A review of the South American cichlid genus Cichla, with descriptions of nine new species (Teleostei: Cichlidae)

Article *in* Ichthyological Exploration of Freshwaters · January 2007

CITATIONS
143

READS
1,858

2 authors:

Sven Kullander
Swedish Museum of Natural History
195 PUBLICATIONS **1,666** CITATIONS

SEE PROFILE

Efrem Jorge Gondim Ferreira
Instituto Nacional de Pesquisas da Amazônia
52 PUBLICATIONS **632** CITATIONS

SEE PROFILE

Verlag Dr. Friedrich Pfeil
ISSN 0936-9902

Ichthyological Exploration of Freshwaters

An international journal for field-orientated ichthyology

Volume 17
Number 4

Ichthyological Exploration of Freshwaters

An international journal for field-orientated ichthyology

Volume 17 • Number 4 • December 2006

pages 289-398, 93 figs., 27 tabs.

Ichthyological Exploration of Freshwaters is published quarterly

Subscriptions should be addressed to the Publisher:

Verlag Dr. Friedrich Pfeil, Wolfratshauser Str. 27, D–81379 München, Germany
PERSONAL SUBSCRIPTION : EURO 100 per Year/volume - 4 issues (includes surface mail shipping)
INSTITUTIONAL SUBSCRIPTION : EURO 180 per Year/volume - 4 issues (includes surface mail shipping)

Manuscripts should be addressed to the Managing Editor:
Maurice Kottelat, Route de la Baroche 12, Case postale 57, CH–2952 Cornol, Switzerland

CIP-Titelaufnahme der Deutschen Bibliothek

Ichthyological exploration of freshwaters : an international journal for field-orientated ichthyology. – München : Pfeil.
Erscheint jährl. viermal. – Aufnahme nach Vol. 1, No. 1 (1990)
ISSN 0936-9902

Vol. 1, No. 1 (1990) –

Printed by Druckerei Wiesendanger, Murnau

ISSN 0936-9902
Printed in Germany

Verlag Dr. Friedrich Pfeil, Wolfratshauser Str. 27, D-81379 München, Germany
Tel. +49-(0)89-7428270 – Fax +49-(0)89-7242772 – E-mail: info@pfeil-verlag.de – www.pfeil-verlag.de

Ichthyol. Explor. Freshwaters, Vol. 17, No. 4, pp. 289-398, 93 figs., 27 tabs., December 2006

A review of the South American cichlid genus *Cichla*, with descriptions of nine new species (Teleostei: Cichlidae)

Sven O. Kullander* and Efrem J. G. Ferreira**

Cichla, with the junior synonym *Acharnes*, is widely distributed in the Amazon, Tocantins, and Orinoco river basins, and in the smaller rivers draining the Guianas to the Atlantic Ocean. Within South America transplantations are recorded from the Paraná and Paraguay river drainages in Paraguay and Brazil, and the Paraíba do Sul and Paraguaçu rivers in Brazil. The genus comprises 15 species recognized by external characters of which colour pattern and meristics are most significant.

In six species juveniles possess three dark blotches on the side and a dark band connecting the posterior blotch to the dark blotch at the caudal-fin base: *Cichla ocellaris* is known from the Guianas, including the Marowijne, Suriname, Corantijn, Demerara, and Essequibo river drainages, and also the upper Rio Branco in Brazil. *Cichla orinocensis* is known from the Negro and Orinoco river drainages in Brazil, Colombia, and Venezuela. *Cichla monoculus* is widespread in the floodplains of the Amazon basin, in Colombia, Peru, and Brazil, and also collected from rivers of Amapá in Brazil, and the lower Oyapock River on the border between Brazil and French Guiana. *Cichla nigromaculata* is known from the upper Rio Orinoco in Venezuela and, tentatively, the middle Rio Negro in Brazil. *Cichla kelberi*, new species, is restricted to the Tocantins river basin, but also found transplanted in the Paraná and Paraíba do Sul river drainages and reported from the Nordeste region of Brazil. *Cichla pleiozona*, new species, occurs in the Madre de Dios, Beni, and Guaporé river drainages in Bolivia and Brazil, and in the Rio Jamari in Brazil. A lectotype is fixed for *Cychla toucounarai* which is a synonym of *Cichla monoculus*.

Juveniles and young of the remaining nine species, in addition to the three midlateral blotches, possess a dark horizontal band extending from the head to the dark blotch at the caudal-fin base: *Cichla mirianae*, new species, is restricted to the upper Tapajós river drainage, in the Juruena and Teles Pires rivers, and the upper Xingu river drainage in Brazil. *Cichla melaniae*, new species, is restricted to the lower Xingu river drainage in Brazil. *Cichla piquiti*, new species, is restricted to the Tocantins river basin, but transplanted in the Paraná river basin in Brazil and Paraguay. *Cichla thyrorus*, new species, occurs in the Rio Trombetas in Brazil, upstream from the Cachoeira Porteira. *Cichla jariina*, new species, occurs in the Rio Jari in Brazil, where it is so far recorded only from the region of the Santo Antonio rapids. *Cichla pinima*, new species, occurs in the lower parts of southern tributaries of the Rio Amazonas in Brazil (Tapajós, Curuá-Una, Xingu), and the lower Tocantins and Capim rivers. Tentatively identified specimens are recorded from the Amapá, Araguari, and Canumã rivers in Brazil. *Cichla pinima* occurs translocated in the Rio Paraguaçu in southeastern Brazil, and is reported as translocated from the northeast of Brazil. *Cichla vazzoleri*, new species, occurs in the Uatumã and lower Trombetas rivers in Brazil. *Cichla temensis* is known from the Negro and Orinoco river drainages in Brazil, Colombia, and Venezuela. It is also recorded from blackwater rivers along the Rio Solimões-Amazonas in Brazil (Tefé, Rio Puraquequara, Rio Uatumã, and Silves). *Cichla intermedia* is restricted to the Casiquiare and Orinoco river drainages in Venezuela.

* Department of Vertebrate Zoology, Swedish Museum of Natural History, POB 50007, SE-104 05 Stockholm, Sweden. E-mail: sven.kullander@nrm.se

** Centro de Pesquisas de Biologia Acuatica, INPA, CP 478, 69083-000 Manaus, AM, Brazil. E-mail: efrem@inpa.gov.br

A phylogenetic analysis suggests that *C. intermedia*, *C. piquiti*, and *C. melaniae* are successive basal species, whereas an unresolved group composed of *C. jariina*, *C. pinima*, *C. temensis*, *C. thyrorus*, and *C. vazzoleri* is the sister group of (*C. mirianae*,(*C. orinocensis*,((*C. ocellaris*, *C. nigromaculata*),(*C. monoculus*, *C. kelberi*, *C. pleiozona*))).

Introduction

Species of the genus *Cichla* are among the major food and game fishes in South America. They are known locally by the collective names tucunaré in most of the Amazon region, pavón in Venezuela, toekoenali in Suriname, and lukanani in Guyana (Kullander, 2003).

Cichla has been the subject of several recent reviews dealing with phylogenetic position (Stiassny, 1982, 1987; Kullander, 1986, 1998), life history (Zaret, 1980), and particular species (Machado, 1971, 1973; Kullander, 1986; Kullander & Nijssen, 1989). There are surprisingly few studies on the ecology and behaviour of *Cichla*. Lowe-McConnell (1969) reported on field observations of *C. ocellaris* in Guyana, and Winemiller (2001) summarised ecological studies on Venezuelan species, which are probably representative for the genus.

Fifteen nominal species are referable to *Cichla* (Table 1). The majority were described in the period 1821-1855 and frequently based on field observations and drawings. Revisions by Günther (1862), Pellegrin (1904), and Regan (1906) distinguished principally only the two species *C. temensis* and *C. ocellaris* with varying synonym lists. Günther (1862) also listed *C. conibos* and *C. multifasciata*, and Regan recognized *C. multifasciata* based on the drawings and sketchy information from Castelnau (1855). Castelnau's names, however, more likely refer to unrecognizable species of *Crenicichla* (Kullander, 1986). Most literature before Machado's (1971) revision mentioned only two species, viz. *C. temensis* and *C. ocellaris*.

Ringuelet et al. (1967: 507) reported *C. chacoensis* (Holmberg, 1891) from Argentina. Holmberg (1891) described the species in the genus *Acharnes*, a synonym of *Cichla*. His description, as well as

Table 1. Nominal species of *Cichla* in chronological order of description.

original combination	author, year	type locality (river basin)	current name
Cichla ocellaris	Schneider, 1801	East India, erroneous	*Cichla ocellaris*
Cichla temensis	Humboldt, 1821	Rio Negro	*Cichla temensis*
Cichla atabapensis	Humboldt, 1821	Rio Orinoco	*Cichla temensis*
Cichla argus	Valenciennes, 1821	Unknown	*Cichla orinocensis*
Cichla orinocensis	Humboldt, 1821	Rio Orinoco, Rio Negro	*Cichla orinocensis*
Cichla monoculus	Agassiz, 1831	Brazilian sea [Amazon basin]	*Cichla monoculus*
Cichla Tucunare	Heckel, 1840	Rio Branco	*Cichla temensis*
Cichla flavo-maculata	Jardine, 1843	Rio Negro	*Cichla temensis*
Cichla nigro-maculata	Jardine, 1843	Rio Negro	*Cichla nigromaculata*
Cichla trifasciata	Jardine, 1843	Rio Negro	*Cichla temensis*
Acharnes speciosus	Müller & Troschel, 1849	Guyana coast, Essequibo River	*Cichla ocellaris*
Cycla toucounarai	Castelnau, 1855	Amazon basin	*Cichla monoculus*
Cichla unitaeniatus	Magalhães, 1931	Rio Negro, Rio Purús	*Cichla temensis*
Cichla bilineatus	Nakashima, 1941	Rio Amazonas, Peru	*Cichla monoculus*
Cichla intermedia	Machado-Allison, 1971	Rio Casiquiare	*Cichla intermedia*
Cichla kelberi	new species, this paper	Rio Tocantins	*Cichla kelberi*
Cichla pleiozona	new species, this paper	Rio Guaporé	*Cichla pleizona*
Cichla mirianae	new species, this paper	Rio Tapajós	*Cichla mirianae*
Cichla melaniae	new species, this paper	Rio Xingu	*Cichla melaniae*
Cichla piquiti	new species, this paper	Rio Tocantins	*Cichla piquiti*
Cichla thyrorus	new species, this paper	Rio Trombetas	*Cichla thyrorus*
Cichla jariina	new species, this paper	Rio Jari	*Cichla jariina*
Cichla pinima	new species, this paper	Rio Curuá-Una	*Cichla pinima*
Cichla vazzoleri	new species, this paper	Rio Trombetas	*Cichla vazzoleri*

that of Ringuelet et al. (1967) clearly suggests a species of *Crenicichla*, and *A. chacoensis* was synonymized with *Crenicichla semifasciata* by Kullander (1981, 2003).

Tertiary cichlid remains from Salta and Catamarca, Argentina, were assigned to the monotypic genus *Palaeocichla* by Casciotta & Arratia (1993), and compared with *Cichla* and *Crenicichla.* There are no character states known that definitively link *Palaeocichla* with *Cichla.*

Machado (1971) provided adequate diagnoses and detailed descriptions of *C. orinocensis* (as *C. ocellaris*) and *C. temensis* based on Venezuelan material, and described a new species from Venezuela, *C. intermedia.* Kullander (1986) resurrected *C. monoculus* from the synonymy of *C. ocellaris* and redescribed the species. Kullander & Nijssen (1989) diagnosed and redescribed the true *C. ocellaris* based on Surinamese materials.

Five species of *Cichla* are thus relatively well known but it has been recognized for some time that several more species exist, and both sport fishing and aquarium literature contains references to populations not conforming to the taxa already named (e.g., Kelber, 1999; Stawikowski & Werner, 2004). The objective of this paper is to address those remaining taxa, providing names and diagnoses, to enable their full recognition for further biological study.

Methods

The major impediment to a revision of *Cichla* has been to assemble sufficient material to represent ontogenetic stages, both sexes and both sexually quiescent and active phases, as well as covering the geographic range of the genus in an even manner. This has not been possible. Adult specimens of *Cichla* collected during surveys and inventories are rarely preserved, and loans between museums of large series are impractical. We have worked mainly with the excellent material from the surveys of Michael Goulding covering the Negro, Branco, Tapajós, and Xingu rivers, and the junior author in the Rio Trombetas, supplemented by other surveys deposited principally in the Instituto Nacional de Pesquisas da Amazônia, Manaus, and the Museu de Zoologia da Universidade de São Paulo.

Morphometry, meristics, and morphology. The descriptions of *C. ocellaris* and *C. monoculus* in Kullander (1986) and Kullander & Nijssen (1989), encompassing general shape, fin shape, scale types, mouth size, gill raker shape, sexual dimorphism, etc., are representative of all *Cichla* except for a limited set of species diagnostic character states. We restrict the descriptions below to general form and species diagnostic characters with emphasis on colour pattern which varies with size and reproductive phase.

Because of the limitations in material size and ontogenetic and geographic coverage, we have worked from a strategy to take detailed notes on just about all lots examined and starting from a rough subdivision into species, subdivided the material into finer diagnosable units as more material has been added. Lack of simultaneous access to samples was remedied by photographing as many specimens as possible and using photographs for species discrimination analysis. The character selection is based on the work of Kullander (1986) and Kullander & Nijssen (1989), employing primarily scale counts and colour pattern. There is some variation in body proportions and other meristics, but generally not useful for discriminating species. We have not observed or examined extensively variation in osteological or soft anatomical characters.

Measurements and counts are summarized in Figs. 2-4 and Tables 2-11; measurement data for each species are summarized in Tables 12-26. Methods for taking measurements and counts follow Kullander (1986) and Kullander & Nijssen (1989). All measurements are taken point to point. Standard length (SL) is taken from the tip of the upper jaw to the middle of the caudal-fin base. Scales in the E1 row are a count of scales in the horizontal row immediately above that containing the lower lateral line. Other counts and measurements should be self-explanatory. Morphometric and meristic information was organized and analysed using SPSS 14 (SPSS, 2005). An unpublished program written by Julian M. Humphries and David L. Swofford was used for performing shearing of principal components.

In species of *Cichla* the lateral line may consist of an anterior sequence of tubed scales extending from the head to below the soft dorsal fin, and a posterior sequence from the caudal fin rostrad to below or slightly posterior to the termination of the anterior sequence, but frequently there are tubed scales bridging the gap between the anterior and posterior sequences and the lateral line consequently appears continuous from the head

to the caudal-fin base. Often, the bridging scales are slightly misaligned and the two principal sequences do not meet, or there may be a scale in the bridging sequence without tube, i.e., the lateral line is subcontinuous. The left and right side may differ with regard to lateral line pattern. In the descriptions we distinguish three character states, i.e., bilaterally discontinuous, bilaterally continuous, and unilaterally continuous (implies that the opposite lateral line is discontinuous). We refer to a subcontinuous state when the upper and lower lateral line follow the same curve, but are separated by one or two normal scales. Actual counts from the right side are summarized in Tables 3-5.

To facilitate comparisons, colour pattern terminology was formalized as follows (Fig. 1a):

Ocellated markings. An ocellus or ocellar blotch is a dark, round marking with a light border, resembling an eye. The caudal blotch in adult *Cichla* is a typical ocellus. However, several other dark markings in *Cichla* may feature white border, either a complete light (white or yellowish) border enclosing the dark marking or light spots lining the dark markings forming an incomplete, collar-like border. Such markings are all referred to as 'ocellated'.

Vertical bars (Fig. 1a)**.** Dark vertical bars, present in all species of *Cichla*, are numbered from 1 to 4. Bar 1 is the one below the anterior spines of the dorsal fin. Bar 2 is the bar below the posterior portion of the spinous dorsal fin. Bar 3 is located below the soft dorsal fin. A fourth major bar (bar 4) occurs only in some species or individuals and is situated on the anterior portion of the caudal peduncle. The precise position of bars relative to countable scales or fin rays may vary slightly between individuals. Thus bar 3 may be located anywhere below the middle or the posterior rays of the soft dorsal fin. In some species of *Cichla* dark vertical bars are present between the three principal bars. These bars are distinguished as bar 1a (between bars 1 and 2) and bar 2a (between bars 2 and 3). The dark bar crossing the nape, and particularly prominent in breeding *C. monoculus*, *C. kelberi*, and *C. pleiozona*, is not numbered, but referred to as the *occipital bar*. This system of numbering vertical bars is different from that usually practised in describing South American cichlid colour patterns (cf. Kullander & Silfvergrip, 1991), which usually feature more vertical markings and in which we count the vertical bars in cephalad direction starting with the bar on the caudal peduncle.

Lateral band. Juveniles and young specimens may possess a complete horizontal dark band extending from the head to the caudal-fin base. In some species, however, a distinct horizontal band is present only caudad from the middle blotch on the side (blotch 2), and is then referred to as an 'abbreviated lateral band'.

Lateral blotches. The colour pattern of several species of *Cichla* includes three large roundish dark blotches arranged serially along the middle of the side, in the same position as bars 1-3. The blotches are numbered according to which vertical bar they correspond to. There are no blotches corresponding to bars 1a, 2a, or 4,

Table 2. Absolute frequencies of scale counts in E1 row in species of *Cichla* (N = 363).

	N	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95
C. ocellaris	44	1	1		4	3	7	3	4	3	7	5	2	2	1		1													
C. orinocensis	29									1	2	2	2	2	5	1		3	2	3	2	2	1	1						
C. nigromaculata	6									1			1		1		1	1	1											
C. monoculus	37		2	1		2	6	7	3	3	3	4	1	2		1		1				1								
C. kelberi	10										1	2	1	1		1	2	2												
C. pleiozona	17																		1	2	3	4		3	1		2	1		
C. mirianae	17						1	1	4	3	1	2	4		1															
C. melaniae	5												1					2	1	1										
C. piquiti	22																	1			1			1	3	1		1	2	3
C. thyrorus	17											1	1	2			2	2	2	2	3	1			1					
C. jariina	5																													
C. pinima	65																				2	1	1	2	3	5	1	1	3	5
C. vazzoleri	33																													1
C. temensis	50																													
C. intermedia	6																													

except in *C. intermedia*.

Occipital bar (Fig. 1a)**.** An intensely pigmented stripe from the gill cover obliquely anteriad and dorsad across the nape, prominent in large specimens of *C. monoculus*, *C. kelberi*, and *C. pleiozona*.

Caudal blotch (Fig. 1a)**.** The caudal blotch starts as a dark spot at the base of the caudal fin, covering two or three rays in the dorsal lobe and one ray in the ventral lobe (generally rays V1 to D2). With increasing body length the dark blotch extends over rays D1-D3, and is margined with a white or silvery ring.

Abdominal blotches. In adults of several species, viz. *C. monoculus*, *C. ocellaris*, *C. nigromaculata*, *C. pleiozona*, and *C. kelberi*, the anterior abdominal side, in the region covered by the adpressed pectoral fin, may feature several irregular black blotches lined by light margins. These blotches probably represent the lower portion of vertical bars, and are corresponding in position to the ventral ocelli developed in *C. thyrorus*, *C. jariina*, *C. pinima*, and *C. vazzoleri*.

Postorbital markings (Fig. 1a)**.** Any black markings represented by a horizontal band caudad from the orbit to the opercular margin in juveniles, and isolated blotches or small spots in adults. Includes a 'dark blotch at anterior, ascending limb of preopercle'.

Halter stripe (Fig. 1a)**.** The halter stripe is a dark stripe continuing the orad margin of the lachrymal to or onto the preopercle. It is present in adults of all species of *Cichla*.

Light spots on side. With the exception of *C. intermedia*, all species of *Cichla* present a pattern of light spots on the side during at least some ontogenetic stages; spots may appear scattered or arranged in regular, horizontal series.

Species concept. The phylogenetic species concept is followed, along the lines of Kullander (1999) and de Pinna (1999). Species are diagnosable units of organisms representing a stable tokogenetic pattern conforming to separate lineages in a phylogenetic hypothesis. Clustered phenotypic character states are taken to indicate both shared phylogenetic ancestry, and at the smallest level self-perpetuating tokogenetic groups.

Phylogenetic analysis. A parsimony analysis was performed and visualized using Nexus Data Editor (Page, 2001) for matrix construction, PAUP* 4.10beta (Swofford, 2001) for analysis, and MrEnt (Zuccon & Zuccon, 2006) for tree drawing.

Species descriptions. The sequence of species descriptions represent an attempt to group similar species in order to facilitate comparisons of text, illustrations, and table data.

Museum codes. BMNH, Natural History Museum, London; CAS, California Academy of Sciences, San Francisco; ICNMHN, Unidad de Ictiologia del Instituto de Ciencias Naturales, Museo de Historia Natural, Universidad Nacional de Colombia, Bogotá; INPA, Instituto Nacional de Pesquisas da Amazônia, Manaus; MBUCV-V, Museo de Biología, Universidad Central de Venezuela, Caracas; MCNG, Museo de Ciencias Naturales, Universidad de Guanare, Guanare; MHNN, Muséum d'Histoire naturelle de Neuchâtel, Neuchâtel;

96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	117	118	119	120	121	123	127	128
		2	2	2	1	1		1																			
				1			1	1		1		1															
9	3	11	6	3	2	4		1	2																		
	3		2	5	4	3	3	2	1	2	2	1	1	2				1									
		1				1			2			1	3	1	5	10	3	3	6	4	3	1	1	1	2	1	1
1		1	1				1		1			1															

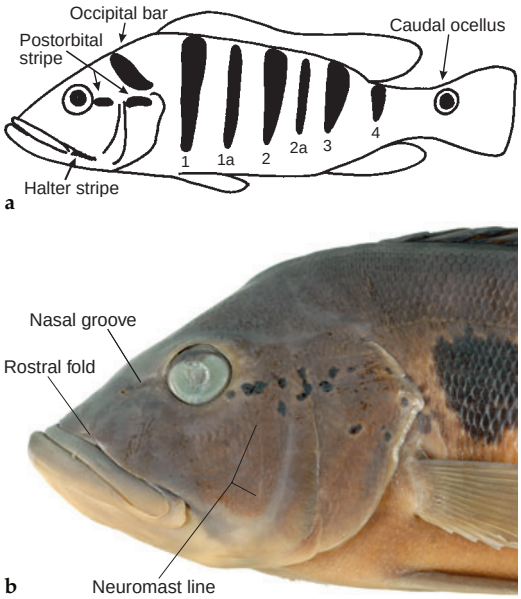

Fig. 1. a, Schematic representation of principal dark markings referred to in descriptions of species of *Cichla*. **b,** *Cichla orinocensis*, NRM 21550, male, 291 mm SL; head, showing rostral fold, nasal groove, and vertical neuromast line cheek.

MNHN, Muséum national d'Histoire naturelle, Paris; MNRJ, Museu Nacional, Rio de Janeiro; MZUSP, Museu de Zoologia da Universidade de São Paulo, São Paulo; NMW, Naturhistorisches Museum, Vienna; NRM, Swedish Museum of Natural History, Stockholm; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.; ZMB, Zoologisches Museum, Humboldt-Universität zu Berlin, Berlin; ZSM, Zoologische Staatssammlung des Bayerischen Staates, München.

Systematic section

Cichla Schneider, 1801

Cichla Schneider, 1801: 336 (type species *Cichla ocellaris* Schneider, 1801, by subsequent designation by Eigenmann & Bray, 1894: 611).

Acharnes Müller & Troschel, in Schomburgk, 1849: 622 (type species *Acharnes speciosus* Müller & Troschel, 1849 = *Cichla ocellaris* Schneider, by monotypy; synonymy discussed in Kullander, 1981).

Diagnosis. Large South American cichlids distinguished by nine putative autapomorphies. (1) Young with *Tylochromis* type pharyngeal apophysis, composed exclusively of parasphenoid; in adults uniquely modified, with lateral one-third of each half of apophysis composed of basioccipital, prootics contributing to lateral wall (Kullander, 1998: 477). (2) Central ligament bifurcate, inserting on tips of ceratobranchials 4 (Kullander, 1998: 473). (3) Dorsomedial part of sternohyoideus muscle originating by long tendon from cleithrum and inserting musculously on urohyal (Stiassny, 1982). (4) Flat anteroventral aponeurosis of pars A1 of adductor mandibularis, extending caudad over anteromedial face of A1, tendon linking maxilla and A1 inserted posteriorly on maxilla instead of on anterior margin as in other cichlids (Stiassny, 1982). (5) Elongate depression behind nostril without opening (Fig. 1b). (6) Absence of semicircular ligament (Stiassny, 1987, 1992). (7) Distinct vertical line across cheek about four scales anterior to preopercle, apparently representing free neuromast row (Fig. 1b). (8)

Table 3. Absolute frequencies of scale counts in continuous lateral line in species of *Cichla* (N = 97). Continuous lateral line not observed in *C. nigromaculata*, *C. monoculus*, *C. kelberi*, *C. mirianae*, and *C. melaniae*. Percent continuous refers to the proportion of continuous to total observations of continuous and discontinuous lateral lines.

	N	71	73	74	75	76	77	78	79	80	81	82	84	85	86	87	88	89	90	92	93	94	95	96
C. ocellaris	26	3	5	1	5	8	1	2	1															
C. orinocensis	1							1																
C. pleiozona	1										1													
C. piquiti	1																				1			
C. thyrorus	12					1	1	4	1	2	1		1		1									
C. jariina	3												1	1								1		
C. pinima	19													1	1	3	2	3	2	2	1	1	2	1
C. vazzoleri	4																1							
C. temensis	25																	1					1	2
C. intermedia	5									1		1			2		1							

Prominent rostral fold on maxilla (Fig. 1b). (9) Unique colour pattern with three dark vertical bars on side, developing from three dark blotches in juveniles.

Field markings. Distinguishing characteristics useful for field identification include: deeply notched dorsal-fin margin; densely scaled caudal and anal fin; large mouth with lower jaw projecting; small scales; frequently continuous lateral line; large, conspicuous ocellus at base of caudal fin.

Descriptive synopsis. Body elongate to moderately deep (21.3-34.6 % SL; Fig. 2), laterally compressed. Mouth large, terminal, low in position, caudally wider than rest of head. Ascending processes of premaxilla extending to behind nostril but not reaching anterior margin of orbit. Caudal part of maxilla well exposed, extending to below orbit. Lower jaw prognathous; articulation below orbit. Upper lip fold interrupted symphysially, but with thickened connection with opposite side fold; caudad a simple fold, not curled inwards. Lower lip fold discontinuous symphysially; widest medially, much reduced in width before attachment caudally to maxilla and dorsally to premaxillary tip ('African type' lips, Kullander, 1986: fig. 9). Postlabial skin fold (rostral cap) discontinuous with lachrymal margin, extended as skin fold laterally on maxilla. Opercular bones entire. Preopercle with uneven straight vertical free margin and rounded ventral margin.

Jaw teeth small, recurved, simple, pointed, smaller and gradually shorter linguad, densely arranged in well-defined bands that widen symphysiad, teeth absent symphysially; upper jaw band wider anteriorly than lower jaw band.

Scales ctenoid. Scales absent from cheek below line continuing labial margin of lachrymal caudad; above that several irregular rows of scales, those

98	99	100	101	102	103	105	107	109	% continuous
									61
									4
									7
									5
									71
									50
									36
	1	1			1				15
1		2	2	4	4	4	2	2	78
									85

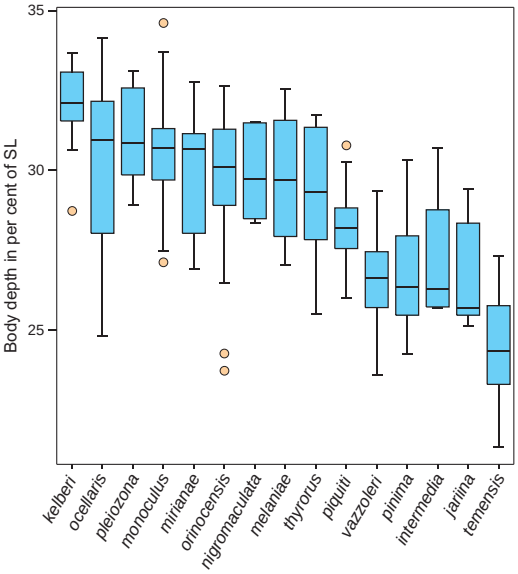

Fig. 2. Box plot of body depth:SL ratio in species of *Cichla* arranged in order of decreasing medians to the right.

dorsally and rostrally of about size of flank scales, ventrally smaller; patch of cycloid scales ventrally; dorsal cheek scale rows continued onto first infraorbital to level of anterior margin of orbit; 4 vertical rows of scales behind orbit; behind upper margin of orbit scales absent from narrow zone caudad to preopercle. Scales absent from preopercle. Opercle, subopercle save for narrow free margin where scales absent, and interopercle posteriorly, densely scaled. Body scales small; slightly larger on flanks and abdomen than along dorsal trunk margins and ventrally anterior to pelvic-fin base. Scales along middle of side (E1 scale row, Table 2), 67-128. Lateral line scales on trunk slightly smaller than adjacent scales. Prepelvic scales very small save for posteromedial about flank scale size. Scales absent from wide area above orbits; predorsal squamation reaching rostrad to not quite anterior margin of orbit. Scales absent from medial portion of predorsal midline. Extension of absence of scales from predorsal midline corresponding to nuchal protuberance when present and reduced in larger specimens

Lateral line continuous, with 71-109 scales (Table 3), or discontinuous with upper and lower lateral line overlapping, with 35-69 and 29-51 scales respectively (Tables 4-5). Flank lateral line continued on caudal fin by a few scales mainly

between rays V1 and V2; on dorsal and ventral lobes of caudal fin long sequences of tubed scales, between rays D3-D4 and V4-V5, respectively.

Scales absent from spinous dorsal fin; present on soft dorsal fin at least from about 150 mm SL, arranged in single or double rows posterior to each ray, in large specimens up to four rows of interradial scales and scales present also between major branches; scales absent on about 2-5 posterior interradial membranes. Anal-fin squamation developing basally in specimens about 50 mm SL; in large adults fin densely scaled with multiple interradial rows forming thick sheath, scales absent only on distal portion of posterior rays

Dorsal-fin spines 15-16, rarely 14 (Table 6); spines increase in length to about 5th (4th-6th) spine, after which spines gradually decrease to very short penultimate spine, followed by slightly longer spine. Spines can be raised or laid back freely, except last spine, which attached to stiff, erect soft-rayed portion of dorsal fin. Dorsal-fin soft rays 16-18, rarely 15 (Table 6); soft-rayed part of dorsal fin about as high as anterior spinous part. Three anal spines, followed by 10-12, exceptionally eight or 13 soft rays (Table 7). Pelvic-fin spine inserted in advance of vertical from pectoral-fin base, followed by five branched rays. Pelvic fin with rounded, subacuminate, or pointed tip formed by first and/or second ray; inner

Table 4. Absolute frequencies of scale counts in upper lateral line in species of *Cichla* (N=213).

	N	35	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	62	63	65	69	Range
C. ocellaris	12						1	3	3	1	1	1	1	1																	8
C. orinocensis	27		1		1		3	3	8	3	2	3	1		1	1															14
C. nigromaculata	5									2	1	1			1																6
C. monoculus	35	1	1	1	2	3	4		8	7	1	2	2		1	1	1														16
C. kelberi	10					2			1		1	1	2	3																	10
C. pleiozona	13											2	1	1	3	2	2	2													7
C. mirianae	15			1		1	1	1		4	2	2		1		2															13
C. melaniae	5							1		1		1		1	1																8
C. piquiti	18							1				1	1		4	1	3	2	1	3		1									15
C. thyrorus	5								1				2	2																	6
C. jariina	3																					1	1					1			8
C. pinima	34									1	1			1	3	2	1	2	6	2	3	3	4	2	2		1				19
C. vazzoleri	23													1	1	1	2	1	2	3		3	1	3	1		2		1	1	23
C. temensis	7																1	1		1			1		1	1			1		15
C. intermedia	1																			1											1

Table 5. Absolute frequencies of scale counts in lower lateral line in species of *Cichla* (N=211).

	N	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	49	51	Range
C. ocellaris	12			3	2	5	1	1														5
C. orinocensis	27		1	2	1	2	7	4	6	4												8
C. nigromaculata	5					3			1	1												5
C. monoculus	33			1	2	4	8	8	6	3		1										9
C. kelberi	10		1	1		2	1	1	3		1											9
C. pleiozona	13		1			2	2	1	3	2	1	1										10
C. mirianae	15	1	2	1	2	3	2	1	1	2												9
C. melaniae	5		1		1		2		1													7
C. piquiti	18				1		2	1	2	5		3	1	2			1					13
C. thyrorus	5				1	1	1							1	1							11
C. jariina	3							2						1								7
C. pinima	34		1		1	1	2	4	4	5	5	4	1	1	3			1		1		20
C. vazzoleri	23				1		1	1	1	1		1	3	1	2	3		2	4	2		18
C. temensis	7							1						1	2		1		1		1	17
C. intermedia	1									1												1

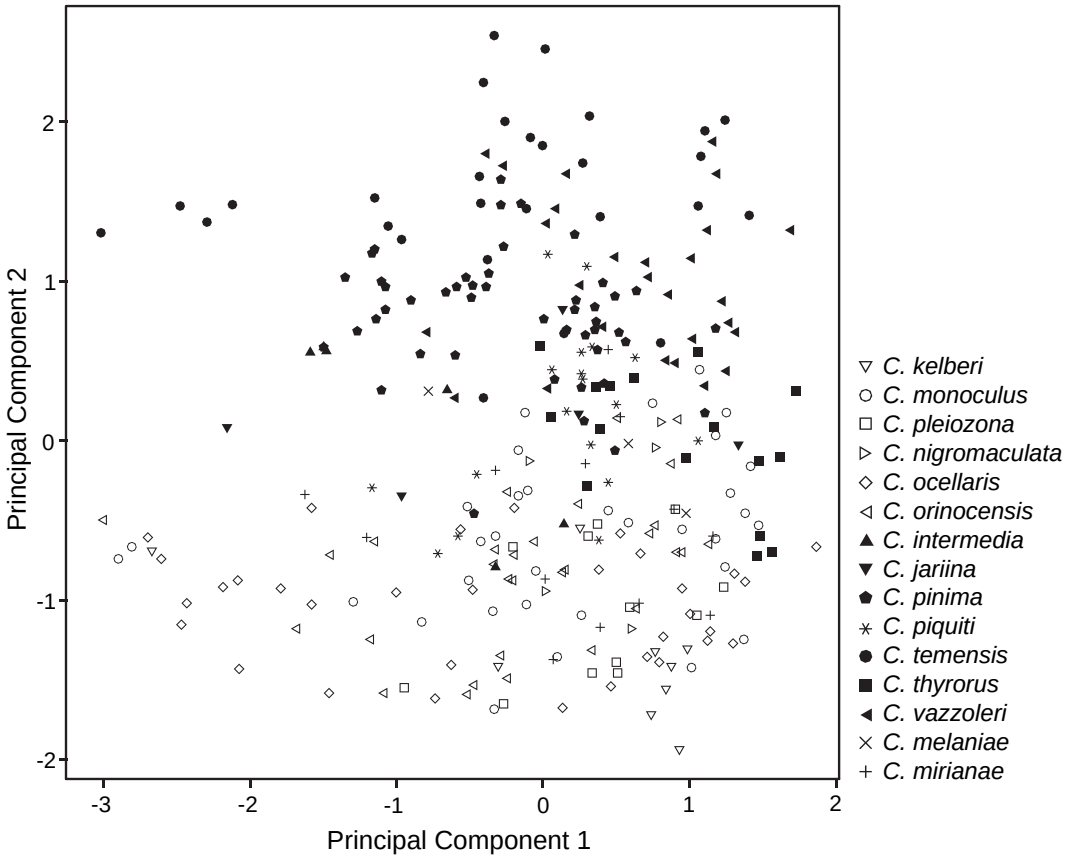

Fig. 3. Principal component scores of morphometric factor 2 against factor 1 for pooled sample of species of *Cichla*.

Table 6. Absolute frequencies of dorsal fin rays, by spines/rays and total spines+rays, in species of *Cichla* (N=357). Modal values in bold.

		XII	XIII				XIV			XV				XVI			Spines+rays				
	N	17	15	16	17	18	16	17	18	15	16	17	18	15	16	17	29	30	31	32	33
C. ocellaris	40							1				**30**	6			3			1	**30**	9
C. orinocensis	42							3	3		7	**24**			3	2			10	**30**	2
C. nigromaculata	5	1										1			**3**		1			**4**	
C. monoculus	37									1	2	**18**	2	3	5	6		1	5	**23**	8
C. kelberi	10											**8**			1	1				**9**	1
C. pleiozona	17										1	**9**	4		1	2			1	**10**	6
C. mirianae	17										3	**9**	1		2	2			3	**11**	3
C. melaniae	7											**7**								**7**	
C. piquiti	24							1			2	**14**	4		2	1			3	**16**	5
C. thyrorus	17							2	1	1	5	**7**	1					1	7	**8**	1
C. jariina	6										**5**	1								**5**	1
C. pinima	60			1			1		1		19	**24**	2	2	7	3	1	1	21	**32**	5
C. vazzoleri	33							1		2	**13**	12			5			2	14	**17**	
C. temensis	36										4	**25**	1		3	3			4	**28**	4
C. intermedia	6										2	**3**			1				2	**4**	

rays gradually shorter. Pectoral fin rounded in juveniles, becoming acuminate in adults, with rays 4 or 5 longest; pectoral-fin rays 14-15, rarely 13 or 16 (Table 8). Caudal fin with 8+8=16 principal rays; posterior margin emarginate in juveniles, truncate, subtruncate or slightly convex in adults.

Supraneurals 2, vertebrae 34-37, usually 18+17, 16+18, or 19+17 (Table 9), free hypurals 5. Haemal arches present on posterior abdominal centra.

Lateralis canal system on head including seven preopercular and five dentary foramina; suborbital series including two contiguous lachrymal bones forming a unit with a total of 5 lateralis foramina, and five tubular infraorbitals (Kullander, 1986: figs. 13A,G).

Bilateral elements of lower pharyngeal jaw separate posteriorly and extensively covered by fine teeth. A row of small tooth plates present on ceratobranchial 4. On first gill arch 7 or 8 epibranchial gill rakers, one in angle, and 12 to 20 cerato- and hypobranchial rakers (Table 10), all strongly denticulate, those caudally on ceratobranchial long, gradually shorter towards arch articulations, anterior three to five becoming plate like in large specimens. Count of emerging lower limb rakers decreases with increasing SL apparently because lower rakers, especially anterior 3, which attached to first hypobranchial, tend to become plate-like and not easily observed or probed on well-preserved specimens. Microbranchiospines with a few spines on exposed face (Kullander, 1986: fig. 14), present on both sides of all gill arches in adults, only externally in young.

Colour pattern ontogenetically variable. Juveniles 20-50 mm long develop an intermediate colour pattern consisting of three dark blotches along middle of side and a lateral band extending either caudad from posterior lateral blotch to caudal-fin base or from cleithrum to caudal-fin

Table 7. Absolute frequencies of number of soft anal fin rays in species of *Cichla* (N=332). Modal values in bold.

	N	8	10	11	12	13
C. ocellaris	39		6	**31**	2	
C. orinocensis	42		3	**29**	9	1
C. nigromaculata	5			**5**		
C. monoculus	37		7	**27**	3	
C. kelberi	10			**7**	3	
C. pleiozona	14		2	**9**	3	
C. mirianae	17			**11**	6	
C. melaniae	7		1	**6**		
C. piquiti	21	1		**16**	4	
C. thyrorus	17		1	**13**	3	
C. jariina	5			**5**		
C. pinima	52		14	**35**	3	
C. vazzoleri	27		2	**22**	3	
C. temensis	33		2	**29**	2	
C. intermedia	6		1	**5**		

Table 8. Absolute frequencies of number of pectoral fin rays in species of *Cichla* (N=317). Modal values in bold.

	N	13	14	15	16
C. ocellaris	33	1	**23**	9	
C. orinocensis	36		**29**	7	
C. nigromaculata	5		**5**		
C. monoculus	37	1	**31**	5	
C. kelberi	10	2	**8**		
C. pleiozona	14	1	**11**	2	
C. mirianae	15	1	**12**	2	
C. melaniae	5	1	**3**	1	
C. piquiti	21		**15**	6	
C. thyrorus	17	1	**14**	2	
C. jariina	6			**5**	1
C. pinima	52		18	**34**	
C. vazzoleri	27		**14**	13	
C. temensis	32		4	**27**	1
C. intermedia	6			**5**	1

Table 9. Absolute frequencies of vertebral counts in species of *Cichla* (N=125). Modal values in bold.

		abdominal/caudal						total			
		18			19						
	N	16	17	18	16	17	18	34	35	36	37
C. ocellaris	6		1	**2**	1	**2**			2	**4**	
C. orinocensis	22		4	7		**9**	2		4	**16**	2
C. nigromaculata	3		1	1		1			1	**2**	
C. monoculus	13		1	**6**		**6**			1	**12**	
C. kelberi	9		1	**7**			1		1	**7**	1
C. pleiozona	9			**8**			1			**8**	1
C. mirianae	13	1	**11**	1				1	**11**	1	
C. melaniae	1		**1**						**1**		
C. piquiti	8		**5**	1	2				**7**	1	
C. thyrorus	3		**3**						**3**		
C. jariina	4	**3**	1					**3**	1		
C. pinima	12	1	**9**			2		1	**11**		
C. vazzoleri	5		**5**						**5**		
C. temensis	11		**8**			3			**8**	3	
C. intermedia	6		1			**5**			1	**5**	

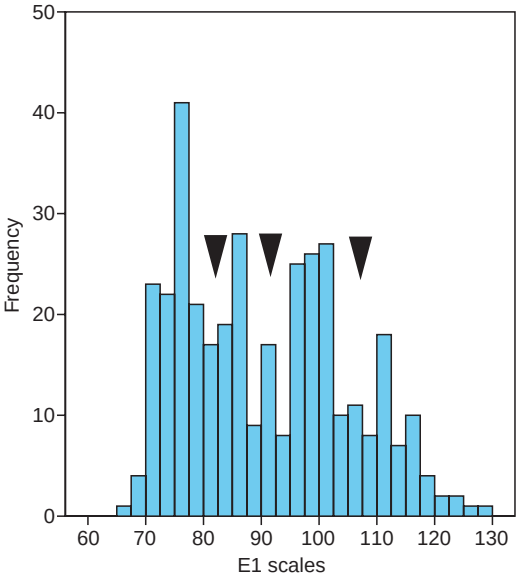

Fig. 4. Frequencies of counts of E1 row scales in species of *Cichla* (N = 362, mean = 90.46 ± 14.119). Each bar represents two scales. Arrows represent potential breaks in distribution of species ranges at 81, 88 and 92-93, and 106-110.

base. Adults with three (bars 1,2,3) or more (bars 1,1a, 2a, 3, 4) vertical bars on side, each commonly containing one to three dark blotches. Dark, round ocellated blotch on caudal-fin base. Suborbital stripe absent. Iridescent markings on side of head absent. Black spot posterodorsally on opercle absent. Ventrally white or yellowish on underside of head, abdomen, and along anal-fin base. Halter stripe present. Dorsal and caudal fins with light spots; other fins typically immaculate.

Size. The largest specimen reliably recorded is Winemiller's (2001) 810 mm SL specimen of *C. temensis*.

Key to species of *Cichla*

1 - Scales in E1 row 67-93; vertebrae 35-37, modally 36; complete lateral band from head to caudal-fin base absent; bars 1 and 2 represented by blotches and blotch representing bar 3 connected to caudal blotch by horizontal band in juveniles, vertical bars 3 or 5 in subadults and adults; occipital bar absent or present, prominent or indistinct. 2

\- Scales in E1 row 72-128; vertebrae 34-36, modally 35; complete lateral band from head to caudal-fin base present in subadults, vertical bars 3 or 5; occipital bar absent. 6

Table 10. Absolute frequencies of gill rakers externally on first gill arch in species of *Cichla* (N = 311). Modal values in bold.

	N	12	13	14	15	16	17	18	19	20
C. ocellaris	32		2	5	6		4	**11**	4	
C. orinocensis	29		3	**14**	7	2	1	1	1	
C. nigromaculata	5			1	2	2				
C. monoculus	30		10	**11**	4	2		2	1	
C. kelberi	5			**4**				1		
C. pleiozona	13	1	4	**6**	2					
C. mirianae	10	1	**4**	2	3					
C. melaniae	12		**9**	1		1	1			
C. piquiti	21		**13**	5		3				
C. thyrorus	17	5	**10**	2						
C. jariina	6		1	**4**			1			
C. pinima	68	1	21	**36**	8		2			
C. vazzoleri	26	1	**14**	10	1					
C. temensis	31		2	5	**11**	4	3	2	2	2
C. intermedia	6		2	1		2		1		

Table 11. Character coefficients in principal components I-III for 13 measurements from pooled material of 285 specimens representing 15 species of *Cichla*. Coefficients contributing most to each component marked in bold.

component	I	II	III
SL	0.467	0.035	–0.003
Head length	0.456	0.010	–0.015
Snout length	0.510	0.020	**–0.034**
Head depth	0.502	–0.031	–0.007
Body depth	0.512	**–0.045**	0.011
Orbit diameter	0.362	–0.011	–0.012
Interorbital width	0.516	**–0.036**	–0.004
Pectoral fin length	0.511	–0.013	0.017
Upper jaw length	0.496	–0.001	–0.019
Lower jaw length	0.476	0.004	–0.015
Caudal peduncle depth	0.495	–0.013	0.013
Caudal peduncle length	0.438	**0.085**	0.008
Dorsal spine length	0.438	0.011	**0.061**
% Variance explained	98.807	0.457	0.220

2 - Abdominal blotches absent, lateral line usually discontinuous; lateral bars 1-3 present as large and oval blotches in juveniles, transformed to roundish ocellar blotches in adults (blotch 1 persistently, blotches 2-3 variably expressed); occipital bar, bars 1a, 2a, and 4 absent (Orinoco and Negro river drainages).
.....*C. orinocensis*

- Abdominal blotches present, lateral line continuous or discontinuous; lateral bars 1-3 present as vertical bars, occasionally bars 1a and 2a present; occipital bar absent or present.
.....3

3 - Occipital bar absent or indistinct, bars 1a, 2a present; bar 4 absent; lateral line continuous or discontinuous.
.....4

- Occipital bar strongly expressed in adults, bars 1a, 2a absent, bar 4 present or absent, lateral line discontinuous.
.....5

4 - E1 scales 67-82; dorsal-fin count modally XV.17; lateral line usually continuous, small black blotches on dorsum absent (Coastal Atlantic rivers in Suriname and Guyana; upper Rio Branco drainage).
.....*C. ocellaris*

- E1 scales 75-84; dorsal-fin count modally XVI.16; lateral line discontinuous, small black blotches on dorsum present or absent (upper Negro and Orinoco river drainages).
.....*C. nigromaculata*

5 - E1 scales 68-79(-87); bar 4 only occasionally present; anal, caudal and pelvic fins immaculate except for caudal blotch (Amazon basin, along Rio Amazonas-Solimões and in lower parts of tributaries, coastal Atlantic rivers between the Oyapock and Amazon rivers).
..... *C. monoculus*

- E1 scales 76-83; bar 4 typically absent; light spots present on anal and pelvic fins and lower lobe of caudal fin in adults (Rio Tocantins drainage).
.....*C. kelberi*

- E1 scales 84-93; bar 4 typically present; anal fin immaculate; E1 scales 84-93 (Bolivian Amazon basin and tributaries of upper Rio Madeira in Brazil).
.....*C. pleiozona*

6 - Vertical bars 1-3, 1a, 2a present, wide and prominent; no ocellated blotches on side; E1 row scales 83-104 (Tocantins and Capim river drainages).
..... *C. piquiti*

- Vertical bars 1a, 2a absent or indistinct and narrow, ocellated blotches on side present or absent; E1 scales 72-128.
.....7

7 - E1 scales 77-128; vertical bars 1a, 2a absent; bars 1-3 relatively wide, prominent in adults, entire or broken up into blotches.
.....8

- E1 scales 72-108; vertical bars 1a, 2a when present indistinct and/or narrow; vertical bars 1-3 moderately wide or narrow, not subdivided into large blotches; row of ocellated blotches along middle of side present or absent in adults.
.....12

8 - E1 scales 98-128; vertical bars 1-3 entire; four regularly arranged horizontal rows of distinct light spots along side (Orinoco and Negro river drainages, blackwater rivers along the Rio Solimões-Amazonas).
.....*C. temensis*

- E1 scales 86-115; vertical bars 1-3 in adults subdivided, each bar represented by 1-3 blotches; light spots on side distinct but usually not regularly arranged.
.....9

9 - E1 scales 77-90; lateral line usually continuous; lateral line scales 76-86 in continuous lines; bars 1 and 2 divided into three ocellated blotches in adults (Rio Trombetas upstream of Cachoeira Porteira).
.....*C. thyrorus*

- E1 scales 86-110; lateral line usually discontinuous; lateral line scales 84-103 in continuous lines; bars 1 and 2 divided into two or three ocellated blotches in adults, or bars 1 and 2 present as ocellated vertical bar.
.....10

10 - E1 scales 100-108; lateral line continuous or discontinuous; scales absent or very few on

soft dorsal fin; bars 1 and 2 divided into three ocellated blotches; dorsal-fin count usually XV.16; vertebrae usually 18+16=34 (Rio Jari). ..... *C. jariina*

- E1 scales 86-113; lateral line usually discontinuous; scales present on soft dorsal fin, bars 1 and 2 divided into two ocellated blotches or forming a continuous ocellated vertical bar in adults, dorsal-fin count modally XV.16 or XV.17, vertebrae usually 18+17=35. 11

11 - E1 scales 95-114; ocellated dark blotch dorsally in bar 3 absent except when other blotches present on side; dorsal blotches present or absent in bars 2 and 3 in large adults (Rio Uatumã and lower Rio Trombetas). .....*C. vazzoleri*

- E1 scales 86-105; ocellated dark blotch persistently present in bar 3 from about 150 mm SL (lower Tapajós, Curuá-Una, Xingu, and Capim rivers, tentatively Amapá, Araguari and Canumã rivers). .....*C. pinima*

12 - E1 scales 96-108; vertical bars 1a, 2a distinct; small ocellated blotches present in bars 1, 1a, 2, 2a, 3, and 4; light spots absent from side at all sizes; lateral line usually continuous (Rio Orinoco and Rio Casiquiare). .....*C. intermedia*

- E1 scales 72-85; vertical bars 1a, 2a indistinct or absent; light spots present or absent on side; lateral line discontinuous. 13

13 - E1 scales 72-80; lateral blotches 1-3 present, ocellated or not, in adults mediated by irregular dark stripe continuing onto caudal peduncle (may be absent or rudimentary in females); vertical bars 1-3 indistinct in adults; bars 1a, 2a absent; light spots on side absent or sparsely distributed in adults (Rio ~~Tocantins~~ and upper Rio Xingu). .....*C. mirianae*

- E1 scales 78-85; ocellated blotches absent from side; lateral band absent in adults; bars 1-3 distinct, narrow; bars 1a, 2a commonly present, narrow, indistinct; numerous light spots covering side (lower Rio Xingu). .....*C. melaniae*

Cichla ocellaris Schneider, 1801
(Figs. 5-8)

Cichla ocellaris Schneider, 1801: 340 (India Orientali), pl. 66 (colour drawing).

