Cichlid fishes from the La Plata basin. Part III. The *Crenicichla lepidota* species group (Teleostei: Cichlidae)

by

Sven O. KULLANDER *

With 12 figures

**ABSTRACT**

*Cichlid fishes from the La Plata basin. Part III. The Crenicichla lepidota species group (Teleostei: Cichlidae).—* A taxonomic study of large-scaled *Crenicichla* from the Paraguay and Paraná river drainages, shows the existence of two species: *Crenicichla lepidota* Heckel, in the Paraguay and Alto Paraná systems, and *C. britskii* n. sp., in the Paraná superior system. Three populations of *C. lepidota* are recognized, one in the Paraguay system, and two in the Alto Paraná system, differing chiefly in meristics. An additional population of *C. lepidota* is found in tributaries of the Lagoa dos Patos in southern Brazil. *Crenicichla lepidota*, *C. britskii*, *C. brasiliensis* (Bloch) (northeast Brazil), and an undescribed species in the São Francisco drainage system, form the *C. lepidota* species group, probably close to *C. saxatilis* auctt. and similar forms in northern South America, but phenetically distinct from all other *Crenicichla* species.

**INTRODUCTION**

The genus *Crenicichla* was first recognized as such by Heckel (1840), although already pre-Linnean authors (Gronovius 1756, Linnaeus 1754, Marcgravius 1648) described and figured species of this genus. The habitus is generally more or less pike-like (Ladiges 1938), with elongate body and prominent jaws. Characteristic of most species is small scales and serrated preoperculum. The distinction versus the more stout-bodied and broad-snouted *Batrachops* Heckel, is not clear, and some authors (e.g. Haseman 1911, Pellegrin 1904) have united the genera. On the other hand, there

* Swedish Museum of Natural History, Section for Vertebrate Zoology, S-104 05 Stockholm, Sweden.
appears to be considerable diversification within *Crenicichla* in the strict sense, and considering that the revisions made (Pellegrin 1904; Regan 1905, 1913) were based on a very meagre material, the genus may be little more than a catch-all taxon for the more elongate pike-like South-American cichlids. The species level taxonomy is unclear, but about 30 valid (or not yet invalidated) species may be encountered in the literature. The genus ranges over most of South America east of the Andes, southwards even into Patagonia (Kullander 1981b), but ranges of particular species are little known.

The Zoological Expedition of the MHNG to Paraguay, 1979, collected a few series of *Crenicichla* in the Paraguay and Alto Paraná drainages, and they provide the basis for the present paper. Additional material comes from collections made by C. Dlouhy in the Alto Paraná in 1980, by myself in the Paraná superior in the same year, and from studies on MZUSP and NRM material.

Because species level taxonomy is somewhat confused and misidentifications common, it is difficult to get a clear idea of which *Crenicichla* species are present in the La Plata basin. It appears, however, partly as a consequence of the present study, that three assemblages of species are encountered, viz. *C. lepidota* like species (two, maybe more), *C. lacustris* like species (*C. niederleinii* (Holmberg) in the Alto Paraná, *C. vittata* Heckel in the Paraguay, *C. lacustris* (Castelnau) in the coastal regions, *C. haroldoi* Luengo & Britski, *C. jaguarensis* Haseman, and *C. jupiaensis* Britski & Luengo in the Paraná superior, maybe additional forms in the Uruguay and Paraná inferior systems), and *C. lenticulata* Heckel (representing the principally Amazonian, small-scaled forms in the upper Paraguay system). I have recently given a redescription of *C. niederleinii* (Kullander 1981a), and also discussed some aspects of the *C. lacustris* group (Kullander 1981b). Below, attention is given to the *C. lepidota* group.

**METHODS**

The terminology employed in the colour descriptions, is adapted from that used in my *Apistogramma* papers (Kullander 1979, 1980a). The preorbital stripe runs between the upper lip and the eye; the suborbital stripe (or spot) runs from the lower margin of the orbit obliquely ventrad and caudad; the postorbital stripe runs from the orbit caudad, and may be continued by a lateral band along the flank; the (vertical) bars are those cross-bands that are found on the sides of the body. The caudal spot is a small, more or less round spot on the dorsal lobe of the caudal fin, slightly behind the base of the fin. Other terms, e.g. humeral (shoulder) blotch (spot), flank blotches (spots), caudal spots (plural), anal and dorsal spots, are of a casual nature.

Measurements and counts are taken as described in Kullander (1979, 1980a, 1980b), except that the squ.tr. count includes the lateral line scale and represents the number of scales between the anal fin origin and the dorsal fin. The squ.long. count expresses the number of scales in the series above the lower lateral line, and is thus different from Regan's (1905, 1913) count above or below the (upper) lateral line.

For testing differences between *C. lepidota* samples (p. 637), I employed the Mann-Whitney non-parametric rank test, as described by Zar (1974).

Abbreviations employed include BMNH (British Museum (Natural History)), MHNG (Muséum d'Histoire naturelle, Genève), MZUSP (Museu de Zoologia da Universidade de São Paulo), NMW (Naturhistorisches Museum, Wien), and NRM (Swedish Museum of Natural History, Stockholm) for museums, and CP (caudal peduncle), CP/CP (caudal peduncle length as per cent of caudal peduncle depth), SL (standard length), and TL (total length), for measurements.
ACKNOWLEDGEMENTS

I am most grateful to the following persons who contributed with their time and efforts: Dr Volker Mahnert, MHNG (specimens), Dr Heraldo Britski, MZUSP (hospitality), Mr Harald Ahnelt, NMW (notes on NMW material), Mr Valdener Garutti, São José do Rio Preto (collecting), Mrs Anita Hogeborn (photos, Figs. 1, 2, 4, 7, 8), and Mrs Britt-Marie Lindkvist (typing). Travel grants were received from the Helge Ax:son Johnson Foundation, C. F. Liljevalch Jr travel grants (University of Stockholm), Yngve Sjöstedt’s Travel Fund, and J. A. Ahlstrand’s Fund (Royal Swedish Academy of Sciences).

Crenicichla lepidota Heckel, 1840 (Figs. 1-5)

ANTECEDENTIA

Literature. I refrain from giving a formal species bibliography here, since so much is still unclear concerning this species. A few comments on the literature may be warranted, though.

Heckel (1840) described Crenicichla lepidota from a specimen collected by J. Natterer in the Rio Guaporé. There are but few later collections in the Bolivian Amazonas drainage, principally those of Haseman (1911, São Antonio de Guaporé; Bastos; San Joaquin) and Pearson (1925, Lake Rogaqua; C. saxatilis from Huachi, Reyes, Cachuela Esperanza, Ixiamas, Popoi River, Rio Iniqui, may be C. lepidota as well). Steindachner (1874) reexamined Natterer’s collections and found in them C. lepidota also from the Paraguay system. Later records of C. lepidota are predominantly from the Paraguay drainage system. The distinction versus C. saxatilis (Linnaeus) has never been clear and for this reason also that name is employed, e.g. by Bouleneger (1895a, b, 1898, 1900) and Devincenzi (1924, 1939). Ribeiro (1918) proposed the combination C. saxatilis var. lepidota. Records of C. lepidota (or C. saxatilis) in the La Plata drainage system range throughout the Paraguay system, close to the Rio Paraguay (e.g. Bouleneger, op. cit., Fowler 1932, Eigenmann & Kennedy 1903, Eigenmann et al. 1907, Haseman 1911 (Puerto Suarez; Sapucay; São Luiz de Caceres; Arequa; Asuncion; Uruécum Mts.; San Francisco; Campos Alegre; Corumba)). But there are also some extreme localities to the west (Bouleneger 1897, San Lorenzo, Prov. Jugu (sic), Argentina; Ringuelet et al. 1967, Luna Muerta, Hickman, Salta), and some authors record C. saxatilis or C. lepidota from the lower Alto Paraná and Paraná medio (e.g. Bonetto et al. 1978, Ringuelet et al. 1967), the Uruguay system (e.g. Haseman 1911 (Cacequy; Uruguayan) or Rio Grande do Sul in Brazil (Lagoa dos Patos basin; e.g. Hensel 1870, Cope 1894, Haseman 1911 (Rio Jacuhy; Porto Alegre)). To the northeast there are records from the Rio Tietê (Haseman 1911, Salto das Cruzes), São Francisco and nearby drainages (Haseman 1911 (Santa Rita, Rio Preto; Joazeiro; Rio Itapicurú; Cidade da Barra; Rio Zinga; Rio Paqui; Queimadas; Propria; Boqueirão)), and even further north, from near Natal (Starks 1913, Lake Papary, Lake Extremoz and Ceará Mirim).

Present report. Examination of the MHNG 1979 material (MHNG 2027.99-100, 2028.1-47, NRM A80-3001) in early 1980 brought the following results: There was no noteworthy variation in external qualitative characters between samples from different localities insofar as the otherwise poor condition of one sample (MHNG 2028.40-47, Itabó Guazú) allowed comparison. However, there was a striking variation in coloration
and body shape associated with sex and reproductive stages, presumably of considerable taxonomic as well as biological significance. A routine series of measurements and counts proved interesting because it showed that the pooled Paraguayan system material and the two Alto Paraná series (Rio Acaray and Arroyo Itabó Guazú) differed considerably from each other. The Itabó Guazú form was characterized by statistically significant higher squ.long. and dorsal spine counts, and narrower caudal peduncle. The Acaray form was intermediate, but not well separated from the Paraguay form statistically. The taxonomic consequences of this situation were not apparent. Complications were provided by literature data showing the distribution of an apparently very variable species to be considerably greater than the area from which my material came. Descriptions of *Crenicichla* material in literature are generally based on very few specimens, so I found it difficult to assess the significance of the observed meristic and morphometric variation on the basis of available material and literature only.

It only appeared quite possible that the differences in meristic characters between the three forms might be due to environmental influence, and that the extensive ranges in e.g. squ.long. counts were remarkable. The caudal peduncle proportion is a character given much consideration in cichlid taxonomy, and it is natural that it would attract attention; however, considering the intermediate condition in the Acaray form, it appeared that it might as well reflect only population differences on an environmental gradient, be they intra- or interspecific. Further, considering the absence of any detectable differences in qualitative characters, it appeared difficult to give much dignity to the observed quantitative differences, except for characterization of populations, or maybe just local samples. Additional material from the Acaray, and from the Brazilian Paraguayan system, was examined as it became available, with the intention of resolving the problem of the significance of the variation observed in the first material. I then concentrated on the squ.long. and dorsal fin counts, which can be made rapidly and show a high degree of repeatability even between different workers. I also had opportunity to examine *C. lepidota* like material from other river systems, which added to the understanding of the problem. The initial results were confirmed by the complementary material; there are distinct populations. It showed also, I believe, that *C. lepidota* is a rather plastic species; that the differences observed between Alto Paraná and Paraguayan system samples cannot be used to distinguish species, although it is still possible that the Itabó Guazú form is specifically distinct. The complementary material also provided reason for considering a much more restricted geographical range for *C. lepidota* than literature indicates.

The present description of *C. lepidota* is characterized by the comparison of the different samples available, grouped according to geographical provenance and characteristics. These groups are termed Paraguayan, Acaray and Itabó Guazú. Most of the description is devoted to the Paraguayan material of 1979, which is abundantly represented. Some parts of the presumed range of *C. lepidota* are not represented in my material, and thus not covered in the description below. An extralimital population (Lagoa dos Patos) is discussed later in this paper (p. 649).

