dorsal fin dusky, base darker; lappet tips white in males; anterior membranes not dark; about 3 terminal spot-stripes; edge of soft part darkened. Anal fin whitish to clear, with dark seam. Caudal fin clear; continuation of lateral band, fainter and narrower posteriorwards, along middle part, to end of fin in males, in females broken up into bars, particularly intense near base of fin, up to 6, wider than interspaces. In males also up to 6 spot-stripes across middle caudal fin rays, near middle band; edges of rays dark. One IRSNB 583 male lacks caudal fin cross-stripes and dark edge. Ventral fin white.

### Size

The largest male (holotype) is 32.5/46.1 mm, the largest female (IRSNB 582) 27.4/36.8 mm long.

### Geographical distribution

Known from the type-locality in the Arquipélago das Anavilhanas, and Lago Jurucuí near Santarem.

### Ecology

Found together with *A. regani* and *A. pertensis* in the Anavilhanas creek. The Lago Jurucuí, a small clear water lake, was described briefly by Marlier (1965, 1967), but *A. gephyra* obviously does not occur in the lake proper.

### Remarks

Superficially this species may be taken for a slightly aberrant *A. agassizii*, but it appears rather to be related to *A. pertensis*, to which it is also very similar. It differs slightly from both these species in colouration, and also meristically and morphometrically but slightly. From *A. pulchra* it is well separated by the longer dorsal fin base (56.3–61.8 % of SL,  $\bar{x}$  = 59.3 %; in *A. pulchra* 55.1–57.8 %,  $\bar{x}$  = 56.2 %). I here place it with *A. pertensis* for reason of the lack of dorsal fin spot, and the few chest scales, but the relationships remain somewhat obscure.

*Apistogramma pulchra* sp. nov.

(Fig. 18)

**Holotype.** IRSNB (Types) 584 — ♂, 32.2 mm SL.

**Type-locality.** Rio Preto, affluent de la rive gauche du Rio Candeias à 25 km de Porto-Velho, Territoire du Rondonia, Brésil. (8°46'S 63°45'W.)

**Diagnosis.** Head length 31.6–33.7 %, body depth 28.6–31.6 % of SL. CP length 80.4–96.3 % of CP depth. D. XIV.7–8, XV.7–8, XVI.7. A. III.6–7. Squ. long. 23. Rakers 1–2. Preoperculum entire. Dorsal fin without produced lappets. Caudal fin rounded. Lateral spot, small pectoral spot, occasionally midventral stripe present. No abdominal stripes or caudal spot. No bars. No chest blotch. Dorsal fin not dark anteriorly. Caudal fin colour pattern varying; immaculate, up to 5 vertical spot-stripes on dorsal lobe, or about 6 stripes on middle; dark-seamed. (8 males, 21.4–32.2 mm SL, 1 female, 19.0 mm SL.)

**Etymology.** *pulchra* (Lat., adj.), handsome, in allusion to the carefully blended colour pattern and the slender body shape.

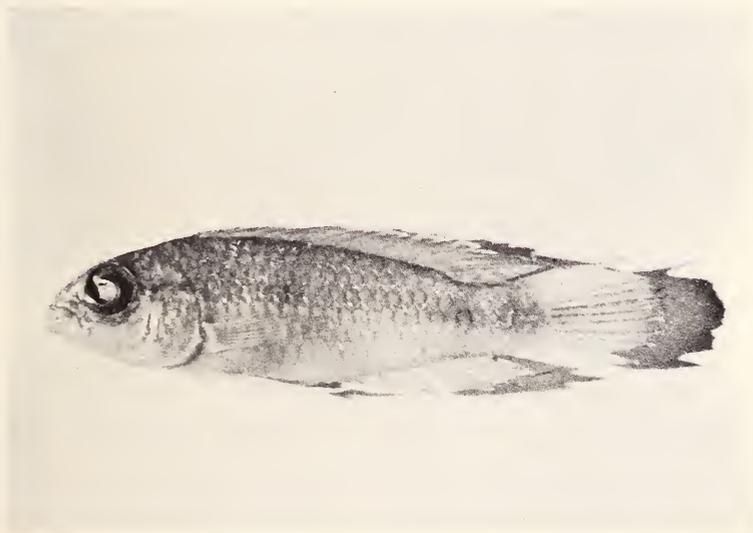


Fig. 18. Holotype of *Apistogramma pulchra*.