Acharnes speciosus Müller & Troschel, in Schomburgk, 1849: 622 (Küste und in der Mündung des Essequibo).

Material examined. 58 specimens, 40.1-345 mm SL, in addition to 245 specimens (largest 414 mm SL) from Kullander & Nijssen (1989). **Guyana: Mahaica River drainage:** CAS 12453, 1; CAS 14696, 1, 345 mm; CAS 20278, 2; Demerara-Mahaica: Lama Stop Off; 1908, C. H. Eigenmann. **Essequibo River drainage:** BMNH 1968.9.26:13-18, 6 juvs.; Upper Takutu-Upper Essequibo: Kajuero, Karanambo, 24 Sep 1957, R. H. Lowe-McConnell. – BMNH 1968.9.26:19-22, 1, 134.5 mm SL; Upper Takutu-Upper Essequibo: Upper Cajuero; 2 Apr 1957; 2, 66.1-70.5 mm SL; Karanambo, 13 Sep 1957; 1, 50.4 mm SL; Morebay; 16 Sep 1957, R. H. Lowe-McConnell. – BMNH 1968.9.26:23-24, 2; Georgetown, Sophia Estate; No date, R. H. Lowe-McConnell. – BMNH 1973.3.26:1-3, 2, 45.3-48.8 mm SL; Upper Takutu-Upper Essequibo: Isherton; 12 Dec 1957, R. H. Lowe-McConnell. – BMNH 1973.3.26:4, 1, 82.1 mm SL; Sophia Trench; 9 Aug 1957, R. H. Lowe-McConnell. – BMNH 1973.3.26:5, 1, 71.8 mm SL; Upper Takutu-Upper Essequibo: Karanambo; 14 Sep 1957, R. H. Lowe-McConnell. – CAS 68102, 1, 325 mm SL; Upper Demerara-Berbice: Rockstone; 1908, C. H. Eigenmann. **Ireng River drainage:** BMNH 1968.9.26:2-12,21, 1, 146.5 mm SL; Upper Takutu-Upper Essequibo: Manari Pools; 18 Dec 1957; 3, 122.5-156 mm SL; Jacaré, 29 Sep 1957; 1, 160 mm SL; Manari Creek; 3 Oct 1957; 1, 148.0 mm SL. Near Manari, 2 Oct 1957; 1, 173.5 mm SL; Jacaré; 7 Dec 1957, R. H. Lowe-McConnell. **Drainage unknown:** BMNH uncat., 1, 337 mm SL; "British Guiana"; Sir R. Schomburgk. – ZMB 1211, 1, ca 100.3 mm SL; Guiana; no date, Schomburgk; holotype of *Acharnes speciosus*. **Suriname: Suriname River drainage:** NRM 46189, 1, 58.9 mm SL; Brokopondo; 1999, A. Stalsberg. **French Guiana: Maroni River drainage**: NRM 28389, 3, 265-302 mm SL; St-Laurent-du-Maroni: Maripasoula, Maroni River at Maripasoula; 20 Apr 1994, S. O. Kullander & F. Fang. – NRM 29437, 2, 109.1-196.1 mm SL; Maroni River; no date, P. Planquette. – NRM 41062, 1, 48.2 mm SL; Maroni River, Antécome [Antecume] Pata; 15 Dec 1985, P. Planquette. **Brazil: Rio Branco drainage: Roraima:** INPA 24094, 3, 220-315 mm SL; Rio Uraricoera drainage, igarapé on Ilha de Maracá; 18 Sep 1987, E. Ferreira. – INPA 24091, 1, 320 mm SL; Rio Uraricoera drainage, swamp on right side of camp road; 17 Sep 1987, E. Ferreira. – INPA 24089, 3, 142-210 mm SL; INPA 24093, 1, 293 mm SL; INPA 24092, 1, 320 mm SL; INPA 24093, 1, 293 mm SL; INPA 24095, 1, 170 mm SL; Rio Uraricoera drainage, rocks in Furo do Maracá; 20 Sep 1987, E. Ferreira. – MZUSP 33104, 2, 40.1-69.8 mm SL; Rio Uraricoera, Ilha

Fig. 5. *Cichla ocellaris*, NRM 19157, 50.0 mm SL; Suriname: Blommestein Stuwmeer.

Fig. 6. *Cichla ocellaris*, NRM 19156, 106.0 mm SL; Suriname: Blommestein Stuwmeer.

de Maracá; 13 Jan 1984, M. Goulding. – MZUSP 33105, 8 (1 measured: 83.9 mm SL); Cachoeira Bem Querer; 8 Jan 1984, M. Goulding. – MZUSP 37023, 1, 168.4 mm SL; Rio Mucajaí, south of Boa Vista; Apr 1962, R. Dente. – ZSM 27743, 1, ca 235 mm SL; swamp on Rio Branco at Boa Vista; 12 Mar 1913, J. D. Haseman.

Diagnosis. Distinguished from all other species of *Cichla* except *C. nigromaculata*, *C. intermedia*, *C. piquiti*, and *C. melaniae*, by presence of bars 1a and 2a. Lateral band abbreviated in juveniles. Distinguished from other species of *Cichla* with abbreviated lateral band by lateral line usually

Table 12. Morphometry of *Cichla ocellaris*. Measurements are in percent of SL, except SL (in mm). Linear regression parameters calculated from original measurements in mm.

	N	min	max	mean	SD	a	b	r
SL (mm)	34	50.0	414.0	180.0				
Head length	34	32.1	36.7	33.7	1.01	1.001	0.329	0.999
Snout length	34	10.8	14.4	11.7	0.83	–1.323	0.128	0.995
Head depth	34	21.4	28.7	24.3	1.76	–2.256	0.262	0.995
Body depth	34	24.8	34.1	30.3	2.71	–4.448	0.341	0.998
Orbit diameter	34	6.5	11.8	8.9	1.31	2.811	0.067	0.984
Interorbital width	34	7.2	9.7	8.3	0.70	–1.708	0.096	0.996
Pectoral fin length	34	20.3	26.2	23.1	1.75	–2.870	0.254	0.997
Upper jaw length	34	13.7	17.0	15.2	0.87	–1.963	0.167	0.997
Lower jaw length	34	17.5	20.5	19.1	0.73	–0.874	0.197	0.997
Caudal peduncle depth	34	10.1	13.2	11.9	0.80	–1.258	0.129	0.998
Caudal peduncle length	34	15.7	18.6	17.2	0.77	1.023	0.164	0.998
Dorsal spine length	33	10.8	14.4	12.9	0.95	1.895	0.116	0.986

Fig. 7. *Cichla ocellaris,* NRM 28389, adult female, 302 mm SL; French Guiana: Maroni River at Maripasoula.

Fig. 8. *Cichla ocellaris*, INPA 24092, adult, 320 mm SL; Brazil: Rio Uraricoera drainage: Furo do Maracá.

continuous vs. discontinuous or nearly always discontinuous in *C. orinocensis* and *C. nigromaculata;* scales in E1 row (67-)70-80(-82) vs. 84-93 in *C. pleiozona*; occipital bar absent or indistinct vs. emphasized in adults of *C. monoculus*, *C. kelberi*, and *C. pleiozona*; abdominal blotches present vs. absent in *C. orinocensis*; vertical bars present at adult size, vs. three midlateral ocellated blotches in *C. orinocensis,* except that an ocellated blotch consistently formed in dorsal portion of bar 3; absence of small black blotches on dorsum, vs. present in *C. nigromaculata*; vertical bars about equally wide across side, vs. wide, occasionally confluent dorsally, and tapering ventrad in *C. nigromaculata*, *C. monoculus*, *C. kelberi*, and *C. pleiozona*. Distinguished from *C. intermedia*, *C. piquiti*, and *C. melaniae* by abbreviated vs. complete juvenile lateral band, less scales in E1 row (67-82 vs. (78)83-108), and presence of ocellated blotch in dorsal portion of bar 3 vs. absence.

Description. Adapted and modified from Kullander & Nijssen (1989), which see for detailed description. Refer to Figs. 5-8 for general shape and colour pattern, Table 12 for morphometrics, and Tables 2-10 for meristics.

Adults moderately deep-bodied (depth 30.2-34.1 % SL, N = 16, 208-414 mm SL). Frontal contour straight or slightly curved; nuchal protuber-

ance present in males from 236 mm SL. Maxilla reaching to below about middle of orbit. Lower jaw prognathous, articulation below about middle or posterior margin of orbit. Lateral line discontinuous in 12, continuous in 26 of 38 specimens.

Dorsal-fin spines 4-6 longest. Soft dorsal fin rounded, extending to middle of caudal peduncle in smallest, little longer in large specimens, but not reaching to caudal-fin base. Soft anal fin rounded; in smallest specimens reaching to middle of caudal peduncle, in larger specimens further, but not attaining caudal-fin base. Caudal-fin hind margin slightly emarginate in smallest specimens; in larger specimens truncate with squared upper corner and rounded lower corner. Pectoral fin short, rounded in young, becoming rather acuminate in large specimens; extending halfway to end of anal-fin base. Pelvic-fin tip rounded; hind edge straight in young, becoming slightly concave in large specimens; first and second rays subequal in extension or second longest.

Scales present on soft dorsal fin in specimens over 150 mm SL, from behind last spine to behind 11th ray, in one or two rows close behind preceding spine or ray; anterior rows reaching to near tips of rays, posteriorly successively shorter, last to ¼ of ray length; interradial scales also on membranes between major ray branches, to near fin margin. Anal fin with heavy basal sheath of ctenoid scales; interradial scales proximally in dense sheath, distad narrower; no scales between ray branches; medially scale sheath slightly wider than half length of longest rays. Caudal fin densely scaled from 140 mm SL, but middle membranes (rays D3-V3) naked along middle, distally narrow zone of cycloid scales and narrow naked fin edge. Scales present or absent from base of pectoral fin. Medial aspect of pelvic fin with basal layer of scales and double series of cycloid interradial scales, extending anteriorly to spine tip, but posteriorly shorter; on lateral side double interradial series of cycloid scales on first two membranes to level of spine tips.

Juveniles about 50 mm SL (Fig. 5) elongate, caudal fin slightly emarginate. Scales absent from fins except bases of caudal and anal fins. At about 170 mm SL, scale cover on dorsal fin almost fully developed in some specimens, but specimens up to almost 200 mm SL may possess only a few scales; at about 140 mm SL anal fin densely scaled.

Colouration in preservative. Juveniles about 50 mm SL (Fig. 5) yellowish white on underside and lower part of head, trunk and caudal peduncle, up to pectoral axilla level. Dorsum brown grey, side lighter. Nape and forehead brownish grey. Cheek silvery dorsally; opercle, preopercle and subopercle greyish with some silver especially anteriorly on opercle and subopercle. Pre- and postorbital dark stripes absent. Pale narrow stripe obliquely dorsad-rostrad across nape from gill cleft. Along middle of side dark brown roundish blotch just posterior to pectoral axilla level, below upper lateral line section, with faint narrow dorsal extension; faint brown blotch above vent, with fainter extensions dorsad and ventrad; dark brown horizontally extended blotch above soft anal fin, with fainter extension along caudal peduncle middle to caudal base blotch. Spinous dorsal fin smoky, soft fin hyaline with dark spot on each ray base. Anal fin hyaline, base narrowly dusky. Pelvic fin hyaline. Caudal fin smoky, especially medially; roundish midbasal blotch, slightly extended caudad; large whitish spot dorsocaudal and ventrocaudal to base blotch.

Short vertical bars develop from 55 mm SL, bar 1 with first blotch in centre, bar 2 replacing second blotch. Specimens about 60-70 mm SL develop large light spots on dorsum, two horizontal dark bands distally in soft dorsal fin; bars 1a and 2a occasionally present as narrow dark vertical shades; bar 3 may show through anterior part of blotch 3; light spots anterior to caudal blotch still indistinct. Specimens about 70-80 mm SL with light spots also on side (or only on side), well-developed vertical bars (1, 1a, 2, 2a, 3; but a bars 1a and 2a not always apparent); blotch 3 tends to become incorporated in bar 3, caudal base blotch tends to be isolated from caudal peduncle pigment and lighter spots around it brighten.

At about 90-100 mm SL (Fig. 6), no clearly defined flank blotches remain, soft dorsal fin light-spotted and isolated caudal base blotch tends to more dorsal position. Specimens about 130 mm SL with light spots on dorsum, flank spots whitish or silvery, caudal blotch ocellated and dorsal to lateral line, bars 1a and 2a always distinguishable. Specimens 160 mm SL and larger with ocellated blotch dorsally in bar 3 (Figs. 7-8) and abdominal blotches appear posterior to pectoral-fin base. Light spots on dorsum and side absent in specimens over 200 mm SL.

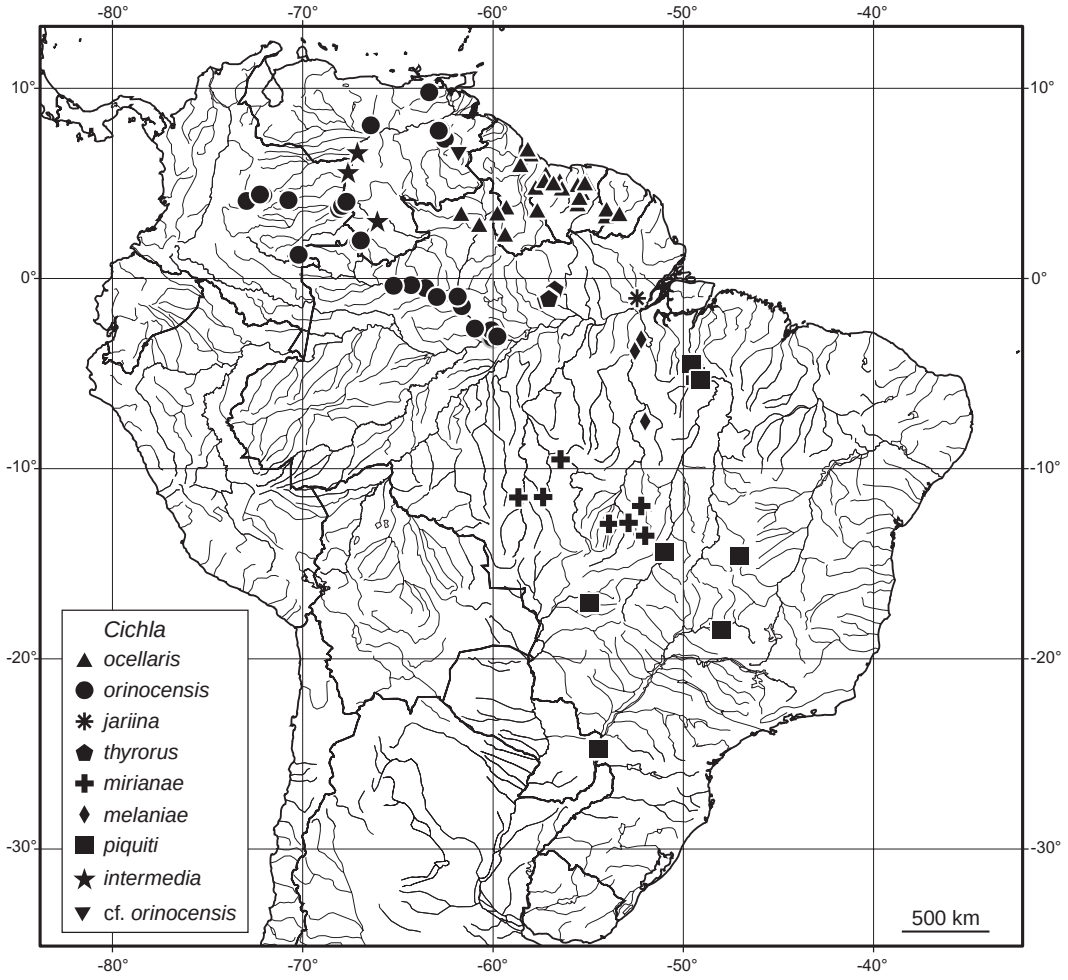

Fig. 9. Collecting localities of *Cichla ocellaris*, *C. orinocensis*, *C. jariina*, *C. thyrorus*, *C. mirianae*, *C. melaniae*, *C. piquiti* (including translocations), *C. intermedia*, and *C.* cf. *orinocensis* (Rio Cuyuni). A symbol may cover more than one collecting site.

Adults (>200 mm SL) more or less greyish or brownish with light underside. Vertical bars pointed ventrally. Ocellus dorsally in bar 3 usually roughly boomerang shaped with apex directed rostroventrad. Occipital blotch (across nuchal midline) or bar more or less evident. Small silvery scale centre spots present in about half of specimens over 200 mm, more or less neatly arranged in horizontal rows on flanks and caudal peduncle; when absent, side indistinctly light/dark marbled.

Large adults about 300 mm SL and larger (Figs. 7-8, Kullander & Nijssen, 1989: fig. 10) with scale centres on back and side light, on back tending to opalescent; on side faint opalescent spot basally on most scales, especially below upper lateral line section. Small, irregular black spots posterior to orbit (on cheek, preopercle, and opercle), more or less ocellated by opalescence. Bars 1a and 2a indistinct; bars 1, 2, and 3 expressed chiefly by large irregularly shaped blotches dorsally (extended vertically to level of lower lateral line section); ringed with white to silvery or opalescent bright spots, most prominent around conspicuous blotch dorsally in bar 3. Abdominal blotches present between pectoral axilla and bar 2, scattered or partly contiguous. Blotch pattern on side highly variable between specimens, and

blotches except for abdominal blotches and bar 3 ocellus may be absent.

Dorsal fin anterior eight interradial membranes blackish brown, pale to opalescent spot present on every second membrane base; posteriorly mottled dark brown and light. Soft fin brownish, paler towards distal margin, covered by large light spots, especially prominent posteriorly. Anal fin mottled brownish, margin narrowly dark. Caudal fin light brownish with large, indistinct light spots on dorsal lobe and along middle; close to base, above lower lateral line section level black caudal blotch contained in white to silvery ring. Pelvic fin brownish outwardly, lighter inwardly.

Live colouration (Fig. 7)**.** Olivaceous, golden sheen to flanks produced by light scale centres. Ocellar markings with golden or silvery ring. Iris bright red. Pelvic, anal and lower lobe of caudal fin dull reddish.

Geographical distribution. French Guiana, Surinam, Guyana, and Brazil, in the Marowijne, Suriname, Saramacca, Nickerie, Corantijn, Berbice, Essequibo, and Branco drainages (Fig. 9). Keith et al. (2000: 65) plotted many records from along most of the main channel of the Marowijne, except the mouth and distant headwaters.

Local names. Lukanani (Guyana; Lowe-McConnell, 1969), Toekoenali, Zonnevisch, Toekanale, Tukanale, Toekoenari (Surinam; Kullander & Nijssen, 1989), Toukounaré, Kounanni, Aboné, Tukunali, Malisamba, Toukounalé, Kunan, Toekoenari, Matawalé, Tucunaré açu (French Guiana; Keith et al., 2000).

Notes. See Kullander & Nijssen (1989) for a detailed redescription of *C. ocellaris* based on Surinamese material. In that paper scales are said to be absent from the pectoral fin, but in subsequently examined specimens scales are present basally on the pectoral fin.

Herein, we refer also material from Guyana and the upper Rio Branco in Brazil to *C. ocellaris* based on the presence of bars 1a and 2a, but with lateral line commonly discontinuous. Guyanese specimens were figured by Eigenmann (1912: pl. 69). References to *C. ocellaris* from outside Guyana and Suriname in literature prior to Kullander (1986) and Kullander & Nijssen (1989) refers to other species, in most cases *C. monoculus*, *C. orinocensis*, and *C. pinima*. Ecological information on *C. ocellaris* is provided by Lowe-McConnell (1969).

Cichla orinocensis Humboldt, 1821
(Figs. 10-19)

Cichla orinocensis Humboldt, in Humboldt & Valenciennes, 1821: 167, pl. 45 fig. 3 (les rives de l'Orénoque et du Guainia ou Rio Negro; île de Dapa).

Cichla argus Valenciennes, in Humboldt & Valenciennes, 1821: 169 ([no locality]).

Material examined. 104 specimens, 29.3- ca. 310 mm SL. **Colombia: Rio Guaviare drainage:** NRM 26209, 5, 52.1-63.9 mm SL; Guainía: Caño Carbón, Cuayare; 28 Jun 1976, T. Hongslo. – NRM 37055, 2, C&S; Guainía: Caño Carbón, Cuayare; 28 Jun 1976, T. Hongslo. **Rio Guarrojo drainage:** NRM 46002, 6, ca 52.5-161 mm SL; Vichada: Finca Boca de Guarrojo, estero close to laguna no. 1; 8 Mar 1972, T. Hongslo. **Rio Meta drainage:** ICN-MHN 16500, 1; Casanare: Caño Guira; 23 Feb 1974, P. Cala. – ICN-MHN 16501, 1; Casanare: Cañada Castrero, tributary to Caño Casiminia; 25 Feb 1971, P. Cala. – ICN-MHN 16502, 1; Meta: Laguna La Venturosa, Hacienda La Venturosa, Puerto López; 30 Mar 1985, C. Román et al. – ICN-MHN 16503, 1; Meta: Puerto López, Laguna Humacita, Hacienda Mozambique; 6 Nov 1972, F. Florez. – ZFMK 13596, 1; Meta: between Santa Rita and Bengalen, tributary to Rio Manacacías; Mar-Apr 1982, H. Linke. **Rio Negro drainage:** NRM 19641, 3, 45.0-49.3 mm SL; Vaupés: Rio Vaupés drainage: Rio Cuduairi, tributary to Rio Vaupés W of Mitú, first rapid upstream; 7-9 Apr 1992, U. Werner et al. **Rio Inírida drainage:** NRM 11255, 1, 43.5 mm SL; Guainía: Puerto Inírida, Caño Conejo; 13 Jun 1972, T. Hongslo. – NRM 11256, 1, 29.3 mm SL; Guainía: Caño Bocón, Pueblo Bretaña; 2-6 Jun 1972, T. Hongslo. – NRM 18346, 2, ca. 60- ca. 88 mm SL; Guainía: Puerto Inírida, Barrio de Indígenas, Caño Conejo and flooded areas; 11 Jul 1976, T. Hongslo. – NRM 26183, 1, 91.6 mm SL; Guainía: Puerto Inírida, flooded caño; 25 Jun 1976, T. Hongslo. – ZSM 25182, 1; Guainía: stream tributary to Rio Inírida; Jan 1976, H. Herkner. **Venezuela: Rio Negro drainage: Amazonas:** USNM 269932, 2, 94.8-98.7 mm SL; depto Rio Negro: laguna NE airport of San Carlos de Rio Negro; 4 Dec 1984, R. P. Vari. – USNM 269933, 1, 154.3 mm SL; depto Rio Negro: Caño Chola where crossed by road from San Carlos de Rio Negro to Solano; 5 Dec 1984, R. P. Vari. – USNM 269934, 2, 152.1- ca 165 mm SL; depto Rio Negro: Caño Manu, tributary of Rio Casiquiare ca 250 m upstream of Solano; 7 Dec 1984, R. P. Vari. **Rio Orinoco drainage:** MCNG 26401, 1, 61.5 mm SL; Amazonas: Rio Atabapo at San Fernando de Atabapo; 18 Jan 1991, L. G. Nico. – MCNG 31915, 1, 207 mm SL; Guárico: Parque Nacional Aguaro-Guariq-

uito, Rio Aguaro on the way towards Hato Aguaro, west of Santa Rita (Garcerito); 10 Jan 1995, D. C. Taphorn et al. – MCNG 33198, 2, 181-190 mm SL; Bolívar: Laguna El Potrero; 23 Apr 1988, M. Rodriguez. – ZSM 25020, 2;Bolívar: Laguna de Palma at San Felix; 29 Mar 1974, H. J. Köpke. – ZSM 25269, 2; Amazonas: Rio Atabapo at San Fernando; 5 Feb 1973, H. J. Köpke & M. Jeschke. – ZSM 23838, 2, 136.2-136.4 mm SL; Monagas: Barrancas, Laguna Los Guateguas; 11 Nov 1963, F. Mago L. **Rio Caroni drainage: Bolívar:** NRM 12038, 1, 57.6 mm SL; Embalse de Guri, 7 km W of El Manteco; 6 Apr 1990, U. Werner et al. – NRM 22918, 2, 79.0-99.6 mm SL; Guri Reservoir-Rio Caroni Los Arrendajos; 4 Dec 1993, J. D. Williams et al. – NRM 21547, 1, 233 mm SL, NRM 21549, 1, 246 mm SL, NRM 21550, 1, 291 mm SL; NE part of Embalse del Guri, Los Arrendajos; 16 Jan 1994, J. D. Williams. – NRM 21548, 1, 267 mm SL; NE part of Embalse del Guri, Zona F, near Dique F; 16 Feb 1994, J. D. Williams. – NRM 22920, 6, 55.6-60.2 mm SL; NE Guri Reservoir, near dique F; 6 Jun 1994. J. D. Williams et al. **Brazil: Rio Negro drainage: Amazonas:** BMNH 1915.11.1:12, 1, 290 mm SL; Manaus; Clark. – MZUSP 92402, 2, 146.2-200 mm SL; vicinity of Manaus; 15-23 Nov 1967, EPA. – MZUSP 6793, 7, 90.4-232 mm SL; Igarapé Tarumãzinho, affluent no. 1; 17-18 Nov 1967, EPA. – MZUSP 6839, 12; Igarapé no 2 tributary to Igarapé Tarumãzinho, N of Manaus; 18 Nov 1967, EPA. – MZUSP 27214, 2; mun. Moura, Pedra do Gavião; 13 Nov 1982, L. Portugal. – MZUSP 92407, 6 juvs.; mun. Novo Ayrão, extreme north of Reserva Ecologica Anavilhanas; 6 Nov 1982, L. Portugal. – MZUSP 32758, 4, 261-278 mm SL; Rio Arirará near mouth; 8 Oct 1979, M. Goulding. – MZUSP 33121, 2 (1 measured, 99.0 mm SL); Ilha de Tamaquaré, central lake; 11 Oct 1979, M. Goulding. – MZUSP 33124, 4; Barcelos; 29 Feb 1980, M. Goulding. – MZUSP 33125, 1; Barcelos; 29 Jan 1980, M. Goulding. – NRM 18347, 1, 65.2 mm SL; Paraná do Marauiá; Jan 1987, M. Goulding – ZSM 23837, 4; Igarapé Castanha at Manaus; 23 Oct 1965; J. Géry & E. J. Fittkau. **Rio Branco drainage:** MZUSP 33122, 1; Roraima: Marará, praia; 26 Oct 1979, M. Goulding. **Rio Amazonas drainage:** MZUSP 6113, 1, 189 mm SL; Amazonas: Lago Puraquequara at mouth of Rio Puraquequara; 17-19 Apr 1967, EPA. **Drainage unknown:** MNHN A.1042 (221-18-1-13), 1, ca. 375 mm TL (ca. 310 mm SL); Brazil; no date, no collector; holotype of *Cichla argus* Valenciennes. **Country unknown: Rio Orinoco drainage:** BMNH 1853.1.11:16, 1, 140.8 mm SL; Orenokko; no date, Frank.

***Cichla* cf. *orinocensis*:** MBUCV-V 10287, 1, 82.3 mm SL; Venezuela: Bolívar: Rio Cuyuni, raudal de Kinotovaca, about 40 km S of El Dorado; 22 Jan 1977, F. Mago Leccia.

Diagnosis. Distinguished from all other species of *Cichla* by typical presence of three large dark ocellated blotches along side (blotches 1, 2, 3), but occasionally blotches 2 and 3 irregularly developed or not ocellated. Lateral band abbreviated in juveniles. Distinguished from other species of *Cichla* with abbreviated juvenile lateral band by absence vs. presence of well defined vertical bars in adults; from *C. ocellaris* also by lateral line nearly always discontinuous vs. nearly always continuous, by absence vs. presence of bars 1a and 2a and absence vs. presence of abdominal blotches; from *C. kelberi*, *C. monoculus*, and *C. pleiozona* also by absence vs. presence of abdominal blotches and occipital bar and presence vs. absence of postorbital markings; from *C. nigromaculata* also by absence vs. presence of bars 1a and 2a, and absence vs. presence of small black blotches on dorsum.

Description. Refer to Figs. 10-19 for general shape and colour pattern, Table 13 for morphometrics, and Tables 2-10 for meristics.

Adults moderately deep (body depth 28.3-32.6 % SL, N = 11, 200-291 mm SL). Frontal contour straight ascending, levelling slightly in advance of dorsal-fin origin; in two large males (NRM 21548, NRM 21550), an incipient nuchal protuberance with sharp flexure indicated. Maxilla reaching to below anterior ¼ of orbit. Lower jaw prognathous, articulation below about posterior ⅕ of orbit. Lateral line bilaterally discontinuous in 39 specimens, unilaterally subcontinuous in one, and unilaterally continuous in three.

Dorsal spines 4-5, 5, or 5-6 longest; soft dorsal fin rounded, not reaching to caudal-fin base. Soft anal fin rounded, reaching to about ¾ of length of caudal peduncle. Caudal-fin margin subtruncate or, usually, slightly convex. Pectoral fin pointed, fourth ray longest, reaching to posterior base of anal fin or middle of caudal peduncle. Pelvic fin pointed (large males) or subacuminate, adjacent branches of first and second ray forming tip, reaching about halfway to base of first soft anal-fin ray, or slightly beyond.

Soft dorsal-fin squamation variable, from one to two rows of scales basally between rays and between branches of longer rays, to densely scaled with four rows of scales between rays and one or two rows between branches. Anal fin densely scaled with three to four interradial scale rows and one or two rows between branches. Caudal fin densely scaled, except narrowly along posterior margin, and middle of membranes between rays D2 and V2. Pectoral fin scaled basally. Pelvic fin densely scaled on both sides along anterior margin.

In juveniles scales absent from fins except base

Fig. 10. *Cichla orinocensis*, NRM 11256, 29.3 mm SL; Venezuela: Guainía: Rio Orinoco drainage: Caño Bocón.

Fig. 11. *Cichla orinocensis*, NRM 19641, 49.3 mm SL; Colombia: Vaupés: Rio Vaupés drainage: Rio Cuduairi.

Fig. 12. *Cichla orinocensis*, NRM 22920, 58.0 mm SL; Venezuela: Bolívar: Rio Caroni drainage: Guri Reservoir (right side, reversed).

of caudal fin; dorsal and anal fins extending only to middle of caudal peduncle; caudal-fin margin slightly concave. At about 100 mm SL, scales present anteriorly on soft dorsal fin, anal fin with basal scale cover, and caudal fin truncate.

Colouration in preservative. In juveniles about 30 mm SL (Fig. 10) markings absent from head. Vertical bars absent; small brownish blotches 1, 2 (indistinct), and 3, and a complete band from blotch 3 to small dark spot at caudal-fin base, as deep as blotch 3 anteriorly, narrower posteriorly.

At about 50 mm SL (Fig. 11) ground colour pale brownish dorsally, lighter ventrally. Indistinct brownish bars 1, 2, and 3, from slightly below dorsal-fin base to level of lower margin of pectoral-fin base. Brown round (or horizontally elongate) blotch on middle of side in bars 1 and 3; lighter, and ovate in bar 2. Dark brown band from blotch 3 to, and continuous with caudal blotch, about three scales wide, including lateral line scale and two scales above. Dark brown blotch

Fig. 13. *Cichla orinocensis*, MCNG 26401, 61.5 mm SL; Venezuela: Amazonas: Rio Orinoco drainage: Rio Atabapo at San Fernando de Atabapo.

Fig. 14. *Cichla orinocensis*, USNM 269934, 152.1 mm SL; Venezuela: Amazonas: Caño Manu, tributary of Rio Casiquiare ca 250 m upstream of Solano.

Fig. 15. *Cichla orinocensis*, MCNG 31915, young female, 207 mm SL; Venezuela: Guárico: Parque Nacional Aguaro-Guariquito, Rio Aguaro (right side, reversed).

covering extrascapular and adjacent area. Snout and nape brownish, lower jaw tip brown; no other distinct head markings. Caudal blotch at caudal-fin base, covering rays D2 to V1, dark brown, caudad narrower to point at about ⅓ of caudal fin. No other distinct fin pigmentation.

At about 60-70 mm SL (Figs. 12-13), bars 1-3 appearing as slightly oval dark brown blotches, bar 1 narrowest, with white anterior and posterior margins. Caudal peduncle band remaining. Extrascapular markings absent. Dark brown blotch between eye and preopercle. Caudal blotch round with slightly lighter margin; dark pigment along middle caudal rays. Soft dorsal fin with indistinct dark band and marginal ½ pigmented. Spinous dorsal fin pigmented, no obvious pattern. Pelvic and anal fins whitish.

At about 150-160 mm SL (Fig. 14) dorsum and top of head brown, side paler brown, ventral side whitish. Preorbital stripe occasionally distinct. Halter stripe from mouth angle to anterior end of preopercle dark brown, distinct. Postorbital markings include narrow dark stripe immediately behind eye, or two minute dark spots in its place, a few scattered spots dorsally on opercle, commonly dark spot on opercle close to subopercular margin, and dark spot at dorsal tip of ascending ramus of subopercle. Sparse white spots on side and caudal peduncle, arranged in five to seven irregular rows on side, about two rows on caudal peduncle; some specimens with indistinct light spots on cheek and preopercle, but spots absent on top of head. Side with bars 1-3, narrow, usually slightly expanded or darker at middle, and with indistinct lighter anterior and posterior margins. No trace remaining of caudal peduncle band. In ZSM 23838 (136 mm SL) and USNM 269334 (ca 165 mm SL) blotches 1-2 (below upper lateral line), and 3 (crossing terminal scales of upper lateral line, or immediately behind upper lateral line) distinct, but specimens pale, and distinctness of blotches may be artefact. Each blotch lined with lighter margin at least anteriorly and posteriorly. Spinous dorsal fin brownish with two or three rows of light spots, or uniformly brownish or blackish; soft dorsal fin light to dark brownish with about three to six irregular rows of hyaline spots. Anal fin brownish to greyish. Pelvic fin brownish or greyish.

Adults about 200-300 mm SL (Figs. 15-19) variable with regard to development of white spots on side and appearance of vertical bars and lateral blotches. Spinous dorsal fin brown with about three rows of light spots, or uniformly brownish or black; soft portion varying from light brown with numerous light spots to dark brown with only indicated spots. Commonly larger black spot on middle of opercle, or scattered black spots immediately behind head, dorsally on opercle and posterodorsally on subopercle, but never a continuous postorbital stripe. Halter stripe conspicuous, preorbital stripe absent. Three large dark brown to blackish blotches on side (blotches 1-3), anterior two below upper lateral line, but blotch 2 may extend above upper lateral line; blotch 3 above lower lateral line, covering terminal part of lateral line or located slightly posterior to it. Blotches ocellated, margined by light, largely confluent spots, and a few white spots scattered over dark blotches. Blotches usually irregularly roundish, but blotches 1-2 may be horizontally or vertically extended. Anal fin brownish or greyish. Caudal blotch roundish, usually completely ocellated; ventral lobe of caudal fin uniformly brownish, dorsal lobe with about seven or eight vertical rows of more or less

Table 13. Morphometry of *Cichla orinocensis*. Measurements are in percent of SL, except SL (in mm). Linear regression parameters calculated from original measurements in mm.

	N	min	max	mean	SD	a	b	r
SL (mm)	33	29.3	291.2	167.7				
Head length	33	29.5	36.3	33.0	1.63	1.364	0.318	0.995
Snout length	33	9.9	13.0	11.3	0.77	–1.847	0.126	0.991
Head depth	33	20.5	26.1	23.4	1.29	–1.853	0.248	0.994
Body depth	33	23.7	32.6	29.7	2.05	–1.506	0.311	0.994
Orbit diameter	33	6.9	12.6	8.7	1.39	3.586	0.060	0.987
Interorbital width	33	6.8	9.0	8.1	0.43	–0.496	0.085	0.993
Pectoral fin length	30	20.2	27.4	24.4	1.81	–3.723	0.269	0.989
Upper jaw length	33	13.9	16.4	15.0	0.71	–1.199	0.159	0.994
Lower jaw length	33	17.9	21.4	19.0	0.87	–0.514	0.194	0.993
Caudal peduncle depth	33	7.8	12.3	11.0	0.89	–0.460	0.114	0.994
Caudal peduncle length	33	16.1	19.5	17.5	0.84	0.780	0.169	0.995
Dorsal spine length	32	10.0	14.6	12.6	1.15	3.366	0.103	0.975

confluent elongate yellow or white spots. Pelvic fin pale grey to blackish.

Large male 291 mm SL from Guri (Fig. 16) unique in having horizontally elongate irregular lateral blotches 2-3 and additional small ocellar blotches along middle of side caudad to caudal-fin base connecting lateral blotches and caudal-fin blotch. Several other large specimens with occasional dark ocellar blotches associated with blotch 3 or scattered on caudal peduncle. Large mature male 267 mm SL from Guri (NRM 21548), with blotch 1 roundish, blotch 2 represented by bar 1, blotch 3 irregularly shaped, none of blotches or bars ocellated, although 1 and 3 with a few marginal light spots. Large females (Fig. 17) with numerous light spots on side and caudal peduncle, opercle, subopercle, and cheek, but absent on top of head. Indistinct un-ocellated blotch 1, bars/blotches 2 and 3 absent or only indicated.

Live colouration. No personal observations. In published photographs of adults (e.g., Román, 1981), and Machado-Allison's (1971) and Winemiller's (2001) descriptions olivaceous to greyish dorsum and olivaceous to yellowish or golden side. Pelvic, anal and lower half of caudal fin orange to reddish. Iris red. Ocellar markings lined with yellow or golden.

Geographical distribution. In the Amazon basin along the Rio Negro from near San Carlos de Rio Negro and from the Rio Uaupés near Mitú downstream to Manaus, and also in the lower Rio Branco, the Rio Puraquequara slightly east of the Rio Negro, and the Rio Casiquiare. Widely distributed in the Orinoco basin including the Inírida, Atabapo, Guarrojo, Guaviare, Meta, Aguaro, and Caroní rivers. Most localities are referable to blackwaters, as suggested by the restriction to Rio Negro and Rio Puraquequara in the Amazon basin, and most collecting sites in the Orinoco drainage are in blackwater rivers (Fig. 9).

Local names. Saupa (Guainía: Ilha de Dapa; Humboldt, 1821), Aketshi (Tamanaco; Humboldt, 1821, referring to Gilj), Pavón (Colombia, Venezuela), Pavón tres estrellas, Pavón mariposa, Pavón amarillo, Marichapa (Venezuela; Román, 1981).

Notes. The original description of *C. orinocensis* (Humboldt, 1821: 167, pl. 45 fig. 3) is apparently based on a field drawing and field notes. No preserved fish specimens are known from Humboldt's collections. The description refers to four blotches of which the last on the caudal fin, arranged in a series. The blotches are described as rounded, blue-black, and margined by a golden area. The drawing shows a very elongate fish with four absolutely round dark blotches with perfectly circular light marginal rings. The unique colour pattern allows identification of the species as the one here referred to as *C. orinocensis*. In addition to the incompatible elongate appearance, small mouth, and other details in the figure that may be attributed to haste or an expression of artistic freedom, the dorsal-fin count is remarkable. According to Humboldt there are 54 pungent rays in the dorsal fin. Since no other fish species is known with 54 spines in the dorsal fin, the count must be an error, but at least it confirms that the dorsal fin includes spines.

Humboldt (in Humboldt & Valenciennes, 1821: 168) reported that he had often eaten *C. orinocensis* both on the Rio Orinoco and the Rio Guainía (Rio Negro), and that the drawing was made in the Guainía valley. The specimen was collected near Ilha de Dapa, said by Humboldt (1819: 472) to be located in the middle of the Rio Guainía, 12 hours by canoe to San Carlos de Rio Negro, and apparently visited on the 5th or 6th of May 1800. Despite the name, the species thus appears to have been described primarily from the Rio Negro basin. We have not been able to locate the Ilha de Dapa on maps available to us.

The type specimen of *C. argus*, MNHN A.1042, 375 mm TL, is a stuffed and mounted skin with glass eyes (Fig. 19). It shows three round brown blotches lined with silver along the middle of the side, and a small black spot at the caudal-fin base. It has about 80 scales in the E1 row and about 42+41 lateral line scales. Fin counts could not be made out with confidence; although we count D. XVIII.13 like Valenciennes (in Humboldt & Valenciennes, 1821), only 15 spines can be positively identified. Valenciennes diagnosed *C. argus* as distinct from *C. orinocensis* on the basis of possession of a caudal ocellus and the dorsal-fin count, 31 instead of 54. On Humboldt's (1821: pl. 45 fig. 3) figure of *C. orinocensis* it looks like the last ocellus is situated on the body instead of on the caudal fin, and this may explain why Valenciennes considered *C. orinocensis* to lack the caudal ocellus. The dorsal-fin count provided by Humboldt for *C. orinocensis* is obviously erroneous (see above). The specimen is labelled as com-

Fig. 16. *Cichla orinocensis*, NRM 21550, adult male, 291 mm SL; Venezuela: Bolívar: Rio Caroni drainage: Embalse del Guri.

Fig. 17. *Cichla orinocensis*, NRM 21549, adult female, 246 mm SL; Venezuela: Bolívar: Rio Caroni drainage: Embalse del Guri.

Fig. 18. *Cichla orinocensis*, NRM 21547, adult male, 233 mm SL; Venezuela: Bolívar: Rio Caroni drainage: Embalse del Guri (right side, reversed).

Fig. 19. *Cichla orinocensis,* MNHN A.1042, ca. 375 mm SL; Brazil; holotype of *Cichla argus*. Photograph by E. Åhlander.

Fig. 20. *Cichla* cf. *orinocensis,* MBUCV-V 10287, 1, 82.3 mm SL; Venezuela: Bolívar, Rio Cuyuni, Raudal de Kinotovaca, ca. 40 km south of El Dorado.

ing from the Musée de Lisbonne, and probably represents part of the Brazilian fish collection made by A. Ferreira 1783-1792. His collection, originally kept in Lisboa, was confiscated by the French army in 1807 and taken to Paris (Araújo, 1983).

The names *C. orinocensis* and *C. argus* were published simultaneously, and *C. orinocensis* has priority by action of the first reviser, Günther (1862: 309), who listed both names in the synonymy under *Crenicichla orinocensis*. We do not designate a neotype of *C. orinocensis* here because there is currently no nomenclatural problem associated with the species.

Cichla orinocensis was identified as a *Crenicichla* species by Günther (1862), probably inspired by the elongate shape of the specimen illustrated by Humboldt (1821). Later authors (e.g., Regan, 1906) synonymized *C. orinocensis* with *C. ocellaris*. Machado-Allison (1971, 1973) provided the so far most detailed descriptive information on *C. orinocensis,* under the name *C. ocellaris*. Román (1981) treated the general natural history of the species with many illustrations, also as *C. ocellaris*. Ecological aspects are covered by Winemiller (2001).

Machado-Allison (1971: 468, figs. 3-4) described and figured the colour ontogeny of *C. orinocensis* from juvenile to adult, corresponding to the description given above. The largest specimen listed in Machado-Allison's table of

material is 220 mm, but he figures a large adult, 360 mm, with three distinct ocelli on the side, and lists a 617 mm specimen from the Sección de Osteologia del Aquarium Agustín Codazzi (no number, not listed in Machado-Allison, 1973: 158) in table 2. Machado-Allison (1973: 158) lists 6 skeletal preparations 215-334 mm SL. Since the 617 mm specimen is the only specimen in that paper stated to possess a continuous lateral line and an elevated number of lateral line scales (97, vs. upper + lower lateral line 73-88 recorded for other *C. orinocensis* in that paper), the identification is recorded here with reservation.

Williams et al. (1998: 178) reported specimens up to 56.5 cm TL (corresponding to ca 46 cm SL) from the Guri reservoir, but their figure of size distributions (fig. 2) shows a specimen in the interval 65-70 cm TL. Winemiller (2001: 98) reported *C. orinocensis* up to 455 mm SL in rivers and 550 mm SL in reservoirs.

Cichla orinocensis can be distinguished from all other *Cichla* species by the adult colour pattern, which typically includes three prominent black, ocellated blotches on the side, but no additional blotches on the dorsum (Fig. 15). The ocellated blotches develop gradually and directly from dark blotches along the midline of the side, and vary considerably in appearance in adults (Figs. 15-19). This variation is well covered by Román (1981), with illustrations of "typical" individuals with distinct ocelli (pp. 19, 27, 36, 49, 53, 70, 73, 105, 113, 122, and 129), varying with respect to the background colour pattern, and both including specimens with golden or silvery specks on the black blotches and specimens with pure black blotches. An adult with an additional prominent ocellus between blotches 1 and 2 is illustrated by Román (1981: 74).

Cichla orinocensis never shows black blotches posterior to the pectoral-fin base as in *C. ocellaris*, *C. monoculus*, *C. kelberi*, or *C. pleiozona*.

Juvenile and young *C. orinocensis* up to 60-70 mm are similar to juvenile and young *C. monoculus*, *C. kelberi* and *C. ocellaris* in colour pattern. Both *C. monoculus* and *C. orinocensis* possess a wide, prominent dark band connecting the bar 3 blotch and the caudal base blotch; in *C. ocellaris* this band is relatively more narrow and lighter. With increasing fish size, the caudal peduncle band disappears in all three species, but the bar 3 blotch transforms differently: in *C. orinocensis* the bar 3 blotch (like the bar 1-2 blotches) develops into an ocellated midaxis blotch; in *C. monoculus* and *C. kelberi* lateral blotches are replaced by vertical bars which more intensely pigmented dorsally and the caudal peduncle band disappears; in *C. ocellaris* the bar 3 blotch remains as an irregular dark blotch unlike the bar 2 and 3 blotches which are replaced by bars.

Adults of the sympatric species *C. temensis* can be separated by scale counts (E1 scales 75-89 in *C. orinocensis* vs. 98-128), absence of lateral ocelli, and postorbital markings wide vs. reduced to a few small blotches in *C. orinocensis*. Juveniles of *C. temensis*, in which scale counts are difficult to obtain, possess a continuous lateral band vs. distinct blotches 1 and 3, and a band caudad from blotch 3.

Although *C. orinocensis* has a fairly wide distribution including two major drainage basins, there is no obvious geographical correlate in the variation in morphometric or meristic characters and the colour pattern variation cannot be organised geographically.

A small specimen, MBUCV-V 10287, 82.3 mm SL, from the Venezuelan part of the Rio Cuyuni (Fig. 20), departs in colour pattern from young *C. ocellaris*, possessing an ocellated blotch 1, a large caudad tapering blotch 3, and the caudal blotch expanded onto the caudal peduncle. This colour pattern agrees with that illustrated by Eigenmann (1912, pl. 69 fig. 2) of a 138 mm specimen from Gluck Island in the Essequibo River identified by Eigenmann as *C. ocellaris*. Eigenmann's other figures of a juvenile and two adults of Guyanan *C. ocellaris* are compatible with *C. ocellaris* as illustrated in this paper and in Kullander & Nijssen (1989). The Cuyuni specimen has 80 scales in the E1 row and lateral line sinistrally discontinuous, dextrally continuous. Measurements fall outside *C. ocellaris* in morphometric PCA analyses. The colour pattern is more similar to that of small *C. orinocensis* (cf. Fig. 13), although the blotches may be considered large also for that species. A photograph of a large adult *Cichla* specimen, MCNG 16565, 225 mm SL, from the Rio Cuyuni (specimen not examined; photograph reproduced by Winemiller, 2001: fig. 1, right center, as *C. ocellaris*), shows a specimen very similar to a large specimen of *C. orinocensis* from the Rio Caroní (Fig. 18). It is thus possible that a population of *C. orinocensis* inhabits the upper Rio Cuyuni and the possible presence of this species in the Essequibo River drainage, suggested by Eigenmann's figure, should be investigated further.

Cichla nigromaculata Jardine, 1843
(Figs. 21-22)

Cychla nigro-maculata Jardine, 1843: 147, pl. 7 ([Rio Negro and Padauiri]).

Material examined. Three specimens, 171-230 mm SL, from the upper Rio Orinoco and Rio Casiquiare, and three specimens, 98.9-263 mm SL, from the Rio Negro tentatively assigned to *C. nigromaculata*. **Venezuela: Rio Orinoco drainage:** MBUCV-V 18632, 1, 173 mm SL; Amazonas: laguna 20 m from the margin of Rio Mavaca about 2 km above the Base Camp; 29 Mar 1988, R. Royero et al. – MCNG 27874, 1, 230 mm SL; Amazonas: Mavaca, isolated laguna in old meander of Rio Mavaca, just above and to the right of the indigenous community; 8 Feb 1991; L. Nico et al. **Rio Casiquiare drainage:** MCNG 12264, 1, 171 mm; Amazonas: Rio Siapa, about 15 km upriver from the Rio Casiquiare (about 2 km upriver from Caño Chimoní); 17 Apr 1985, L. Nico et al. **Brazil: Rio Negro drainage: Amazonas:** MZUSP 92401, 2, 254-263 mm SL; Arirará; 8 Oct 1979, M. Goulding. – MZUSP 33121, 1, 98.9 mm SL; Ilha de Tamaquaré; 11 Oct 1979, M. Goulding.

