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Phylogeny and Taxonomic Revision of the Endemic Malagasy Genus *Ptychochromis* (Teleostei: Cichlidae), with the Description of Five New Species and a Diagnosis for *Katria*, New Genus

MELANIE L. J. STIASSNY[1] AND JOHN S. SPARKS[1]

ABSTRACT

The Malagasy cichlid genus *Ptychochromis* is revised and five new species are described, one of which is presumed to be extinct. The three valid nominal species, *P. oligacanthus*, *P. grandidieri*, and *P. inornatus*, are redescribed with diagnoses provided for each. A phylogeny of ptychochromin cichlids, derived from the simultaneous analysis of morphological features and nucleotide characters from a combination of mitochondrial and nuclear genes is presented. *Ptychochromis* is diagnosed by a suite of derived features of the pharynx, infraorbital series, and palatine morphology. In addition, the sister taxon to *Ptychochromis*, *Ptychochromoides katria*, is removed from *Ptychochromoides* and placed in its own genus, *Katria*, which is described herein as new. *Katria* is diagnosed by a unique pigmentation pattern, the absence of paired anterior gas bladder chambers that approach the neurocranium, an elevated vertebral count, and a slender caudal peduncle. An unnamed clade comprising *Ptychochromis* and *Katria* is diagnosed by a suite of derived features of the pharynx, sensory canal system, supraneural patterning, and palatine morphology.

INTRODUCTION

Historically *Ptychochromis* Steindachner, 1880 was widely distributed in freshwaters throughout much of northwestern, southwestern, and eastern Madagascar (Kiener, 1963: pl. 14). However, as for many other Malagasy taxa, recent surveys indicate that populations throughout the island, especially in the southwestern and northwestern regions, have become increasingly rare and highly restricted in distribution or, in the case of

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the southwestern Onilahy drainage population, may have become extinct (de Rham and Nourissat, 2002; Sparks and Stiassny, 2003; and fig. 1).

A hypothesis of relationships for *Ptychochromis*, based on the simultaneous analysis of nucleotide characters from multiple mitochondrial and nuclear genes, was recently published by Sparks and Smith (2004). Examination of newly collected material and of museum holdings representing collections from throughout the island, in conjunction with the results reported by Sparks and Smith (2004), suggests that several novel species of *Ptychochromis* are present on Madagascar (see also, de Rham and Nourissat, 2002), including two new species not included in the analysis of Sparks and Smith (2004).

To date, four species of *Ptychochromis* have been formally described: *P. oligacanthus* (Bleeker, 1868), including what Bleeker referred to as var. *nossibeënsis*; *P. grandidieri* Sauvage, 1882; *P. madagascariensis* Sauvage, 1891; and *P. inornatus* Sparks, 2002. Prior to the study by Sparks (2002), only a single species, *P. oligacanthus*, was considered valid; both *P. madagascariensis* and *P. grandidieri* were considered junior synonyms of *P. oligacanthus* by Pellegrin (1904). Pellegrin's (1904) synonomies were apparently based on the examination of very few specimens, most of which are now, and may have been at the time the synonymies were proposed, in poor condition (Sparks, 2002). Furthermore, at best only vague collection-locality information accompanied most specimens examined by Pellegrin, which in any event probably represented a very restricted portion of the geographic range of the genus. As discussed below, most of the morphological characters useful for species discrimination within the genus are coloration and/or internal anatomical features, none of which were discussed by Pellegrin.

Pellegrin (1904) also synonymized *Tilapia* (now *Ptychochromoides*) *betsileanus* (Boulenger, 1899) with *Ptychochromis oligacanthus*; a synonymy apparently based upon examination of a single specimen (now lost) from Lac Itasy in the central highlands of Madagascar (Pellegrin, 1904). This specimen (MNHN 93-62 Lac Itasy: Grandidier) was either a *Ptychochromis* erroneously identified as *Tilapia betsileanus*, or was in very poor condition, as the two genera are readily distinguished (see Reinthal and Stiassny, 1997; Sparks, 2001, 2002). Pellegrin (1907) removed *Ptychochromis betsileanus* from synonymy with *Ptychochromis oligacanthus* but with no justification beyond the statement that he believed the species to be valid. Kiener and Maugé (1966) subsequently designated *Ptychochromis betsileanus* the type species of a new genus, *Ptychochromoides*.

Here we present a revision of the genus *Ptychochromis* and describe five new species. A phylogenetic hypothesis for a subset of ptychochromine cichlids (sensu Sparks and Smith, 2004), that are herein informally termed the ptychochromins (fig. 2), and that comprise the genera *Ptychochromis*, *Ptychochromoides*, *Oxylapia*, and a new genus, *Katria*, provides the framework for our focus on resolution of the relationships of the genus *Ptychochromis* and its placement within the ptychochromin clade. Our hypothesis is based on the simultaneous analysis of both morphological and molecular character data from representative taxa of all Malagasy and South Asian lineages, as well as basal Neotropical (*Retroculus*) and African (*Heterochromis*) genera (for a full listing of comparative material examined, see Materials and Methods below).

MATERIALS AND METHODS

Morphological Studies

Counts and morphometric measurements follow Barel et al. (1977), unless noted otherwise. Measurements were recorded to the nearest 0.1 mm using digital or dial calipers. Vertebral counts exclude the terminal, hypural-bearing vertebra; vertebral and fin spine/ray counts and measurements were obtained from radiographs or cleared-and-stained skeletal preparations. The terminal dorsal and anal soft fin rays are counted as a single element, even if branched and split to the fin base, as this element is associated with a single supporting pterygiophore. Gill raker counts correspond to the lower limb of the first arch and exclude the raker in the angle of the arch

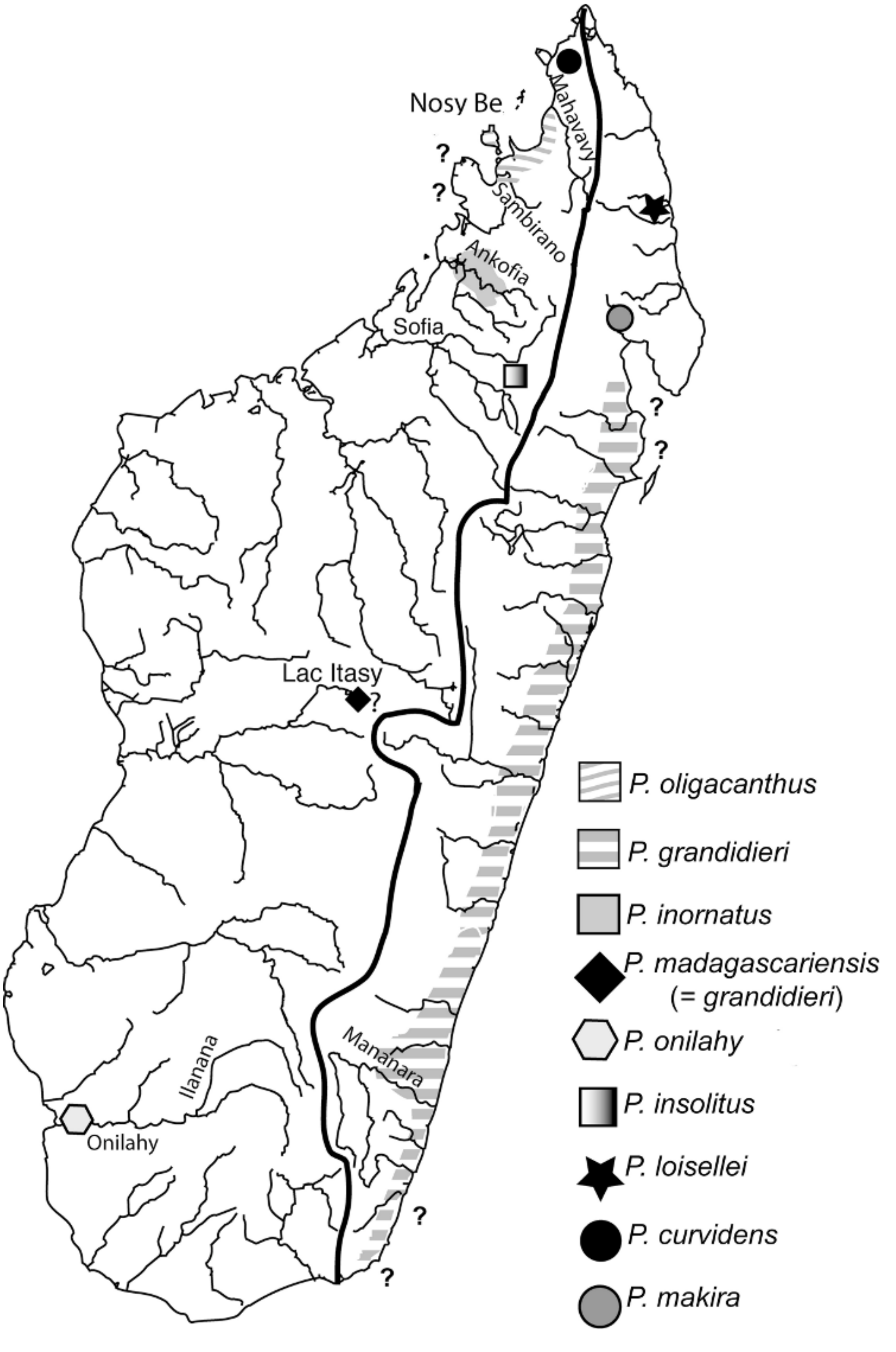

Fig. 1. Map of Madagascar indicating the verified geographic ranges for currently recognized species of *Ptychochromis*.