**Material**

**Holotype.** IRSNB (Types) 584 — ♂, 32.2 mm. Brasil (Rondônia), R. Preto (8°46'S 63°45'W). 1967.11.24. Leg. S. M. le roi Léopold de Belgique & J.-P. Gosse (IMA 1967: Sta. 182).

**Paratypes.** IRSNB (Types) 585 — 7 ♂, 21.4, 25.5, 26.0, 26.4, 27.6, 29.4, 31.2 mm; ♀, 19.0 mm. Same data as holotype.

## Description

All specimens in excellent condition.

Body elongate. Head moderately elongate. Predorsal contour gently curved, descending from dorsal fin origin, steeper on snout. Preventral head contour less steep, about straight or gently arched. Snout rounded, rather broad, dorsal profile steeper, arched, ventral more or less concave. Orbit tangential. Tip of maxilla exposed, to anterior margin of orbit or slightly behind. Preoperculum entire.

Predorsal scales cycloid, laterally posteriorwards to vertical from preoperculum vertical edge. Opercular and posteriormost cheek scales ctenoid. Squ. prd. 9–10; squ. prv. 9–10. Upper lateral line usually with 1–2 terminal pores, and occasionally 1–2 subserial pores or canals; lower with (0)1–3 pores; a caudal pore on one side in one specimen. 1/5 to 1/4 of caudal fin scaled; squ. caud. 4–5; all ctenoid.

Dorsal spines subequal from 7th, increasing in length to last. Lappets moderately long, more or less truncate. Soft part pointed, in the largest male prolonged, 2nd or 3rd ray to almost caudal fin end; to 1/3 of caudal fin or less, without elongation, in the smaller specimens. Soft anal fin similar, but shorter. D. XIV.7(1), XIV.8(2), XV.7(4), XV.8(1), XVI.7(1).  $D_{\text{tot}}$  21(1), 22(6), 23(2). A. III.6(6), III.6.i(1), III.7(2).  $A_{\text{tot}}$  9(6), 10(3). Pectoral fin to about vent. Ventral fin pointed, short prolongation of first ray to middle of soft anal fin base at most. Caudal fin rounded.

Dentition biserial in both jaws. The outer series of 40–50 teeth, the inner short, little more than symphyseal. Anteriormost teeth notably stronger and well spaced.

Colouration: Yellowish, somewhat darker dorsally, with brown markings and conspicuously dark-rimmed scales. No bars, but in the female hardly apparent light spots along band above and below, reflecting bar interspaces. Back dark along dorsal fin base, broadening rostrally to nape, not or only little extended into dorsal fin base (*A. agassizii* back pattern). Lateral band from narrow postorbital stripe, 1 scale deep to lateral spot, posteriorly 1½–2 scales deep into caudal fin on middle rays narrowing, not past middle of fin length. Scale edges conspicuously dark also in band. Band almost vanished in the two largest specimens.

Suborbital stripe absent or a very pale ill-defined spot below the eye; superorbital stripe in the smallest specimen only. Pectoral spot small. No abdominal stripes. A midventral stripe in one male only. No caudal spot.

Dorsal fin dusky, lappets clear; soft part clear or dusky, edge clear; not black on anterior membranes. Anal fin clear to whitish, dusky-seamed. Caudal fin dark-

seamed as in *A. gephyra*, but narrower. Three types of caudal fin pattern: a) up to 5 ill-defined vertical spot-stripes on dorsal half near middle in upper lobe, b) immaculate, c) about 6 bars along middle, continuing band continuation and broader than it. Ventral fin white.

## Size

The holotype is the largest male known, 32.2/43.9 mm long. The only female is 19.0/26.8 mm in length.