Diagnosis. Distinguished from all other species of *Cichla* except *C. intermedia*, *C. ocellaris*, *C. melaniae*, and *C. piquiti* by presence of bars 1a and 2a; similar to *C. ocellaris* in possession of dark blotch dorsally in bar 3. Different from *C. piquiti* in lower scale count (E1 row scales 75-84, vs. 83-104), and in having bars relatively narrow and short instead of uniformly wide across the side and reaching to the lower abdominal side; from *C. melaniae* by presence of prominent dark blotch dorsally in bar 3, and absence of numerous small light spots on side; from *C. intermedia* by lower scale count (E1 row scales 75-85 vs. 96-108), absence of horizontal lateral band, and vertical bars most prominent on dorsum rather than along midaxis. Different from *C. ocellaris* in possession of small black spots on dorsal side, discontinuous lateral line (vs. usually continuous); more scales (E1 scales 75-84 vs. 67-82); narrower caudal peduncle (depth 10.3-11.4 % SL vs. 11.9-13.2 % SL in specimens over 100 mm SL); vertical bars 1-3 wide dorsally, tapering to a point below middle of side (vs. usually relatively narrow and about equally wide from dorsum to ventral end); absence of postorbital markings (vs. presence); and presence of distinct occipital bar (vs. absent or indistinct).

Description. Based on Casiquiare and Orinoco specimens. Refer to Figs. 21-22 for general shape and colour pattern, Table 14 for morphometrics, and Tables 2, 4-10 for meristics.

Moderately deep (depth 28.3-31.5 % SL; N = 3, 230-263 mm SL). Frontal contour about straight ascending. Maxilla reaching to below middle of orbit. Lower jaw articulation below posterior ¾ of orbit. Lateral line discontinuous on both sides in all specimens.

Dorsal spines 3-4 broken; soft dorsal fin rounded, not reaching to caudal-fin base. Soft anal fin rounded, reaching beyond middle of caudal peduncle. Caudal fin rounded. Pectoral fin pointed, reaching halfway to middle of caudal peduncle, or (in MBUCV-V 18632) halfway to end of anal-fin base. Pelvic fin subacuminate, first ray longest, reaching halfway to middle of anal-fin base.

Table 14. Morphometry of *Cichla nigromaculata*. Measurements are in percent of SL, except SL (in mm). Linear regression parameters calculated from original measurements in mm.

	N	min	max	mean	SD	a	b	r
SL (mm)	5	171.4	262.5	217.9				
Head length	5	31.7	33.1	32.3	0.60	0.340	0.321	0.995
Snout length	5	10.3	11.8	11.1	0.54	–4.173	0.130	0.992
Head depth	5	22.3	25.2	23.7	1.05	–5.690	0.264	0.988
Body depth	5	28.3	31.5	29.9	1.55	4.654	0.277	0.967
Orbit diameter	5	7.9	9.3	8.6	0.60	5.042	0.062	0.953
Interorbital width	5	8.0	8.5	8.3	0.17	–1.077	0.088	0.998
Pectoral fin length	5	24.2	27.4	25.8	1.19	6.060	0.230	0.968
Upper jaw length	5	13.9	15.8	14.7	0.74	1.653	0.140	0.977
Lower jaw length	5	18.2	20.1	18.9	0.73	2.533	0.177	0.987
Caudal peduncle depth	5	10.3	11.4	11.0	0.44	–1.474	0.117	0.990
Caudal peduncle length	5	17.2	18.8	18.0	0.67	–0.481	0.182	0.986
Dorsal spine length	5	11.8	14.7	13.2	1.08	7.146	0.098	0.934

Fig. 21. *Cichla nigromaculata,* MCNG 12264, 171 mm SL; Venezuela: Rio Siapa.

Fig. 22. *Cichla nigromaculata,* MCNG 27874, adult female, 230 mm SL; Venezuela: Rio Mavaca.

Soft dorsal fin densely scaled basally and anteriorly to near distal margin, but scales absent from last four interradial membranes; two or three scale rows posterior to each ray, reduced to one row posteriorly, a few scales between major branches of anterior rays. Anal fin densely scaled basally, anteriorly also to near distal margin. Caudal fin densely scaled, covering almost all of fin except posterior margin and middle interradial membrane. Pelvic fin scaled anteriorly on lateral side, basally and on anterior rays also distally on medial side. Pectoral fin scaled basally.

Specimens 171-173 mm (Fig. 21) slightly more elongate. Fin squamation less extensive and scales absent from pectoral-fin base. Dorsal-fin spines 3-4 the longest. Caudal fin subtruncate.

Colouration in preservative. Adult female 230 mm (Fig. 22) discoloured, overall brownish from preservative and right side with several deep incisions to some extent obscuring colour pattern. Pattern of dark markings slightly different on each side of specimen. Distinct dark brown spot anterodorsally on opercle on right side only. Occipital bar present but indistinct due to damage from net. No other markings on head. On side three vertical brown bars from close to dorsal-fin base, gradually narrower down the side, bar 1 from below anterior half of dorsal fin to level of lower lateral line, bar 2 below posterior ⅓ of dorsal fin, to level of pectoral-fin base, bar 3 below soft anal fin, extending little ventral to lower lateral line. Bars 1a and 2a obsolete and much narrower than bars 1, 2, and 3; bar 1a not evident of left side. On left side, a black irregularly shaped

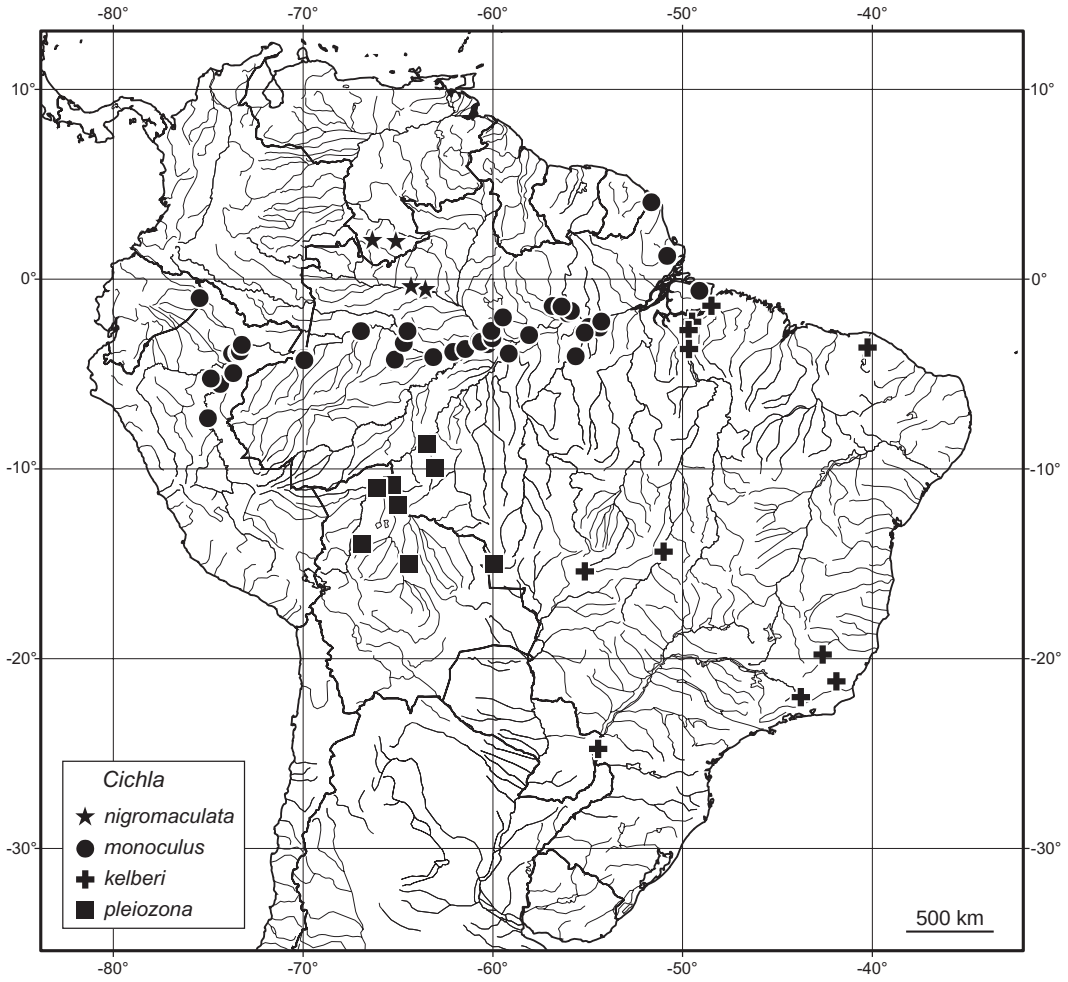

Fig. 23. Collecting localities of *Cichla kelberi* (including translocations), *C. monoculus*, *C. nigromaculata*, and *C. pleiozona*. A symbol may cover more than one collecting site.

blotch in bar 3 above upper lateral line, on right side some smaller black spots in the same area but no major blotch. Dorsal side with scattered irregular brown or black spots most prominent in bars 1a and 2a. Several larger black spots on middle of side between bars 1-2 and 2-3. Brown, more indistinct spots between pectoral-fin base and bar 2.

Dorsal-fin spinous portion black; soft portion brownish with two lighter cross bands distally. Anal fin brownish, lighter posteriorly. Pelvic fin brownish-greyish. Caudal fin light brownish with no markings other than black, almost round blotch ventrally at base of upper lobe, with complete light margin.

Specimens 171-173 mm (Fig. 21) overall lighter, probably slightly faded. Bars 1a and 2a distinct, widest dorsally, tapering to a point ventrally, similar to bars 1-3. Dorsal roundish blotch marking upper end of bar 3 distinct. Diffuse dark pigmentation in extrascapular area, but no distinct occipital bar. Dark brown spots on back restricted to two or three spots in bar 2a dorsally. Brownish spots between pectoral-fin base and bar 3 indistinct, in 173 mm specimen only one spot below bar 1 and one spot terminating bar 3.

Live colouration. No information available.

Rio Negro specimens. Three specimens (MZUSP 92401) from the middle Rio Negro are tentatively referred to *C. nigromaculata*. A morphometric PCA (not shown) of *C. ocellaris* and *C. nigromaculata* clusters the Rio Negro specimens with Orinocoan *C. nigromaculata* rather than with *C. ocellaris*, but in the total analysis (Fig. 3) they fall within the overlap with the *C. temensis* group, together with *C. monoculus* and *C. orinocensis*. The larger specimens are overall dark, with dark vertical bars not contrasted, and without distinct pattern of black spots on the side. All possess distinct bars 1-3, which widest dorsally and gradually narrower almost to a point ventrally; and with less distinct bars 1a and 2a.

Geographical distribution. Upper Orinoco and Casiquiare tributaries and the middle Rio Negro (Fig. 23).

Notes. Jardine (1843) reported four species of *Cichla* observed and drawn by Schomburgk in the Rio Negro basin. *Cichla argus* is identifiable from the drawing as *C. orinocensis*. *Cichla trifasciata* and *C. flavomaculata* possess the typical narrow dark bars on the side, and *C. flavomaculata* also the regular lines of yellow spots along the side, characteristic of *C. temensis*. The drawing of *C. nigromaculata* (Jardine, 1843: pl. 7) shows a fish with green dorsal side, yellowish lower side, blue dorsal fin and upper half of caudal fin, and reddish pelvic, anal and lower part of caudal fin. Numerous black blotches are present on the head, dorsum, and abdominal side, and on the dorsal side one can distinguish four, maybe five principal dark blotches, which appear to be narrowly ocellated. The colour pattern resembles that of *C. monoculus*, which, however, is not known from the upper Rio Negro. *Cichla ocellaris* is the next most similar species in the area, but it does not show more than three prominent blotches or bars on the dorsal side. None of the species of *Cichla* in the upper Rio Negro shows numerous large black spots on the side of the head. The figure is apparently not correct to details, but is understood by us to depict a *Cichla* with prominent black markings on the side.

Three specimens from the upper Rio Orinoco and Casiquiare, here identified as *C. nigromaculata*, depart from other *Cichla* in the area in displaying five dark bars dorsally on the side, and the larger specimen also several black blotches, whereby it resembles the colour pattern on the drawing of *C. nigromaculata* (Jardine, 1843: pl. 7). They differ from that drawing in absence of dark blotches on the side of the head, in having a more prominent caudal-fin ocellus, and in having well defined vertical bars instead of dorsal blotches. Two of the specimens are immature and do not show extensive black blotches dorsally on the side. The third is an adult female with a significant number of black blotches on the side. The drawing probably shows a breeding male as indicated by the prominent nuchal hump, and it is possible that males are more speckled than females.

The two species of *Cichla* confirmed for the Rio Negro, *C. orinocensis* and *C. temensis*, never show a colour pattern with extensive dark markings on the side. The colour pattern of *C. nigromaculata* as illustrated by Jardine (1843) is compatible with that of *C. monoculus*, *C. ocellaris*, and the species herein reported as *C. nigromaculata*.

The three Orinoco-Casiquiare specimens come from distant localities in the upper Rio Orinoco region, in rivers eroding the Serra Parima, separating the Orinoco from the Rio Branco headwaters, but a region travelled by Schomburgk. Three other, tentatively assigned specimens were collected in the middle Rio Negro together with *C. orinocensis*, and not far from the Rio Padauiri, mentioned by Schomburgk as an observation site for *C. nigromaculata*.

The material that we identify as *C. nigromaculata* is most similar to *C. ocellaris*, particularly in the presence of bars 1a and 2a, and the enlarged dorsally positioned blotch in bar 3. However, the absence of postorbital markings, and suggested strongly pigmented occipital bar in the large female from Rio Mavaca are more indicative of *C. monoculus*.

Cichla nigromaculata differs from *C. ocellaris* from the Rio Branco and the Guianas in average higher E1 row scale counts (75-84, vs. 67-82; Table 2). *Cichla nigromaculata* always has an interrupted lateral line, whereas in *C. ocellaris* the condition is variable. In practically all specimens of *C. ocellaris* from the Suriname and Marowijne rivers the lateral line is continuous (Kullander & Nijssen, 1989: 13), but in Guyana and the Rio Branco the condition varies. In 10 specimens of *C. ocellaris* from the Rio Branco the lateral line is continuous bilaterally in one, and on one side in two. *Cichla nigromaculata* has a shallower caudal peduncle than *C. ocellaris* of similar size: depth 10.3-11.4 % SL vs. 11.9-13.2 % SL in specimens over 100 mm SL. In the colour pattern, the shape

of the principal vertical bars in *C. nigromaculata* may be distinctive. In this species they are very wide dorsally, tapering to a point ventrad, whereas in *C. ocellaris* they are usually about equally wide, and comparatively narrow. Dark spots above the lateral line have not been observed in *C. ocellaris*, but scattered dark blotches may occur along the middle of the side (Fig. 8). Based on a single specimen, an emphasized occipital bar may be present in *C. nigromaculata*, typical of *C. monoculus, C. kelberi,* and *C. piquiti,* but the character needs confirmation from a larger sample.

Considering the variability of the colour pattern in *C. ocellaris*, it may be premature to suggest diagnostic characters in the colour pattern, and the material of *C. nigromaculata* is too limited for a definite assessment of morphometric or meristic differences. We nevertheless maintain *C. nigromaculata* for upper Orinoco and Negro river drainages, noting that the delineation versus *C. ocellaris* needs further work.

A colour photograph of a fresh captured specimen of what may represent *C. nigromaculata* from the Rio Emoni in the Rio Siapa drainage is provided by Winemiller (2001: fig. 1, upper right, as *C.* cf. *monoculus*; reproduced too small and too dark to show details), who gives a maximum recorded standard length of 346 mm for this species.

Cichla monoculus Agassiz, 1831
(Figs. 24-27)

Cychla Monoculus Agassiz, in Spix & Agassiz, 1831: 100, pl. 63 (as *Cichla Monoculus*) (mari Brasiliae).

Cycla toucounarai Castelnau, 1855: 17, pl. 10 fig. 1 (le lac des Perles de la province de Goyaz; le Tocantins; l'Amazone).

Cichla bilineatus Nakashima, 1941: 73, fig. [3] (los lagos y rios de Sudamérica tropical [cercanías del Puerto de Iquitos]).

Material examined. 153 specimens, 39.8-344 mm SL, in addition to material listed in Kullander (1986). **Peru: Rio Amazonas drainage: Loreto:** BMNH 1977.3.10:240, 1, 112.7 mm SL; Bueno Caño; 30 May 1974, M. Chapman. – NRM 18028, 1, 106.1 mm SL; Rio Tahuayo drainage, Caño Huayti, gramalotales. 7 Jul 1986. S. O. Kullander et al. – NRM 19148, 3, 130.5-142.3 mm SL; Iquitos, Belén market; 4 Aug 1986, S. O. Kullander. **Rio Nanay drainage: Loreto:** MHNG 2394.55, 1; Santo Tomás, Quebrada Santa Clara, tributary of Rio Nanay; 29 Aug 1987, H. Ortega. – MHNG 2394.62, 2; San Juan, Rio Chambira; 17 May 1987, V. Montreuil, S. Tello. – NRM 19135, 1, 136.0 mm SL; Rio Nanay, Yarina Cocha; 28 Jul 1986, S. O. Kullander. **Rio Ucayali drainage.** MZUSP 16204, 9; Ucayali: Cashibococha; 26 Jun 1978, H. Ortega. **Rio Samiria drainage.** NRM 18027, 1, 119.5 mm SL: Loreto: Quebrada Santa Elena, playa and small bay; 11 Aug 1986. S. O. Kullander et al. **Colombia:** NRM 32663, 2, 276-282 mm SL; Amazonas: Rio Amazonas, Leticia; 1995; P. Cala. **Brazil: Locality unknown:** MNHN A.9490, 2, 230.0-278.6 mm SL; "Amazone"; No date, F. de Castelnau. Syntypes of *Cycla toucounarai* Castelnau. **Rio Solimões drainage: Amazonas:** BMNH 1890.2.25:31, 1, 326 mm SL; Codajás; No date, L. Agassiz. – BMNH 1925.10.28:358, 2; Manacapuru; 29 Aug 1928, W. Ehrhardt. – BMNH 1925.10.28:359-360, 2, 270-325 mm SL; Manacapuru; no date, W. Ehrhardt. – MZUSP 5927. 1; Lago Jacaré, upstream of Manacapuru; 29-31 Mar 1967, EPA. – MZUSP 5980. 2; mouth of Rio Purús; 1-5 Apr 1967, EPA. – MZUSP 6499, 8; Lago Jacaré on left bank of Rio Solimões upstream of Manacapuru; 11 Nov 1967, EPA. – MZUSP 6652. 10; igarapé of Lago Manacapuru; 13 Nov 1966, no collector. – MZUSP 27253, 2; mun. Tabatinga, Costa Teresina, Lago Caial; 7-12 Oct 1982, L. Portugal. – MZUSP 50593, 6; Coari; 28 Sep 1968, EPA. – MZUSP 50596, 5; Lago Janauacá and surroundings; Sep 1976-Jan 1977, Alpha Helix. – MZUSP 50597, 1; Rio Içapó, mouth of Rio Jutaí; 22 Oct 1968, EPA. – NRM 5579, 1, 344 mm SL; Codajás; [1865-1866, Thayer Expedition.] – NRM 11309, 1, 248 mm SL; Rio Solimões system; no date, no collector. **Rio Tefé drainage: Amazonas:** BMNH 1897.12.1:248-275, 26, 39.8-45.8 mm SL; Tefé; no date, T. Bach. – MZUSP 50592, 6; Tefé; 30 Oct 1968, EPA. – NRM 24098, 1, 141.6 mm SL; Rio Tefé, 'Lagoa No 2', a few km downstream of RS-TEFE-4, which ca 150 km upstream of Tefé; 12 Sep 1993, R. Stawikowski. **Rio Japurá drainage:** MZUSP 36136, 2, 305-315 mm SL; Amazonas: Lago Urini at mouth of Rio Japurá; 29 Aug 1979, R. Barthem. **Rio Negro drainage: Amazonas:** BMNH 1929.11.18:18, 1, 153 mm SL; Manaus; no date, C. E. Turner. – BMNH 1970.4.2:1, 1, 59.2 mm SL; Manaus; no date, D. Kershaw. – MZUSP 6743, 3; vicinity of Manaus; 15-23 Nov 1967, EPA. – MZUSP 92402, 1; Igarapé Tarumãzinho, affluent no. 1; 17-18 Nov 1967, EPA. **Rio Uatumã drainage: Amazonas:** INPA 14736, 2; Igarapé Abonari, Km 5 below bridge; 18 Feb 1983, Equipe de Ictiologia do INPA. – INPA 14734, 1; Igarapé Catitu. 19 Oct 1983, Equipe de Ictiologia do INPA. – INPA 14739, 1; Rio Uatumã upstream of mouth of Igarapé Catitu. 23 Feb 1983, Equipe de Ictiologia do INPA. – INPA 14732, 1; Igarapé do Miriti. 25 Apr 1983, Equipe de Ictiologia do INPA. – INPA 14737, 8; Rio Uatumã. Nov 1984, Equipe de Ictiologia do INPA. – INPA 24077, 2; Igarapé da Arraya; 15 Apr 1983, Equipe de Ictiologia do INPA. **Rio Trombetas drainage: Pará:** INPA uncat., 1, 305 mm; Lago Tapagem; 13 Apr 1985; M. Jégu, E. Ferreira. – INPA uncat. 3, 245-285 mm; Área Shell-Alcoa, lower course of river. 19 Nov 1982, C. Vazzoler. – NRM 19494, 1, 136.5 mm SL; Lago de Sapucuá, Cabeceira Cururi ca 5-7 km upstream

Fig. 24. *Cichla monoculus,* NRM 18052, 46.6 mm SL; Peru: Rio Napo drainage: Aucapoza Cocha.

Fig. 25. *Cichla monoculus,* NRM 18412, 146.7 mm SL; Brazil: Pará: Santarém, Rio Tapajós shore opposite Santarém, Igarapé Açu.

of Oriximiná; 3 Oct 1991, B. Kilian & C. Seidel. – NRM 51804, 1, 52.6 mm SL; Lago Caipuru; 8 Sep 1998, R. Stawikowski. **Rio Canumã drainage:** MZUSP 7074, 2; Amazonas: Rio Canumã; 28-29 Sep 1967, EPA. **Rio Tapajós drainage: Pará:** MZUSP 3211, 2; Santarém, Rio Maicá; 19-27 Oct 1971, EPA. – MZUSP 22065, 1; Lago da Santa Clara, Monte Cristo; 5 Dec 1970, EPA. – MZUSP 50591, 5; island lake at Monte Cristo. 8 Dec 1970. EPA. – MZUSP 50598, 2; Igarapé Jacaré on right bank of Rio Tapajós, near Boim. 27 Oct 1970. EPA. – NRM 18412, 1, 146.7 mm SL; Santarém, Rio Tapajós shore opposite Santarém, peninsula, Igarapé Açu; 3 Oct 1992, R. Stawikowski et al. – NRM 27104, 2, 65.9-78.3 mm SL; 1 km below Alter do Chao, small bay; 23 Sep 1992, F. Warzel et al. **Rio Amazonas drainage:** BMNH 1929.7.30:28, 1; Pará: Rio Maycuru; no date, Flemming. – CAS uncat., 1; Pará: Santarém, Amazon River; Aug 1924, C. Ternetz. – MNRJ uncat., 1; Amazonas: Paraná do Ramos; Jul 1982, C. M. L. Ferreira. **Rio Arari drainage:** MZUSP 3596, 3; Pará: Ilha Marajó, Lago Arari; Oct 1944, A. Campos. **Rio Araguari drainage:** MNRJ 11614, 1, 190 mm SL; Amapá: Fazenda Modelo Aporema; May 1981, G. W. Nunan et al. **Rio Oiapoque drainage:** MNHN 1981-594, 2, 159-165 mm SL; Amapá: Junilan, savane; 20 Sep 1977, M. Fily.

Diagnosis. Similar to *C. kelberi* and *C. pleiozona* in possession of three dark vertical bars on side, presence of a pronounced occipital bar in large specimens, absence of black or ocellated markings laterally on head, and presence of irregular dark blotches on anterior abdominal side. Distinguished from *C. pleiozona* by less scales in a lateral row (68-87 vs. 84-93 in *C. pleiozona*) and typical absence of dark vertical bar anteriorly on caudal peduncle, and from *C. kelberi* by absence of light spots on anal and pelvic fins and lower caudal fin.

Fig. 26. *Cichla monoculus*, freshly captured adult male, not preserved; Brazil: Amazonas: Tefé, Rio Tefé. Photograph by R. Stawikowski.

Fig. 27. *Cichla monoculus*, MHNN 2188, 365 mm TL; from the Brazilian collection of Spix and von Martius, but of doubtful type status. Photograph by M. Kottelat.

Description. Modified from Kullander (1986). Refer to Figs. 24-27 for general shape and colour pattern, Table 15 for morphometrics, and Tables 2-10 for meristics.

Moderately deep (body depth 28.0-32.5 % SL, N = 15, 211-344 mm SL). Frontal contour straight ascending or slightly curved to slightly in advance of dorsal-fin origin; only a few specimens about 300 mm SL and longer with slight to prominent (Fig. 26) nuchal protuberance. Maxilla reaching ⅓ or middle of orbit. Lower jaw prognathous, articulation below posterior margin or, in juveniles, middle of orbit. Lateral line discontinuous on both sides in all specimens.

Dorsal-fin spines 4-6 longest. Soft dorsal and anal fins rounded, never extending to caudal-fin base. Caudal fin in young specimens slightly emarginate, with squared dorsal and rounded ventral hind corner, in adults hind margin very slightly and evenly convex. Pectoral fin acuminate, 4th

ray longest, reaching halfway to end of anal-fin base. Pelvic fin with tip formed by subequally long 1st and 2nd rays, inner branch of 1st usually slightly the longest, extending about halfway to anal-fin origin, relatively longer in juveniles.

Dorsal fin from behind last spine to behind 11th or 12th ray with small scales in one or two, in large specimens up to four rows close behind preceding spine or ray and in deeper ray branches. Anal fin with thick basal layer and most of fin except distal parts of posterior rays covered by scales. Caudal fin densely scaled, distal ⅔ of median portion of central membrane and, narrowly, hind margin of fin naked. Pectoral fin with small cycloid scales proximally. Pelvic-fin lateral side with dense pluriserial layer of scales between spine and second ray, extending to near fin tip; medial side with one or two rows of cycloid interradial scales between spine and first ray, first and second ray, and basally between second and third ray; dense layer of scales over base of fin; also scales between major branches of outer rays.

Juveniles 45-50 mm SL similar to adults, but slenderer. Dorsal, pectoral and pelvic fins naked, almost half of caudal fin scaled, and anal fin scaled basally. Dorsal and pelvic fin squamation present from about 100 mm SL, pectoral fin scales present from 175 mm SL.

Colouration in preservative. Juveniles 45-50 mm SL (Fig. 24) whitish ventrally; dorsum, occiput and dorsal part of caudal peduncle greyish, side dusky down to about level of horizontal band. Snout, preorbital, projecting part of lower jaw dark grey. Bars 1-3 dark grey, extending from back at dorsal-fin base onto abdominal side; each including black vertically extended spot on middle of side, less intense in bar 2. Wide black band from caudal spot rostrad to bar 3, and fainter to bar 2. Caudal fin smoky except white horizontally elongate spots on each side of proximal half of black band continuing band on body to hind margin of fin; band pigmentation more intense basally on fin. Anal and pelvic fins white or hyaline. Spinous dorsal fin with some dark pigment basally and along margin, but no pattern formed; horizontal dark stripe may be present along middle of soft dorsal fin.

Specimens about 100 mm SL with horizontal band remaining, dark grey, from caudal blotch to bar 4 position, band absent in specimens longer than about 120 mm SL. Anal fin and dorsal part of pelvic fin greyish; spinous and soft dorsal fin blackish, with two and three series of white spots, respectively; caudal fin dark grey with indistinct light spots in dorsal lobe, generally better expressed in larger specimens; caudal ocellus fully formed, in dorsal rather than midaxial position, black nuclear part of pupil diameter, white ventrally incomplete ring of eye diameter. Specimens 100-140 mm SL may possess indistinct scattered small light spots along middle of side. Light dorsal-fin spots retained in specimens about 140-150 mm SL (Fig. 25), apparently lost from spinous portion in those larger. Bar 3 may be reduced to blotch above lateral line level, with some adjacent silvery spots large specimens (Kullander, 1986: pl. 3 fig. 2; 175 mm SL).

Young adult 211 mm SL (Kullander, 1986: pl. 3 fig. 1). Ground colour grey, light on flanks, dark

Table 15. Morphometry of *Cichla monoculus*. Measurements are in percent of SL, except SL (in mm). Linear regression parameters calculated from original measurements in mm.

	N	min	max	mean	SD	a	b	r
SL (mm)	35	44.3	343.9	200.5				
Head length	35	31.5	35.3	33.5	0.93	0.446	0.331	0.998
Snout length	35	9.2	13.0	11.3	0.79	–1.932	0.126	0.994
Head depth	35	21.2	29.7	24.1	1.57	–2.292	0.255	0.988
Body depth	35	27.1	34.6	30.6	1.56	–0.190	0.309	0.995
Orbit diameter	35	6.8	11.3	8.5	1.05	2.477	0.069	0.984
Interorbital width	35	7.7	9.9	8.8	0.58	–1.586	0.098	0.995
Pectoral fin length	33	22.6	28.9	25.1	1.45	–2.221	0.265	0.992
Upper jaw length	35	13.8	16.8	15.2	0.84	–2.286	0.167	0.995
Lower jaw length	35	18.0	21.2	19.4	0.76	–1.128	0.201	0.995
Caudal peduncle depth	35	9.9	12.6	11.1	0.58	–0.154	0.112	0.993
Caudal peduncle length	35	15.2	20.2	18.3	1.05	1.461	0.174	0.989
Dorsal spine length	35	11.2	16.0	13.8	1.21	3.531	0.117	0.980

on back, nape and dorsally on caudal peduncle; most flank scales with light centre and dark edge. Lower regions, including prepelvic area and abdomen back along ventral surface of caudal peduncle yellowish white. Head side grey-brown, lower jaw smoky, whitish branchiostegal membrane dusky dorsally, intermandibular region whitish with some dark pigment. Blackish halter stripe present. Lips, preorbital area, snout, forehead, dark grey. Chest and pectoral axilla dirty greyish; pectoral axilla internally dark grey. Black blotch, including light scale centra, covering extrascapulars. Black, not contrasted vertical bar across nape between levels of orbit and preopercle. Three blackish bars on side, from back close to dorsal-fin base down to below (bars 1-2) or to (bar 3) lower lateral line level, none ocellated. Dark scattered spots between bars give mottled appearance to flanks.

Spinous dorsal fin black, immaculate; soft dorsal fin dark grey, with about seven vertical rows of white spots. Anal fin dark grey. Caudal-fin ventral lobe uniformly grey, dorsal lobe lighter with about six vertical rows of silvery or white spots. Caudal fin ocellus of about diameter of orbit; black nucleus on and above lower lateral line level, ring silvery. Pelvic fin dorsally with rays and scale layer blackish; ventral side unpigmented but dorsal side pigment showing through.

In adults 275 mm SL and larger, black bars often short, restricted to dorsum, blotch-like and contrasting against light side (Figs. 26-27), and black occipital bar pronounced. Blotches may be narrowly ocellated and usually additional scattered small dark spots present on dorsum or middle side. Abdominal blotches present with considerable variation, either as numerous smaller blotches or single elongate blotch extending caudad to bar 2. Spinous dorsal fin contrastingly black. This colouration found among specimens of both sexes, and tentatively regarded as breeding colour pattern because males with this pattern possess distinct nuchal protuberance.

Live colouration (Fig. 26)**.** Adults dull olivaceous or yellowish to golden or dark greenish with golden sheen on side, white ventrally. Narrow orange to yellow band from mouth angle to lower caudal fin base marking ventral extent of yellow/golden side. Caudal ocellus ringed with golden. Pelvic, anal, and lower half of caudal fin orange to dark red. Iris yellowish red. Vertical bars dark grey, not contrasted, or deep black, concentrated to dorsal blotches in large specimens and much more contrasted in living than in preserved specimens. Juveniles olivaceous with faint brassy sheen, ventrally white.

Geographical distribution. Rio Solimões-Amazonas along the main channel and lower courses of tributaries (Fig. 23); in Peru from Yarina Cocha on the Ucayali north to the lower Napo in Peru and Ecuador; in Colombia at Leticia, in Brazil from Tabatinga to the Marajó island, including lower parts of the Tefé, Trombetas and Tapajós rivers. Also present in the Araguari and lower Oyapock rivers north of the Amazon. The species is probably much more widespread in the lowland Amazon basin than our records show.

Habitat. *Cichla monoculus* has been collected in a number of different biotopes, but most commonly in floodplain lakes. In Peru adults were caught along the shoreline of both blackwater and whitewater floodplain lakes (Kullander, 1986).

Local names. Tucunaré, Tucunari (Peru; Kullander, 1986). Toukounaré, Kounanni, Aboné, Tukunali, Malisamba, Toukounalé, Kunan, Toekoenari, Matawalé, Tucunaré açu (French Guiana; Keith et al., 2000). In Brazil, Tucunaré açu or Tucunaré comum seem to be widely deployed for this species, but it is obvious that açu (large) is also used for big *C. temensis*. *Cichla monoculus* is generally not distinguished from similar species, such as *C. kelberi* or *C. pleiozona* in the first place, and the general name tucunaré is applied on all.

Notes. *Cichla monoculus* is identified with reference to the description and, particularly, the figure in Spix & Agassiz (1831). The description was made by Agassiz, the plate under Spix's supervision (Kottelat, 1988). Agassiz cited as reference for his description of *Cychla monoculus* a 13" long specimen in spirit of wine, with the locality 'mari Brasiliae'. The Spix and von Martius collection was destroyed when the Munich Museum was bombed in 1944. Kottelat (1984), however, recognized some material from that collection in the Museum d'Histoire naturelle de Neuchâtel (MHNN), where it was brought by Agassiz. One stuffed specimen of *Cichla*, MHNN 2188, was identified by Kottelat (1984, 1988) as

potential type specimen of *C. monoculus*. The specimen, 218 mm SL, 373 mm TL (Kottelat, 1988), is mounted on a wood plate with the left side toward the plate (Fig. 27). Kullander (1986) provided arguments for not considering the MHNN specimen as the holotype of *C. monoculus*. Although two similar species are now described, *C. kelberi*, and *C. pleiozona*, we do not consider that there is any real confusion concerning the identity of *C. monoculus*, and the species can be identified on the basis of the drawing and original description. There is thus presently no need for a neotype of *C. monoculus*. Authorship citation for Spix & Agassiz (1829-1831) here follows Kottelat (1988).

It is not known if any type material may exist of *C. bilineatus*, but the information in the original description (Nakashima, 1941) strongly suggests that it is a synonym of *C. monoculus* (Kullander, 1986).

Cichla monoculus was already described to detail, and figured from specimens of different sizes by Kullander (1986), and we have no substantial addition to that description. Measurement data provided here (Table 15) includes Peruvian material and previously unreported specimens from elsewhere, and the geographical distribution is considerably expanded by new material.

Cichla monoculus, *C. pleiozona*, and *C. kelberi* are similar in general appearance, and share a common colour pattern which includes three distinct dark vertical bars (bars 1-3), and variably (present in *C. pleiozona*, typically absent in *C. monoculus* and *C. kelberi*) a fourth dark vertical bar anteriorly on the caudal peduncle; vertical bars 1-3 in large adults intensified, expanded and blotch-like adjacent to base of dorsal fin; a pronounced wide occipital bar in large specimens; absence of black or ocellated stripes or spots on the head posterior to the orbit or on the gill cover. The three species can be distinguished from each other by E1 scale counts (84-93 in *C. pleiozona*, 68-87 in *C. monoculus*, and 76-83 in *C. kelberi*) and details of the colour pattern. *Cichla kelberi* is uniquely distinguished by light spots on the pelvic and anal fins, and the lower half of the caudal fin. *Cichla pleiozona* almost invariably shows bar 4 at the root of the caudal peduncle, whereas this bar is extremely rare in the other two species. *Cichla nigromaculata* may be a member of the same group if observations on presence of emphasized occipital bar and absence of postorbital spots are confirmed in better preserved specimens, but differs in the presence of bars 1a and 2a.

The E1 scale counts (Table 2) in *C. monoculus* cluster between 70 and 80, and the extreme values 85 and 87 belong two specimens from the Rio Trombetas drainage (INPA uncat.) whereas other Trombetas specimens are below 80. Most of our data come from western Amazonian specimens, and geographical variability was not targeted for analysis.

Cichla kelberi, new species
(Figs. 28-32)

Holotype. MZUSP 92397, 276 mm SL; Brazil: Pará: Tucurui; 1987, P. Formagio.

Paratypes. 52 specimens, 16.0-263 mm SL. **Brazil: Rio Araguaia drainage:** MZUSP 3855; 3, 150-195 mm SL; Mato Grosso: Rio das Mortes; 1950, Expedição Butantan. – MZUSP 50602, 2; Goiás: Lago Rico, near Cocalinho; Mar 1976, EMGOPA. – NRM 18023, 1, 246 mm SL; Mato Grosso: Rio das Mortes, cachoeira under bridge of MT-130 road; 20 Oct 1989, S. O. Kullander et al. **Rio Tocantins drainage: Pará:** MZUSP 38410, 34 (4 measured, 251-263 mm SL); Tucurui; 1987, P. Formagio. – MZUSP 46067, 1; Tucurui, Igarapé Muru; 12 Sep 1970, EPA. – MZUSP 50594, 1; Baião, Igarapé do Limão, Rio Tocantins; 9 Sep 1970, EPA. – MZUSP 50599, 6; Cametá, Igarapé Aricura; 7 Sep 1970, EPA. – MZUSP 50601, 4, 16.0-48.4 mm SL; Igarapé do Grilo, Rio Tocantins, Pindobazinho; 3 Sep 1970, EPA. – MZUSP 50620, 1; Utinga, Belém; no date, no collector.

Non-types, all translocations. Brazil: Rio Doce drainage: Minas Gerais: MZUSP 28964, 2; Lagoa Jacaré, Rio Doce; 29 Jun - 17 Jul 1983, J. R. Verani. – MZUSP 36654, 1; Lago Carioca, Vale do Rio Doce; Nov 1985, J. R. Verani. – MZUSP 36676, 2; Lago Dom Helvécio, Vale do Rio Doce; 27 Nov-13 Dec 1985, J. R. Verani. – MZUSP 36686, 1; Dom Helvécio, Rio Doce; no date, R. Haddad Rezek. **Rio Paraíba drainage: Rio de Janeiro:** MNRJ uncat., 18; Resende, Represa do Funil; 7-9 May 1982, G. W. Nunan. – MNRJ uncat., 1; Rio Muriaé 20 km downstream of Itaperuna, mun. Itaperuna; Aug 1989, no collector. **Drainage?: Ceará:** MZUSP 3268, 2; Açude Pau Cerrado; no date, A. Marques. **Paraguay: Rio Paraná drainage:** Alto Paraná: NRM 41915, 1, 30.1 mm SL; Rio Limoy, Reserva de Limoy; 2 Mar 1998, S. O. Kullander et al. – NRM 42401, 1, 60.0 mm SL; Rio Limoy, Reserva Limoy de Itaipú; 1 Mar 1998, S. O. Kullander et al.

Diagnosis. Distinguished from all other species of *Cichla* by presence in adults of small light spots on pelvic and anal fins, and lower lobe of caudal fin. Similar to *C. monoculus* and *C. pleiozona* in possession of three dark vertical bars on side, presence of a pronounced occipital bar in large specimens, absence of black or ocellated markings laterally on head, and presence of irregular dark blotches on anterior abdominal side. Distinguished from *C. pleiozona* by less scales in a lateral row (76-83 vs. 84-93 in *C. pleiozona*) and typical absence of bar 4.

Description. Refer to Figs. 28-32 for general shape and colour pattern, Table 16 for morphometrics, and Tables 2-10 for meristics.

Adults relatively deep (depth 31.7-33.7 % SL, N = 6, 246-276 mm SL). Predorsal contour straight, smoothly arched anterior to dorsal fin, large males with indicated (MZUSP 38410) to pronounced (in holotype) nuchal elevation. Maxilla reaching to below middle of orbit. Lower jaw prognathous, articulation below posterior margin of orbit. Lateral line discontinuous on both sides in all specimens.

Dorsal spines 3-6 or 4-6 longest; soft dorsal fin rounded, not quite reaching to caudal fin base; in large males subacuminate, reaching to or slightly beyond caudal fin base. Soft anal fin rounded, reaching beyond middle of caudal peduncle; in large males subacuminate, to caudal fin base. Caudal fin rounded, upper corner angled, lower corner rounded. Pectoral fin pointed, fourth ray longest, reaching halfway to end of anal fin base. Pelvic fin subacuminate, first or second ray longest, reaching halfway to beginning of soft anal fin base or middle of anal fin base.

Spinous dorsal fin naked, soft dorsal fin densely scaled except for posteriormost and distal portion, up to four rows of scales basally and one row on each side along with each ray. Anal fin densely scaled except distally, with two or three rows of scales associated with each ray. Caudal fin densely scaled, scales covering almost all of fin except posterior margin and middle interradial membrane. Pelvic fin densely scaled anteriorly on both medial and lateral side. Pectoral fin scaled or naked basally.

Juveniles (Figs. 28-29) elongate, scales absent on fins in the smallest. Caudal fin markedly emarginate.

Colouration in preservative. Juveniles ca 17 mm SL (Fig. 28) with brown blotch anteriorly on side, indistinct pigmentation representing second blotch, and third blotch barely distinguishable from succeeding brown band which ends with slightly more intense small spot at base of caudal fin. Fins hyaline.

Juvenile 48 mm SL (Fig. 29) with indistinct greyish vertical bar across anterior side, below lateral line and below posterior part of spinous dorsal fin, both bars with dark brown blotch at middle. Similar bar and blotch below anterior soft portion, but blotch connected to narrow dark brown horizontal stripe running on lower lateral line to dark blotch at middle of caudal fin base. Fins hyaline except for faint dark stripe across soft dorsal fin. Caudal base blotch dark brown, lanceolate, becoming narrower and fainter caudad

Table 16. Morphometry of *Cichla kelberi*. Measurements are in percent of SL, except SL (in mm). Linear regression parameters calculated from original measurements in mm. HT, holotype (MZUSP 92397).

	N	min	max	mean	SD	HT	a	b	r
SL (mm)	10	48.1	275.5	212.0		275.5			
Head length	10	31.9	35.3	33.4	1.03	33.1	0.596	0.330	0.997
Snout length	10	10.2	12.1	11.5	0.55	11.6	–1.017	0.121	0.997
Head depth	10	22.0	25.7	23.9	1.34	25.4	–3.626	0.259	0.992
Body depth	10	28.7	33.7	32.0	1.50	33.1	–3.983	0.343	0.998
Orbit diameter	10	7.4	11.0	8.2	1.08	7.4	2.461	0.068	0.993
Interorbital width	10	7.9	9.7	8.9	0.53	9.2	–1.281	0.096	0.993
Pectoral fin length	10	22.7	27.6	25.5	1.64	25.2	–3.931	0.277	0.989
Upper jaw length	10	14.1	16.7	15.9	0.74	16.2	–1.808	0.169	0.998
Lower jaw length	10	18.9	21.2	19.9	0.76	20.3	–1.844	0.209	0.995
Caudal peduncle depth	10	11.3	12.3	11.6	0.35	11.3	0.236	0.115	0.994
Caudal peduncle length	10	15.0	21.0	16.8	1.77	16.6	3.307	0.149	0.981
Dorsal spine length	9	11.3	14.6	12.6	0.98	11.3	1.342	0.118	0.984

to posterior margin of caudal fin.

Young male, and young unsexed specimens, 150-195 mm SL (Fig. 31), overall brownish with dark brown markings. Extrascapular marking distinct, consisting of dark proximal and distal blotches. Three dark vertical bars on side (bars 1-3), dorsally slightly separated from dorsal fin base, becoming gradually narrower ventrally, extending for ⅔ of side. Dark spot on many scales on back form short irregular rows of spots in larger specimens; in 150 mm SL specimen entire dorsum to level of upper lateral line, including caudal peduncle marbled with dark brown spots and lighter ground colour. Vertical bar on caudal peduncle absent. Small dark spots scattered on side only in 189 mm SL specimen; two larger specimens with irregular dark, light-margined spots behind pectoral fin base caudad to bar 3. Dorsal fin spinous portion dark, soft part with more or less distinct light spots distally. Anal fin with 3-4 rows of light spots distally; obsolete in 150 mm SL specimen. Up to five vertical rows of hyaline spots present posterodorsally on caudal fin. Caudal blotch round or slightly irregular, with complete or nearly complete light margin. Pelvic fin with a few light spots in 195 mm SL specimen.

In adult female 246 mm SL (NRM 18023) dorsum and dorsal margin of caudal peduncle dark greyish brown, nape and snout grey. Side light brown, abdomen, chest and ventral aspect of caudal peduncle yellowish white. Side of head brown, light or dark spots absent. Black spot marking region of proximal extrascapular. Four black vertical bars (bars 1-4); anterior below anterior half of spinous dorsal fin, second below posterior third of spinous dorsal fin, third below soft dorsal fin, fourth anteriorly on caudal peduncle. Bars wider dorsally, but about uniform in width across side; bars 1-2 extend to level of lower pectoral fin base, bar 3 slightly shorter, bar 4 to little below lower lateral line.

Small black spot on medial side of pectoral fin base and on adjacent side. Side, but not dorsum, with numerous scattered, partly confluent, small brownish spots; posterior to bar 2, including caudal peduncle, also many scattered small silvery spots. Spinous portion of dorsal fin black. Soft dorsal fin brown, light spots cannot be traced. Anal fin brown, soft portion distally grey with successively more obvious light spots distally on soft portion, three cross rows of hyaline spots distally on soft portion. Caudal blotch black, round, with almost complete silvery ring with short interruption dorsally and ventrally. Caudal fin brown, paler ventrally, and with indistinct pattern of alternating dark and light vertical bars posteriorly on dorsal lobe. Pelvic fin laterally brown with about four cross rows of white spots and lighter margin; medial side grey with some light spots visible from opposite side.

Large males (Fig. 32) light brown, caudal peduncle, abdomen and head ventrally whitish. Snout and occiput dark brown. Postorbital dark markings absent. Black occipital bar extending from above gill cover obliquely anteriad across nape. Dark brown vertical bars 1-2 below spinous dorsal fin ventrally to about level of pectoral fin base, bar 3 below anterior half of soft dorsal fin ventrally to slightly below lower lateral line. Dark brown blotch anterior to pectoral fin base. Several dark irregular blotches on abdominal side under adpressed pectoral fin. Scattered small dark spots between bars 1 and 2, and dorsally between bars 2 and 3. Dorsal surface of caudal peduncle dark brown. Spinous dorsal fin black, soft part brown with indistinct light spots on three posterior interradial membranes. Anal fin greyish brown with indistinct light spots on five posterior interradial membranes. Caudal fin brownish basally, otherwise greyish. Caudal blotch black, ringed with silvery or light spots. Pelvic fin greyish brown, lighter posteriorly. In 276 mm SL specimen (holotype, Fig. 32), anal fin with silvery white spots on inner ¾ of scaled portion, and all of naked posterior membranes; lower lobe of caudal fin with about six irregular vertical rows of silvery white spots; lateral aspect of pelvic fin with silvery white spots on two anterior membranes and long stripes of same colour on posterior membranes. MZUSP 38410 specimens generally not well preserved, and details of the pigment pattern on fins cannot be unambiguously determined.

Live colouration. Photographs show breeding males with yellow or golden side, greenish head without black spot, white chest, abdomen and ventral aspect of caudal fin base, but side duskied close to anal fin base. Vertical bars black. Yellow colour of side interspersed with numerous small black spots dorsally. Spinous dorsal fin black, with only few light spots. Soft dorsal fin, anal fin, and lateral aspect of pelvic fin grey to blackish with scattered contrasting white or yellow spots. Caudal fin ocellus with white to yellow ring.

Several light spots on proximal half of caudal fin. Large, partially confluent black spots with white or yellow margin on abdominal side between pectoral fin and middle vertical bar. Nuchal hump prominent, dark grey.

Breeding female NRM 18023 yellowish to golden on side yellowish on cheek and gill cover, with pattern as preserved specimen. Lower jaw, chest, abdomen and ventral side of caudal peduncle white. Branchiostegal membrane orange. Light spots posterodorsally on side, light ring of caudal ocellus and spots on anal fin yellow. Light spots on pelvic fin white.

Other large adults, without nuchal hump, greyish to olive on side, lower part of head, abdomen and ventral margin of caudal peduncle white; greyish on side next to anal fin base. Orange stripe from angle of mouth to lower part of subopercle, and often indistinct pale orange along abdominal side. Spots on fins white. Anal fin and lower lobe of caudal fin maroon.

Etymology. Named for Dieter Kelber, in recognition of his promotion of *Cichla* as sport fishes, and for supporting our study with information and images of the tucunaré amarela *(C. kelberi)* and tucunaré azul *(C. piquiti)*.

Geographical distribution. Rio Araguaia drainage and the lower Rio Tocantins drainage (Fig. 23). Introduced in reservoirs in Rio Grande do Norte, Minas Gerais and Ceará (Chellappa et al., 2003, as *C. monoculus;* Fontenele, 1948, as *C. ocellaris*), in the Rio Paraíba do Sul (State of Rio de Janeiro), and the Rio Paraná.

Kelber (1999) listed Tucunaré amarela from the Itaipu, Porto Primavera, Jupiá, Três Irmãos, Ilha Solteira, São Simão, Porto Colômbia, Volta Grande, Jaguara, Estreito, Promissão, Igaratá and Paraibuna dams in the Brazilian Paraná basin, the Funil and Ribeirão das Lajes dams in the Rio Paraíba do Sul drainage, the Xingó dam in the Rio São Francisco drainage, the Pacoti-Riachão dam near Fortaleza in Ceará, the Serra da Mesa dam in the Rio Tocantins drainage. The Tucunaré amarela corresponds to *C. kelberi* according to photographs provided by D. Kelber.

Local names. Tucunaré amarela (São Paulo, Brazil; Kelber, 1999), Tucunaré comum (Northeast of Brazil; Fontenele, 1948).

Notes. *Cichla kelberi* has long been confused with *C. monoculus* (e.g., Fontenele, 1958, as *C. ocellaris*), which it resembles in shape and general colour pattern. We have not found any diagnostic character other than the light-spotted pelvic, anal and caudal fins, to separate the two species, but since this character state is unique in the genus, we are confident about species distinctness. The lateral scale count is within the higher range of *C. monoculus,* and below the range of *C. pleiozona*.