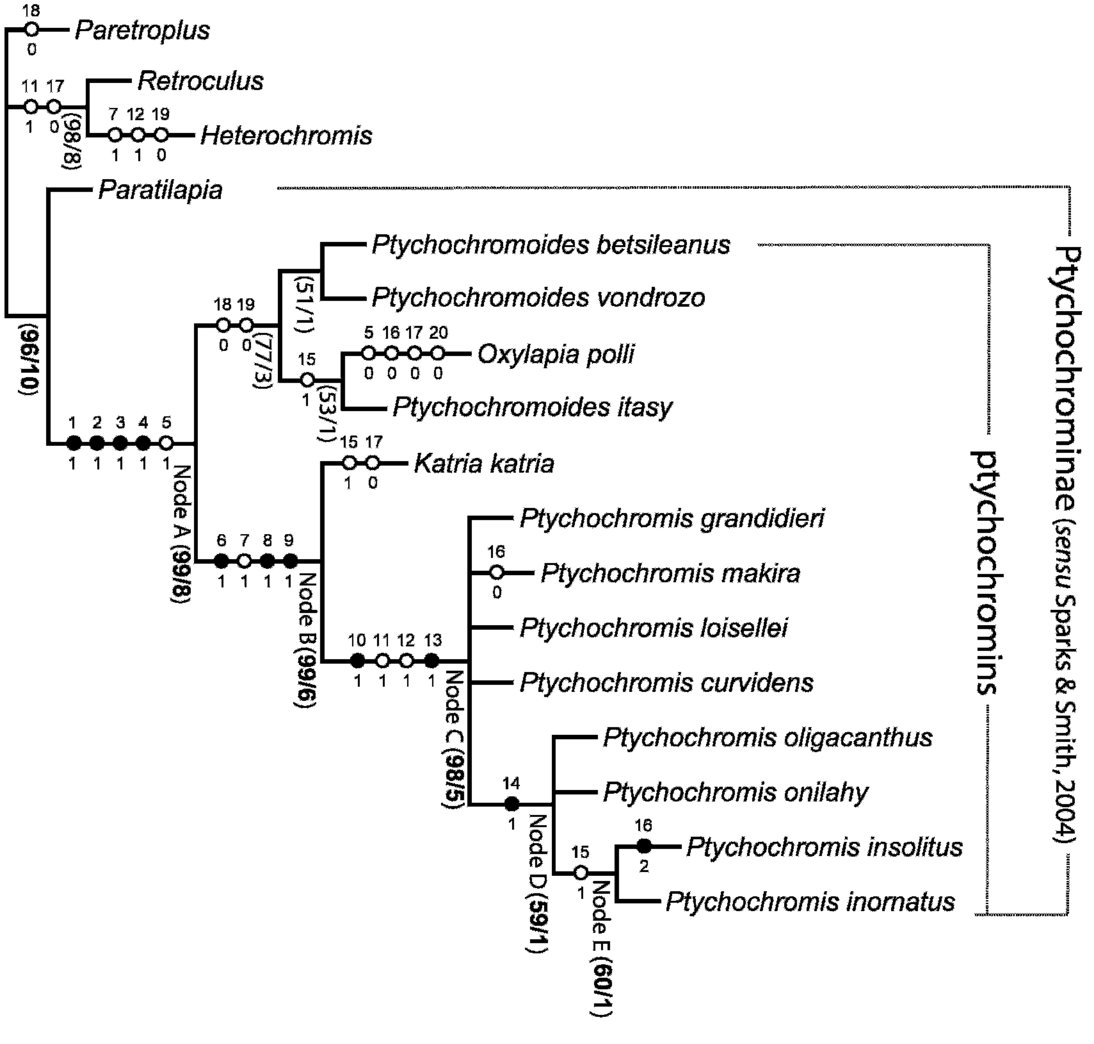

Fig. 2. Strict consensus of nine equally most-parsimonious trees (length 1014, CI = 0.67, RI = 0.61) recovered, based on the simultaneous analysis of 2029 aligned mitochondrial and nuclear nucleotide characters and 21 morphological transformations. Unambiguously optimized morphological features supporting recovered nodes are designated by solid (unique feature) and open (homoplasious feature) circles. Character numbers and states correspond to the morphological transformations listed in table 1. Support indices at nodes are presented in parenthesis (Jackknife/Bremer support).

marking the transition from ceratobranchial to epibranchial.

Comparative material comprised formalin-fixed specimens stored in 70–75% ethanol, non-formalin–fixed specimens stored in 70–95% ethanol and specimens cleared and stained (C&S) for bone and cartilage using a modified protocol based on Taylor and Van Dyke (1985). When sufficient material was available multiple C&S specimens were prepared and examined for each species. Institutional abbreviations follow Leviton et al. (1985). The following comparative materials have been included in this study and are arranged geographically and alphabetically by genus and species (values after catalog number indicate number of specimens examined, and do not necessarily correspond to the total number of specimens in the lot; C&S = cleared and stained preparation; SL = standard length).

South Asian Cichlids: *Etroplus canarensis*: AMNH 217754, 1 ex., River Kumaradhara at Kalikai, southern Canara, India; AMNH 233642, 131 ex., 5 ex. C&S, Canara, India. *Etroplus maculatus*: AMNH 215904, 7 ex. C&S; AMNH 217755, India; AMNH 217758, Sri Lanka. *Etroplus suratensis*: AMNH 217756, 1 ex., District Salem T.V., Mettur Dam Reservoir, Madras, India; AMNH 217757, 32 ex., 7 ex. C&S, Negombo Lagoon, Sri Lanka.

