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REVISION OF THE NEOTROPICAL CICHLID GENUS *GYMNOGEOPHAGUS* RIBEIRO, 1918, WITH DESCRIPTIONS OF TWO NEW SPECIES (PISCES, PERCIFORMES)

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ABSTRACT

The Neotropical cichlid genus Gymnogeophagus *Ribeiro, 1918 is revised. The following species are considered valid and are redescribed:* G. rhabdotus *(Hensel, 1870),* G. gymnogenys *(Hensel, 1870),* G. labiatus *(Hensel, 1870),* G. balzanii *(Perugia, 1891) and* G. australis *(Eigenmann, 1907). In addition, two new species are described:* G. lacustris, *sp. n., from the coastal region of southern Brazil and* G. meridionalis, *sp. n., from the lower Rio Paraná and Rio Uruguay systems. Lectotypes are designated for* Geophagus bucephalus *Hensel, 1870 (=* G. labiatus*) and* Geophagus scymnophilus *Hensel, 1870 (=* G. labiatus*) and the phylogenetic relationships among the species are analyzed. An osteological description based mainly on* G. meridionalis *is presented. A map of species distribution and a key to the species are provided.*

INTRODUCTION

The genus *Gymnogeophagus* was originally proposed by Ribeiro, 1918 and included a single species: *G. cyanopterus* (= *G. balzanii*), from southern Brazil. Gosse, 1976, in his "Revision du genre *Geophagus*...", distinguished four species sharing two important osteological characters — the absence of supraneurals, and the presence of a forward directed spine on the top of the first dorsal pterygiophore: *G. balzanii* (= *G. cyanopterus* and *Geophagus duodecimspinosus* Boulenger, 1895), *G. gymnogenys* (= *G. labiatus, G. bucephalus, Geophagus pygmaeus* Hensel, 1870 and *G. scymnophilus*), *G. rhabdotus* (= *Geophagus camurus*

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Cope, 1894 and *Geophagus brachyurus* Cope, 1894) and *G. australis*. The synonymy proposed by Gosse is significantly re-arranged in the present paper. That author united the four species as a monophyletic assemblage he termed the genus *Gymnogeophagus*. In his study, however, Gosse primarily used long preserved color-less specimens, resulting in a poor definition of species and a useless key.

Kullander, 1981 studying some specimens from Rio Grande do Sul recognized a thick-lipped *Gymnogeophagus* species, resurrecting *G. labiatus* from the synonymy of *G. gymnogenys*.

The two characters used by Gosse in redefining *Gymnogeophagus* are reinterpreted in light of Hennig's, 1966 principles. The spine on top of the first dorsal pterygiophore has proved to be a synapomorphy for the genus, being unique among Neotropical cichlids. The absence of supraneurals, however, although a very good key-character, must be used with caution in a phylogenetic analysis. This reduction seems likely to have occurred independently in various cichlid genera. However, within Geophagines — a probably monophyletic assemblage (Kullander, 1980a), including those genera with an epibranchial lobe: *Acarichthys, Biotodoma, Geophagus, Gymnogeophagus, Papiliochromis Retroculus, Apistogramma, Apistogrammoides, Biotoecus* and *Taeniacara* — this reduction evidently occurred only once and may be assumed to be synapomorphic for *Gymnogeophagus*.

MATERIAL AND METHODS

Description are base on alcohol preserved specimens except where otherwise stated, from collections in the following Institutions:

ANSP: Academy of Natural Sciences of Philadelphia, Philadelphia.
BM (NH): British Museum (Natural History), London.
CAS: California Academy of Sciences, San Francisco.
CECN: Centro de Estudios de Ciências Naturales, Montevideo.
CIMLP: Museo de La Plata, La Plata.
DZUFRGS: Departamento de Zoologia, Universidade Federal do Rio Grande do Sul, Porto Alegre.
FMNH: Field Museum of Natural History, Chicago.
IUM: Indiana University Museum (specimens now at CAS).
MACN: Museo Argentino de Ciências Naturales "Bernardino Rivadavia", Buenos Aires.
MAPA: Museu Anchieta, Porto Alegre.
MCP: Museu de Ciências da Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre.
MCZ: Museum of Comparative Zoology, Cambridge.
MHNG: Muséum d'Histoire Naturelle de Genève, Genève.

MZUSP: Museu de Zoologia da Universidade de São Paulo, São Paulo.
NRM: Naturhistoriska Riksmuseet, Stockholm.
USNM: National Museum of Natural History, Smithsonian Institution, Washington, D.C.
ZMB: Museum für Naturkunde der Humboldt-Universität, Berlin.

The material examined of each *Gymnogeophagus* species is listed before the description of each species and comparative material is given at the end of the paper. Data include museums abbreviations and catalogue number, number of specimens in parenthesis, collecting locality, date and collectors.

The synonymy for each species are limited to original species descriptions. The morphometric and meristic data were taken as shown on figure 1. Proportions are expressed as ratios in table 3, with minimum and maximum values given and the mean in parenthesis. The regression data were computed through routine statistical methods and are presented in table 4.

Description of color in life are based on observations of living specimens and/or color photos taken just after collection of the specimen.

The osteological observations were made on cleared and alizarin-stained material (Taylor, 1967 enzyme method) and the drawings sketched with a stereomicroscope and "camera lucida". At least two specimens of each *Gymnogeophagus* species, except *G. australis,* were cleared, alizarin-stained and dissected for osteological observations. Radiographs were made of *G. australis* paratypes. An attempt was made to use specimens of aproximately the same size. Larger specimens were also prepared, in order to look for ontogenetic differences.

The phylogenetic analysis follows the principles of Hennig, 1966 and further contributions by several other authors.

Definition of counts and measurements
(Fig. 1)

1. Scales in a longitdinal series.
2. Scales in upper portion of lateral line.
3. Scales in lower portion of lateral line.
4. Scales between dorsal fin origin and upper portion of lateral line.
5. Scales between anal fin origin and upper portion of lateral line.
7. Body depth (BD): taken at the point of maximum depth; ratio expressed in HL.
8. Eye diameter (ED): taken horizontally between the orbital bony margins; ratio expressed in HL.
9. Head depth (HD): taken vertically from the lower point of the interopercule; ratio expressed in HL.
10. Head length (HL): from upper lip to posterior bony margin of oper-

cle; ratio expressed in SL.

11. Head width (HW): taken at the point of maximum width; ratio expressed in HL.
12. Interorbital width (IW): taken at the point of least bony width; ratio expressed in HL.
13. Length of caudal peduncle (CpL): from the end of dorsal-fin base to the hypural joint; ratio expressed in HL.
14. Post-orbital length (PoL): from posterior rim of orbit to the bony posterior margin of opercle; ratio expressed in HL.
15. Pre-orbital length (PrL): from the lower margin of the lachrimal (just above the maxilla) to the orbital rim; ratio expressed in HL.
16. Snout length (SnL): from the projection of a line from anterior margin of the upper lip to anterior orbital rim; ratio expressed in HL.
17. Standard length (SL): from upper lip to the hypural joint; expressed in millimetres.

List of abbreviations:

		IHY	Interhyal
		IO	Infraorbital
AA	Anguloarticular	IOP	Interopercle
BB	Basibranchial	LAC	Lachrymal
BH	Basihyal (= Glossohyal)	LET	Lateral ethmoid
BOC	Basioccipital	LPTP	Lower pharyngial toothplate
BPT	Basipterygium	M	Maxilla
BR	Branchiostegal rays	MET	Mesethmoid
BSP	Basisphenoid	MPT	Metapterygoid
CB	Ceratobranchial	N	Nasal
CHY	Ceratohyal	NAP	Neurapophysis
CL	Cleithrum	NS	Neural spine
Cl&St	Cleared and stained specimen	OP	Opercle
COR	Coracoid	P	Palatine
D	Dentary	PAR	Parietal
DHHY	Dorsal hypohyal	PB	Pharyngobranchial
DP	Dorsal pterygiophore	PHY	Parhypural
DPCL	Distal postcleithrum	PM	Premaxilla
DS	Dorsal spines	POO	Prootic
EB	Epibranchial	POP	Preopercle
ECT	Ectopterygoid	PPCL	Proximal postcleithrum
EHY	Epihyal	PS	Parasphenoid
ENT	Entopterygoid	PS1	First pterygiophore spine
EP	Epural	PT	Posttemporal
EPO	Epiotic	PTO	Pterotic (= Supratemporal)
EXO	Exoccipital	PTS	Pterosphenoid
EXSC	Extrascapular	Q	Quadrate
F	Frontal	RA	Retroarticular
FM	Foramen magnum	RS	State of Rio Grande do Sul
HAP	Hemapophysis	S	Symplectic
HB	Hypobranchial	SC	State of Santa Catarina
HY	Hypural	SCA	Scapula
HYM	Hyomandibular	SCL	Supracleithrum
HYO	Hyoid	SO	Supraoccipital
IC	Intercalar	SOP	Subopercle
		SPO	Sphenotic

TL	Total length	UTP4Fourth	
U	Urostyle	V	Vomer
UH	Urohyal	VHHF	Ventral hypohyal
UN	Uroneural	VR	Ventral rays

Gymnogeophagus Ribeiro, 1918

Gymnogeophagus Ribeiro, 1918: 790-1 (Type-species by monotypy: *Gymnogeophagus cyanopterus* Ribeiro, 1918 — junior synonym of *G. balzanii*).

Etymology: From the greek: *gymno,* meaning naked, probably after its naked snout; *geo,* meaning earth and *phagus,* meaning eater, probably after its hypothesized nearest relative, *Geophagus.* Gender masculine.

Diagnosis: The genus *Gymnogephagus* is distinguished from other Neotropical cichlid genera by the combination of the absence of supraneurals and the presence of a small bony forwardly directed spine on the top of the first dorsal pterygiophore (Fig. 13).

Description: *Gymnogeophagus* species are among the large geophagines (sensu Kullander, 1980a). *G. balzanii* is apparently the larger species, with a maximum SL of 169 mm. *Gymnogeophagus meridionalis* seems to be the smallest species with maximum SL of 88 mm.

Body laterally compressed. Dorsal contour strongly and evenly arched *(G. balzanii)* or cnspicuously divided in two segments with different degrees of arching: a steep anterior portion from snout tip to origin of dorsal fin (somewhat straight in *G. rhabdotus*) and a less steep arched segment from that point to caudal peduncle. Ventral profile gently arched, with somewhat straight segment between insertions of pelvic and anal fins. Caudal peduncle shape highly variable among species; uniform within each species.

Head roughly triangular; mouth terminal. Numerous conical small teeth in upper and lower jaws; outer teeth more strongly developed than inner ones. Teeth moderately recurved posteriorly distally and not arranged into conspicuous series.

Body covered with ctenoid scales, except for pre-ventral region which may bear cycloid scales. Cheeks with an area of variable size covered with ctenoid and cycloid scales (size of scaled area differs with species). Operculum with some cycloid and ctenoid scales, usually irregulary scattered. At least proximal third of caudal fin covered with ctenoid scales regularly arranged into a single series between rays. In *G. balzanii* at least proximal half of fin is scaley with two or more series of scales between rays.

Dorsal fin with 12 to 15 spines and 8 to 15 branched rays. Anal fin with 3 spines, except for a few aberrant individuals with two - or four-spined anal fins.

All species have a typical color pattern of double vertical cross bands and a more or less conspicuous dark spot on the flank. Body, head and fins of living fish highly colored, with distinctive pattern for each species.

The secondary sex dimorphism not always conspicuous; large males with tips of anal and dorsal fins slightly longer than females which, in turn, are usually more palid than males. Nuptial males (?) develop a small *(G. rhabdotus)* to very big *(G. gymnogenys)* adipose hump on top of head. Exact origin and behavioral aspects of this hump deserve further studies.

Very little is known about chromosomes in *Gymnogeophagus* species with only a study by Pereira, 1983 on *G. rhabdotus* available. In five specimens of *G. rhabdotus* that author found that for the species 2n = 48 with three metacentric chromosomes, ten chromosomes with short arms (including hardly discernible sub-metacentric and acrocentric ones) and eleven telocentric chromosomes.

Gymnogeophagus species are, as typical for cichlids, brood-caring fishes. *Gymnogeophagus balzanii, G. gymnogenys, G. labiatus* and *G. lacustris* are mouth-breeders while *G. rhabdotus* and *G. meridionalis* are substrate-breeders. No information is available on the habits of *G. australis.*

The following common names are used for various *Gymnogeophagus* species: Brazil — Cará, Acará, Cará-cartola, Cará-topete, Cará-manteiga and Palometa; Uruguai — Castañeta and Chanchita; Argentina — Castañeda and Chanchita; Paraguay — Pirámbocadyá (for *G. balzanii,* after Fowler, 1954).

Distribution: La Plata basin and small river systems flowing into the Atlantic in Uruguay and Rio Grande do Sul and Santa Catarina states of Brazil (see maps on Figs. 2, 3). A single record of *G. balzanii* (CAS 48828) is known from the Amazon River basin, in the Guaporé river, which has natural connection with the headwaters of the Paraguayan tributary Rio Jaurú around 15°S and 59°W (Lowe-McConnell, 1975:47), where the species seems to be very common. Also very interesting is the fact that prior to the construction of the Itaipu hydreletric dam, no *Gymnogeophagus* species were found in the Paraná River basin upstream of Guaíra, Paraná state. The absence of the genus from that portion of the basis was probably a consequence of the major falls "Sete Quedas", at Guaíra, which acted as a natural barrier for upstream dispersion. With the construction of the Itaipu dam in 1983 and consequent disappearance of this natural barrier, *Gymnogeophagus,* as well as other fish, may invade the Paraná river and its tributaries upstream of Guaíra.

Although the available geographic cladogram (after Beurlem, 1970 reconstruction of tertiary-quaternary development of most South American drainage basins) is partially congruent with our phylogenetic reconstruction within *Gymnogeophagus,* no biogeographic hypothesis is made as a consequence of the absence of distributional data from several localities. Furthermore, no other phylogenetic reconstruction of another group found in the region was available for comparison with *Gymnogeophagus* making a vicariance analysis impossible.

From the distributional data of *Gymnogeophagus* and its sister-group (one of the large Geophagines, all present in the Amazon basin) one can infere that the genus *Gymnogeophagus* might have evolved from a vicariant event of isolation of the Paraná-Paraguay drainage basin from the northern basins occurred in the late tertiary (Beurlen, 1970).

Gymnogeophagus lacustris is restricted to the coastal lagoon system of Southern Brazil, which is geologically very recent, derived from the Holocenic regression (Jost, 1971). Either it is a very new species — that is, product of a very recent speciation event — or it has become totally extinct outside this area.

Key to the *Gymnogeophagus* species

1. Longitudinal series with 22-25 scales 2
1'. Longitudinal series with 26-28 scales 3
2. Dorsal and anal fins with well-defined circular dots (Fig. 18) ....
.... *G. meridionalis* sp. n.
2'. Dorsal and anal fins with small stripes (Fig. 19) ....
.... *G. rhabdotus*
3. Dorsal fin with 12-15 branched rays; caudal fin almost completely scaled, with lateral line ramus in its lower lobe ....
.... *G. balzanii*
3'. Dorsal fin with 8-12 branched rays; caudal fin with scales restricted to the proximal third or half, without lateral line ramus in its lower lobe 4
4. Dark band extends posteroventrally from the dorsal fin origin; well-defined circular dots on dorsal, anal and especially caudal fins 6
4'. Dark band from nape to cheek crossing the eye instead of the band described above; dorsal, anal and especially caudal fins with rather small stripes 5
5. Lips thick, extremely well developed, lower lip deeply notched medially .... *G. labiatus*
5'. Lips normal, not excessively developed or notched ....
.... *G. lacustris* sp. n.
6. Dorsal profile of body anterior to dorsal fin origin very steep (Fig. 19); soft dorsal fin scaly; caudal peduncle depth 0.9 in its length ......
.... *G. australis* (*)
6'. Dorsal profile of body anterior to dorsal fin origin not as steep (Fig. 19); soft dorsal fin rarely scaled; caudal peduncle depth 1.0-1.4 in its length .... *G. gymnogenys*

(*) Based on type-specimens only; distinctions between this species and *G. gymnogenys* is tentative — see discussion in Remarks.

Osteology

The osteological drawings and comments are primarily based on a 60 mm SL specimen of *G. meridionalis* (MAPA 2225). Only significant differences in the other species are discussed. The relative position and shape of individual bones are not described since complete drawings are presented.

Infraorbital series: (Fig. 4). The first infraorbital is fused to the "lachrymal" (Kullander, 1983), forming a roughly squarish plate with four sensory canal pores, herein named lachrymal. In larger specimens the lachrymal tends to be relatively more elongate than in small individuals. Infraorbitals 3 and 4 are also fused into a single bone with two terminal and a median pore indicating such a fusion. Infraorbitals 3 + 4 and 5 are occasionally fused together. Infraorbitals 2 and 3 + 4 are laminar in *G. rhabdotus* and *G. meridionalis*. In *G. labiatus* and *G. gymnogenys* the laminar wings are very small and in *G. lacustris* and *G. balzanii* the bones are instead tubular. Infraorbitals 5 and 6 (dermosphenotic) are always tubular.

The nasal is tubular (Fig. 6 and 9), bearing the supraorbital sensory canal and with a broad lateral wing along half its length.