The type material of *Cycla toucounarai* is represented by two preserved specimens, MNHN A.9490, labelled simply as coming from the "Amazone", although the description (Castelnau, 1855) also mentions "le lac des Perles de la province de Goyaz", and the Rio Tocantins. They were referred to *C. monoculus* by Kullander (1986). Both specimens have characteristic blotches on the abdominal side posterior to the pectoral fin base. The larger syntype (Kullander, 1986: pl. 4 fig. 1) is a male with nuchal hump, the smaller specimen a female. The pigmentation of the smaller specimen is slightly faded on both sides, and it shows no traces of light spots on the pelvic, anal, or caudal fins. The larger specimen possesses a black occipital stripe, three prominent vertical bars dorsally on the side, and trace of a dark blotch dorsally at the root of the caudal peduncle. The pigmentation of the right side is significantly faded, but the dark pigmentation is relatively well preserved on the left side. The anal fin is brownish with indicated lighter patches distally on the scaled portion of the anterior five soft rays. The ventral half of the caudal fin is brownish with indistinct lighter mottling but without light distinct spots. The pelvic fin is brownish anteriorly with two lighter patches on anterior soft rays. The caudal spot is ringed with a prominent silvery ring in both specimens.

Castelnau's description and drawing disagree with the preserved syntypes. The drawing shows a specimen without occipital bar, and without dark blotches on abdominal side, but with three distinct vertical bars below the dorsal fin and one anteriorly on the caudal peduncle, and some red spots on the anal fin. The description apparently partly refers to the drawing, but the total length agrees with the larger syntype. Both syntypes have D. XVI.17, the drawing shows XV.18, Castelnau gives XV.17. He counts A. II.11, we count A. III.11. The pectoral fin count, 14 is in agreement. We count approximately 79 (larger syntype) and 71 (smaller syntype) scales along the midline, but

Fig. 28. *Cichla kelberi*, paratype, MZUSP 50601, 17.2 mm SL; Brazil: Pará: Igarapé do Grilo, Rio Tocantins, Pindobazinho.

Fig. 29. *Cichla kelberi*, paratype, MZUSP 50601, 48.4 mm SL; Brazil: Pará: Igarapé do Grilo, Rio Tocantins, Pindobazinho.

many scales are lost, and a through-going perforation likely caused by an arrow or spear through the larger syntype perforates the E1 row; Castelnau gives the range 72-75.

In the description, Castelnau says that "l'anale est piquetée de rouge et de noir", i.e., the anal fin is spotted with red and black. This is significant because *C. kelberi* is diagnosed particularly by its anal fin colouration. One of us re-examined the existing syntypes with special emphasis on the possible presence of spots on the pelvic and anal fins, which were not mentioned by Kullander (1986). Whereas the pigmentation on these fins is indeed not uniform, we cannot recognize light spots of the kind displayed by some freshly preserved adults of *C. kelberi* although the silvery caudal blotch ring is well preserved in the syntypes. Close to imperceptible light mottling of the otherwise brownish scaled portions of the pelvic, anal, and caudal fins does not permit ambiguous identification as homologous with light spots in fresh specimens of *C. kelberi*, and is at least partly referable to lost scales. The light anal fin patches are located anteriorly on the fin in the transition between the scaled portion and the scaleless margin, a condition which is different from fresh specimens in which the light spots are located on the posterior soft rays. Whereas the light mottling of the anal fin possibly can be correlated with the red spots described and figured by Castelnau, it does not match the white or yellow spots observed in fresh preserved specimens of *C. kelberi*, and is doubtfully distinct from uneven artifactual discolouration of fins in other old specimens of *Cichla*.

Whereas the larger syntype has 79 scales in the E1 row, which is in the upper portion of the range of counts of *C. monoculus* and near the median of the slightly higher range of *C. kelberi*, the smaller syntype has 71 scales, which is far

Fig. 30. *Cichla kelberi*, NRM 42401, 60.0 mm SL; Paraguay: Alto Paraná: Rio Limoy, Reserva Limoy de Itaipú (right side, reversed).

Fig. 31. *Cichla kelberi*, paratype, MZUSP 3855, 195 mm SL; Brazil: Mato Grosso: Rio das Mortes.

Fig. 32. *Cichla kelberi*, holotype, MZUSP 92397, adult male, 276 mm SL; Brazil: Pará: Tucurui.

below counts observed in *C. kelberi*, and near modal for *C. monoculus*.

Castelnau (1855) included material from several localities in his concept of *C. toucounarai*. He relates that he first saw this fish in the lac des Perles in Goiás, later it was found in the Tocantins, and finally in the "Amazone". "It is known locally everywhere as Toucounarai. The Chambioas of the Araguaia gave it the name of Kini-teray. Its flesh is very good, and it reaches sometimes double the size that we have indicated." [Translated from the French.]

Castelnau (1855) expresses that he hesitates to describe *C. toucounarai* as a new species because it would be very close to *C. monoculus*, differing by the constant absence of spots from the abdomen, assured by observation of an "immense quantity" of individuals of *C. toucounarai*. It would be close also to *C. flavomaculata* but differing in the absence of yellow spots from the body and the colouration.

Quite clearly, the description of *C. toucounarai* includes observations of *Cichla* from the Tocantins, Araguaia, and the rest of the Amazon. The syntypes seem to have been preserved from the later part of the expedition, from Western Amazonia. The sketch for the drawing may have been made in the Tocantins basin, or the colouring of the plate based on field notes from the Tocantins basin. We also suspect that Castelnau may be including *C. piquiti* in his concept of *C. toucounarai*. That species does not have dark blotches on the abdominal side and is quite common in the Tocantins basin.

Cichla kelberi frequently displays black blotches behind the pectoral fin base, like the syntypes of *C. toucounarai*, but in contrast with the drawing and description. The anal fin spots are white, yellow or silvery, not red. Species of *Cichla* frequently display some red colour on the anal fin, but not in the form of small spots.

Even specimens of *C. kelberi* in a poor state of preservation may maintain light markings in the anal fin. Inasmuch as the syntypes of *C. toucounarai* do not display anal fin markings, and since the description is ambiguous and may refer to three or even more species, we continue to consider *C. toucounarai* a synonym of *Cichla monoculus*. To fix the name, we select the larger syntype of *C. toucounarai* as lectotype. It can be recognized by the morphological information above, and is figured by Kullander (1986: pl. 4 fig. 1).

Cichla pleiozona, new species
(Figs. 33-36)

Holotype. MZUSP 92398, adult male, 340 mm SL; Brazil: Mato Grosso: Rio Alegre, tributary to Rio Guaporé, ca 30 km from Vila Bela da Santíssima Trindade; 28-30 Sep 1984, J. C. Garavello et al.

Paratypes. 21 specimens, 108.8-320 mm SL. **Brazil: Rio Jamari drainage: Rondônia:** INPA 24065, 1, 220 mm SL; 15 km upstream of UHE Samuel; 19 Sep 1986, G. M. Santos. – INPA 24068, 2, 205-210 mm SL; Rio Canaã, Ariquemes, escalvado; 3 Apr 1986, G. M. Santos. – INPA 24069, 1, 240 mm SL; Ariquemes, Lago Fortaleza; 24 Jun 1985, G. M. Santos. – INPA 24071, 3, 210-240 mm SL; Lago Espanha, 20 km downstream of UHE Samuel; 17 Jun 1985, G. M. Santos. – INPA 24074, 3, 165-235 mm SL; Rio Canaã, Lago Fortaleza, ca 10 km upstream Ariquemes; 9 Jun 1984, G. M. Santos. **Rio Guaporé drainage:** MZUSP 37251, 1, 204 mm SL; Mato Grosso: Vila Bela da Santíssima Trindade; 28-30 Sep 1984, J. C. Garavello et al. – MZUSP 37499, 4, 212-320 mm SL; Mato Grosso: Rio Alegre, tributary to Rio Guaporé, ca 30 km from Vila Bela da Santíssima Trindade; 28-30 Sep 1984, J. C. Garavello et al. – INPA 24064, 1, 205 mm SL; Rondônia: Surpresa; 16 Jun 1985, G. M. Santos. **Rio Mamoré drainage:** INPA 24073, 1, 217 mm SL; Rondônia: Guajará Mirim, Rio Pacaas Novos; 16 Nov 1984, G. M. Santos. **Bolivia: Rio Mamoré drainage:** NRM 19131; 1, 108.8 mm; Beni: Laguna Mocovi; 28 Apr 1985, G. Loubens. **Rio Guaporé drainage:** NRM 19130, 1, 212 mm SL; Beni: mouth of Rio Machupo; 31 Aug 1984, G. Loubens. **Rio Madre de Dios drainage:** NRM 19129, 2, 149.8-157 mm SL; Pando: Rio Madre de Dios near Riberalta; 18 May 1982, G. Loubens.

Non-types. Bolivia: Rio Mamoré drainage: ZSM 23839, 3; Beni: cañada to Tarupal; 26 Apr 1954, O. Schindler. – ZSM 23840, 1; Beni: cañada to Tarupal; 23 Apr 1954, O. Schindler. – ZSM 23841, 5; Beni: 'Lange Lagune' at Espíritu; 14-17 Apr 1954, O. Schindler. – ZSM 23842, 2; Beni: Carnaval, floodlands; Apr 1954, O. Schindler & Foster. **Rio Beni drainage:** CAS IU 17065, 1, 267 mm SL; Beni: Lago Rogoagua; Nov 1921, N. E. Pearson.

Diagnosis. Similar to *C. kelberi* and *C. monoculus*, and distinct from all remaining species of *Cichla* in combination of possession of three dark vertical bars on side, presence of pronounced occipital

bar in large specimens, absence of black or ocellated markings laterally on head, and presence of irregular dark blotches on anterior abdominal side. Distinguished from *C. kelberi* and *C. monoculus* by more scales in lateral row (84-93 vs. 76-83 in *C. kelberi* and 68-87 in *C. monoculus*) and presence (with occasional exceptions) of dark vertical bar (bar 4) anteriorly on caudal peduncle which is typically absent in both *C. kelberi* and *C. monoculus*, and from *C. kelberi* by absence of light spots on anal and pelvic fins and lower lobe of caudal fin.

Description. Refer to Figs. 33-36 for general shape and colour pattern, Table 17 for morphometrics, and Tables 2-10 for meristics.

Adults moderately deep-bodied (body depth 28.9-31.2 % SL, N = 11, 204-340 mm SL). Predorsal contour straight ascending, smoothly arched on nape except in three large males, 278, 310, and 340 mm SL with nuchal protuberance immediately anterior to dorsal fin. Maxilla reaching to below anterior margin of orbit or slightly beyond. Lower jaw prognathous, articulation below about middle of orbit. Lateral line discontinuous on both sides in 13 specimens, continuous on one side in three specimens, subcontinuous on one side in two other specimens.

Dorsal spines 3-5 or 4-5 longest; soft dorsal fin rounded, not reaching to caudal fin base. Soft anal fin rounded, reaching beyond middle of caudal peduncle. Caudal fin damaged in many specimens, otherwise with angled dorsal corner, rounded ventral corner, and slightly convex posterior margin. Pectoral fin pointed, fourth or 5th ray longest, reaching halfway to end of anal fin base or middle of caudal peduncle. Pelvic fin subacuminate, first ray longest, reaching halfway to soft anal fin origin.

Dorsal fin scaled basally in smallest specimen, 109 mm SL, with single rows along rays, in the next largest 150-157 mm SL single rows along anterior rays; in large specimens densely scaled basally and in branches, in two or three rows. Anal fin densely scaled anteriorly, and on proximal two thirds of soft portion in 109 mm SL specimen, densely scaled, to close to margin in larger specimens. Caudal fin densely scaled, in adults scales covering almost all of fin except posterior margin and middle interradial membrane. Pelvic fin scaled basally in young, in larger specimens densely scaled on both sides of fin along anterior margin. Pectoral fin scaled basally in all specimens.

Colouration in preservative. Vila Bela specimens much darker than Bolivian specimens, reflecting different preservation, whitish parts showing as dull yellowish to pale brownish.

Young, 109 mm SL (Fig. 33) light brownish on top of head and dorsum; lighter on side. Lower head, abdomen, anal-fin base, underside of caudal peduncle whitish. Nape markings absent. Very faint oblique, slightly dorsad running dark band from orbital margin to middle of opercle. Narrow brown vertical bars from base of dorsal fin to level of lower pectoral fin base (bars 1 and 2), or little below lower lateral line (bar 3); bar 1 below

Table 17. Morphometry of *Cichla pleiozona*. Measurements are in percent of SL, except SL (in mm). Linear regression parameters calculated from original measurements in mm. HT, holotype (MZUSP 92398).

	N	min	max	mean	SD	HT	a	b	r
SL (mm)	14	108.8	340.0	223.6		340.0			
Head length	14	31.2	35.0	33.1	1.14	33.7	1.798	0.321	0.993
Snout length	14	10.6	13.0	11.9	0.60	12.6	–2.159	0.129	0.985
Head depth	14	21.9	29.0	24.1	1.80	25.1	–4.269	0.262	0.976
Body depth	14	28.9	33.1	31.0	1.47	33.1	–3.655	0.327	0.985
Orbit diameter	14	7.3	8.7	7.9	0.48	7.6	2.183	0.068	0.986
Interorbital width	14	8.4	10.1	9.1	0.45	10.1	–2.323	0.102	0.988
Pectoral fin length	13	22.5	25.6	24.2	0.96	25.0	–1.669	0.250	0.991
Upper jaw length	14	15.0	17.2	15.8	0.54	17.2	–2.945	0.172	0.992
Lower jaw length	14	18.5	21.3	19.6	0.85	21.3	–3.272	0.211	0.987
Caudal peduncle depth	14	10.8	11.8	11.2	0.32	11.0	0.384	0.110	0.995
Caudal peduncle length	14	15.2	17.9	16.7	0.76	15.2	2.608	0.155	0.984
Dorsal spine length	13	11.0	14.0	12.2	0.93		6.260	0.091	0.986

Fig. 33. *Cichla pleiozona*, paratype, NRM 19131, 108.8 mm SL; Bolivia: Beni: Laguna Mocovi.

Fig. 34. *Cichla pleiozona*, paratype, NRM 19129, 157 mm SL; Bolivia: Pando: Rio Madre de Dios near Riberalta.

anterior ⅓ of spinous dorsal fin, bar 2 below posterior spinous dorsal fin, bar 3 below about middle of soft dorsal fin. Indistinct dark grey band from bar 3 caudad to caudal fin base (on left side) or limited to caudal peduncle (right side). Light spots on side absent. Dorsal spinous portion not well preserved, but possesses dark and hyaline portions; soft part hyaline with brownish band across middle, and brownish tip. Anal fin whitish basally, naked part greyish; pelvic fin whitish. Caudal fin brownish yellow, lower lobe also duskied; a few large white spots on middle membranes. Caudal blotch elongate with white ring except posteriorly.

Specimens 150-157 mm (Fig. 34) with conspicuous blackish occipital bar from dorsal margin of gill cover obliquely rostrad across nape. Postorbital markings absent, or some dark pigment behind orbit and on opercle. In addition to three dark bars (bars 1-3) on side a dark bar (bar 4) on caudal peduncle anteriorly, from dark dorsal margin of peduncle to slightly below lower lateral line. A few small brownish spots between bars 2 and 3 under pectoral fin. Dorsal fin spinous portion grey, soft portion yellowish grey with some hyaline spots posteriorly. Anal fin greyish on scaled part, hyaline posteriorly. Caudal ocellus round, with more or less complete silvery ring; remainder of caudal fin pale brownish yellow, smoky, posteriorly grey with transverse row of white spots. Pelvic fin greyish anteriorly, lighter posteriorly on both sides.

Young adult female, 240 mm SL (INPA 24069), light brownish, to whitish abdominally, on lower part of head and underside of caudal peduncle. Pronounced blackish band along anteroventral

Fig. 35. *Cichla pleiozona*, paratype, MZUSP 37499, probable male, 212 mm SL; Brazil: Mato Grosso: Rio Alegre, tributary to Rio Guaporé, ca 30 km from Vila Bela da Santíssima Trindade.

Fig. 36. *Cichla pleiozona*, holotype, MZUSP 92398, adult male, 340 mm SL; Brazil: Mato Grosso: Rio Alegre, tributary to Rio Guaporé, ca 30 km from Vila Bela da Santíssima Trindade (right side, reversed).

margin of cheek. Blackish irregular blotch on middle of opercle. Blackish spot posterodorsal to orbit. Wide black bar obliquely anteriad across nape covering extrascapular series. Three dark brown vertical bars on side, bar 1 below anterior ⅓ of spinous dorsal fin, bar 2 below posterior part of spinous dorsal fin, bar 3 below middle of soft anal fin. Bars about uniformly pigmented to about middle of side, where gradually fainter to approximately horizontal level of dorsal pectoral fin base. Scattered dark brown blotches under adpressed pectoral fin. Dorsal fin blackish; soft portion dark greyish. Anal fin light basally, duskied distally.

Young adult female 212 mm SL (NRM 19130) with dorsum and nape light brownish, light grey side; chest, abdomen, side adjacent to anal fin and underside of caudal peduncle pale yellowish. Lower jaw white. Side of head yellowish whitish, somewhat reflecting. Anterior side slightly slivery. Dorsum and upper side with numerous, indistinct small lighter spots.

Dark brown band across nape, obliquely anteriad from dorsal margin of opercle, covering extrascapulars and some scales anterior to extrascapular series. Bars 1-2 brownish from dorsal fin base to about level of pectoral fin base, grading into a mottled pattern of scattered brown, silver ringed spots behind pectoral fin base. Bar 3 including darker irregular pigment subdorsally, including 3-4 silvery dots, ventrad greyish brown to below lower lateral line. Bar 4 indistinct, to

slightly below lower lateral line. Indistinct whitish spots along middle of caudal peduncle. No postorbital markings, except a tiny black ocellated spot at posterodorsal tip of opercle. Dark blotch immediately anterior to pectoral fin base. Spinous dorsal fin brown, soft part greyish yellow, a white cross band posteriorly in soft dorsal fin. Anal fin pale brownish yellowish. Caudal fin brownish yellow; indistinct light vertical rows of spots posteriorly. Black irregular spot at base with complete silvery ring. Pelvic fins yellowish with white anterior margin.

In probable male 212 mm SL (Fig. 35) dorsum, top of head, dorsal part of opercle, and dorsal side with dense pale spots separated by narrow light brown interspaces. Dark occipital bar from gill cover across nape indistinct, mostly obscured by pattern of light spots. Two dark brown vertical bars (bars 1-2) below spinous dorsal fin, becoming narrower ventrally, extending to level of pectoral fin base; dark vertical bar (bar 3) below middle of soft dorsal fin, becoming narrower ventrally, extending to lower lateral line; dark vertical bar (bar 4) across root of caudal peduncle, laterally extending to lower lateral line. A few indistinct dark spots under adpressed pectoral fin. Dorsal fin grey with black lappet margins, soft dorsal fin greyish with lighter cross-band close to margin. Anal fin brownish, distally light greyish. Pelvic fins light brown. Caudal fin ocellus complete with light ring; caudal fin pale brownish, with a few indistinct lighter spots on median membranes.

Three large specimens 278-340 mm SL (MZUSP 37499; Fig. 36), probably all males, brown on side, dorsum and head, lower aspects paler. Postorbital markings absent. Black irregular oblique occipital bar from above gill cover to hump or across nape. Vertical bars (1-3) positioned as described above but deep black dorsally and mediated by black pigment along base of dorsal fin, extending to level of lower lateral line but fading below upper lateral line (extending to middle of side in 278 mm SL specimen); bar 4 distinct from the rest, restricted to dorsal surface of caudal peduncle. Black blotches of varying size and variously connected under and around adpressed pectoral fin. Irregular black or dark brown blotch or smaller spots anterior to pectoral fin base. Spinous dorsal fin black; soft dorsal fin dark brown to blackish. Anal fin light brownish. Pelvic fin laterally brownish grey, medially greyish. Caudal fin brownish, without light spots; caudal base blotch black, with complete light ring. In specimen 277 mm SL (MZUSP 37499), without nuchal hump, band of abdominal side blotches narrower, and vertical bars not confluent close to dorsal fin base.

Live colouration. A photograph of a freshly captured specimen from Surpresa, Rio Guaporé: Side olivaceous. Underside of head, chest, abdomen, side adjacent to anal fin base, and underside of caudal peduncle white. Dark grey vertical bars 1-3 distinct, also a dark grey vertical bar across middle of caudal peduncle. Blackish blotch at pectoral peduncle. Dorsal fin blackish. Anal fin dark grey anteriorly, reddish posteriorly. Ring around caudal blotch silvery. Lower caudal fin lobe dull reddish. Pectoral fin dark grey anteriorly, inner rays reddish.

Geographical distribution. The Bolivian Amazon basin including the Rio Madre de Dios, Beni, Mamoré, and Guaporé river drainages in Bolivia and Brazil, and in the Rio Jamari, which is a tributary of the Rio Madeira (Fig. 23).

Etymology. Named *pleiozona* for reason of the additional vertical bar on the caudal peduncle, in contrast to *C. monoculus* and *C. kelberi*, recognizing also the usually distinct occipital bar; from the Greek *pleios,* more, and *zona*, girdle. To be treated as a noun in apposition.

Notes. Almost all specimens of *C. pleiozona* possess a distinct dark vertical bar on the caudal peduncle, which is very rarely seen in *C. monoculus,* and *C. kelberi*. Out of 22 specimens of *C. pleiozona*, the fourth bar is missing only in the 109 mm specimen (NRM 19131) and one adult specimen (INPA 24069) from Lago Fortaleza. Three other specimens from Lago Fortaleza (INPA 24074) however, possess the fourth bar. There are no morphometric differences between *C. monoculus, C. pleiozona*, and *C. kelberi*.

We are unaware of preserved specimens of the species of *Cichla* introduced into the Rio Chagres drainage in Panamá, and reported by Zaret & Paine (1973), but photographs in Zaret (1980), and posted on websites by recreational fishermen consistently show four dark vertical bars (bars 1-4), and the Chagres species may thus be *C. pleiozona*. According to Zaret & Paine (1973) the introduced stock was brought from rearing tanks in Buga, Colombia, in 1965. Buga is located in the Cauca Valley, which has no natural occurrence

of *Cichla*, and the stock must have originated elsewhere.

Cichla mirianae, new species
(Figs. 37-43)

Holotype. MZUSP 92399, adult female, 236 mm SL; Brazil: Mato Grosso: Rio Arinos, município Porto dos Gauchos, forest pool; 19 Aug 1984, M. Goulding et al.

Paratypes. 22 specimens, 64.2-520 mm SL. **Brazil: Rio Tapajós drainage:** MZUSP 33095, 4, 230-310 mm SL (1 measured, 276 mm SL); Mato Grosso: Rio Arinos, mun. Porto dos Gauchos, forest pool; 19 Aug 1984, M. Goulding et al. – MZUSP 50616, 3, 315- ca 520 mm SL; Pará/Mato Grosso: Rio Teles Pires; Jul 1973, Instituto de Pesca. – NRM 46003, 2, 207-303 mm SL, NRM 50264, 1, 90.7 mm SL; Mato Grosso: Rio Juruena at ferry crossing, 60 km E of Juína; 14 Oct 1989, S. O. Kullander et al. – USNM 199192, 1, 96.3 mm SL; Mato Grosso: upper Rio Juruena; 27 Aug 1962, H. Schultz. – USNM 199230, 2, 81.3- ca 83.8 mm SL; Mato Grosso: upper Rio Juruena; 1962, H. Schultz. – USNM 199231, 1, 152 mm SL; Mato Grosso: upper Rio Juruena; 8 Jul 1962, H. Schultz. **Rio Xingu drainage: Mato Grosso:** BMNH 1985.6.20:1106, 1, 235 mm SL; Corrego do Gato; Apr 1986, R. H. Lowe-McConnell. [Rio Suiá Missu, May 1968 fide Lowe-McConnell, in litt.] – MZUSP 33101, 3 (2 measured 175-182 mm SL); confluence of Rio Culuene and Rio Sete de Setembro, canal; 23 Aug 1984, M. Goulding et al. – NRM 12007, 5, 64.2-84.1 mm SL; tributary to Rio Suiá-Missu between São José do Xingu and Alô Brasil, close to and north of Liquilandia, collected from nest, raised in aquarium; 21 Jul 1988, U. Werner et al. – USNM 235641, 1, 218 mm SL; Rio Batovi [Tamitatoala], small tributary and shallow lake; Aug-Sep 1964, H. Schultz. – USNM 235642, 1, 196 mm SL; Rio Batovi [Tamitatoala]; Aug-Sep 1964, H. Schultz.

Diagnosis. Uniquely distinguished by colour pattern, which includes dark lateral band along side in young, and three blackish ocellated blotches along middle of side from at least 90 mm SL; adults retaining portions of lateral band as black irregular stripes connecting ocellar blotches and continuing on caudal peduncle. Similar only to *C. orinocensis* in possession of three lateral ocelli; different from *C. orinocensis* in possession of horizontal band (vs. absent in *C. orinocensis*). Three indistinct vertical bars in young and adults vs. five or more vertical bars in *C. intermedia*, *C. nigromaculata*, and *C. piquiti*. Lateral scales 72-80. Lateral line discontinuous (vs. continuous in *C. intermedia*, *C. ocellaris*, *C. temensis*, and *C. thyrous*).

Description. Refer to Figs. 37-43 for general shape and colour pattern, Table 18 for morphometrics, and Tables 2-10 for meristics.

Large adults moderately deep (depth 27.1-32.8 % SL, N = 7, 207-315 mm SL). Predorsal contour smoothly arched, nuchal protuberance minute to small in three large males 303, 430 and 520 mm SL. Maxilla reaching to slightly behind orbital margin. Lower jaw prognathous, articulation

Table 18. Morphometry of *Cichla mirianae*. Measurements are in percent of SL, except SL (in mm). Linear regression parameters calculated from original measurements in mm. HT, holotype (MZUSP 92399).

	N	min	max	mean	SD	HT	a	b	r
SL (mm)	14	81.3	315.0	197.3		236.0			
Head length	14	31.6	35.8	33.4	1.23	31.8	4.158	0.309	0.998
Snout length	14	10.9	12.7	12.0	0.57	12.1	–1.318	0.128	0.995
Head depth	14	22.5	25.9	24.1	0.91	22.5	–0.999	0.246	0.993
Body depth	14	26.9	32.8	29.7	1.92	27.1	–4.511	0.325	0.992
Orbit diameter	14	6.3	10.8	8.3	1.30	7.7	3.977	0.059	0.959
Interorbital width	14	7.1	8.9	8.0	0.50	7.5	–0.787	0.085	0.992
Pectoral fin length	13	20.8	23.9	22.5	0.85	21.4	0.151	0.224	0.994
Upper jaw length	14	14.5	16.4	15.5	0.51	14.8	0.271	0.154	0.996
Lower jaw length	14	17.9	21.4	19.4	0.85	18.1	1.874	0.184	0.992
Caudal peduncle depth	14	10.6	12.2	11.3	0.49	10.9	–1.345	0.121	0.995
Caudal peduncle length	14	14.6	19.7	17.1	1.29	16.5	2.918	0.154	0.973
Dorsal spine length	14	10.2	15.5	12.9	1.48	12.1	5.918	0.094	0.970

Fig. 37. *Cichla mirianae*, paratype, NRM 12007, 78.7 mm SL; Brazil: Mato Grosso: tributary to Rio Suiá-Missu between São José do Xingu and Alô Brasil.

Fig. 38. *Cichla mirianae*, paratype, USNM 199192, 96.3 mm SL; Brazil: Mato Grosso: upper Rio Juruena.

Fig. 39. *Cichla mirianae*, paratype, USNM 199231, 152 mm SL; Brazil: Mato Grosso: upper Rio Juruena.

below middle or posterior margin of orbit. Lateral line discontinuous; continuous on right side in one specimen only (NRM 50264).

Dorsal spines 3-6 longest; soft dorsal fin rounded, not reaching to caudal fin base or slightly shorter. Soft anal fin rounded, reaching beyond middle of caudal peduncle. Caudal fin truncate or subtruncate. Pectoral fin pointed,

reaching halfway to middle of anal fin base. Pelvic fin pointed, first ray longest, reaching halfway to anal fin origin.

Dorsal fin naked in all specimens to 152 mm SL, in larger specimens sparsely scaled on proximal ⅓ of soft portion, with single row of scales along anterior and posterior margin of rays. Anal fin densely scaled anteriorly in adults, on proximal half or less in specimens up to 152 mm SL. Caudal fin densely scaled, in adults scales covering almost all of fin except posterior margin and middle interradial membrane. Pelvic fin naked in young, progressively densely scaled on both sides along anterior margin. Pectoral fin scaled basally in specimens over 200 mm SL.

Colouration in preservative. Smallest specimens, about 60-80 mm SL (Fig. 37) with dark brown to blackish lateral band from cleithrum to caudal fin base. White, partly contiguous spots bordering lateral band dorsally and ventrally; additional one or two rows of indistinct light spots on dorsum dorsal to lateral line. Short, narrow, dark brown vertical bars 1-3 (in one specimen indicated bar 4) from about lateral line, fading on abdominal side; expanded into oval or round blotch where crossing lateral band. Dark brown blotch immediately posterior to orbit and dark brown horizontal stripe dorsally on opercle. Dorsal fin dusky, both spinous and soft portion with large white or hyaline spots. Anal fin whitish anteriorly, colourless posteriorly. Black caudal blotch, small, rounded, contiguous with lateral band, and extended by blackish stripe along ⅘ of middle of caudal fin; blotch midbasal in 64.2 mm SL specimen, slightly superior in remainder. Rest of caudal fin grey with large white spots on dorsal half. Pelvic fin whitish.

In specimens about 90 mm SL and larger (Figs. 38-39) lateral band much less distinct than vertical bars/blotches and gradually transformed to narrow stripe. Dorsum, nape and snout brown with yellow spots on top of snout, nape and in two rows on dorsum close to dorsal fin. Side of head light brownish, ventrally yellowish, large yellow spots in brownish area. A dark brown spot ventrally on opercle. Dark horizontal stripe from snout to orbit, from orbit horizontally across opercle, brownish and distinct. Stripe continued, indistinct, brownish, along middle of side, immediately above level of lower lateral line tube row, lighter anteriorly, to caudal fin base. Stripe crossed by three short vertical bars confined to middle third of side, containing an approximately round dark brown blotch at intersection. Large light spots in a row dorsally and ventrally along horizontal band; an irregular row of large light spots on dorsal side, another along abdominal side. Dorsal fin brown, spinous portion with two, soft portion with three rows of large hyaline spots. Anal fin hyaline, pelvic fin smoky on both sides.

Large adult male, 330 mm SL (Fig. 40) with dark brown back, nape and snout dorsally, lighter brown side, chest yellowish white, abdomen dirty white, ventral aspect of caudal peduncle duskied. Side of head brown. Lower jaw grey, chest and throat dusky on white ground (unique for this specimen). Row of irregularly arranged black spot in horizontal succession from orbit to posterior margin of opercle, scattered black spots on opercle. Extrascapular series marked by a black oblique stripe. Spinous dorsal fin brown, soft portion brown with seven cross-rows of lighter spots and grey distal margin. Anal fin brown, darker distally. Caudal fin brown with about 10 vertical rows of lighter spots on dorsal lobe. Pelvic fin dark brown on posterior side, grey on anterior side. Pectoral fin greyish.

Indistinct dark vertical bars (bars 2-3) containing distinct irregular black blotches at level slightly above upper lateral line. Anteriorly on side, above pectoral fin, a large black blotch. Side close to major black blotches partially, especially anterior blotch, slightly lighter than rest of side. Caudad from cleithrum an irregular row of irregularly shaped black spots connecting major black blotches, continued beyond posterior blotch as gradually narrower band of blotches to about middle of caudal peduncle. Numerous irregularly arranged and irregularly shaped black blotches on lower side associated with bars 2 and 3, on pectoral fin base and under adpressed pectoral fin. Caudal blotch slightly elongate, margined by narrow silvery circle; on both sides of fin also minute dark spot dorsally on ventral lobe, margined by light spots. Other large males similarly dark with dark brown to black spinous dorsal fin and black spots on anterior abdominal side. Lower jaw, throat and branchiostegal membrane whitish or yellowish without blackish pigmentation.

Breeding female, 207 mm SL (Fig. 41) similar to male, but anterior two blotches brown, posterior blotch black and most prominent. Five series of light spots in dorsal fin. Only some indistinct brownish markings on abdominal side. No light

Fig. 40. *Cichla mirianae*, paratype, NRM 46003, adult male, 303 mm SL; Brazil: Mato Grosso: Rio Juruena at ferry crossing, 60 km E of Juína (right side, reversed).

Fig. 41. *Cichla mirianae*, paratype, NRM 46003, adult female, 207 mm SL; Brazil: Mato Grosso: Rio Juruena at ferry crossing, 60 km E of Juína.

spots on head, flank or dorsum. Probable female 152 mm SL retains white spots on nape, dorsum and side. Black spots on gill cover. Lateral band indistinct, faded on posterior part of caudal peduncle, and in transition to rows of dark spots of larger specimens. Female 315 mm SL similar, with small light spots scattered on side and densely on side of head, but only limited faint brownish markings representing the horizontal band.

Holotype, 236 mm SL (MZUSP 92399, Fig. 42), light brown on dorsum, with small light spots on dorsal side. Spinous dorsal fin brownish with about three rows of light spots on spinous portion, five rows on soft portion, Anterior two lateral blotches dark brown, posterior blotch black, connected by smaller irregular dark brown blotches in narrow band continued short distance posterior to posterior black blotch; all dark markings margined with dull whitish or silvery spots. Otherwise similar to 207 mm SL female.

Live colouration. Male, NRM 46003, freshly captured, olivaceous to yellowish on lower part of head and lower flanks.

Geographical distribution. Known from the upper Rio Tapajós drainage, in the Juruena and Teles Pires rivers, and from the middle and upper Rio Xingu drainage, in the Fresco, Batovi, Culuene and Suiá-Missu rivers (Fig. 9).

Lowe-McConnell (1991), reported *Cichla* 'xingu' as abundant in the Rio Suiá-Missu, and present in Suiá-Missu lakes, and observed in the Córrego do Gato (also a tributary of the Rio Suiá-Missu). The only specimen preserved, however, comes from the Córrego do Gato. Other records

Fig. 42. *Cichla mirianae,* holotype, MZUSP 33095, adult female, 236 mm SL; Brazil: Mato Grosso: Rio Arinos, município Porto dos Gauchos.

Fig. 43. *Cichla mirianae,* paratype, USNM 235641, adult female, 218 mm SL; Brazil: Mato Grosso: Rio Batovi.

are from nearby, at the confluence of the Culuene and Sete de Setembro rivers, and without precise locality in the Rio Batovi (shown as Rio Tamitatoala on current maps). The Córrego do Gato is also the type locality of *Crenicichla rosemariae* (Kullander, 1997).

Etymology. Named for Mirian Leal-Carvalho, who participated in the collection of part of the type series.

Notes. Small specimens of *C. mirianae* display an indistinct continuous lateral band from snout to caudal peduncle (Fig. 37), and retain this band as adults displaying as irregular blackish blotches arranged in a narrow band connecting the three lateral ocellar blotches and continuing onto the caudal peduncle. This development of the colour pattern is similar to that of *C. intermedia*, but in that species, the juvenile lateral band is wider and more prominent, and whitish spots covering body and head of *C. mirianae* are absent. *Cichla intermedia* lacks the prominent lateral ocelli of *C. mirianae* and has about 6 narrow vertical bars across the side. Adult *C. mirianae* are similar to *C. orinocensis* in possession of three prominent ocellated blotches along the side, but juvenile *C. orinocensis* do not possess a continuous horizontal band along the side.

The *Cichla* material from the upper Rio Tapajós and upper Rio Xingu drainages are referred to the same species. There are no morphometric or meristic differences between the two geographical samples. Whereas all specimens from the Rio Tapajós drainage display prominent ocelli on the side from small sizes, the lateral blotches are less prominent in Xingu specimens, and also large specimens possess distinct white

spots on the head (Fig. 43). Colour slides of two adult *Cichla* specimens made by Harald Schultz and labeled *Cichla ocellaris*, Alto Xingu, Soojah-Karaja Ind. [Suiá-Carajá indians], November 1960, show a colour pattern very similar to that of Tapajós specimens, with three distinct ocellar blotches mediated by stripes of small black blotches. Among Schultz's slides the same locality and date is given on a colour slide of *Crenicichla rosemariae*, so far only known from the Rio Suiá-Missu drainage, confirming at least that Schultz photographed fishes in the Suiá-Missu area in 1960. A popular article (Schultz, 1962) describing Suiá fishing in the Suiá-Missu, probably near Diauarum, mentions a "large *Crenicichla* species with olive-green body and many rows of dark-red dots and a dorsal fin which was attractively edged with red", corresponding to the slide of *C. rosemariae*, and *Cichla ocellaris* is mentioned as present. Since all adult Xingu specimens at hand are females, except one discoloured young male (MZUSP 33101, 175 mm SL), and none of them in breeding condition, we suggest that the differences in colour pattern reflect absence of preserved breeding adults among the Xingu specimens.

Cichla melaniae, new species
(Figs. 44-48)

Holotype. MZUSP 92400, adult female, 230 mm SL; Brazil: Pará: Rio Xingu, Cachoeira do Espelho (3°48'S 52°32'W); 23-26 Oct 1986, P. E. Vanzolini.

Paratypes. Six specimens, 40.6-290 mm SL. **Brazil: Pará: Rio Xingu drainage:** MZUSP 36878, 2, 124.7- ca 290 mm + 2, 40.6-44.3 mm SL; Cachoeira do Espelho; 23-26 Oct 1986, P. E. Vanzolini. – MZUSP 35791, 1, 275 mm; mun. São Felix do Xingu, Gorotire, Rio Fresco; Aug 1983, M. Petrere. – NRM 45594, 1, 130.9 mm; Balneário do Pedral, ca 8 km S of Altamira; 25 Sep 1988, R. Stawikowski et al.

Diagnosis. Uniquely distinguished by narrow vertical bars 1-3, and numerous minute white spots scattered over flanks, including many ocellated spots. Bars 1a and 2a commonly present, narrow, indistinct. Complete lateral band present in juveniles. Lateral line discontinuous. Similar to *C. mirianae*, but light spots absent from side of head (vs. present or absent), large midlateral ocelli absent from side (vs. present), and E1 scales 78-85 (vs. 72-80).

Description. Refer to Figs. 44-48 for general shape and colour pattern, Table 19 for morphometrics, and Tables 2-10 for meristics.

Large adults moderately deep (depth 30.6-32.6 % SL, N = 2, 230-275 mm). Predorsal contour smoothly arched. Nuchal protuberance absent from specimens examined (young or females); present in large photographed specimens (Fig. 48). Maxilla reaching to vertical from anterior margin or middle of orbit. Lower jaw prognathous, articulation below middle or posterior margin of orbit. Lateral line bilaterally discontinuous in all specimens.

Dorsal spines 3-6 longest; soft dorsal fin rounded, not reaching to caudal fin. Soft anal fin rounded, reaching beyond middle of caudal peduncle. Caudal fin truncate or subtruncate, upper corner angled, lower corner rounded. Pectoral fin pointed, reaching halfway to soft anal fin origin. Pelvic fin with rounded tip, first ray longest, reaching about halfway to middle of anal fin base.

Soft dorsal fin scaled basally in 131 mm SL specimen, a few interradial scales only in 125 mm SL specimen; in adults with two rows of scales immediately posterior to each ray except posteriorly. Anal fin densely scaled anteriorly. Caudal fin densely scaled, in adults scales covering almost all of fin except posterior margin and middle interradial membrane. Pectoral fin scaled basally in specimens over 200 mm. Pelvic fin scaled on anterior lateral face in 125 and 131 mm SL specimens, in larger specimens progressively densely scaled on both sides along anterior margin.

Two juveniles from the type locality, 40.6-44.3 mm SL, terete. Fins, except caudal fin basally, naked. Caudal fin with slightly concave posterior margin.

Colour pattern in preservative. Juveniles 40-6-44.3 mm SL yellowish white. Dorsum, snout, side of head light brownish. No light spots on head or side. Faint straight band from orbit, horizontal across opercle, continued on side at level just above and including lower lateral line tube series to end of caudal peduncle. Indistinct narrow dark vertical bars (bars 1-3) from dorsum to horizontal band, bar 1 below anterior half of spinous dorsal fin, bar 2 below posterior spinous dorsal fin, bar 3 below anterior half of soft dorsal fin. Prominent

dark roundish blotch formed at intersection of bars with horizontal band. Indistinct dark stripe from snout tip to orbit. Dorsal fin spinous portion hyaline with indistinct dark band along middle, and greyish outer margin. Soft portion of dorsal fin hyaline with 1-2 indistinct dark horizontal stripes and duskied outer margin. Pectoral, pelvic and anal fins hyaline. Caudal fin duskied, but yellowish at base next to caudal base blotch. Caudal base blotch black, lanceolate, from middle of caudal fin base, gradually narrower to end of caudal fin.

Young 124.7-130.9 mm SL (Fig. 44) with brown dorsum, side pale grey brown. Ventral aspects of head, abdomen and caudal peduncle whitish. Distinct blackish band from snout tip to orbit, from orbit to margin of gill cover, continued along side to caudal peduncle end above lower lateral line, more indistinct in 130.9 mm SL specimen (Fig. 44) in which only faint brownish trace anteriorly on side. Brownish to blackish narrow vertical bars 1-3, from close to dorsal fin base ventrally to close to abdominal margin. Whitish spots in horizontal row along dorsal and ventral margin of horizontal band on side; in 130.9 mm SL specimen (Fig. 44) scattered white or silvery spots over side. Numerous irregularly arranged small whitish spots present on nape and dorsum. White spots absent from snout and side of head. Dark spot at ventral tip of opercle absent. Spinous dorsal fin with three rows of light spots; soft portion with four large white spots basally and two rows of partially confluent white spots distally, distal margin light. Anal fin dusky whitish to greyish. Caudal fin with black blotch basally and ventrally in dorsal lobe, posterodorsal ¼ margined with light band and one or two light spots anteriorly; dorsal lobe with about four irregular white vertical bars or rows of white spots posterior to caudal ocellus; ventral lobe grey or pale brownish. Pelvic fin near whitish.

Adult female 290 mm SL (Fig. 45) with brownish dorsum, nape, and snout. Side and side of head paler brown. Abdomen, chest, ventral side of head and caudal peduncle yellowish white. Three straight, brown vertical bars (1-3) from dorsum to level of ventral margin of caudal peduncle. Bar 1 below anterior portion of spinous dorsal fin, bar 2 below posterior portion of spinous dorsal fin, bar 3 below posterior part of soft dorsal fin. Posterior to orbit and on opercle scattered small dark brown spots with whitish margin; similar spots on middle of anterior side, caudad to posterior vertical bar, mixed with white spots which also occur on dorsal side and on caudal peduncle. Light spots absent from head. Spinous dorsal fin grey with about three horizontal rows of indistinct light spots. Soft dorsal fin light brown with dense, irregularly arranged rows of light oblong spots, each covering two interradial membranes and one ray. Anal fin light grey. Caudal fin with black blotch ventrally at base of dorsal lobe, ocellated with silvery, almost complete ring. Dorsal lobe with about 7 rows of yellowish spots, and additional spots more irregular dorsally. Ventral lobe of caudal fin brownish-greyish. Pelvic fin greyish brown laterally, variegated with grey medially.

Holotype, female 230 mm SL (Fig. 46), similar, but black ocellated spots absent; white spots scat-

Table 19. Morphometry of *Cichla melaniae*. Measurements are in percent of SL, except SL (in mm). Linear regression parameters calculated from original measurements in mm. HT, holotype (MZUSP 92400).

	N	min	max	mean	SD	HT	a	b	r
SL (mm)	4	124.7	275.0	190.2		230.0			
Head length	4	32.5	33.0	32.7	0.18	33.0	0.011	0.327	1.000
Snout length	4	11.5	13.0	12.1	0.75	13.0	–2.835	0.138	0.998
Head depth	4	21.2	24.1	22.6	1.41	23.5	–6.352	0.264	1.000
Body depth	4	27.0	32.5	29.7	2.37	30.6	–10.501	0.359	0.998
Orbit diameter	4	7.2	8.8	8.0	0.86	7.3	3.737	0.058	0.999
Interorbital width	4	7.1	8.4	7.7	0.57	8.1	–2.559	0.093	1.000
Pectoral fin length	4	21.3	23.4	22.3	0.89	22.0	–3.143	0.241	0.997
Upper jaw length	4	14.3	15.8	14.9	0.76	15.2	–3.505	0.170	1.000
Lower jaw length	4	18.1	19.5	18.8	0.56	18.9	–2.344	0.202	0.999
Caudal peduncle depth	4	11.2	12.4	11.8	0.50	12.0	–2.160	0.131	1.000
Caudal peduncle length	4	17.4	18.4	17.7	0.48	17.6	1.045	0.171	0.999
Dorsal spine length	3	11.9	13.6	12.9	0.88	13.6	3.091	0.113	0.979

Fig. 44. *Cichla melaniae*, paratype, NRM 45594, 130.9 mm SL; Brazil: Pará: Balneário do Pedral, ca 8 km S of Altamira.

Fig. 45. *Cichla melaniae,* paratype, MZUSP 36878, adult female, 290 mm SL; Brazil: Pará: Rio Xingu, Cachoeira do Espelho.

Fig. 46. *Cichla melaniae,* holotype, MZUSP 92400, adult female, 230 mm SL; Brazil: Pará: Rio Xingu, Cachoeira do Espelho.

Fig. 47. *Cichla melaniae,* not preserved, photographed alive. Brazil: Pará: Rio Xingu upstream of Altamira. Photograph by U. Werner.

Fig. 48. *Cichla melaniae,* large adults, not preserved, photographed fresh. Brazil: Pará: Rio Xingu, Balneário do Pedral, 8 km S Altamira. Photograph by R. Stawikowski.

tered over entire side and dorsum. Pectoral fin base dark. Possible male, 275 mm SL (MZUSP 35971), similar to adult females, but less numerous ocellated spots on side.

Live colouration. Young specimen from near São Felix do Xingu, photographed alive just after capture and estimated to have been about 70 mm SL, dull silvery, white abdominally, with a well demarcated blackish stripe from snout tip to

caudal fin base, blackish blotch at caudal fin base, and narrow greyish vertical bars 1-3. Light spots visible on dorsum.

In young specimen photographed alive near Altair (Fig. 47), estimated to be about 150 mm SL, horizontal band absent, bars 1-3 distinct, crossing side from dorsum to below level of pectoral fin base, also one or two very narrow dark vertical markings between principal bars. Dorsum and middle side with about five irregular rows of yellowish spots.

Large adult, estimated length 300 mm SL, photographed alive in São Felix do Xingu (Stawikowski & Werner, 2004: 39, upper photo) overall blue green with yellow branchiostegal membrane. Colour pattern obscured by reflections, but obviously including narrow vertical bars and small light spots on middle of side and caudal peduncle.

Two adult market specimens (Fig. 48) photographed at Balneário do Pedral display small nuchal protuberances, and may be in breeding colour. Side yellowish, abdomen and underside of head white. Black vertical bars prominent, from dorsum to about level of pectoral fin base. Numerous minute, light-margined black spots scattered over side; similar small spots also on side of head but few and much smaller. Indications of a medial bar 1a in one specimen and bar 2a in one specimen. Caudal ocellus ringed with gold.

Geographical distribution. Only three localities in the lower Rio Xingu drainage are verified by preserved material (Fig. 9). The Balneário do Pedral is located on the Rio Xingu about 8 km from Altamira. The type locality, Cachoeira do Espelho is located 13 km south of Altamira. The third locality, Gorotire, is located on the lower course of the Rio Fresco. At Balneário do Pedral, specimens were collected in shallow water, pH 6.5, less than 1 dGH, and temperature 30-32 °C, in strong current among lava rocks (Stawikowski & Werner, 2004: 40).

Etymology. Named for Melanie L. J. Stiassny, Curator of Fishes in the American Museum of Natural History, in recognition of her significant contribution to cichlid systematics.

Notes. *Cichla melaniae* occurs in the Xingu river drainage downstream from localities of *C. mirianae*. Because both species are known only from few localities and few specimens from each locality it may, however, be premature to conclude that they are allopatric.

The two species differ in the colour pattern of young and adults. No juveniles are known of *C. mirianae*, but specimens about 100 mm are known from both species. At this size, *C. mirianae* displays distinct lateral ocelli, whereas *C. melaniae* displays only narrow vertical bars. This colour difference persists in larger specimens, and *C. melaniae* also displays a pattern of minute black and white spots on the middle side as adult commonly with the black spots margined with white, unlike *C. mirianae* which never shows minute black spots on the side except for those contained in the irregular lateral band, which in turn is absent (but cf. below) from *C. melaniae*.

Photographs of large specimens of *Cichla* in the aquarium trade said to come from the Rio Xingu, exemplified by Stawikowski & Werner (2004: 39, lower photo), depart in colour pattern from that of preserved specimens and photographs of fresh caught specimens by displaying a narrow, irregular black horizontal band along the side, margined with white, only faint greyish vertical bars, and one or two vertical bars of same colour between the principal bars.

Cichla piquiti, new species
(Figs. 49-54)

Holotype. MZUSP 40296, young male, 219 mm SL; Brazil: Pará: Rio Itacaiúnas at Caldeirão; Apr-May 1983, M. Goulding.

Paratypes. 56 specimens, ca. 20-430 mm SL. **Brazil: Rio Araguaia drainage:** MZUSP 50240, 4, 184-249 mm SL; Mato Grosso: Rio das Mortes; 1950, Expedição Butantan. – MZUSP 50242, 3, 212-214 mm SL; Goiás: Lago Rico, near Cocalinho; Mar 1976, EMGOPA. **Rio Tocantins drainage:** INPA 24063, 2, 207-220 mm SL; Pará: Rio Tocantins, Itupiranga; Nov. 1980, Equipe de Ictiologia do INPA. – MZUSP 40397, 3, 127.9- ca 143 mm SL; Goiás: mun Flores de Goiás, Fazenda Fortaleza, Rio Macacos, tributary to Rio Macaquinhos; 10 Sep 1988, J. C. de Oliveira et al. – MZUSP 40926, 1, 298 mm SL, 2, ca 43- ca 68 mm SL; Goiás: mun Flores de Goiás, Fazenda Olho d'Agua, Poço do Gandaia, marginal lake of Rio Paranã; 21 Jan 1989, J. C. de Oliveira et al. – MZUSP 50256, 4, 97.1-126.3 mm SL; Pará: lagoa at Jatobal; 16 Sep 1970, EPA. – NRM 12711, 1, 146.6 mm SL; Pará: harbour

in Marabá, river bank; 18 Sep 1990, R. Stawikowski et al. **Rio Itacaiúnas drainage: Pará:** MZUSP 33140, 5, to ca 430 mm SL, MZUSP 40296, 1, 218.8 mm SL, NRM 12878, 4, 196.6-233 mm SL; Caldeirão; Apr-May 1983, M. Goulding. – MZUSP 32755, 25, ca 20 mm SL; Rio Itacaiúnas, Caldeirão; 14 Oct 1983, M. Goulding. – MZUSP 33139, 7, 140-190 mm SL; Caldeirão, pedral; Nov 1983, M. Goulding. – MZUSP 33141, 3, 180-350 mm SL; Caldeirão, Igarapé Boa Vista. Nov 1983. M. Goulding. – MZUSP 33142, 1, 103.1 mm SL; Caldeirão, Igarapé Aguas Claras; Nov 1983, M. Goulding. – MZUSP 33143, 1, 65.2 mm SL, MZUSP 33756, 7, 230-250 mm SL; Caldeirão, Cachoeira Carreira Comprida, rocky pool; 14 Oct 1983, M. Goulding.