**Paraguayan material**

Included are thirty-five specimens from the republic of Paraguay (MHNG and NRM material listed on p. 656) and forty-five specimens from Brazil (MZUSP material listed on p. 656). The description was made on the basis of study of the MHNG + NRM material only; the Brazilian material examined chiefly for selected counts.
Description (based primarily on two specimens, MHNG 2028.1-26, 106.1 (male) and 88.4 (female) mm SL). Elongate, moderately compressed laterally. Abdomen pouch-like in gravid females; in others depth of trunk portion rather uniform. Snout moderately pointed. Mouth large; lower jaw slightly projecting before upper; articulation below posterior part of orbit. Tip of maxilla slightly exposed, reaching to below anterior third or orbit. Premaxillary processes reaching to above middle of orbit. Lips moderately wide. Cephalic lateralis pores as shown in Fig. 12. Nostril halfway between tip of upper lip and center of orbit.

Scales cycloid predorsally and anteriorly on back above upper lateral line, just behind and on pectoral axilla, on chest, throat and just behind ventral fin bases on belly; all other body scales ctenoid, except that belly pouch scales cycloid in female. Squ. long. 34-45. Head scales all cycloid and small; on most of cheek, operculum, and suboperculum; two dorsocaudal scales on interoperculum; preoperculum and dorsocaudal cutaneous projection of gill-cover naked. Lateral line scales slightly smaller, equal or slightly larger than adjacent scales; two tubed scales continuing lower lateral line on caudal fin. Less than half of caudal fin scaled; basal scales ctenoid, distal cycloid. Preopercular serrations well developed.

Dorsal fin origin above posterior edge of operculum; spines increasing in length to last, but little from about 7th; lappets rather long, pointed; soft portion pointed, 9th ray produced, reaching beyond middle or even end of caudal fin (adult males), pointed, not produced, to one-third of caudal fin (adult females), or to just behind caudal fin base (young). Soft anal fin similar, not produced, to one-fourth of caudal fin or shorter. D XVI.15, XVIII.12-15, XVIII.13-14, XIX.13; spines 16-19, $\bar{x} = 17.2 \pm 0.06$; $D_{\text{tot}}$ 29-32, $\bar{x} = 30.9 \pm 0.09$ (see also Table 2). A. III.8 (1), III.9 (24), III.10 (9); $A_{\text{tot}}$ 11-13, $\bar{x} = 12.3 \pm 0.09$ (MHNG & NRM material). Caudal fin rounded, tending to sublanceolate. One male, 96.8 mm SL (MHNG 2028.1-26), with 8th caudal ray produced (TL 125.9 mm, prolongation 15.5 mm). Pectoral fin symmetrical, rounded, reaching halfway to first or second anal ray. Ventral fin pointed, first and second rays equal in length or second slightly longer; reaching halfway to first to third anal spine.

Teeth in (2)3-4 series anteriorly in each jaw, pointed, slightly recurved, outer fixed, inner depressible.

Ovaries in a gravid female (76.9 mm) paired, the left one about 20 mm long, the right one about 22 mm long (slightly injured), voluminous and somewhat irregular in shape. Eggs elliptic, yellowish, tightly packed, length about 2.1 mm; between them large amounts of very small globular structures.

Coloration. Three colour phases are recognized, (1) Non-breeding, as seen in young, and in slender females, (2) breeding females, with well-rounded bellies, and (3) breeding males, as seen in the largest males.

Non-breeding (description chiefly from a female, MHNG 2027.99-100, but valid for all juveniles and non-breeding adults): Greyish, countershaded; abdomen, throat, chest, ventral parts of head white; back greyish, gradually paler ventrally. Forehead and dorsal part of snout greyish. Operculum lead grey, lateral parts of head otherwise greyish white. Brownish stripe between mouth and orbit (preorbital stripe), almost straight horizontal, below nostril, narrower than pupil. Below posterior portion of orbit wedge-shaped, caudoventrally directed short stripe across the upper part of the cheek (suborbital stripe). Brownish black stripe from orbit to caudal edge of operculum, of pupil width initially, widening caudalwards (postorbital stripe); distinct pale zone bordering dorsally. Shoulder blotch about size of orbit plus diffuse partial light border just behind gill-cover, below and on, very little above lateral line. Pocket under pectoral axilla black, pigmentation extended onto pectoral girdle under dorsal projection of gill-cover (pectoral spot). Below
dorsal fin 7 or possibly 8 (one below dorsal fin origin dubious) very weak greyish lateral bars extending ventrally to lateral horizontal band; partly with pale spots along middle part. Another bar on dorsal part of caudal peduncle. A similarly colored diffuse horizontal band continues the postorbital stripe to caudal fin, on and above lower lateral

Fig. 1-3.

Fig. 1. Crenicichla lepidota Paraguay. Adult male, 91.0 mm SL, from Arroyo Tagatya-Mi (NRM A80-3001). Photo A. Hogeborn. — Fig. 2. Crenicichla lepidota Paraguay. Breeding female, 76.9 mm SL, from Arroyo Tagatya-Mi (NRM A80-3001). Photo A. Hogeborn. — Fig. 3. Crenicichla lepidota Paraguay. Breeding female, 88.4 mm SL, from Arroyo Tagatya-Mi (MHNG 2028.1-26).
line, about two scales wide, edges unsharp. Lateral lines appearing like pale stitches. Dorsal fin pale greyish, without apparent colour zones. On soft part irregularly arranged pale spots. Anal fin greyish, darker marginally; about four spot-series over terminal rays. Caudal fin greyish, with pale submarginal zone, blackish distal edge and scattered darker spots over middle part. Proximally on dorsal lobe a black, pale-ringed spot; diameter with pale ring less than that of orbit. Ventral fins white.

Breeding females: Dark, blackish grey, slightly paler on chest. Seven to 10 vertical bars below dorsal fin and a horizontal band variously distinct, more apparent in more slender specimens. Shoulder blotch larger than orbit, just below or extending slightly above upper lateral line, not ocellated. Lateral lines not distinctly light-coloured. Head stripes and pectoral spot as in non-breeding specimens. Caudal fin ocellus only indicated in some specimens; caudal fin base otherwise generally dark or with a continuation of the horizontal body band. Dorsal fin blackish to dark grey; at least on soft part, but also commonly far forwards on spinous part, a pale inframarginal band consisting of more or less confluent colourless spots, one on each membrane; distally coloured like proximally, but ultimate margin deep black; no other spots on fins. Anal fin blackish grey. Caudal fin blackish grey, corner of each lobe with more or less pronounced black edge. Ventral fins pale greyish.

Breeding males: Dark, but not almost black as breeding females. Vertical and horizontal bands of flank distinct or vanishing in the dark general colour. Countershading indicated but lower regions still dark. Head stripes and shoulder blotch like in breeding females; suborbital stripe sometimes connected with preorbital stripe along margin of orbit. Lateral lines more or less light. Unpaired fins blackish grey. Dorsal fin without pale inframarginal stripe, but with more or less distinct spots on soft part; anal fin similar. Unocellated dark spot on caudal fin usually distinguishable; fin margin not darkened; about 8 vertical dark spot-series across middle portion more or less distinct. Ventral fins pale greyish.

**Determination.** The Paraguay system material agrees well with Heckel's (1840) original description of *C. lepidota*, based on a single specimen from the Rio Guaporé with D. XVI.15, A. III.10, squ.long. 44, L1 23/10. Steindachner (1874) redescribed Heckel's specimen together with remaining Natterer material of the same species from the Rios Paraguay and Guaporé. He recorded a variation in counts of D.XVI-XVIII. 14-16, A.III.9-10, squ.long. 41-45, L1 21-24/7-10, squ.tr. 3½/10-11. Steindachner also mentioned filamentously prolonged soft dorsal and anal fins, reaching almost to the end of the caudal fin, as a male characteristic. Other reports of *C. saxatilis* or *C. lepidota* from the Paraguay system are commonly not accompanied by descriptive data, but to the extent that they are, these are in agreement with those of the present material. I see no reason to hesitate in assigning the present material to a species originally described from the Amazonas drainage, although, in view of the variation found in La Plata basin material and the recognition of similar species in other river systems, the present report suffers somewhat from the lack of comparative data on Amazonian material.

**ACARAY MATERIAL**

Included are nine specimens, MHNG 2028.31-39, 44.8-87.5 mm, fifteen specimens, MHNG 2061.90-100, 2062.1-3, NRM unreg., 50.9-130.9 mm, and fourteen specimens, MHNG 2088.38-51, 57.5-90.5 mm.

The smaller series agrees well with the Paraguayan material, i.e. there are no apparent differences in qualitative characters examined or in colour pattern. The 44.8, 64.5, and
62.5 mm specimens are young with the non-breeding coloration described above, including spotted unpaired fins and distinct shoulder and caudal ocelli. The remainder are apparently females, without fin spots except for the unocellated caudal spot. The dorsal fin is uniform in two specimens, both slender, but with a pale inframarginal stripe in four specimens, three of which have rounded bellies. Neither coloration nor shape suggest that these females are in the very advanced reproductive state of most of the Tagatya-Mi specimens.

The specimens in the largest series show non-breeding coloration, but a lateral band is not clearly expressed, and the caudal ocellus is occasionally not apparent. There are

Fig. 4-5.

Fig. 4. Crenicichla lepidota Acaray. Probably a male, 75.5 mm SL, from the Acaray barrage lake (MHNG 2061.90-100, 2062.1-3). Photo A. Hogeborn. — Fig. 5. Crenicichla lepidota Itabó Guazú. Two young specimens, 63.3 (upper) and 49.7 (lower) mm SL, from Arroyo Itabó Guazú (MHNG 2028.40-47).
no particularly dark specimens or any with pronounced belly region. The males have spotted unpaired fins, the females almost immaculate dorsal and anal fins. In the females there is but a vaguely indicated zonation of the dorsal fin.

Amongst the fourteen MHNG 2088.38-51 specimens, are a few more or less dark females, but none gravid. One of them (70.7 mm) has blackish fins, the caudal fin black-seamed with pale submarginal zone, the dorsal fin with narrow black margin and light inframarginal band posteriorly, pale lappets anteriorly.

There are no apparent differences from the Paraguayan material in coloration or in other qualitative characters. D. XVI.15, XVII.14-16, XVIII.13-14; D spines 16-18, \( \bar{x} = 17.3 \pm 0.09 \); Dtot 31-33, \( \bar{x} = 31.6 \pm 0.09 \) (see also Table 5). A. III.9 (3), III.10 (6), in MHNG 2028.31-39 (see also Table 1).

**Itabó guazú material**

The Itabó Guazú material (MHNG 2028.40-47, eight specimens, 49.7-112.5 mm SL) is similar to the Paraguayan material, but unfortunately it is in a rather poor condition, except for two young specimens, 49.7 and 63.3 mm SL. In the others, the coloration is largely lost, faded to a pale, whitish principal colour. The scales are also lost to a great extent, so scale counts are partly from counting scale pockets. All specimens are slender. In the largest specimen there are five series of teeth anteriorly in the upper jaw, four in the lower, in the others three to four series in both jaws. The soft dorsal fin reaches at most to one-third of caudal fin; soft anal fin at most to slightly behind caudal fin base. Dorsal fin counts in Table 2; Dtot 31-32, \( \bar{x} = 31.4 \pm 0.18 \), A. III.10 in all specimens. The 112.5 mm specimen is a female with immature ova contained in paired ovaries which are elongate, cucumber-shaped, but ventrally flattened, dorsally convex. The right ovary is 22.5 mm, the left ovary 20.5 mm long. The eggs are tightly packed, of irregular shapes, and about one millimeter in diameter. The 91.1 mm specimen is a male with long slender testes, the left one 21.4 mm, the right one 16.7 mm long. What remains of the coloration is in agreement with that of the Paraguayan C. lepidota. Only in the large female the dorsal fin pattern appears to present an important difference (cf. below).