Neurocranium: (Fig. 6-9). The specimen in MAPA 2225 has a 16.1 mm long skull (from vomer tip to basioccipital condyle). The skull is roughly triangular in lateral view. The supraoccipital and the frontals form a well-developed crest with a widely grooved edge specially in larger specimens. The frontal has four openings for the supraorbital sensory canal, the anterior most in contact with the nasal and the last one adjoining the pterotic. The pterotic has three sensory pores with the most anterior in contact with the frontal. A lateral crest extending along the frontal, parietal and epiotic bones is also present. This crest is smaller in *G. gymnogenys*, *G. lacustris* and *G. labiatus*. The outer portion of epiotic is attached to the posttemporal. The ventral portion of parasphenoid is somewhat laterally compressed and has a large pharyngial apophysis attached to the third pharyngobranchial.

Gill-cover: (Fig. 5). The caudal portion of subopercle is unossified even in large specimens. The preopercle bearing a bone-enclosed sensory canal, with two terminal and four medial pores; its postero-ventral margin is entirely smooth.

Suspensorium and jaws: (Fig. 5). The hyomandibular has an articulation condyle with two points of contact with the skull and a smaller opercular articulation process. The metapterygoid, symplectic, quadrate, ectopterygoid and entopterygoid are rather laminar bones. The palatine has a long rostral process articulating with the maxilla. The maxilla has an inner premaxillary articular condyle and a flattened ventral wing reaching the dentary. The premaxilla has a long ascending process. The dentigerous premaxilla arm is short and laterally flattened. The anguloarticular with two sensory canal pores, one facing the inferior preopercular pore and the other facing the first dentary pore. The retroarticular is small and separated from the anguloarticular by a hardly visible suture. The dentary with five sensory canal openings, the first one facing the last anguloarticular pore.

Hyoid and branchial arches: (Fig. 10-13). The hyoid arches have five branchiostegal rays. The interhyal is short, articulating with the cartilage separating the symplectic and the hyomandibular. The basihyal is long, covering part of the first basibranchial in dorsal view.

There are four gill-arches. The fourth ceratobranchial has 2-5 small dentigerous plates (2-3 in *G. rhabdotus* and *G. meridionalis,* 3-5 in *G. lacustris* and 2-4 in remaining species). The well-developed lower pharyngial tooth-plate is roughly triangular in dorsal aspect. Of three dissected *G. rhabdotus* one has small rakers on lower pharyngeal tooth-plate margin. No other dissected specimen of *Gymnogeophagus* bears such rakers. The phylogenetic value of this character is doubtful, but the presence of such rakers in other Geophagines may indicate a plesiomorphy. The first epibranchial has widely separated medial arms (Fig. 10) — which become very close in larger specimens — and a large flattened ventral expansion which supports the characteristic fleshy lobe. Second epibranchial also with a large laminar expansion. Upper pharyngeal jaw paired and slightly separated, including the second and third pharyngobranchial and corresponding tooth-plates and the fourth upper tooth-plate. Upper pharyngeal jaw attachment to the skull is via the first pharyngobranchials and by the articular process on the dorsal surface of the third pharyngobranchial. Such an articulation is extremely movable, allowing complex pharyngeal jaws movements.

The urohyal is roughly triangular in lateral view, with paired ventral wings and a conspicuous spiny process dorsally. The caudal margin of urohyal may be very irregular.

Pectoral girdle: (Fig. 17). Four bones bear sensory canals, the supracleithrum, posttemporal and two extrascapulars. The supracleithrum of *G. lacustris* is very narrow, surely an autapomorphy (see Phylogenetic Relationships section). Attachment to the skull is via the posttemporal-epiotic union. A very small tubular third extrascapular may be rarely present (this third extrascapular is show in Fig. 17). The cleithra of both sides are united ventrally by a symphyseal attachment. Scapula and coracoid widely attached to the cleithrum and conspicuously separated from each other. The scapula with a large median foramen. Proximal and distal postcleithrum are rather laminar and posteroventrally directed. Pectoral fins with 13 soft rays modally, the third the longest.

Pelvic girdle: (Fig. 16). The basipterygium reaching the ventral tip of cleithrum. Well-developed anterior and posterior median process are present. One spine and five branched soft rays are always present.

Dorsal fin: (Fig. 14). No supraneurals are present. Ventral tips of both first and second pterygiophore lying vertically between first and second neural spines. First pterygiophore with a well-developed forward directed spine — the main synapomorphy for the species of *Gymnogeophagus.*

Caudal fin: (Fig. 15). Three upper and two lower separate hypurals. The parhypural supports a slender parhypural-spine which is highly variable in size, being frequently of different size on either side of the same individual. The parhypural as well the second hemapophysis are autogenous. The second neurapophysis is short and broadly contacts the uroneural. Two epurals, the first of which may be in contact with the second neurapophysis. Proximal tip of the first epural in different individuals ranges from truncate to very irregularly shaped. Urostyle also with considerable variability in size and shape. Eighty principal and three to five procurrent rays are present in both the superior and the inferior lobes.

Gymnogeophagus balzanii (Perugia, 1891)
(Fig. 18)

Geophagus balzanii Perugia, 1891 (Type-locality: Vila Maria, Mato Grosso, Brazil).

Geophagus duodecimspinosus Boulenger, 1895 (Type-locality: Paraguay).

Gymnogeophagus cyanopterus Ribeiro, 1918 (Type-locality: Itaqui, Rio Grande do Sul, Brazil. Type-species of *Gymnogeophagus*).

Etymology: *Geophagus balzanii* was named in honour of Luigi Balzani, collector of the holotype.

Holotype: number 7683 in Museu Civico di Storia Naturale "Giacomo Doria", Genova (102 mm TL).

Specimens examined

Type-material: MZUSP 2549 (holotype of *G. cyanopterus),* Itaqui, RS, Brazil, 1914, E. Garbe leg.

Argentina:
MACN 3956 (3 ex.), Lagunas del Regimiento, Camino de Barranqueras, Chaco, H. Arrenti leg. MAPA 2215 (3 ex.), Bela Vista, Corrientes.

Bolivia:
FMNH 54210 (5 ex.), Puerto Suarez, 1909, J. D. Haseman leg.

Brazil:
CAS 48828 (2 ex.), Rio Guaporé at Santo Antônio de Guaporé, Brazil, 23.VII.1909, J. D. Haseman leg. FMNH 54206 (1 ex.), Campos Alegres, Mato Grosso, 1909, J. D. Haseman leg. FMNH 54209 (3 ex.), São Luiz de Cáceres, Mato Grosso, 1909, J. D. Haseman leg. FMNH 54208 (6 ex. 2 Cl&St), Corumbá, Mato Grosso do Sul, 1909, J. D. Haseman leg.

FMNH 54207 (1 ex.), Uruguaiana, RS, 1909, J. D. Haseman leg. MAPA 2304 (1 ex.), Rio Uruguai at Vila São Marcos, Uruguaiana, RS, 6. V. 1984, R. E. Reis leg. MAPA 2508 (5 ex.) and 2520 (1 ex.), Barragem de São Marcos, Uruguaiana, RS, 17.XI.1984, R. E. Reis & L. R. Malabarba leg. USNM 270288 (2 ex.), Rio Quaraí, Barra do Quaraí, RS, 16.XI.1984, L. R. Malabarba & R. E. Reis leg.

Paraguay:

FMNH 52570 (2 ex.), Asunción, J. D. Anistis leg. MCZ 15240 (2 ex.), Paraguay, mid-1800's, Capt. Page leg. MCZ 15763 (1 ex.), Paraguay, mid-1800's, Capt. Page leg.

Description

Standard length of examined specimens 28 to 169 mm. Other meristic and morphometric data are summarized in tables 2 and 3.

Body very deep and robust. Predorsal contour somewhat straight in specimens up to about 80 mm SL or gently arched in larger individuals. Body contour at dorsal fin base strongly convex. Caudal peduncle very deep and short with slightly concave dorsal profile and usually straight ventral profile. Ventral contour gently arched from lower lip to last anal-fin ray.

Preorbital length usually equal to snout length. Eye diameter equal to snout length in specimens of about 60 mm SL; smaller in larger specimens.

Body scales moderately large and ctenoid; smaller in preventral region. Cheek and gill-cover almost completely covered with typically ctenoid scales; isthmus under branchiostegal membrane with very small ctenoid scales. Spiny dorsal with few scales; soft dorsal fin almost completely covered with mainly ctenoid scales. Anal fin base with a few ctenoid scales. At least proximal half of caudal fin covered with minute ctenoid scales, usually in two series between rays.

Dorsal fin usually originating anterior to a vertical line through posterior bony margin of opercle. Fifth to eighth dorsal fin rays the longest, reaching caudal fin base in young, and sometimes reaching caudal fin tip in large specimens. Pectorals reaching middle of anal fin base. Pelvics reaching to or falling slightly short of anal fin origin, except for very large specimens, in which pelvics may reaches third anal spine. Anal fin reaching caudal fin base in small specimens or extending one-third length of caudal in larger individuals. Caudal fin assymetric in adult specimens, with inferior lobe shorter than superior, bearing one or two branches of latero-sensory canal in lower lobe.

Color in life: ground color of dorsal surface light-olivaceous, yellowish ventrally. About seven transverse double dark cross-bands and an indistinct midlateral spot uniting third and fourth cross-band, just below upper segment of lateral line. Distinct dark band from nape to below eye, usually reaching inner angle of preopercle. Iris and snout darker than back. Abdomen in front of ventrals, isthmus and branchiostegal membranes yellowish. Small bright-blue dots of various sizes and shapes scattered on cheek, gill-cover and over flank. Pectorals hyaline; ventrals yellowish with bright-blue marks. Dorsal fin reddish with small obliquous bars in spined anterior portion and small whitish dots on soft part. Anal fin reddish with blue marks. Proximal half of caudal fin slightly reddish, hyaline distally. Color in alcohol: general appearance in preserved specimens paler. The bright-blue marks disappears and the red pigmentation become dark-olivaceous to gray-brown.

Remarks

Apparently the only *Gymnogeophagus* species inhabiting the Paraguay River system, as well as the only one known from the Amazon basin (see comments on "Distribution" of the genus for details).

Reproductive habits are described in aquarium literature: see Axelrod & Vorderwinkler, 1974:528-9 for a color photo of a female *G. balzanii* with young in its mouth.

Gymnogeophagus rhabdotus (Hensel, 1870)
(Fig. 22)

Geophagus rhabdotus Hensel, 1870 (Type-locality: Rio Cadeia, Rio Grande do Sul, Brazil).

Geophagus brachyurus Cope, 1894 (Type-locality: Rio Grande do Sul, Brazil — restricted herein).

Etymology: From the greek: *rhabdotus,* meaning striated.

Lectotype: ZMB 7464 (110 mm TL) Lectotype designation by Gosse, 1976:114.

Specimens examined

Type-material: ZMB 7464 (Paralectotype of *G. rhabdotus* - 62 mm SL), Rio Cadeia, RS, Brazil. ANSP 21881 (Paratype of *Geophagus brachyurus*), (?) San José do Rio Negro and Chapada, Matto Grosso, Brazil, H. H. Smith leg.

Brazil:

MAPA 2139 (1 ex.), Arroio Passo dos Buracos at road between Santa Maria and Cruz Alta, km 248, RS, 10.II.1982, L. R. Malabarba & J. R. Stehmann leg. MZUSP 22159 (1 ex.), Santos Reis, Montenegro, RS, 27.II.1965, R. Leal leg. MCZ 61070 (2 ex.), Small creek at Passo da Taquara, Gravataí, RS, 5.VII.1981, P. A. Buckup, L. R. Malabarba & R. E. Reis leg. MZUSP 27153 (2 ex.), Rio dos Sinos at São Leopoldo, RS, 31.II.1967, R. Leal leg. MAPA 0376 (1 ex.), Dead arm of Rio Jacui, Rio Pardo, RS, 14.XII.1976, P. A. Buckup leg. MZUSP 27160 (6 ex.), Rio dos Sinos at São Leopoldo, RS, 22.IV.1966. leg. MAPA 1955 (2 ex.), Small creek at Vila Restinga, Porto Alegre, RS, 20.IV.1983, R. E. Reis leg. USNM 270287 (2 ex.), Small creek tributary of Rio dos Sinos, distrito de Mato Grande, Canoas, RS, 12.X.1984, L. R. Malabarba, C. A. S. Lucena & J. J. Bertoletti leg. DZUFRGS 0188 (1 ex.), Saco das Garças, delta do Rio Jacui, Canoas, RS, 11.VI.1977, C. L. L. Santos leg. MAPA 0678 (1 ex.), Sitio Refúgio, estrada da Branquinha, Viamão, RS, 25.V.1978, P. A. Buckup leg. MZUSP 27146 (16 ex.), Arroio Chapéu Virado at Belém Novo, Porto Alegre, RS, 21.IX.1977, Exp. MZUSP & USNM leg. MZUSP 16217 (2 ex.), Arroio Fiúza at Passo do Fiúza, Viamão, RS, 9.XII.1979, Exp. MZUSP & USNM leg. MZUSP 16220 (2 ex.), Small creek at estrada do Passo das Pedras, Viamão, RS, 9.XII.1979, Exp. MZUSP & USNM leg. MZUSP 16218 (1 ex.), Riacho Passo Comprido (affluent of Arroio Fiúza), Passo D'Areia, Viamão, RS, 9.XII.1979, Exp. MZUSP & USNM leg. MAPA 0607 (1 Cl&St), Delta do Rio Jacui, Porto Alegre, RS, 4.XII.1977, P. A. Buckup leg. MAPA 2278 (1 Cl&St), Rio Jacui basin, RS, 1983, R. E. Reis leg. MAPA 2185 (1 ex.), Lagoa da Cerquinha, Pinhal, Tramandaí, RS, 16.X.1982, R. E. Reis & L. R. Malabarba leg. DZUFRGS 3173 (1 ex.), Lagoa da Cerquinha, Pinhal, Tramandaí, RS, 1.III.1981, L. R. Malabarba leg. MAPA 2184 (1 ex.), Rio Vacacaí at São Gabriel, RS, 19.XII.1982, R. E. Reis & L. R. Malabarba leg. MCP 9016 (12 ex.), Cachoeira do Sul, RS, 27.IV.1978, leg.? MAPA 0487, 0488 and 0489 (1 ex.), Artificial dam near Lagoa Formosa, Tapes, RS, 17.II.1977, P. A. Buckup leg. MZUSP 27154 (1 ex.), Rio Pelotas, near bridge of road BR-116, Pelotas, RS, 10.V.1967, R. Leal leg. MCP 9021 (3 ex.), Headwaters of Rio Negro at road BR-293, Bagé, RS, 25.X.1982, C. A. Lucena & L. R. Malabarba leg. MAPA 2186 (6 ex.), Rio Negro at road between Bagé and Pinheiro Machado, RS, 22.XII.1982, R. E. Reis & L. R. Malabarba leg. MZUSP 27162 (1 ex.), Arroio Chasqueiro at road between Pelotas and Jaguarão, RS, 14.XII.1979, Exp. MZUSP & USNM leg. MZUSP 16221 (1 ex.), Arroio Grande at Road between Pelotas and Jaguarão, Arroio Grande, RS, 14.XII.1979, Exp. MZUSP & USNM leg. DZUFRGS 3172 (4 ex. 1 Cl&St), Taim Ecological Station, Rio Grande, RS, 7/8.V.1981, R. E. Reis & J. R. Stehmann leg. DZUFRGS 0680 (1 ex.), Taim Ecological Station, Rio Grande, RS, 7/8.V.1981, R. E. Reis & J. R. Stehmann leg. MAPA 2274 (1 Cl&St), specimen from aquarium trade (Jacuí basin).

Paraguay:
MHNG 2027.67-69 (2 ex.), Rio Acaray, Pto. Pte. Stroessner, 8.XI.1979, Exp. Zool. Mus. Genève leg. MHNG 2027.92-95 (4 ex.), Itabó-guaçu, Alto Paraná, 5.XI.1979, Exp. Zool. Mus. Genève leg. MHNG 2027.96-98 (2 ex.), Rio Carapé, Alto Paraná, 2.XI.1979, Exp. Zool. Mus. Genève leg.

Uruguay:
BM(NH) 1893.7.31:4-5 (1 ex.), Tributary of Rio Negro near Muccoco, 31.VII.1893, leg.?

Description

Standart length of examined specimens 40.4 to 120 mm. Other meristic and morphometric data are summarized in tables 2 and 3.

Body deep and compressed laterally. Predorsal profile straight to slightly convex. Body contour at dorsal fin base gently arched. Caudal peduncle deeper than long, with straight ventral and dorsal profiles. Ventral contour gently arched from lower lip to base of last anal fin ray.

Interorbital width and post-orbital length usually identical. Eye diameter also equal to interorbital width in specimens up to about 40 mm SL, smaller in large specimens. Ontogenetic differences in eye diameter conspicuous; eye larger than pre-orbital length in specimens up to about 60 mm SL and smaller in larger specimens.

Body scales moderately large and ctenoid, except for small preventral cycloid ones. Cheek almost completely covered with typically cycloid scales. Gill-cover partially covered with irregularly scattered ctenoid scales. Isthmus under branchiostegal membrane without scales. Soft dorsal fin rarely with a few ctenoid and cycloid scales. Proximal third of caudal fin with small ctenoid scales, arranged into single series between rays.