Non-types (translocations). Brazil: Rio Paraná drainage: MZUSP 38912, 1, 125.0 mm SL; Minas Gerais: Rio Paranaíba, projeto UHE Bocaina; Nov 1987 - Apr 1988, Leme Engenharia S/A. – MZUSP 45118, 5; Minas Gerais: Represa de Embarcação (Rio Paranaíba); no date, no collector. **Rio Paraguai drainage:** MZUSP 36762, 1 adult; Mato Grosso do Sul: Itiquira, dam in Fazenda Santo Antonio do Paraíso; 21 Oct 1980, J. H. B. Medeiros & J. C. de Oliveira. **Paraguay: Rio Paraná drainage:** NRM 50336, 2, 46.3-54.7 mm SL; Alto Paraná: Rio Limoy, Reserva Limoy de Itaipú; 1 Mar 1998, S. O. Kullander et al.

Diagnosis. Uniquely distinguished from other species of *Cichla* by the combination of 83-104 scales in E1 row and adult colour pattern including five wide dark vertical bars below the dorsal fin (bars 1-3, 1a, 2a).

Description. Based on the holotype (219 mm SL) and selected specimens of similar length unless otherwise stated. Refer to Figs. 49-54 for general shape and colour pattern, Table 20 for morphometrics, and Tables 2-10 for meristics.

Adults moderately elongate (depth 26.0-30.7 % SL, N = 12, 202-298 mm SL). Predorsal contour smoothly arched; largest specimen examined, 430 mm SL, with incipient nuchal protuberance. Maxilla extending to below middle of orbit. Lower jaw prognathous, articulation below posterior margin of orbit or slightly posterior. In 21 specimens, lateral line bilaterally discontinuous in 18 specimens, continuous on right side in one, continuous on left side in one, subcontinuous on right side in one.

Dorsal fin rays 4-6 longest; soft dorsal fin rounded, not reaching to caudal fin base. Anal fin rounded, not reaching to caudal fin base. Caudal fin subtruncate or slightly convex, with more angled dorsal corner and rounded lower corner. Pectoral fin pointed, extending halfway to origin or middle of soft anal fin. Pelvic fin subacuminate, with tip formed by rays 1-2, ray 1 longest, extending halfway to anal fin origin or slightly beyond.

Dorsal fin scaled from behind last spine, scales behind each ray, in three rows, posteriorly gradually reduced to one row, last membrane naked; scales also in deeper branches. Anal fin with thick basal and anterior scale cover, posterodistally less densely scaled, only last two membranes naked. Caudal fin extensively scaled in adults, except for posterior margin and middle membranes. Pectoral fin basally with a few small cycloid scales.

Table 20. Morphometry of *Cichla piquiti*. Measurements are in percent of SL, except SL (in mm). Linear regression parameters calculated from original measurements in mm. HT, holotype (MZUSP 40296).

	N	min	max	mean	SD	HT	a	b	r
SL (mm)	20	65.2	298.0	192.6		219.0			
Head length	20	30.6	35.0	31.8	0.96	31.4	3.680	0.297	0.999
Snout length	20	10.3	12.0	11.4	0.44	11.6	–0.755	0.118	0.995
Head depth	20	20.9	23.6	22.0	0.70	22.6	–0.470	0.223	0.994
Body depth	20	26.0	30.7	28.3	1.22	30.3	–2.914	0.299	0.987
Orbit diameter	20	6.7	11.2	7.9	1.09	7.5	4.655	0.052	0.984
Interorbital width	20	6.9	8.1	7.5	0.35	7.8	–0.581	0.078	0.989
Pectoral fin length	18	22.1	25.1	23.2	0.89	25.1	–3.488	0.251	0.989
Upper jaw length	20	14.2	15.6	14.7	0.34	14.9	–0.822	0.151	0.995
Lower jaw length	20	18.2	20.1	18.7	0.47	19.0	0.636	0.183	0.998
Caudal peduncle depth	20	10.0	12.1	11.1	0.68	12.1	–0.178	0.112	0.975
Caudal peduncle length	20	16.0	19.9	17.8	0.93	17.7	0.585	0.174	0.982
Dorsal spine length	20	11.1	13.7	12.5	0.59	11.9	1.579	0.117	0.984

Fig. 49. *Cichla piquiti,* paratype, MZUSP 33143, 65.2 mm SL; Brazil: Pará: Caldeirão, Cachoeira Carreira Comprida (right side, reversed).

Fig. 50. *Cichla piquiti,* NRM 50336, 55.7 mm SL; Paraguay: Alto Paraná: Rio Limoy, Reserva Limoy de Itaipú (right side, reversed).

Fig. 51. *Cichla piquiti,* paratype, NRM 12711, 146.6 mm SL; Brazil: Pará: Marabá (right side, reversed).

Pelvic fin laterally densely scaled on first two membranes, and basally on third; medially densely scaled between spine and first ray and on first soft ray, gradually more reduced squamation proximad on rest of fin.

Juveniles up to about 50 mm SL with naked

Fig. 52. *Cichla piquiti*, paratype, MZUSP 40397, 136.7 mm SL; Brazil: Goiás: Flores de Goiás, Fazenda Fortaleza, Rio Macacos, tributary to Rio Macaquinhos.

Fig. 53. *Cichla piquiti*, holotype, MZUSP 40296, young male, 219 mm SL; Brazil: Pará: Rio Itacaiúnas at Caldeirão (right side, reversed).

Fig. 54. *Cichla piquiti*, adult specimen photographed in aquarium, not preserved. Photograph by U. Werner.

fins and caudal fin margin concave. Anal and caudal fins scaled basally in 65.3 mm specimens.

Colouration in preservative. Juveniles about 20 mm SL yellowish white with blackish lateral band from head to caudal fin. Lateral band including an elongate blotch close behind head and another above anal fin origin, and terminating with caudad acutely tapering black spot on caudal fin base.

In young specimens lateral band distinct and prominent in 56 mm SL specimen (Fig. 49), but in 65 mm SL specimen (Fig. 50) lateral band faint, affected by preservation. Three narrow brown vertical bars extending down from dorsal fin base (two below spinous portion, one below soft portion) to slightly below lateral band, widening and forming blotches where crossing lateral band. Bars 1a and 2a absent or indistinct. Dark preorbital stripe from eye to mouth. Spinous dorsal fin light with darker lappets, soft dorsal fin dusky with a few large light blotches. Caudal spot still integrated with lateral band, not ocellated, succeeded caudally by dark grey stripe.

Specimens 140-150 mm SL from Marabá and Itacaiunas with distinct lateral band, emphasized preorbital stripe and midbasal caudal spot. Marabá specimen (Fig. 51) with ventral parts (underside of head, chest, belly and caudal peduncle) white, contrasting with side which greyish with yellowish tint. Head and dorsum light greyish. Grey halter stripe extending back from mouth, bordered above by white. Wide blackish lateral band slightly widened and intensified where crossing vertical bars and margined above and below by rows of white spots which partly confluent. Dark grey vertical bars 1-3, 1a, and 2a, running from dorsal fin base down to contrasted white ventral area, bars 1, 1a, 2 below spinous dorsal fin, bars 2a, 3 below soft portion of dorsal fin. Bars 1-3 wider and darker than bars 1a and 2a. Only a few, indistinct white spots on dorsum and side. Dorsal fin greyish with two rows of white spots on spinous portion and three rows of white spots on soft portion. Anal fin whitish proximally, shading to greyish distally. Caudal fin grey with large white spots in dorsal lobe. Caudal spot black and nearly completely ocellated. Pelvic fin grey anteriorly on lateral face, otherwise white. In another young specimen, 137 mm SL (Fig. 52), lateral band remaining only as black stripe on caudal peduncle.

From about 150 mm SL three black spots present posterior to orbit, of which one on cheek; one, sometimes doubled, dorsally on opercle; and one, sometimes doubled, dorsally on subopercle; spots may be light ringed in large specimens. Scattered white spots appear on side, and on top and side of head, but disappear gradually again between 200 and 250 mm SL in preserved specimens. Lateral band disappears completely between 150 and 200 mm SL, and vertical bars become dominant lateral markings. Number of rows of light spots in dorsal fin increasing to five. Caudal spot ocellated, ringed with whitish; 5-6 vertical rows of light spots in dorsal lobe of caudal fin.

Holotype, adult male 219 mm SL, not breeding, may represent average size adult colour pattern (Fig. 53). Dorsum and nape brown, gradually lighter ventrally. Underside of head and body including, chest, abdomen, narrow area close to anal fin base and underside of caudal peduncle, white, shading to yellowish. Vertical bars dark brown, bars 1, 1a, 2 from spinous dorsal fin base, bars 2a, 3 from soft dorsal fin base, wider than interspaces proximally, slightly narrower down side, ending just before entering light ventral body colour. Bars gradually slightly paler ventrally, but distinct throughout. Vertical bar absent from caudal peduncle. Dark vertical bar, similar in width and colour to posterior bars, from predorsal midline immediately anterior to dorsal fin to anterior portion of lateral line. Ocellated spots absent from side. Scattered white spots on side few and indistinct. Numerous white spots on nape, cheek and opercular bones. Indistinct narrow blackish stripe from orbit toward mouth along anterodorsal margin of lachrymal, fading anteriorly.

Spinous dorsal fin in holotype dark brown with three rows of large white spots, soft dorsal fin dark brown with five rows of white spots, those in proximal row larger than rest. Anal fin yellowish basally, turning greyish distally. Caudal fin ventral half greyish, dorsal half brownish with six vertical rows of vertically elongate whitish spots. Caudal ocellus including light ring of same size as eye, black center extending between rays D1 and D3, ring between rays V1 and D4. Pelvic fin medially greyish, laterally brownish, lighter posteriorly.

White spots on head and body indistinct in holotype, not at all apparent in similar sized males but more numerous and distinct in female 202 mm

SL from same sample. It is not obvious to what extent respectively sexual dimorphism, ontogenetic change of colour pattern and state of preservation contribute to variation in expression of light spots on head and body.

Specimen 298 mm SL, apparently a breeding female, light greyish with intense contrasting blackish vertical bars without light margins. Black spots on head behind eye prominent; two small black spots on anterior part of caudal peduncle. Caudal spot ringed with brilliant white spots, not seen in any other specimen. Spinous dorsal fin uniformly black.

Largest specimen examined, 430 mm SL, male with small soft nuchal hump, agreeing largely in colour with specimens half its size. Ground colour light brownish, with lighter underside and vertical bars prominent. White spots on side and head absent. Fins immaculate save for caudal ocellus.

Live colouration. Photos are available of transplanted fishes from Brazilian dams, a fresh captured specimen from the Araguaia (Stawikowski & Werner, 2004: 38), as well as various sport fishing magazine photos without locality information and illustrated here by aquarium specimens (Fig. 54). General body colour varies from pale grey (usually) to yellow, with contrasted black bars. Bars 1a and 2a usually slightly narrower or paler than bars 1-3. Light ring around caudal blotch always silvery to white. Very large males (40-50 cm estimated size) with reddish, prominent nuchal protuberance, and white spots absent from fins. Other specimens, estimated size 30-40 cm SL, possibly females, feature small white spots on spinous and soft dorsal fins and upper half of caudal fin as well as on side of head; body side with or without light spots; anal and pelvic fins and lower half of caudal fin yellowish to reddish.

Geographical distribution. Natural occurrences are recorded from the lower (Rio Itacaiunas, Marabá, Itupiranga), and upper Rio Tocantins (Rio Paranã), as well as in the Araguaia drainage (Cocalinho and Rio das Mortes) (Fig. 9).

Cichla piquiti is extensively stocked in reservoirs in the Paraná river drainage, and the States of Minas Gerais and São Paulo. Kelber (1999) lists tucunaré azul from the Itaipu, Porto Primavera, Jupiá, Três Irmãos, Ilha Solteria, São Simão, Jaguara, Estreito, Peixoto, Furnas, Avanhandava, and Promissão dams in the Rio Paraná drainage, the Tres Marias dam in the Rio São Francisco drainage, and the Serra da Mesa dam in the Rio Tocantins drainage, as well as from the Rio Piquiri in the upper Rio Paraguay drainage. The tucunaré azul corresponds to *C. piquiti*, according to photographs provided by D. Kelber. Photos of large adults were made available by D. Kelber from Tres Irmãos (Rio Tietê), collected in 1995, and Itumbiara (Rio Paranaíba). Preserved material is available from Embarcação and Bocaina, also in the Rio Paranaíba drainage.

A specimen of *C. piquiti* from Itiquira on the Rio Piquirí in the Rio Paraguay drainage was sampled already in 1980, although Nascimento et al. (2001) date the first introduction of *Cichla* (presumably *C. piquiti*) into the Piquirí to 1982. Nascimento et al. (2001) surveyed extensively the Piquirí and São Lourenço rivers between 1992 and 1995 but found *Cichla* only in the Rio Piquirí. Marques & Resende (2005) extended the distribution to the Pantanal just north from Corumbá. *Cichla piquiti* was found together with *C. kelberi* in the Rio Limoy (Paraguay) (Figs. 9, 23). Although there are practically no fish collections available from the Rio Paraná in the region of the Itaipu dam before the construction of reservoirs, introduction seems more likely than natural occurrence.

Etymology. The species epithet *piquiti* is a Tupi-Guarani word meaning striped, and is here used as a noun in apposition.

Local names. Recorded as tucunaré by Costi et al. (1977) and as tucunaré azul by Kelber (1999).

Notes. *Cichla piquiti* is known as tucunaré azul among Brazilian recreational fishermen (Kelber, 1999), with reference to an overall light bluish impression of living specimens.

Cichla piquiti bears some resemblance to *C. ocellaris* and *C. nigromaculata* in the presence of five wide vertical bars on the side, but ocellar markings are absent from the side, and the vertical bars reach more ventrally on the side. *Cichla piquiti* can be distinguished from the sympatric *C. kelberi* by the absence of light spots on the anal fin, presence of bars 1a and 2a, absence of abdominal blotches, and absence of occipital bar. It may be confused at small sizes with *C. pinima*, which also occurs in the lower Rio Tocantins, but the two species appear to be only narrowly parapatric (cf. Figs. 23 and 60).

Cichla thyrorus, new species
(Figs. 55-59)

Holotype. INPA 3503, 1, 355 mm SL; Brazil: Pará: Igarapé Caxipacoré; 16 Oct 1985, E. Ferreira & L. R. Py-Daniel.

Paratypes. 27 specimens, 67.2, 183-430 mm SL. **Brazil: Pará: Rio Trombetas drainage:** INPA 2144, 1, 430 mm SL; Rio Cachorro; 19 Oct 1985, E. Ferreira. – INPA 2145, 1, 430 mm SL; Igarapé Caxipacoré; 15 Oct 1985, E. Ferreira. – INPA 3060, 1, 207 mm SL; upstream of Cachoeira Porteira; 25 Nov 1987, E. Ferreira. – INPA 3061, 2, 198-207 mm SL; downstream of Cachoeira Vira-Mundo; 25 Nov 1987, E. Ferreira. – INPA 3063, 2, 240-248 mm SL; Rio Cachorro; 2 Dec 1988, E. Ferreira. – INPA 3499, 1, 67.2 mm SL; Rio Trombetas above Cachoeira Porteira; 15 Apr 1985, E. Ferreira. – INPA 3500, 2, 183-193 mm SL; Igarapé Caxipacoré; 21 Apr 1985, E. Ferreira & M. Jégu. – INPA 3587, 1, 282 mm SL; Rio Trombetas upstream of Cachoeira Porteira; 23 May 1986, E. Ferreira & G. M. Santos. – INPA 3588, 2, 240-295 mm SL; Rio Mapuera, Cachoeira da Égua; 17-19 May 1986, E. Ferreira & G. M. Santos. – INPA 3590, 2, 220-225 mm SL; Igarapé Caxipacoré; 17 Oct 1985, E. Ferreira & L. R. Py-Daniel. – INPA 3591, 2, 213-216 mm SL; Rio Cachorro; 18 Oct 1985, E. Ferreira & L. R. Py-Daniel. – INPA 3593, 1, 405 mm SL; Igarapé Caxipacoré; 15 Oct 1985, E. Ferreira & L. R. Py-Daniel. – INPA 3594, 1, 420 mm SL; downstream of Cachoeira Vira-Mundo; 7 Oct 1985, E. Ferreira. – INPA 24072, 1, 375 mm SL, INPA 24075, 2, 380-395 mm SL, INPA 24078, 3, ca 305-355 mm SL; Igarapé Caxipacoré; 21 Apr 1985, E. Ferreira & M. Jégu. – INPA 24076, 1, 353 mm SL; downstream of Cachoeira Quebra-Pote; 9 Oct 1986, E. Ferreira & L. R. Py-Daniel. – NRM 13503, 1, 365 mm SL; Igarapé Caxipacoré; 16 Oct 1985, E. Ferreira & L. R. Py-Daniel.

Diagnosis. Most similar to *C. jariina*, *C. pinima*, *C. temensis*, and *C. vazzoleri* in presence of rows of distinct light spots along the side, and presence of large ocellated blotches replacing vertical bars in adults. Scales in E1 row 77-90 (vs. 95-114 in *C. vazzoleri*, 100-108 in *C. jariina*, 98-128 in *C. temensis*, and 96-108 *C. intermedia).* Lateral line usually continuous (vs. discontinuous in *C. melaniae*, and *C. mirianae*, usually discontinuous in *C. pinima*, *C. piquiti*, and *C. vazzoleri*).

Vertical bars 1-3 complete in subadults, expressed as vertical row of ocellated blotches in adults (three in bars 1 and 2, two in bar 3, latter including small blotch close to dorsal fin base (vs. typically vertical bars represented by ocellated blotch close to dorsal fin, and vertical ocellated marking extending ventrally from middle of side in *C. vazzoleri*, and dorsal blotches in bars 1 and 2 typically absent from *C. pinima*). Dark blotch on anterodorsal process of subopercle usually present in large adults, shared with *C. jariina* and *C. vazzoleri*, vs. absent from *C. pinima* and *C. temensis.*

Description. Refer to Figs. 55-59 for general shape and colour pattern, Table 21 for morphometrics, and Tables 2-10 for meristics.

Moderately elongate, (body depth 27.3-31.7 % SL, N = 14, 230-405 mm SL). Predorsal contour smoothly curved; minor nuchal elevation present in four males 353-395 mm SL. Maxillary tip below anterior margin of orbit or middle of orbit, usually below anterior ⅓-½. Lower jaw slightly prognathous, lower jaw articulation below posterior margin of orbit. Lateral line usually bilaterally continuous, never bilaterally discontinuous; discontinuous or subcontinuous on one side in seven of 17 specimens.

Dorsal fin spines 4-6 longest; soft dorsal and anal fins rounded, reaching to procurrent rays of caudal fin or slightly shorter. Caudal fin truncate or subtruncate, upper corner angled, lower corner rounded. Pectoral fin extending halway to ⅘ distance to vertical from anal fin origin. Pelvic fin acuminate, first and second rays contributing to tip, extending almost as far as pectoral fin.

Dorsal fin scales present from behind first soft ray; thick basal scale layer, on each interradial membrane a few cycloid scales in single row close to ray slightly distal to base and between major ray branches, five last interradial membranes naked. Anal fin densely scaled especially anteriorly, last three membranes naked. Caudal fin densely scaled. Scales usually absent from pectoral fin (present in three of 15). Pelvic fin inside densely scaled along margin, on outside distally on two outer membranes.

Single small specimen available (67.2 mm SL, Fig. 55) elongate; caudal fin emarginate; anal fin scaled basally, caudal fin scaled to beyond middle; lateral line bilaterally continuous; pectoral fin extending halfway to end of anal fin base, pelvic fin halfway to anal fin origin.

Fig. 55. *Cichla thyrorus*, paratype, INPA 3499, 67.2 mm SL; Brazil: Pará: Rio Trombetas above Cachoeira Porteira.

Fig. 56. *Cichla thyrorus*, paratypes, INPA 3591, upper 216 mm SL, lower 213 mm SL; Brazil: Pará: Rio Cachorro.

Colouration in preservative. Small specimen, 67.2 mm SL (Fig. 55), greyish dorsally, whitish ventrally, snout with indicated dark band from side of snout to orbit. Irregular dark stripe from cheek behind orbit to posterior tip of gill cover. Dark band along middle of side, 4-5 scales wide posteriorly and with pigment reaching to scales of lower lateral line but not further ventrally, from close behind head to end of caudal peduncle, contiguous with dark elongately roundish blotch at base of caudal fin. Bars 1-3 present, indistinct, intensified pigmentation where bar 1 and bar 3 cross lateral band.

Young, 180-190 mm SL, with faint vertical bars 1-3 present, lateral band absent. Five horizontal rows of whitish spots, in somewhat more regular rows than in large adults, and not extending onto caudal peduncle, one above and one below lower lateral line scale series, one further ventrally, and two further dorsally. Slightly larger specimens, 213-225 mm SL (Fig. 56) greyish brownish, lower side and ventral aspect whitish. Vertical bars and

horizontal band absent, but slightly darker where ocelli formed in larger specimens. No ocellar markings on body. Five or six irregular rows of whitish spots along side extending caudad onto caudal peduncle; some white spots may also be present on gill cover. Dark stripe from snout to orbit; between orbit and posterior tip of opercle indistinct, irregular dark stripe. Caudal ocellus with black nuclear blotch and two separate light semicircular blotches anteriorly and posteriorly. Dorsal fin dark; spinous dorsal fin with two or three light spots on each interradial membrane; soft dorsal fin with four or five rows of light spots. Caudal fin with four to six transverse rows of yellow spots dorsally, extending onto ventral lobe.

Female, 240 mm SL (Fig. 57) with completely ocellated caudal spot, and spots absent from ventral lobe of caudal fin. Middle ocellus of bar 2 indicated. Large whitish spots present on cheek and gill cover.

Adult male, 355 mm SL (Fig. 58), with nape and forehead dark grey. Head and side light grey, belly and chest yellowish white. Lower part of head and branchiostegal membrane duskied with grey. Markings on head including row of black white-margined spots from eye to opercular tip and scattered spots on cheek and gill cover. Vertical bars absent, instead three vertical rows of irregular ocelli: (1) below dorsal spines 4 and 5, one blotch halfway between dorsal fin and upper lateral line, partly dissolved into four small spots, another blotch below lateral line and third blotch behind and below pectoral axilla; (2) below last two dorsal spines blotch consisting of four small spots, another blotch below lateral line integer, third blotch at level of pectoral fin, faint and vertically narrow; (3) both blotches situated above lateral line, upper close to dorsal fin, near end of soft dorsal fin, consisting of three small spots, lower blotch just above lower lateral line level and integer. Soft dorsal fin brownish with scattered yellowish spots; spinous dorsal fin dark, but pattern damaged. Anal fin greyish brown. Pelvic fin dirty greyish, lighter inwardly. Caudal fin greyish brown, dorsal lobe with many small yellowish spots. Caudal ocellus black, round, ringed with silver, different shape dextrally and sinistrally.

In other large males (Fig. 59) small white spots in about 5 irregular rows on the side present or absent, when present larger and more distinct around ocellar blotches. Dark blotches or groups of blotches on back may be indistinct, and blotches in median series dominant. Yellow spots in soft dorsal and caudal fins increase in number with body size. Number and shape of dark spots on cheek and gill cover variable.

Large female, 310 mm SL, similar to large males but with much lighter, indistinct ocellar blotches, dark spots absent from head, but numerous white spots present in about five horizontal rows along side.

Live colouration. No information available.

Geographical distribution. Rio Trombetas near Cachoeira Porteira, only upstream of the falls (Fig. 9).

Table 21. Morphometry of *Cichla thyrorus*. Measurements are in percent of SL, except SL (in mm). Linear regression parameters calculated from original measurements in mm. HT, holotype (INPA 3503).

	N	min	max	mean	SD	HT	a	b	r
SL (mm)	16	183.0	405.0	286.6		355.0			
Head length	16	31.2	34.0	32.4	0.74	32.1	–5.901	0.346	0.998
Snout length	16	10.8	14.4	12.5	0.90	12.5	–7.589	0.153	0.990
Head depth	16	21.0	25.2	22.8	1.24	23.1	–10.779	0.268	0.996
Body depth	16	25.5	31.7	29.3	2.11	31.6	–16.966	0.356	0.993
Orbit diameter	16	6.1	7.9	7.2	0.44	6.9	3.939	0.057	0.979
Interorbital width	16	7.6	8.9	8.2	0.44	8.9	–3.845	0.096	0.993
Pectoral fin length	16	20.5	25.1	22.7	1.42	24.5	–10.315	0.265	0.988
Upper jaw length	16	13.9	16.6	15.1	0.80	15.1	–7.829	0.181	0.997
Lower jaw length	16	17.7	19.8	18.5	0.62	18.3	–5.120	0.204	0.996
Caudal peduncle depth	16	10.8	12.3	11.4	0.39	11.7	–0.863	0.117	0.991
Caudal peduncle length	16	15.3	18.4	17.0	0.97	16.0	4.406	0.153	0.977
Dorsal spine length	16	10.9	13.3	12.2	0.60	11.7	3.700	0.108	0.982

Fig. 57. *Cichla thyrorus*, paratype, INPA 3588, young female, 240 mm SL; Brazil: Pará: Rio Mapuera: Cachoeira da Égua.

Fig. 58. *Cichla thyrorus*, holotype, INPA 3503, adult male, 355 mm SL; Brazil: Pará: Rio Trombetas drainage: Igarapé Caxipacoré.

Fig. 59. *Cichla thyrorus*, paratype, NRM 13503, adult male, 365 mm SL; Brazil: Pará: Rio Trombetas drainage: Igarapé Caxipacoré.

Etymology. The species epithet *thyrorus* is from the Greek noun thyroros, meaning doorkeeper or porter, in reference to the geographical distribution in the Cachoeira Porteira, the Portuguese word porteira meaning gate or entrance.

Notes. The Rio Trombetas apparently has a distinctive endemic fauna from the Cachoeira Porteira upstream. Kullander & Ferreira (2005) listed seven cichlid species that are known only from that region, and examples from other fish families. They concluded that the lower rapids of the Trombetas may constitute a distribution barrier to some species, but at least three species are rheophilic. The lower rapids certainly are a barrier to upstream dispersal, as lowland Amazonian cichlid species are absent from the Rio Trombetas upstream from the Cachoeira Porteira, but present immediately below, e.g., *Apistogramma pertensis* listed by Kullander & Ferreira (2005). Among species of *Cichla*, this geographical separation is evident in *C. thyrorus* being present upstream and *C. vazzoleri* only in and downstream of the Cachoeira Porteira.

Cichla thyrorus can be distinguished from *C. vazzoleri* by the number of scales in the E1 row, 77-90, vs. 95-110 in *C. vazzoleri*. Most specimens of *C. thyrorus* available are of fairly large size, above 200 mm and many above 300 mm SL, but a lateral horizontal stripe is absent from all specimens 183 mm and larger, and vertical bars are present, and faintly expressed only in the two smallest subadults, 183-193 mm SL. Specimens larger than 300 mm all possess three vertical rows of ocelli, the anterior two rows with three ocelli each, and the posterior row with two ocelli (the ventralmost absent), whereas in *C. vazzoleri* the vertical bars usually form a complete bar down from the middle of the side, leaving an isolated small blotch close to the dorsal fin base. *Cichla jariina* may be the most similar species in colour pattern, uniquely sharing with *C. thyrorus* the subdivision of the two anterior vertical bars into three blotches, but possessing smaller scales (E1 row scales 100-108 vs. 77-90 in *C. thyrorus).*

Cichla jariina, C. pinima, *C. temensis*, *C. thyrorus,* and *C. vazzoleri* are distinguished from remaining species of *Cichla* by two colour characters. In subadults, as the dark lateral band fades away, the marginal light spots become more apparent and are supplemented by one regular row of light spots dorsally and one ventrally. These light spots form a distinctive pattern, most marked in *C. temensis* in which the spots are somewhat elongate whereas in remaining species they are round. Additional short rows of light spots appear anterodorsally on the side and may also occur ventrally. In *C. jariina* and *C. thyrorus* the pattern is less regular than in the other species, but irregularities occur in specimens of all the species concerned. In large adults, apparently representing the breeding colour, and best expressed in males, the vertical bars (bars 1-3) give way to large ocellated blotches which remain entire in *C. temensis*, but further subdivided in the remaining species.

Except for *C. thyrorus,* and shared only with *C. intermedia* and *C. piquiti,* these species have the highest counts of E1 scales in the genus, rarely below 90 scales (Table 2). With the exception of *C. thyrorus,* with modally 14 pectoral fin rays like *C. melaniae, C. mirianae*, *C. piquiti,* and species of the *C. ocellaris* group, the group tends to have more pectoral fin rays, modally 15, than remaining species of *Cichla* (Table 8). In *C. vazzoleri*, 14 is modal, but 15 nearly equally frequent, and also *C. intermedia* has a mode of 15 pectoral fin rays.

Cichla thyrorus is distinguished particularly by its lower scale count (77-90, vs. 100-108 in *C. jariina,* 86-110 (usually more than 90) in *C. pinima,* 98-128 in *C. temensis*, and 95-114 in *C. vazzoleri*), and the colour pattern of adults, with vertical bars modified to rows of blotches, typically three blotches vertically in bars 1 and 2, and two blotches in bar 3. In the other species with blotches in place of bars in adults, viz. *C. jariina*, *C. pinima*, and *C. vazzoleri*, the first species is like *C. thyrorus*, but in *C. pinima* and *C. vazzoleri*, dorsal blotches develop while the ventral part of bars 1 and 2 remains entire, without further subdivision, except that the midlateral portion of bar 1 may be expanded into a sizable blotch.

Cichla temensis differs from the other three species particularly in colour pattern, possessing three complete vertical bars at all sizes, vs. variously modified into blotches, and it also has the highest scale count in the genus, a few specimens recorded with scale counts down to 98, the majority with more than 110 scales (Table 2). Large *C. temensis* retain a complete postorbital stripe, whereas in the other species of *Cichla* the stripe is either absent or replaced by a few scattered black spots.

Cichla jariina, new species
(Figs. 60-63)

Holotype. INPA 3504, adult male, 340 mm SL; Brazil: State of Pará: Rio Jari downstream of Cachoeira Santo Antonio; 15 Jun 1987, E. Ferreira & S. Amadio.

Paratypes. Five specimens, 62.1-205 mm SL. **Brazil: State of Pará: Rio Jari drainage:** INPA 1382, 1, 62.1 mm SL; Rio Jari, Cachoeira Itacara, pool; 25 Jun 1987, M. Jégu & J. Zuanon. – INPA 3505, 1, 114.7 mm SL, NRM 13505, 1, 205 mm SL; Rio Jari, upstream of Cachoeira Santo Antonio, at level of Ilha Carapatinho; 23 Jun 1987, M. Jégu & J. Zuanon. – INPA 24066, 1, 180 mm SL; Rio Jari, downstream of Cachoeira Santo Antonio, 11-15 Jun 1987; E. Ferreira & S. Amadio. – INPA 24067, 1, 195 mm SL; Rio Jari, upstream of Cachoeira Santo Antonio; 20 Jun 1987, M. Jégu & J. Zuanon.

Diagnosis. Most similar to *C. pinima*, *C. temensis*, *C. thyrorus*, and *C. vazzoleri* in presence of distinct rows of light spots along side, and presence of large ocellated blotches replacing vertical bars in adults. Uniquely distinguished by absence or extreme reduction of squamation of dorsal fin. Scales in E1 row 100-108 (vs. 77-90 in *C. thyrorus*). Similar only to *C. pinima* in having ocellated black spot just below soft dorsal fin. Only breeding male known has three blotches ocellated by white dots representing bars 1 and 2, similar to *C. thyrorus* but different from *C. pinima*, *C. temensis*, and *C. vazzoleri* in which bars below upper lateral line typically entire and dorsal ocellar markings frequent only in *C. vazzoleri*. Dorsal fin count modally XV.16, shared only with *C. vazzoleri* (vs. XV. 17 in other species of *Cichla*) and vertebral count modally 18+16=34 (vs. 18+17=35, 18+18=36 or 19+17=36 in other species of *Cichla*).

Description. Refer to Figs. 60-63 for general shape and colour pattern, Table 22 for morphometrics, and Tables 2-10 for meristics.

Adults relatively elongate (depth 25.1-29.4 % SL in four specimens 180-340 mm SL). Nuchal protuberance only indicated in holotype, other specimens with smoothly arched predorsal contour. Maxilla reaching to anterior ⅕ or ⅓ of orbit. Lower jaw prognathous, articulation below posterior ⅕ or middle of orbit. Lateral line continuous (bilaterally in one), anterior and posterior joined beneath anterior half of soft dorsal fin, subcontinuous or discontinuous (bilaterally in one), equal or different on left and right side.

Dorsal spines 3-4, or clearly fourth longest; soft dorsal fin rounded, reaching beyond middle of caudal peduncle but not to caudal fin base. Soft anal fin rounded, reaching beyond middle of caudal peduncle. Ventral lobe of caudal fin damaged in holotype, in other specimens caudal fin subtruncate. Pectoral fin pointed, reaching halfway to middle of anal fin base. Pelvic fin pointed, first ray longest, reaching halfway to anal fin origin.

Dorsal fin naked in all specimens, except 6 scales bilaterally medially on fin between rays 5 and 6 in 205 mm specimen. Pelvic fin densely scaled on both sides along anterior margin. Pectoral fin scaled basally. Anal fin moderately

Table 22. Morphometry of *Cichla jariina*. Measurements are in percent of SL, except SL (in mm). Linear regression parameters calculated from original measurements in mm. HT, holotype (INPA 3504).

	N	min	max	mean	SD	HT	a	b	r
SL (mm)	6	62.1	340.0	182.8		340.0			
Head length	6	31.6	37.2	33.1	2.12	32.3	2.348	0.312	0.999
Snout length	6	10.5	12.5	11.6	0.69	12.5	–1.771	0.127	0.994
Head depth	6	20.7	23.4	21.8	1.28	23.4	–3.510	0.241	0.996
Body depth	6	25.1	29.4	26.6	1.79	29.4	–5.955	0.305	0.995
Orbit diameter	6	6.8	11.9	8.6	1.79	6.8	4.204	0.057	0.999
Interorbital width	6	7.1	8.1	7.5	0.37	8.1	–0.873	0.080	0.994
Pectoral fin length	5	21.5	23.3	22.4	0.80	23.1	–1.402	0.233	0.998
Upper jaw length	6	14.3	15.6	14.9	0.53	15.4	–0.952	0.154	0.998
Lower jaw length	6	17.9	21.1	19.0	1.09	19.0	0.349	0.186	0.998
Caudal peduncle depth	6	9.7	11.8	10.9	0.74	10.5	0.604	0.106	0.994
Caudal peduncle length	6	16.0	20.3	17.7	1.54	16.0	3.304	0.154	0.994
Dorsal spine length	6	12.6	13.1	12.8	0.27	12.6	0.338	0.126	0.999

Fig. 60. *Cichla jariina*, paratype, INPA 1382, 62.1 mm SL; Brazil: Amapá: Rio Jari, Cachoeira Itacara.

Fig. 61. *Cichla jariina*, paratype, INPA 3505, 114.7 mm S; Brazil: Amapá: Rio Jari, upstream of Cachoeira Santo Antonio, at level of Ilha Carapatinho

densely scaled. Caudal fin densely scaled. In smallest specimen, 62.1 mm SL, pectoral and pelvic fins naked, anal fin scaled basally, caudal fin scaled only up to half of fin.

Colouration in preservative. Young 62.1 mm SL (Fig. 60) with dorsum brownish, nape and snout pale brownish, side greyish, ventrally white. Chest silvery. Brown horizontal band from eye across opercle, continued along midaxis of side to caudal fin base, more distinct posteriorly than anteriorly, continuous with caudal base spot, and extended on middle caudal fin rays to end of caudal fin. Horizontal band crossed by three (four on left side, one bar interspersed anterior to third bar of right side) horizontal brownish vertical bars, from slightly above level of upper lateral line to level of lower margin of pectoral fin base. Indistinct light spots marginal to horizontal band dorsally and ventrally. Spinous portion of dorsal fin greyish with light band along middle of fin; soft dorsal fin basally dusky, followed in succession by grey band, hyaline band and wide dusky margin. Anal fin hyaline. Brown spot at base of caudal fin contiguous with horizontal band on side and dark pigment caudally on caudal fin, margined by light elongate blotches dorsally and ventrally. Pelvic fin whitish.

Specimen 114.7 mm SL (Fig. 61) with incipient ocellated blotch below soft dorsal fin. Faint dark band from snout tip to caudal fin, and faint dark vertical bars (bars 1-3) across middle of side. A few light spots on side of head. Large round light spots on side; one horizontal row dorsally and one row ventrally along horizontal band, a few spots along abdominal side and one horizontal row on dorsal side. Two rows of light spots on spinous dorsal fin. Two rows of contiguous yellowish spots crossing soft dorsal fin. Anal fin hyaline. Dark blotch at dorsal caudal fin base

Fig. 62. *Cichla jariina*, paratype, NRM 13505, young female, 205 mm SL; Brazil: Amapá: Rio Jari, upstream of Cachoeira Santo Antonio (right side, reversed).

Fig. 63. *Cichla jariina*, holotype, INPA 3504, adult male, 340 mm SL; Brazil: Amapá: Rio Jari downstream of Cachoeira Santo Antonio.

margined by light curved bars anteriorly and posteriorly; caudal fin crossed by two light vertical bars. Pelvic fin whitish.

Probable male 180 mm SL light brownish, lighter below. Dark band from snout tip to caudal fin base extremely faint; crossed by three obscure vertical bars (bars 1, 2, 3) from dorsum to horizontal level of lower margin of pectoral fin base. Posteriormost bar includes a blackish blotch at the upper end. About four irregular rows of small light spots along middle of side, reduced to two rows on caudal peduncle. Light spots also on head side, but not on nape. Spinous portion of dorsal fin greyish with about two rows of light spots; soft portion greyish with some light spots. Caudal fin with black blotch at base, above midaxis, almost completely encircled with light ring.

Females 195-205 mm SL (Fig. 62) like 180 mm SL specimen, but no horizontal band; caudal ocellus almost complete. Three rows of yellow spots in dorsal fin.

Holotype, adult male 340 mm SL (Fig. 63) with dorsum, snout, nape grey, side pale grey. Underside of head, chest ventrally, belly, anal-fin base and lower margin of caudal peduncle whitish. Small black ocellated spots in row behind orbit and on opercle, dark spot in opercular/subopercular junction. Dark bars 1-3 represented by three vertical rows of black blotches with white or silvery spots marking margins of blotches; along middle of side scattered white spots. Anterior row of black blotches below anterior dorsal spines including small blotch above upper lateral line, large blotch slightly below upper lateral line, and

large blotch under and below pectoral fin base. Middle row of blotches below posterior third of spinous dorsal fin including blotch above upper lateral line, another just below upper lateral line, and third, indistinct, at horizontal level of third blotch in anterior row. Posterior row of blotches includes one most prominent blotch close to soft dorsal fin and on right side faint dark bar across side below it. Spinous dorsal fin hyaline, distally grey. Soft dorsal fin greyish with about six rows of light spots. Anal fin grey. Caudal ocellus round, almost completely ringed with silver. More or less indistinct light spotting in dorsal lobe of caudal fin on greyish ground. Pelvic fin grey marginally on upper surface.

Live colouration. No information available.

Geographical distribution. Known only from the Rio Jari, in the region of Cachoeira Itacari and Cachoeira Santo Antonio (Fig. 9).

Etymology. Named with reference to the type locality, the Rio Jari; an adjective with alternative endings *-inus* and *-inum*.

Notes. *Cichla jariina* is a distinctive species with diagnostic support from colour pattern and extreme meristic values. The adult colour pattern of *C. jariina* is close to that of *C. thyrorus*, from which it can be distinguished by the number of scales in the E1 row (100-108 in *C. jariina* vs. 77-90 in *C. thyrorus*) (Table 2), and similar to that of *C. pinima* in the possession of a distinctive blotch dorsally in bar 3 already in subadults. *Cichla jariina* overlaps with *C. intermedia*, *C. pinima*, *C. piquiti*, *C. temensis*, and *C. vazzoleri* in E1 scale counts (Table 2), and also like those species has relatively many scales in the upper lateral line (56-63) (Table 4), and in the complete lateral line (84-94) (Table 2). The pectoral fin count (mode 15) also agrees with the slightly higher mode in those species, vs. mode 14 in other species of *Cichla* (Table 8).

Although the sample is small, low vertebral (18 + 16 = 34) and dorsal fin counts (XV.16, total 31) appear significant. Of 125 radiographed specimens of *Cichla*, only one specimen of *C. marianae* and one specimen of *C. pinima* have 18 + 16 = 34 vertebrae (Table 9). The modal dorsal fin count, XV.16 is shared only with *C. vazzoleri* in which species XV.17 is almost as frequent (Table 6). Although all remaining species of *Cichla* have modally XV.17, it is only in *C. intermedia*, *C. pinima*, *C. thyrorus*, and *C. vazzoleri* that XV.16 is proportionally significant.

With the exception of a few scales in the the 205 mm specimen in which observed only after careful manipulation under transmitted light, scales appear to be absent from the dorsal fin in *C. jariina*, which is unique for the genus. Development of dorsal fin scales in *Cichla* is relatively late in ontogeny, and additional large specimens are needed to verify the diagnostic value of the relative absence of dorsal fin scales in *C. jariina*. The other fins are scaled to an extent comparable with other species of *Cichla*.

The type series was obtained from both upstream and downstream of the Cachoeira Santo Antonio, which is a major waterfall separating the upper Rio Jari from the Amazon lowland. It would seem impassable at least in low water stands, but obviously forms no barrier to *C. jariina*.

The radiograph of the smallest specimen available, 62.1 mm SL, shows two articulated specimens of ostariophysans curled up in the stomach, apparently swallowed whole.

Cichla pinima, new species
(Figs. 64-73)

Holotype. INPA 691, adult male, 300 mm SL; Brazil: Pará: Rio Curuá-Una, Km 30; 6 Feb 1983, E. J. G. Ferreira.

Paratypes. 400 specimens, 22.6-520 mm SL. **Brazil: Pará: Rio Curuá-Una drainage:** INPA 688, 1, 210 mm SL; Rio Curuá-Una, Km 30; 6 Feb 1983, E. Ferreira. – INPA 689, 1, 310 mm SL; Rio Curuá-Una, Km 80; 7 Nov 1982, E. Ferreira. – MZUSP 50254, 4, 119-214 mm SL; mun. Santarém, Rio Curuá-Una above and below barrage; 6-12 Jul 1979, A. Darwich et al. **Rio Xingu drainage:** MZUSP 33097, 32, to 430 mm SL, NRM 52916, 1, 247 mm SL, NRM 52917, 5, 190-223 mm SL; Belo Monte; Jul-Aug 1983, M. Goulding. – MZUSP 33098, 18 (6 measured, ca 77-120.1 mm SL); Belo Monte; 25 Sep 1983, M. Goulding. – MZUSP 33100, 3; Belo Monte, cachoeira; 26 Sep 1983, M. Goulding. – BMNH 1929.7.30:27, 1, 185.3 mm SL; Rio Xingu; Jul 1928, K. Lako. **Rio Tapajós drainage:** BMNH 1890.2.25:32, 1, 295 mm SL; Tapajós; no date, L. Agassiz. – BMNH 1896.6.29:15-16, 2, 51.3-52.9 mm SL; Santarém; no date, Austen & Cam-

bridge. – BMNH 1902.11.7:15, 1, 197 mm SL; Santarém; Paris Museum. – MZUSP 5731, 1, 68.4 mm SL; Rio Tapajós, Santarém; Feb-Mar 1967, EPA. – MZUSP 8470, 3, 123.6-132.1 mm SL; Alter do Chão; 23 Dec 1967, EPA. – MZUSP 8550, 2, 112.2-121.4 mm SL; Rio Tapajós, Santarém; 26-27 Dec 1967, EPA. – MZUSP 21853, 1, 97.1 mm SL; Cachoeira Lombo de Anta near São Luis; 6 Nov 1970, EPA. – MZUSP 22016, 4, 26.5-151 mm SL; São Luis, rocky pool in river; 8 Nov 1970, EPA. – MZUSP 23729, 4; pool in Rio Tapajós, Barreirinha near São Luiz; 23 Nov 1970, EPA. – MZUSP 25317, 1, 220 mm SL; Ilha Grande, upstream of PARNA camp; 15-31 Jul 1979, J. C. de Oliveira. – MZUSP 25486, 1, 395 mm SL, MZUSP 25487, 1, 520 mm SL; Pará: Rio Tapajós left bank at sede of PARNA; 21-25 Jul 1979, J. C. de Oliveira. – MZUSP 25565, 1, 360 mm SL; Rio Tapajós left bank at Km 64-67 of BR-230; 4-6 Jan 1979, J. C. de Oliveira. – MZUSP 25577, 1, 400 mm SL; Ilha da Montanha, km 163, BR-230; 1-2 Feb 1979, J. C. de Oliveira. – MZUSP 25613, 2, ca 138-195 mm SL; left bank of Rio Tapajós, defronte ao Ramal Saita (igapó), PARNA; 23-26 Jan 1979, J. C. de Oliveira. – MZUSP 33099, 11; Rio Tapajós between Itaituba and São Luiz; Sep-Oct 1983, M. Goulding. – MZUSP 33130, 2; São Luiz upstream of Itaituba; 22 Oct 1983, M. Goulding. – MZUSP 33134, 2; Alter do Chão, beach; 25 Nov 1983, M. Goulding. – MZUSP 33135, 1, 95.3 mm SL; Rio Tapajós between Itaituba and São Luiz; Sep-Oct 1983, M. Goulding. – MZUSP 92408, 2; Rio Tapajós; 1970, EPA. – MZUSP 50250, 47, ca. 20 mm SL; MZUSP 50253, 4, 99.0-151 mm SL; Cachoeira do Maranhãozinho, near São Luis; 6-7 Nov 1970, EPA. – MZUSP 50272, 5, 103.5-156 mm SL; island lake opposite Monte Cristo; 8 Dec 1970, EPA. – MZUSP 50247, 116 juv.; lake on island opposite Monte Cristo; 8 Dec 1970, EPA. – MZUSP 50245, 5, 160-180 mm SL; Ilha Tapaiuna; 26-27 Oct 1970, EPA. – MZUSP 50252, 1, 109.6 mm SL; Rio Tapajós, Barreirinha; Nov 1970, EPA. – NRM 18474, 2, 138.6-140.5 mm; Itaituba, shore or "harbour"; 24 Sep 1992, R. Stawikowski et al. – NRM 18475, 1, 78.9 mm SL; Rio Tapajós, São Luís do Tapajós area, ca 2 km upstream fazenda (ca 5 km downstream Pimentel), backwater pool on right shore; 27 Sep 1992, R. Stawikowski et al. – NRM 18476, 1, 88.4 mm SL; Rio Tapajós, between first and second cachoeira upstream São Luiz do Tapajós, backwater pool and lakes on left shore; 26-30 Sep 1992, R. Stawikowski et al. – NRM 18478, 6, 91.0-147.0 mm SL, NRM 18479, 5, 92.5-140.2 mm SL; Rio Tapajós, Brasilia Legal, gravel shore ("harbour"); 23 Sep 1992, R. Stawikowski et al. – NRM 18549, 1, 43.4 mm SL; Rio Tapajós, Aveiro, sand shore ("harbour"); 22 Sep 1992, R. Stawikowski et al. – NRM 35587, 1, 144.9 mm SL; Rio Tapajós about 5 km upstream of São Luis do Tapajós, small bay; 30 Aug 1995, F. Warzel. **Mixed:** BMNH 1849.11.8:23 + 1853.3.19:57, 2; Rio Cupari and Rio Capim; no date [H.W. Bates.] **Rio Tocantins drainage:** INPA 3595, 1, 210 mm SL; Poço do Paulo; 24 Jun 1980, Equipe de Ictiologia do INPA. – INPA 3475, 2, 185-190 mm SL; Icangui; Nov 1980, Equipe de Ictiologia do INPA. – INPA 3592, 1, 205 mm SL; Tucuruí market; 13 Mar 1982, Equipe de Ictiologia do INPA. – MZUSP 38409, 13 (7 measured: 210-247 mm); Rio Tocantins at Tucuruí; 1987, P. Formagio. – MZUSP 50246, 83 juv.; Rio Tocantins at Baião; 9-10 Sep 1970, EPA. – MZUSP 50249, 2, 56.2-56.7 mm SL; lagoa near Canal do Capitariquara, near Jatobal; 18 Sep 1970, EPA. **Rio Capim drainage: Pará:** BMNH 1849.11.8:24, 1, 171 mm SL; Pará: Rio Capim; no date, [H. W. Bates.] – MZUSP 50267, 1, 247 mm SL; near Caranandéua; 16-17 Aug 1970, EPA. – MZUSP 50244, 2, ca 166-183 mm SL; Rio Capim, Lago Maria Preta; 18 Aug 1970, EPA. – MZUSP 50248, 1, 46.2 mm SL; Lago Maria Preta; 18 Aug 1970, EPA. – MZUSP 92409, 1 juv.; Lago Jururundéua; 19 Aug 1970, EPA. – MZUSP 50270, 1 juv.; Lago Bernardino, near Badajós; 20 Aug 1970, EPA. – NRM 37016, 2, 107.7-127.6 mm SL; Rio Guamá ca 4 km upstream of Ourém; 18 Sep 1988, R. Stawikowski et al. **Rio Amazonas drainage:** BMNH 1926.10.27:414; 1, 280 mm SL; Monte Alegre; no date, C. Ternetz. – MZUSP 3721, 1, 166 mm SL; Lago Arari; no date, no collector., listed in Appendix 1.