The 49.7 and 63.3 mm specimens have the juvenile, non-breeding coloration described for C. lepidota. The shoulder ocellus reaches to slightly above the upper lateral line. There are 9 vertical bars below the dorsal fin, and also one before and one behind. The caudal fin ocellus is distinct. Dorsal, anal and caudal fins are spotted. The 112.5 and 91.1 mm specimens have a caudal spot lacking pale ring, and the distal edges of the caudal fin are dark. In the 91.1 mm specimen the unpaired fins are spotted. The female has a basically dark dorsal fin. Inframarginally is a paler zone containing a horizontal series of black spots, one on each membrane from about the middle of the spiny portion to the middle of the soft portion. The edge is black. Because of the condition of the specimen, it is not possible to decide on the exact nature of the coloration of the dorsal fin and hence I hesitate to put much emphasis on the apparent difference (see description of breeding female C. lepidota for comparison).

**Analysis of sample characteristics**

Reasons for distinguishing between the samples of C. lepidota from the Acaray, Itabó Guazú and Paraguay localities are given in the Antecedentia above (p. 629). It may itself be interesting to compare data of material from different river systems, in this case the Alto Paraná and the Paraguay. The Paraguayan population here recognized
has a somewhat vast geographic connotation compared to those called Acaray and Itabó Guazú. The Paraguayan population may be defended on the ground of assumed continuity only. It is important to note that possible continuity of the Alto Parana

![Scatter diagram](image)

**Fig. 6.**

Scatter diagram, and linear regression of caudal peduncle length plotted against caudal peduncle depth in *Crenicichla lepidota* Paraguay (MHNG 2028.1-26, ten specimens, Tagatya-Mi; black circles; $y = 0.41 + 0.84x$, $r = 0.94$), *C. lepidota* Acaray (MHNG 2028.31-39; open squares; $y = 0.48 + 0.87x$, $r = 0.96$), and *C. lepidota* Itabó Guazú (MHNG 2028.40-47; open circles; $y = 1.23 + 0.92x$, $r = 0.99$).

populations with the Paraguayan emerges from the comparative study, so distinguishing these by reference to geographical situation only, appears a valid procedure.

*Qualitative characters.* As noted, there may be a trenchant character in the dorsal fin pattern in adult females of the Itabó Guazú and the Tagatya-Mi material, but it should be examined in better material from the Itabó Guazú. None of the females of the Acaray material has such a conspicuous spotting of the dorsal fin as have the breeding females of the Tagatya-Mi series; but because the development of the dorsal fin pattern
appears to be correlated with sexual maturity, it is evident that females in a more advanced reproductive stage are required for a conclusive comparison. Otherwise, qualitative characters offer no points of separation for any part of the *Crenicichla* material under consideration, except, to some extent, between specimens in different stages of reproductive maturity (slender to gravid females) or between sexes (males always slender and with prolonged unpaired fins).

**Morphometry and meristics.** Data from the three sample groups indicate distinctness particularly of the Itabó Guazú sample. The Acaray material is close to the Tagatya-Mi material. Tables 1-4 summarize the data under consideration. The morphometric data are more or less influenced by allometric growth and must be used with caution. Aside from the apparently narrower caudal peduncle in the Itabó Guazú material, the very short caudal fin in this series may be noted. The caudal peduncle depth: length ratio is characteristic of each sample recognized, although the difference is very small. In the meristics particularly the dorsal, squ.long, squ.tr. and Ll 2 counts attract attention because of distinctly higher numbers in the Itabó Guazú material. Evidently, the Itabó Guazú material has, on the whole, more scales. To check the consistency of the difference in dorsal and squ.long. counts, counts were taken from all remaining specimens. In addition, a small number of specimens was radiographed in search for internal differences. Apparently, only vertebral counts offer any potentially interesting aspects, and they are discussed below. The CP ratios, dorsal, squ.long., and vertebral counts were subjected to the non-parametric Mann-Whitney rank test (Zar 1974), and the results are illustrated in Table 5.

**Statistical analysis.** The morphometric and meristic data just considered are discussed below in the context of the statistical analysis (Table 5). Characters chosen for this analysis were, with the exception of the vertebral count, those that appeared, from raw data only, to distinguish one or more of the samples.

**Caudal peduncle ratios** (Tables 1 and 5, Fig. 6). Statistically significant differences were found between the Itabó Guazú and the other samples. The Itabó Guazú material is unique within the *lepidota* group in having, in average, a longer than deep caudal peduncle (cf. pp. 648 and 650), so some weight must be given to this circumstance, although it should be apparent that value intervals on a continuous scale are considered. With the data available, the Itabó Guazú sample has to be considered as distinct, but the intermediacy of Acaray values suggest that there may be a clinal series (cf. CP depth means in Table 1; regression lines of Fig. 6).

**Dorsal fin counts** (Tables 2 and 5). Whereas the Itabó Guazú specimens all have 18 spines, the other material shows a minor variation in spine number, ranging from 16 to 19. The Itabó Guazú material is clearly distinct statistically with regard to spine number. The Acaray material is distinguished by the total dorsal count from the Paraguay material; the range is nevertheless within that of the Paraguayan, and the situation goes back to the concentration of Paraguayan counts on XVII.14, whereas in the Acaray material XVIII.14 (modal) and XVII.14 are almost equally common. Looking at these figures (Table 2), it seems rather that we may have a bimodal Acaray population, what is interesting in view of the restricted range of values. The Acaray material is thus probably intermediate also in dorsal fin counts, even if it appears to have a higher mean total count.

**Squ.long. counts** (Tables 3 and 5). Characteristic of this count is the wide ranges within each group recognized in Table 3. There is a clear tendency towards central values in the Paraguay and Acaray material, but there are no decidedly central values at all
Morphometry and meristics of *Crenicichla lepidota* from the Paraguay system (Tagatya-Mi, MHNG 2028.1-26, NRM A80-3001, 10 specimens), and the Alto Paraná system (Acaray, MHNG 2028.31-39, 9 specimens; Itabó Guazú, MHNG 2028.40-47, 8 specimens). Measurements are expressed as per cent of SL, except CP/CP, which is CP length as per cent of CP depth, and SL, which is in mm.

<table>
<thead>
<tr>
<th></th>
<th>Itabó Guazú</th>
<th></th>
<th>Acaray</th>
<th></th>
<th>Tagatya-Mi</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Range</td>
<td>$\bar{x} \pm s_{\bar{x}}$</td>
<td>n</td>
<td>Range</td>
<td>$\bar{x} \pm s_{\bar{x}}$</td>
</tr>
<tr>
<td>SL</td>
<td>49.7-112.5</td>
<td>7</td>
<td>8</td>
<td>44.8-87.5</td>
<td>9</td>
</tr>
<tr>
<td>Head length</td>
<td>30.9-32.8</td>
<td>31.9 ± 0.24</td>
<td>7</td>
<td>32.2-33.7</td>
<td>32.9 ± 0.17</td>
</tr>
<tr>
<td>Head depth</td>
<td>15.5-17.3</td>
<td>16.2 ± 0.21</td>
<td>8</td>
<td>16.8-18.3</td>
<td>17.6 ± 0.16</td>
</tr>
<tr>
<td>Body depth</td>
<td>22.9-27.0</td>
<td>24.4 ± 0.55</td>
<td>7</td>
<td>25.1-29.2</td>
<td>26.4 ± 0.43</td>
</tr>
<tr>
<td>Orbit diameter</td>
<td>7.6-9.9</td>
<td>8.5 ± 0.30</td>
<td>8</td>
<td>8.8-10.7</td>
<td>9.4 ± 0.22</td>
</tr>
<tr>
<td>Snout length</td>
<td>6.5-9.1</td>
<td>7.6 ± 0.29</td>
<td>8</td>
<td>6.6-7.7</td>
<td>7.1 ± 0.12</td>
</tr>
<tr>
<td>Interorbital width</td>
<td>6.0-7.6</td>
<td>6.6 ± 0.18</td>
<td>8</td>
<td>6.6-7.7</td>
<td>7.0 ± 0.11</td>
</tr>
<tr>
<td>Upper jaw length</td>
<td>11.0-13.1</td>
<td>11.6 ± 0.27</td>
<td>8</td>
<td>11.4-13.4</td>
<td>12.3 ± 0.20</td>
</tr>
<tr>
<td>Lower jaw length</td>
<td>15.5-17.2</td>
<td>16.0 ± 0.20</td>
<td>7</td>
<td>16.0-17.3</td>
<td>16.6 ± 0.12</td>
</tr>
<tr>
<td>Pectoral fin length</td>
<td>19.1-21.5</td>
<td>20.6 ± 0.43</td>
<td>5</td>
<td>21.0-23.2</td>
<td>21.8 ± 0.43</td>
</tr>
<tr>
<td>Last dorsal spine length</td>
<td>11.5-13.5</td>
<td>12.3 ± 0.24</td>
<td>7</td>
<td>11.4-13.7</td>
<td>12.7 ± 0.27</td>
</tr>
<tr>
<td>Caudal fin length</td>
<td>25.2-26.6</td>
<td>25.9 ± 0.27</td>
<td>7</td>
<td>28.4-29.9</td>
<td>29.0 ± 0.30</td>
</tr>
<tr>
<td>CP depth</td>
<td>11.5-12.2</td>
<td>11.9 ± 0.10</td>
<td>7</td>
<td>12.3-12.9</td>
<td>12.6 ± 0.06</td>
</tr>
<tr>
<td>CP length</td>
<td>11.8-13.4</td>
<td>12.6 ± 0.21</td>
<td>7</td>
<td>10.5-12.2</td>
<td>11.6 ± 0.18</td>
</tr>
<tr>
<td>CP/CP</td>
<td>98.1-114.9</td>
<td>106.0 ± 2.18</td>
<td>7</td>
<td>83.9-96.2</td>
<td>92.2 ± 1.37</td>
</tr>
<tr>
<td>A tot</td>
<td>13</td>
<td>13.0 ± 0.00</td>
<td>8</td>
<td>12-13</td>
<td>12.7 ± 0.17</td>
</tr>
<tr>
<td>P</td>
<td>15-16</td>
<td>15.4 ± 0.18</td>
<td>8</td>
<td>15-16</td>
<td>15.4 ± 0.18</td>
</tr>
<tr>
<td>Squ.tr.</td>
<td>16-17</td>
<td>16.5 ± 0.19</td>
<td>8</td>
<td>14-15</td>
<td>14.7 ± 0.17</td>
</tr>
<tr>
<td>Li1</td>
<td>21-23</td>
<td>22.0 ± 0.22</td>
<td>7</td>
<td>20-23</td>
<td>21.9 ± 0.40</td>
</tr>
<tr>
<td>Li2</td>
<td>8-11</td>
<td>9.6 ± 0.43</td>
<td>7</td>
<td>7-9</td>
<td>8.0 ± 0.24</td>
</tr>
<tr>
<td>Rakers</td>
<td>9-10</td>
<td>9.9 ± 0.13</td>
<td>8</td>
<td>9-11</td>
<td>9.7 ± 0.29</td>
</tr>
</tbody>
</table>
Table 2.
Dorsal fin counts frequency in *Crenicichla lepidota* group forms from various regions.