Dorsal fin usually originating anterior to or just over posterior bony margin of opercle. Fourth or fifth soft rays longest, usually reaching proximal third of caudal fin. Pectorals usually reaching middle of base of anal fin. Pelvics reaching or slightly beyond origin of anal fin. Fourth or fifth soft rays longest, reaching proximal third of caudal fin. Caudal fin usually truncated.

Color in life: ground color of dorsal surface of body olivaceous, lighter ventrally. About six transverse, inconspicuously double, dark cross-bands and distinct midlateral spot on third transverse cross-band, just below upper portion of lateral line. Distinct dark band from nape to below eye, often reaching outer angle of preopercle. About eight longitudinal bright-blue stripes laterally on flank. Bright-blue dots distributed on cheek, gill-cover and postorbital region, a few dots somewhat aligned on infraorbital bone series. The iris yellowish to light-olivaceous with dark superior and inferior medial segments. Abdominal region yellowish; branchiostegal membranes often with diffuse to deep dark pigmentation. Pectoral fins hyaline to slightly yellowish. Ventral fins pale olivaceous with bright-blue marks. Dorsal, anal and caudal fins yellow to reddish with whitish to bright-blue small bars. Caudal fin sometimes with roundish marks and often with both superior and inferior red edges.

Color in alcohol: general appearance of preserved specimens paler. The bright-blue marks tend to be faint and the red pigmentation becomes light- to dark-olivaceous or disappears totally. Dark marks usually remain well-preserved.

Remarks

The synonymy of *G. rhabdotus* deserves discussion. The examined type-material of *Geophagus brachyurus* was erroneously labelled as *"Geophagus camurus"* - actually synonym of *G. gymnogenys*. Cope's 1894 description and illustrations of these two *Geophagus* species are, however, fortunately sufficiently good as to allow a reliable re-identification of the type-specimens. The holotype of *G. brachyurus* (ANSP 21751) was correctly catalogued by Fowler, then curator of ANSP. However, four paratypes in ANSP 21880-21883 and four syntypes of *G. camurus* in ANSP 21885-21888, all from "Brazil, Matto Grosso, San Jose to Rio Negro and Chapada" (sic), were mixed up and interchanged by Fowler (Smith-Vaniz, in litt.).

This fact clearly explains Gosse's 1976 synonymy of *G. rhabdotus (G. brachyurus* and *G. camurus)* as he examined two mislabelled syntypes of *G. camurus* (actually paratypes of *G. brachyurus*) and the holotype of *G. brachyurus*.

Furthermore, we have some doubts concerning the collecting locality of these previously confused type-specimens. Besides these specimens there are no records of *G. rhabdotus* or *G. gymnogenys* from the Paraguay River system, the nearest record being more than one thousand kilometers South of "Rio Negro in Matto Grosso" (now Mato Grosso do Sul State). We believe this locality was also erroneously catalogued by Fowler, since Cope's paper deals with Rio Grande do Sul fishes - he clearly wrote: "Besides the addition of seventeen species to the fauna of the Jacuhy River ..." and also "Mr. Smith obtained near Chapada in Matto Grosso from the headwaters of the Paraguay, *Tetragonopterus lineatus* Steind. and *T. moorei* Boul. From the headwaters of the Tocantins, not far from the same locality, he obtained a species close to *T. caudimaculatus* Gthr." If such is the case, the correct type-locality should be the Jacuí River system, in Rio Grande do Sul.

We have tentatively included within this species a population inhabiting the Paraná River and its tributaries near Fóz do Iguaçu (Brazil). The specimens examined (MHNG 2027.67-69, 2027.92-95 and 2027.96-98), previously identified as *Gymnogeophagus* cf. *australis* by Kullander, 1981, show minor morphological differences chiefly in body shape (a little little longer caudal peduncle) and coloration.

The specimens from the Rio Grande do Sul coastal lagoon system may demonstrate a few small roundish bright-blue marks on soft dorsal and caudal fins, while the specimens from the headwaters of Rio Negro, near Bagé, RS, have a very strong longitudinal striping.

The range of *G. rhabdotus* includes very different habitats. This species is usually found in lagoons, creeks and small rivers with sandy, more rarely muddy or loose-stoned bottom, and light to slightly strong water flow. Waters with dense submerged vegetation are usually preferred.

In spite of *G. rhabdotus* being very commom in the area we collected, we have no notes on its reproductive habits. According to Kullander, 1983, *G. rhabdotus* is a substrate-brooder species.

Gymnogeophagus meridionalis, sp. n.
(Fig. 19)

Etymology: From the Latin *meridionalis,* after its southern distribution. This new species is the only *Gymnogeophagus* species found south of Buenos Aires. The new name was suggested by Jorge Casciotta of CIMLP.

Type-locality: Headwaters of Rio Negro at road BR-153, (Uruguay River system), Bagé, Rio Grande do Sul, Brazil.

Type-specimens

Holotype: MZUSP 28461, Rio Negro at road BR-153, Bagé, RS, 22.XII.1982, R. E. Reis, L. R. Malabarba & K. L. Leyler leg.

Paratypes: Argentina:
CIMLP 26.IV.84.1 (12 ex.), Laguna Camino Bella Vista/San Roque, frente a Escuela nº 12, Corrientes, XI.1978 (not measured, SL 44.4 to 70 mm). MACN 7466 (formerly 3905) (5

ex.), Parque Ludeña, Rosario. MAPA 2228 (10 ex.), Los Talas, Berisso, Buenos Aires.

Brazil:

MZUSP 2557 (11 ex. 2 Cl&St), Itaquí, RS, 1914, E. Garbe leg. MZUSP 1805 (5 ex.), Rio Uruguay at Itaquí, RS, 1914, E. Garbe leg. MCP 9317 (5 ex.), Arroio Jaguari at São Francisco de Assis, RS, 15.IX.1983, C. A. S. Lucena, L. R. Malabarba & R. E. Reis leg. MCZ 61067 (1 ex. formely MCP 9317), Arroio Jaguari at São Francisco de Assis, 15.IX.1983, C. A. S. Lucena, L. R. Malabarba & R. E. Reis leg. MCP 9456 (2 ex.) USNM 270286 (2 ex.), Rio Caraí-Passo near São Francisco de Assis, RS, 15.IX.1983, C. A. S. Lucena, L. R. Malabarba & R. E. Reis leg. MCP 9465 (7 ex.), NRM A84/1983372.3035 (1 ex. formerly MCP 9465), ZMB 31372 (1 ex. formely MCP 9465) and MHNG 2169.59 (1 ex.), Sanga do Rio Toropi at road BR-453, São Vicente do Sul, RS, 13.IX.1983, C. A. S. Lucena, L. R. Malabarba & R. E. Reis leg. MCP 9036 (1 ex.), Rio Santa Maria at road BR-293, km 246, Dom Pedrito, RS, 26.X.1982, C. A. S. Lucena & L. R. Malabarba leg. MAPA 2225 (1 Cl&St), 2226 (1 Cl&St), 2227 (2 ex.) and DZUFRGS 3178 (2 ex.), Rio Negro at road BR-153, Bagé. RS, 22.XII.1982, R. E. Reis & L. R. Malabarba leg. MCP 9022 (6 ex.), Headwaters of Rio Negro at road BR-293, Bagé, RS, 25.X.1982, C. A. S. Lucena & L. R. Malabarba leg. MCP 9032 (17 ex.), Arroio Valente at road BR-153 (Rio Negro system), Bagé, RS, 25.X.1982, C. A. S. Lucena & L. R. Malabarba leg.

Description

Standart length of examined specimens 39.3 to 88 mm. Other meristic and morphometric data are summarized in tables 2 and 3.

Body deep and laterally compressed. Dorsal contour evenly arched from snout to last dorsal fin ray. Ventral contour gently arched from lower lip to last anal-fin ray. Caudal peduncle squarish or deeper than long.

Head length usually equal to its depth. Eye diameter usually smaller than post-orbital length. Interorbital width shorter than pre-orbital length in specimens up to about 60 mm SL and longer than pre-orbital length in larger specimens.

Body scales moderatelly large and ctenoid, except for small, sometimes cycloid preventral scales. Cheek almost completely covered with cycloid scales. Gill-cover partially covered with irregularly scattered cycloid and ctenoid scales. Isthmus under branchiostegal membrane without scales. Dorsal and anal fins without scales. Proximal third of caudal fin with small ctenoid scales, arranged into single series between rays.

Dorsal fin usually originating anterior to vertical through the posterior bony margin of operculum. Fifth or sixth soft dorsal fin ray longest, reaching proximal third of caudal fin. Pectorals usually reaching middle of base of anal fin. Pelvic spines usually half length of first soft ray, which reaches origin of anal fin base. Fourth to sixth anal rays the longest, usually reaching proximal third of caudal fin. Caudal truncated to slightly concave.

Color in life: ground color of dorsal portions of body gray-brown to olivaceous, lighter ventrally. About six transverse, inconspicuously double, dark cross-band and distinct midlateral spots on third transverse cross-band, just below upper portion of lateral line. Distinct dark band from

nape to below eye, often reaching outer angle of preopercle. About seven longitudinal bright-blue stripes laterally on flank. Bright-blue dots distributed on cheek, gill-cover and post-orbital region; a few dots irregulary aligned on infra-orbital bone series. Iris light with dark inferior and superior segments. Abdomen yellowish to deep-orange below pectoral insertions, and from inferior lip to anal papillae. Branchiostegal membranes often with dark diffuse pigmentation. Pectoral fins hyaline; ventral fins dark-blue. Dorsal and anal fins reddish to deep-red with whitish to light-blue small roundish dots. Proximal half of caudal fin reddish with small whitish to light-blue roundish dots; fainter distally.
Color in alcohol: general appearance of preserved specimens paler. Bright-blue mark are very faint and red and dark-blue pigmentation are dark-olivaceous.

Remarks

This species has been frequently misidentified as *G. australis* by some authors (Iwaszkiw & Sendra, 1981 and Gosse, 1976). Besides aspects of color and body proportions, *G. meridionalis* may be readily distinguished from *G. australis* by the longitudinal scale count.

This new species is found in a broad area including the Paraná and Uruguay River systems. We have collected *G. meridionalis* in several different habitats including small pools, creeks and large rivers with sandy or muddy bottom and with transparent to dark muddy water. This species is a substrate-brooder (J. Casciotta, pers. comun.).

Gymnogeophagus australis (Eigenmann, 1907)
(Fig. 21)

Geophagus australe Eigenmann, 1907 (Type-locality: Buenos Aires, Argentina).

Etymology: From the Latin, *australis,* meaning austral.

Type-material: Holotype and three paratypes formerly in the Museum of Princeton University, later transferred to FMNH. These four specimens were not found. Three existing paratypes in CAS 51440.

Specimens examined

Type-material: CAS 51440 (formerly in IUM 11352 - 2 of 3 ex.), Buenos Aires, Argentina, W. B. Scott leg.

Argentina:
CIMLP 17.III.1980-1 (1 ex.), Lagoon in front of Clube Tifon, Santa Fé, 9.XII.1957. CIMLP 11.IX.1961-3 (8 ex. of various), Lago Parque Sur, Santa Fé. MACN 3143 (1 ex.), Gualeguaychu, Entre Rios, collected before 1943, J. A. H. Rossi leg.

Description

This description is based on two paratypes - 108 and 110 mm SL. Other meristic and morphometric data, including the non-type-specimens examined, are summarized in tables 2 and 3.

Body slightly elevated and robust, laterally compressed. Predorsal contour elevated and strongly steep. Body contour at base of dorsal fin gently arched. Caudal peduncle squarish, slightly deeper than long. Ventral contour gently arched from lower lip to the last anal fin ray.

Body scales moderately large and ctenoid, except for small preventral scales. Scales near branchiostegal membrane cycloid. Isthmus under branchiostegal membrane without scales. Upper half of cheeks covered with irregulary scattered ctenoid elements. Dorsal fin with a few scales between the rays (no scales found in type-material). Proximal third of caudal fin covered with small ctenoid scales, arranged into single series between rays.

Dorsal fin originating along vertical line through posterior bony margin of preopercle. Sixth dorsal ray longest, reaching proximal third of caudal fin. Pectorals reaching middle of anal fin base. Pelvics reaching origin of anal fin. Fifth anal fin ray longest, reaching proximal third of caudal. Caudal fin slightly concave.
Color in alcohol: the examined paratypes of *G. australis* are presently quite discolored. Except for a few small and very faint roundish dots on the dorsal and anal fins in one paratype, the fishes are completely colorless. Eigenmann, 1907:454-5, wrote in the original description: "A dark area across back in front on the dorsal; bases of some of the scales of the back frequently very dark brown; side with about six cross-bands, each of those on middle of side composed of double dark lines with a band of light of equal width between them; no dark spot on side; pectoral light; ventrals blue-black; dorsal dusky, with ascending light stripes which are largely replaced by light spots on the soft dorsal; caudal dusky, with round hyaline spot on the rays similar to those on soft dorsal; anal with similar but smaller and less distinct spots; no spot or ocellus on the caudal".

The non-types examined agree with the general pattern described by Eigenmann but are also rather discolored.

Remarks

The designation of an holotype - "Type" - by Eigenmann, which could not be located at FMNH (the Princeton University Museum material from the expedition to Patagonia is now at the FMNH), prevents the possibility of designation of a lectotype, as already pointed out by Gosse, 1976:136. Gosse, however, designated an invalid lectotype in the table of page 134.

Gymnogeophagus gymnogenys (Hensel, 1870)
(Fig. 23)

Geophagus gymnogenys Hensel, 1870 (Type-locality: Rio Cadeia, Rio Grande do Sul, Brazil).
Geophagus pygmaeus Hensel, 1870 (Type-locality: Rio Guaíba, Porto Alegre, Rio Grande do Sul, Brazil).
Geophagus camurus Cope, 1894 (Type-locality: Rio Grande do Sul, Brazil - restricted herein).

Etymology: From the greek *gymno,* meaning naked and *genys,* meaning cheek.

Lectotype: ZMB 7465 (125 mm SL) Lectotype designation by Gosse, 1976:119.

Specimens examined

Type-material: ZMB 22269 (Paralectotype of *Geophagus gymnogenys* - 82 mm SL), Rio Cadeia, RS, Brasil.

Argentina:
MACN 6456 (4 ex.), Rio Gualeguaychu at Gualeguaychu, Entre Rios, F. Santos leg. BM(NH) 1937.6.21:1-2 (2 ex.), Rosário de Santa Fé, 21.VI.1937, Arnold (donor).

Brazil:
DZUFRGS 3177 (11 ex.), 3376 (1 ex.), 3179 (1 Cl&St) and 3220 (1 Cl&St), Rio Piratini at Coimbra, Santo Ângelo, RS, 15/16.II.1982, L. R. Malabarba & J. R. Stehmann leg. MZUSP 27147 (1 ex.), Dam of Rio Jacuí at Fazenda dos Shell, Maraú, RS, 1.I.1972, G. Q. Benvegnú leg. MZUSP 27156 (1 ex.), Rio Jacuí at Barragem Ernestina, near Passo Fundo, RS, 20.IX.1977, Exp. MZUSP & USNM leg. MAPA 2203 (2 ex.), Rio Taquari at road BR-386, RS, 17.II.1982, leg.? MZUSP 16059 (6 ex.), and 27149 (1 ex.), Rio Forqueta at Marquês de Souza, Lageado, RS, 7.XII.1979, Exp. MZUSP & USNM leg. MAPA 2189 (4 ex.), and MCZ 61069 (3 ex.), Rio Caí at São Sebastião do Caí, RS, P. A. Buckup, C. F. M. Souto, L. R. Malabarba & R. E. Reis leg. MAPA 2193 (3 ex.), Arroio do Salso at Rosário do Sul, RS, 20.XII.1982, R. E. Reis, L. R. Malabarba, K. L. Leyser & M. C. Lima leg. MAPA 2205 (3 ex.), Dam of Rio Caí near Montenegro, São Sebastião do Caí, RS, 19.I.1979, P. A. Buckup leg. MZUSP 27158 (2 ex.), Rio Paranhama at confluence with Rio dos Sinos, Taquara, RS, 3/5.I.1979, J. Casado Neto leg. MAPA 2229 (1 ex.), Rio da Ilha, between Vila Rio da Ilha and Padilha, Taquara, RS, 21.III.1982, R. E. Reis leg. MZUSP 27152 (2 ex.), Rio dos Sinos at São Leopoldo, RS, 22.IV.1966, leg.? MZUSP 27148 (2 ex.), Rio dos Sinos at São Leopoldo, RS, 31.III.1967, R. Leal leg. MCP 9357 (1 ex.), Rio Saicã, Cacequi, RS, 13/14.IX.1983, C. A. S. Lucena, L. R. Malabarba & R. E. Reis leg. MAPA 2202 (1 ex.), Dam at Parque Saint Hilaire, Viamão, RS, 10.VIII.1981, R. E. Reis & L. R. Malabarba leg. MAPA 0311 (1 ex.), and 0312 (1 ex.), Rio Guaíba, southern of Ilha Grande dos Marinheiros, Porto Alegre, RS, 27.XI.1976, P. A. buckup leg. USNM 270290 (2 ex.), Rio Guaíba at Morro do Sabiá, Porto Alegre, RS, 25.IV.1984, R. E. Reis leg. MAPA 2204 (5 ex.), Arroio dos Ratos at Road BR-290, limit between Guaíba and São Jerônimo, RS, 19.I.1979, P. A. Buckup, C. F. M. Souto & D. Wilhelm Fº leg. MAPA 2201 (2 ex.), Lagoa da Cerquinha, Pinhal, Tramandaí, RS, 4.IV.1981, P. A. Buckup, R. E. Reis & L. R. Malabarba leg. DZUFRGS 3176 (2 ex.), Lagoa da Cerquinha, Pinhal, Tramandaí, RS, 1.III.1981, L. R. Malabarba leg. MAPA 2206 (1 ex.), Lagoa da Cerquinha, Pinhal, Tramandaí, RS, 16.X.1982, R. E. Reis & L. R. Malabarba leg. MAPA 2197 (4 ex.) and 2198 (1 Cl&St), Rio