Non-types. Brazil: Rio Tapajós drainage: NRM 18480, 3, heads only; Pará: Rio Tapajós, Aveiro, sand shore ("harbour"); 22 Sep 1992, R. Stawikowski et al. – NRM 18481, 3, heads only; Pará: Rio Tapajós, Aveiro, sand shore ("harbour"); 22 Sep 1992, R. Stawikowski et al. **Brazil: Rio Paraguaçu drainage (introduced):** USNM 298108, 3, 65.7-134.2 mm SL. Bahia: Rio Paraguaçu near Iaçu, side channel from main river channel forming pool with current flowing through; 25 Jul 1988, S.L. Jewett et al. **Brazil: drainage unknown:** MZUSP 1796, 2; Maranhão, Boa Vista; 1907, Swanda. – NRM 11306, 1, 73.7 mm SL; Pará: Belém; Received 1868, da Silva Castro. **Origin unkown:** MZUSP 50273, 3, 177-288 mm SL; no locality; no date, Museu Goeldi. [Probably from Museu Goeldi pond culture.]

Cichla cf. *pinima*. **Brazil: Rio Amapá Grande drainage:** MZUSP 33094, 15, to 295 mm SL (5 measured, 135.9-186.3 mm SL); Amapá: Cachoeira Grande, river

Fig. 64. *Cichla pinima*, paratype, NRM 18549, 43.4 mm SL; Brazil: Pará: Rio Tapajós, Aveiro.

Fig. 65. *Cichla pinima*, paratype, NRM 18475, 78.9 mm SL; Brazil: Pará: Rio Tapajós, São Luís do Tapajós area.

Fig. 66. *Cichla pinima*, paratype, NRM 18479, 104.2 mm SL; Brazil: Pará: Rio Tapajós, Brasilia Legal.

channel; Feb 1984, M. Goulding. – MZUSP 33131, 3; Amapá: Cachoeira Grande; no date, M. Goulding. **Rio Araguari drainage:** MNRJ 11615, 1, 307 mm SL; Amapá: lake on property of AMCEL; May 1981, G. W. Nunan et al. – MNRJ 11616, 1, 385 mm SL; Amapá: Fazenda Modelo Aporema; Apr 1981, G. W. Nunan et al. – MNRJ 11617, 1, 207 mm SL; Amapá: Fazenda Modelo Aporema; May 1981, G. W. Nunan et al.

Cichla cf. *pinima/vazzoleri*. **Brazil:** NRM 18477, 2, 110.6-134.8 mm SL; Pará: cachoeira where Rio Aruá joins with Rio Arapiuns, Vila de Cachoeira de Aruá; 4 Oct 1992, R. Stawikowski et al. **Rio Canumã drainage:** MZUSP 7075, 5, 143.4-260 mm SL; Amazonas: Rio Canumã; 28-29 Sep 1967, EPA.

Diagnosis. Most similar to *C. jariina*, *C. temensis*, *C. thyrorus*, and *C. vazzoleri* in possession of four or more horizontal rows of light spots along side in subadults and large females, and prominent

Fig. 67. *Cichla pinima*, paratype, NRM 52917; young female, 217 mm SL; Brazil: Pará: Belo Monte.

Fig. 68. *Cichla pinima*, paratype, NRM 52917; young male, 190 mm SL; Brazil: Pará: Belo Monte.

Fig. 69. *Cichla pinima*, paratype, NRM 52916; adult female, 247 mm SL; Brazil: Pará: Belo Monte.

black, light-margined vertical bars or blotches in adults. Uniquely distinguished by an ocellated dark blotch dorsally in bar 3, which absent in *C. temensis*, absent or present only in the breeding pattern together with other ocellated blotches in *C. thyrorus* and *C. vazzoleri*. Scales in E1 row 86-105, vs. 77-90 in *C. thyrorus*. Lateral line commonly discontinuous, vs. usually continuous in *C. temensis* and *C. thyrorus*. Distinguished from *C. temensis* by less scales in E1 row, 86-105, usually less than 100, vs. 98-128, usually more than 110, and vertical bars of adults blotch-like and bar 1 often appearing as round blotch or divided into 2-3 blotches, instead of straight vertical and

about uniformly wide. Distinguished from *C. vazzoleri* by larger scales (86-105 vs. 95-114), but ranges overlap, and common absence of row of light spots along the abdominal side (vs. persistent in *C. vazzoleri*). Breeding *C. pinima* possess three ocellated bars, which continuous above upper lateral line when extending above it, and isolated blotches on dorsum usually not present (vs. dorsal blotches present or absent in *C. vazzoleri*, and typically three vertical rows of 3, 3, and 2 blotches in *C. jariina* and *C. thyrorus*).

Description. Based on the holotype and selected specimens of similar length unless otherwise stated. Refer to Figs. 64-74 for general shape and colour pattern, Table 23 for morphometrics, and Tables 2-10 for meristics.

Adults relatively elongate (depth 24.9-30.3 % SL, N = 21, 204-310 mm SL). Predorsal contour gently curved. Nuchal hump observed in three specimens, 260, 307 and 430 mm SL. Maxilla extending to below anterior ⅓ or middle of orbit. Lower jaw prognathous, articulation below posterior margin of orbit. Lateral line bilaterally discontinuous in 32, unilaterally discontinuous in 27, bilaterally continuous in 10 of 69 specimens.

Dorsal fin spines 3-4, 4 or 4-5 longest; soft dorsal fin rounded, reaching posterior to middle of caudal peduncle. Soft anal fin rounded, reaching to middle of caudal peduncle. Caudal fin subemarginate or subtruncate with angled dorsal corner and rounded ventral corner. Pectoral fin pointed, extending to halfway to posterior end of anal fin base. Pelvic fin subacuminate, tip formed by rays 1-2, ray 1 longest, extending halfway to first spine or soft ray of anal fin.

Dorsal fin naked in specimens up to about 140 mm SL, smallest specimen with a few scales on dorsal fin anteriorly 147 mm SL; specimens about 200 mm SL with single scale row along posterior margin of anterior and middle rays; from about 250 mm SL extensively scaled with up to three rows of scales anteriorly, reduced to one row posteriorly, and scales present between major fin ray branches. Anal fin scaled basally on anterior rays in specimens 100-150 mm SL, in specimens about 200 mm SL and larger extensively scaled except naked posterodistally. Caudal fin densely scaled in adults, scales absent only from distal half of middle of membranes between rays V2 and D2 and posterior margin of fin. Pectoral fin in large specimens naked or few basal scales present. Pelvic fin scaled anteriorly on both sides.

Juveniles (Fig. 64) terete, all fins naked, except caudal fin base. Caudal fin distinctly emarginate.

Colouration in preservative. Juveniles, ca 20 mm SL, yellowish white with a dark lateral band from head to caudal fin. Band includes dark postorbital spot, short horizontal stripe dorsally on opercle, and greyish band along middle of side containing three roundish black blotches, of which two below spinous dorsal fin and one below soft dorsal fin. Fins hyaline except for blackish, horizontally extended caudal spot.

At about 40 mm SL (Fig. 64) bars 1-3 present but still very faint, extending height of side. Often

Table 23. Morphometry of *Cichla pinima*. Measurements are in percent of SL, except SL (in mm). Linear regression parameters calculated from original measurements in mm. HT, holotype (INPA 691).

	N	min	max	mean	SD	HT	a	b	r
SL (mm)	49	91.7	310.0	175.9		300.0			
Head length	49	30.1	33.9	31.7	1.04	33.2	0.316	0.315	0.994
Snout length	49	10.3	12.5	11.1	0.54	12.5	–1.763	0.122	0.989
Head depth	49	19.6	23.9	21.1	0.88	22.6	–2.958	0.230	0.992
Body depth	49	24.2	30.3	26.6	1.49	28.0	–4.404	0.294	0.989
Orbit diameter	49	6.8	9.6	7.8	0.70	7.3	2.936	0.060	0.983
Interorbital width	49	6.7	8.3	7.3	0.37	8.3	–1.424	0.082	0.991
Pectoral fin length	48	18.6	24.2	21.6	1.42	23.3	–5.072	0.247	0.988
Upper jaw length	49	13.3	16.3	14.2	0.61	16.3	–2.325	0.157	0.991
Lower jaw length	49	16.7	19.5	18.1	0.72	19.5	–1.227	0.188	0.992
Caudal peduncle depth	49	9.8	12.3	10.6	0.62	10.9	–1.467	0.116	0.983
Caudal peduncle length	49	16.6	20.6	18.7	1.04	16.6	3.577	0.165	0.985
Dorsal spine length	47	10.5	15.0	12.7	0.91	12.9	–1.853	0.139	0.984

dark spot included in band at root of caudal peduncle. Fins hyaline. At about 50-60 mm SL dark stripe across soft dorsal fin. In slightly larger specimens (Fig. 65) lateral band distinct, blotches and bars faint. At about 100 mm SL (Fig. 66) more or less distinct preorbital stripe present; lateral band extending distinct from head to caudal fin. Vertical bars distinct, bar 3 reaching up to soft dorsal fin base. Round white spots extend in rows along side; minimally (Fig. 66) one row along dorsal margin of lateral band from slightly anterior to bar 2 caudally to end of caudal peduncle; another row immediately below lateral band, confined to distance between bars 1 and 2; two rows may be present on dorsum above lateral line. Full rows of white spots may also be present along dorsal and ventral margins of lateral band. Spinous dorsal fin dusky with one row of light spots; soft portion with two rows. Anal and pelvic fins hyaline. Dark pigment may be present along middle caudal-fin rays, otherwise usually immaculate or with a few yellowish spots in dorsal lobe. Caudal blotch rounded and slightly removed from caudal fin base, light spot bordering caudally.

Lateral band maintained distinct in specimens 100-200 mm SL. At about 150 mm SL bar 1 faded, except for pigment included in band, bar 3 including an intensified black spot close to dorsal fin base, with one or a few highlighted marginal white spots. At this size caudal blotch may be completely ringed with white. About four rows of white spots in soft dorsal fin and in dorsal lobe of caudal fin. Well preserved specimens with short greyish halter stripe, margined with white dorsally. White spots may appear on dorsal head side.

Non-breeding adults about 200-300 mm SL (Figs. 67-68) with dorsum and top of head brown, slighly lighter on side, underside whitish. Bars 1-3 dark grey, narrow, well separated, bars 1-2 below spinous dorsal fin, bar 3 below soft dorsal fin, extending from close to dorsal fin base distinct to middle of side, or to white ventral area. Irregularly round, black blotch dorsally in bar 3, usually with highlighted white spots along periphery. Incipient expansions of bar 1 to develop a blotch, or marginal light areas along bars, precursors of breeding colour pattern (below), frequent, but typically only dorsal ocellus in bar 3 and caudal ocellus prominently black. Numerous white spots seemingly irregularly distributed over side, varying in number and intensity among specimens; two principal horizontal rows of spots from caudal peduncle rostrad, often one row on abdominal side, and always one or two rows on dorsum. Dark bars devoid of white spots, but white spots tend to be larger and highlighted at periphery of dark markings, contributing to irregular-appearing pattern. Nape, cheek and opercular bones with numerous white spots with narrow interspaces; occasionally wanting from cheek and head side, mostly probably due to fading in preservative. Dark postorbital spots present, but appear as interrupted dark stripe and not ocellated. Preorbital stripe usually indistinct, occasionally not apparent. Some dark pigment in mouth angle, but no distinct halter stripe. Spinous dorsal fin grey with two or three rows of whitish spots, soft portion with five rows, proximal spots larger than distal spots. Upper half of caudal fin with five or six vertical rows of vertically extended white or yellowish spots. Caudal ocellus size of eye, usually with white or silvery border only anteriorly and posteriorly.

Colour pattern characterized by ocellated blotches or bars on side occurs in both males and females from ca 250 mm SL (Figs. 69-72). Practically all specimens above 300 mm SL show this colour pattern and it is possible that it represents a final phase rather than a particular breeding colour pattern. Some specimens over 300 mm SL, however, possess a colour pattern appearing intermediate between that shown by most 200-300 mm SL specimens, and most of those over 300 mm SL, featuring both white spots and rather faint ocellar blotches or bars with white spots arranged along margins of dark markings. No obvious sexual dimorphism, except that light spots may be completely absent in males and retained to some extent on dorsum in females; material available insufficient for decision. Grey on nape and dorsum, paler grey on side, underside white. Lips grey, location of halter stripe marked by grey pigmentation. Light margins of ocellar markings white or silvery. Bars each form three major ocellar markings which may be further subdivided or have smaller ocelli associated with them. Bar 1 marking an irregularly rounded deep black blotch bordered dorsally by lateral line; either perfectly round and then not extending below level of pectoral fin base or extending as bar down to white underside (i.e., tracing bar 1); black roundish ocellated blotch also often present above lateral line. Bar 2 with roundish ocellated blotch in series with blotch in bar 1 or, usually,

Fig. 70. *Cichla pinima*, holotype, INPA 691, adult male, 300 mm SL; Brazil: Pará: Rio Curuá-Una, Km 30.

Fig. 71. *Cichla pinima*, paratype, MZUSP 33097, adult male, 430 mm SL; Brazil: Pará: Belo Monte.

Fig. 72. *Cichla* cf. *pinima*, NRM 18477, 110.0 mm SL; Brazil: Pará: cachoeira where Rio Aruá joins with Rio Arapiuns, Vila de Cachoeira de Aruá.

extending ventrally as black bar to white ventral region; round ocellus almost always present above lateral line but may be incorporated in bar 2 or contiguous with it. Bar 3 represented by deep black, irregular roundish ocellated blotch close to soft dorsal fin base, usually contiguous or continuous with black bar extending ventrally to white ventral region. Black postorbital spots ocel-

Fig. 73. *Cichla pinima*, fresh caught adult specimen, not preserved. Brazil: Para: Rio Guamá, downstream of Ourém. Photograph by F. Warzel.

Fig. 74. *Cichla* cf. *pinima*, MZUSP 22094, 161 mm SL; Brazil: Amapá: Cachoeira Grande.

lated with narrow white ring appear in three positions, one on postorbital portion of cheek, one dorsally on opercle, and one on posterodorsal tip of subopercle; occasionally one marking in each position, but normally several small spots in each position. In holotype an ocellated blotch present at ventral tip of opercle, but no dark blotch observed at anterodorsal process of preopercle. Dorsal and caudal fins nearly uniformly dark, immaculate or with light spots similar to non-breeding specimens. Caudal ocellus black with complete white ring; size same as eye. Anal fin whitish basally, turning greyish distally. Pelvic fin all white or grey on lateral face.

Specimens 111-135 mm SL from the blackwater Rio Arapiuns (Fig. 73) much darker than all Tapajós specimens, featuring contrasting yellowish white spots on body similar to much larger specimens (non breeding adults, see above), including rows accompanying lateral band, two or three rows on dorsum, and one row of a few spots only on abdominal side. In similar sized Tapajós and Xingu specimens yellow spots found only along lateral band and commonly only along dorsal border of band. Specimens 66-134 mm SL from the Rio Paraguaçu similar to Arapiuns specimens in colour pattern.

Live colouration. Live or freshly killed specimens in breeding pattern (Fig. 74) yellow, especially

intense on lower head side, turning greenish dorsally and on caudal peduncle, ventral parts white. Iris yellowish. Bars or blotches black, ocellar margins white. Branchiostegal membrane may be orange and lower half of caudal fin as well as anal fin may be yellowish. Nuchal hump dark grey in specimens showing this feature (Fig. 72).

Geographical distribution. Lower Rio Tapajós, Rio Curuá-Una, lower Rio Xingu, lower Rio Tocantins, and Rio Capim (Fig. 75); uncertain localities in southern Amapá and Rio Arapiuns, introduced in Rio Paraguaçu in eastern Brazil, and probably elsewhere in northeastern Brazil.

Etymology. The species epithet *pinima* is a Tupi-Guarani adjective meaning spotted with white, and is here used as a noun in apposition.

Local names. We propose tucunaré pinima as Brazilian name for this species, selecting a name already in use.

Notes. Tucunaré pinima is applied as a local name on the current species at least in the Nordeste region of Brazil, where it forms self-sustaining stocks following introductions into numerous reservoirs in the 1940s (Fontenele, 1948; Braga, 1952, 1953; Menezes, 1953; Bezerra e Silva et al., 1980; as *C. temensis*). According to Menezes (1953: 382-383) tucunaré pinima was the name used locally by the Serviço de Piscicultura in Fortaleza (Ceará) for the species sent there by Museu Goeldi as tucunaré-açu. Santos et al. (1985), in a catalog of fishes from the Tucurui dam, illustrate the adult as *C. ocellaris,* tucunaré-açu, and the young as *C. temensis*, tucunaré-pinima. Nomura (1984: 454-455) included tucunaré-pinima as a synonym of tucunaré-açu as well as tucunaré-tinga, identified as *C. temensis*, and identified tucunaré-comum as *C. ocellaris.* His illustration of *C. ocellaris* is a reproduction of Spix & Agassiz's (1831: pl. 63) illustration of *C. monoculus*. Santos (1981:156) uses the vernacular tucunaré putanga, referring to a lecture by Carlos Estevão (then director of the Museu Goeldi in Belém) at the Rotary Clube do Pará, and indicating that it would have been reproduced also in Ceará, but is possibly not his species.

Sawaya (1946) conducted experiments on *Cichla* and *Astronotus* in ponds in Museu Goeldi and reported on tucunaré putanga as well as a hybrid *C. temensis* × C. *ocellaris*, but without clues to their identity. Sawaya & Maranhão (1946) reported on tucunaré açú *(Cichla ocellaris)*, tucunaré putanga (species not yet well determined), tucunaré tinga *(C. temensis)* and the 'hybrid'. Sawaya & Maranhão (1946) considered the putanga to be more elongate than the tucunaré-açu, with more elongate head and smaller interorbital space. The lateral line is said to be broken in the young and never turning entire in the adults. The small whitish spots would always be absent, in adults as well as juveniles. There is no further information from Museu Goeldi or elsewhere on the putanga. There is a possibility that the name putanga, of unknown meaning, resulted from a misunderstanding or misapplication involving the names pinima and tinga.

There seems to have been considerable confusion over what species was being studied in Museu Goeldi as well as in the fisheries station at Fortaleza. For certain, *C. pinima* was studied in Ceará, as evidenced by photos and illustrations in Braga (1953), Fontenele (1948) and Bezerra e Silva et al. (1980). Also *C. kelberi,* identified as *C. ocellaris* (tucunaré comum) by Fontenele (1948), was cultivated. Three specimens that we refer to *C. pinima*, MZUSP 50273, 177-288 mm SL, labeled Museu Goeldi, have an aspect indicating stunted growth. They have deeper head, deeper body, longer pectoral fin, and larger eye than other *C. pinima* of similar length, and separate from a cluster formed by the other species in a morphometric canonical discriminant analysis (not shown). They also have relatively low E1 scale counts (78, 84, 88). We thus excluded those specimens from the morphometric analysis, although the colour pattern agrees with *C. pinima.*

Cichla pinima is widely distributed, and there are large, well preserved series chiefly from the lower Rio Tapajós drainage supplemented by well preserved material from the lower Rio Xingu. The species is characterized by the early appearance, below 100 mm SL, of a blackish, more or less ocellated blotch dorsally in bar 3, close to the dorsal fin base. In large males this blotch is increased in size and highly prominent, but then similar in appearance to the corresponding blotch in several other *Cichla* species. In *C. vazzoleri*, there is no ocellated blotch close to the dorsal fin except in large adults (about 300 mm and larger). In adult *C. vazzoleri*, *C. jariina,* and *C. thyrorus* is typically present a dark brown or black blotch at the anterodorsal process of the subopercle, usually absent in *C. pinima.*

Fig. 75. Collecting localities of *Cichla temensis*, *C. pinima* (including translocation), *C. vazzoleri*, and *C.* cf. *pinima*. A symbol may cover more than one collecting site.

Cichla pinima and *C. vazzoleri* share a distinctive adult breeding colour pattern, best expressed in males. The vertical bars become deep black and the dorsal portion of each bar may separate as a dark ocellated blotch above the upper lateral line, regularly in *C. vazzoleri* but rarely in *C. pinima*. In *C. pinima* the middle portion of the first bar forms a large prominent ocellus and the ventral part becomes obsolete or forms a blotch under the pectoral fin; the middle portion of bar 2 may be slightly expanded and blotch-like, but usually there is a complete ocellated vertical bar extending to the abdominal side; the third bar, below the dorsal blotch, remains vertically extended, and is usually contiguous with the dorsal blotch. In *C. vazzoleri* the pattern is similar to that of *C. pinima*, although the vertical bars are usually narrower, and the middle ocellus in bar 1 is not as well formed as in *C. pinima*.

All populations sharing the development of the blotch in the dorsal portion of bar 3 were assigned to *C. pinima*, although samples other than those from the Tapajós and Xingu river drainages generally do not contain large breeding males in which breeding colour could be verified. Samples from southern tributaries assigned to *C. pinima* on the basis of colour markings turned out to be highly variable in fin ray and particularly scale counts. E1 row counts show some geographic variation and are generally higher to the west and

lower to the east, but alone the Tapajós population spans 91-105 (N = 31), the Xingu 95-102 (N = 12). Either our heterogenous samples contain distinctive geographical populations or species, or there is a gradient in average scale counts, which cannot be analysed properly because some geographical samples are small.

The pectoral fin count (Table 8) includes a high frequency of 14 rays, mostly derived from the Tapajós sample (Arari 15 (1); Capim 14 (3), 15 (2); Tocantins 14 (3), 15 (6); Xingu 14 (1), 15 (11); Curuá-una 14 (3), 15 (4); Tapajós 14 (8), 15 (10)). Total variation in the anal fin ray count (Table 8) reflects high frequencies of 10 rays in Xingu and Tapajós samples (Arari 11 (1); Capim 10 (2), 11 (3); Tocantins 10 (1), 11 (7), 12 (1); Xingu 10 (5), 11 (6); Curuá-una 10 (1), 11 (5), 12 (1); Tapajós 10 (5), 11 (13), 12 (1)).

Specimens from the Rio Curuá-una possess E1 row scales 86-91, and the lateral line is discontinuous on one (N = 4) or both (N = 2) sides.

No large breeders were examined from the Tocantins or Capim river drainages, but a photograph is available of a large specimen in adult colouration from the Rio Guamá (Fig. 75). Scale counts range 87-101 (N = 14). The lateral line is usually discontinuous on both sides (N = 12) or continuous on both sides (N = 3) or on one side only (N = 4).

Specimens from Cachoeira Grande, Amapá (Fig. 76) do not include breeding males. E1 row scales 85-93, and abdominal vertebrae 19 (N = 5), vs. 18 in the other samples (N = 12) except Tocantins (N = 2). The lateral line is discontinuous on both sides (N = 3), or on one side (N = 1), or not determinable (N = 1). Numerous small light spots are present on the top and side of the head. A photograph of a *Cichla* specimen from the Rio Araguari (Stawikowski & Werner, 2004: 37, upper photo) is similar to the Cachoeira Grande sample, and displays a prominent ocellus dorsally in bar 3. Three preserved specimens from the Rio Araguari possess 94, 104, 105 E1 scales. Two of these are breeding males, referable to *C. pinima* by colour pattern, the third a female similar to the Araguari specimen (Stawikowski & Werner, 2004: 37, upper photo).

One large male (MZUSP 7075, 1, ca 260 mm SL) from the Rio Canumã, a tributary to the lower Rio Madeira, has a deformed caudal peduncle, and critical counts and measurements cannot be made. However, the ocellus adjacent to the soft dorsal fin base is absent, and a dark blotch at the anterodorsal process of the subopercle is present, suggesting that it is not *C. pinima*, but rather *C. vazzoleri*. Four smaller specimens (MZUSP 7075, 143.4-195.0 mm SL, all females) from the same locality, depart from *C. pinima* in somewhat high E1 row scale counts, 100, 102, 108, 112, but do display a minor blotch adjacent to the soft dorsal fin base. Two specimens (NRM 18477, 110.6-134.8 mm SL) from the Rio Arapiuns drainage also depart in high scale counts, 104-112, and are overall darker than similar sized *C. pinima* from the adjacent lower Rio Tapajós, but the distinctive dark blotch adjacent to the soft dorsal fin is already present. Both the Arapiuns and Canumã rivers are black water rivers in contrast to all other localities of *C. pinima*, which are clear water habitats as far as could be ascertained. Additional collections from the Canumã and Arapiuns are required to clarify whether *Cichla* from these localities are distinctive.

Cichla vazzoleri, new species
(Figs. 76-80)

Holotype. INPA 3501, adult male, 295 mm SL; Brazil: Pará: Rio Trombetas drainage: Area Shell-Alcoa, lower Rio Trombetas; 19 Nov 1982, Gelso Vazzoler.

Paratypes. 316 specimens, 26-410 mm SL. **Brazil: Rio Trombetas drainage: Pará:** INPA 3062, 1, 345 mm SL; Lago Abuí; 22 May 1988, E. Ferreira. – INPA 3571, 1, 260 mm SL; praia on left bank of Rio Trombetas, upstream of camp of Reserva Biológica do Trombetas; 13 Apr 1985, M. Jégu & E. Ferreira. – INPA 3572, 2, 160-182 mm SL; downstream of Cachoeira Porteira; 13 Apr 1985, E. Ferreira & M. Jégu. – INPA 3573, 3, 196-225 mm SL, INPA 3574, 2, 165-175 mm SL, INPA 3575, 1, 188 mm SL; Lago Tapagem; 12 Apr 1985, E. Ferreira & M. Jégu. – INPA 3576, 14, 26-41 mm SL, INPA 3577, 166, ca 30-40 mm SL; left bank praia 10 m upstream of mouth of Lago Tapagem; 13 Apr 1985; E. Ferreira & M. Jégu. – INPA 3578, 5, 38.1-66.8 mm SL; Cachoeira Porteira below furo at exposed rock. 19 Apr 1985. E. Ferreira. – INPA 3579, 1, 39.8 mm SL; Cachoeira Porteira, furo at exposed rock on right bank; 19 Apr 1985, E. Ferreira. – INPA 3570, 6, 205-330 mm SL; Pará: Area Shell-Alcoa; 20-21 Nov/19 Dec 1982, G. Vazzoler. – INPA 3569, 7, 275-335 mm SL; Pará: Area Shell-Alcoa, Lago da Cruz Alta; 4-18 Oct 1982, G. Vaz-

zoler. – MZUSP 5501, 1; Rio Trombetas; no date, no collector. – MZUSP 5536, 3, 200-410 mm SL; Lago Jacupá; No date, EPA. – MZUSP 5580, 1, 340 mm SL; Oriximiná, Lago Paránacui; 9 Feb 1967, EPA. – MZUSP 9441, 1, 365 mm SL; mouth of Rio Cuminá, near Oriximiná; 20-27 Jan 1968, EPA. – MZUSP 12114, 1; Oriximiná; 16-18 Dec 1967, EPA. – MZUSP 15677-15678, 2; Reserva Biológica do Trombetas, igapó of Lago Leonardo; 9 Jul 1979. R. M. C. Castro. – MZUSP 15797, 1; Reserva Biologica de Trombetas; 14 Jul 1979, R. M. C. Castro. – MZUSP 15817, 1, 310 mm SL; Reserva Biológica do Trombetas, lago upstream of mouth of Lago Jacaré; 14 Jul 1979, R. M. C. Castro. – MZUSP 15962, 1; island at mouth of Lago Erepecu, Reserva Biológica do Trombetas; 20 Jul 1979, R. M. C. Castro. – MZUSP 33096, 3; Cuminá, river shore; Oct-Nov 1983, M. Goulding. – MZUSP 33129, 12; Rio Trombetas, 20 km upstream from mouth; Oct-Nov 1983, M. Goulding. – MZUSP 33132, 22; Cuminá, river shore; Oct-Nov 1983, M. Goulding. – MZUSP 50622, 6; Lago Jacaré; 29 Nov-13 Oct 1965, Departamento de Zoologia and Museu Goeldi. – MZUSP 92410, 1; Oriximiná; 16-18 Dec 1967, EPA. – NRM 43055, 2, 76.0-106.7 mm SL; Lago Caipuru; 8 Sep 1998; R. Stawikowski. **Rio Uatumã drainage: Amazonas:** INPA 3494, 3, 125.5-207 mm SL; Rio Uatumã upstream of mouth of Igarapé Catitu; 23 Feb 1983, Equipe de Ictiologia do INPA. – INPA 3586, 1, 255 mm SL; Igarapé do Barreto; 27 Apr 1983, Equipe de Ictiologia do INPA. – INPA 3580, 2, 183-320 mm SL, INPA 3581, 2, 270-300 mm SL; Amazonas: Rio Uatumã; Nov 1984, Equipe de Ictiologia do INPA. – INPA 3582, 2, 325-335 mm SL; Igarapé Catitu; 19 Oct 1983, Equipe de Ictiologia do INPA. – INPA 3583, 1, 310 mm SL; Igarapé do Arraia, at confluence with Rio Uatumã; 26 Jan 1985, Equipe de Ictiologia do INPA. – INPA 3584, 1, 280 mm SL; Nazaré; Mar 1985, Equipe de Ictiologia do INPA. – INPA 3585, 42, 36-46 mm SL; Igarapé do Nazaré, pedral do Jacaré; 16 Sep 1985, M. Jégu. – NRM 13494, 1, 268 mm SL; Rio Uatumã upstream of mouth of Igarapé Catitu; 23 Feb 1983, Equipe de Ictiologia do INPA.

Diagnosis. Similar to *C. jariina*, *C. pinima*, *C. temensis*, and *C. thyrorus* in possession of four horizontal rows of light spots along side in subadults and large females, and prominent black, light-margined vertical bars or blotches in adults. Scales in E1 row ca 100-110, exceptionally 95-114, vs. 77-90 in *C. thyrorus*. Lateral line nearly always discontinuous, vs. usually continuous in *C. temensis* and *C. thyrorus*. Vertical bars of breeding specimens ocellated and modified, typically with small blotch close to dorsal fin base, below that ocellated vertical bars, or bar 1 with two separate or contiguous blotches, one on midaxis and one under pectoral fin, posterior bars rarely modified into blotches (vs. typically three vertical rows of 3, 3, and 2 blotches in *C. jariina* and *C. thyrorus*). A dark blotch at anterodorsal process of preopercle is nearly always present in adults over 200 mm SL (vs. usually absent in *C. pinima*).

Distinguished from *C. pinima* also by smaller scales (95-114 vs. 86-105), but ranges overlap, and consistent presence of row of light spots along abdominal side (vs. commonly absent in *C. pinima*). Breeding *C. pinima* have three ocellated bars which continuous above upper lateral line when extending above it, and usually no isolated blotches on dorsum; subadult and adult specimens of *C. pinima* possess an ocellated blotch dorsally in bar 3, which never occurs single in *C. vazzoleri* but only in breeding pattern together with other ocellated blotches. *Cichla temensis* generally possesses more E1 scales, 98-128, usually more than 110, and vertical bars of adults entire, extending from dorsum to abdominal side.

Description. Refer to Figs. 76-80 for general shape and colour pattern, Table 24 for morphometrics, and Tables 2-10 for meristics. Specimens 26 to 410 mm SL were available from the lower Rio Trombetas (downstream of Cachoeira Porteira). Most are adults in breeding colouration. The description is based primarily on the adult Trombetas material. Specimens 36-335 mm were available from the Rio Uatumã, and the smaller size range was used in the description below.

Relatively elongate (depth 25.2-29.3 % SL, N = 20, 200-410 mm SL). Predorsal contour ascending gently curved; or in large males straight, with soft nuchal swelling projecting from predorsal midline. Maxilla reaching to vertical from anterior margin or middle of orbit, lower jaw distinctly prognathous, its articulation below middle of orbit. Lateral line usually discontinuous, bilaterally continuous in two of 33 specimens; free ends of discontinuous sections usually with long overlap.

Dorsal fin spines 4-5 longest: soft dorsal fin rounded, not reaching to caudal fin base. Soft anal fin rounded, reaching halfway to middle of cau-

Fig. 76. *Cichla vazzoleri*, paratype, INPA 3494, 125.5 mm SL; Brazil: Amazonas: Rio Uatumã drainage, upstream from Igarapé Catitu.

Fig. 77. *Cichla vazzoleri*, paratypes, INPA 3574, top 174 mm SL, bottom 165 mm SL; Brazil: Pará: Rio Trombetas drainage, Lago Tapagem.

dal peduncle or slightly shorter. Caudal fin truncate, upper corner angled, lower corner rounded. Pectoral fin pointed, reaching little more than halfway to vertical from anal fin origin. Pelvic fin pointed, first ray longest, not reaching as far as pectoral fin.

Dorsal fin scaled from behind last spine, last five interradial membranes naked. Narrow short scale rows close behind each soft ray and between some of branches, and thick basal scale layer. Anal fin densely scaled anteriorly, less dense posteriorly. Caudal fin densely scaled. Pectoral fin naked, or scaled basally. Pelvic fin scaled along outer margin on both sides.

Juveniles 30-40 mm SL, terete, caudal fin emarginate, scales absent from fins except caudal fin base.

Fig. 78. *Cichla vazzoleri*, holotype, INPA 3501, adult male, 295 mm SL; Brazil: Pará: Rio Trombetas drainage, Shell-Alcoa.

Fig. 79. *Cichla vazzoleri*, paratype, INPA 3583, adult female, 310 mm SL; Brazil: Amazonas: Rio Uatumã, Igarapé do Arraia.

Fig. 80. *Cichla vazzoleri*, paratype, NRM 13494, adult male, 268 mm SL; Brazil: Amazonas: Rio Uatumã drainage, Igarapé Catitu.

Colouration in preservative. At ca 30-40 mm SL whitish with conspicuous black lateral band from snout to end of caudal fin including intensified portions above pectoral fin base, above tip of pectoral fin, and below soft dorsal fin. Caudal spot contained within lateral band, horizontally extended, to about middle of caudal fin, posteriorly less intense dark pigmentation.

Specimens 60-70 mm SL yellowish whitish with greyish back. Lateral band distinct, dark grey to black, extending from eye to end of caudal fin, caudal spot still contained within band and elongate; preorbital stripe faint. Three faint vertical bars across middle of side in position of band intensifications seen in smaller specimens. No light spots on body or fins. Dark stripe across middle of soft dorsal fin.

Specimen 126 mm SL (Fig. 76) with back darker. Lateral band deep black, with contiguous white spots bordering above and below. White spots appear in dorsal and caudal fins. Specimen 138 mm SL from same locality has lateral band indistinct, and is similar to specimens 160-190 mm (below) except for absence of spots on head.

Specimens 160-190 mm SL (Fig. 77) with brownish or greyish side, darker dorsally. Vertical bars and lateral band about equally intense, extending from dorsum at or slightly below dorsal fin base, to white ventral area. Postorbital stripe inconspicuous, not subdivided into blotches. Conspicuous yellowish or whitish, round or very slightly elongate spots in row along each margin of lateral band, one row on abdominal side between bars 1 and 3, and along dorsal side. Light spots also on side of head (above eye and on cheek) with only narrow brownish interspaces, but not as contrasted as flank spots. Dorsal fin with three rows of light spots; dorsal half of caudal fin with vertical rows of light spots. Caudal blotch black, round, distinct from lateral band, with light posterior margin or partly ocellated with light areas both anteriorly and posteriorly.

Adults of both sexes 260-410 mm SL (Figs. 79-90) may show ocellated pattern as in holotype (Fig. 79) regarded as breeding colour. Other adults up to 330 mm SL (Fig. 80, and of both sexes, may show colour pattern more similar similar to 160-190 mm SL specimens, with brownish back and side.

Breeding colour pattern identical in both sexes. Side grey, darker on top of head and snout, close along dorsal fin base and on top of caudal peduncle; underside whitish or yellowish white. Seemingly scattered black, white margined spots behind eye and on gill cover; one blotch on cheek between eye and preopercle, one blotch or a group of up to five blotches dorsally on opercle, one or two blotches posterodorsally on subopercle, one blotch at anterodorsal process of subopercle, often also a spot at border cheek/preopercle at same vertical level as lower subopercular blotch. One or more of dark head spots occasionally missing.

Vertical bars deep black, modified into separate blotches or bars: Bar 1 represented by small black, usually ocellated spot above upper lateral line, deep black, white margined blotch between upper lateral line and level of pectoral fin base, continued narrower down to white underside or pigmentation under pectoral fin forming separate

Table 24. Morphometry of *Cichla vazzoleri*. Measurements are in percent of SL, except SL (in mm). Linear regression parameters calculated from original measurements in mm. HT, holotype (INPA 3501).

	N	min	max	mean	SD	HT	a	b	r
SL (mm)	27	125.5	410.0	257.8		295.0			
Head length	27	28.6	33.7	31.7	1.12	31.7	–4.5843	0.336	0.996
Snout length	27	10.1	13.0	11.9	0.86	11.9	–4.9827	0.1397	0.989
Head depth	27	18.9	25.2	21.7	1.44	23.2	–6.9401	0.2465	0.986
Body depth	27	23.6	29.3	26.5	1.36	27.5	–4.9939	0.2861	0.991
Orbit diameter	27	6.6	8.5	7.3	0.53	6.9	2.9929	0.0608	0.977
Interorbital width	27	6.9	8.6	7.6	0.50	7.8	–2.1675	0.0856	0.982
Pectoral fin length	27	20.2	23.8	22.2	0.91	21.8	–4.3556	0.2402	0.995
Upper jaw length	27	13.0	16.1	14.6	0.81	14.9	–4.7685	0.166	0.992
Lower jaw length	27	16.9	19.9	18.2	0.75	18.6	–4.0364	0.1994	0.994
Caudal peduncle depth	27	9.6	11.5	10.5	0.57	10.2	0.7738	0.1013	0.979
Caudal peduncle length	27	16.7	20.2	18.5	0.94	18.9	3.5716	0.1704	0.983
Dorsal spine length	27	10.4	12.8	11.6	0.62	12.2	2.4533	0.1055	0.984

ocellated blotch. Bar 2 represented by small black spot (usually ocellated) above upper lateral line and wide black, white-margined bar from upper lateral line down to level of lower margin of pectoral fin base. Bar 3 represented by small dark spot (usually ocellated) above level of upper lateral line and a black bar or blotch below it, commonly ocellated. White margins bordering black markings may consist of aggregates of white spots or complete white borders. Light spots on side and head characteristic of smaller specimens absent or very indistinct.

Spinous dorsal fin blackish, soft dorsal fin brown with few light spots posteriorly or immaculate. Anal fin brownish. Caudal fin brown, usually without pattern of light spots. Caudal ocellus above level of lower lateral line, ringed with silver. Pelvic fin brownish grey.

Two large females, 290-310 mm SL, have both pattern of white spots and ocellated bars; bars more prominent dorsally. One male, 325 mm SL, shows intermediate pattern with both bars and white spotting.

Live colouration. No information available.

Geographical distribution. *Cichla vazzoleri* is recorded from the middle Rio Uatumã and lower Rio Trombetas including but not above the Cachoeira Porteira, to the Oriximiná region at the mouth of the Rio Cuminá (Fig. 75).

Etymology. Named in honour of Gelso Vazzoler (1929-1987), collector of part of the type series, former head of the Departamento de Biologia Acuática, INPA, Manaus.

Notes. *Cichla vazzoleri* is most similar to *C. pinima*. Refer to comparison under that species.

Jégu et al. (1989) described *Mylesinus paraschomburgkii*, a rheophilic characid from the Rio Trombetas (Cachoeira Vira-Mundo and upstream) and Rio Uatumã (Cachoeira do Miriti and upstream). This species appears to be restricted to rapids, and thus presents different dispersal options than the *Cichla* species. Although the distribution pattern of *M. paraschomburgkii* is similar to that of *C. vazzoleri*, which is present in both the Uatumã and the Trombetas, *C. vazzoleri*, although collected from rapids in both rivers, is present in the lower Rio Trombetas chiefly in lowland conditions. We are unaware of other fish species restricted to the Uatumã and lower Trombetas rivers, but we also cannot conclude that this is the total distribution of *C. vazzoleri*.

There is no significant difference in proportional measurements or meristics between Trombetas and Uatumã samples. There is no clear modality in the counts of soft dorsal and pectoral fin ray counts of the species. This is also the case within populations for the pectoral fin count (Trombetas 14(7), 15(7), Uatumã 14(7), 15(6)), whereas the Uatumã sample has a clear mode in soft dorsal fin rays, and the mode of combined spines and rays is different (Trombetas XIV.17(1), XV.16(5), XV.17(9), XVI.16(5), Uatumã XV.15(2), XV.16(8), XV.17(3)). The distribution of E1 scales is similar in the two geographical samples (ranges: Trombetas 97-114, Uatumã 95-108).

Cichla temensis Humboldt, 1821

(Figs. 81-89)

Cichla temensis Humboldt, in Humboldt & Valenciennes, 1821: 169 (Temi).
Cichla atabapensis Humboldt, in Humboldt & Valenciennes, 1821: 168 (l'Orénoque; Rio Atabapo).
Cichla Tucunare Heckel, 1840: 409 (Rio-branco).
Cychla flavo-maculata Jardine, 1843: 145, pl. 6 (Rio Negro and Padauiri).
Cychla trifasciata Jardine, 1843: 151, pl. 9 (Rio Negro; Padauiri).
Cichla unitaeniatus Magalhães, 1931: 225 (Rio Negro e do Purus).

Material examined. 73 specimens, 25.6-375 mm SL. **Guyana: Ireng River drainage:** BMNH 1968.9.26:1, 1, 218 mm SL; Pirara Stop-Off; 30 Sep 1957, R. H. Lowe-McConnell. **Colombia: Rio Orinoco drainage:** ICN-MHN uncat., 2; Vichada: Rio Elvita, Puerto Carreño; May 1974, P. Cala. **Venezuela: Rio Negro drainage:** USNM 269330, 1, 112.5 mm SL; Amazonas: shore of Rio Negro ca 1/2 h above San Carlos de Rio Negro; 4 Dec 1984, R. P. Vari. **Rio Orinoco drainage:** USNM 269931, 1, 113.0 mm SL; Amazonas: Laguna Provincial ca 20 km N of Puerto Ayacucho; 1 Dec 1984, R. P. Vari. – ZSM 25019, 2; Bolívar, Laguna de Palma at San Felix; 29 Mar 1974, H. J. Köpke. **Rio Caroni drainage: Bolívar:** NRM 21551, 1, 199 mm SL; NE part of Embalse del Guri, Zona F, near Dique F; 18 Jan 1994, J. D. Williams. – NRM 22919, 2, 58.1-71.0 mm SL; NE Guri Reservoir-Near dique F; 6 Jun 1994, J. D. Williams et al. – NRM 22921, 1, 25.6 mm SL; Campamento Guri, in the marina by the tub boat; 19 Jun 1994, J. D. Williams & L. J. Gessner. – NRM 22922, 3, 52.6-62.9 mm SL; ventral part of Guri Reservoir near Budare; 14 Jul 1994, J. D. Williams & K.

M. Ryan. **Brazil: Rio Jamari drainage:** INPA 3493, 1, 290 mm SL; Rondônia: lake of Rio Verde, 70 km downstream of UHE Samuel; 5 Apr 1986, G. M. dos Santos. **Rio Negro drainage: Amazonas:** MZUSP 1792, 5; Igarapé Tarumãzinho, affluent no 1; 17-18 Nov 1967, EPA. – MZUSP 6169, 4, 159-345 mm SL; Rio Negro upstream of Manaus; 22-25 Apr 1967, EPA. – MZUSP 6213, 1; Igarapé Jaraqui on left bank of Rio Negro upstream Manaus; 22-24 Apr 1967, EPA. – MZUSP 92403, 1; vicinity of Manaus; 15-23 Nov 1967, EPA. – MZUSP 26952, 1; Lago Janauacá and vicinity of Manaus; Nov-Dec 1976, Alpha-Helix. – MZUSP 27223, 1; mun. Caracarai, Rio Jufari, Baia Grande, São Bento; 10 Nov 1982, L. Portugal. – MZUSP 27229, 4, 83.0-96.9 mm SL; município Novo Ayrão, extreme north of Reserva Ecologica Anavilhanas; 6 Nov 1982, L. Portugal. – MZUSP 27233, 2; município Ayrão Velho, mouth of Rio Padauari; 8 Oct 1982, L. Portugal. – MZUSP 32703, 1, 158 mm SL; Arquipélago das Anavilhanas, island margin; Sep 1980. M. Goulding. – MZUSP 32704, 1, 168 mm SL; Ilha Tamaquaré, lake; 11 Oct 1979, M. Goulding. – MZUSP 32705, 1, 178 mm SL; Arquipélago das Anavilhanas, margin of igapó; Aug 1980, M.Goulding. – MZUSP 32706, 2, 189-193 mm SL; Rio Marauiá, Cachoeira de Bicho-açu; 13 Oct 1979, M. Goulding. – MZUSP 32707, 6 (5 measured, 176-314 mm SL); Rio Arirará near mouth; 8 Oct 1979, M. Goulding. – MZUSP 32991, 1, 45.5 mm SL; Anavilhanas, capimzal; Feb 1982, M. Goulding. – MZUSP 33136, 2, ca 50-ca 62 mm SL; Arquipélago das Anavilhanas; 21 Sep 1979, M. Goulding. – MZUSP 33138, 1, 123 mm SL; Barcelos, island lake; 29 Feb 1980, M. Goulding. – MZUSP 92411, 1; Rio Cuieiras and tributaries; Jan 1977, Alpha Helix. – NRM 11308, 1, 228 mm SL; Rio Uaupés at Taracuá; 14 Feb 1924, Svenska Amazonas-Expeditionen 1923-1925. – **Rio Uatumã drainage: Amazonas:** INPA 3566, 6, 109.3-114.5 mm SL; Amazonas: Lago Samaúma; 7 Feb 1985, Equipe de Ictiologia do INPA. – INPA 3567, 1, 200 mm SL; Amazonas: Lago Samaúma; 3 Aug 1987, S. Amadio et al. – INPA 3568, 1, 157 mm SL; Amazonas: Cachoeira Morena; 7 Oct 1987, E. Ferreira et al. – MZUSP 9558, 7, 114.9-169 mm SL; Amazonas: São Sebastião do Uatumã; 5-8 Sep 1968, EPA. – **Rio Amazonas drainage: Amazonas:** MZUSP 5815, 1; Silves, Lago Saracá; 17-18 Mar 1967, EPA. – MZUSP 6079, 3, 153-154 mm SL; Rio Preto da Eva near Manaus; 13 Apr 1967, EPA. – MZUSP 92406, 2, 190-375 mm SL; Lago Puraquequara at mouth of Rio Puraquequara; 17-19 Apr 1967, EPA. **Rio Solimões drainage: Amazonas:** MZUSP 50268, 2; Amazonas: Lago Janauacá and vicinity; Sep 1976 - Jan 1977, Alpha-Helix. – NRM 5580, 1, 262 mm SL; Tefé; [1865-1866, Thayer Expedition.] – NRM 11307, 1, 251 mm SL; small whitewater river near Manaus; 25 Nov 1923, Svenska Amazonas-Expeditionen 1923-1925.

Diagnosis. Large, elongate species with small scales (E1 row scales 98-128, usually more than 110, vs. usually less than 110 in other species of *Cichla*). Postorbital band present, entire, may be irregular but does not consist of scattered spots, vs. absent or present as scattered spots in other species of *Cichla*. Lateral line usually continuous. Most similar to *C. pinima* and *C. vazzoleri*, sharing subadult to young adult colour pattern including dark midlateral band and four rows of regularly arranged light spots along side, but light spots slightly elongate instead of round. Different from *C. pinima* and *C. vazzoleri* in absence of dark lateral blotches with intensified light margins; vertical bars when expressed entire, never forming round blotches; ocellated blotches on dorsal side absent at all sizes; postorbital band entire vs. expressed as scattered dark blotches; dark blotch associated with preopercle absent (present in *C. vazzoleri*); lateral line nearly always continuous vs. usually discontinuous in *C. vazzoleri*.

Description. Refer to Figs. 81-89 for general shape and colour pattern, Table 25 for morphometrics, and Tables 4-10 for meristics.

Elongate (depth 24.5-27.3 % SL, N = 11, 202-375 mm SL). Frontal contour slightly curved or straight ascending, levelling slightly in advance of dorsal fin origin; nuchal protuberance absent in preserved specimens examined. Maxilla reaching to anterior about ⅓ of orbit. Lower jaw prognathous, articulation below about posterior ⅕ of orbit. Lateral line usually continuous (N = 42), rarely bilaterally (N = 3) or unilaterally (N = 8) discontinuous, anterior and posterior sequences overlapping beneath anterior half of soft dorsal fin.

Dorsal-fin spine 4 longest; soft dorsal fin rounded, reaching to about middle of caudal peduncle. Soft anal fin rounded, reaching to about middle of caudal peduncle. Caudal-fin margin truncate. Pectoral fin pointed, fifth ray longest, reaching to middle or posterior base of anal fin. Pelvic fin pointed or subacuminate, first ray forming tip, reaching almost halfway to base of first anal-fin ray.

Soft dorsal fin squamation consisting of 2 rows of scales basally between rays and a few scales between branches of longer rays. Anal fin densely scaled basally with 4 interradial scale rows, but no scales between between branches. Caudal fin densely scaled, except narrowly along posterior margin, and middle of membranes between rays D2 and V2. Pelvic fin densely scaled on both side basally and along first ray on lateral side. Pectoral fin scaled basally.

Small specimens elongate (21.3-23.8 % SL, N = 7, 45.0-122.7 mm SL); fins naked except base

Fig. 81. *Cichla temensis*, NRM 22921, 25.6 mm SL; Venezuela: Bolívar: Guri Reservoir.

Fig. 82. *Cichla temensis*, MZUSP 32991, 45.5 mm SL; Brazil: Amazonas: Anavilhanas.

Fig. 83. *Cichla temensis*, NRM 22919, 71.0 mm SL; Venezuela: Bolívar: Guri Reservoir (right side, reversed).

Fig. 84. *Cichla temensis*, MZUSP 33138, 122.7 mm SL; Brazil: Amazonas: Barcelos.

of caudal fin; dorsal and anal fins extending only to middle of caudal peduncle; caudal fin margin slightly concave. At about 100 mm SL scales present anteriorly on soft dorsal fin, anal fin with basal scale cover, and caudal fin truncate.

Colouration in preservative. Juvenile, 25.6 mm SL from Guri (Fig. 81) whitish, back greyish close to dorsal fin base. Brown blotch immediately behind orbit and dorsally on opercle. Brown stripe along middle of side, incorporating dark brown, round blotch 1 little behind cleithrum and intensified in dark brown band from above about origin of anal fin, narrower caudally to end at caudal fin base; blotch 2 appears as slight intensification of lateral band. Middle of caudal fin base with round, slightly caudad extended dark brown spot; fins otherwise hyaline except duskied along middle of caudal fin. Bars absent also in slightly larger specimens (Fig. 82), blotches 1, 2, and 3 showing as slight intensifications of lateral band. Caudal spot extended by dark pigment along middle rays of caudal fin.