<table>
<thead>
<tr>
<th></th>
<th>Paraguay</th>
<th>Acaray</th>
<th>Itabó Guazú</th>
<th><em>C. britskii</em></th>
<th>Patos</th>
<th>S. Francisco</th>
<th>Nordeste</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>D</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>XVI.15</td>
<td>1</td>
<td>2</td>
<td>2</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>XVII-</td>
<td>2</td>
<td></td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>XVII.12</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>XVII.13</td>
<td>14</td>
<td></td>
<td>3</td>
<td>2</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>XVII.14</td>
<td>28</td>
<td>12</td>
<td>4</td>
<td>5</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>XVII.15</td>
<td>8</td>
<td>8</td>
<td>1</td>
<td></td>
<td>4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>XVII.16</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>XVIII.13</td>
<td>8</td>
<td>2</td>
<td>5</td>
<td>1</td>
<td>1</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>XVIII.14</td>
<td>3</td>
<td>13</td>
<td>3</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>XVIII.15</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>XIX.13</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>D spines</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>16</td>
<td>1</td>
<td>2</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>17</td>
<td>53</td>
<td>21</td>
<td>8</td>
<td>12</td>
<td>2</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>18</td>
<td>11</td>
<td>15</td>
<td>8</td>
<td>1</td>
<td>4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>19</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Dₜₜ</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>29</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>30</td>
<td>14</td>
<td></td>
<td>3</td>
<td>2</td>
<td>1</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>31</td>
<td>37</td>
<td>16</td>
<td>5</td>
<td>7</td>
<td>6</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>32</td>
<td>12</td>
<td>21</td>
<td>3</td>
<td>1</td>
<td>6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>33</td>
<td></td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

In *C. britskii* or *C. lepidota* Patos. Some of the variation at least is due to irregularities in the scale pattern. When these, as is usual, are bilaterally asymmetrical, the left side count is closer to the mean or modal value(s) observed in the whole group. The ranges overlap greatly, but the means are different. The Paraguayan and Alto Paraná forms are statistically different from each other (see also p. 637), and the means are in a series. The range of the Itabó Guazú material is virtually disjunct, and although only few specimens were analysed, the frequency distribution in Table 3 is strongly indicative of the distinctness of this form.

Vertebral counts (Tables 4 and 5). A limited number of specimens were radiographed. All specimens lack a supraneural spine. The vertebral counts of the Itabó Guazú material average slightly higher than those of the Tagatya-Mi material, probably due to more caudal vertebrae (abdominal/caudal vertebrae ratios: Itabó Guazú: 1.1-1.3, $\bar{x} = 1.2$, Acaray: 1.2-1.4, $\bar{x} = 1.3$; Tagatya-Mi: 1.2-1.5, $\bar{x} = 1.4$). The Acaray material takes an intermediate position. The data are insufficient for a decisive analysis of differences, but it is worth noting that the findings are in agreement with those for dorsal and squ. long. counts. The Itabó Guazú material has higher figures than the other material, and the Acaray material has slightly higher figures than the Paraguayan material.
Table 3.

Squ. long. counts of *Crenicichla lepidota* group forms from different regions.

|                | 33 | 34 | 35 | 36 | 37 | 38 | 39 | 40 | 41 | 42 | 43 | 44 | 45 | 46 | 47 | 48 | 49 | 50 | 51 | 52 | Range  | $\bar{x} \pm s_{\bar{x}}$ |
|----------------|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|-----|--------------------------|
| *C. lepidota* Paraguay | 1  | 1  | 2  | 8  | 13 | 13 | 11 | 7  | 5  | 2  | 34-45 | 41.0 ± 0.25 |
| *C. lepidota* Acaray    | 1  | 1  | 1  | 6  | 4  | 9  | 7  | 7  | 1  | 1  | 38-47 | 43.0 ± 0.31 |
| *C. lepidota* Itabó Guazú | 1  | 1  | 3  | 3  | 47-52 | 50.8 ± 0.59 |
| *C. lepidota* Patos     | 2  | 1  | 3  | 1  | 4  | 1  | 1  | 1  | 1  | 42-52 | 45.6 ± 0.70 |
| *C. britskii*           | 2  | 3  | 2  | 1  | 3  | 1  | 2  | 33-40 | 35.9 ± 0.62 |
| *C. sp.* São Francisco  | 2  |    |    |    |    |    |    | 39  | 39.0 ± 0 |
| *C. brasiliensis*       | 1  | 3  | 1  |    |    |    |    | 47-50 | 48.8 ± 0.49 |
Table 4.

Vertebral counts from Paraguayan (MHNG 2028.1-26, NRM A80-3001; Tagatya-Mi) and Alto Paraná (MHNG 2028.31-39, 2061.90-100, 2062.1-3, NRM unreg., Acaray; MHNG 2028.40-47, Itabó Guazú) Crenicichla lepidota.

<table>
<thead>
<tr>
<th>Sample</th>
<th>Count</th>
<th>f</th>
<th>abdominal</th>
<th>caudal</th>
<th>total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>$\bar{x} \pm s_{x}$</td>
<td>$\bar{x} \pm s_{x}$</td>
<td>$\bar{x} \pm s_{x}$</td>
</tr>
<tr>
<td>Itabó Guazú</td>
<td>18 + 15 = 33</td>
<td>5</td>
<td>18.1 ± 0.14</td>
<td>15.1 ± 0.14</td>
<td>33.3 ± 0.18</td>
</tr>
<tr>
<td>n = 7</td>
<td>18 + 16 = 34</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>19 + 15 = 34</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Acaray</td>
<td>18 + 14 = 32</td>
<td>2</td>
<td>18.4 ± 0.15</td>
<td>14.7 ± 0.14</td>
<td>33.1 ± 0.21</td>
</tr>
<tr>
<td>n = 11</td>
<td>18 + 15 = 33</td>
<td>5</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>19 + 14 = 33</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>19 + 15 = 34</td>
<td>3</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tagatya-Mi</td>
<td>18 + 14 = 32</td>
<td>1</td>
<td>18.7 ± 0.18</td>
<td>13.9 ± 0.26</td>
<td>32.6 ± 0.20</td>
</tr>
<tr>
<td>n = 7</td>
<td>18 + 15 = 33</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>19 + 13 = 32</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>19 + 14 = 33</td>
<td>3</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 5.

P-values from Mann-Whitney ranking test of identity in caudal peduncle depth/length ratio (CP/CP), dorsal fin, squ.long. and vertebral counts in Crenicichla lepidota from the Alto Paraná (Acaray and Itabó Guazú) and Paraguay river systems. $H^0$ = samples are not different; rejected at $P > 0.05$ ($^-$).

<table>
<thead>
<tr>
<th>Samples compared</th>
<th>CP/CP</th>
<th>D spines</th>
<th>D tot</th>
<th>Squ. long.</th>
<th>Vertebrae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Paraguay-Acaray</td>
<td>0.20-</td>
<td>&gt; 0.05-</td>
<td>&lt; 0.001</td>
<td>&lt; 0.001</td>
<td>0.20-</td>
</tr>
<tr>
<td>Acaray-Itabó Guazú</td>
<td>&lt; 0.001</td>
<td>&lt; 0.01</td>
<td>&gt; 0.20-</td>
<td>&lt; 0.001</td>
<td>&gt; 0.20-</td>
</tr>
<tr>
<td>Paraguay-Itabó Guazú</td>
<td>&lt; 0.001</td>
<td>&lt; 0.001</td>
<td>&gt; 0.05-</td>
<td>&lt; 0.001</td>
<td>&gt; 0.10-</td>
</tr>
</tbody>
</table>

The vertebral counts agree with those for Amazonian and Orinocoan C. saxatilis like material in averaging about 33, a rather low figure for the genus (unpubl. data; based on NRM material). Crenicichla lacustris from Puerto Madryn, Argentina, has 19 + 16 or 19 + 17 (Kullander 1981b), and C. niederleinii 19 + 17 (Kullander 1981a). Pelligrin (1904) gave 24 + 17 for C. brasiliensis (nee Bloch) (obviously various C. johanna like forms), and 20 + 16 for C. saxatilis. Crenicichla multispinosa Pellegrin has 23 + 18 according to Vandewalle (1971). Regan (1905) counted 23 + 18 in C. johanna
Heckel, and 20 + 15 in *C. saxatilis*. In *C. britskii* there are 18 + 14 vertebrae (abdominal/caudal ratio 1.3). *Crenicichla* species with high vertebral counts also have high dorsal and squ. long. counts.

**Conclusions.** It appears that the Itabó Guazú material is clearly distinguished from the Acaray and Paraguay material in some characters. I would regard this material as representing a distinct population, but it cannot be distinguished specifically, because a) the characters studied are rather few and distinctness is apparent only through statistical analysis, and b) there is an apparent shift of means, modes, and ranges in the sample series Paraguay - Acaray - Itabó Guazú, possibly indicating a continuous series of populations that may be distinct or as well grading into each other. The differences in meristics between the Acaray and Paraguay materials are small and in view of the rather large samples and the absence of colour or other qualitative differences, there may be justification only for regarding the Acaray material as a local population of *C. lepidota*. There is no indication of geographical isolation of the Acaray form from the Paraguay form; but upon comparison of geographical location and relative distinctness, such is postulated relative the Itabó Guazú form.

**Distribution**

Paraguayan *C. lepidota* evidently occurs in late October (breeding specimens in MHNG 2028.1-26). Krieg collected fry (18.3-20.5 mm) in January and February at Nueva Germania (Schindler 1939). A female in breeding coloration, 89.8 mm SL, was taken at Campo do Jofre, Poconé, 10-19 February (MZUSP unreg.). Haseman (1911) collected an 8 cm specimen near Corumbá on 2 May 1909, which was “very dark” and had “the dorsal fin . . . edged with black, beneath which is a lighter streak, and the base is dark brown”, probably a breeding female. In the Paraguay area rain falls chiefly between October and April, and reproduction may be timed with flooding.

**Crenicichla britskii** n. sp. (Fig. 7)

*Holotype.* MZUSP 16004, adult female, 83.2 mm SL. Brasil, Estado de São Paulo, mun. Promissão, R. Tietê system, km 143 on BR-153, above road in small brook. 28 August 1980. Leg. V. Garutti & S. O. Kullander (Sta. SOK 4).

**Bibliography**


**Diagnosis.** A species of the *Crenicichla lepidota* group, characterized by a rather deep head (18.2-20.0% of SL), long caudal fin (28.0-30.4% of SL), caudal peduncle
proportions (CP/CP 75.8-100%), low squ.long. (33-40), pectoral fin (14-15, mean 14.8) and upper lateral line (20-22) counts, and few gill-rakers (8-9). Breeding females with uniformly dark or black-edged dorsal fin. Adults with a series of spots along side or uniform flank colour except for humeral spot.

Description. Based chiefly on the holotype, additional data from NRM paratypes. Notes on MZUSP paratypes are given at the end of this section. Counts and measurements are summarized in Tables 2, 3 and 6; but some are presented here only.