Santa Maria at Rosário do Sul, RS, 31.IX.1982, L. R. Malabarba leg. MAPA 2196 (1 ex.), Rio Santa Maria at Rosário do Sul, RS, 20.XII.1982, R. E. Reis & L. R. Malabarba leg. MAPA 2194 (3 ex.), Arroio Santa Maria Chico at road BR-293, Dom Pedrito, RS, 21.XII.1982, R. E. Reis & L. R. Malabarba leg. MAPA 1949 (2 ex.), Arroio do Ribeiro at road BR-116, Barra do Ribeiro, RS, 12.IX.1982, R. E. Reis & L. R. Malabarba leg. MAPA 2192 (3 ex.), Açude dos Garcia, Barra do Ribeiro, RS, 12.IX.1982, R. E. Reis & L. R. Malabarba leg. MAPA 2200 (11 ex.), Sanga (small creek) at km 52 of road between Rosário do Sul and Dom Pedrito, RS, 20.XII.1982, R. E. Reis & L. R. Malabarba leg. MAPA 2195 (1 ex.), Rio Ibicuí da Cruz, Santana do Livramento, RS, 20.XII.1982, R. E. Reis & L. R. Malabarba leg. MAPA 2187 (1 ex.), and 2190 (7 ex.), Arroio Piraí at road between Dom Pedrito e Bagé, RS, 21.XII.1982, R. E. Reis & L. R. Malabarba leg. MAPA 2191 (4 ex.), Rio Negro at road BR-153, Bagé, RS, 22.XII.1982, L. R. Malabarba, R. E. Reis & K. L. Leyser leg. MCP 9033 (5 ex.), Arroio Valente (affluent of Rio Negro) at road BR-153, Bagé, RS, 25.X.1982, C. A. S. Lucena & L. R. Malabarba leg. MAPA 2199 (4 ex.), Rio Negro at road between Bagé and Pinheiro Machado, RS, 22.XII.1982, R. E. Reis & L. R. Malabarba leg. MAPA 2188 (1 ex.), Arroio Quebracho at road between Bagé and Pinheiro Machado, RS, 22.XII.1982, R. E. Reis & L. R. Malabarba leg. MCP 9023 (26 ex.), headwaters of Rio Negro at bridge of road BR-293, Bagé, RS, 25.X.1982, C. A. S. Lucena & L. R. Malabarba leg. MZUSP 27161 (2 ex.), Arroio Chasqueiro at road between Pelotas and Jaguarão, RS, 14.XII.1979, Exp. MZUSP & USNM leg. DZUFRGS 0679 (1 ex.), Taim Ecological Station, Rio Grande, RS, 7/8.V.1981, R. E. Reis & J. R. Stehmann leg. DZUFRGS 3174 (1 ex.), and 3175 (2 ex.), Canal flowing into Lagoa do Nicola, Taim Ecological Station, Rio Grande, RS, 1981, L. R. Malabarba leg.

Uruguay:

ANSP 54073 (1 ex.), Cerro Largo, Montevideo (?), 1932, F. Felippone leg. ANSP 84616 (1 of 3 ex.), Rio Santa Lucia at Canelones, X. 1935, L. P. Barattini leg. ANSP 84615 (1 ex.), Uruguay, 1935, F. Felippone leg.

Description

Standart length of examined specimens 40 to 125 mm. Other meristic and morphometric data summarized in tables 2 and 3.

Body elongate, compressed laterally. Predorsal contour slightly arched. Some adult males show a very large adipose hump. Body contour at dorsal fin base slightly arched. Caudal peduncle rectangular, longer than deep, with straight to slightly concave dorsal and ventral profiles. Body contour gently arched between lower lip and last anal fin ray, with a somewhat straight segment between pelvic and anal fin insertions.

Interorbital width usually smaller than eye diameter in specimens up to about 55 mm SL or larger than eye diameter in larger specimens. Postorbital lenght usually identical to eye width in specimens up to about 40-60 mm SL, or larger than eye in larger specimens.

Body scales moderately large and ctenoid, except for cycloid and ctenoid small-scaled pre-ventral area. Cheeks with very few or no scales, when present usually ctenoid. Gill-cover with a few ctenoid and cycloid scales. Soft dorsal fin occasionally with few small ctenoid and cycloid scales. Proximal third of caudal fin with small ctenoid scales, arranged into single series between rays.

Dorsal fin usually originating anterior to vertical line through posterior bony margin of opercle. Small specimens with short dorsal, reaching just to caudal fin base; large individuals with fifth or sixth dorsal-fin rays longest, usually reaching proximal half of caudal fin. Pectorals usually reaching middle of anal fin base. Pelvics reaching to or slightly beyond anal fin origin. Anal fin usually reaching caudal fin base. Caudal fin truncated to slightly concave.

Color in life: ground color of dorsal portions of body yellowish to light-olivaceous, yellowish ventrally. About five to six transverse, usually inconspicuously double dark cross-bands, first short and more intensely pigmented, originating below first dorsal spine. Large midlateral spot on third transverse band, just below upper portion of lateral line. Dark band from inferior rim of orbit to inner angle of preopercle. Cheek and gill-cover richly covered with small irregularly shaped bright-blue dots. Post-orbital area reddish; upper lip usually bright-blue. About eight longitudinal series of flank scales with small bright-blue dots. Isthmus and branchiostegal membranes yellowish to deep-orange. Pectoral fins hyaline; ventral fins with diffuse blue pigmentation. Dorsal, anal and caudal fins reddish to deep-red with whitish to light-blue roundish dots.
Color in alcohol: general appearance of preserved specimens paler. Bright-blue marks disappear and red pigmentation becomes pale gray-brown. Isthmus and branchiostegal membranes becomes whitish.

Remarks

Kullander's 1981 synonym of *G. gymnogenys* is correct, except for the exclusion of *Geophagus pygmaeus,* which was synonymized with *G. labiatus*. Hensel's 1870 description of *G. pygmaeus,* including specimens of 23 mm of maximum SL chiefly agree with young *G. gymnogenys* color pattern.

G. gymnogenys, in the sense here adopted, may prove to be a group of species through future work. We have tentatively included within this species a few populations from headwaters of Rio Negro (MAPA 2191, MAPA 2199 and MCP 0673), Rio Santa Maria (MAPA 2196, 2197 and 2198) and Rio Piratini (DZUFRGS 3376) which show a few differences, chiefly in body proportions and coloration. These differences, however, are completely overlapping when analyzed together (more than two hundred specimens were analysed). At one extreme of this variation are the specimens examined of *G. australis,* which may also be included in a "*G. gymnogenys* species-group".The limit between these two species is presently hardly distinguishable.

Gymnogeophagus gymnogenys is usually found in large rivers and lagoons with sandy bottom and sparse to absent vegetation, being scarcer than *G. rhabdotus* in smaller environments.

This species is a mouth-breeder one. We have collected a mouth breeding female in December (MAPA 2187).

Gymnogeophagus labiatus (Hensel, 1870)
(Fig. 20)

Geophagus labiatus Hensel, 1870 (Type-locality: Rio Santa Maria, Taquara, Rio Grande do Sul, Brazil).

Geophagus bucephalus Hensel, 1870 (Type-locality: Rio Cadeia, Rio Grande do Sul, Brazil).

Geophagus scymnophilus Hensel, 1870 (Type-locality: Rio Cadeia, Rio Grande do Sul, Brazil).

Etymology: From the Latin, *labiatus,* after it very thick lips.

Holotype: ZMB 7467 (146 mm SL), Rio Santa Maria, Rio Grande do Sul, Brazil.

Specimens examined

Type-material: ZMB 31373 (formerly ZMB 7466), Lectotype of *Geophagus bucephalus* by present designation, Rio Cadeia, Nova Petrópolis, RS, Brazil, R. Hensel, leg. ZMB 31374 (formerly ZMB 22293), Lectotype of *Geophagus scymnophilus* by present designation, Rio Cadeia, Nova Petrópolis, RS, Brazil, R. Hensel leg.

Brazil:

DZUFRGS 1016 (1 ex.), Rio Jordão at Jordão Baixo, Sideropólis, SC, 2/9.XII.1977, C. L. L. Santos leg. MZUSP 27150 (1 ex.), Rio Pique at road between Araranguá and Meleiro, Morro Cortado, SC, 22.IX.1977, Exp. MZUSP & USNM leg. DZUFRGS 2169 (1 ex.), Rio Morto at Meleiro, SC, 1.V.1983, C. B. UFSC leg. MZUSP 27155 (2 ex.), Rio Jacui at Barragem Ernestina, near Passo Fundo, RS, 20.IX.1977, Exp. MZUSP & USNM leg. MZUSP 16062 (1 ex.), Rio Fão at Vila do Fão, Lageado, RS, 7.XII.1979, Exp. MZUSP & USNM leg. MZUSP 27157 (3 ex.), Rio Forqueta at Marquês de Souza, Lageado, RS, 20.IX.1977, Exp. MZUSP & USNM leg. MZUSP 16060 (1 ex.), Rio Forqueta at Marquês de Souza, Lageado, RS, 7.XII.1979, Exp. MZUSP & USNM leg. MAPA 2213 (3 ex.), Rio Maquiné at Maquiné, Osório, RS, 20.II.1983, R. E. Reis & C. M. Penz leg. MAPA 2214 (5 ex.), Arroio Água Parada at Maquiné, Osório, RS, 20.II.1983, R. E. Reis & C. M. Penz leg. MAPA 1234 (1 ex.), Rio Caí near Feliz, RS, 12.VIII.1980, Sec. Saúde leg. MAPA 2208 (2 ex. not measured), Left bank of Rio Caí at road between São Sebastião do Caí and Feliz, RS, 14.XII.1982, P. A. Buckup, R. E. Reis & L. R. Malabarba leg. MZUSP 16061 (12 ex.), Rio Caí, ca. 5 km of São Sebastião do Caí, RS, 8.XII.1979, Exp. MZUSP & USNM leg. DZUFRGS 1019 to 1022 (4 ex.), Dam of Rio Cai, near Montenegro, São Sebastião do Caí, RS, 19.I.1979, P. A. Buckup, C. F. M. Souto & D. Wilhelm F° leg. MAPA 2209 (6 ex.), Rio dos Sinos at bridge to Nossa Senhora do Monte Serrat, Santo Antônio, RS, 13.VI.1982, R. E. Reis & L. R. Malabarba leg. MAPA 2212 (8 ex.), 2210 (1 Cl&St), 2211 (1 Cl&St), 2267 (1 Cl&St), MCZ 61068 (2 ex.), and USNM 270291 (3 ex.), Rio dos Sinos at second bridge upstream of Nossa Senhora do Monte Serrat, Santo Antônio, RS, 13.VI.1982, R. E. Reis & L. R. Malabarba leg. MAPA 2207 (2 ex.), Rio dos Sinos, 2 km northeastern of Vila Caraá, Santo Antônio, RS, 13.VI.1982, R. E. Reis & L. R. Malabarba leg. MAPA 1228 (1 ex.), Rio dos Sinos at Canoas, RS, 19.VIII.1980, Sec. Saúde leg. DZUFRGS 1018 (1 ex.), Arroio dos Ratos, limit between Guaíba and São Jerônimo, RS, 29.VIII.1981, R. E. Reis & L. R. Malabarba leg. MAPA 0172 (1 ex.), Rio Guaíba at Belém Novo, Porto Alegre, RS, 8.XII.1975, J. A. Gay leg. MCP 8823 (1 ex.), Rio Camaquã at "eixo da barragem", RS, X.1974, J. J. Bertoletti & M. Fábio leg. DZUFRGS 1012 (1 Cl&St), Rio Camaquã at Road BR-116, limit between Camaquã and São Lourenço do Sul, RS, 7.V.1981, P. A. Buckup, R. E. Reis & L. R. Malabarba leg. DZUFRGS 1013 to 1015 (3 ex.), Rio Camaquã near road BR-116, limit between Camaquã and São Lourenço do Sul, RS, 7.V.1981, R. E. Reis & J. R. Stehmann leg. MAPA 0515 (1 ex.), specimen bought in a public market in Porto Alegre, RS, 18.III.1977.

Description

Standard length of examined specimens 36.9 to 138.3 mm. Other meristic and morphometric data summarized in tables 2 and 3.

Body very elongate, compressed laterally. Predorsal profile convex, often with straight segment above eyes. Body contour at dorsal fin base gently arched. Caudal peduncle longer than deep with straight dorsal and ventral profiles. Ventral profile gently arched to nearly straight between lip and origin of anal fin.

Head longer than deep. Eye diameter larger than interorbital width and pre-orbital lenght in specimens up to about 70 mm SL, and smaller in larger specimens.

Body scales moderately large and ctenoid, except for the small embebed cycloid scales in preventral area. Upper cheek with deeply embeded ctenoid scales; few embeded scales in lower half of cheek. Gill-cover with large ctenoid and smaller cycloid scales, irregularly scattered. Isthmus under branchiostegal membrane without scales. Dorsal and anal fins naked. Proximal third of caudal fin covered with small ctenoid scales, arranged into single series between rays.

Dorsal fin usually originating along vertical through posterior bony margin of opercle. Longest dorsal soft ray usually reaching base of caudal fin. A few large males have fifth or sixth ray reaching proximal third of caudal fin. Pectorals hardly reaching origin of anal fin. Pelvics short, just reaching first or second scale anterior to anal fin. Longest anal ray reaching base of caudal fin; a few males, however, with fourth or fifth ray reaching caudal proximal third. Caudal fin slightly concave.

Color in life: ground color of dorsal portions of body olivaceous, lighter and yellowish ventrally. About nine double, dark cross-bands and distinct midlateral spot uniting third and fourth cross-bands, just below upper portion of lateral line. Distinct dark band from nape to below eye, usually reaching inner angle of preopercle. Snout, cheek and gill-cover darker than trunk. A few bright-blue dots on the cheeks, often aligned on the infra-orbital series. Iris yellowish with both superior and inferior dark segments. Most scales on flank with bright-blue dots. Branchiostegal membranes deep-orange. Lips and ventral fins light- to deep-orange. Pectoral fins hyaline; dorsal and anal fins light-olivaceous to slightly reddish with whitish to bright-blue small bars or ovate marks. Caudal fin light-olivaceous to slightly reddish.

Color in alcohol: general appearance of preserved specimens paler and ground color yellowish. Bright-blue marks disappears and ventral orange coloration become whitish. Fins light-olivaceous with whitish marks.

Remarks

This species was recently resurrected from the synonymy of *G. gymnogenys* by Kullander, 1981. The name *labiatus* was preferred by Kullander instead of *bucephalus* or *scymnophilus* since it characterizes this species very well. This choice, however, introduced another difficulty. The type-locality of *Geophagus labiatus* is "Rio Santa Maria at the primeval forest of Rio Grande do Sul" (our translation from Hensel, 1870). In Rio Grande do Sul, however, there are two Santa Maria rivers. A large sandy bottomed affluent of Uruguay River, in which *G. labiatus* is apparently absent (based on a fruitless intensive collecting attempt) and a small little-known loose-stone bottomed river (Jacuí River system), where *G. labiatus* does exist. In a previous paper Hensel (1867) described the German colonies along the Rio Santa Maria, allowing us to discern that the Santa Maria River referred to in the original description of *G. labiatus* is the Rio Santa Maria at Taquara County, RS, Brazil.

Gymnogeophagus labiatus is usually found in small rivers and creeks with a loose-stone bottom and strong current, the water being usually very transparent and cool. One exception is the sandy bottomed Rio Camaquã, where this species seems to be commom.

Gymnogeophagus lacustris, sp. n.

(Fig. 24)

Etymology: This species is named from the Latin after its common habitat: the Southern Brazilian coastal lagoons system.

Type-locality: Lagoa da Cerquinha at Pinhal, Tramandaí, RS, Brazil.

Type-material

Holotype: MZUSP 28462, Canal between Lagoa da Cerquinha and Lagoa da Rondinha, Pinhal, Tramandaí, RS, Brazil, 16.X.1982, R. E. Reis & L. R. Malabarba leg.