Table 20. Morphometry and meristics of *Apistogramma pulchra*. For explanation, see Tab. 5.

	n	Range	$\bar{x}$	$s(\bar{x})$	$s^2$
<b>Measurements</b>					
Head length	9	31.6–33.7	32.6	0.21	0.40
Head depth	9	24.2–26.1	25.1	0.23	0.47
Head width	9	14.4–16.8	15.4	0.26	0.59
Body depth	9	28.6–31.6	30.0	0.28	0.73
Orbit diameter	9	12.1–14.2	12.8	0.21	0.41
Snout length	9	5.9– 7.2	6.7	0.16	0.23
Cheek depth	9	5.1– 5.8	5.6	0.08	0.05
Interorbital width	9	6.3– 7.1	6.7	0.09	0.07
Preorbital depth	9	1.9– 2.3	2.1	0.05	0.03
Dorsal base	9	55.1–57.8	56.2	0.33	1.00
Anal base	9	16.7–20.2	18.2	0.35	1.11
CP depth	9	14.2–15.6	14.9	0.15	0.21
CP length	9	11.9–14.1	13.3	0.23	0.49
Last D spine	9	14.2–18.0	16.4	0.49	2.12
Last A spine	9	14.6–17.3	15.7	0.30	0.81
CP/CP	9	80.4–96.3	89.2	1.97	34.85
<b>Counts</b>					
Squ. long.	8	23	23.0		
Ll <sub>1</sub> (c)	8	12–15	12.9	0.35	0.98
Ll <sub>1</sub> (cp)	8	13–15	14.4	0.26	0.55
Ll <sub>2</sub> (c)	8	4– 6	4.6	0.26	0.55
Ll <sub>2</sub> (cp)	8	6– 8	7.0	0.27	0.57
Cheek scales	9	2– 3	2.8	0.15	0.19
Squ. op.	8	8–12	10.6	0.46	1.70
Squ. sop.	9	4– 6	5.0	0.24	0.50
Squ. iop.	9	2– 3	2.6	0.18	0.28
D spines	9	14–16	14.8	0.22	0.44
D <sub>tot</sub>	9	21–23	22.1	0.20	0.36
A <sub>tot</sub>	9	9–10	9.3	0.17	0.25
P	9	11	11.0		
Rakers	9	1– 2	1.1	0.11	0.11
Serrations	9	0	0.0		

## Geographical distribution

Known but from the type-locality, a small river tributary of the R. Candeias, itself a tributary of the R. Madeira, near Pôrto Velho.

## Remarks

This is the first species in the genus to be reported with certainty from the R. Madeira system in Brazil. Several species are known from the Bolivian tributaries and the R. Guaporé, however, e.g. *A. Juelingi* in the R. Chapare (Kullander, 1976), and *A. trifasciata* in the R. Guaporé (e.g. Haseman, 1911c).

Its characters place it in the *pertensis* group, but it is distinguished from its closest relatives there by the colour pattern, rather few dorsal spines (14–16,  $\bar{x} = 14.8$ ; 14–16,  $\bar{x} = 14.9$  in the others), etc. (see also pp. 96, 130, and 134).

*A. trifasciata* is closest geographically (a sample from Igarapé de Palheta, above Guajará-Mirim, R. Mamoré, IRSNB 18.603), but it is morphologically distinct (produced dorsal fin lappets in males, more robust shape, a stripe obliquely between pectoral and anal fins).

### *Apistogramma roraimae* sp. nov.

(Fig. 19)

**Holotype.** IRSNB (Types) 565 — ♀, 20,5 mm SL.

**Type-locality.** Igarapé Uazinho à environ 10 km de Boa Vista sur la route Boa Vista — Caracarai, Territoire du Rio Branco, Brésil. (2°49'N 60°40'W.)

**Diagnosis.** Head length 31.7–36.3 %, body depth 32.2–37.6 % of SL. CP length 73.7–83.9 % of CP depth. D. XV.6.i–7. A. III.6–7. Squ. long. 22–23. Rakers 1–2. Preoperculum entire. Dorsal fin without produced lappets. Caudal fin rounded. Lateral spot present. No pectoral spot, abdominal stripes, midventral stripe, caudal spot, bars or chest blotch. Dorsal fin not dark anteriorly. Caudal fin immaculate except for lateral band continued on middle rays. (5 specimens of both sexes; 18.3–23.4 mm SL.)

**Etymology.** *roraimae* for the Território Roraima (Rio Branco).

## Material

**Holotype.** IRSNB (Types) 565 — ♀, 20.5 mm. Brasil (Roraima), 10 km on road Boa Vista — Caracarai, Igarapé Uazinho (2°49'N 60°40'W). 1962.11.29. Leg. J.-P. Gosse (IMA 1962: Sta. 21).