Malagasy Cichlids: *Katria katria*: AMNH 217739, holotype, eastern Madagascar, Tamatave Province, River Nosivolo, below Zule's Village, large side-pool off mainstream; AMNH 93701, 20 ex., 10 ex. C&S, eastern Madagascar, Tamatave Province, River Nosivolo below Ampasimaniona Village, 26 km east-northeast of Marolambo; UMMZ 240358, 1 ex. C&S, eastern Madagascar, Marolambo. *Oxylapia polli*: AMNH 97111, 10 ex., 1 ex. C&S, eastern Madagascar, Tamatave Province, Mangoro drainage, village of Marolambo, Nosivolo River; AMNH 97150, 4 ex., 1 ex. C&S, eastern Madagascar, Tamatave Province, River Nosivolo by Ambarimasina Village, ca. 16 km east northeast of Marolambo; UMMZ 235046, 1 ex. C&S, eastern Madagascar, Tamatave Province, Nosivolo River, near village of Marolambo, Mangoro drainage. *Paratilapia polleni*: AMNH 216068, 25 ex, eastern Madagascar, large baylake, behind dunes 1 km south of turnoff from Marolambo-Mananjary road, ca. 100 meters from sea; UMMZ 235043, 2 ex. C&S, northeastern Madagascar, Lac Anjavibe, Nosy be; UMMZ 235045, 2 ex. C&S, southeastern Madagascar, Sahapindra River, near Vevembe. *Paretroplus dambabe*: AMNH 11707, 2 ex., northeastern Madagascar, Lake Kinkony; UMMZ 235024, paratypes, 39 ex., 3 ex. C&S, northwestern Madagascar, Majunga Province, south of Mitsinjo, Mahavavy (du sud) drainage basin, Lake Kinkony. *Paretroplus damii*: AMNH 231248, 4 ex., northeastern Madagascar, main channel of Mahanara River at Antsirabe; UMMZ 235021, 1 ex. C&S, northwestern Madagascar, Anjingo River, east of Antsohihy; UMMZ 235022, 1 ex. C&S, northwestern Madagascar, Lac Andrapongy, north basin, northeast of Antsohihy. *Paretroplus kieneri*: AMNH 97365, 6 ex., 1 ex. C&S, northeastern Madagascar, Mahajanga Province, Ambomboa River, west of Mandritsara; UMMZ 235018, 5 ex., 1 ex. C&S, northwestern Madagascar, Lac Ravelobe, near Ampijoroa Forestry station; UMMZ 236592, 4 ex., 1 ex. C&S, Northwestern Madagascar, Lac Kinkony, near Mahajanga. *Paretroplus maculatus*: AMNH 97362, 1 ex., northwestern Madagascar, Mahajanga Province, Lac Ravelobe, Ampijoroa Forestry Station; UMMZ 235019, 2 ex. C&S, northwestern Madagascar, Lac Ravelobe, near Ampijoroa Forestry Station. *Paretroplus maromandia*: UMMZ 234790, holotype, northwestern Madagascar, Antalaha province, region of Maromandia, Maintsomalaza River, immediately south of Maromandia. *Paretroplus menarambo*: AMNH 97364, 3 ex., 1 ex. C&S, northwestern Madagascar, Mahajanga Province, Lac Sarodrano; UMMZ 235014, 2 ex. C&S, northwestern Madagascar, Lac Sarodrano, near village of Sarodrano, approx. 30 km north of Mampikony. *Paretroplus nourissati*: AMNH 229554, 2 ex., northeastern Madagascar, Ambomboa River, near confluence with Mangarahara River; UMMZ 235205, 1 ex. C&S, northeastern Madagascar, Amboaboa River, near Mandritsara. *Paretroplus petiti*: MNHN 1928-282, holotype, northwestern Madagascar, Maintimaso River, Province of Majunga, Ambila (Ambanja?). *Paretroplus polyactis*: AMNH 98171, 3 ex., 2 ex. C&S, eastern Madagascar, Tamatave Province, baylake behind first dune, ca. 100 m from sea, 1 km south of turnoff from Marolambo-Mananjary road; UMMZ 235016, 1 ex. C&S, southeastern Madagascar, Farafangana market. *Ptychochromoides betsileanus*: BMNH 1882.2.25:69, lectotype, Betsileo, Madagascar; BMNH 1882.2.25:70, paralectotype, Betsileo, Madagascar; AMNH 217753, 1 ex., southwestern Madagascar, Ilanana River, near Ranohira, Onilahy drainage; AMNH 217763, 1 ex., south-central Madagascar, Manantanana River, headwaters near Iaritsena, Ambalavao Region, Mangoky drainage; UMMZ 238115, 5 ex., dry skeletons, south-central Madagascar Ilanana River, south of Isalo National Park. *Ptychochromoides itasy*: AMNH 2336643, 1 ex., Madagascar; MNHN 1919-11, 1 ex. C&S, paratype, Madagascar, central highlands, Region of Antananarivo, Lake Itasy. *Ptychochromoides vondrozo*: AMNH 228488, 2 ex., paratypes, southeastern Madagascar, Fianarantsoa Province, Region of Vondrozo, near Village of Vevembe, Mananara drainage; UMMZ 235294, 3 ex., 1 ex. C&S, paratypes, southeastern Madagascar, Fianarantsoa Province, Region of Vondrozo, near Village of Vevembe, Mananara drainage.

African Cichlids: *Heterochromis multidens*: AMNH 5963, 1 ex., Poko, Bomokandi River; CU 88258, 8 ex., 1 ex. C&S, Likouala River, Odzala National Park; MRAC 60893, 1 ex. C&S, Buta.

Neotropical Cichlids: *Retroculus lapidifer*: AMNH 97347, 1 ex., Rio Tocantins; MNRS 12910, 27 ex., 1 ex. C&S, Goiás, Minaçu, Rio Tocantins, Brazil.

Text and Figure Abbreviations

The following abbreviations are used in the figures and text:

Cb4	fourth ceratobranchial
Cb4-tp	fourth ceratobranchial toothplate

Ep2-tp	second epibranchial toothplate
LPJ	lower pharyngeal jaw
Pb2	second pharyngobranchial
Pb3	third pharyngobranchial
Up4-tp	fourth upper toothplate
UPJ	upper pharyngeal jaw

Principal Components Analysis (PCA)

As an aid in the revision of *Ptychochromis*, multivariate analysis of 13 morphometric variables was accomplished using a sheared principal components analysis (PCA; Humphries et al., 1981; Bookstein et al., 1985). Variables with missing data and variables that were not measured from fixed homologous landmarks from form to form were excluded. Principal components were factored from the covariance matrix of log-transformed variables. Sheared PCA is designed to eliminate size effects, and was necessary to ensure size-free shape comparisons, particularly among groups of individuals of nonoverlapping size classes. The PCA was conducted in *Sheared PCA*, a freeware program written by Norman Macleod for the Macintosh operating system (http://www.nhm.ac.uk/hosted_sites/paleonet/ftp/ftp.html).

Phylogenetic Analysis

For the phylogenetic analysis, 2029 equally weighted nucleotide characters (based on the implied alignment [Wheeler, 2003b]) from the four gene fragments used by Sparks and Smith (2004; mitochondrial: ~530 bps from the large ribosomal subunit (16S) and ~649 bps from cytochrome *c* oxidase subunit I (COI); nuclear: ~334 bps from histone H3 and ~506 bps from Tmo-4C4) and 21 unordered morphological transformations (see Morphological Character Data below) were simultaneously analyzed under the optimality criterion of parsimony. Methods for sequence acquisition are presented in Sparks and Smith (2004) and GenBank accession numbers for specimens included in this study are presented here in appendix 1.

The parsimony analysis was conducted using direct optimization (Wheeler, 1996) as implemented in the program POY (Wheeler et al., 2003), and run on a Macintosh G4 computer. The method of direct optimization is used to avoid the potential biases inherent in traditional sequence-alignment procedures (e.g., manual alignment), which may not necessarily result in the most parsimonious topology due to a potentially suboptimal alignment (Slowinski, 1998). Unlike traditional multiple-sequence alignment, which is divorced from the search for optimal tree topologies, direct optimization combines alignment and tree-search into a single procedure (i.e., nucleotide homology is dynamic) to produce globally most parsimonious trees. This is achieved by including insertions and deletions, in addition to transitions and transversions, as forms of character transformation during optimization.

The analysis began by generating 12 random addition sequences (RAS) per random replicate for 17 replicates. These 204 RAS were improved with TBR branch swapping during the searches, an additional round of TBR branch swapping of all trees within 0.5% of the shortest tree(s) found per replicate, and 340 parsimony ratchet replicates (Nixon, 1999; 20 rounds in each of the 17 replicates with ratchetpercent 20 and ratchetseverity 2 or 4). In addition to TBR branch swapping and ratcheting within each replicate, all resulting trees within 1.0% of the shortest trees were examined in an additional round of TBR branch swapping. The random replicates from these initial searches resulted in nine equally most parsimonious trees. These nine trees were submitted to POY for further tree searching using the commands *iterative pass* (Wheeler, 2003a) and *exact* (Wheeler et al., 2003). This second step of the analysis began by tree fusing (Goloboff, 1999) the nine submitted topologies and 20 additional RAS. The resulting trees were submitted to additional analyses including 100 rounds of parsimony ratcheting (ratchetpercent 20, ratchetseverity 2 or 5), and a final round of tree fusing and TBR branch swapping.

The length of the resulting implied alignment (Wheeler, 2003b) was verified in NONA (Goloboff, 1998) and PAUP* (Swofford, 2002). To estimate the "robustness" of the recovered phylogenetic hypotheses, Bremer supports (Bremer, 1988, 1995) were calculated using Tree Rot (Sorenson, 1999) in conjunction with PAUP*, and Jackknife resampling analyses were performed using NONA (1000 replications, heuristic searches, 10 random additions per replication), via the WinClada interface (Nixon, 2000).

For the 21 morphological features analyzed, consistency indices (CI, Kluge and Farris, 1969) and retention indices (RI, Farris, 1989) follow the individual character descriptions (table 1). Patterns of character evolution were examined using NONA in conjunction with WinClada. Unambiguous morphological transformations common to all most parsimonious dichotomized trees are used to diagnose clades (Goloboff, 1995).