The holotype is an adult female in what appears to be breeding coloration; it is not very deep, however, and a short cut through the abdominal wall reveals ripening but apparently not mature ova in what can be seen of the ovaries. The juveniles are more slender. Snout rather short, moderately pointed in lateral aspect, rounded as seen from above. Mouth large; lower jaw slightly projecting, articulation below posterior half of orbit. Tip of maxilla partly exposed, reaching to below one-third of orbit (slightly shorter in juveniles). Premaxillary processes reaching to above middle of orbit (slightly shorter in juveniles). Lips moderately wide. Nostril closer to orbit than postlabial snout tip. Preopercular serrations weak, apparent only after removal of skin. Gill-rakers short. Cephalic lateralis pores as in C. lepidota, except that the pore medial to that behind nostril bilaterally doubled in holotype and one NRM paratype, and doubled unilaterally in one NRM paratype.

Scales cycloid predorsally and anteriorly on back above lateral line to about middle of dorsal fin, on chest, pectoral axilla, throat and along midline of abdomen (anterior abdominal squamation mixed); all other body scales weakly ctenoid. Head scales all cycloid and small; on most of cheek (c. 7 series), operculum and suboperculum; three dorsocaudal scales on interoperculum; preoperculum and dorsocaudal cutaneous projection of gill-cover naked. Squ.long. 35 in holotype. Lateral line scales about equal in size to those adjacent, except that upper lateral line scales slightly smaller than those immediately below; two (one or two in NRM paratypes) tubed scales continuing lower lateral line on caudal fin; two scale series between lateral lines. About two-fifths of caudal fin scaled; basal scales ctenoid, distal cycloid.

Dorsal fin origin above posterior edge of operculum; spines increasing in length to last, but little from 7th; lappets pointed, soft portion rounded, reaching to one-third of caudal fin (to one-fourth in juveniles). Soft anal fin similar, to one-fifth of caudal fin (just behind caudal fin base in juveniles). D.XVI.15, A.III.10 in holotype. Soft anal rays 9 (1), 9.i (1) and 10 (2) in NRM paratypes. Caudal fin rounded, tending to ovate (rounded in juveniles). Pectoral fin nearly symmetrical, rounded, reaching almost halfway to third anal ray (slightly longer in juveniles). Ventral fin rounded; second ray longest; reaching halfway to second anal spine (longer in juveniles).

Teeth in three series anteriorly in upper jaw; four series in lower jaw. Pointed, slightly curved, outer fixed, inner depressible.

Vertebræ 18 + 14, no supraneural (holotype and NRM paratypes).

Coloration. Holotype: The dark coloration compares well with the breeding coloration of C. lepidota females, so I assume that this is the breeding coloration of female C. britskii, although the specimen is apparently not in a very advanced state of reproduction. Blackish grey, lower parts of head, chest and anterior abdomen dirty whitish, slightly lighter also on posterior ventral sides. Cheek brownish grey; lips and preorbital area pale greyish. No vertical bars or lateral band apparent. A large shoulder blotch may be discerned especially on the slightly lighter anterior margin; below upper lateral line. Pectoral axilla spot black against lighter ground. Lateral lines not light-colored. Preorbital stripe not apparent. Suborbital stripe black, short, from lower margin.
or orbit obliquely backwards to about middle of cheek, continued forwards along orbital rim to dark upper portion of preorbital. Postorbital stripe sharp-edged, black, broadening on gill-cover. Unpaired fins blackish grey, immaculate; dorsal fin spinous part posteriorly narrowly black-edged, soft part broadly black-edged. Caudal spot not appearing. Ventral fins greyish white.

In life, the holotype had much the same colours, but the dark body and fins had a bluish tint.

Juveniles (NRM paratypes): NRM SOK/1980354:3127 is faded, but agrees otherwise well with the others (described below). In life this specimen was greyish above, whitish below, distinguished by a red ring around the pupil and a red spot anterior to the humeral spot, not seen in the others and probably indicative of different habitat types (water turbidity?).

Ground colour yellowish white, markings greyish to brownish, countershaded. Cheek and lower parts of head pale. Lateral lines appearing like white stitches. Humeral
ocellar below upper lateral line; clearly ocellated in 35.8 mm specimen only. Caudal ocellus prominent, diameter less than that of orbit, above level of lower lateral line and a little behind caudal fin base. Preorbital stripe indistinct, below nostril; postorbital stripe with sharp, even edges, widening on operculum. Upper lip and, anteriorly and on lateral edge, lower lip dark grey. Suborbital stripe a brown spot in the two smaller specimens, in the largest specimen like in holotype. Pectoral spot black, prominent. The 51.1 mm specimen with almost uniform flank coloration; vertical bars and lateral band not distinct. Dorsal fin greyish, with two horizontal series of small white dots on outer half (also on spinous portion); caudal fin greyish with about five vertical series of darker spots across middle portion, posterior edges white; anal fin greyish with a few darker spots posteriorly; ventral fins pale greyish, anteriorly a narrow grey margin. The 41.5 mm specimen with partly spoiled flank coloration; horizontal band not distinct. Dorsal fin greyish, with two horizontal series of small white dots on outer half (also on spinous portion); caudal fin greyish with about five vertical series of darker spots across middle portion, posterior edges white; anal fin greyish with a few darker spots posteriorly; ventral fins pale greyish, anteriorly a narrow grey margin. The 41.5 mm specimen with partly spoiled flank coloration; horizontal band not well defined; similar to 51.1 mm specimen in fin coloration. The 35.8 mm specimen with well defined lateral band continuing the postorbital stripe, on and above level of lower lateral line, to caudal fin base which is of the same brownish colour; vertical bars: one before dorsal fin to slightly above gill-cover; eight below dorsal fin, narrow, uneven, particularly the middle ones appearing like spots below upper lateral line; one indistinctly on caudal peduncle (SOK/1980354:3127 and MZUSP paratypes have but seven bars below dorsal fin); similar to 51.1 mm specimen in fin coloration, but ventral fin paler.

### Table 6.

Measurements and counts from holotype and NRM paratypes of *Crenicichla britskii*. Measurements are in mm, except ranges and means, which are in per cent of SL, and CP/CP, which is CP length as per cent of CP depth.

<table>
<thead>
<tr>
<th></th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>SL</strong></td>
<td>35.8-41.5</td>
</tr>
<tr>
<td>Head length</td>
<td>12.1-14.4</td>
</tr>
<tr>
<td>Head depth</td>
<td>6.6-7.6</td>
</tr>
<tr>
<td>Body depth</td>
<td>9.3-11.3</td>
</tr>
<tr>
<td>Orbit diameter</td>
<td>4.2-4.8</td>
</tr>
<tr>
<td>Snout length</td>
<td>2.2-2.9</td>
</tr>
<tr>
<td>Interorbital width</td>
<td>2.5-3.1</td>
</tr>
<tr>
<td>Upper jaw length</td>
<td>3.6-4.6</td>
</tr>
<tr>
<td>Lower jaw length</td>
<td>5.4-6.6</td>
</tr>
<tr>
<td>Pectoral fin length</td>
<td>8.7-9.5</td>
</tr>
<tr>
<td>Last D spine length</td>
<td>5.0-6.6</td>
</tr>
<tr>
<td>Caudal fin length</td>
<td>10.1-12.6</td>
</tr>
<tr>
<td>CP depth</td>
<td>4.4-5.3</td>
</tr>
<tr>
<td>CP length</td>
<td>4.4-5.3</td>
</tr>
<tr>
<td>CP/CP</td>
<td>100.0-200.0</td>
</tr>
</tbody>
</table>

| A<sub>tot</sub> | 13-15 |
| P              | 15-14 |
| L<sub>1</sub>  | 20-22 |
| L<sub>2</sub>  | 9-7   |
| Rakers         | 8-9   |
The colour pattern of these juveniles corresponds to the non-breeding pattern of *C. lepidota*, but is distinguished by the upper flank spots, shown clearly, however, by only one of the specimens.

**Additional data from MZUSP paratypes.** A gravid female from the córrego do Abrigo, 63.0 mm, is dark (chocolate brown, paler on chest and lower head), with dark unpaired fins. The dorsal fin is possibly narrowly black-edged, but there is no black/white zonation. A large unocellated shoulder blotch extends upwards to the lateral line; the caudal spot is indistinct. The vertical bars give rise to about seven vertical spots instead of a lateral band. Another gravid female (Jupiá, 84.8 mm) also has uniform fins. A large male, 118.3 mm, from the córrego do Abrigo, has spotted unpaired fins. The humeral ocellus is irregular in shape and reaches to above the lateral line; it also has a small caudal ocellus. Behind the humeral ocellus is a series of about eight irregular spots between the levels of the lateral lines, and apparently developed from the faint vertical bars. A slender female, 91.1 mm, in the same series, has immaculate, pale grey fins, is otherwise similar to the male.

**Distribution.** *Crenicichla britskii* replaces *C. lepidota* in the Paraná superior system. Collections are from Guaira, Jupiá, and Promissão.

**Ecology.** Gravid females or females in breeding coloration have been collected in late August, September, and December; but collections from other times of the year are not available.

My Sta. 3 (Fig. 9) was an exposed, large isolated water-hole, one of several, excavated through human agency, close to the bank of the R. Tietê, below the Promissão barrage lake. The water was turbid, the bottom (depth more than two meters) clayey. There was no submerged vegetation. Water temperature, 17.9° C, was measured in a similar water-hole next-to. Small Cheirodontinae (*Cheirodon notomelas* Eigenmann, *Ch. stenodon* Eigenmann, *Cheirodon* sp., and *Aphyocheirodon hemigrammus* Eigenmann) were extremely common; other fishes taken (all characoids) included: *Acestrorhynchus lacustris* (Reinhardt), *Characidium fasciatum* (Reinhardt), *Hyphessobrycon callistus* (Boulenger), *Curimata gilbert* Quoy & Gaimard, *Leporinus bahiensis* Steindachner, *Moenkhausia intermedia* (Eigenmann), *Astyanax bimaculatus* (Linnaeus), *Paralobioscarus pintoi* (Campos), and *Hemigrammus marginatus* Ellis.

The type-locality (Sta. 4; Fig. 10) was a narrow and very shallow brook almost choked with vegetation. The water was clear and slow-running. Fishing was made in a shallow, vegetation-free section, in open water in the vegetation margin. Associated species were *Curimata vanderi* Britski, *Hoplias malabaricus* (Bloch), *Characidium fasciatum Moenkhausia sanctaeilomenae* (Steindachner), *Hemigrammus marginatus*, *Gymnotus carapo* Linnaeus, *Corydoras macrosteus* Regan, *Cichlasoma* sp. (undescribed), and the very common *Phalloceros caudimaculatus* (Hensel) and *Cheirodon notomelas*.

**Etymology.** Named in honour of Dr Heraldo A. Britski (Museu de Zoologia da Universidade de São Paulo), in appreciation of his valuable help during my stay in São Paulo, *e.g.* in arranging the excursion during which the type-material was collected.