**Paratypes.** IRSNB (Types) 566 — sex indet., 18.3 mm. Same data as holotype.  
IRSNB (Types) 588 — ♂, 23.4 mm; ♀ 18.6 mm. Brasil (Roraima), 4 km west of road Boa Vista — Caracarai, small temporary pool (2°49'N 60°40'W). 1962.11.29. Leg. J.-P. Gosse (IMA 1962: Sta. 22).  
IRSNB (Types) 589 — sex indet., 19.9 mm. Brasil (Roraima), Boa Vista, R. Mucajai left bank, Igarapé Bucabal (2°49'N 60°40'W). 1962.11.29. Leg. J.-P. Gosse (IMA 1962: Sta. 23).



Fig. 19. Holotype of *Apistogramma roraimae*.

## Description

The condition leaves something to be desired. All specimens have had their belly cut and the viscera removed, and the colouration is rather faded. The holotype is apparently a breeding female judging from the swollen genital papilla and the more contrasting colouration, especially the black ventral fins. The larger male has had its branchial apparatus demolished, and was thus less suitable as reference specimen.

Body moderately elongate. Head moderately deep. Predorsal contour very little arched or straight from dorsal fin origin or occiput, an inconspicuous notch between orbits. Preventral head contour about as steep, arched. Snout rather short, rounded, profiles about equal. Orbit tangential. Tip of maxilla exposed, to about anterior margin of orbit. Preoperculum entire.

Predorsal scales cycloid, laterally posteriorwards to between preoperculum and dorsal fin origin, beyond latter 4 scales close to dorsal fin base. Dorsal opercular and posterior cheek scales ctenoid. Squ. prd. 9–10; squ. prv. 8 (possible to

count in holotype only). Upper lateral line with 1–3 terminal pores except on one side in one specimen; 1–2 subserial pores on one side in two specimens; 0–5 pores in lower line; no caudal fin pores or canals.  $1/5 - 1/4$  of caudal fin scaled; squ. caud. 3–4; all ctenoid or outer cycloid.

Dorsal spines subequal in length from 4th or 5th, the last longest. Lappets moderately long, pointed. Soft part pointed, without prolongation, to little behind caudal fin base. Soft anal fin similar. D. XV.6.i(2), XV.7(3).  $D_{tot}22(5)$ . A. III.6(4), III.7(1).  $A_{tot}9(4)$ , 10(1). Pectoral fin to vent. Ventral fin pointed, first ray not produced, to anal fin origin at most. Caudal fin rounded.

Table 21. Morphometry and meristics of *Apistogramma roraimae*. For explanation, see Tab. 5.

	n	Range	$\bar{x}$	$s_{(\bar{x})}$	$s^2$
<b>M e a s u r e m e n t s</b>					
Head length	5	31.7–36.3	34.2	0.90	4.05
Head depth	5	26.3–27.7	27.2	0.24	0.27
Head width	5	16.1–17.2	16.4	0.21	0.22
Body depth	5	32.2–37.6	34.8	0.95	4.54
Orbit diameter	5	12.6–13.4	13.0	0.15	0.12
Snout length	5	5.9– 6.8	6.2	0.18	0.17
Cheek depth	5	5.5– 7.3	6.1	0.31	0.47
Interorbital width	5	7.5– 8.1	7.8	0.10	0.05
Preorbital depth	5	2.0– 2.2	2.1	0.04	0.01
Dorsal base	5	55.2–59.5	57.3	0.85	3.62
Anal base	5	18.3–21.4	19.5	0.52	1.37
CP depth	5	15.1–16.2	15.7	0.22	0.23
CP length	5	12.0–12.9	12.6	0.15	0.11
Last D spine	3	12.7–15.1	13.6	0.74	1.65
Last A spine	5	12.7–15.6	14.6	0.55	1.50
CP/CP	5	73.7–83.9	80.1	1.73	14.91
<b>C o u n t s</b>					
Squ. long.	5	22–23	22.8	0.20	0.20
Ll <sub>1</sub> (c)	5	12–14	12.4	0.40	0.80
Ll <sub>1</sub> (cp)	5	13–15	14.0	0.45	1.00
Ll <sub>2</sub> (c)	4	1– 4	3.3	0.75	2.25
Ll <sub>2</sub> (cp)	4	6– 8	6.5	0.50	1.00
Cheek scales	5	2– 3	2.8	0.20	0.20
Squ. op.	4	8– 9	8.3	0.25	0.25
Squ. sop.	3	3– 4	3.3	0.33	0.33
Squ. iop.	5	3	3.0		
D spines	5	15	15.0		
$D_{tot}$	5	22	22.0		
$A_{tot}$	5	9–10	9.2	0.20	0.20
P	5	11–12	11.2	0.20	0.20
Rakers	4	1– 2	1.8	0.25	0.25
Serrations	5	0	0.0		

Dentition biserial in both jaws, outer series of about 40 teeth, inner little more than symphyseal.