RESULTS

Phylogenetic Analysis

Simultaneous analysis of the 21 morphological transformations (table 1) and the four gene fragments used by Sparks and Smith (2004), comprising a total of 2050 characters, resulted in nine equally most parsimonious trees with lengths of 1014 steps (298 phylogenetically informative characters, CI of 0.67, and RI of 0.61, when uninformative characters are retained). A strict consensus topology of these optimal trees is presented in figure 2 on which all unambiguously optimized morphological features are indicated with a numeration that matches the character descriptions in the text below. Support indices at nodes are presented in parentheses (Jackknife/Bremer support). Below we discuss the morphological character support for the monophyly and intrarelationships of ptychochromins derived from the combined analysis of morphological features and nucleotide characters.

Ptychochromin Relationships: Morphological Character Data

Node A: Ptychochromins (*Ptychochromoides* + *Oxylapia* + *Katria* + *Ptychochromis*)

Character 1. **Configuration of median frontal pores (NLF_0):** Among cichlids the median NLF_0 pores of the neurocranial laterosensory system may either be widely separated or broadly coalesced in the midline. In ptychochromins NLF_0 pores are invariably widely separated, whereas in all other cichlids these pores are more or less coalesced in the midline. Possession of widely separated NLF_0 pores was interpreted by Stiassny (1991) as the plesiomorphic cichlid condition and subsequent authors have followed that assessment; however, based on the current analysis, this condition is resolved as a unique and unreversed ptychochromin synapomorphy (fig. 2).

Character 2. **Tooth form:** Reinthal and Stiassny (1997) included the possession of a bilaterally symmetrical bicuspid oral dentition as a synapomorphy of *Ptychochromis* and *Ptychochromoides*. Sparks and Reinthal (2001) noted that although the oral dentition in *Oxylapia* is variable, in many individuals some bilaterally symmetrical, bicuspid teeth are interspersed among the otherwise distally expanded, dorsally flattened unicupid oral dentition. In the present analysis the possession of bilaterally symmetrical bicuspid teeth (coded as polymorphic for *Oxylapia*, table 1) unambiguously optimizes at Node A (fig. 2) and is interpreted here as a synapomorphy of the ptychochromins.

Character 3. **Anterior dorsal-fin pterygiophore:** Reinthal and Stiassny (1997) and Sparks and Reinthal (2001) follow Cichocki (1976) in noting the presence of a well-developed procurrent spur on the first dorsal-fin pterygiophore (fig. 3) in various ptychochromin genera. In *Oxylapia* (fig. 3D) the procurrent spur is less well developed than in other ptychochromins, but is clearly present and contrasts with the condition in non-ptychochromins (fig. 3E). In the current analysis the presence of a procurrent spur on the first dorsal-fin pterygiophore unambiguously optimizes at Node A and is interpreted as a synapomorphy of ptychochromins. The presence of an independently derived procurrent spur on the first dorsal-fin pterygiophore also characterizes members of the South American genus *Gymnogeophagus* (Gosse, 1976).

Character 4. **Supraneural shape:** Sparks and Reinthal (2001) noted that *Ptychochromis*, *Ptychochromoides* (at the time including *Katria*) and *Oxylapia* share the presence of supraneural (predorsal) elements shaped in the form of an inverted "L". Our own examination confirms this finding, but we note that this is most marked in the first supraneural element (see fig. 3C, D) and it is only among

TABLE 1

Morphological Character Matrix and Character Descriptions for Species of *Ptychochromis* and Outgroups

Inapplicable character assignments are designated by (–). "A" = character states 0 and 1. Consistency index (CI) and retention index (RI) follow the individual character descriptions in the format [CI, RI].

	Characters																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Paretroplus damii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0
Retroculus	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	1	0	0
Heterochromis	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1	0	1	0	–	0
Paratilapia polleni	0	0	0	0	0	0	0	0	0	0	A	0	0	0	0	0	1	1	A	–	0
Oxylapia polli	1	A	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	A	0	0
Ptychochromoides betsileanus	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0
Ptychochromoides itasy	1	1	1	1	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0
Ptychochromoides vondrozo	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0
Katria katria	1	1	1	1	1	1	1	1	1	0	0	0	0	0	1	1	0	1	1	1	0
Ptychochromis oligacanthus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	0
Ptychochromis insolitus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	0
Ptychochromis onilahy	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	0
Ptychochromis inornatus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
Ptychochromis grandidieri	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1	1	1	1	1
Ptychochromis makira	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	1	1	1	1	1
Ptychochromis loisellei	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1	1	1	1	1
Ptychochromis curvidens	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1	1	1	1	1

Character 1. *Median frontal laterosensory pores* (NLF_0): state 0, pores broadly coalesced in midline; state 1, pores widely separated. [1.00, 1.00]

Character 2. *Oral dentition*: state 0, unicuspid, tricuspid, or asymmetrically bicuspid; state 1, bilaterally symmetrically bicuspid. [1.00, 1.00]

Character 3. *Anterior dorsal-fin pterygiophore*: state 0, no procurrent spur; state 1, procurrent spur present. [1.00, 1.00]

Character 4. *Supraneural shape*: state 0, anterior supraneural uniform size; state 1, anterior supraneural in shape of an inverted "L". [1.00, 1.00]

Character 5. *Anal-fin spines*: state 0, graded in size; state 1, anterior spine very short, second and third spines elongate and of more or less similar lengths. [0.50, 0.75]

Character 6. *Inner margin of Cb4*: state 0, smooth; state 1, bearing a characteristically elongate process and deeply rounded indentation. [1.00, 1.00]

Character 7. *Cephalic laterosensory canals and pores*: state 0, not markedly enlarged; state 1, markedly enlarged and inflated. [0.50, 0.83]

Character 8. *Supraneural pattern*: state 0, supraneurals separated by first neural spine; state 1, both supraneurals located anterior to first neural spine. [1.00, 1.00]

Character 9. *Palatine lateral ethmoid process*: state 0, process absent or weakly developed; state 1, process well-developed and expansive. [1.00, 1.00]

Character 10. *"Free" epibranchial 2 toothplate*: state 0, no separate toothplate; state 1, separate toothplate present. [1.00, 1.00]

Character 11. *Infraorbital 2 (IO2)*: state 0, IO2 included in orbit; state 1, IO2 excluded from orbit by IO3. [0.50, 0.80]

Character 12. *Palatine groove*: state 0, no groove on palatine head; state 1, deep groove on palatine head. [0.50, 0.85]

Character 13. *Palato-palatine ligament insertion*: state 0, palato-palatine ligament inserts directly or via a small process onto dorsal face of each palatine; state 1, palato-palatine ligament insertion ventrally displaced onto small nublike process on dorsolateral face of each palatine. [1.00, 1.00]

Character 14. *Palatine type*: state 0, not as "western type"; state 1, "western type" with compact palatine head and elevated lateral ethmoid process, both with an upright orientation. [1.00, 1.00]

Character 15. *Scale ctenoidy*: state 0, body scales cycloid or weakly ctenoid with only the central portion of each scale margin bearing small cteni; state 1, body scales strongly ctenoid with the entire caudal scale margin bearing extremely well-developed cteni. [0.33, 0.50]

Character 16. *Number of infraorbital elements (including lachrymal):* state 0, 6 infraorbitals; state 1, 7 infraorbitals; state 2, 5 infraorbitals. [0.40, 0]

Character 17. *Anterior gas bladder*: state 0, anterior gas bladder horns absent or weakly developed and not approaching the exoccipital region of the neurocranium; state 1, anterior gas bladder horns well developed and contacting exoccipital region of neurocranium. [0.33, 0.33]

Characer 18. *Palatine splint*: state 0, no palatine splint; state 1, palatine splint present. [0.50, 0.75]

Character 19. *Pharyngobranchial 2 (Pb2) toothplate*: state 0, single row of teeth on Pb2; state 1, two or more rows of teeth on Pb2. [0.50, 0.66]

Character 20. *Configuration of ceratobranchial 4 (Cb4) toothplates*: state 0, Cb4 toothplates separate from outer row gill rakers; state 1, Cb4 toothplates confluent (fused) with outer row gill rakers. [0.50, 0.50]

Character 21. *Palatine type*: state 0, not "eastern type"; state 1, "eastern type" palatine head with horizontal orientation, and both elongate palatine prong and posterior palatine lamina more or less horizontally aligned. [0.50, 0.66]