At about 70 mm SL (Fig. 83) whitish, top of head and dorsum above lateral line grey. Snout and lips grey. Indistinct darker grey preorbital stripe. Dark brown stripe from orbit to opercular tip; continued on body side by wide band to caudal fin, dark brown anteriorly, deep black and slightly wider from interception with third vertical bar. Three narrow, straight vertical bars (bars 1-3) from dorsal fin base down to white ventral area, two below spinous, one below soft dorsal fin. Bar 1 slightly intensified (black) where crossing lateral band, bar 2 not or only slightly intensified where crossing lateral band. Dorsal fin hyaline; faint grey stripe across soft-rayed portion. Pectoral, pelvic and anal fins hyaline. Caudal fin with black stripe continuing lateral band to middle or ⅘ of caudal fin, margined dorsally and ventrally at least basally by yellowish stripes; rest of fin greyish.

Specimens about 120 mm SL (Fig. 84) with dorsum and upper parts of head greyish. Preorbital stripe indistinct. Vertical bars faint. Abdominal side above white ventral area greyish. Blackish lateral band gradually more intense and wider caudad, but of uniform width and intensity from above anal fin. White stripe or series of partly contiguous white spots bordering band above and below except where crossed by vertical bars. One row of a few white spots above anterior portion of lateral line. Dorsal fin greyish with two rows of white spots across both spinous and soft portion, spots in soft portion partly contiguous. Anal fin hyaline. Caudal fin greyish brown except black stripe along middle and white borders to black stripe. Caudal blotch barely distinguishable within band. A few light spots in dorsal lobe of caudal fin. Pelvic fin dusky basally on lateral side. USNM 269931, 113 mm SL, from the Orinoco drainage (Fig. 85), overall very light, with vertical bars better expressed than lateral band.

Specimens about 150-170 mm SL (Fig. 86) with three, increasing to four rows of white spots on side, one on back above lateral line, two from eye to caudal fin base along middle of side, and one along abdominal side slightly below pectoral fin base level developing later. Spots in

Table 25. Morphometry of *Cichla temensis*. Measurements are in percent of SL, except SL (in mm). Linear regression parameters calculated from original measurements in mm.

	N	min	max	mean	SD	a	b	r
SL (mm)	31	45.5	375.0	193.1				
Head length	31	29.9	33.9	31.7	1.07	0.527	0.313	0.998
Snout length	31	10.0	12.0	11.0	0.55	–1.693	0.121	0.997
Head depth	31	18.2	21.8	19.9	1.00	–2.390	0.214	0.995
Body depth	30	21.3	27.3	24.5	1.54	–3.630	0.269	0.996
Orbit diameter	31	6.0	10.5	7.8	1.08	2.904	0.059	0.992
Interorbital width	31	6.2	8.0	7.0	0.39	–1.054	0.076	0.996
Pectoral fin length	31	18.7	25.3	21.7	1.66	–4.502	0.245	0.991
Upper jaw length	31	12.7	15.1	13.9	0.68	–2.108	0.151	0.996
Lower jaw length	31	16.7	19.2	17.9	0.69	–1.416	0.187	0.997
Caudal peduncle depth	30	8.6	11.3	9.9	0.58	–0.171	0.100	0.994
Caudal peduncle length	31	16.9	21.3	19.3	1.22	2.023	0.180	0.991
Dorsal spine length	30	10.4	13.3	12.1	0.68	1.585	0.112	0.991

two middle rows may be contiguous to some extent. Caudal ocellus dark brown, located above mid-axis, with yellow peripheral fields but not completely ocellated. Light spots absent from nape and cheeks.

Specimens over 200 mm SL (Figs. 87-89) with light brown side, slightly darker dorsally. Halter stripe dark brown, extending back to jaw articulation. Preorbital stripe blackish, well expressed. Dark brown to blackish wide stripe with wide white margin from eye to opercular tip, not interrupted over preopercle. Horizontal lateral band not evident except occasionally as narrow dark brown stripe dorsally on caudal peduncle. Vertical bars faint. White spots in two horizontal rows along back, one row along abdominal side and two rows representing rows marginal to absent lateral band. Spots generally roundish and distinct except in latter rows in which spots elongate or to some extent confluent. Cheek, gill cover, and top of head with numerous white spots increasing in number and decreasing in relative size with increasing specimen length. Dorsal fin grey with two rows of white spot on spinous portion, four rows of white spots on soft portion. Anal fin whitish, shading to brownish distally. Pelvic fin brownish on lateral side, otherwise whitish. Caudal fin with round, dark brown spot, completely ringed with yellow stripe. Dorsal lobe otherwise brownish with about six rows of whitish spots; ventral lobe brownish or yellowish.

Large adults, over 300 mm SL (Fig. 89), have the postorbital stripe partly fragmented and with a few additional black spots dorsally on subopercle and cheek, all with white borders. Anal fin brownish. Ocellar markings absent other than those formed by postorbital blotches and caudal spot. Specimens clearly representing breeding colour or sexual dimorphism absent in preserved material.

Live and fresh preserved colours. Juvenile photographed at Rio Cadauiri yellowish with white underside and black lateral stripe.

Large adults, known or estimated to be over 500 mm SL apparently sexually dimorphic. Specimens probably representing males, with well developed nuchal hump, yellowish with greenish grey back and hump. Vertical bars evident, though not contrasted, light spots only indicated on side or, usually, completely absent from head, body and fins. Lower half of caudal fin, anal and pelvic fins, a band along abdominal side, branchiostegal membrane, and iris bright red or orange. Large specimens without hump, assumed to be females, with white spots on body, head and fins, but fins, branchiostegal membrane, side and iris red as in males. Vertical bars in those large adults proportionally wider than in young specimens; of about uniform width across side, and may appear to have slightly lighter margin, but do not form ocellar markings. Black, light-margined postorbital markings well evident and contrasted especially in large males.

Geographical distribution. Restricted to black-water rivers and their tributaries (Fig. 75), recorded from many localities along the Rio Negro in Brazil and Venezuela, many localities in the Rio Orinoco drainage, a few localities only in the Rio Branco drainage. Along the Rio Solimões-Amazonas recorded from Tefé, Rio Puraquequara, lower Rio Uatumã, Rio Preto da Eva, and Lago Saracá, all black-water habitats. Reported by Lowe-McConnell (1969) from the Rio Branco drainage in Guyana.

An adult specimen from the Rio Jamari (INPA 3493) and a small specimen from Lago Genipapo (INPA uncat.) on the Rio Aripuanã are questionably referred to *C. temensis*, but regrettably there is nearly no other *Cichla* material available from the Brazilian portion of the Madeira drainage to permit an understanding of the distribution of *C. temensis* in this region.

Local names. Sarabiana (Natterer, in Heckel, 1840: 413, Rio Negro); tucunaré (Natterer in Heckel, 1840: 409, Boa Vista area); pintado (Schomburgk in Jardine, 1843:145, Rio Negro); Lucanari Grande (Schomburgk, in Jardine, 1843: 151, Rio Negro); tucunaré sorubiana (Magalhães, 1931: 225, errata, Rio Negro); pavón pintado, pavón trucha, pavón venado (Román, 1981: 76, Venezuela); Pavón cinchado (large specimens; Román, 1981: 82).

Both the appelation pintado and sorubiana refer to the pimelodid catfish species *Pseudoplatystoma fasciatum*, known as surubi (Tupi-Guarani) or bagre pintado (Spanish).

Notes. The smallest specimen (Fig. 81) was identified by the very small scales, estimated at 100 in the E1 row but a precise count not possible.

None of the preserved specimens show a nuchal protuberance; sport fishing web sites, however, frequently display large *C. temensis*,

Fig. 85. *Cichla temensis*, USNM 269931, 113.0 mm SL; Venezuela: Amazonas: Laguna Provincial ca 20 km N of Puerto Ayacucho.

Fig. 86. *Cichla temensis*, INPA 3568, 157 mm SL; Brazil: Amazonas: Rio Uatumã at Cachoeira Morena, freshly preserved.

Fig. 87. *Cichla temensis*, NRM 21551, young female, 202 mm SL; Venezuela: Bolívar: Guri Reservoir.

Fig. 88. *Cichla temensis*, NRM 11308, young male, 228 mm SL; Brazil: Amazonas: Taracuá.

Fig. 89. *Cichla temensis*, MZUSP 6113, 375 mm SL; Brazil: Amazonas: Rio Puraquequara.

estimated to be about 0.8-1 m long, and with a prominent nuchal protuberance.

Cichla temensis is the most elongate species in the genus (Fig. 4), manifest above all at larger sizes, where it overlaps with *C. vazzoleri* but is more slender than *C. pinima* and *C. thyrorus*. The colour pattern and the ontogenetic development of principal dark markings, distinguish it from all other species of *Cichla*. The smallest specimens at 25 mm feature spot 1, and a caudal peduncle band, but spot 2 is only indicated (Fig. 81); by 45 mm there is a complete dark band along the middle of the side, though intensifications in position of spots 1 and 2 suggest that this band conceals spots developed in other small *Cichla* (Fig. 82); and at about 60 mm vertical bars 1-3 are distinct. At sizes over 200 mm, the midlateral band has faded, but four straight horizontal rows of white spots run along the side, and the vertical bars remain distinct. The white spots are large, often horizontally elongated and closely approximated or even to some extent contiguous in the two middle rows. At very large sizes, over 350 mm, light spots become obsolete, and the dark vertical bars, which originate close to the dorsal fin base and extend the depth of the side, may be enhanced by lighter margins.

Cichla temensis can be distinguished from other species of *Cichla* by the high E1 scale count (98-128, usually more than 100 scales, Table 2). Three small specimens from Guri (NRM 22919, 22922, 58.1-62.9 mm SL), have low scale counts, 98-105, whereas a small specimen (MZUSP 32991, 45.5 mm SL) from the Rio Negro has 113. Since another small Guri specimen (NRM 22919, 71.0 mm SL) has 115 scales, and no small *C. temensis* were identified from elsewhere, it remains to investigate if the counts at small sizes correlate with size or geographic location. The only other *Cichla* species with small scales are *C. piquiti*, *C. jariina*,

C. pinima, *C. vazzoleri*, and *C. intermedia* (Table 2). Among those *C. pinima* and *C. vazzoleri* are most similar in colour pattern.

Most specimens of *C. temensis* have bilaterally continuous lateral line, whereas in *C. pinima* the common condition is to have discontinuous lateral line, and in *C. vazzoleri* almost all specimens have discontinuous lateral line. Unlike *C. vazzoleri* and *C. pinima*, *C. temensis* never develops dark ocellated blotches on the dorsum, and the vertical bars remain entire and at all sizes instead of at least bar 1 forming a distinct ocellated blotch. At some medium sizes, however, the dorsal blotches of *C. vazzoleri* may be overlooked and the general appearance is similar to *C. temensis*, e.g., in the specimen shown in Figure 80, especially since the light spots along the side may be slightly elongate in *C. vazzoleri*.

Even with a synonymy of six names, no type material is available for any of the nominal species and the synonymy of *C. temensis* has to be established on the basis of descriptions. As there is no difference in opinion between different recent authors as to the identity of *C. temensis*, and the published descriptions and figures for the nominal species included in *C. temensis* give a fair or strong idea of what species is considered, there seems to be no need for a neotype designation at this moment.

The original descriptions of *C. atabapensis* and *C. temensis* (Humboldt & Valenciennes, 1821: 168-169) are very brief and there are no figures to facilitate recognition of the species. Humboldt writes (translated from the French):

"I have noted in my diary two more species of *Cichla* [in addition to *C. orinocensis*], with the following characters.

"Cichla atabapensis.
"*Pavon of Rio Atabapo*: same form as *Cichla orinocensis*, but instead of four blotches, four transverse very broad, blue-black areas bordered with gold. It is also encountered in the portions of the Orinoco where the waters are not so fast; but the variety most agreeable for food is the one from the Rio Atabapo, a river with black, crystalline waters" (M. Valenciennes supposes, with reason, that C. atabapensis in my manuscript is C. ocellaris, Schneid., Pl. LXVI.)

"C. temensis.
"*Pavon of Temi*: same shape; no transverse bands, but four rows of small yellow spots. A single very large spot on the tail.

"[Latin diagnosis, translated:] Green body, decorated with small yellow spots arranged in four longitudinal rows. A single large blue yellow-margined spot on tail."

It is thus evident that no specimens were ever preserved of either *C. temensis* of *C. atabapensis*. The species can be identified only with reference to the colour pattern in combination with the geographic distribution indicated by Humboldt. Of the species occuring in the area only one species displays a prominent pattern of four (or five) horizontal rows of yellow (or white) spots along the side (young and non-breeding adults, possibly breeding females) as well as three (although Humboldt counts four) prominent, wide, black, thinly light-margined vertical bars on the side, and that species is here identified as *C. temensis*. Kullander (2003: 621) placed *C. atabapensis* in the synonymy of *C. temensis*, thereby acting as first reviser, fixing the priority order of the names.

The other species occurring or expected to occur in the upper Rio Orinoco area, *C. orinocensis* and *C. intermedia*, can be distinguished by their colour pattern. The former was correctly distinguished by Humboldt as *C. orinocensis* and is characterised by three prominent ocellar blotches on the side. *Cichla intermedia* has a series of several narrow vertical bars along the middle of the side. Amazonian species, particularly *C. vazzoleri* and *C. pinima*, would equally well suit Humboldt's colour pattern description, but occur outside Humboldt's collecting area.

No types are preserved of either *Cychla flavomaculata* or *C. trifasciata* Jardine (1843), both reported from the Rio Negro and Rio Padauiri. The colour description and painting of *C. flavomaculata* agree with *C. temensis*, and there is no similar species with black bars and horizontal rows of light spots in the area:

"The body is greenish lake, with three black bars, three rows and several scattered yellow spots; on the head several black spots, and a peacock-eye on the insertion of the tail. Dorsal fin and upper part of tail, indigo spotted with light blue; ventral, anal, and lower half of caudal fin vermilion; pectoral greenish; gill-rays vermil-

ion; belly lighter than the other parts of the body." (Jardine, 1843: 145).

The description of *C. trifasciata* derives mainly from a drawing provided by Schomburgk. The local appellation provided, Lucanari Grande, is a Guyanese-Spanish mix, and not likely to derive from the Brazilian portion of Rio Negro, where the corresponding Tupi-Guarani would have been Tucunaré-açu. Nonetheless, the drawing (Jardine 1843: pl. 9) shows a fish clearly referable to *C. temensis*. It is apparently a breeding male as it features a small but distinct hump. The body is greenish, with grey dorsum, three wide dark vertical bars, black spots on the head side apparently representing the postorbital stripe and associated spots on the gill cover, but no yellow spots or lines on the side. Lower fins, iris and branchiostegal membrane are painted dull or bright red.

Heckel's *Cichla tucunare* is based on a stuffed specimen 2 feet long from Rio Branco, probably more precisely Forte do Rio-branco (= Forte or Fortaleza de São Joaquim, near Boa Vista), where the local name was recorded (Heckel, 1840: 409). The holotype cannot now be located, but the description agrees very well with *C. temensis*. *Cichla tucunare* is diagnosed as having continuous lateral line and 110-120 scales; three vertical bars on the side, a narrow postorbital stripe, a caudal ocellus and rows of milky white spots behind the caudal ocellus. Heckel also mentions traces of yellowish spots on the body and dorsal fin. Heckel (1840: 413) apparently also had one or more specimens of *C. temensis* from Rio Negro, but those were smaller specimens (13 inches TL) showing characteristic rows of light spots along the side.

The description of *Cichla unitaeniatus* Magalhães (1931) may have been unintentional, and is not so precise as to permit unequivocal identification of the species. It is contained in a note headed "Nota: TUCUNARÉ-SUBIANA – Chichla uitaeniatus, ? – Rio Negro" (corrected in the errata to tucunaré sorubiana, *Cichla unitaeniatus*). Magalhães never observed a specimen, but describes the species on characters supplied by "credible persons": "Whitish tucunaré with a dark band along the lateral line; this band starting a little behind the gill opening and runs to the base of the caudal fin, forming a slight curve". The species is further said to be the largest tucunaré species in the Negro and Purús, attaining 80 cm total length, but is not as common as *C. ocellaris*. Given the distribution, the large size, the name sorubiana (cf. sarabiana of Natterer), and the compatible colour pattern (typical of young *C. temensis* only), it seems likely that the description refers to *C. temensis* and not to any other Mid-Amazonian species of *Cichla*. However, at commercial sizes none of the *Cichla* species would show a horizontal stripe as described by Magalhães.

Steindachner (1883: 3, pl. 1 fig. 3), reports a 26 cm SL specimen of C. *temensis* from Iquitos in Peru said to have 95 scales along the side, and provided a figure stated to show a juvenile specimen. He also reports a 22 cm SL specimen of *C. ocellaris* from the Rio Huallaga, but illustrats the species with a juvenile (1883: 3, pl. 1 fig. 2). The figure of *C. temensis* shows a juvenile *C. temensis* or possibly *C. pinima*, whereas the figure of *C. ocellaris* shows a young *C. orinocensis*. The illustrations apparently do not show Peruvian specimens, but are probably based on material from the Thayer Expedition, traveling only within Brazil, from which specimens of *C. temensis* and *C. orinocensis* were deposited in NMW. Steindachner (1883: 3) states that he would provide detailed descriptions of the variability within *C. ocellaris* in the second part of his paper on Amazonian cichlids. The first part (Steindachner, 1875) dealt almost exclusively with Thayer Expedition material. This second part, however, was never published. The Peruvian *Cichla* specimens were deposited in the Museum für Tierkunde, Dresden. The *C. temensis* specimen was discarded in 1909, and the *C. ocellaris* specimen was identified by Kullander (1986: 60), as a probable *C. monoculus*.

Although *C. temensis* may be the largest species of *Cichla*, and consequently the largest species of cichlid in South America, precise measurements of large specimens are scarce, and it is not always documented whether lengths are standard or total lengths. There appear to be no really large specimens in museum collections. The sport fishing weight record is 27 lbs (12.25 kg) (IGFA data at http://www.peacockbassassociation.com/). Jepsen et al. (1999) reported a maximum length of 750 mm SL and maximum weight of 9.2 kg in *C. temensis* from the upper Rio Negro. Winemiller (2001: p. 98) gives maximum sizes 810 mm SL in rivers and 621 mm SL in reservoirs in Venezuela. Román (1981: 83) has a photo of a 710 mm SL specimen. Other species of *Cichla* generally do not exceed 500 mm in SL, and rarely more than

400 mm SL. Large specimens are recorded of *C. orinocensis* (617 mm by Machado-Allison, 1971; 410-565 mm by Jepsen et al., 1999), and *C. intermedia* (429 mm by Jepsen et al., 1999).

Cichla intermedia Machado-Allison, 1971
(Figs. 90-92)

Cichla intermedia Machado-Allison, 1971: 473, fig. 7 (río Casiquiare, Territorio Federal Amazonas. Holotype MBUCV V-6489).

Material examined. Six specimens, 87.6-192 mm SL. **Venezuela: Rio Orinoco drainage:** MBUCV-V 3477, paratypes, 3, 87.6-137.3 mm SL; Apure, Rio Cinaruco; 6 Mar 1966, V. E. Ogilvie. – MBUCV-V 6498, 1, 192 mm SL; Apure, Rio Cinaruco; 26 Feb 1964. C. Rivero. – MBUCV-V 6496, paratype, 1, 153 mm SL; Amazonas, Quiritare, 4 h before mouth of Rio Cunucuna; 3 Oct 1966, R. Campos & C. Duque. – MBUCV-V 12819, 1, 88.9 mm SL; Amazonas, Rio Cataniapo, ca 300 m from mouth, in small caño. 3 Jul 1981, R. Royero et al.

Diagnosis. Juveniles with uninterrupted dark band along middle of side, young and adults uniquely distinguished among species of *Cichla* by colour pattern with lateral band transformed to row of irregular dark blotches and six or seven narrow dark vertical bars across side below dorsal fin (corresponding in position to bars 1, 1a, 2, 2a, 3, additional bar below end of soft dorsal in base, and occasionally one anteriorly on caudal peduncle). Adults with several small black blotches posterior to orbit and on gill cover. Light spots on side absent at all sizes (vs. present in most other species of *Cichla*). Lateral line almost always continuous; scales in E1 row 96-108.

Description. Refer to Figs. 90-92 for general shape and colour pattern, Table 26 for morphometrics, and Tables 2-10 for meristics.

Relatively elongate (depth 25.7-30.7 % SL, N = 6, 88-192 mm SL). Frontal contour straight ascending, gently curved between eye and dorsal fin origin. Nuchal hump absent in specimens observed by us, but present in specimens on published photographs (Román, 1981: 68). Maxilla reaching to below middle of orbit, lower jaw to below posterior margin of orbit. Lateral line continuous on both sides in four specimens, continuous on one side in one specimen, and bilaterally discontinuous in one.

Dorsal-fin spine 4 longest; soft dorsal fin rounded, reaching about middle of caudal peduncle in small specimens, slightly beyond middle in specimen 192 mm SL. Soft anal fin rounded, extending as far as soft dorsal fin. Caudal fin emarginate, with angled corners in specimen 89 mm SL, concave with angled upper corner and rounded lower corner in 137 mm specimen, in larger specimens generally injured, shape not unambiguously determinable. Pectoral fin rounded in specimen 89 mm SL, rays 5 and 6 longest, reaching about halfway to anterior anal fin rays; in larger specimens subacuminate or acuminate, ray 4 longest, reaching halfway to soft anal fin. Pelvic fin rounded in specimen 89 mm SL, rays 1-2 longest, reaching about halfway to anterior anal fin rays; in larger specimens becoming subacuminate, tip terminated by ray 1, extending

Table 26. Morphometry of *Cichla intermedia*. Measurements are in percent of SL, except SL (in mm). Linear regression parameters calculated from original measurements in mm.

	N	min	max	mean	SD	a	b	r
SL (mm)	6	87.6	191.9	125.2				
Head length	6	31.5	35.5	33.0	1.51	2.7221	0.3058	0.994
Snout length	6	11.0	12.3	11.5	0.55	–0.2685	0.1175	0.992
Head depth	6	20.5	23.2	21.7	1.19	–3.3703	0.2461	0.995
Body depth	6	25.7	30.7	27.2	2.05	–5.3279	0.319	0.988
Orbit diameter	6	7.8	10.0	9.0	0.89	3.2846	0.061	0.999
Interorbital width	6	6.5	8.2	7.3	0.64	–2.3048	0.0932	0.997
Pectoral fin length	6	17.2	23.6	20.5	2.21	–7.7116	0.2727	0.997
Upper jaw length	6	14.1	15.5	14.6	0.57	–0.4633	0.1504	0.995
Lower jaw length	6	18.2	20.0	18.8	0.66	0.1854	0.1859	0.997
Caudal peduncle depth	6	9.1	10.9	10.2	0.65	–1.8005	0.1178	0.996
Caudal peduncle length	6	16.8	19.5	18.2	1.16	4.0503	0.1464	0.997
Dorsal spine length	6	11.1	12.9	11.9	0.89	–1.8308	0.1351	0.987

Fig. 90. *Cichla intermedia*, MBUCV-V 12819, 88.9 mm SL; Venezuela: Amazonas: Rio Cataniapo.

Fig. 91. *Cichla intermedia*, paratype, MBUCV-V 3477, 137.3 mm SL; Venezuela: Apure: Rio Cinaruco.

Fig. 92. *Cichla intermedia*, MBUCV-V 6498, young female, 192 mm SL; Venezuela: Apure: Rio Cinaruco.

about halfway to anal fin origin.

Scales absent from dorsal fin in small specimens, in specimen 137 mm SL a few scales present basally on soft dorsal fin, in specimen 192 mm SL double rows in single band behind each soft ray, except on last four interrradial membranes, squamation extending for about ¾ of length of rays. Scales present on anal fin in all specimens, in 89 mm specimen only on spinous portion and bases of anterior soft rays, in specimen 192 mm

SL anal fin densely scaled anteriorly, scales in bands of up to three scale rows anteriorly, gradually fewer and restricted to basal part of fin posteriorly. Scales present on caudal fin, reaching to ⅘ of dorsal and ventral lobes in specimen 89 mm SL, but on middle rays only to middle of fin; in specimen 192 mm SL squamation extending to near posterior margin of fin, except that scales absent along middle portion of median interradial membranes for most of their length. Scales absent from pectoral fin. Scales present anteriorly on lateral aspect of pelvic fin, in specimen 192 mm SL also on medial aspect.

Colouration in preservative. Specimen 89 mm SL (Fig. 90) with light brown dorsum, nape and dorsal snout, paler on side; underside of head, chest, abdomen and ventral aspect of caudal peduncle whitish. Indistinct greyish preorbital stripe. Dark brown band from orbit to tip of opercle. Along middle of side a dark brown band, about four to five scales wide anteriorly, six or seven scales wide posteriorly, from supracleithrum to caudal fin base, continuous with caudal blotch, and covering lower lateral line scales. Band lined dorsally and ventrally by indistinct paler border. Six narrow brownish bars across side: bar 1 below first spines of dorsal fin, bar 1a below dorsal-fin spines 6-7, bar 2 below dorsal spines 10-11, bar 2a below last two dorsal-fin spines, bar 3 below about dorsal-fin soft rays 3-4; and one more indistinct bar below end of dorsal fin base. Bars extend to horizontal level of lower pectoral-fin base or shorter. Dorsal fin hyaline, soft part with brown cross bar marking proximal ⅓. Anal and pelvic fins colourless. Caudal blotch contained in extension of lateral band, but more deeply pigmented, situated above lower lateral line level; darker brown, gradually narrower on middle, unscaled caudal fin to middle of fin; middle membranes of caudal fin brownish distally, lobes greyish.

Medium sized specimens (Fig. 91: 137 mm SL) with light brown dorsum, nape, snout, dorsal aspect of caudal peduncle; somewhat lighter on side. Preorbital stripe absent. One or two dark brown blotches behind orbit, one on preopercle, irregular band dorsally on operculum, dot on membrane distal to supopercle dorsal tip. Dark spot anterior to pectoral fin base dextrally. Dark spot on margin of opercle adjacent to subopercle sinistrally. Lateral band dark brown, uneven, with widenings where crossing vertical bars, posteriorly at least one scale above lateral line scales; narrowly connected to caudal blotch. Lighter ground colour adjacent to lateral band. Bars 1, 1a, 2, 2a, 3 only indicated. Spinous dorsal fin not pigmented. Soft dorsal fin light greyish with cross rows of white spots. Caudal blotch black, horizontally oval, above lower lateral line level, irregular, with light border. Along middle of caudal fin alternating dark and light spots.

Young adult 192 mm SL (Fig. 92) overall brownish, discoloured. Indistinct preorbital stripe. Dark brown spots between eye and preopercular tip; spots medially on opercular dorsal margin and distally at opercular tip. Vertical bars relatively faint, only reaching little below lower lateral line level; irregularly spaced, six on right side, seven on left side, last below posterior part of dorsal-fin base. Dark brown, irregular horizontal band extended into blotches where crossing vertical bars, extending to penultimate vertical bar, posteriorly as row of scattered blotches to middle of caudal peduncle well above lateral line. Dorsal-fin spinous part brownish, soft part brownish with five cross rows of light spots. Anal fin brownish, lighter posteriorly. Pelvic fin brownish, lighter distally and medially. Caudal fin brownish, lighter along middle rays. Caudal blotch horizontally oval, black, with complete light ring.

Published photographs of large adults (Machado-Allison, 1971: figs. 7, 9, 320-375 mm SL; Winemiller, 2001 fig. 1, lower left; Román, 191: 67-68, 81): Lateral band consisting of row of blotches, variously contiguous or discrete where crossed by bars 1-4, followed by a row of irregular blotches along dorsal half of caudal peduncle. Spots on opercle and behind eye small, deep black. Caudal spot round with contrasting light ring. Dorsal fin blackish throughout.

Live colours. "Body generally greenish blue; abdomen white along midline and orange on the side. A discontinuous black band along middle of side (continuous in juveniles); eight or nine transverse bands less apparent than the one preceding. Dorsal fin and upper half of caudal bluish with clear spots. The membranes of the gill opening, pelvic fins and anal fin intensely orange, sometimes a vivid red. Lower half of caudal fin brick red. Pectoral fin colourless. Head bluish dorsally and yellow or greenish yellow on the side. Lower jaw and branchiostegal membrane orange. Eye with black pupil and the iris dark red" (Machado Allison, 1971: 473, translated, also

ibid., fig. 7). Winemiller (2001: 97, fig. 1, lower left) described the ground colour as varying from a dull grey-green to a brilliant turquoise green depending on environmental conditions and reproductive state.

Geographical distribution. Specimens at hand are from the Rio Cinaruco in Apure state, and from the Rio Casiquiare (Rio Cunucuna, Rio Cataniapo), reflecting the fragmented range given by Machado-Allison (1971: fig. 13, also including the Rio Siapa drainage) (Fig. 9). Winemiller (2001: fig. 2) also included the lower Rio Caura in the distribution. There are no records from Colombia, although the species is probably present also in that country.

Local names. Pavón real (Román, 1981: 79).

Notes. The original description of *C. intermedia* (Machado-Allison, 1971) is fairly detailed and well illustrated, with consideration of the ontogenetic variation in colour pattern. We cannot make out adult caudal fin shape in our specimens, but Machado's (1971: fig. 7) photo of a large male suggests a rounded hind margin, with angled dorsal corner and rounded ventral corner. Also at this size (375 mm) the body shape is relatively elongate.

Machado-Allison (1971: table 4) gave lateral line counts as follows [our reported counts on the same specimen in brackets], 84, 54+42 [54/37], 48+39 [86], 93 [86], 94 [88], 40+38, 47+35, 45+38 [80], 50+41, contrasting with our observation that a continuous lateral line is more common (in five of six specimens examined). Machado-Allison's higher counts suggest that scales on the caudal fin base were included.

The type series of *C. intermedia* includes the holotype, MBUCV V-6489, 277 mm SL, and five paratypes, MBUCV V-160, MBUCV V-3477, and MBUCV V-6496. In Machado-Allison (1971), table 4, giving measurements and count, the holotype is not included, but the paratypes, and two additional specimens, MBUCV V-6498 (211 mm SL), and SOAAC No. 3 (375 mm SL). There is no illustration of the holotype, and the illustrations present do not provide catalogue numbers. Machado-Allison's (1971) figure 7, in colour, probably shows SOAAC 3 (legend states length 375 mm), figure 8 shows MBUCV V-3477 (agrees with specimens examined by us), and figures 10-11 (upper fish) show MBUCV V-6498 (agrees with specimen examined by us). Figure 11 is captioned "Juveniles de *Cichla ocellaris* (a) y *Cichla intermedia* (b)", but is only a reduced copy of fig 10, showing adults of *C. intermedia*, *C. ocellaris* [= *C. orinocensis*], and *C. temensis*. Figure 9 shows three adult *C. intermedia*, 200-320 mm according to the caption, suggesting that the smallest specimen is MBUCV V-160, the 320 mm specimen is undocumented, but the intermediate-sized specimen could then be the holotype.

Román (1981: 67) argued that the name "Cichla nigrolineatus" introduced by Ogilvie (1966) is available, and thus has priority over *C. intermedia*. Ogilvie (1966) is an internal report written in an informal style and apparently intended chiefly for circulation within the Florida Game and Fresh Water Fish Commission. We have not been able to examine an original of the report, but we have xerox copies of originals from two different sources. The report is unbound and in type writing and definitely gives the impression of having been distributed as xerox copies or produced by some other copying method. It may be printed in agreement with International Code of Zoological Nomenclature Article 8.4, which permits hectographing or mimeographing, but it was not published in the sense of the International Code of Zoological Nomenclature Article 8.1.1, and maybe also Article 8.1.2.

In Ogilvie's (1966) report, *C. intermedia* is consistently referred to as *Cichla U4*, and recognized as distinct from four other species reported on as U1, U2, U3, and U5. The header for the descriptive account is: "*Cichla U4* (suggested species name *Cichla nigrolineatus* by Ogilvie 1966)." There is no further use of "nigrolineatus" in the report. Román (1981) consistently used the designations "*C. nigrolineatus*" and "*C. nigrolineatus* o *C. intermedia*", referring to Ogilvie (1966) for the name, and explicitly identifying "C. nigrolineatus" and *C. intermedia* as the same species. We consider this usage unavailable because Román did not explicitly state any intent to the effect of making the name available. He was just arguing that Ogilvie (1966) was an available publication.

The largest specimen of *C. intermedia* recorded was 429 mm SL (Jepsen et al., 1999; Winemiller 2001: 98).

Discussion

Species diversity. Despite being one of the most colourful, well-known, and most commercial of the genera of cichlids, of importance to artisanal as well as tourism based sport fishing, and among the largest fishes in the Neotropics, the taxonomic confusion in *Cichla* has remained considerable.

A major source of confusion has been the obvious acceptance in species of *Cichla* of much more than modest variability in colour pattern, both ontogenetic and between individuals, as well as a traditional recognition of just a few species. This has been possible because most authors have only dealt with very few specimens or a restricted geographical region. In this paper, covering a wider geographic area, we have been able to organise phenotypic variation within the genus into spatially clustered units representing 15 distinct phylogenetic species.

The species diversity of *Cichla* is thus demonstrated to be much greater than indicated by current literature. Nevertheless, we believe the work on a revision of *Cichla* has just started. Our species accounts include references to samples that cannot be satisfactorily assigned, and some species are still known only from a few specimens. Huge areas within the geographical range of the genus have not been sampled for fishes. We expect that there may likely exist between 20 and 30 species of *Cichla*, which require large series of specimens and more extensive sampling to be located and diagnosed. Hopefully, this revision can inspire more efforts in further revising the genus.

Morphometric and meristic variation. Scale and fin counts are moderately efficient in separating species, and are summarised in Tables 2-10. The lateral scale counts (Table 2) span from 67 to 128, comparable only to *Crenicichla* and *Teleocichla* among other Neotropical cichlid genera. Intraspecific ranges varies from 8 to 32, apparently correlated both with sample size and maximum scale number. Large-scaled species, *C. ocellaris, C. orinocensis, C. nigromaculata, C. monoculus, C. kelberi, C. pleiozona, C. melaniae, C. melaniae,* and *C. thyrorus* generally possess less than 90 E1 scales, whereas remaining, small-scaled species, generally possess more than 90 scales (*C. piquiti* and *C. pinima* down to 83 and 86 respectively). The overlap is considerable in the genus as a whole, and there are no instances of normal distribution. The slender species tend to have more scales. Three potential low frequency counts occur in the distribution (Table 2, Fig. 4), potentially distinguishing classes of scale counts. The first at 81 scales (3 specimens) separates *C. ocellaris*, *C. monoculus* and *C. mirianae* as having lower scale counts. At 88 scales (2 specimens) *C. orinocensis*, *C. nigromaculata*, *C. kelberi*, *C. melaniae*, and *C. thyrorus* are separated from the small-scaled species *C. piquiti*, *C. jariina*, *C. pinima*, *C. vazzoleri*, and *C. intermedia*, and at about 110 scales (3 specimens) *C. temensis* separates from the rest. With this interpretation, only *C. kelberi* significantly spans over the drop at 88 scales. Alternatively, a drop at 92-93 scales (3 specimens each) separates large-scaled and small-scaled species, with two species transcending, *C. piquiti* and *C. pinima*.

Cichla is occasionally diagnosed as having a continuous lateral line as young, frequently becoming discontinuous in the adult (Eigenmann, 1912; Newsome, 1971; Stiassny, 1982, Webb, 1990) in contrast with most cichlids, which have a dorsal anterior lateral line section and a midaxial posterior section at all sizes. However, a continuous lateral line (Table 3) occurs frequently (61-85 % of the specimens) only in four species, viz. *C. ocellaris*, *C. thyrorus*, *C. temensis*, and *C. intermedia*. The condition is exceptional (4-7 %) in *C. orinocensis, C. pleiozona,* and *C. piquiti*, and infrequent in *C. pinima* (36 %) and *C. vazzoleri* (15 %). Three of six specimens of *C. jariina* possess continuous lateral line. As with the E1 scale counts, there is no normal distribution and ranges overlap for lateral line scale counts, with small-scaled species tending to have more lateral line scales.

Discontinuous lateral line occurs in all species of *Cichla*. Counts of scales in the upper lateral line (Table 4) vary similar to scale counts in the E1 row and continuous lateral line. The number of scales in the lower lateral line (Table 5) is more restricted, with *C. temensis, C. vazzoleri, C. pinima,* and *C. piquiti* having slightly higher numbers than the rest, but also greater variation. The overlap between species is almost complete. There is no indication of an ontogenetic transition from continuous to discontinuous state in any of the species. The early development of the lateral line tubes is bidirectional (cf. Webb, 1990), with caudad succession in the anterior (upper) sequence and rostrad succession in the posterior (lower) sequence. Some of the variation in species usually possessing a continuous lateral line, observed

as tubed scales, may thus be influenced by misalignment or small size. The smallest specimens recorded with a continuous lateral line are 45.5 (*C. temensis*), 50.0 (*C. ocellaris*), and 62.1 mm SL (*C. jariina*).

The total number of dorsal fin spines and rays (Table 6) is modally 32 in all species except *C. jariina* with 31. All species have modal count XV.17 except *C. jariina* (XV.16), *C. vazzoleri* (XV.16), and *C. nigromaculata* (XVI.16). Also *C. pinima* and *C. thyrorus* have a high frequency of XV.16. The frequency distribution of anal fin rays (Table 7) shows little variation, with 11 rays modal for the genus and all species. The pectoral fin count (Table 8) varies between 14 and 15, with occasional 13 or 16. Higher numbers occur principally in the more elongate species, viz. *C. pinima, C. vazzoleri, C. temensis,* and *C. intermedia,* but also in *C. jariina*.

Vertebral counts (Table 9) separate species into two groups, those with modally 36 vertebrae (18+18 or 19+17), and those with 35 (almost exclusively 18+17), and *C. jariina* exceptional with 34 vertebrae.

Gill rakers (Table 10) were counted as distinguishable units, and since the anteriormost gill rakers become flat and contiguous in large specimens, the variation in counts to some extent reflects the length of the specimens in the sample. Our only conclusion is that gill-raker counts are generally between 13 and 15, with juveniles having up to 20. The higher numbers in *C. temensis* may reflect a later transformation as well as a higher average.

Morphometric information is available from 304 specimens 29.3-414 mm SL (Tables 12-26). In a principal component analysis of morphometric distance data (Fig. 3, Table 11), there are only traces of allometry, except in the orbital diameter, and shearing factor 2 did not alter the scatter. Species with complete or abbreviated juvenile lateral band tend to cluster apart on factor 2, but show considerable overlap. Variation mainly refers to body depth, which tends to be less in several species with complete juvenile lateral band (particularly *C. intermedia, C. jariina, C. pinima, C. temensis*, and *C. vazzoleri)* compared to species with abbreviated juvenile band (*C. kelberi, C. monoculus, C. ocellaris*, *C. orinocensis*, *C. pleiozona*, and probably *C. nigromaculata*), and caudal peduncle length, which tends to be correspondingly longer. *Cichla piquiti* and *C. thyrorus* cluster in the midrange, and *C. mirianae* and *C. melaniae* span both major clusters. In comparing similar species, there are no trenchant morphometric differences. Proportional measurements for each species are summarized in Tables 12-26. Whereas some species of there is variation between extremes the overlap prevents use of proportional characters to identify specimens to species. Figure 4 illustrates the gradual variation in body depth expressed as per cent of SL, with species with abbreviated juvenile lateral band having body depths up to 31.5-34.6 % SL, the more deep-bodied species of species with complete lateral band up to 30.7-32.8 % SL, and the slender species (particularly *C. intermedia, C. jariina, C. pinima, C. temensis,* and *C. vazzoleri*) maximum body depths 27.3-30.7 % SL, with *C. temensis* at the extreme with a variation 21.3-27.3 % SL (Tables 12-26). A comparison including only large specimens (>199 mm SL; graph not shown) produces the same general graphic pattern, but with less confidence and excluding *C. intermedia* of which no large specimens were available.

In the morphologically diverse South American cichlid genus *Crenicichla* body depth varies from 12.5 % SL in small, elongate species, to 32.4 % (N = 590) (pers. obs.). In genera representing a "normal" South American cichlid body plan, and with very little interspecific differences, the variation is 37-45 % of SL (N = 475) in *Aequidens*, and 34-45 % SL (N = 322) in *Satanoperca* (pers. obs.). The magnitude of variation in *Cichla* is thus comparable with *Aequidens* and *Satanoperca* albeit values are contained within the upper range of *Crenicichla*.

Juvenile colour pattern. Comparatively little is known about larval and juvenile cichlid colour pattern ontogeny, although it is potentially phylogenetically informative. *Cichla* and *Crenicichla* are the only genera of South American cichlids with a juvenile colour pattern including a horizontal midlateral stripe (Figs. 37, 49, 50-51, 55, 60, 64-66, 72, 74, 76-77, 81-85, 88, 90-91), and some species of *Cichla* are unique in the possession of an abbreviated lateral band extending only between the posterior lateral blotch and the caudal fin base (Figs. 5, 10-13, 24, 28-30).

Species with a complete lateral band include *C. intermedia, C. jariina, C. melaniae, C. mirianae*, *C. pinima, C. piquiti*, *C. temensis, C. thyrorus*, and *C. vazzoleri*. In these species, the lateral band remains to at least 100-150 mm SL, in *C. mirianae* and *C. intermedia* it remains as an irregular stripe

in large adults. Species with an abbreviated lateral band include *C. kelberi*, *C. monoculus*, *C. ocellaris*, *C. orinocensis*, and *C. pleiozona*. In these species, the band fades away before or at about 100 mm SL. In the smallest specimen of *C. pleiozona* (109 mm SL, Fig. 33), the caudal peduncle band is about to fade away. Juveniles of *C. nigromaculata* have not been available.

In the smallest specimens available, about 20-30 mm SL, the lateral band is present along with blotches 1 and 3, and the lateral band is more intense caudally in *C. temensis* (Fig. 81), but only blotches 1 and 3, and the caudal portion of the lateral band is present in *C. orinocensis* (Fig. 10), and *C. kelberi* (Fig. 28). Blotch 2 is absent or rudimentary. Small juveniles available to us were generally not purposefully preserved, and since the diagnostically helpful scale count cannot be used at least not without damaging the specimen, identification relies to some extent on presence of larger specimens from the same collecting event or site. Although it appears that there is a difference between species with complete or abbreviated band already at very small sizes, the material at hand is insufficient for conclusions. Specimens 40-60 mm SL are available of most species. At this size the two different juvenile colour patterns are clearly demonstrable and includes a recognizable blotch 2. The abbreviated lateral band is, however, reflected in species with a complete band, in which it may appear as a caudal intensification of the lateral band (e.g., Fig. 81).

Small juveniles of *Crenicichla* (10-19 mm SL) display a continuous black band from snout to caudal fin, but no blotches or vertical bars. In *Crenicichla*, the lateral band is retained into the adult stage in many species, but is commonly lost in adults of the larger species. Several species of *Crenicichla* are vertically barred as adult, but there is no information about early colouration ontogeny in those species. A juvenile, 21.6 mm SL of *C. semifasciata*, a species with a series of blotches along the middle of the side as adult, has a near-continuous lateral band. We have not been able to examine juvenile *Teleocichla*, a genus closely related to *Crenicichla*.

Adult colour pattern. In juveniles of all species there is some dark pigment in a band from the orbit caudad to the margin of the gill cover, much less intense in species with abbreviated juvenile lateral band than in species with complete lateral band. In adults, only *C. temensis* retains this postorbital band, whereas it is absent from *C. kelberi*, *C. monoculus*, and *C. pleiozona*, and either absent or represented by a few scattered small black spots in *C. ocellaris* and *C. orinocensis*, and probably in *C. nigromaculata*. It is represented by a few large, usually ocellated blotches in *C. intermedia*, *C. jariina*, *C. pinima*, *C. piquiti*, *C. thyrorus*, and *C. vazzoleri*, and usually associated with a few similar blotches on the opercle, but in *C. melaniae* and *C. mirianae* the postorbital blotches are notably minute. In adults, a black marking may be present on the anterodorsal process of the preopercle, either round or extended as a short stripe. This marking was observed only in *C. intermedia*, *C. jariina*, *C. mirianae*, *C. thyrorus*, and *C. vazzoleri*, and variably in *C. pinima*.

Several species with complete juvenile lateral band share a common pattern of relatively regular horizontal rows of light spots, including two rows marginal to the lateral band, and one more dorsal and one more ventral, viz. *C. jariina*, *C. pinima*, *C. temensis*, *C. thyrorus*, and *C. vazzoleri*. Among those species, the rows are most neatly linear in *C. temensis*, but commonly include irregularities in the other species. In *C. melaniae*, and *C. mirianae* there are many scattered small spots on the side. In *C. piquiti* these spots may be absent, although young specimens possess light margins to the lateral band. In remaining species of *Cichla* a pattern of distinct light spots never shows; however, a very dense mottling by small light spots has been observed in at least some specimens of *C. kelberi*, *C. monoculus*, *C. ocellaris*, *C. orinocensis*, and *C. pleiozona*, apparently producing a golden sheen to the side in living specimens (Figs. 9, 26).

Each species of *Cichla* possesses a distinctive adult colour pattern, which is more contrast rich in males, and in most species includes large black blotches on the side lined with silver or golden. These ocellar markings derive from vertical bars and are believed, in the absence of systematic gonadal or field behavious surveys, to represent breeding markings. The only exceptional species may be *C. piquiti*. In *C. kelberi*, *C. monoculus*, and *C. pleiozona*, the breeding colouration is dominated by intensified blotch-like dorsal portions of the vertical bars best exemplified by Fig. 26, see also Figs. 27, 32, 36). In *C. ocellaris* and *C. nigromaculata* there may be dorsal blotches (Figs. 8, 22), but other specimens of *C. ocellaris* possess ocellated markings retracing portions of the bars

(Kullander & Nijssen, fig. 10). *Cichla orinocensis* and *C. mirianae* are unique in possessing a series of three distinct ocellated blotches along the middle of the side, formed directly from the juvenile lateral blotches. In *C. mirianae* the blotches are mediated by the lateral band whereas in *C. orinocensis* they are usually separate. In *C. intermedia* minute ocellated blotches may develop in several of the vertical bars, and are mediated by the irregular lateral band. No adult breeding males have been available of *C. melaniae*, but it seems that in this species sides are sprinkled with ocellated spots, and the vertical bars are deep black and narrow (Fig. 48). *Cichla jariina*, *C. pinima*, *C. thyrorus*, and *C. vazzoleri* possess ocellated blotches tracing portions of the precursory vertical bars (Figs. 58-59, 63, 69-72, 78-79). In *C. temensis*, vertical bars remain wide and distinctive but are not, or only narrowly margined with light.

Species of *Cichla* differ in the number of vertical bars on the side. Three principal dark bars in homologous position occur in all species, and less intensely pigmented dark bars appear between the principal bars in *C. melaniae*, *C. nigromaculata*, *C. ocellaris*, and *C. piquiti*. The observational basis for this character state is somewhat weak in *C. melaniae*, based on one preserved specimen and photographs. *Cichla intermedia*, *C. pleiozona*, and individuals of other species frequently possess a bar anteriorly on the caudal peduncle. In *C. intermedia* with typically six bars, the bars are somewhat irregularly arranged and there may be additional bars. The pattern of three prominent dark markings on the side (blotches in juveniles, bars in adults) is highly unusual among cichlids, which typically possess several vertical dark bars and a dark blotch approximately at the middle of the side. Among Neotropical cichlids, only *Satanoperca daemon* (two blotches) and *S. acuticeps* (three blotches) stand out having more than one prominent, more or less ocellated blotch on the side. Adults of *Boulengerochromis microlepis*, a large cichlid species in Lake Tanganyika, possesses three large blotches along the middle of the side. Among riverine African cichlids the larger species of *Hemichromis* and the large tilapia species *Oreochromis andersonii* also possess three large midlateral blotches. All these species have multiple vertical bars. Many other cichlids possess a series of dark blotches along the side, in the position of vertical bars.

Cichla is apparently unique in starting in early ontogeny with two to three midlateral blotches, and developing a barred state later in ontogeny. Very small specimens of *Cichla* have not been available. The smallest specimens reliably identified are 16 mm SL and already well past the larval stage. Free swimming *Cichlasoma dimerus*, a cichlasomatine South American cichlid, possess pigment patches gradually developing into vertical bars already at about 5 mm length (Meijide & Guerrero, 2000). The lateral blotches in juvenile *Cichla* may correspond positionally to the bar immediately posterior to the pectoral fin (bar 1) and above the anal fin (bar 3) in *C. dimerus* (Meijide & Guerrero, 2000: fig 8b), corresponding to bars 6 and 4-5 respectively in *Cichlasoma amazonarum* in Kullander (1983: fig. 4). It is not clear if the midlateral blotch in those cichlasomatine cichlids (bar 6 in Kullander, 2003: fig. 4) is a portion of the anterior juvenile bar (bar 7) or an independent pigment patch, but could correspond to the middle blotch/bar (bar 2) in *Cichla*.

Further study is needed to investigate the homology of colour markings in cichlids including *Cichla*, but the preliminary comparison suggests that the blotches and bars in *Cichla* may be homologous with elements in other Neotropical cichlids in which juvenile vertical markings are variously split, resulting in a basic pattern of 8 serially homologous dark bars in the adults of the majority of species (Kullander & Silfvergrip, 1991: 412). In the multibarred *Cichla* species, viz. *C. intermedia*, *C. nigromaculata*, *C. ocellaris*, *C. piquiti*, and to some extent *C. melaniae*, caudal peduncle bars cannot be observed, but taking the bar above the anal fin as fixed common homologue, the five bars below the dorsal fin correspond to bars 2-8 (4-5 being a divided bar) in the scheme of Kullander (1983) and 3-7 in that of Kullander & Silfvergrip (1991). Bar 8 in Kullander & Silfvergrip (1991) is a dark marking anterior to the dorsal fin, which is usually indistinct in *Cichla*. The caudal blotch in most Neotropical cichlids forms as a vertical marking and gradually becomes a dorsal blotch (Kullander, 1983: fig. 7), but in *Cichla* and *Crenicichla* it starts as a somewhat elongate mid-basal blotch continuous with the lateral band, and the blotch ends up in adults in a slightly more dorsal position as an effect of relative growth of adjacent areas. In *Crenicichla* the caudal ocellus is formed already at 20-25 mm SL.