Colouration: Apparently faded, whitish yellow, markings brown. No bars, but not confluent spots very close to and little into dorsal fin base. Lateral band from moderate postorbital stripe, broadening to lateral spot, behind it about 1 scale deep; lower edge sharp; to caudal fin base, above and on lower lateral line. Lateral spot round, not outside band, very intensely pigmented.

Suborbital stripe straight, moderately wide; superorbital stripe faint. No pectoral spot, abdominal stripes, midventral stripe or caudal spot.

Fins clear or almost clear. Dorsal fin not dark anteriorly. In the holotype very weak cross stripes on middle of caudal fin, and anterior ventral fin membranes black. Indistinctly a continuation of lateral band on basal caudal fin.

### Size

The largest specimen recorded is a male 23.4/32.6 mm (IRSNB 588), the largest female 20.5/27.8 mm (holotype).

### Geographical distribution

Known only from a restricted area in the Roraima territory near Boa Vista.

### Ecology

The type-series was collected in late November in igarapés and a small temporary pool. The holotype, a 20.5 mm female, is probably in breeding condition (strong pigmentation, swollen genital papilla).

### Remarks

The relationships are obscure. It is a rather deep species, but it lacks bars and dorsal fin spot. It is also the first and still only species to be reported from the R. Branco system. Eigenmann (1912) found *A. steindachneri* in the R. Ireng, a source river of the R. Branco, but that species is essentially Guianan, and so far not found further downstream in the R. Branco. It is true, however, that the R. Branco is one of the least collected rivers in South America, and it is hardly possible to discuss seriously its fish fauna at the moment. *A. steindachneri* differs considerably from *A. roraimae* in fin shape and colouration.

The sexed individuals appear sexually mature, and this species may be the smallest in the genus, and as such the smallest cichlid species, although maturity is no criterion of maximum size.

### Supplementary descriptions

#### *Apistogramma taeniata*

*Mesops taeniatus* Günther, 1862. Catal. Fish Brit. Mus. 4: 312.

**Holotype.** BMNH 1853.3.19: 71 — ♂, 42.1 mm. "Rio Cupai. Bates". [Brasil (Pará), R. Cupari. 1852. Leg. H. W. Bates.]

The holotype and only known specimen is a very old and poorly preserved fish which has lost its colours and most of its scales. The fins are also so damaged that their shape cannot be determined. The following brief description may be given, with additional data from Günther (1862) in parenthesis: Head length 33.5 %, head depth 27.8 %, head width 15.2 %, body depth 34.9 %, orbit diameter 11.9 %, snout length 5.5 %, cheek depth 9.0 %, interorbital width 9.3 %, preorbital depth 3.5 %, CP depth 15.7 %, CP length 15.4 %, dorsal base 63.2 %, anal base 21.0 %, D spine 24.7 %, A spine 18.3 % of SL. Cheek scale series 3, squ. long. (est.) 23, D.XV.6, A. III.6, P. 12, rakers 3, serrations 0.

Head rounded; predorsal contour straight descending to above middle of orbit, steep on snout; preventral head contour gently arched, less steep. Snout blunt; mouth subinferior; maxilla angle less than 45°; tip of maxilla exposed, to middle of orbit. No produced dorsal fin lappets; dorsal spines increasing in length to last. (Caudal fin rounded.) (Brownish, a black band along the middle of the side to caudal spot; suborbital and preorbital stripes present.)

In Regan's (1906a) description is also indicated a postorbital stripe and stated that the first 3 dorsal spines are blackish, and the vertical fins more or less distinctly spotted. A faint, vertically extended caudal spot, a narrow preorbital stripe, a broad suborbital stripe to inner edge of preoperculum angle, 2 terminal spot-stripes in the dorsal and anal fins, and a dark ventral fin spine remain of the colouration now.