Paratypes: Brazil:
MCP 8664 to 8673 (10 ex.), Florianópolis, SC, XI.1968, leg?. MCP 8676 to 8678 (3 ex.), Lagoa Itapeva, Torres, RS, X.1968, leg?. MCP 8412 (1 ex.), Pisciculture Station at Lagoa dos Quadros, Osório, RS, 27.I.1983, C. A. S. Lucena, H. Tiago & D. Morais leg. MAPA 2220 (4 ex.), Rio Maquiné between road BR-101 and Lagoa dos Quadros, Osório, RS, 19.I.1978, P. A. Buckup leg. MAPA 2222 (1 ex.), Rio Maquiné at road BR-101, Osório, RS, 3.I.1981, R. E. Reis leg. DZUFRGS 3171 (1 ex.), Lagoa dos Quadros at Cornélios, Osório, RS, 1983, C. A. Bello leg. MAPA 2221 (3 ex.), and 2279 (2 Cl&St), Mouth of Rio Cornélios at Cornélios, Osório, RS, 19.II.1983, R. E. Reis & C. M. Penz leg. MAPA 2223 (1 ex.), Canal do João Pedro (between Lagoa dos Quadros and Lagoa da Pinguela), Osório, RS, 3.I.1981, R. E. Reis & J. L. Reis leg. DZUFRGS 1010 and 1011 (2 ex.), Lagoa da Cerquinha, Pinhal, Tramandaí, RS, II.1980, L. R. Malabarba leg. MAPA 2218 (1 ex.), and 2219 (1 Cl&St), Lagoa da Cerquinha, Pinhal, Tramandaí, RS, 4.IV.1981, P. A. Buckup, R. E. Reis & L. R. Malabarba leg. DZUFRGS 1017 (1 ex.), Lagoa da Cerquinha, Pinhal, Tramandaí, RS, 1.III.1981, L. R. Malabarba leg. MAPA 2216 (3 ex.), and 2217 (1 Cl&St), same data of holotype. USNM 270289 (1 ex.), and NRM A84/1983487.3036 (1 ex.), Lagoa da Cerquinha, Pinhal, Tramandaí, RS, 4.XII.1983. L. R. Malabarba leg.

Description

Standard length of type-material 48.4 to 146 mm. Other meristic and morphometric summarized in tables 2 and 3.

Body very elongate, compressed laterally. Predorsal profile slightly convex. Body contour at dorsal fin base gently arched. Caudal peduncle longer than deep with slightly concave dorsal and ventral profiles. Ventral profile straight to gently convex between lower lip and anal fin origin.

Head length longer than deep. Eye diameter longer than interorbital width and pre-orbital length in specimens up to about 60-70 mm SL, smaller in larger specimens.

Body scales moderately large and ctenoid, except for the small cycloid pre-ventral scales. Isthmus under branchiostegal membrane without scales. Cheeks with ctenoid scales restricted to the upper half. Gill-cover with large ctenoid and small cycloid irregularly scattered scales. Dorsal and anal fins without scales. Proximal third of caudal fin covered with small ctenoid scales, arranged into single series between rays.

Dorsal fin usually originating anterior to vertical through posterior bony margin of opercle. Seventh soft dorsal ray usually longest, reaching proximal third of caudal fin in large specimens. Pectorals reaching or falling slightly short of middle of anal fin base. Pelvics usually reaching anus. Anal longest rays usually reaching caudal fin base. Caudal fin slightly concave.

Color in life: ground color of dorsal portions of body light-olivaceous, lighter ventrally. Usually nine double, dark cross-bands and distinct midlateral spots uniting the third and fourth transverse cross-bands, just below upper portion of lateral line. Distinct dark band from nape to below eye, usually reaching inner angle of preopercle. Snout, cheek and gill-cover darker than trunk. Few bright-blue dots on cheek, often aligned on infra-orbital bone series. Most scales of flank with small bright-blue dots. Lips, branchiostegal membranes and isthmus orange. Lips of large nuptial males impressively deep-orange. Pectoral hyaline; dorsal and anal fins light-olivaceous to slightly reddish with whitish to light-blue small bars or ovate marks. Anal fins sometimes with roundish dots. Proximal half of caudal fin light-olivaceous to slightly reddish, fainter distally.

Color in alcohol: general appearance of preserved specimens paler. Ground color of dorsal surface of body yellowish. Bright-blue marks disappear and ventral orange coloration become whitish. Fins are light- to deep-olivaceous with whitish marks.

Remarks

This species is rectricted to a very narrow area, the coastal lagoons system of Rio Grande do Sul and Santa Catarina States. The lagoons are sandy- and often muddy-bottomed, with submerged vegetation. Most emergent plants are Gramineae and Cyperaceae.

Gymnogeophagus lacustris is a mouth-breeder species. We found a specimen (not preserved) caring young in the mouth in February.

Phylogenetic relationships

The proposed hypothesis of phylogenetic relationships within *Gymnogeophagus* is illustrated in the cladogram in Fig. 25 and is based on Hennig's 1966 principles. Polarity decisions are mainly based on out-group comparisons. Kullander, 1980a has included *Gymnogeophagus* in a monophyletic assemblage consisting of large-Geophagines: *Acarichthys, Biotodoma, Geophagus, Gymnogeophagus, Papiliochromis* and *Retroculus* — see Introduction — not taking into consideration, however, the phylogenetic relationships among the Geophagine genera. For this reason and assuming Geophagines as monophyletic, out-group comparisons include the large-Geophagine genera. Most data on these genera are from the literature, mainly from Gosse, 1963, 1971 and 1976 and Kullander 1977, 1980a, 1980b and 1983.

Since the Hennigian principles have been reviewed in detail by several subsequent authors, we believe it is not necessary to discuss them again. However, it is useful and profitable to emphasize two important aspects: (1) the fact that polarity decisions and the small number of available characters are the main problems with phylogenetic analysis in lower level groups such as species; and (2) the state of a scientific hypothesis (in the Popperian sense) that phylogenetic reconstructions assume when Hennigian principles are employed. The establishment of a monophyletic group, based on shared derived characters states, which are the basis for phylogenetic reconstructions, may be tested (and hence falsified) by the examination of new characters. Furthermore, a high degree of predictivity, never attained by others systematic approaches is achieved (for further discussion see Wiley, 1981).

In cichlid literature a deep-body is usually regarded as a derived character state over an elongate body. We believe this statement is only acceptable in higher groups such as families within an order or even genera within a family. Within *Gymnogeophagus,* however, if we assumed that a deep body were synapomorphic relative to an elongate body then we would have to consider that character 7, 8, 12, 13 and 14 evolved more than once.

Below we present a discussion of the characters used in the cladogram numbered in table 1. The position of *G. australis* in the cladogram is rather tentative, since very few specimens were available and no accurate osteological observations were possible.

Character discussion:

1. The forward directed spine on top of first dorsal pterygiophore is the main synapomorphy of *Gymnogeophagus*. This character is not found in Neotropical cichlids outside this genus.
2. Despite the loss of supraneurals in cichlids seems likely to have occurred more than once in different lineages (e.g., *Gymnogeophagus, Crenicichla, Batracops*), within Geophagines this reduction evidently occurred only once and is, therefore, assumed to be a synapomorphy for *Gymnogeophagus* species.
3. The elevated dorsal contour of *G. balzanii* — see description — is considered autapomorphic by out-group comparison, since this condition is not found in the remaining *Gymnogeophagus* species and other Geophagines.
4. The high number of dorsal soft rays in *G. balzanii* (12-15) may be related to the elevation of the dorsal contour. By the criterion of out-group comparison (usually less than 12 in out-group but 11-14 in *Geophagus brasiliensis*), this character state is considered autamorphic.
5. The assymetric shape of caudal fin of *G. balzanii,* that is, the possession of a ventral lobe shorter than the dorsal, is considered autapomorphic by the ontogenetic and out-group criterious — young *G. balzanii* have a symmetric caudal fin, similarly to adults of remaining *Gymnogeophagus* species and other Geophagines.
6. *Gymnogeophagus balzanii* has a rostro-caudal shortening in the supraoccipital crest which may be related to the development of the disk-like shape of adults, and is not found in other species of cichlid examined. This characteristic supraoccipital crest shape is regarded as autapomorphic.
7. Within cichlids dense squamation on the fin is usually regarded as plesiomorphic relative to weak squamation. We believe that a reduction of dense to weak fin squamations has occurred several times independently in Neotropical cichlids even within Geophagines. Within *Gymnogeophagus,* a monophyletic genus, only *G. balzanii* shows dense fin squamation, which is regarded as plesiomorphic relative to the reduced state of the squamation in the remaining species.
8. Most cichlid genera have a well-developed ramus of lateral sensory canal prolonged in scales on the caudal fin. Within *Gymnogeophagus,* however, only *G. balzanii* has a prolonged sensory canal in the lower lobe of caudal fin. In the remaining species the canal is reduced to two or three proximal caudal fin scales. This reduction may be related with the general reduction of caudal fin squamation — see discussion of character 7. This reduced state is assumed as synapomorphic as a consequence of out-group comparisons.

9. *Gymnogeophagus rhabdotus* and *G. meridionalis* share a lower number of scales in the longitudinal series: 22-25 instead 26 or more in the remaining species of *Gymnogeophagus* and most Geophagine genera. By out-group comparison the lower number of longitudinal scales is regarded as derived.
10. The characteristic longitudinal brigh-blue flank striping of *G. rhabdotus* and *G. meridionalis* are not found in other *Gymnogeophagus* species (not present in *G. australis* according to Eigenmann's description) and are also unknown in Geophagines outside this genus. The presence of this longitudinal striping is therefore assumed to be a derived condition.
11. The conspicuously higher supraoccipital crest of *G. rhabdotus* and *G. meridionalis* is herein considered synapomorphic, since no other *Gymnogeophagus* species possesses such a supraoccipital crest shape.
12. The fronto-parietal crest is consistently well developed in several genera examined and in three *Gymnogeophagus* species. Such a crest is, however, somewhat reduced in *G. gymnogenys, G. labiatus* and *G. lacustris,* and is presumed to be reduced in *G. australis.* Although we believe the polarity decision on this character is questionable, the reduced state is tentatively assumed to be derived.
13. The first transverse dark stripe on the flank is usually very short and diffuse in most Geophagines. In *G. gymnogenys* and *G. australis,* however, this mark is conspicuously sharper and longer than in the other species, forming a posteroventrally directed dark band extending from the nape. This sharper mark, described for *G. australis* by Eigenmann, 1907 as "A dark area across back in front of the dorsal;..." and hardly visible in Eigenmann illustration, is regarded as synapomorphic.
14. A dark band from the nape to below the eye is a very commom feature in Neotropical cichlids. In *G. gymnogenys* the segment from the nape to upper orbital rim has disappeared, with only the mark on the cheek persisting. This disappearance may be an autapomorphy of *G. gymnogenys* or, most probably, a synapomorphy shared with *G. australis* — the specimens examined were very poorly colored — which also has the apomorphic state of character 13. This character state is tentatively assumed as synapomorphic for these two species.
15. Deep-orange lips are found in *G. labiatus* and *G. lacustris.* This state is extremely strong in adult males of *G. lacustris* and is assumed to be synapomorphic for these two species by out-group comparison.
16. Thick lips are a condition found in a few reophilic cichlids, and seems likely to have evolved independently in different lineages. Within *Gymnogeophagus, G. labiatus* is the only consistently reophilic species and shows very thick lips, herein regarded as an autapomorphy, by out-group comparison.

17. The supracleithrum of all Geophagines examined as well all *Gymnogeophagus* species except *G. lacustris* has a roughly ovate form in lateral aspect (Fig. 17). *Gymnogeophagus lacustris,* however, shows a reduction in the longitudinal lenght of the supracleithrum, the bone being narrower than in other species. This narrow bone is regarded as autapomorphic by out-group comparisons.

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COMPARATIVE MATERIAL EXAMINED

Aequidens portalegrensis (Hensel, 1870)
MAPA 0258 (1 ex.), MAPA 0673 (2 ex.), MAPA 1888 (4 ex.), MAPA 2270 (1 Cl&St)
Cichlasoma dimerus (Heckel, 1840)
MAPA 1282 (1 ex.)
Cichlasoma facetum (Jenyns, 1842)
MAPA 1959 (1 ex.), MAPA 2160 (1 ex.), MAPA 2269 (2 Cl&St)
Cichlasoma pusillum Kullander, 1983
MAPA 2310 (8 ex.)
Crenicichla lacustris (Castelnau, 1855)
MAPA 0603 (1 ex.), MAPA 0777 (1 ex.), MAPA 0826 (1 ex.)
Crenicichla lepidota Heckel, 1840
MAPA 0563 (1 ex.), MAPA 0956 (1 ex.), MAPA 1948 (1 ex.), MAPA 2273 (1 Cl&St)
Papiliochromis ramirezi (Myers & Harry, 1948)
MAPA 2277 (2 Cl&St)
Symphysodon discus Heckel, 1840

MAPA 2275 (1 Cl&St)
Pterophylum sp.
MAPA 2276 (2 Cl&St)
Apistogramma sp.
MCP 9380 (2 ex.)

REFERENCES

Axelrod, H. & W. Vorderwinkler, 1974. *Encyclopedia of tropical fishes*. TFH Publications, Neptune City, 631p. il.

Beurlen, K. 1970. *Geologie von Brasilien*. Sttutgart, 444p.

Boulenger, G. A. 1895. Abstract of a report on large collection of fishes formed by Dr. C. Ternetz at various localities in Matto Grosso and Paraguay; with description of new species. *Proc. Zool. Soc. London,* London, *2*(34):523-9.

Cope, E. D. 1894. On the fishes obtained by naturalist expedition in Rio Grande do Sul. *Proc. Amer. Philo. Soc.*, Philadelphia, *33*(144):84-108 pls. 4-9.

Eigenmann, C. H. 1907. On a collection of fishes from Buenos Aires. *Proc. Wash. Acad. Sci.*, Washington, *8*:449-58, pls. 21-3.

Fowler, H. W. 1954. Os peixes de água doce do Brasil. *Arqs. zool. Est. S. Paulo,* São Paulo, *9*:1-400.

Gosse, J. P. 1963. Descriptions de deux cichlides nouveaux de la region Amazonienne. *Bull. Inst. r. Sci. nat. Belg.*, Bruxelles, *39*(35):1-7.

Gosse, Y. P. 1971. Revision du genre *Retroculus* (Castelnau, 1855) (Pisces, Cichlidae) designation d'un neotype de *Retroculus lapidifer* (Castelnau, 1855) et descriptions de deux espèces nouvelles. *Bull. Inst. r. Sci. nat. Balg.*, Bruxelles, *47*(43):1-13, pls. 1-5.

Gosse, Y. P. 1976. Revision du genre *Geophagus* (Pisces, Cichlidae). *Mém. Acad. r. Bélg. Cl. Sci.*, Bruxelles, *19*(3):1-172.

Hennig, W. 1966. *Phylogenetic Systematics*. Univ. illinois Press, Illinois, xv + 263p.

Hensel, R. 1867. Beiträge zur näheren Kenntnis der brasilianischen Provinz São Pedro do Rio Grande do Sul. *Zeitschrift der Gesellschaft für Erdkunde,* Berlin, *2*:227-69.

Hensel, R. 1870. Beiträge zur Kenntnis der Wilbertiere Südbrasiliens Fische. *Archiv. F. Naturgesch.*, *1*:50-91.

Iwaszkiw, J. M. & E. D. Sendra, 1981. Nuevas citas para la ictiofauna de la laguna Chascomús y análisis de las relaciones merísticas en *Gymnogeophagus australis* (Gosse) (Cichlidae) y *Plecostomus commersonii* (Val.) (Loricariidae). *Limnobios,* La Plata, *2*(4):247-52.

Jost, H. 1971. O quaternário da planície costeira do Rio Grande do Sul. I — A Região norte. *XXV Congresso Brasileiro de Geologia, Anais,* São Paulo, :53-62.

Kullander, S. O. 1977. *Papiliochromis* gen n., a new genus of South American Cichlid fish (Teleostei, Perciformes). *Zool. Scripta, 6*:253-4.

Kullander, S. O. 1980a. A redescription of the South American cichlid fish *Papiliochromis ramirezi* (Myers & Harry, 1948) (Teleostei: Cichlidae). *Studies on Neotropical Fauna and Environment,* Amsterdam, (15):91-108.

Kullander, S. O. 1980b. A taxonomical study of the genus *Apistogramma* Regan, with a revision of the Brazilian and Peruvian species. *Bonn. zool. Monogr.*, *14*:1-152.

Kullander, S. O. 1981. Cichlid fauna from the La Plata basin. Part I. Collections from Paraguay in the Muséum d'Histoire naturelle de Genève. *Rev. suisse Zool.*, *88*(3):675-92.

Kullander, S. O. 1983. *Taxonomic studies on the percoid freshwater fish family Cichlidae* *in South America. Part II. Review of the South America Cichlidae*. Stockholm, University of Stockholm, p.297-440. Ph. D. Thesis.

Lowe-McConnell, R. H. 1975. *Fish communities in tropical freshwater*. Longman, New York, xvii + 338p.

Pereira, A. N. 1983. Estudio cromosomico de *Gymnogeophagus rhabdotus* (Perciformes, Cichlidae). *Res. com. jorn. c. nat.*, Montevideo, p.8.

Perugia, A. 1891. Appunti sopra alcuni pesci sud-americani conservati nel Museo Civico di Storia Naturale di Genova. *Ann. Mus. Ci. Sto. Nat. Genova*, Genova, 2nd serie, *10*:605-57.

Ribeiro, A. M. 1918. Dois gêneros e três espécies novas de peixes Brasileiros determinados nas coleções do Museu Paulista. *Revta. Mus. Paulista*, São Paulo, *10*:787-91.

Taylor, W. R. 1967. An enzyme method of clearing and staining small vertebrates. *Proc. U.S. Nat. Mus.*, Washington, *122*(3596):1-17.

Wiley, E.O. 1981. *Phylogenetics, the theory and practice of phylogenetics systematics*. John Wiley & Sons, New York, xv + 439p.