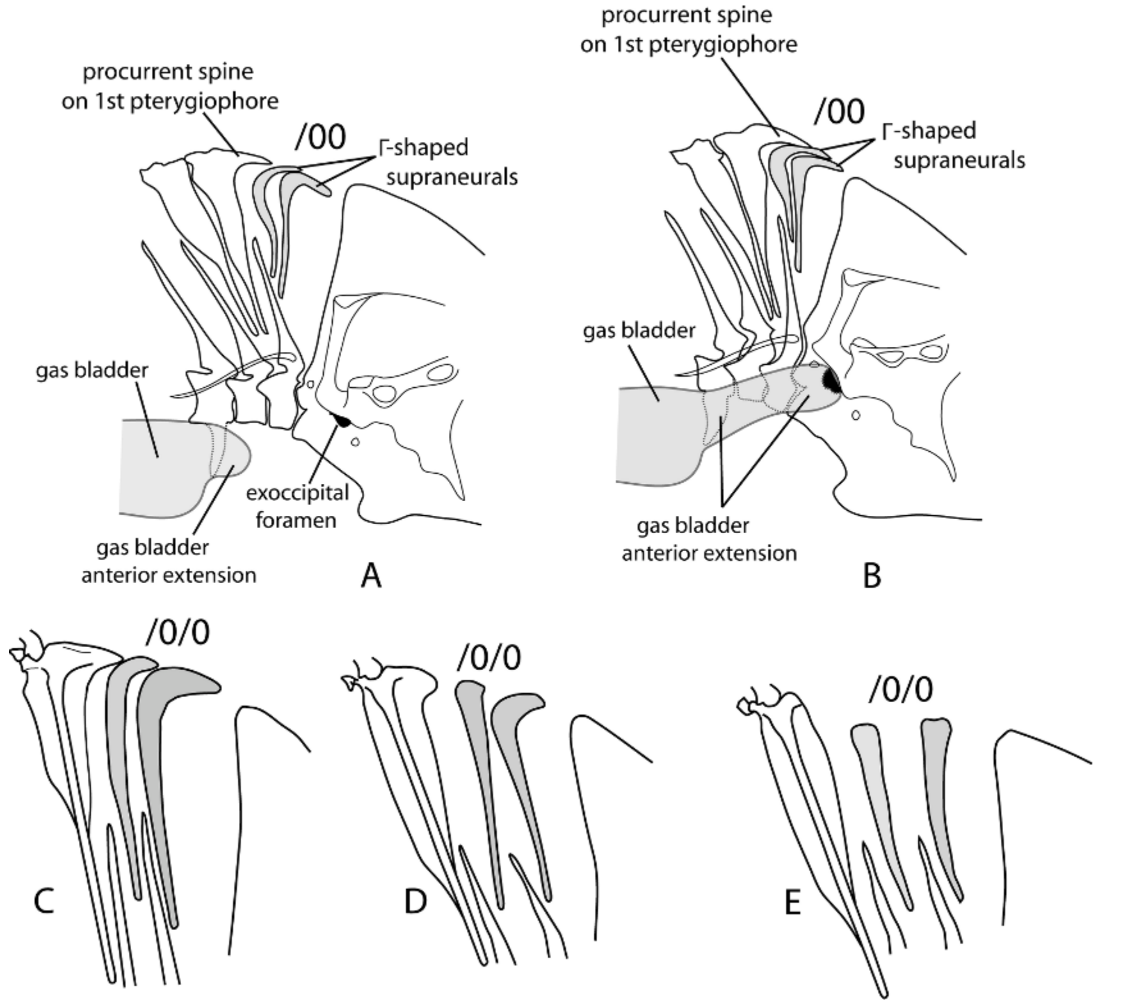

Fig. 3. Posterior neurocranium and associated structures (lateral view) in (A) *Katria* and (B) *Ptychochromis*, and isolated dorsal-fin pterygiophores and supraneural elements in (C) *Ptychochromoides*, (D) *Oxylapia*, and (E) *Paratilapia*.

Ptychochromis and *Katria* (fig. 3A, B) that the second supraneural is also markedly recurved. In the current analysis the presence of an inverted L-shaped first supraneural is resolved as a ptychochromin synapomorphy.

Character 5. **Anal spines:** Reinthal and Stiassny (1997) noted that in *Ptychochromis* and *Ptychochromoides* (at the time including *Katria*) the first anal-fin spine is extremely short, while the succeeding two spines are long and of more or less equal length. In the current analysis the presence of an extremely short first anal-fin spine followed by two long spines of more or less equal length unambiguously optimizes at Node A (fig. 2). This character is apparently reversed in *Oxylapia* where the first, second, and third anal-fin spines are uniformly graded in length.

Note on the Configuration of Fourth Ceratobranchial Toothplates (Character 20): Cichocki (1976) considered the possession of fourth ceratobranchial toothplates (Cb4-tp) that are contiguous (fused) with the outer row gill rakers (fig. 4B) to be plesiomorphic for cichlids, and Stiassny (1991) concurred. Although in the current analysis this feature fails to optimize unambiguously at a single node, we note that contiguous Cb4-tp

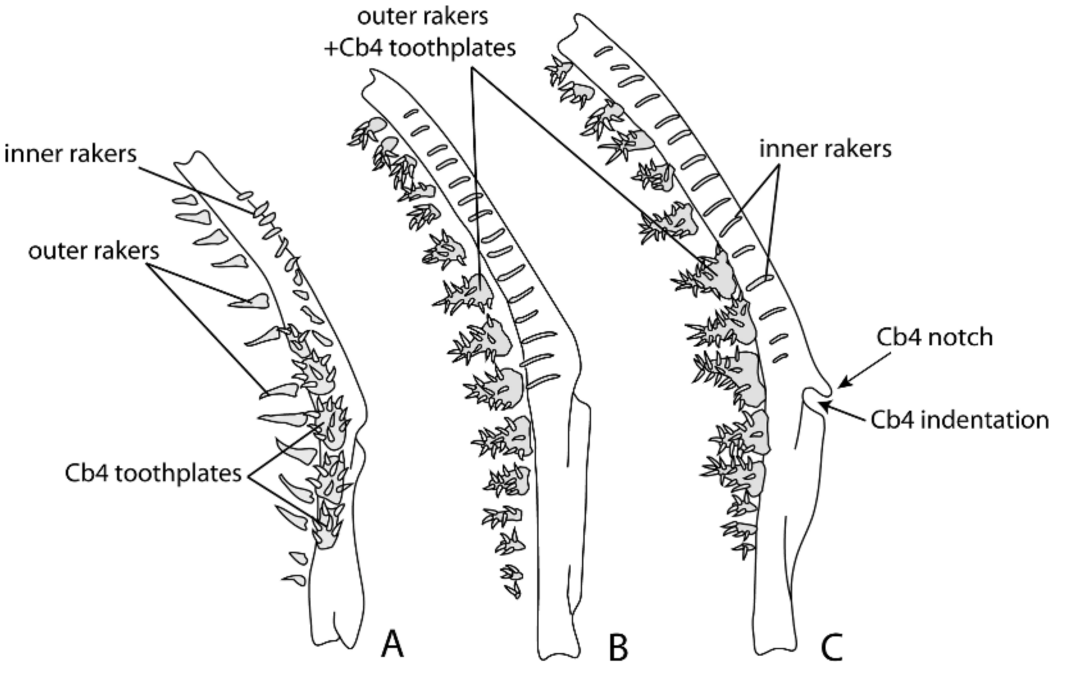

Fig. 4. Isolated fourth ceratobranchial elements and associated structures (dorsomedial view) in (A) *Etroplus*, (B) *Ptychochromoides*, and (C) *Katria*.

and outer gill rakers are present only in *Ptychochromoides*, *Katria*, and *Ptychochromis* (*Oxylapia* retains separate Cb4-tp and outer row rakers). In *Paretroplus* and *Etroplus* (fig. 4A) outer row gill rakers are separate from the Cb4-tp's, and a similar condition is exhibited in *Retroculus* (and all other Neotropical cichlids which retain Cb4-tp's). *Heterochromis* (and all other African cichlids) and *Paratilapia* lack toothplates on Cb4, and therefore this character has been coded as inapplicable for those taxa (table 1). Despite the lack of an unambiguous optimization for this feature, we note here that a confluence of Cb4-tp's and the outer row gill rakers is uniquely present in ptychochromins (reversed in *Oxylapia*), and this state may resolve as a ptychochromin synapomorphy in future analyses.