**Remarks.** *Crenicichla britskii* is very similar to *C. lepidota*, and there appears to be no reason to doubt a close phyletic relationship. Indeed, it may be questioned why I regard the Paraná superior form as a distinct species, but include the Alto Paraná and Patos forms in *C. lepidota* with the Paraguay form taken as “basic” within the group. Actually, it is rather the tendency for character state gradients, lack of critical colour pattern data, and very restricted ranges of the available material of non-Paraguayan forms which suggests the action taken in this paper. *Crenicichla britskii* is readily reco-
The dorsal fin counts (Table 2) are frequently low, distinguishing *C. britskii* from *C. lepidota* Itabó Guazú; there is also an unclear tendency for lower counts than encountered in *C. lepidota* Paraguay, Acaray and Patos. The squ.long. counts (Table 3),

Fig. 9. Water-holes near the Promissão hydroelectric power plant, habitat of *Crenicichla britskii* (Sta. 3, 28 August 1980). — Fig. 10. A small brook near the Promissão hydroelectric power plant, at Km 143 on BR-153, type-locality of *Crenicichla britskii* (Sta. 4, 28 August 1980).
are concentrated on the range 33-37, but extended to 40. There is a clear distinction here relative all other *C. lepidota* group forms, except that in the São Francisco system. Other low counts (gill-rakers and upper lateral line particularly) may be noted, but here small specimens may be influential.

In the measurements (Table 6), it appears that *C. britskii* has a slightly deeper head than the forms covered in Table 1. The apparently long pectoral fin is probably characteristic rather of small specimens, than a species characteristic. Caudal peduncle measurements from six additional MZUSP paratypes extend the ranges given in Table 6, due to size allometry (CP length and CP/CP decreasing, CP depth increasing with increasing SL). For \( n = 11 \), CP length 10.5-12.8, \( \bar{x} = 11.7 \pm 0.25\% \) of SL; CP depth 12.3-14.3, \( \bar{x} = 13.4 \pm 0.19\% \) of SL; CP/CP 75.8-100.0, \( \bar{x} = 87.2 \pm 2.66 \). Regression line for CP/CP is given by \( y = 1.56 + 0.69x \) (\( r = 0.99 \)) (cf. Fig. 6), *i.e.* a lesser slope than in any *C. lepidota* form. The caudal peduncle is deeper than in *C. lepidota* Itabó Guazú, but the means of CP length, CP depth and CP/CP come out nearly identical with those of the Tagatya-Mi *C. lepidota* (Table 1).

The colour pattern distinguishes *C. britskii* more than anything else. Most important are the spots the sides and the plain or modestly black-edged dorsal fin of breeding females. In the holotype, the flanks are almost uniformly dark, as in breeding *C. lepidota* females, so it is important to put both those character states in the diagnosis.

*Crenicichla britskii* can hardly be said to differ more in meristics or proportions from *C. lepidota* Paraguay than does *C. lepidota* Itabó Guazú. There is one more character available for study, however, *viz.* the color pattern, and I regard it as important in this group of species. Also, *C. britskii* is encountered over a rather wide geographical area, which, it appears, is hydrographically separated from that of *C. lepidota* by the Sete Quedas falls and the mountainous divide between the Paraguay and Paraná superior drainages. *Crenicichla britskii* does not appear to be involved in a character state gradient as may be the case with *C. lepidota* forms. Its geographically closest form, *C. lepidota* Itabó Guazú has squ.long. and dorsal fin counts severely disturbing any potential cline connecting *C. lepidota* Paraguay with *C. britskii*, via the Alto Paraná. But in its low meristics *C. britskii* resembles somewhat *C. lepidota* Paraguay, and it may be that meristics are correlated with geographical location, characterized by *e.g.* altitude, or more likely latitude. I do not think, however, that the available data allows the proposal of a reasonable explanation of character variation within the *lepidota* group. Consequently, I do not feel that there is much ground either for a discussion of the relationships of *C. britskii*. There remains not only a more extensive study of morphological variation within the *lepidota* group in the La Plata basin, but the forms in the São Francisco system and in northeast Brazil have to be thoroughly studied, and the *saxatilis*-like forms in northern South America probably should be included in a study of phyletic relationships.

From the other Paraná superior *Crenicichla* species, all belonging to the *C. lacustris* group (p. 653), *C. britskii* differs greatly. In these the maxilla reaches backwards only to about the margin of the orbit, and neither a humeral nor a pectoral spot is encountered. *Crenicichla jaguarensis* Haseman, has black dots along the lateral lines, and D. XIX-XXI.11-12, squ.long. 47-54. *Crenicichla haroldoi* Luengo & Britski also has black dots along the lateral lines, and D. XX-XXI.10, squ.long. 53-56. *Crenicichla jupiaensis* may be recognized on the more than ten narrow vertical bars across the sides, anteriorly naked cheek and few gill-rakers (5-6); D.XIX-XX.9-10, squ.long. 49-55. *Crenicichla britskii* resembles these forms in the rather low meristics, compared to closely related species outside the Paraná superior system.

The *lepidota*-like Ceará form resembles *C. britskii* in having a flank spot pattern; it seems to differ in a greatly reduced suborbital stripe, and in higher dorsal (D.XVIII.13)
and squ.long. (47-50) counts. The São Francisco form appears to lack the suborbital stripe completely.

Only Haseman (1911) appears to have reported this form previously, as C. lepidota. His 8 cm specimen from the Salto das Cruzes (not located on maps available), Rio Tietê, is said to have D.XVIII.15, A.III.9, Ll. 23 + 9, depth 3.75, head length 2.8 times in body length and eye diameter 5 times in head length. Fins and body were uniform dark brown with spots above the base of pectorals, at base of caudal, and in base of soft dorsal. That specimen would thus have a dorsal count not found in my material. The colour pattern resembles somewhat that of the holotype except for the dorsal fin spots.

**THE CRENICICHLA LEPIDOTA SPECIES GROUP**

*Diagnosis*. Although already referred to above, this group remains to be characterized: Medium-sized Crenicichla species in the La Plata river system, Lagoa dos Patos affluents, and northeastern coastal Brazilian rivers from the São Francisco system northwards to the state of Ceará. Scales large, squ.long. 33-52. Dorsal fin counts low, (XVI) XVII-XVIII (XIX). (12) 13-15 (16), D<sub>go</sub> (29) 30-32 (33). Vertebral count low, 18-19 + 13-16, total 32-34. Maxilla to one-third of orbit or slightly shorter. Lower jaw articulation behind middle of orbit. Lower jaw slightly prognath. CP/CP 75.8-114.9%. Gill-rakers 7-10. Preoperculum serrated. Nostril nearer orbit than snout tip. Sex dimorphism: males larger, soft dorsal fin pointed, prolonged; females with rounded soft dorsal fin, and well-rounded bellies when breeding. Sex dichromatism: both sexes darker when breeding, but females may become almost uniformly dark, to the extent that flank markings (spots, bands, vertical bars) do not appear; males with small spots on unpaired fins, females with more or less uniform unpaired fins, often with dark or light horizontal stripes in the dorsal fin, with or without contrasting black-on-white spots. Non-breeding color pattern in adults includes humeral ocellus below upper lateral line, above pectoral fin; black spot bordering pectoral axilla dorsally; caudal ocellus above lower lateral line level, and usually an uninterrupted suborbital stripe. No dorsal fin ocellus; suborbital stripe not in the shape of dots.

**INCLUDED SPECIES**

The diagnosis is based on *Crenicichla britskii*, the three populations of *C. lepidota* discussed above, and, as far as relevant data could be obtained, three more forms, described below. One of these cannot be separated from *C. lepidota*. The other two are essentially similar to *C. lepidota*, but nevertheless readily distinguished; they are regarded as distinct species. Thus, the group includes four species, with a southerly distribution in South America (Fig. 11):

*Crenicichla lepidota* (Rios Guaporé, Paraguay, Alto Paraná, Lagoa dos Patos system)

*Crenicichla britskii* (Rio Paraná superior)
*Crenicichla sp.*, undescribed (Rio São Francisco system)
*Crenicichla brasiliensis* (northeast Brazilian rivers)

*Crenicichla lepidota* Patos. The taxonomic status of the available material (p. 657) depends to some extent on the evaluation of the status of the Itabó Guazú form. There are no apparent distinguishing features in colour pattern or in other qualitative characters, compared to *C. lepidota* Paraguay. The unpaired fins are plain in females, spotted in
males; no females are available that show breeding coloration comparable to that of gravid Tagatya-Mi females. There is much variation in dorsal fin counts, but spine counts compare well with *C. lepidota* Acaray and Paraguay (cf. Table 2). One specimen has squ.long. 52 on both sides, but the scale pattern of that specimen is extraordinarily irregular and the squ.long. counts of the remaining specimens compare well with the values obtained in *C. lepidota* Acaray and Paraguay. It is nevertheless somewhat higher, with a mean clearly above that of *C. lepidota* Paraguay (cf. Table 3). The caudal peduncle is deeper than long (CP/CP 81.3-96.7%, \( \bar{x} = 88.9 \pm 1.21 \), for \( n = 15 \)), shorter (length 10.8-12.7% of SL, \( \bar{x} = 11.6 \pm 0.16 \) for \( n = 14 \)) and deeper (depth 12.2-13.5% of SL, \( \bar{x} = 13.0 \pm 0.10 \), for \( n = 14 \)) than in *C. lepidota* Itabó Guazú, similar to that of *C. lepidota* Paraguay and Acaray. The only character state shared with *C. lepidota* Itabó Guazú, distinct from that in the other forms, is the short caudal fin (25.4-26.2% of SL, \( \bar{x} = 26.3 \pm 0.33 \), for \( n = 4 \) (SL 56.1-120.3 mm). The gill-rakers are slightly fewer than in Paraguayan or Alto Paraná material of *C. lepidota* (8-11, \( \bar{x} = 9.4 \pm 0.21 \), for \( n = 15 \)).

The Patos form is certainly distinct from Paraguayan and Alto Paraná *C. lepidota* in the following combination of character states: squ. long. 42-49 (52), \( \bar{x} = 45.6 \); gill-rakers few, 8-11, \( \bar{x} = 9.4 \); dorsal spines mode 17; caudal peduncle deeper than long; caudal fin short, 25.4-26.2% of SL. It is different from *C. britskii, C. brasiliensis,* and *Crenicichla* sp. (São Francisco) in the color pattern, which is like that of *C. lepidota* Paraguay.

I regard the Patos form as a population of *C. lepidota* only provisionally, awaiting more material from especially the area between the Lagoa dos Patos affluents and the Rio Paraguay. It would seem to be differentiated e.g. by its own particular range of squ.long. count, but since that count is suspected to be merely a population characteristic within *C. lepidota*, too much stress cannot be placed on it. Including the Patos form in *C. lepidota* would have to be reconsidered.

*The São Francisco form.* I have examined only two specimens of this form (MZUSP unreg.). They are like *C. lepidota* Paraguay in normal coloration, but there is no trace of a suborbital stripe. The maxilla appears to be shorter, reaching only slightly beyond the margin of the orbit. The caudal peduncle is slightly deeper than long (CP/CP 85.2 and 92.8%). Dorsal fin counts XVII.13-14, squ.long. 39, gill-rakers 7.

*Haseman* (1911) reported *C. lepidota* from several localities in the State of Bahia, most of them in the São Francisco basin (p. 629, this paper). These had D. XVI.12-15, A. III.8-9, squ.long. 34-44 (method of counting not known). Haseman stressed the absence of “bars beneath the eyes”, so it appears that this character state may be characteristic of the São Francisco form. Interestingly, Haseman distinguished two forms, with a “complete series of intergradations”, exemplified by his series CM 2680 from Lagoa.
Pereira (cf. also CM 2693, same locality). One form showed “spots in the vertical fins, an ocellated caudal, and pectoral [humeral] spots”, and a body depth of 4.33 in body length. The other form was characterized by dark-edged, immaculate vertical fins, lack of caudal and humeral spots, and a depth of 4.17 in body length. Comparing with data on sex dimorphism in C. lepidota and C. britskii, it appears likely that the two forms are male (spotted fins) and female (dark-edged fins) of the same species.