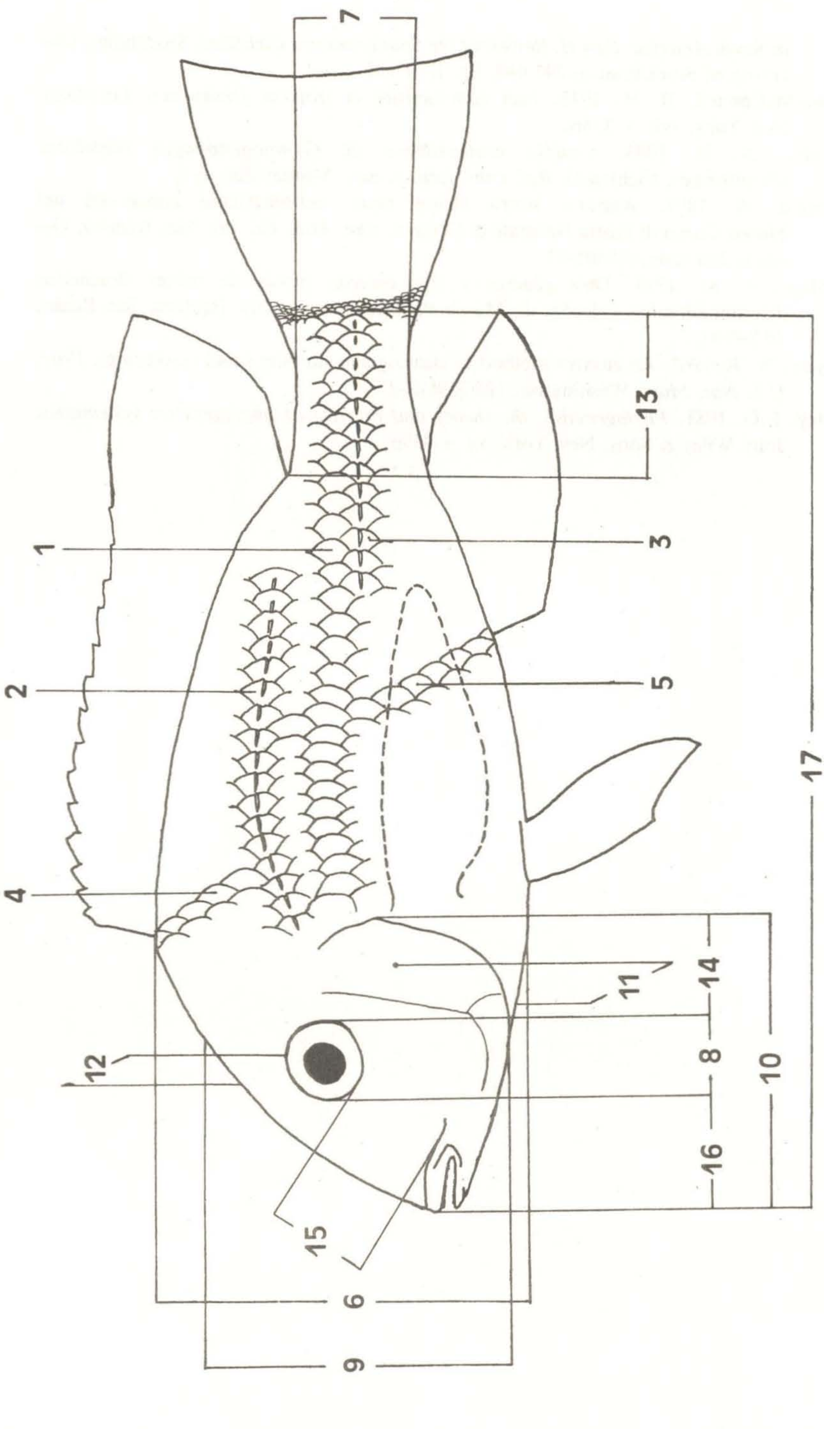


Fig. 1: An hypothetical *Gymnogeophagus* showing the counts and measurements made.

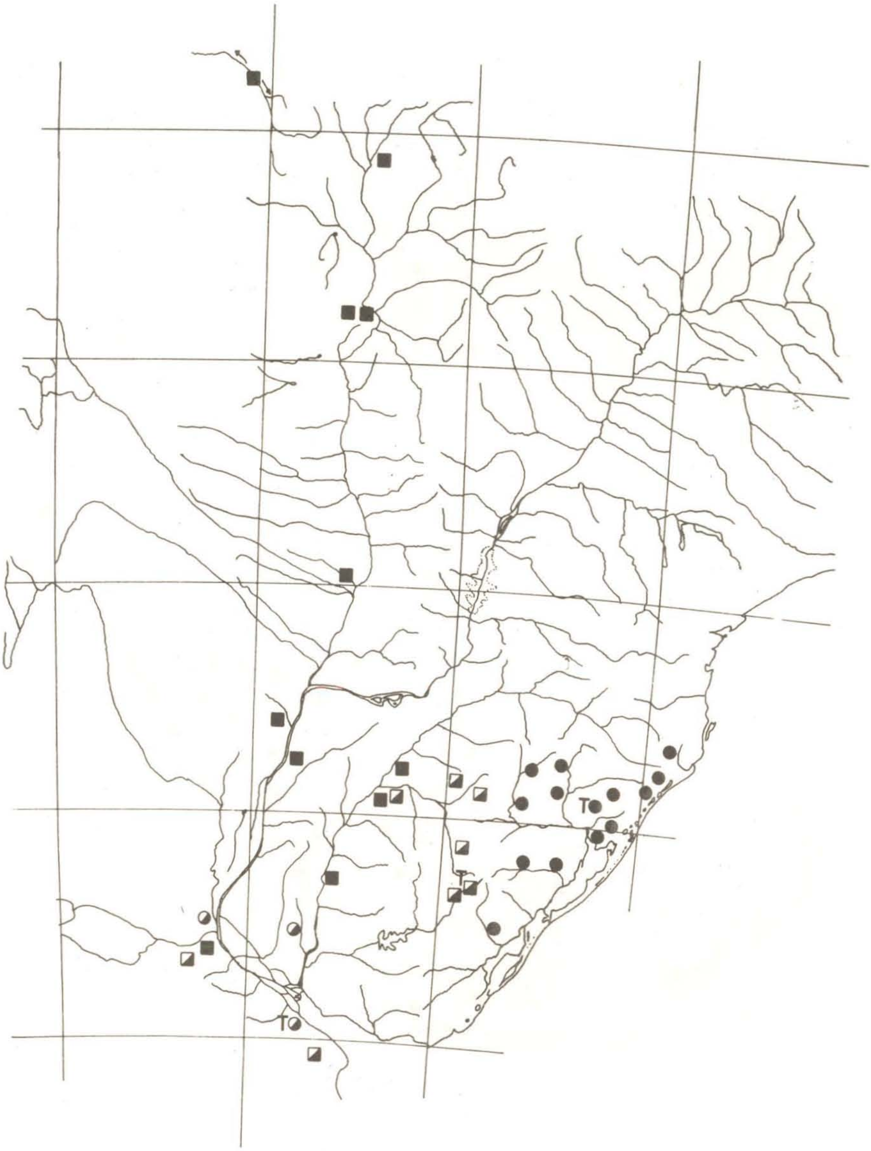


Fig. 2: Map showing the localities of *Gymnogeophagus* species. Black circle: *G. labiatus;* black square: *G. balzanii;* black and white circle: *G. australis* and black and white square: *G. meridionalis* sp. n. One sign may cover several localities. T = type-locality.

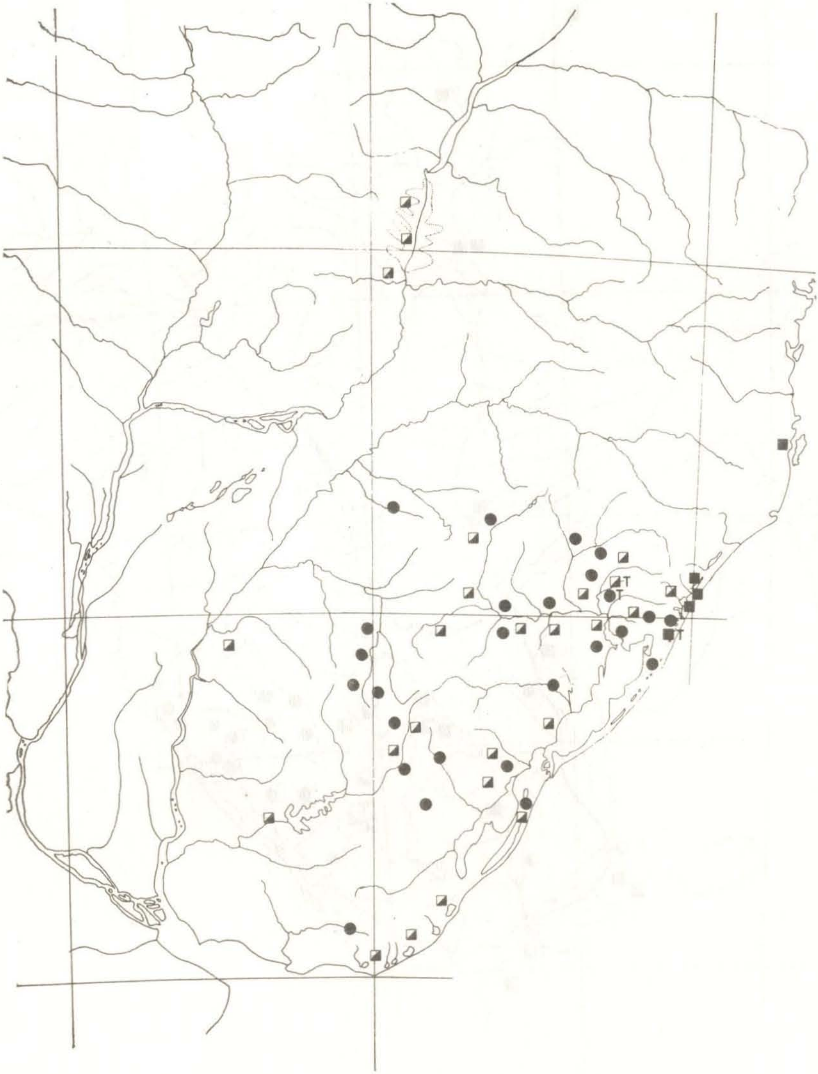
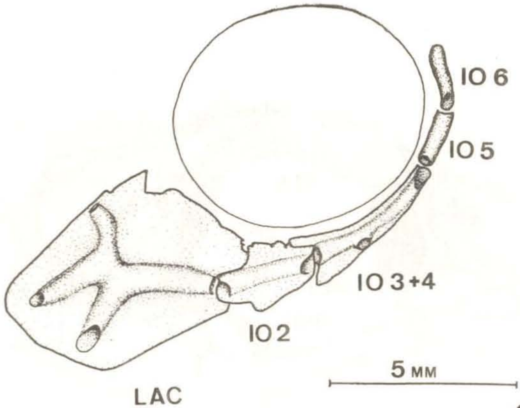


Fig. 3: Map showing the localities of *Gymnogeophagus* species. Black circle: *G. gymnogenys;* black square: *G. lacustris* sp. n. and black and white square: *G. rhabdotus.* One sign may cover several localities. T = type-locality.



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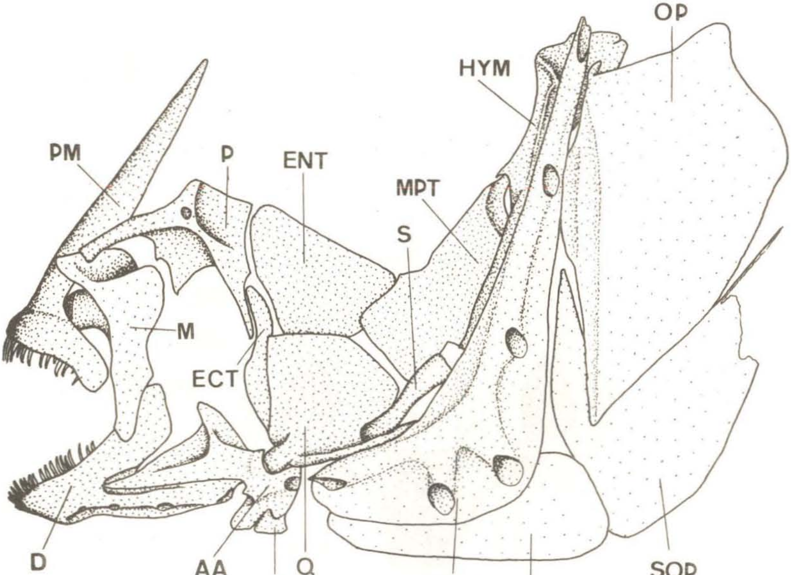

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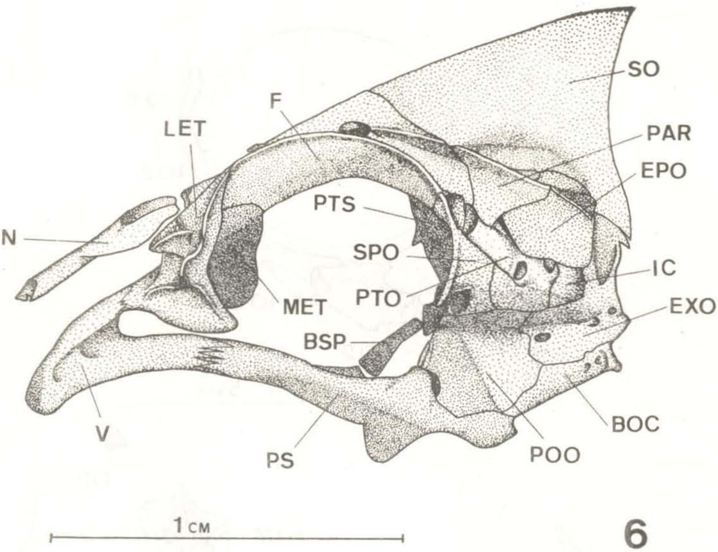
Fig. 4,5: *G. meridionalis* MAPA 2225. 4. Left lateral view of the infraorbital series. 5. Left lateral view of the jaws, suspensorium and operculum.



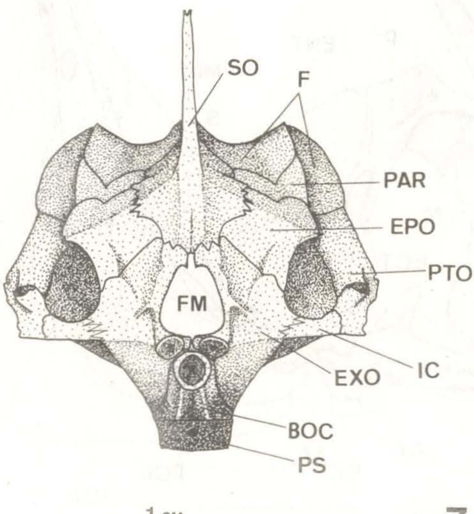
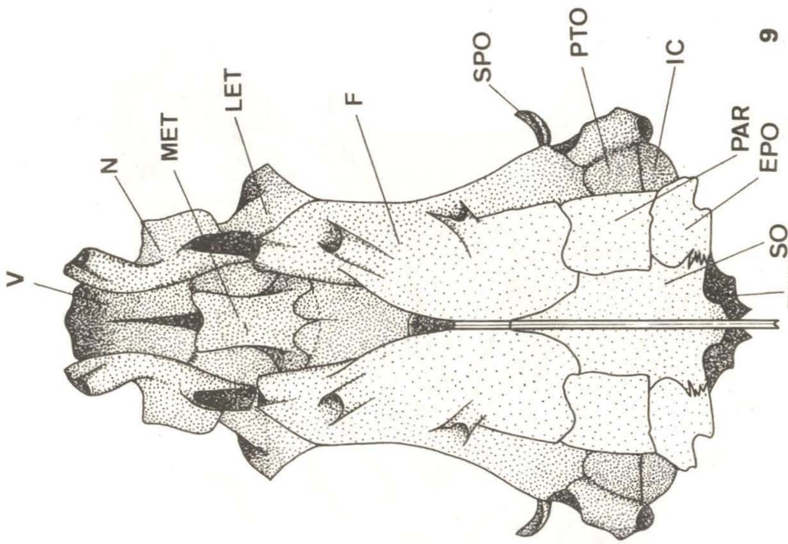


Fig. 6,7: G. meridionalis MAPA 2225. 6. Left lateral view of the neurocranium. 7. Posterior view of the neurocranium.



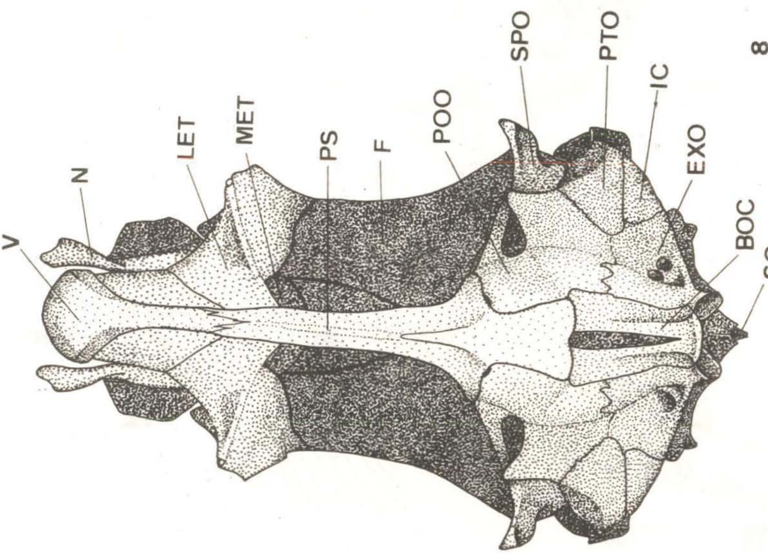


Fig. 8,9: *G. meridionalis* MAPA 2225. 8. Ventral view of the neurocranium. 9. Dorsal view of the neurocraium.