Kullander (1998) notes that the extremely heavy denticulation of the outer gill rakers of *Ptychochromis* is noteworthy and probably a derived feature within the family. We concur and add that similar heavily toothed outer rakers on Cb4 are found also in *Katria* (fig. 4C) and *Ptychochromoides* (fig. 4B) (reversed in *Oxylapia*).

Node B: Unnamed Clade (*Katria* + *Ptychochromis*)

Character 6. **Shape of inner margin of the fourth ceratobranchial:** In *Ptychochromis* and *Katria* (fig. 4C) the fourth ceratobranchial bone (Cb4) bears a characteristically elongate process and deeply rounded indentation on its inner margin. This feature is herein interpreted as a unique and unreversed synapomorphy of *Katria* and *Ptychochromis*.

Character 7. **Cephalic laterosensory canals:** Sparks (2004) noted that *Ptychochromis* and *Ptychochromoides katria* (now *Katria*) share a marked hypertrophy of the laterosensory canal system of the neurocranium, preopercle, and mandible. In these taxa the laterosensory canals are enlarged and the pores are markedly expanded (see fig. 5B). While a marked hypertrophy of the laterosensory system on the head and jaws optimizes unambiguously at Node B (fig. 2) and is interpreted as a synapomorphy of *Katria* and *Ptychochromis* in this analysis, the feature is homoplasious with respect to the condition in the African genus *Heterochromis*.

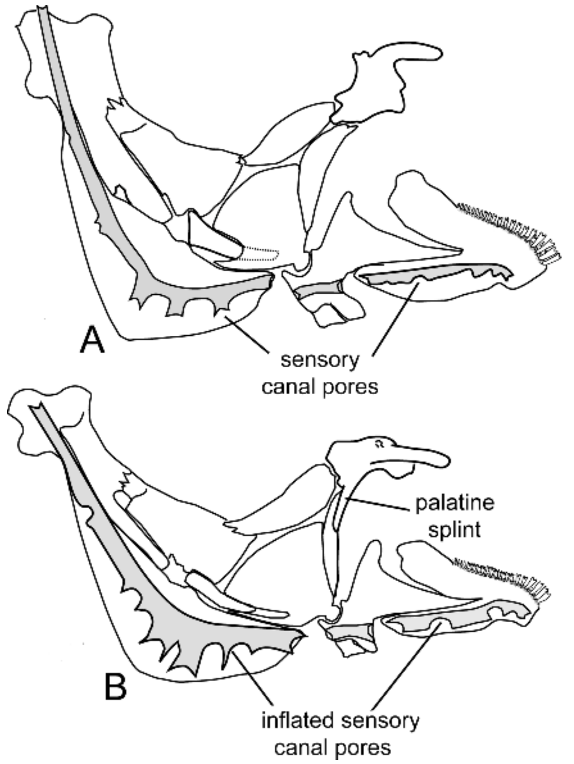

Fig. 5. Suspensorium and lower jaw (lateral view) of (A) *Ptychochromoides vondrozo* (UMMZ 235294) and (B) *Ptychochromis grandidieri* (AMNH 88102).

Character 8. **Supraneural pattern:** Uniquely in *Katria* and *Ptychochromis* two supraneural elements are located anterior to the first neural spine (fig. 3A, B). In all other taxa with two supraneurals, those supraneurals are separated by an intervening neural spine (fig. 3C, D, E). The possession of two supraneural elements located anterior to the first neural spine is interpreted as a unique and unreversed synapomorphy of a clade comprising *Katria* and *Ptychochromis*. The plesiomorphic arrangement of supraneurals with respect to neural spines may be annotated as /0/0 (where "/" denotes a neural spine and "0" denotes a supraneural) and the derived condition as /00 (see fig. 3).

Character 9. **Lateral ethmoid process of the palatine:** The palatine bone of *Katria* (fig. 6E) and *Ptychochromis* (Fig 6F, G) bears a well-developed, expansive, and dorsally elevated lateral ethmoid process on the dorsal margin of the palatine head, with a broad articulation surface on the medial face. This condition is contrasted with that in the remaining Malagasy and South Asian cichlids (fig. 6A–D), *Retroculus* (fig. 6H) and *Heterochromis* (fig. 6I), in which such a process and medial articulation facet is absent or only weakly developed. Whereas a similarly developed lateral ethmoid process is present in a few Neotropical and many African taxa, the feature optimizes unambiguously at Node B in this analysis and its presence is interpreted here as a synapomorphy of *Katria* + *Ptychochromis*.

Node C: *Ptychochromis*

Character 10. **Free second epibranchial toothplate:** Stiassny (1991) followed Cichocki (1976) in interpreting the presence of a free second epibranchial toothplate (Ep2-tp) as the plesiomorphic condition for cichlids. A free Ep2-tp is present in all species of *Ptychochromis* (fig. 7A) and is absent in all

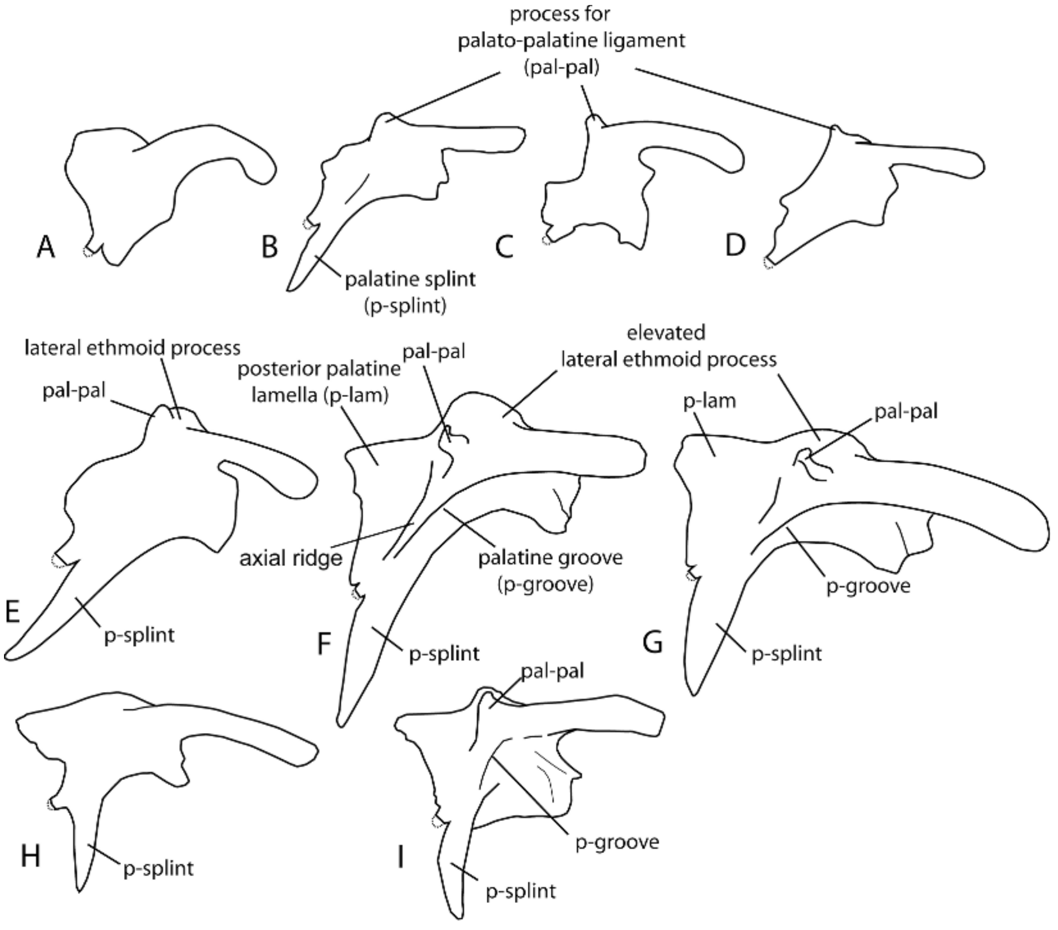

Fig. 6. Isolated palatine bones (lateral view) of (A) *Paretroplus*, (B) *Paratilapia*, (C) *Oxylapia*, (D) *Ptychochromoides*, (E) *Katria*, (F) *Ptychochromis oligacanthus* ("western type"), (G) *Ptychochromis grandidieri* ("eastern type"), (H) *Retroculus*, and (I) *Heterochromis*.

other cichlids (as in *Katria*, fig. 7B). In the current analysis, the presence of a free Ep2-tp optimizes unambiguously at Node C (fig. 2) and is interpreted herein as a unique and unreversed synapomorphy of *Ptychochromis*.