The Nordeste form (C. brasiliensis). Only five specimens have been available for study, labelled simply Ceará 1972. Under the gill-covers are attached a small piece of paper stating the local name, Jacundá. All have D. XVIII.13; the squ.long. count varies slightly, 47-50. The suborbital stripe is reduced to a faint spot below the orbit. The flank pattern consists in a humeral ocellus, reaching upwards to the lateral line, a lateral band to the caudal ocellus, and above the lateral band six spots connected by faint bars with the dorsal fin. I tentatively regard these specimens as representing a distinct form within the lepidota group, characterized by the flank spots and the feebly developed suborbital stripe.

Fowler’s (1941) C. saxatilis from Lago Papari (Rio Grande do Norte), Rio Salgado, Icó and Rio Choró (Ceará), and Rio Pianci (Paraiba), Menezes (1953) Jacundá from Rio Malcozinhado (Ceará), and Piau Sabão from Brejão, Barbalha (Ceará), and Stark’s (1913) C. lepidota from Lago Papari, Lago Extremoz and Ceará Mirim (Rio Grande do Norte) may be referable to the Nordeste form. Starks described the life colours in some detail, distinguishing three phases, the first two of which may be of males, the third of a female, as a comparison with data on sex dimorphism in C. lepidota and C. britskii would suggest.

Since the Nordeste form has spots on the flanks, it is possible that it should be identified as C. brasiliensis (Bloch, 1792). That species is based on the Nhaquunda (variant spelling of Jacundá) in Marcgravius (1648), most likely described from material taken somewhere along the northeastern coast of Brazil, within the Dutch Brazilian colony (1637-1644). Bloch appears to have had no preserved material, but relied on earlier descriptions, and manuscript notes by the Count Moritz von Nassau. If a type-specimen would be discovered it would be of greatest interest, however, because neither Marcgravius’ (1648), nor Bloch’s (1792) descriptions and figures are of any greater use.

Comparing Marcgravius’ and Starks’ descriptions, a certain similarity becomes apparent; both forms obviously have a series of spots along the side. But these spots appear to be quite small in the Nhaquunda. I am not certain whether C. lacustris, which also has spotted body and dorsal fin, can be excluded from consideration, except by reference to distribution. The Dutch Brazilian colony extended from Ceará to Sergipe (Schneider 1938), including thus parts of the ranges of the Nordeste and São Francisco forms, but the northermost coastal locality for C. lacustris is Salvador (type-locality).

Pellegrin (1904) applied the name Crenicichla brasiliensis on several small-scaled Crenicichla forms, presently regarded as full species (C. strigata Günther, C. vittata Heckel, C. lenticulata Heckel, C. lugubris Heckel, C. johnna Heckel, C. cincta Regan, and C. marmorata Pellegrin). None of these is known from even anywhere near the range likely to have produced Marcgravius’ Nhaquunda material. Regan (1906) suggested that C. brasiliensis might be a senior synonym of Cichla temensis Humboldt, on the basis of apparent similarity of Bloch’s figure with two C. temensis juveniles from Santarém (BMNH 1896.6.29:151). I agree with Regan on the point of similarity, but Marcgravius’ species is said by him to grow to “seven, eight, or even ten fingers” (inches). At that size the C. temensis juveniles would have looked quite different had they been allowed to grow. Certainly, it is possible that the Nhaquunda/brasiliensis figures were based on
juveniles (cf. Regan 1905), but I would hold that for unlikely. Besides, the Crenicichla habitus of the Nhaquunda cannot be ignored. My proposal of C. brasiliensis as the name for the Nordeste form of the C. lepidota group, has one advantage besides referring to a degree of similarity, viz. the geographical location, otherwise it is no less a conjecture than Pellegrin’s or Regan’s suggestions. A final decision will have to wait until the northeast Brazilian Crenicichla species are subjected to a more thorough study.

**Comparison with other Crenicichla species**

Data on other Crenicichla species can be found in Regan (1905; 1913), Britski & Luengo (1968), Luengo & Britski (1974), Norman (1926) Kullander (1981a, b), and below. The lepidota group occupies the lower part of the squ.long. count range of the genus (33-130); the snout shape is also particularly distinctive, with the maxilla reaching as far as one-third of the orbit and the lower jaw only slightly prognathous. The component species are all very similar to each other, and probably closely related to each other phylogenetically. Because of insufficient data on the rest of the genus, nothing can be said about the phylogenetic position. Phenetically, there is a close affinity to C. saxatilis (Linnaeus) and similar species in central and northern South America; hence, these forms are given particular attention below.

The Crenicichla lacustris species group. All remaining Crenicichla species with a southerly distribution were recently referred to a lacustris group (Kullander 1981b). It is more heterogenous, and of a more provisional character than the lepidota group. The 16 nominal forms are distinguished by the extension of the maxilla (only to about the margin of the orbit), many dorsal spines (rarely 19, usually 20-23), moderate number

---

![Figure 12](image-url)

Heads of Crenicichla lacustris (left; MHNG 2027.87-90, 74.7 mm SL, Puerto Madryn, Argentina) and C. lepidota (right; MHNG 2028.1-26, 74.4 mm SL, Tagatya-Mi) illustrating differences between lepidota and lacustris group species in snout shape and suborbital stripe. Cheek markings vary in the lacustris group, but the spotted kind shown here is found in lacustris group species only. Cephalic lateralis pores indicated. Semischematic. The line represents 10 mm.
of squ.long. scales (about 60-70 generally, rarely as few as 45 or as many as 90), absence of humeral ocellus, frequently occurring large ocellus (or ocelli) on the middle of the dorsal fin, and frequently smooth preopercle margin. Sex dimorphism is not known. *Crenicichla vittata* Heckel is further distinguished by the very many lateral line scales on the caudal fin (up to 16 scales) and is maybe distinct. The endemic Paraná superior forms are distinguished by their low squ.long. and dorsal fin counts (see p. 648), and appear to represent an autochthonous, probably polyphyletic group within the *lacustris* group. The relationships of the group are obscure. It is similar to most northern forms in the high dorsal spine count and extension of the maxilla, possibly ancestral character states. There is nothing suggesting close relationship with the *lepidota* group.

*Crenicichla saxatilis* and similar forms. *Crenicichla saxatilis* is often mentioned in connection with *C. lepidota*, and these species are occasionally synonymized (cf. p. 629). Whereas the name *C. lepidota* is usually applied on large-scaled *Crenicichla* in the La Plata basin, and eastern and northeastern Brazilian river systems, the *Crenicichla* of similar appearance in the Amazonas and Orinoco basins and the Guianas, with but slightly higher squ.long. counts (more than 50) are commonly called *C. saxatilis*. A few similar forms are distinguished, and of these at least *C. alta* Eigenmann, 1912 (Guyana and Surinam), and *C. lucius* Cope, 1870 (Peruvian Amazon), appear to be specifically distinct. Boeseman (1960) suggested that *C. alta* may be a junior synonym of *C. frenata*, but confer Eigenmann's (1912) comment on their similarity in position of shoulder ocellus; also, one of the two syntypes of *C. vaillanti* Pellegrin, 1903 (MNHN 2993, Essequibo) agrees with *C. alta* (the second syntype, from La Mana, Guyane française, represents another species of uncertain affinity). Other nominal species close to or identical with *C. saxatilis auctt.* are *Cychla labrina* Spix, 1831 (mari Brasiliae), *Searus pavoninus* Gronovius (Gray), 1854 (Surinam), *Crenicichla pterogramma* Fowler, 1914 (Rupununi River, British Guiana), *C. saxatilis albopunctata* Pellegrin, 1904 (Surinam; Guyane anglaise; Guyane française), *Crenicichla frenata* Gill, 1858 (Trinidad, W.I.), *Crenicichla vaillanti* Pellegrin, 1903 (Essequibo; La Mana), *Cychla rutilans* Jardine, 1843 (Rio Branco; synonymized with *C. saxatilis* by Regan (1905), status not apparent to me), *Batrachops nemopterus* Fowler, 1940 (Contamana, Peru), *Crenicichla anthurus* Cope, 1872 (Ambyiacu), *C. proteus* Cope, 1872 (Ambyiacu River), and *C. proteus argynnis* Cope, 1872 (Ambyiacu River).

*Crenicichla saxatilis auctt.*, and to a greater or lesser degree the other species listed above resemble *C. lepidota* in the colour pattern, including humeral and caudal spot or ocellus and sex dimorphism; the scale and fin counts are only slightly higher. The confused taxonomic situation makes it difficult to evaluate the relationship of the *lepidota* group to the *saxatilis*-like forms, although the vicarying distributions and morphological similarity would seem to justify the assumption that these fishes are phyletically more close to each other than to any other *Crenicichla* species.

The description of *C. lepidota* (p. 631) extends the range of variation within that species considerably, so it would seem even that its distinction versus *C. saxatilis auctt.* is in danger. However, the latter species is not well defined. It is highly doubtful whether all *C. saxatilis* reported in the literature belong to a single species or are conspecific with *C. saxatilis* of Linnaeus. It appears that Bloch's figure (1792, pl. 307) has become the practical iconotype, and that all later determinations are for the species figured (cf. e.g. Eigenmann 1912). The Linnaean type-material has been completely ignored.

My preliminary conclusion, based on a literature survey and superficial study of Guianas, Orinocoan and Amazonian material, is that *C. saxatilis auctt.* is a composite, the component species of which are not recognizable until a larger material is subjected
to critical study. It is relevant to note here that most records of *C. saxatilis auett.* are founded on study of very limited material from particular localities. It thus appears to me that both nomenclatural and taxonomic objections can be raised against the identification of e.g. the Itabó Guazú form with *C. saxatilis*, although it would key out as that species using Regan’s (1913) key. Apparently, there are also some differences in counts: Two specimens (NRM 5583, 5585) that may possibly represent Linnaeus’ material of *Sparus saxatilis* (presumably from Surinam), both have the dorsal count XVIII.14; squ.long. counts are 52 and 53. The material is not in good condition and in other respects rather uninformative. Various *C. saxatilis* like material from the Amazonas and Orinoco drainages available, has generally 18 or 19 dorsal spines and squ.long. 55 to 63, conforming to *C. saxatilis sensu Regan* (1905; 1913 in part) and Pellegrin (1904), with slightly higher modal dorsal and squ.long. counts than *C. lepidota*, and also *C. semicincta* (cf. below).

Gronovius’ type-specimen of *Scarus pavoninus* Gronovius, 1854 (also a syntype of *C. saxatilis*) is a dried skin, described at length by Wheeler (1958). With only 17 dorsal spines and squ.long. c. 46 (my count) it is somewhat below *C. saxatilis*, to which species it is usually referred (e.g. by Wheeler 1958). In addition to the markings described by Wheeler, there is a trace of a suborbital streak. The specimen conforms better with *C. lepidota* than with *C. saxatilis auett.*, but not exactly with either.