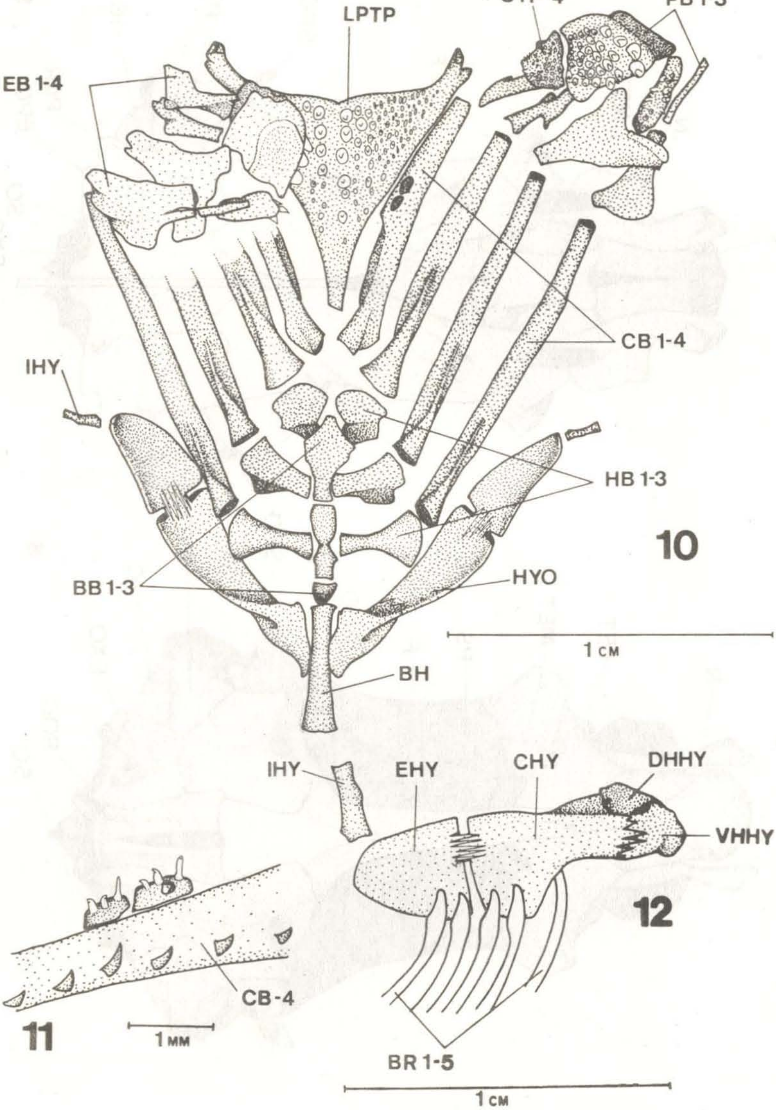
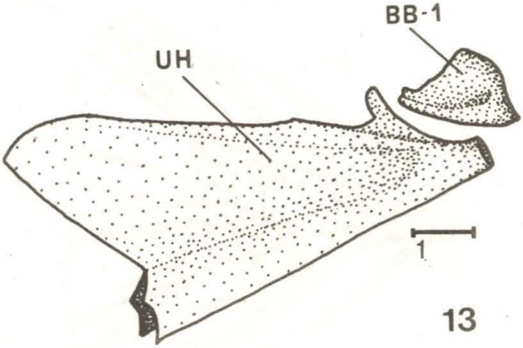


Fig. 10-12: *G. meridionalis* MZUSP 2557. 10. Dorsal view of the branchial skeleton. Upper parts of left side in ventral view. 11. Lateral view of the left fourth ceratobranchial tooth-plate. 12. Right lateral view of the hyoid arch.



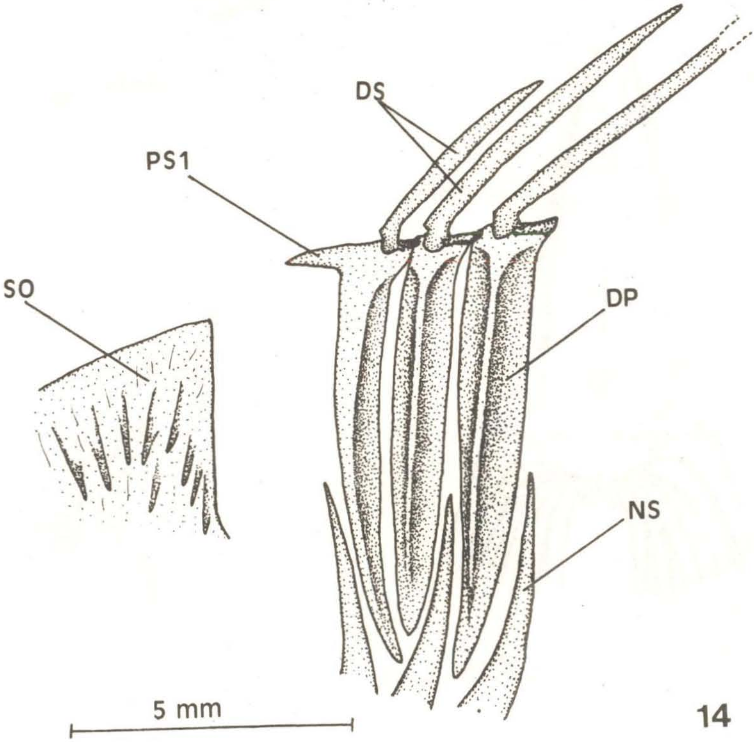
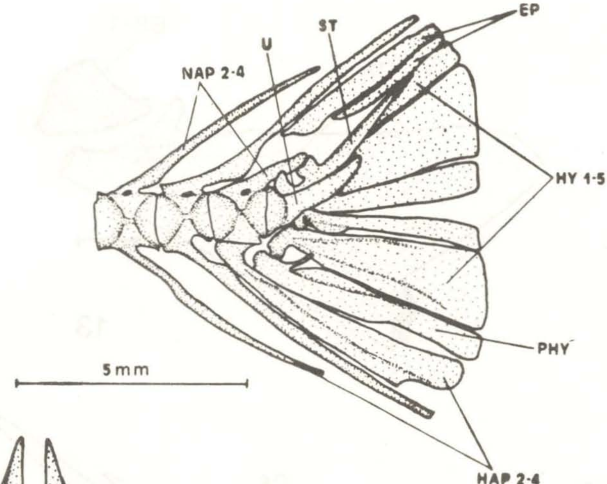


Fig. 13-14: *G. meridionalis*. 13. MZUSP 2557. Right lateral view of the uruhyal plus first basibranchial. 14. MAPA 2225. Left lateral view of the dorsal fin osteology.



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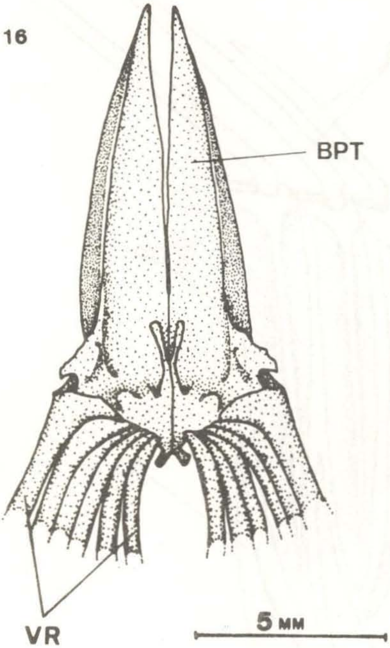

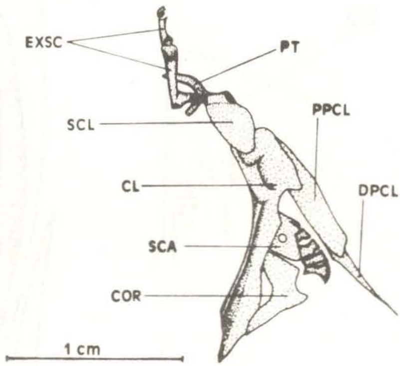

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Fig. 15-17: *G. meridionalis* MAPA 2225. 15. Left lateral view of the caudal fin osteology. 16. Ventral view of the pelvic girdle osteology. 17. Left lateral view of pectoral girdle osteology.

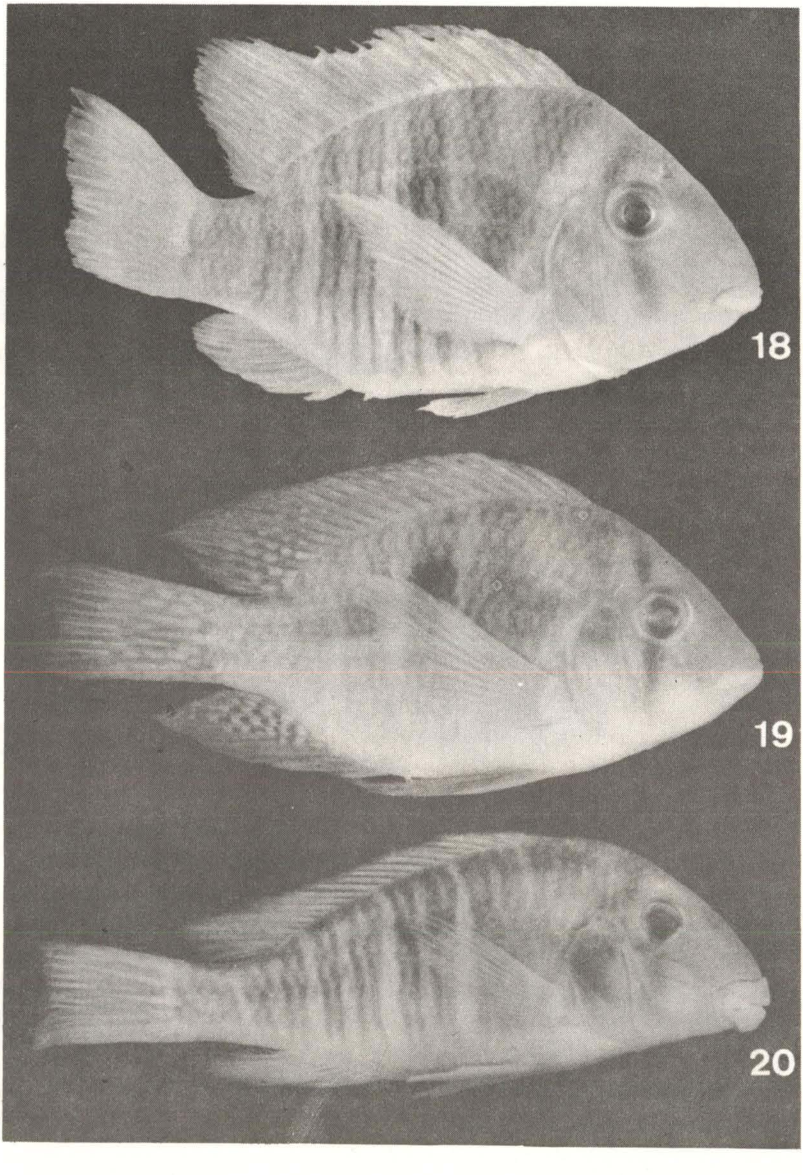


Fig. 18-20: 18. MAPA 2520 *Gymnogeophagus balzanii*, SL = 93.5 mm. 19. MZUSP 28461 Holotype of *Gymnogeophagus meridionalis* sp. n., SL = 80.3 mm. 20. DZUFRGS 1015 *Gymnogeophagus labiatus*, SL = 101.8 mm.

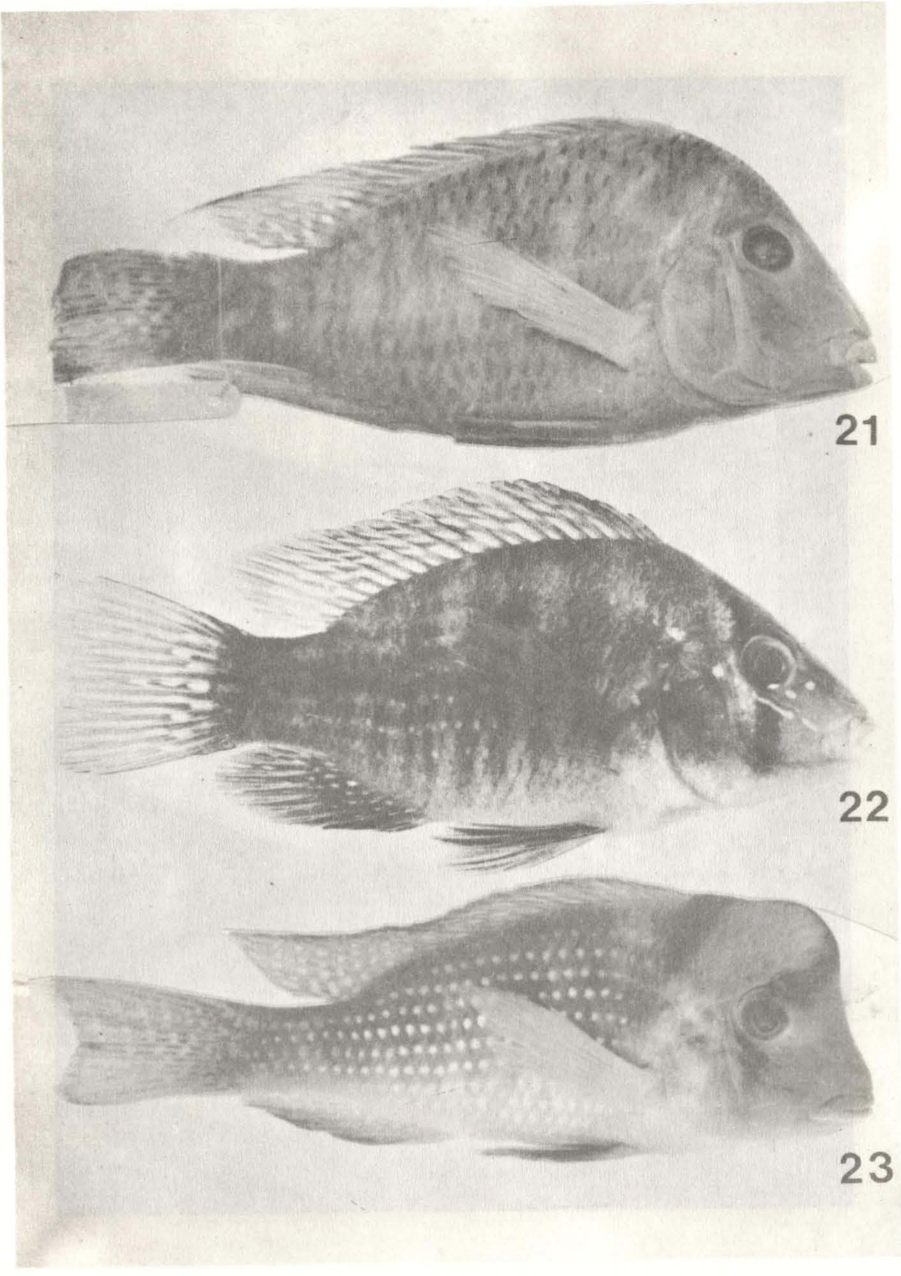
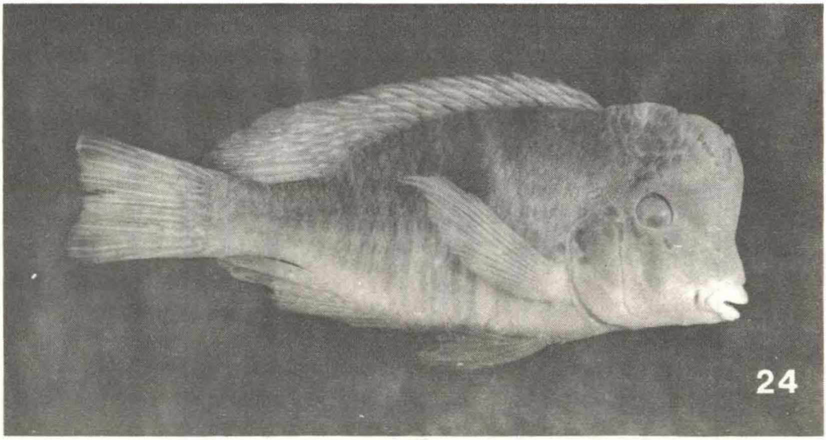


Fig. 21-23: 21. CAS 51440 paratype of *Gymnogeophagus australis*, SL = 110.0 mm. 22. DZUFRGS 0680 *Gymnogeophagus rhabdotus*, SL = 57.0 mm. 23. MAPA 0311 *Gymnogeophagus gymnogenys* SL = 112.0 mm.