Character 11. **Infraorbital 2 (IO2):** In most Malagasy and South Asian cichlids the lachrymal (first infraorbital) is broadly contiguous with the second canal-bearing infraorbital (IO2), which is also platelike (see Cichocki, 1976; Stiassny, 1991; Kullander, 1998). In most of these taxa IO2 is positioned such that its dorsal margin forms part of the infraorbital ring beneath the orbit (fig. 8A–E). In *Ptychochromis* (fig. 8f) IO2 is completely excluded from the orbit by the third infraorbital element (IO3). Although a similar exclusion of IO2 from the orbital margin by IO3 is found also in *Retroculus* (fig. 8G) and *Heterochromis* (fig. 8H), exclusion of IO3 from the orbital margin optimizes unambiguously at Node C (fig. 2) and is interpreted herein as a synapomorphy of *Ptychochromis*.

Character 12. **Palatine groove:** In *Ptychochromis* the palatine bears a well-developed axial palatine ridge (Cichocki, 1976) and, as a result, a deep groove is formed beneath the palatine prong (fig. 6F, G). This condition is contrasted with that in the remaining Malagasy and South Asian cichlids (fig. 6A–E), which lack a well-defined axial ridge and

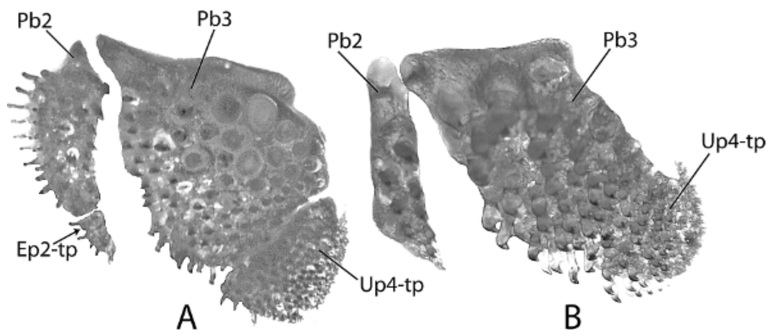

Fig. 7. Isolated upper pharyngeal jaw (ventral view) of (A) *Ptychochromis onilahy* (MNHN 1962-0201) and (B) *Katria katria* (AMNH 93701). *Ptychochromis* is diagnosed among cichlids by the presence of a "free" toothplate associated with, but not fused to, the second epibranchial bone (indicated by arrow).

palatine groove. Whereas a similarly developed ridge and groove is present in a few Neotropical and African taxa (e.g., *Heterochromis*, fig. 6I), this feature optimizes unambiguously at Node C in this analysis and its presence is interpreted here as a synapomorphy of *Ptychochromis*.

Character 13. **Attachment of the palato-palatine ligament:** In most cichlids the palato-palatine ligament attaches directly, or via a small process, onto the dorsal margin of the palatine head (fig. 6A–E, H, I). In *Ptychochromis* insertion of the palato-palatine ligament is ventrally displaced and attaches via a small nublike process that is situated on the lateroventral aspect of the palatine head (fig. 6F, G). Ventral displacement of the palato-palatine ligament insertion optimizes unambiguously at Node C in this analysis and its presence is interpreted here as a synapomorphy of *Ptychochromis*. We note, however, that a similar lateral displacement of the

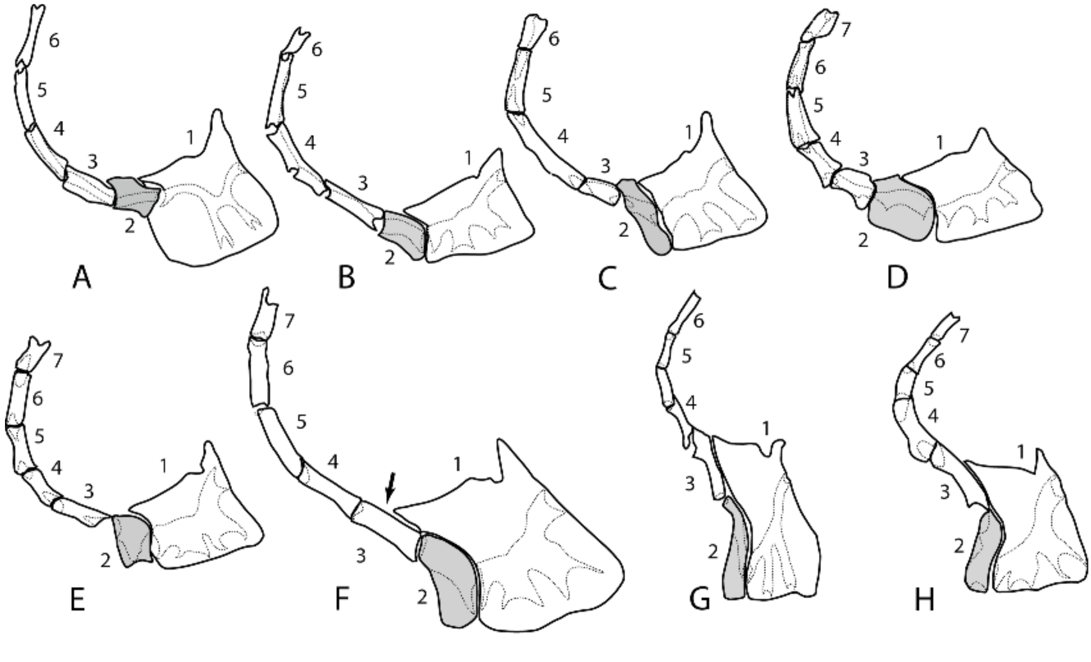

Fig. 8. Infraorbital series, IO2 shaded grey, in (A) *Etroplus*, (B) *Paratilapia*, (C) *Oxylapia*, (D) *Ptychochromoides*, (E) *Katria*, (F) *Ptychochromis*, (G) *Retroculus*, and (H) *Heterochromis*.

insertion of the palato-palatine ligament is found in a few African taxa.

Node D: "Western Clade" *Ptychochromis*

Character 14. **Palatine type:** Two distinctive palatine morphologies are exhibited within *Ptychochromis*. One, referred to here as the "western type" (fig. 6F), has a compact palatine head with a markedly elevated lateral ethmoid process and upright orientation. This is contrasted with the alternate condition, here termed the "eastern type", which has a markedly horizontal orientation with both an elongate palatine prong and the posterior palatine lamina more or less horizontally aligned. In the eastern-type palatine the lateral ethmoid process is also less prominent than in the alternative western type (fig. 6G). Counter to expectation and based on a consideration of morphological data alone, in our combined analysis of morphological and molecular evidence the western-type palatine optimizes unambiguously at node D (fig. 2), whereas the eastern-type palatine has no unambiguous optimization on the tree. As a result, the possession of a western-type palatine is interpreted here as a synapomorphy of *P. oligacanthus, P. onilahy, P. insolitus*, and *P. inornatus*.

Node E: Unnamed Clade

Character 15. **Ctenoidy:** In *Ptychochromis* most scales are ctenoid, although usually weakly so, with only the central portion of each scale margin bearing small cteni. Strongly ctenoid scales, with the entire caudal scale margin bearing extremely well-developed cteni are present in *P. insolitus* and *P. inornatus*, a feature that optimizes unambiguously as a synapomorphy uniting these two species in the current analysis.

Additional morphological characters utilized in this analysis are listed in table 1 and discussed in the text below.

Principal Components Analysis (PCA)

A sheared principal components analysis of 13 morphometric variables separated species of *Ptychochromis* exhibiting the western-type palatine configuration into four nonoverlapping clusters (fig. 9 and table 2). Sheared PC2 loaded heavily for caudal peduncle width, whereas the variables that loaded most heavily on sheared PC3 were preorbital depth, snout length, upper jaw length, and orbit diameter (table 2). Complete discrimination of *Ptychochromis insolitus*, new species, from the other species with a western-type palatine configuration occurred along sheared PC3. Sheared PC3 also essentially discriminates *P. onilahy*, new species, and *P. inornatus*, whereas sheared PC2 clearly separated *P. oligacanthus* from both *P. onilahy* and *P. inornatus*.

In a sheared principal components analysis of 13 morphometric variables for species of *Ptychochromis* exhibiting the eastern-type palatine configuration *P. curvidens*, new species, forms a distinct cluster (fig. 10 and table 3). Sheared PC2 loaded heavily for caudal peduncle width, whereas the variables that loaded most heavily on sheared PC3 were preorbital depth, interorbital width, and lower jaw length (table 3). Complete discrimination of *Ptychochromis curvidens* from the other species occurred along sheared PC2. Sheared PC2 and PC3 were unable to discriminate among the other three species with an eastern-type palatine configuration, *P. grandidieri*, *P. loisellei*, new species, and *P. makira*, new species, although there was only slight overlap between *P. grandidieri* and *P. loisellei* along sheared PC3.