The material described by Steindachner (1892) as “*Crenicichla saxatilis* Lin. (Var. *semicincta* Steind.)” from “Bolivia, Provinz Yuracares, im oberen Chaparé bei Puerto de San Mateo” (NMW 33482-33484; 9½, 10 and 17 cm total length), have 48, 50 and 52 scales in a series from the upper edge of the gill cleft to the base of the middle caudal rays as counted by Steindachner. No fin counts are given, and the rest of Steindachner’s description does not suffice to identify the material as belonging to any particular *lepidota* group form, although it is of interest as coming from a locality close to the Rio Guaporé, type-locality of *lepidota*. It may be noted though, that a pectoral spot is not mentioned. On my request, Harald Ahnelt has reexamined the specimens with regard to squ.long. and dorsal fin counts: With squ.long 50 (1) and 51 (2), according to my method, and D. XVIII.15 (2), XVIII.14 or 15 (1; posterior part of dorsal fin injured), this Bolivian form approaches Amazonian *C. saxatilis* rather than *C. lepidota* as defined in this paper. Only a more throughout study of Bolivian material can tell if *semicincta* is distinct from *C. lepidota*.

Pellegrin (1904) regarded *semicincta* as a “variété” (var.) of *C. saxatilis*, possibly a distinct species, but it is not certain what Steindachner intended with the name. On page 383, Steindachner (1892) lists his material in an “Übersicht der beschriebenen Arten” simply as “*Crenicichla saxatilis* sp. L.”, whereas “*Trygon pastinaca* sp. L., var. *marmorata*” occurs as such in the list, “Übersicht” and “Erklärung der Tafeln” (page 384). Any more recent reference to this form by Steindachner is lacking. The most straightforward conclusion is that *semicincta* is to be regarded as a subspecific name, with reference to the International Code of Zoological Nomenclature, Art. 45 (e) (i): “Before 1961, the use of either of the terms “variety” or “form” is not to be interpreted as an express statement of either subspecific or infrasubspecific rank, and their use is therefore to be interpreted as denoting subspecific rank.” No evidence given that *semicincta* is indeed a subspecies of *C. saxatilis*, it may be regarded as a full species of uncertain validity until a revision is made. Regan (1905) lumped it in the synonymy of *C. saxatilis*, but it should be noted then that he did not recognize infraspecific taxa and apparently never examined Steindachner’s material.

The Cabeza amarga of Uruguay determined as *Crenicichla saxatilis* by e.g. Devincenzi (1939) and Luengo (1971) appears to have about 50 to 60 scales in a horizontal
series and 17 to 21 dorsal spines. A comparison with Amazonian or Guianas material has evidently not been made, and I would regard the identifications as doubtful although the published data are far too insufficient to allow further speculations. It would be of interest rather to compare the Patos and Itabó Guazú forms of *C. lepidota* with the Uruguayan “*C. saxatilis*”. A specimen of *C. saxatilis* from Concordia, Entre Ríos, Argentina, figured by Ringuelet et al. (1967) is evidently a misidentified *C. lacustris* group species to judge from counts and colour pattern.

**MATERIAL**

*Crenicichla brasiliensis*

MZUSP 16055. Five specimens, 67.2, 68.8, 72.4, 72.9, 78.8 mm. Ceará. 1972.

*Crenicichla britski*


*Crenicichla lepidota* (Paraguay)

MHNG 2027.99-100. One ♂, 63.4 mm; one ♀, 83.1 mm. Paraguay, depto. Concepción, Puerto Max, Estancia El Postillón, small affluent of Arroyo León. 19 October 1979. Leg. Exp. MHNG to Paraguay, 1979 (Loc. 4). — MHNG 2028.1-26, NRM A80-3001. Fifteen ♂♂, 72.8*, 81.7, 86.2, 87.2, 87.9*, 91.0*, 91.4, 96.8, 96.8, 96.8, 98.0, 98.3, 103.0*, 103.3, 106.1* mm; eight ♀♀, 73.1, 74.0*, 75.4*, 76.9*, 78.1*, 78.6, 83.1, 88.4* mm; five juvs. (unsexable), 67.6, 68.0, 74.4, 74.5, 78.7 mm. Paraguay, depto. Concepción, Arroyo Tagatyá-Mi (about 30 km E Puerto Max). 20 October 1979. Leg. as preceding (Loc. 5). (Asterisk indicates material included in Table 1.) — MHNG 2028.27-29. Three juvs. (unsexable), 57.2, 61.1, 66.7 mm. Paraguay, depto. Concepción, between Estancia Estrellas and Estancia Primavera, (temporary ?) swamp in connection with Riacho La Paz. 16 October 1979. Leg. as preceding (Loc. 3). — MHNG 2028.30. One ♂, 69.8 mm. Paraguay, depto. Concepción, small arroyo, affluent of Tagatyá-Guazú, near Estancia Garay-Cué. 16-23 October 1979. Leg. as preceding (Loc. 6). — MZUSP 16023. Six specimens, 46.7, 73.1, 76.9, 77.1, 82.2, 123.4 mm. Brasil, Est. Mato Grosso, mun. Cáceres, Santo Inácio, la ponte da Rodovia Cáceres-Porto Limão. 26 March 1977. Leg. CEPIPAM. (D and squ. long, counts.) — MZUSP 16024. Four specimens

_Crenicichla lepidota (Acaray)_

MHNG 2028.31-39, Six ♀♀, 69.4, 70.5, 76.4, 77.5, 79.1, 87.5 mm; three juvs. 44.8, 62.5, 64.5 mm. Paraguay, depto. Alto Parana, R. Acaray, under road bridge near Puerto Presidente Stroessner. 8 November 1979. Leg. Exp. MHNG to Paraguay, 1979 (Loc. 8.) — MHNG 2061.90-100, 2062.1-3, NRM unreg. Four ♂♂, 94.3, 95.2, 106.9, 130.9 mm; four ♀♀, 74.9, 87.6, 98.2, 101.2 mm; seven juvs. (unsexable), 50.9, 52.3, 67.8, 75.2, 75.5, 75.7, 76.4 mm. Paraguay, depto. Alto Paranan, barrage lake Acaray. 30 April 1980. Leg. C. Dlouhy (coll. no. 637). — MHNG 2088.38-51. One ♂, 90.5 mm; nine ♀♀, 63.9, 67.6, 69.6, 70.7, 71.2, 72.3, 75.8, 78.3, 79.0 mm; four juvs., 57.5, 66.8, 68.1, 68.6 mm. Paraguay, depto. Alto Paranã, Arroyo Acaray, below the barrage. 7 October 1980. Leg. C. Dlouhy (coll. no. 770).

_Crenicichla lepidota (Itabó Guazu)_

MHNG 2028.40-47. One ♂, 91.1 mm; one ♀, 112.5 mm; six juvs. and unsexable, 49.7, 57.3, 63.3, 75.5, 84.5, 87.5 mm. Paraguay, depto. Alto Paranã, Arroyo Itabó Guazu, near confluence with R. Alto Parana. 5 November 1979. Leg. Exp. MHNG to Paraguay, 1979 (Loc. 7).

_Crenicichla lepidota (Patos)_

141.6, c. 190 mm; one ♀, 149.4 mm. Same data as preceding. — MZUSP 16035. Six specimens, 51.4, 56.9, 57.5, 63.1, 72.5, 78.5 mm. Brasil, Est. Rio Grande do Sul, valley at km 16 on BR-116 (Porto Alegre-Pelotas). 21 September 1977. Leg. Expedition of the MZUSP and USNM. — MZUSP 16036. Two ♂♂, 62.8, 120.3 mm; one ♂, 71.3 mm; one juv., 56.1 mm. Brasil, Est. Rio Grande do Sul, road Rio Grande — Cassino, Arroio do Vieira. 11 December 1979. Leg. Expedition of the MZUSP and USNM.

Crenicichla sp. (São Francisco)


Comparative material


Summary

The taxonomy of the genus Crenicichla, with about 30 strictly South American species, is unclear both at genus and species level (p. 627). In this paper, an attempt is made towards a revision of the large-scaled forms in the La Plata drainage system. The results are not definitive, due probably rather to limited material than to uncertainty about character states. A major problem encountered is, however, the evaluation of
statistical differences between samples of what is here regarded as *Crenicichla lepidota*. In the absence of qualitative distinguishing features, I have regarded the slight morphometric and meristic differences as representing population differences. Geographical populations distinguished in addition by colour pattern are given species rank (pp. 642, 650, 652). All of the large-scaled *Crenicichla* studied show great conformity with respect to body shape and colour pattern, and may also be distinguished from all other *Crenicichla* species by the rather low counts, so that it appears warranted to recognize a species group, called here the *lepidota* group (p. 649). But this is largely a phenetic unit, because similar forms in northern South America remain to be studied and compared to the *lepidota* group species. These northern species are *C. saxatilis* and over a dozen similar nominal species of mostly uncertain status (p. 654).

The *Crenicichla lepidota* group contains four species:

*Crenicichla lepidota* (p. 629), originally described from the Rio Guaporé. Four populations are recognized: Paraguay, in the Paraguay system; Acaray, from Alto Paraná (Rio Acaray) samples; Itabó Guazú, from a single Alto Paraná series (Arroyo Itabó Guazú); Patos, from series collected in Lagoa dos Patos tributaries. The populations differ chiefly in scale and dorsal fin counts. Sex dimorphism is strong in at least *C. lepidota Paraguay*, of which breeding specimens are available. These are very dark-coloured compared to non-breeding specimens. Females are plump, with short, immaculate fins, and a contrasting pale submarginal zone in the dorsal fin. Males are slender and grow larger; the unpaired fins are spotted and the soft dorsal fin extended.

*Crenicichla britskii* is described from the Paraná superior (p. 642). It has rather low counts and a series of blotches along the side.

*Crenicichla* sp. Säo Francisco (p. 650), remains to be formally described. Characteristically, it lacks the stripe across the cheek found in the other *lepidota* group species. It is apparently endemic to the Säo Francisco drainage system in Brazil.

*Crenicichla brasiliensis* (p. 652), is the name given to the *lepidota* group species in the Nordeste of Brazil. It may be characterized by flank spots and reduced suborbital stripe. The identification with *Perca brasiliensis* Bloch, 1792, an insufficiently described species of which no type-material is known, is far from certain, but represents apparently the best conjecture so far.

**LITERATURE**


THE CRENICICHLA LEPIDOTA SPECIES GROUP


**View This Item Online:** [https://www.biodiversitylibrary.org/item/128872](https://www.biodiversitylibrary.org/item/128872)

**DOI:** [https://doi.org/10.5962/bhl.part.82465](https://doi.org/10.5962/bhl.part.82465)

**Permalink:** [https://www.biodiversitylibrary.org/partpdf/82465](https://www.biodiversitylibrary.org/partpdf/82465)

**Holding Institution**
Smithsonian Libraries and Archives

**Sponsored by**
Biodiversity Heritage Library

**Copyright & Reuse**
Copyright Status: In Copyright. Digitized with the permission of the rights holder.
Rights Holder: Muséum d'histoire naturelle - Ville de Genève
License: [http://creativecommons.org/licenses/by-nc-sa/3.0/](http://creativecommons.org/licenses/by-nc-sa/3.0/)
Rights: [https://www.biodiversitylibrary.org/permissions/](https://www.biodiversitylibrary.org/permissions/)

This document was created from content at the Biodiversity Heritage Library, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at [https://www.biodiversitylibrary.org](https://www.biodiversitylibrary.org).