The dentition is triserial; the outer series of upper jaw of about 52 teeth, the innermost short, the middle symphyseal; the outer series of lower jaw of about 42 teeth, the innermost as long, the middle teeth almost symphyseal, irregular, rather forming two middle series.

The very long last dorsal spine, rather deep cheek, wide interorbital, and snout and mouth shape obviously place this species apart from all other members of the genus of which it is the type-species. It is very desirable to collect again at the type-locality to find fresh specimens that may allow a redescription of the species.

#### "*Apistogramma*" *amoena*

*Geophagus amoenus* Cope, 1872. Proc. Acad. nat. Sci. Philadelphia 23:250.

**Holotype.** Lost (W.G. Saul, in litt. 1977). Loc. River Ambyiacu [= R. Ampí-yacú, Departamento Loreto, Perú].

The brief, incomplete, partly seemingly impossible description given by Cope of what apparently was only one specimen, embodies our total knowledge of this species. Although stated by Cope to be allied to *A. taeniata*, and assigned to *Apistogramma* (or equivalent taxon) by later authors, it cannot even be taken for granted that it is a species of this genus. Cope was not particularly reliable in his assignments of his specimens to genera (e.g. *Geophagus badiipinnis* Cope, 1872 = *Chaetobranchius flavescens*; *Uarus centrarchoides* Cope, 1872 = *Cichlasoma severum*; *Acara compressus* Cope, 1872 = *Astronotus ocellatus*).

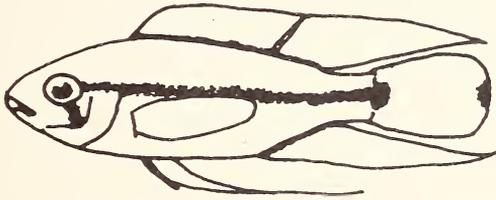


Fig. 20. An attempt to draw a figure of the holotype of *Geophagus amoenus*, on basis of Cope's (1872) data. Approximately natural size.

If it is an *Apistogramma* species, it appears most likely to be an elongate species, but no such is known with 25 scales in a longitudinal series (may include caudal fin scales [Steindachner, 1875]), a preorbital depth 50 % of the orbit diameter, immaculate fins except a black spot at tip of caudal fin, and is not to be expected to exist. With some imagination the description could be taken for one of an *A. cacatuoides* male with the caudal fin ocellus representing the caudal fin tip spot. But *A. cacatuoides* males have a fin shape that surely would not have passed Cope unnoticed. Very probably his specimen had no dorsal fin lappets or caudal rays produced, but was also very probably a male (dorsal and anal fins with prolonged rays to beyond caudal fin, ventral fin beyond base of anal fin). Fig. 20 is an attempt to reconstruct Cope's fish on basis of his description, but not, for convenience, exactly true to it. It is asserted in the reconstruction that the specimen represents an *Apistogramma* species, otherwise the result would have looked quite different.

In Cope's description there is much that reminds of an *Apistogramma* species, but of no particular, and not definitely, and no other genus in particular is indicated. Alone new collections from the R. Ampí-yacú will possibly show what genus and species Cope intended. Until such an effort has been made, the name *G. amoenus* should not be given up.

*Apistogramma parva*

*Apistogramma parva* Ahl, 1931. Sber. Ges. natf. Freunde Berlin, 1931:210.

**Holotype.** ZMB 23410 — sex indet., 15.8 mm. "Rio Capim." [Brasil (Pará), R. Capim. Late 1928?. Leg. H. Böker.]

The status of this taxon must remain uncertain till more collecting has been made in the R. Capim. The holotype and only known specimen is a juvenile fish, probably representing an elongate species.

There are no traces of bars, but that may be due to fading. A faint lateral band to caudal fin base, still fainter continued on caudal fin, a roundish lateral spot, and head stripes make up the colour pattern. Ahl, while the specimen was fresher, observed also about 8 to 9 very obscure dark transverse bars, and a spot, less apparent than the lateral spot, behind the gill-cover. There are no cheek scales; squ. long. 24; Ll counts 8/1 (right side), and 10/1 (left side); D. XVI.4.ii; A. III.4.ii; P. 12; 1 raker.