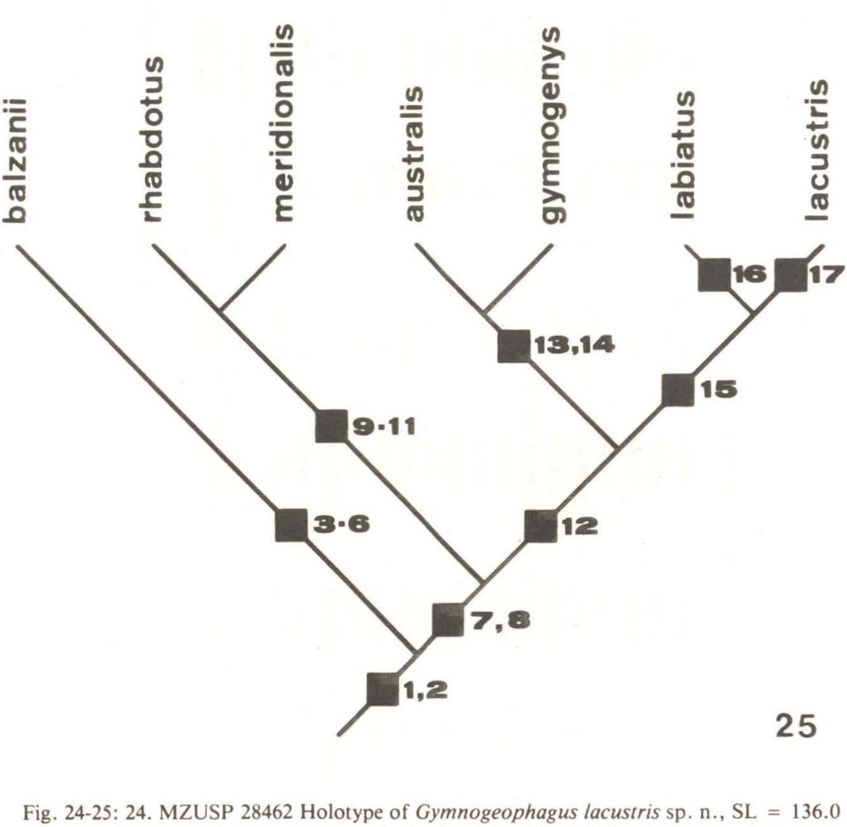


Fig. 24-25: 24. MZUSP 28462 Holotype of *Gymnogeophagus lacustris* sp. n., SL = 136.0 mm. 25. Cladogram depicting the hypothesized relationships within *Gymnogeophagus* species. Solid bars are synapomorphies, numbered according to the Table 1.

Table 1 - Apomorphic (capitals) and plesiomorphic characters states used in the cladogram.

Characters	G. balzanii	rhabdotus	meridionalis	australis	gymnogenys	labiatus	lacustris
1) First dorsal pterygiophore spine	PRESENT	PRESENT	PRESENT	PRESENT	PRESENT	PRESENT	PRESENT
2) Supraneural	ABSENT	ABSENT	ABSENT	ABSENT	ABSENT	ABSENT	ABSENT
3) Dorsal contour	ELEVATED	not elevated	not elevated	not elevated	not elevated	not elevated	not elevated
4) Dorsal soft rays	MANY	few	few	few	few	few	few
5) Assymetric caudal fin	PRESENT	absent	absent	absent	absent	absent	absent
6) Shortened supraoccipital	PRESENT	absent	absent	absent	absent	absent	absent
7) Fins squamation	strong	WEAK	WEAK	WEAK	WEAK	WEAK	WEAK
8) Sensory canal on caudal fin	long	REDUCED	REDUCED	REDUCED	REDUCED	REDUCED	REDUCED
9) Number of longitudinal scales	high	LOWER	LOWER	high	high	high	high
10) Bright-blue striping	absent	PRESENT	PRESENT	absent	absent	absent	absent
11) Supraoccipital crest depth	not elevated	ELEVATED	ELEVATED	not elevated	not elevated	not elevated	not elevated
12) Fronto-parietal crest	wide	wide	wide	REDUCED	REDUCED	REDUCED	REDUCED
13) First transverse band	short	short	short	ELONGATED	ELONGATED	short	short
14) Supraorbital band	present	present	present	ABSENT	ABSENT	present	present
15) Orange lips	absent	absent	absent	absent	absent	PRESENT	PRESENT
16) Very thick lips	absent	absent	absent	absent	absent	PRESENT	absent
17) Supracleithrum shape	ovate	ovate	ovate	ovate	ovate	ovate	NARROW

Table 2 - Frequency of spines, rays and scales in Gymnogeophagus species. A - scales between dorsal origin and upper portion of lateral line; B - scales between anal origin and upper portion of lateral line; * = data of paratypes only.

	dorsal spines				dorsal rays								anal spines			anal rays					scales longitudinal series							
	XII	XIII	XIV	XV	8	9	10	11	12	13	14	15	II	III	IV	6	7	8	9	10	22	23	24	25	26	27	28	29
balzanii	3	18	7						2	12	12	2		27	1		2	11	10	5					10	18		
rhabdotus		3	27	13	9	21	11	2						43			1	35	7		1	5	24	11				
meridionalis		27	10			8	26	3						37			1	19	15	2		7	25	4				
australis*		1	1				1	1						2				1	1							2		
gymnogenys		29	68	7	2	17	43	36	6					104			9	60	34	1					6	25	10	1
labiatus		11	29	2	1	7	22	9	3				1	41		1	12	27	2						3	20	13	
lacustris	8	19	3				4	20	6				1	29				7	23						3	16	11	

	scales upper lateral line										scales lower lateral line										A			B			
	12	13	14	15	16	17	18	19	20	21	4	5	6	7	8	9	10	11	12	13	4	5	6	7	8	9	10
balzanii					1	4	3	8	9	3				1	1	9	10	6				22	6		2	15	11
rhabdotus			9	13	12	6	1	1					2	8	20	5	5	1			27	15		4	38		
meridionalis	1	2	1	4	12	14	1	1			3	2	5	15	6	4	1				10	10			19	1	
australis*					1	1												2			2				1	1	
gymnogenys			1	1	4	15	17	4					6	3	7	7	7	9	3		39	3			28	14	
labiatus			1	1	4	7	13	7	5					2	3	5	9	15	3	1	24	13		1	32	4	
lacustris					3	15	8	3	1					4	6	7	5	5	3		21	7				30	

Table 3 - Morphometric data of *Gymnogeophagus* species. n= number of specimens measured. *= data of paratypes only.

	G. balzanii	*rhabdotus*	*meridionalis*	*australis*	*gymnogenys*	*labiatus*	*lacustris*
n	28	43	21	11	94	40	29
Standard length	28-126 mm	40.4-120 mm	39.3-88 mm	80-110 mm	40-125 mm	26.9-138.3 mm	48.4-146 mm
Body depth / SL	1.8-2.4 (2.0)	2.1-2.4 (2.2)	1.9-2.8 (2.2)	2.0-2.2 (2.2)	2.3-2.9 (2.6)	2.2-3.1 (2.6)	2.3-2.9 (2.5)
Head length / SL	2.6-3.1 (2.8)	2.5-3.0 (2.7)	2.6-2.9 (2.8)	2.8-3.1 (2.9)	2.6-3.3 (2.9)	2.8-3.3 (2.9)	2.7-3.2 (2.9)
Head depth / SL	0.7-1.0 (0.8)	0.9-1.2 (1.0)	0.9-1.1 (1.0)	0.8-0.8 (0.8) *	0.8-1.2 (1.1)	0.9-1.3 (1.1)	0.8-1.2 (1.0)
Head width / HL	1.6-2.0 (1.8)	1.7-2.1 (1.9)	1.7-2.0 (1.8)	1.7-2.1 (1.9)	1.7-2.1 (1.8)	1.7-2.2 (1.9)	1.7-2.3 (1.9)
Eye diameter / HL	2.4-4.4 (3.3)	2.8-4.8 (3.7)	3.1-3.8 (3.3)	3.1-4.4 (3.5)	2.6-5.0 (3.6)	2.3-5.1 (3.8)	3.1-4.9 (3.6)
Interorbital width / HL	2.1-3.7 (2.7)	2.5-3.8 (3.1)	2.4-3.5 (3.1)	2.7-3.6 (3.3)	2.0-4.2 (3.3)	1.8-4.3 (3.4)	2.4-4.3 (3.3)
Post-orbital length / HL	2.6-3.9 (3.2)	2.6-3.8 (3.0)	2.6-3.7 (3.0)	2.4-3.5 (2.9)	2.5-3.5 (2.9)	2.5-3.3 (3.0)	2.7-3.4 (3.0)
Pre-orbital length / HL	2.1-4.4 (2.9)	3.2-4.3 (3.7)	3.0-4.5 (3.9)	2.5-3.4 (2.9)	2.5-5.0 (3.9)	2.4-5.7 (3.9)	2.5-4.5 (3.7)
Snout length / HL	2.1-3.9 (2.8)	2.1-3.0 (2.6)	2.5-3.3 (2.8)	2.2-2.8 (2.4)	2.0-3.5 (2.7)	1.8-4.5 (2.5)	2.2-3.0 (2.5)
Length caudal peduncle / CpD	0.4-0.9 (0.6)	0.6-1.0 (0.8)	0.6-0.9 (0.8)	0.9-1.1 (1.0)	1.0-1.4 (1.2)	1.2-1.6 (1.3)	1.1-1.6 (1.3)

Table 4 - Linear regression data of morphometric characters for *Gymnogeophagus* species. a = regression constant (linear coefficient) ± standard deviation; b = regression coefficient (angular coefficient) ± standard deviation; r^2 = coefficient of determination; n = number of specimens.

	G. balzanii (n=28)			*G. meridionalis* (n=21)			*G. labiatus* (n=40)		
	a	b	r^2	a	b	r^2	a	b	r^2
BD/SL	-4.97 (±0.59)	0.59 (±0.011)	0.99	-6.54 (±1.55)	0.58 (±0.046)	0.96	-2.87 (±1.14)	0.41 (±0.034)	0.95
HL/SL	-0.18 (±0.62)	0.36 (±0.020)	0.99	0.74 (±0.51)	0.35 (±0.025)	0.99	0.78 (±0.57)	0.33 (±0.021)	0.98
HD/HL	-4.54 (±1.17)	1.43 (±0.027)	0.98	-3.34 (±0.60)	1.18 (±0.024)	0.99	-5.58 (±0.97)	1.13 (±0.031)	0.96
HW/HL	-0.82 (±0.33)	0.59 (±0.018)	0.99	-0.85 (±0.41)	0.59 (±0.033)	0.98	0.56 (±0.43)	0.49 (±0.031)	0.96
ED/HL	2.16 (±0.28)	0.21 (±0.045)	0.94	0.95 (±0.25)	0.26 (±0.047)	0.96	2.20 (±0.50)	0.17 (±0.089)	0.70
IW/HL	-2.66 (±0.36)	0.49 (±0.024)	0.98	-2.19 (±0.50)	0.44 (±0.053)	0.94	-1.13 (±0.72)	0.35 (±0.070)	0.82
PoL/HL	1.46 (±0.31)	0.25 (±0.040)	0.96	0.25 (±0.48)	0.32 (±0.068)	0.91	0.53 (±0.22)	0.22 (±0.025)	0.97
PrL/HL	-3.69 (±0.54)	0.52 (±0.035)	0.97	-2.36 (±0.35)	0.38 (±0.043)	0.96	-3.61 (±0.42)	0.43 (±0.036)	0.95
SnL/HL	-3.44 (±0.56)	0.52 (±0.036)	0.97	-0.88 (±0.54)	0.40 (±0.062)	0.93	-3.78 (±0.50)	0.56 (±0.032)	0.96
CpD/CpL	-1.22 (±1.35)	1.80 (±0.078)	0.84	-1.68 (±0.88)	1.52 (±0.077)	0.89	0.41 (±0.33)	0.72 (±0.034)	0.96
CpD/SL	-0.68 (±0.33)	0.19 (±0.021)	0.99	-1.27 (±0.43)	0.18 (±0.041)	0.97	-0.08 (±0.26)	0.13 (±0.026)	0.97
CpL/SL	1.51 (±0.61)	0.09 (±0.076)	0.85	0.77 (±0.40)	0.11 (±0.061)	0.93	-0.32 (±0.43)	0.17 (±0.031)	0.96
HD/SL	-5.23 (±0.81)	0.52 (±0.019)	0.99	-2.59 (±0.60)	0.41 (±0.025)	0.99	-4.87 (±1.02)	0.38 (±0.033)	0.96
ED/PrL	3.78 (±0.27)	0.39 (±0.545)	0.92	2.60 (±0.20)	0.65 (±0.052)	0.95	3.76 (±0.35)	0.40 (±0.089)	0.70
SnL/PrL	0.57 (±0.59)	0.97 (±0.049)	0.94	1.62 (±0.31)	1.04 (±0.051)	0.95	1.23 (±0.38)	1.27 (±0.035)	0.95
ED/PoL	1.22 (±0.43)	0.80 (±0.057)	0.91	1.26 (±0.46)	0.72 (±0.086)	0.86	1.97 (±0.53)	0.55 (±0.089)	0.70
ED/SnL	3.74 (±0.31)	0.39 (±0.062)	0.90	1.86 (±0.37)	0.58 (±0.079)	0.88	3.41 (±0.37)	0.31 (±0.086)	0.72
ED/IW	3.40 (±0.29)	0.42 (±0.055)	0.92	2.51 (±0.35)	0.53 (±0.085)	0.86	2.76 (±0.27)	0.51 (±0.060)	0.86
	G. gymnogenys (n=94)			*G. rhabdotus* (n=43)			*G. lacustris* (n=30)		
BD/SL	-3.99 (±0.57)	0.45 (±0.019)	0.97	-1.95 (±0.91)	0.48 (±0.027)	0.97	-4.38 (±0.78)	0.46 (±0.021)	0.99
HL/SL	2.01 (±0.43)	0.31 (±0.020)	0.96	-1.36 (±0.76)	0.38 (±0.028)	0.97	2.62 (±0.70)	0.30 (±0.028)	0.98
HD/HL	-5.09 (±0.82)	1.18 (±0.029)	0.92	-1.00 (±1.19)	1.03 (±0.044)	0.92	-9.95 (±1.63)	1.36 (±0.043)	0.95
HW/HL	-0.67 (±0.29)	0.56 (±0.022)	0.95	0.40 (±0.51)	0.51 (±0.038)	0.94	-0.43 (±0.58)	0.53 (±0.039)	0.96
ED/HL	2.35 (±0.25)	0.17 (±0.053)	0.74	2.64 (±0.43)	0.16 (±0.088)	0.68	2.81 (±0.41)	0.17 (±0.081)	0.81
IW/HL	-1.11 (±0.36)	0.36 (±0.041)	0.85	-1.88 (±0.56)	0.41 (±0.051)	0.89	-3.82 (±0.62)	0.46 (±0.048)	0.93
PoL/HL	0.94 (±0.22)	0.30 (±0.031)	0.91	1.53 (±0.44)	0.27 (±0.060)	0.85	0.23 (±0.32)	0.33 (±0.036)	0.96
PrL/HL	-3.38 (±0.33)	0.42 (±0.033)	0.90	-1.13 (±0.31)	0.32 (±0.038)	0.94	-4.78 (±0.59)	0.47 (±0.045)	0.94
SnL/HL	-2.42 (±0.38)	0.48 (±0.033)	0.90	-2.17 (±0.55)	0.49 (±0.043)	0.92	-1.96 (±0.51)	0.48 (±0.039)	0.96
CpD/CpL	-0.16 (±0.35)	0.84 (±0.036)	0.88	0.48 (±1.52)	1.25 (±0.109)	0.51	0.16 (±0.41)	0.73 (±0.039)	0.96
CpD/SL	0.08 (±0.18)	0.13 (±0.021)	0.96	-0.65 (±0.34)	0.16 (±0.030)	0.96	-0.05 (±0.33)	0.13 (±0.032)	0.97
CpL/SL	1.17 (±0.31)	0.14 (±0.031)	0.91	2.89 (±0.64)	0.07 (±0.098)	0.61	0.04 (±0.47)	0.17 (±0.034)	0.97
HD/SL	-3.49 (±0.64)	0.38 (±0.025)	0.94	-2.99 (±1.19)	0.41 (±0.041)	0.93	-7.29 (±0.90)	0.43 (±0.026)	0.98
ED/PrL	4.13 (±0.19)	0.35 (±0.067)	0.59	3.39 (±0.37)	0.48 (±0.092)	0.65	4.75 (±0.32)	0.33 (±0.100)	0.72
SnL/PrL	2.07 (±0.31)	1.06 (±0.042)	0.84	0.24 (±0.63)	1.44 (±0.059)	0.86	3.21 (±0.44)	0.96 (±0.052)	0.92
ED/PoL	2.27 (±0.31)	0.52 (±0.062)	0.65	2.49 (±0.56)	0.50 (±0.102)	0.57	2.85 (±0.45)	0.50 (±0.087)	0.79
ED/SnL	3.60 (±0.22)	0.31 (±0.064)	0.63	3.86 (±0.42)	0.27 (±0.109)	0.52	3.77 (±0.42)	0.33 (±0.098)	0.73
ED/IW	3.54 (±0.26)	0.39 (±0.069)	0.56	3.95 (±0.41)	0.32 (±0.109)	0.51	4.55 (±0.37)	0.33 (±0.105)	0.69