The species most similar to other cichlids with regard to bar development is *C. intermedia* in which the typically six bars are relatively similar in width and intensity. Small juveniles have not

been available of that species, the smallest specimen examined 88 mm SL, at which size bars and horizontal band are well developed (Fig. 90).

Juvenile and subadult individuals of *Cichla* are fairly uniform in colour within samples and largely within species, and effects of preservation differences may account for most variation in museum specimens. There is variation in life colours of adults which has been related to habitat (Winemiller, 2001) and which also includes intensification of particularly red pigment in breeding individuals (Winemiller, 2001). Large adults in breeding colour, however, show considerable individual variation not only in intensity of markings but notably in the shape and distribution of ocellated components, and in the presence of various additional markings, observable in preserved specimens. The two sides of an individual may be quite differently patterned. We consider this variability to be highly unusual for adult cichlid fishes. In other South American cichlids, there may be variation particularly in intensity of markings, e.g., in *Symphysodon* (Bleher, 2006), but large conspicuous markings tend to be similar in expression between all individuals. We have three possible explanations for the variability of ocellated markings in adult *Cichla*, which we interpret as reduced or absent selection for a uniform colour pattern. Actually, variation in expression of colour markings among cichlids is usually considered as species markers.

a) Scale. *Cichla* species are among the largest cichlid species and the concerned markings are proportionally large. In a small cichlid, variation in expression of markings is likely to be less conspicuous than in a very large cichlid. In contrast, the other large cichlids, including species of *Crenicichla*, *Boulengerochromis microlepis*, *Caquetaia umbrifera*, *Oreochromis andersonii*, and *Parachromis dovii*, do not display the same variability. None of these species, however, possesses an elaborate pattern of conspicuous large markings on the body.
b) Individual recognition markings. In *Cichla* parental care and pair-formation during breeding may be facilitated by markings permitting individual recognition. Because of the large size, adult *Cichla* may have very few predators. There are almost no predatory fishes in South America that can attack and kill *Cichla* of sizes between 20 and 60 cm SL. Exceptions may be even larger *Cichla*, *Arapaima gigas*, large *Hoplias* and *Hoplerythrinus* and some large catfish species. The cost of a conspicuous breeding colour for breeders may thus be very low in relation to visibility to predators. The conspicuous colouration may also have a function in deterring smaller predators from approaching the brood, but could also signal presence of brood to brood predators. Biparental care is common among cichlid fishes, and usually involves some degree of sexual dichromatism, which facilitates sex recognition but not necessarily individual recognition. It remains to test why it would be more important in *Cichla species* to have individual recognition.
c) Relative growth. Colour pattern is related to surface dimensions such that growth patterns determine the development of colour markings. Under a steady growth to fixed adult size, genetically determined colour markings may be expected to produce identical patterns, as seems to be the case in small, early-maturing fishes. In large, late-maturing species which suffer several seasonal fluctuations in food availability, growth may be more irregular and development of pigment patches relative to body proportions may yield significant differences. This hypothesis requires further testing for correlation between pigment patch size and body proportions.

The caudal ocellus of *Cichla* and other large South American cichlid species has been interpreted as an anti-cannibalism marking (Zaret, 1977) or as an eye mimic deterring fin-eating piranhas (Winemiller, 1990). Those studies were based on species in which additional ocellar markings are absent from the body or other fins *(C. monoculus*, and *Astronotus* cf. *rubroocellatus)*, and should be extended to more prominently ocellated species. In *Crenicichla* species the caudal ocellus is fully formed at very small sizes (about 20-25 mm SL), at which size fin nipping by piranhas does not seem to be a major predatory threat, and the presence of the ocellus must have some other explanation. Nevertheless, we can confirm that piranha bites on the caudal fin are very rare in *Cichla*, although we are unable to judge if the low proportion is less than in sympatric species which lack a caudal ocellus. Figures 45 and 48 (lower specimen) demonstrate bites in the anal fin, presumably by piranhas; Figure 69 shows a bite in the lower part of the caudal fin. In large *Cichla*

specimens, the lower rays of the caudal fin commonly appear regenerated, with irregular scale cover, but we cannot directly relate such anomalies to fin predation.

Species phylogeny. The present paper makes use principally of external characters with the objective of formal description of diagnosable species. Diagnostic characters ideally are species autapomorphies, and the total number of characters available for hierarchical clustering methods remains limited; nevertheless the characters used should contain phylogenetic information. As detailed above, variability in morphometric characters (body proportions) is limited, with considerable overlap between species, and meristic variation is either very limited, irreconcilable between species, or highly variable. Colour pattern is most useful for constructing a character state matrix (Table 27), although some characters could not be assessed with confidence in all species (e.g., juvenile colour pattern). We offer the following analysis as a platform for discussion rather than as a strong hypothesis about a historical scheme of diversification.

Polarisation of character states is problematic because at the basal level at which *Cichla* resides in the cichlid phylogeny, characters used here are difficult to correlate with those of other cichlids. The outgroup applied for rooting represents *Retroculus*, which is the basal Neotropical cichlid taxon in Kullander's (1998) analysis, and *Crenicichla*, which is the sister group of *Cichla* in morphological phylogenetic analyses (Stiassny, 1987; Kullander, 1998) though not in molecular analyses (López-Fernández et al., 2005). For *Crenicichla* information was sampled from the *Crenicichla saxatilis* species group, which is morphologically most similar to cichlids in general.

The outgroup is coded to have bars 1a and 2a because they have more than three vertical markings, as discussed above. The abbreviated juvenile lateral band in *Cichla* is unique among cichlids and probably a wider group of fishes, whereas a complete band is present from *Crenicichla*. The occipital bar and potential homologue in other cichlids is moderately pigmented or absent in other cichlids. Postorbital markings of some kind are commonly present in cichlids, like in *Crenicichla*, but absent in *Retroculus*. No other cichlids have regular light spots along the side, and very few have any light spots on the side at all. The lateral line is discontinuous in almost all cichlids, except some *Cichla* and some extremely terete other cichlids *(Teleogramma*, *Teleocichla)*. Ocellated midline blotches are unique to some *Cichla* among cichlids (cf. above). Small species of cichlids generally have a low pectoral fin count, but large species usually have more than 14, e.g., 15-18 in *Crenicichla*, 15 in *Geophagus* and *Astronotus*, 16 in *Retroculus*. Total vertebral counts in cichlids are generally lower than 30; in the outgroup they vary between 32 and 34 in *Retroculus* and about 33-35 in *C. lepidota* and similar species. Ocellated vertical bars as in some species *(C. jariina*, *C. thyrorus*, *C. vazzoleri*, *C. pinima)* are unique to those taxa. Other cichlids except *Crenicichla* generally have much less than 67 E1 row scales, see above for discussion on possible subdivision into character states within *Cichla*. E1 scale counts vary between 34 and 40 in *Retroculus*, and generally between 35 and 60 in *C. saxatilis* group species.

Parsimony analysis using the branch-and-

Table 27. Character state matrix for species of *Cichla*. *Retroculus* and the *Crenicichla saxatilis* species group included as outgroup. Characters: **1**, a bars, 0 = present, 1 = absent; **2**, juvenile band, 0 = absent, 1 = complete, 2 = abbreviated; **3**, occipital bar, 0 = absent or faint, 1 = emphasized; **4**, postorbital marks, 0 = present, 1 = absent; **5**, light spots along side, 0 = absent, 1 = present, irregular, not persistent, 2 = regular rows; **6**, lateral line, 0 = usually or always discontinuous, 1 = usually or always continuous; **7,** ocellated midline blotches, 0 = absent, 1 = present; **8**, modal pectoral fin rays, 0 = 15 (or more in outgroup), 1 = 14; **9,** modal total vertebrae, 0 = 34, 1 = 35, 2 = 36; **10**, ocellated vertical bars, 0 = absent, 1 = present; **11**, principal variation in E1 scales, 0 = 30-60, 1 = 67-80, 2 = 81-88, 3 = 89-110, 4 = 111-128.

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**
Retroculus	0	0	0	0	0	0	0	0	0	0	0
Crenicichla	0	1	0	1	0	0	0	0	{0/1}	0	0
C. ocellaris	0	2	0	0	1	1	0	0	2	0	1
C. orinocensis	1	2	0	1	1	0	1	0	2	0	{1/2}
C. nigromaculata	0	?	0	0	?	0	0	0	2	0	{1/2}
C. monoculus	1	2	1	0	1	0	0	0	2	0	1
C. kelberi	1	2	1	0	1	0	0	0	2	0	1
C. pleiozona	1	2	1	0	1	0	0	0	2	0	{2/3}
C. mirianae	1	1	0	1	1	0	1	0	1	0	1
C. melaniae	0	1	0	1	1	0	0	0	1	0	2
C. piquiti	0	1	0	1	0	0	0	0	1	0	3
C. thyrorus	1	1	0	1	2	1	0	0	1	1	3
C. jariina	1	1	0	1	2	{0/1}	0	1	0	1	3
C. pinima	1	1	0	1	2	0	0	1	1	1	3
C. vazzoleri	1	1	0	1	2	0	0	{0/1}	1	1	3
C. temensis	1	1	0	1	2	0	0	1	1	1	4
C. intermedia	0	1	0	1	0	1	1	1	2	0	3

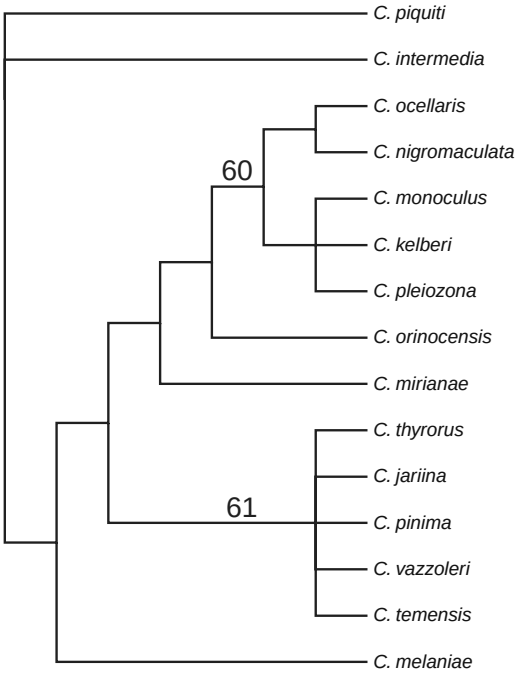

Fig. 93. Strict consensus tree of 14 most parsimonious trees of species of *Cichla*, based on 11 characters (Table 27). Multistate characters unordered, all characters of equal weight, multistate taxa treated as variable, tree length = 28, consistency index = 0.6071, retention index = 0.7755, rescaled consistency index = 0.4708. Numbers at nodes are bootstrap values (100 replicates) over 50 %.

bound algorithm in PAUP* (Swofford, 2001), results in a relatively well resolved consensus tree (Fig. 93), despite being based on more taxa than characters, and with only low bootstrap support for unresolved groups formed by *C. monoculus*, *C. kelberi*, and *C. pleiozona* (60 %), and *C. temensis*, *C. vazzoleri*, *C. pinima*, *C. thyrorus*, and *C. jariina* (61 %). In a majority of the trees *C. thyrorus* comes out as sister to remaining species in the latter clade.

Based on this preliminary analysis, we propose that *Cichla* phylogeny is characterized by a major branching represented by the species with abbreviated lateral band on one side, and the species with regular rows of light spots on the other side, and subsequent diversification in allopatry within these potential clades. The basal taxa, *C. melaniae (*lower Xingu), *C. piquiti* (Tocantins), and *C. intermedia* (parts of the Orinoco drainage) recover the Guiana and Brazilian shields, and the basal position fits with the position of *C. mirianae* (upper Xingu, Tapajós) at the base of the branch to the species with abbreviated juvenile band. With one exception, the widespread *C. monoculus*, all species of *Cichla* are associated with the Guianas and Brazilian shields, and generally with clear or black waters.

The elongate species with light spots are endemic to the Guiana shield, except *C. pinima* which is mainly collected from the southern bank of the Amazon, and *C. temensis* which is reported from the Madeira and Solimões.

Molecular divergence of *C. monoculus* + *C. orinocensis* vs. *C. temensis* is suggested in the trees of Farias et al. (2001, cytochrome b). In López-Fernandez et al. (2004, 2005), *C. intermedia* and *C. orinocensis* are sister to *C. temensis*, based on a morphological analysis and the mitochondrial ND4 gene, compatible with our conclusion.

Andrade et al. (2001) sequenced the rRNA 16S gene in *Cichla* samples identified as *C. temensis*, *C. monoculus*, and what they considered as intermediate possible hybrids based on external aspects. Their photographs suggest that their *C. temensis*, and two hybrid forms represent *C. pinima* (male, female). The photograph of *C. monoculus* may be correctly identified. The material list and tree suggests that *C. monoculus* (Clade B2), *C. kelberi* (Clade B3) and *C. vazzoleri* may also be included, and the 'hybrids' may just be ontogenetic stages or females. Although the cluster analysis (UPGMA) supports two major clusters ('*C. monoculus*' and '*C. temensis*' lineages), no further conclusions are possible without proper identification of the samples included.

Brinn et al. (2004) identified karyological evidence of hybridization between *C. monoculus* and *C. temensis* in the Rio Uatumã. Their illustrations show *C. monoculus* with aberrant colour pattern (fig. 1A), a *C. temensis* (fig. 1B), and two specimens identified as hybrids from the "juncture of Lake Balbina with the Uatumã River", but which we recognize as *C. vazzoleri* (fig. 1C, probable female; fig. 1D, probable male). The Balbina dam was completed in 1987. We identified *C. monoculus*, *C. temensis* and *C. vazzoleri* in pre-dam collections from rapids or close to rapids, dating back to 1983, and we identify the 'hybrid' *(C. vazzoleri)* also in the lower Rio Trombetas drainage. We thus suggest that there must be alternative interpretations of the karyological data.

Autapomorphies of *Cichla*. Stiassny (1982) diagnosed *Cichla* by four autapomorphic character states, viz. (1) bilateral elements of lower pharyngeal jaw united anteriorly, posteriorly diverging before sweeping laterad to form posteriorly directed muscular processes; dentigerous area covering almost all of dorsal face; (2) a dorsomedial part of the sternohyoideus muscle originating by a long tendon from the cleithrum and inserting musculously on the urohyal; (3) a flat anteroventral aponeurosis of the pars Al of the adductor mandibularis, extending caudad over the anteromedial face of the Al, the tendon linking maxilla and Al inserted nearer the neurocraniad condyle of the maxilla than in other cichlids, (4) a cartilaginous plate uniting hypurals 2 and 3.

A hypural cartilage is present also in *Geophagus* and *Biotodoma* (Kullander, 1986: 128). The appearance of the lower pharyngeal jaw, resembling the modal percoid condition, has been debated (Kullander, 1988, 1998; Stiassny, 1987). The semicircular ligament is present in percomorphs, including all cichlids except *Cichla*, and is possibly another autapomorphy; however, it is possibly absent also in some species of *Crenicichla* (Stiassny, 1992).

Kullander's morphological analysis of South American cichlids (1998, fig. 11, but states for characters 13, 38, 39, 47 with incorrect symbols) provided twelve homoplastic derived character states for *Cichla*. Two character states, however, were proposed as uniquely derived. (1) In small *Cichla* specimens, the basicranial apophysis for articulation with the upper pharyngeal bones is morphologically like in most other South American cichlids ("*Tylochromis*" type), composed exclusively of the parasphenoid, but in large specimens the apophysis is uniquely modified, with the basioccipital making up a large part of the apophysis and its walls supported by the prootics. There is no other record of a transformation from a *Tylochromis* type apophysis to a *Haplochromis* type apophysis among cichlids, and the formation of the apopysis by caudad elongation of the parasphenoid, may be different from the formation in African cichlids in which the basioccipital participates in the apophysis. Ismail et al. (1982) interpreted early ontogeny of the apophysis in the African haplochromine species *Astatotilapia elegans* as a succession of adult types *Tylochromis–Tilapia–Tropheus–Haplochromis*, and the final apophysis apparently depending on anteroventrad growth of the basioccipital. (2) The bifurcate central ligament from the fifth ceratobranchial inserts on the tips of the ceratobranchials 4.

In this study we have observed four further potential autapomorphies that were not previously recorded:

(1) Elongate groove posterior to nostril (Fig. 1b). This depression fills about half the distance between the nostril and the orbital margin and is more prominent in large specimens.
(2) Distinct vertical line across cheek about 4 scales anterior to preopercle, apparently representing a free neuromast row (Fig. 1b). It corresponds in position to the "vertical row of free lateralis organs in front of preopercle" illustrated by Freihofer (1978: fig. 7, PCL) in *Polycentrus schomburgkii* (Polycentridae). This character state will require further investigation in a wider group of perciforms, but at least it is absent in a selection of cichlids screened including *Astronotus, Retroculus* and *Crenicichla*.
(3) Prominent rostral fold on maxilla (Fig. 1b). The rostral fold starts laterally on the anterolateral face of the maxilla, and continues as the rostral cap across the snout shielding the postlabial portion of the ascending processes of the premaxillae when the mouth is closed. A deep incision appears where the maxillary fold emerges exposed parallel with the orad margin of the lachrymal. In other cichlids there is a smooth transition from the lachrymal margin to the rostral cap, the maxillary skin does not form a prominent fold continuous with the rostral cap, and the conspicuous incision separating rostral cap and lachrymal is not present.
(4) Unique colour pattern with three dark vertical bars on the side, developing from three dark blotches in juveniles. Above, we attempt to homologize the bars with those of other cichlids, but the expression of three vertical markings remains unique for *Cichla*.

According to Newsome (1971) the nostrils [on each side of the head] are double in young of *Cichla*, but in adults the one nostril closes and disappears. All juvenile specimens of *Cichla* that we have examined, however, have a single nostril on each side of the head. A secondary opening close to the nostril was described for *Apistogramma alacrina* by Kullander (2004), otherwise all cichlids have a single nostril on each side of the head. In *Cichla* is present a minimal unpig-

mented, apparently mucus-filled, circular area slightly posterior to the nostril and at the dorsal margin of the nasorbital depression. This area represents probably a free neuromast; it can be probed into the skin, but does not seem to represent an opening to the nasal sac, instead it may be related to the multiple perforations connecting to the anterior nasal lateralis canal opening. Preliminary observations suggest that this character is also present in other cichlids.

Geographical distribution. Most species of *Cichla* now known conform to a general pattern of allopatric distribution, although several species are sympatric or even syntopic. This suggests that *Cichla* is a component of a general species distribution pattern in tropical South America. Limiting factors are sometimes obvious, with elements of isolation to or above major rapids (*C. thyrorus*, *C. melaniae*, *C. mirianae*, *C. jariina*), restriction to certain water conditions, e.g., blackwaters (*C. temensis*, *C. orinocensis*) or clearwater rivers (*C. piquiti*, *C. melaniae*, *C. mirianae*, *C. thyrorus*, *C. jariina*), as is known from other cichlids. The historical patterns are more obscure. The species pattern does not retrace that of other cichlid genera and the tree (Fig. 93) shows a complex geographic branching.

Essentially, the distribution of the genus recovers the Guianan and Brazilian highlands. *Cichla monoculus* is exceptional in its wide floodplain distribution in the western Amazon basin, but there is too little information about the fish fauna of tributaries to conclude if it is really restricted to floodplains. *Cichla monoculus* extends eastwards to the mouth of the Amazon and occurs also in the Oyapock drainage. It is represented by similar species in Bolivia *(C. pleiozona)* and the Rio Tocantins *(C. kelberi)*. *Cichla ocellaris* is the only species occurring in several rivers in the Guianas, but also in the Rio Branco. The putative sister species is *C. nigromaculata* in the upper Orinoco and Negro rivers.

Cichla vazzoleri and *C. pinima* occur in tributaries below major rapids east of the Rio Negro and Rio Madeira, but restricted to opposite sides of the Rio Amazonas. *Cichla* from the Amapá are identified as *C. pinima*, but based on limited material. Two species, *C. orinocensis* and *C. temensis* are distributed over two major river drainages, the Negro and the Orinoco, which, however, are incompletely separated being connected across the Rio Casiquiare. *Cichla ocellaris* is recorded from both the Rio Branco and several rivers in Guyana and Suriname.

Species of *Cichla* are remarkably similar to each other in body proportions and most meristics. Colour variation provides the best species diagnostic characters. In this regard *Cichla* conforms to other genus-level taxa of cichlids in South America, which are morphologically distinct, but within each genus species differ principally in colour pattern. Since cichlids are diurnal, and effect an elaborate behaviour including visual clues in social interaction, this is not surprising. More surprising is that other morphological differentiation tends to be limited. Possible explanations could be that the generic subdivisions among cichlids are biased towards recognizing units separated by morphological gaps, that morphological key innovations are functional in stable communities not permitting radiating evolution, or biased or incomplete character sampling.

Clearly, patterns of variation in colour and meristics are easier to perceive than other aspects of the type of organisms represented by *Cichla* and other cichlids. Silfvergrip (1996), working with a genus of nocturnal catfishes over the entire Neotropics, found surprisingly few species in a total analysis approach, where others have easily described species by comparing just selected geographical samples. The conclusion is that colour variation greatly facilitates species recognition. Whereas genera of cichlids are recognized by gaps, phylogenetic morphological and molecular analyses support about the same branching patterns of genera (e.g., Kullander, 1988; Farias et al., 2001), and it thus seems likely that morphological characters are reasonably well sampled and consequently genera are reasonable approximations of monophyletic morphology-based clades. Clearly, ecological functional constraints may be the most plausible explanation for the pattern shared by *Cichla* and other cichlid genera with a more or less consistent allopatry of included species – whenever there is vicariance followed by speciation, colour divergence is the most obvious marker of speciation. It is hard to think that all intrageneric cichlid speciation would represent very recent isolation, with insufficient time for further differentiation.

Under this functional constraint hypothesis, changes in characters not affecting the basic body plan and consequently feeding ecology, would have little effect on the ecological function of the new species, but mutations relating to the com-

munity function would be selected against. Thus, species of *Cichla* may be locked in the role as the large cichlid predator in each new community derived from an ancestral community with *Cichla* present. The hypothesis is compatible with vicariance biogeography, and thus suggests that sympatry of *Cichla* species is secondary. Where *Cichla* species co-exist, they must either be actively competing for resources, be morphologically differently specialised, or the environment is so fluctuating that no niche structuring occurs. The major sympatry among species of *Cichla* is in the Rio Negro/Orinoco drainages. In this region, there are two species of the *C. ocellaris* group, and two species of the *C. temensis* group, but in a model where niches are limiting, we would expect sympatry to appear where communities are not stable. Interestingly, the one case of sympatry referable to ephemeral syntopy is the occurrence of *C. monoculus* with other species along the Rio Amazonas in Brazil, i.e., in regions of contact between the whitewater and blackwater floodplain and clearwater tributaries.

Acknowledgments

Special thanks are due to Michael Goulding for collecting such large series of specimens of Amazonian fishes, and for making available his large collections from all over the Amazon basin. Heraldo Britski, José Lima de Figueiredo, Naércio Menezes, Mário de Pinna and Osvaldo Oyakawa (MZUSP), Donald C. Taphorn (UNELLEZ), Antonio Machado-Allison and Francisco Mago Leccia (MBUCV), Plutarco Cala (ICNMHN), the late P. Planquette (INRA, Kourou), Gérard Loubens (ORSTOM, Bolivia), Oliver Crimmen and Gordon Howes (BMNH), Tomio Iwamoto and David Catania (CAS), Gustavo Nunan and Paulo Buckup (MNRJ), Rainer Hacker and Harald Ahnelt (NMW), Richard P. Vari and Susan L. Jewett (USNM), Hans-Joachim Paepke (ZMB), and Maurice Kottelat (then ZSM), made available collections. Patrice Pruvost (MNHN) kindly hand-carried the syntypes of *C. toucounarai* to Thessaloniki for re-examination. Field assistance was received from Jansen Zuanon, Geraldo Mendes dos Santos, and other staff at INPA, Kenny Tanizaki, Marco Túlio de Lacerda (Rio de Janeiro), Walter Gill Morlis (Itaipú Binacional, Ciudad del Este), Mirtha Medina, Dario Mandelburger and other members of the PROVEPA project at the Museo Nacional de Historia Natural, Paraguay, and the late Andrés Urteaga (Iquitos). Dieter Kelber, Rainer Stawikowski, Uwe Werner, Frank Warzel, Leo Nico, Michel Jègu. Rosemary H. Lowe-McConnell, and many others, shared photographs, specimens and information about *Cichla*. Rainer Stawikowski, Uwe Werner, Frank Warzel, and Maurice Kottelat kindly granted permission to use their photos. Financial support enabled visits to Brazil (Swedish Natural Science Research Council, No. B-BU 4568 to SOK), and field work in Paraguay (Swedish International Development Agency, No 16-243/1993 to SOK) and French Guiana (Swedish Natural Science Research Council U-FR 04568-312 to SOK).

Literature cited

Andrade, F., H. Schneider, I. Farias, E. Feldberg & I. Sampaio. 2001. Análise filogenética de duas espécies simpátricas de tucunaré (*Cichla*, Perciformes), com registro de hibridização em diferentes pontos da bacia da Amazônica. Revista Virtual de Iniciação Acadêmica da UFPA, 1 (1): 1-11.

Araújo Moreira Neto, C. 1983. Introdução. Pp. 13 -37 in A. R. Ferreira, Viagem filosófica ao rio Negro. Museu Paraense Emílio Goeldi, Belém, 775 pp.

Bezerra e Silva, J. W., J. de Oliveira Chacon, E. P. dos Santos, J. T. C. de Mello & E. de A. Duarte. 1980. Curva de rendimento do tucunaré pinima, *Cichla temensis* (Humboldt, 1833), do açude público "Estevam Marinho" (Curemas, Paraíba, Brasil). Revista Brasileira de Biologia, 40: 203-206.

Bleher, H. 2006. Bleher's discus. Volume 1. Aquapress Publishers, Miradolo Terme.

Braga, R. A. 1952. Ninhos de tucunarés, "*Cichla temensis*" Humboldt e "– *Cichla ocellaris*" Bloch & Schneider. Revista Brasileira de Biologia, 12: 273-278

— 1953. Crescimento de tucunaré pinima, *Cichla temensis* Humboldt, em cativeiro. Dusenia, 4: 41-46.

Brinn, M. N. A., J. I. R. Porto & E. Feldberg. 2004. Karyological evidence for interspecific hybridization between *Cichla monoculus* and *C. temensis* (Perciformes, Cichlidae) in the Amazon. Hereditas, 141: 252-257.

Casciotta, J. & G. Arratia. 1993. Tertiary cichlid fishes from Argentina and reassessment of the phylogeny of New World cichlids. Kaupia, 2: 195-240.

Castelnau, F. de. 1855. Animaux nouveaux ou rares recueillis pendant l'expédition dans les parties centrales de l'Amérique du sud, de Rio de Janeiro à Lima, et de Lima au Para exécutée par ordre du gouvernement français pendant les années 1843 à 1847 sous la direction du Comte Francis de Castelnau. Poissons. Paris, xii + 112 pp.

Chellappa, S., M. R. Câmara & N. T. Chellappa. 2003. Ecology of *Cichla monoculus* (Osteichthyes: Cichlidae) from a reservoir in the semi-arid region of Brazil. Hydrobiologia, 504: 267-273.

Costi, C. G., C. C. Bello Rodrigues, D. L. Paiva Filho & J. B. Rozas Rodrigues. 1977. Estudo preliminar da ictiofauna do Polo Araguaia-Tocantins. Brasilia, 177 pp

Eigenmann, C. H. 1912. The freshwater fishes of British Guiana, including a study of the ecological grouping of species and the relation of the fauna of the plateau to that of the lowlands. Memoirs of the Carnegie Museum, 5: xxii + 578 pp.

Eigenmann, C. H. & W. L. Bray. 1894. A revision of the American Cichlidae. Annals of the New York Academy of Sciences, 7: 607-624.

Farias, I. P., G. Ortí, I. Sampaio, H. Schneider & A. Meyer. 2001. The cytochrome *b* gene as a phylogenetic marker: the limits of resolution for analyzing relationships among cichlid fishes. Journal of Molecular Evolution, 53: 89-103

Fontenele, O. 1948. Um caráter sexual secundário extragenital nos tucunarés (Actinopterygii, Cichlidae). Revista Brasileira de Biologia, 8: 185-188.

Freihofer, W. C. 1978. Cranial nerves of a percoid fish, *Polycentrus schomburgkii*, a contribution to the morphology and classification of the order Perciformes. Occasional Papers of the California Academy of Sciences, 128: 1-78.

Günther, A. 1862. Catalogue of the fishes in the British Museum. Volume fourth. British Museum, London, 534 pp.

Heckel, J. 1840. Johann Natterer's neue Flussfische Brasilien's nach den Beobachtungen und Mittheilungen des Entdeckers beschrieben. (Erste Abtheilung, die Labroiden.) Annalen des Wiener Museums der Naturgeschichte, 2: 327-470.

Holmberg, E. L. 1891. Sobre algunos peces nuevos o poco conocidos de la República Argentina. Revista Argentina de Historia Natural, 1: 180-193.

Humboldt, A. von. 1819. Voyage aux régions équinoxiales du Nouveau Continent: fait en 1799, 1800, 1801, 1803 et 1804 par Al. de Humboldt et A. Bonpland. Tome second. 722 pp.

— 1907. Personal narrative of travels to the equinoctial regions of South America during the years 1799-1804, vol. 2. [Translation]. George Bell & Sons, London. Project Gutenberg Ebook http://www.gutenberg.net/etext04/qnct210.txt

Humboldt, [A.] de, [A.] Valenciennes & [Gay-Lussac. 1821.] Recherches sur les poissons fluviatiles de l'Amérique équinoxiale. Pp. 145-216 in [A.] de Humboldt & [A.] Bonpland (1813-1832), Voyage de Humboldt et Bonpland. Deuxième partie. Observations de Zoologie et d'Anatomie comparée. Paris.

International Commission on Zoological Nomenclature, 1999. International code of zoological nomenclature, 4th ed. International Trust for Zoological Nomenclature, London, 306 pp.

Ismail, M. H., W. Verraes & A. Huysseune. 1982. Developmental aspects of the pharyngeal jaws in *Astatotilapia elegans* (Trewavas, 1933) (Teleostei: Cichlidae). Netherlands Journal of Zoology, 32: 513-543.

Jardine, W. (ed.). 1843. The naturalist's library [vol. 38]. Ichthyology Vol. V. Fishes of Guiana. Part II. Edinburgh, 214 pp. [Also as Vol. XXXI. Ichthyology. Fishes of British Guiana. Part 2nd. Two pl. 18 listed in text and Contents, but only one present.]

Jégu, M., G. M. dos Santos & E. Ferreira. 1989. Une nouvelle espèce du genre *Mylesinus* (Pisces, Serrasalmidae), *M. paraschomburgkii*, décrite des bassins du Trombetas et du Uatumã (Brésil, Amazonie). Revue d'Hydrobiologie Tropicale, 22: 49-62.

Jepsen, D. B., K. O. Winemiller, D. C. Taphorn & D. Rodriquez O. 1999. Age structure and growth of peacock cichlids from rivers and reservoirs of Venezuela. Journal of Fish Biology, 55: 433-450.

Keith, P., P.-Y. Le Bail & P. Planquette. 2000. Atlas des poissons d'eau douce de Guyane, Tome 2, Fascicule I. Batrachoidiformes, Mugiliformes, Beloniformes, Cyprinodontiformes, Synbranchiformes, Perciformes, Pleuronectiformes, Tetraodontiformes. Patrimoines Naturels (Muséum National d'Histoire Naturelle, Service du Patrimoine Naturel), 43 (1): 1-286.

Kelber, D. 1999. Tucunaré uma paixão internacional. Coleção pescarte 02, Editora Arte & Ciencia, São Paulo, 96 pp.

Kottelat, M. 1984. Catalogue des types du Musée d'Histoire naturelle de Neuchâtel. I. Pisces. Bulletin de la Société Neuchâteloise des Sciences Naturelles, 107: 143-153.

— 1988. Authorship, dates of publication, status and types of Spix and Agassiz's Brazilian fishes. Spixiana, 11: 69-93.

Kullander, S. O. 1981. Cichlid fishes from the La Plata basin. Part I. Collections from Paraguay in the Muséum d'Histoire naturelle de Genève. Revue Suisse de Zoologie, 88: 675-692.

— 1983. A revision of the South American cichlid genus *Cichlasoma*. Swedish Museum of Natural History, Stockholm, 296 pp.

— 1986. Cichlid fishes of the Amazon River drainage of Peru. Swedish Museum of Natural History, Stockholm, 431 pp.

— 1997. *Crenicichla rosemariae*, a new species of pike cichlid (Teleostei, Cichlidae) from the upper Rio Xingu drainage, Brazil. Ichthyological Exploration of Freshwaters, 7: 279-281.

— 1998. A phylogeny and classification of the South American Cichlidae (Teleostei: Perciformes). Pp. 461-498 in L. R. Malabarba, R. E. Reis, R. P. Vari, Z. M. S. Lucena & C. A. S. Lucena (eds.), Phylogeny and classification of Neotropical fishes. Edipucrs, Porto Alegre.

— 1999. Fish species – how and why. Reviews in Fish Biology and Fisheries, 9: 325-352.

— 2003. Family Cichlidae (Cichlids). Pp. 605-656 in R. E. Reis, S. O. Kullander & C. J. Ferraris (eds.), Check list of the freshwater fishes of South and Central America. Edipucrs, Porto Alegre, xi + 729 pp.

— 2004. *Apistogramma alacrina*, a new species of cichlid fish (Teleostei: Cichlidae) from Colombia. Ichthyological Exploration of Freshwaters, 15: 41-48.

Kullander, S. O. & E. J. G. Ferreira. 2005. Two new species of *Apistogramma* Regan (Teleostei: Cichlidae) from the rio Trombetas, Pará State, Brazil. Neotropical Ichthyology, 3: 361-371.

Kullander, S. O. & H. Nijssen. 1989. The cichlids of Surinam. Brill, Leiden, xxxiii + 256 pp.

Kullander, S. O. & A. M. C. Silfvergrip. 1991. Review of the South American cichlid genus *Mesonauta* Günther with descriptions of two new species. Revue Suisse de Zoologie, 98: 407-448.

López-Fernández, H., R. L. Honeycutt & K. O. Winemiller. 2004. Molecular phylogeny and evidence for an adaptive radiation of geophagine cichlids from South America (Perciformes: Labroidei). Molecular Phylogenetics and Evolution, 34: 227-244.

López-Fernández, H., R. L. Honeycutt, M. L. J. Stiassny & K. O. Winemiller. 2005. Morphology, molecules, and character congruence in the phylogeny of South American geophagine cichlids (Perciformes, Labroidei). Zoologica Scripta, 34: 627-651.

Lowe-McConnell, R. H. 1969. The cichlid fishes of Guyana, South America, with notes on their ecology and breeding behaviour. Zoological Journal of the Linnean Society, 48: 255-302.

— 1991. Natural history of fishes in Araguaia and Xingu Amazonian tributaries, Serra do Roncador, Mato Grosso, Brazil. Ichthyological Exploration of Freshwaters, 2: 63-82.

Machado-Allison, A. 1971. Contribución al conocimiento de la taxonomía del género Cichla en Venezuela. Parte I. Acta Biológica Venezuelica, 7: 459-497.

— 1973. Contribución al conocimiento de la taxonomía del género Cichla en Venezuela. Parte II. Osteologia comparada. Acta Biológica Venezuelica, 8: 155-205.

Magalhães, A. Couto de. 1931. Monographia brazileira de peixes fluviaes. São Paulo, 260 pp.

Marques, D. K. S. & E. K. Resende. 2005. Distribuição do Tucunaré *Cichla* cf. *monoculus* (Osteichthyes, Cichlidae) no Pantanal. Boletim de Pesquisa e Desenvolvimento, Embrapa Pantanal, 60: 1-24

Meijide, F. K. & G. A. Guerrero. 2000. Embryonic and larval development of a substrate-brooding cichlid *Cichlasoma dimerus* (Heckel, 1840) under laboratory conditions. Journal of Zoology, London, 252: 481-493.

Menezes, R. S. de. 1953. Listas dos nomes vulgares de peixes de aguas doces e salobras da zona seca do Nordeste e Léste do Brasil. Arquivos do Museu Nacional, 42: 343-388.

Müller, J. & F. H. Troschel. 1849. Horae Ichthyologicae. Beschreibung und Abbildung neuer Fische. Drittes Heft. Von Veit, Berlin, 28 pp.

Nakashima, S. 1941. Algunos peces del Oriente peruano. Boletín del Museo de Historia Natural Javier Prado, 5: 61-78.

Nascimento, F. L., A. C. Catella & A. S. Moraes. 2001. Distribuição espacial do tucunaré, *Cichla* sp (Pisces, Cichlidae), peixe amazônico introduzido no Pantanal, Brasil. Boletim de Pesquisa e Desenvolvimento, Embrapa Pantanal, 24: 1-17.

Newsome, Y. L. 1971. Comparative osteology and relationships of Neotropical cichlid fishes. Unpublished Ph.D. dissertation, University of Illinois, Chicago, 303 pp.

Nomura, H. 1984. Dicionário dos peixes do Brasil. Brasília, 482 pp.

Ogilvie, V. E. 1966. Report on the Peacock Bass Project including Venezuelan trip report and a description of five *Cichla* species. Florida Game and Fresh Water fish Commission, 42 pp, unpaginated.

Page, R. D. M. 2001. NEXUS Data Editor for Windows, version 0.5.0.

Pellegrin, J. 1904. Contribution à l'étude anatomique, biologique et taxinomique des poissons de la famille des Cichlidés. Mémoires de la Société Zoologique de France, 16: 41-399.

Pinna, M. C. C. de. 1999. Species concepts and phylogenetics. Reviews in Fish Biology and Fisheries, 9: 353-373.

Regan, C. T. 1906. A revision of the fishes of the South-American cichlid genera *Cichla*, *Chaetobranchus*, and *Chaetobranchopsis*, with notes on the genera of American Cichlidae. Annals and Magazine of Natural History, Ser. 7, 17: 230-239.

Ringuelet, R. A., R. H. Arámburu & A. A. de Arámburu. 1967. Los peces argentinos de agua dulce. Provincia de Buenos Aires, Comisión de Investigación Científica, La Plata, 602 pp.

Román, B. 1981. Los pavones. Colección: Los peces de los llanos de Venezuela I. Fundación Científica Fluvial de los Llanos, Caracas, 143 pp.

Santos, E. 1981. Peixes da agua doce. Belo Horisonte, 267 pp. (Zoologia brasilica, vol. 2* reprint of 1954 ed., with new colour plates).

Sawaya, P. 1946. Sobre o consumo de oxigenio por alguns peixes fluviais neotropicos (Cichlidae – gen. *Cichla* e *Astronotus*). Boletim da Faculdade de Filosofia, Ciências e Letras da Universidade de São Paulo, Zoologia, 11: 335-355.

Sawaya, P. & A. de Albuquerque Maranhão. 1946. A construção dos ninhos e a reprodução de alguns peixes neotrópicos (Cichlidae – gen. *Cichla* e *Astronotus*). Boletim da Faculdade de Filosofia, Ciências e Letras da Universidade de São Paulo, Zoologia, 11: 357-372

Schneider, J. G. (ed.). 1801. M. E. Blochii systema ichthyologiae. Berolini, lx + 584 pp.

Schultz, H. 1962. Komdu and the Suya indians. Tropical Fish Hobbyist Magazine, 1962 (March): 19-20, 23-24, 26, 29-31, 34-37.

Shafland, P. L. 1995. Introduction and establishment of a successful butterfly peacock fishery in southeast Florida canals. American Fisheries Society Symposium, 15: 443-451.

Silfvergrip, A. M. C. 1996. A systematic revision of the neotropical catfish genus *Rhamdia* (Teleostei, Pimelodidae). Department of Zoology, Stockholm Uni-

versity and Department of Vertebrate Zoology, Swedish Museum of Natural History, Stockholm, 156 pp.

Spix, J. B. & L. Agassiz. 1829-1831. Selecta genera et species piscium quos in itinere per Brasiliam annis MDCCCXVII-MDCCCXX jussu et auspiciis Maximiliani Josephi I. Bavariae regis augustissimi peracto collegit et pingendos curavit Dr. J. B. de Spix. Monachii, 138 pp. [1829, pp. 1-82, 1831, pp. 83-138].

SPSS. 2005. SPSS 14.0 for Windows. SPSS Inc., Chicago.

Stawikowski, R. & U. Werner. 2004. Die Buntbarsche Amerikas. Band 3: Erdfresser, Hecht- und Kammbuntbarsche. Ulmer, Stuttgart, 478 pp.

Steindachner, F. 1875. Beiträge zur Kenntniss der Chromiden des Amazonenstromes. Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften, Wien, Mathematisch-Naturwissenschafliche Classe, 71: 61-137.

— 1883. Beiträge zur Kenntniss der Flussfische Südamerika's. (IV.). Denkschriften der Kaiserlichen Akademie der Wissenschaften, Wien, Mathematisch-Naturwissenschafliche Classe, 46: 1-44.

Stiassny, M. L. J. 1982. The relationships of the neotropical genus *Cichla*: a phyletic analysis including some functional considerations. Journal of Zoology, London, 197: 427-453.

— 1987. Cichlid familial intrarelationships and the placement of the neotropical genus *Cichla*. Journal of Natural History, 21: 1311-1331.

— 1992. Atavisms, phylogenetic character reversals, and the origin of evolutionary novelties. Netherlands Journal of Zoology, 42: 260-276.

Swofford, D. L. 2001. PAUP* 4.0 beta 10 for 32-bit Microsoft Windows. Sinauer Associates, Sunderland.

Webb, J. F. 1990. Ontogeny and phylogeny of the trunk lateral line system in cichlid fishes. Journal of Zoology, London, 221: 405-418.

Williams, J. D., K. O. Winemiller, D. C. Taphorn & L. Balbas. 1998. Ecology and status of piscivores in Guri, an oligotrophic tropical reservoir. North American Journal of Fisheries Management, 18: 274-285.

Winemiller, K. O. 1990. Caudal eyespots as deterrents against fin predation in the neoptropical [sic] cichlid *Astronotus ocellatus*. Copeia, 1990: 665-673.

— 2001. Ecology of peacock cichlids (*Cichla* spp.) in Venezuela. Journal of Aquariculture and Aquatic Sciences, 9: 93-112.

Zaret, T. M. 1977. Inhibition of cannibalism in *Cichla ocellaris* and hypothesis of predator mimicry among South American fishes. Evolution, 31: 421-437.

— 1980. Life history and growth relationships of *Cichla ocellaris*, a predatory South American cichlid. Biotropica, 12: 144-157.

Zaret, T. M. & R. T. Paine. 1973. Species introduction in a tropical lake. Science, 182: 449-455.

Zuccon A. & D. Zuccon. 2006. MrEnt v1.2. Department of Vertebrate Zoology & Molecular Systematics Laboratory, Swedish Museum of Natural History, Stockholm.

Received 30 June 2006
Revised 17 November 2006
Accepted 19 November 2006

Ichthyological Exploration of Freshwaters

An international journal for field-orientated ichthyology

INSTRUCTIONS TO CONTRIBUTORS

Warning

Prospective authors should read carefully the following instructions and follow them when submitting a manuscript. Doing so significantly hasten publication and save money and efforts. Manuscript which do not satisfy the instructions below may be rejected at the Editor's discretion and will not be returned.

Types of papers

1) Major Articles and Notes. These manuscripts are submitted to two referees for evaluation.

2) Rapid communications. These articles will be reports on exciting new results or discoveries within the scope of the journal. They are evaluated by the Editor and the Editorial Board and are either accepted or rejected.

Submission of manuscripts

The original manuscript and two copies should be sent to the Editor, Maurice Kottelat, Route de la Baroche 12, Case postale 57, CH-2952 Cornol, Switzerland. Do not send a disk or original of figures at this stage. A letter of transmittal is requested, giving:

1) the name, postal and email addresses and telephone of the corresponding author;

2) the names, postal and email adresses of up to four persons outside the authors' institutions who are qualified to review the paper;

3) a statement that the material has not been published and is not considered for publication elsewhere and that it will not be submitted elsewhere unless it is rejected or withdrawn. In submitting a manuscript, the author(s) accept transfer of the copyright to the Publisher.

Co-authors, corresponding author

Authors are those who have played a *significant* role in designing and conducting the research and in writing the manuscript. Individuals who have only collected data, provided material or financial support, or reviewed the manuscript should be listed in acknowledgments. Honorary authorship is not accepted.

Co-authors should designate a single corresponding author to whom correspondence and proofs will be sent. All correspondence regarding the paper should go through the corresponding author. Correspondence will not be sent to other co-authors and correspondence from other co-authors regarding the manuscript will neither be answered nor taken into consideration.

Format

Text. All manuscripts are subject to editorial revision before final acceptance for publication. The manuscript should be printed, double spaced and with at least 2.5 cm right, left and bottom margins. Pages must be numbered. Nothing in the manuscript should be underlined. Titles with numerical series designations are not permitted. Titles should be brief, fewer than 20 words and should indicate clearly the field of study and the group of fishes investigated. All abbreviations should be explained in the Method section (or figure caption when appropriate) or a reference to published explanations should be provided; exceptions are very common abbreviations, such as mm, km, kg, sec, min, yr, vs, SL. Footnotes are not permitted. Do not end a line of text with a hyphen. All measurements must be in metric units. The first page should include: title of the paper, author(s), addresses and abstract, all left justified. The text should be followed by Material Examined (if appropriate), Acknowledgments (if any), Appendix (if any) and Literature Cited, in that order. Keys are desirable in taxonomic papers. They should be dichotomous and not serially indented.

Nomenclature. Names of living organisms should follow the appropriate and current International Codes of Nomenclature. Formal names of genera and species should be written in italics. Names of authors and publication dates of scientific names should appear only when nomenclatural problems are involved.

Language. Manuscripts should be written in English, French or German, but English is strongly encouraged. All papers must have a concise but informative abstract in English. Manuscripts in French or German must have an extensive summary in English. In taxonomic papers, the abstract must include at least clear diagnosis of the new taxa. A second abstract, provided by the author(s), in the language of the country or area concerned by the text is acceptable. A maximum of two abstracts is permitted.

Acknowledgments. Identify individuals by name(s) and surname. Do not list titles, position or institution. Acknowledge individuals, not positions. Idiosyncrasy and private jokes are not permitted.

Literature Cited. Format for Literature Cited is that of the most recent issue. Abbreviate names of well known journals, but provide in full the names of lesser known journals. For books, give full name of publishing company or institution, city and country. Manuscripts in preparation or submitted, abstracts, in-house reports and other literature not obtainable through normal library channels cannot be cited.

Tables. Each table should be on a separate sheet, numbered sequentially with Arabic numerals; they should have concise but self-explanatory headings. Do not insert frames, vertical rules, dotted lines or footnotes. The location of first citation of each table should be clearly indicated.

Figures. Do not submit originals for the review; send originals with the revised manuscript. All maps, graphs, charts, drawings and photographs are regarded as figures and are to be numbered consecutively and in the sequence of their first citation in the text. When several charts or photographs are grouped as one figure, they must be trimmed and spaced as intended for final reproduction. Each part of such a group figure should be lettered with a lower case block letter in the lower left corner. Scale should be indicated on the figure by a scale bar. Figures should never be mounted on hard cardboard. Do not mark or write on the back of the figures.

All illustrations should be designed to fit a width of 68 or 140 mm and a depth no greater than 200 mm. Prints should be of high contrast and glossy. Lettering should be large enough to be easily seen when reduced onto a journal column (68 mm). Legends for figures must be typewritten on a separate sheet. Identify each illustration with the author's name, figure number and direction of top margin.

Colour illustrations should preferably be slides. Slides should be framed and properly labelled. For the review, they should be submitted as three sets of prints, pasted on sheets of paper, or as a series of color photocopies. Prints to be used for publications should never be mounted and never labelled on the back.

The decision to print in colour or in black and white any figure originally submitted in colour remains with the editor and publisher. This decision will be based on scientific justification, quality of the original, layout and other editorial, financial and production contraints. By submitting colour originals, the authors know and accept that they may be published in black and white.

Even if photographs or line drawings are processed with graphics programs, original slides, negatives or drawings must always be submitted.

Software texts. The whole text should be left justified. Do not right-justify. Do not underline. Never use "L" or "I" for the numeral 1 or "O"/"o" for "0". Do not hyphenate any word. Do not format the text. Text should be on 3.5" disks, readable on IBM-compatibles with MS-DOS. Do not send a disk, when submitting the manuscript. Revised manuscript must be accompanied by a disk satisfying above criteria, or will not be accepted.

Review

Each manuscript will be sent to two reviewers for confidential evaluation. When justified, the reviewer's comments will be forwarded to the author. When submitting a revised manuscript, authors should *briefly* indicate which comments have been incorporated and the reasons for disregarding any suggestion regarded as unacceptable. Remember that if a reviewer had questions or did not understand you, other readers may make the same experience and the answers should be in the manuscript and not in a letter to the editor. *Changes in style, format and layout requested by the Editor are non-negotiable and non-observance will usually result in rejection of the manuscript*.

Revised manuscripts received more than 6 months after the reviewers' comments had been sent will not be considered or will be treated as new submissions.

Proofs, Reprints and Page Charges

One set of proofs will be sent to the corresponding author; they should be checked and returned to the Editor within one week. Proofs not received within this delay may be corrected by the Editor, at the author's risks. Authors may be charged for any changes other than printer's error. Reprint orders must be forwarded with the corrected proofs on the form supplied by the editor. The corresponding author is responsible for contacting the co-authors and forwarding their reprint orders.

The authors will obtain 20 reprints free of charge, additional reprints may be ordered at cost. There will be no page charges and no charges for justified colour illustrations.

Ichthyological Exploration of Freshwaters

An international journal for field-orientated ichthyology

Volume 17 • Number 4 • December 2006

CONTENTS

Cover photograph:
Cichla piquiti (photograph by U. Werner)
Sven O. Kullander and Efrem J. G. Ferreira
(this volume pp. 289-398)

Articles appearing in this journal are indexed in:

AQUATIC SCIENCES and FISHERIES ABSTRACTS
BIOLIS - BIOLOGISCHE LITERATUR INFORMATION SENCKENBERG
CAMBRIDGE SCIENTIFIC ABSTRACTS
CURRENT CONTENTS/AGRICULTURE, BIOLOGY & ENVIRONMENTAL SCIENCES and SCIE
FISHLIT
ZOOLOGICAL RECORD