*Apistogramma sweglesi*

*Apistogramma sweglesi* Meinken, 1961. Aquar. Terr. Z. 14: 136.

**Holotype.** Lost? — ♂, 50 mm Körperlänge. "bei Letitia in Peru" [Leticia, Comisaria Amazonas, Colombia. 1960?.] Leg. K. Swegles. Ded. E. Schmidt-Focke. (Data from Meinken, 1961a).

According to Meinken (1961a), the type-material (including also 2 paratypes) would be sent to the Zoologisches Staatsinstitut in Hamburg (= ZIMH) after the appearance of the description. But they are not there (H. Wilkens, in litt. 1977), and obviously they remained in Meinken's personal collection at least till January 1966 (H. Meinken, in litt. to W. Ladiges, 1966), when the trace is lost. According to Meinken all his *Apistogramma* were eventually sent to the SMF (in litt. 1976), but the specimens described by Meinken in 1961 (also his *A. borellii* in 1961b), are apparently not there either.

I am optimistic about finding the type-specimens again, and believe that a discussion of the species must wait till they have been restudied. Meinken's description is not of much use. It suggests that his species is based on over-size import specimens of *A. bitaeniata*, the head of the holotype deformed, but is not sufficient for a definite decision.

*Apistogramma ambloplitoides*

*Apistogramma ambloplitoides* Fowler, 1940. Proc. Acad. nat. Sci. Philadelphia 91: 281.

**Holotype.** ANSP 68681 — ♂?, 77.4 mm. Ucayali River basin, Contamana, Peru, 1937.07—08. Leg. W. C. Morrow.

Fowler's data are on the whole confirmed by the reexamination of the holotype. However, it is apparent from the description and the figure that this is no *Apistogramma* species, and the reexamination shows clearly that it is a small specimen of *Acaronia nassa* (Heckel, 1840).

## 5. SUMMARY

This study deals with the taxonomic history, nomenclature, generic characteristics, geographical distribution, and relationships of the South American cichlid genus *Apistogramma* Regan, 1913. 18 species are described, 12 of which are new, and notes are given on four additional species.

The genus contains more than 40 species, 36 of which are formally recognized as valid with this paper. The distribution includes the Amazonas, Paraguay, and Orinoco basins, the Guianas, and the East Brazilian rivers Caeté, Apeu, Capim, and Parnaíba. All species are small, the largest specimen known a 63 mm standard length male of *A. steindachneri*. Diagnostic characters are (in combination): presence of gill-rakers on the sides of the lower pharyngeal tooth-plate; a compressed lobe on the first epibranchial, with rakers on its edge; 3, rarely 4 or 6, anal spines; 14—18 dorsal spines. Morphological characteristics of the genus, in particular the epibranchial lobe, gill-arches and colour pattern, are described at length. The genus is related to *Apistogrammoides*, and belongs to the group of genera called the geophagines. The gender of the name is feminine. *Pintoichthys* is considered to be a junior subjective synonym.

*A. agassizii*, *A. bitaeniata*, *A. geisleri*, *A. gibbiceps*, *A. cacatuoides*, and *A. pertensis* are described. *A. kleei* and *A. klausewitzi* are junior subjective synonyms of *A. bitaeniata*. The type-locality of *A. bitaeniata* is emended to "environments of Letícia", that of *A. cacatuoides* to "R. Amazonas basin between 69° and 71°W". A lectotype is designated for *A. agassizii* and for *A. bitaeniata*. Five species are described as new from the R. Uaupés: *A. uaupesi*, *A. meinkeni*, *A. personata*, *A. elizabethae*, and *A. brevis*. Other new species are from the R. Branco (*A. roaimae*), the R. Moá (*A. moae*), the R. Madeira (*A. pulchra*), the R. Caeté and Apeu (*A. caetei*), the R. Parnaíba (*A. piauiensis*), or the R. Amazonas (*A. regani*, *A. gephyra*). Notes are given on *A. taeniata*, *A. amoena* (holotype lost), *A. parva*, and *A. sweglesi* (type-series lost), the status of which are uncertain. Most species can be assigned to one of 7 species groups that are defined.

## 6. ZUSAMMENFASSUNG

Die Studie enthält die taxonomische Geschichte, Nomenklatur, Gattungsmerkmale, geographische Verbreitung und die verwandtschaftlichen Beziehungen der Gattung *Apistogramma* Regan, 1913. Die Gattung umfaßt mehr als 40 Arten. 38 davon sind in der vorgelegten Arbeit erfaßt. Davon wurden 24 Arten früher genannt, 12 Arten sind neu, und zwei Arten sind noch nicht beschrieben worden.

Die Gattung zeichnet sich durch folgende Merkmalkombination aus: An den Seiten der unteren Schlundknochen sind Kiemenrechen vorhanden. Ein komprimierter Anhang sitzt am oberen Teil des ersten Kiemenbogens. Die Afterflosse besitzt 3, selten 4 oder 6 Stacheln. 14 bis 18 Stacheln trägt die Rückenflosse. 9 Arten haben gezähnte Präopercularknochen wie *Papiliochromis* Kullander. Die Kieferzähne sind in 2 bis 4 Reihen angeordnet, von denen die äußere meistens 60 Zähne trägt. Der Epibranchialanhang ist aus einem Fortsatz des ersten Epibranchiale gebildet. Er ist nicht mit dem sogenannten "hanging pad" einiger afrikanischer Cichliden identisch, dessen Knochenkern ein Fortsatz des zweiten Epibranchiale ist. Weiter-

hin ist die Gattung mit einem Supraneurale und 22 bis 24 Rückenwirbeln ausgestattet. Dunkle Elemente im Farbmuster sind die folgenden: 7 senkrechte Binden, eine horizontale Seitenbinde, ein Fleck auf der Kreuzung von 3. senkrechter Binde und horizontaler Seitenbinde, ein schwarzer Fleck über der Basis der mittleren Schwanzflossenstrahlen, Binden vom Auge bis in den Nacken, zum Maul, zur Seitenbinde und zum Interoperculum, Abdominalstreifen unter und parallel zur Seitenbinde, ein Streifen vom After nach vorne, ein Fleck auf der Innenseite des Bauchflossenstiemes, ein Fleck auf der rostralen Rückenflossenmembran.

Alle Arten sind kleinwüchsig. Das größte Exemplar einer *Apistogramma*-Art war ein Männchen von *A. steindachneri* (Regan) von 63 mm Standardlänge. Die Gattung ist in Orinoco-, Amazonas- und Paraguay-Becken, den Guyana-Ländern und den ostbrasilianischen Flüssen Caeté, Apeu, Capim und Parnaíba verbreitet. Mehrere Arten haben eine sehr begrenzte Verbreitung, einige finden sich entlang großer Strecken des Amazonas, nur eine einzige Art fand sich in zwei Becken.

Es werden 12 neue Arten beschrieben: *A. uaupesi*, *A. meinkeni*, *A. personata*, *A. elizabethae*, *A. brevis* (alle aus dem R. Uaupés), *A. roraimae* (R. Branco), *A. moae* (R. Moá), *A. pulchra* (R. Madeira), *A. caetei* (R. Caeté und R. Apeu), *A. piauiensis* (R. Parnaíba), *A. regani* (R. Negro und R. Amazonas) und *A. gephyra* (R. Negro und R. Amazonas). Es werden auch Beschreibungen von sechs früher genannten Arten gegeben: *A. agassizii* (Steindachner), *A. bitaeniata* Pellegrin, *A. geisleri* Meinken, *A. gibbiceps* Meinken, *A. cacatuoides* Hoedeman und *A. peritensis* (Haseman). Von vier weiteren Arten werden Angaben gemacht: *A. taeniata* (Günther), *A. amoena* (Cope) (Holotypus verloren), *A. parva* Ahl und *A. sweglesi* Meinken (das Typenmaterial nicht auffindbar). *A. klausewitzi* Meinken und *A. kleei* Meinken sind als Synonyme von *A. bitaeniata*, *A. ambloplitoides* Fowler als Synonym von *Acaronia nassa* (Heckel) anzusehen.

*Apistogramma* ist am nächsten verwandt mit *Apistogrammoides* Meinken. Beide gehören zusammen mit *Geophagus* Heckel, *Biotodoma* Eigenmann & Bray, *Acarichthys* Eigenmann und anderen in die Gattungsgruppe der Geophaginen.

*Acara geayi* Pellegrin wird als eine *Acarichthys*-Art angesprochen, ist also keine *Aequidens*-Art, sondern gehört zu den Geophaginen.

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