SYSTEMATIC ACCOUNTS

Ptychochromis Steindachner, 1880

Diagnosis: A ptychochromin genus diagnosed by the presence of a free second epibranchial toothplate (fig. 7A, *Character 10: 1*), the third infraorbital (IO3) excluded from the orbit by IO2 (fig. 8F, *Character 11:1*), the presence of a well-developed palatine groove (fig. 6F–G, *Character 12:1*), and ventral displacement of the palatine-palatine ligament insertion (fig. 6F–G, *Character 13:1*).

Ptychochromis onilahy, new species
Figures 11–12, Plate 2A, Table 4

Ptychochromis oligacanthus, race du Sud-Ouest: Kiener, 1963.
Ptychochromis oligacanthus, race géographique "Sud-Ouest": Kiener and Maugé, 1966, fig. 26.

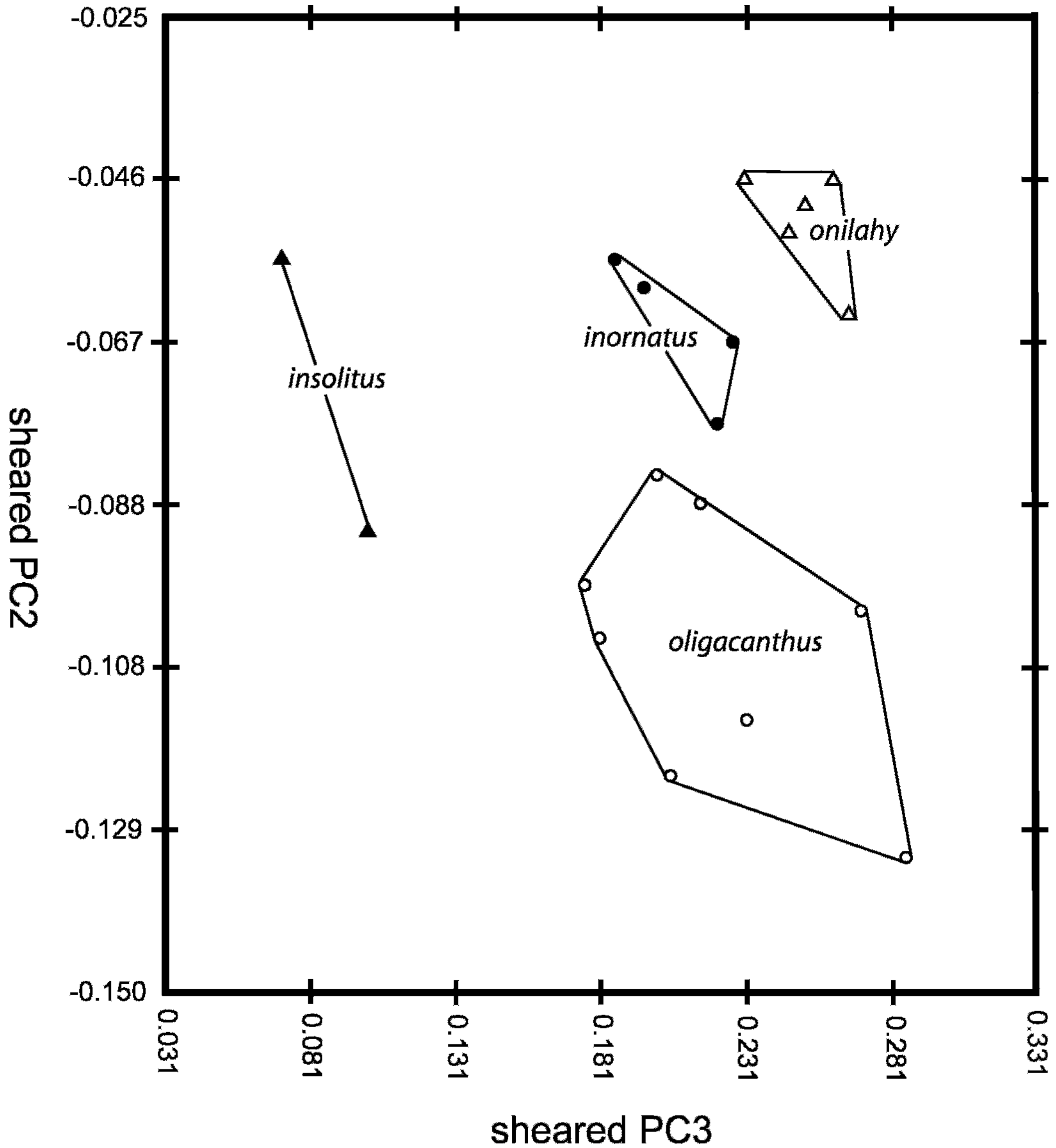

Fig. 9. Scatterplot of sheared second and third PC scores of 13 log-transformed morphometric variables for species of *Ptychochromis* exhibiting the western-type palatine configuration: *P. oligacanthus* (open circles), *P. inornatus* (solid circles), *P. onilahy* (open triangles), and *P. insolitus* (solid triangles).

Ptychochromis sp. "sud-ouest Riv. Onilahy": de Rham and Nourissat, 2002.

Ptychochromis n. sp. "onilahy": Sparks, 2003.

Ptychochromis nov. sp. "kotro/onilahy": Sparks and Stiassny, 2003: table 9.1.

HOLOTYPE: MNHN 1962-0201, 84.3 mm SL; southwestern Madagascar, Province of Tulear, Onilahy River, A. Kiener.

PARATYPES: AMNH 237130, 1 ex. (C&S in part), 76.8 mm SL; data as for holotype. MNHN 2006-0780, 3 ex., 66.4–85.8 mm SL; data as for holotype.

DIAGNOSIS: A *Ptychochromis* exhibiting the western-type palatine morphology (fig. 12A) and distinguished from all congeners by the presence of a lachrymal plate that extends

TABLE 2
Loadings of Morphometric Variables in Sheared Principal Components Analysis for Species of *Ptychochromis* Exhibiting the Western Type Palatine Configuration (figs. 6F, 9)

Variable	Sheared PC2	Sheared PC3
Standard length	0.040	0.003
Head length	0.063	−0.215
Body depth	0.133	0.161
Snout length	0.162	−0.363
Lower jaw length	0.068	−0.309
Upper jaw length	−0.023	−0.355
Interorbital width	0.094	0.067
Preorbital depth	0.402	0.453
Caudal peduncle depth	0.304	0.271
Caudal peduncle length	−0.067	0.215
Caudal peduncle width	−0.807	0.309
Orbit diameter (horizontal)	−0.147	−0.351
Orbit depth	−0.017	−0.181

ventrally to cover a portion of the upper lip. It is further distinguished from all congeners except *P. oligacanthus* by the presence of cycloid scales above the upper lateral line on the flanks, and only two inner rows of teeth in both upper and lower jaws. *Ptychochromis onilahy* is distinguished from *P. oligacanthus* by a higher number of lateral line scales (33–34 vs. 29–31 in *P. oligacanthus*), a shorter head length (32.8–34.7 vs. 35.9–40.0% SL in *P. oligacanthus*). Additionally, *P. onilahy* lacks all trace of the black blotch or bar covering the dorsoposterior margin of the opercle, diagnostic of *P. oligacanthus*.

DESCRIPTION: Morphometric and meristic data presented in table 4. Morphological characteristics and general pigmentation pattern in preservation can be observed in figure 11 and plate 2A. Body deep and laterally compressed. Lateral snout outline straight. Predorsal head profile convex from midorbit to dorsal-fin origin. Dorsal body profile from dorsal-fin origin smoothly convex. Ventral body profile more or less straight. Caudal peduncle short, deep, and laterally compressed. Dorsal-fin origin located anterior to vertical through pectoral-fin insertion. Pelvic-fin origin located well posterior to vertical through pectoral-fin insertion.

Total vertebral count 26 or 27, with a formula of 13 + 13 or 13 + 14 precaudal and caudal vertebrae, respectively.

Jaws isognathous. Oral dentition bilaterally symmetrical and bicuspid, with crowns somewhat expanded distally and slightly recurved. Outer row teeth of both jaws enlarged and graded in size laterally. Rostrally, outer row teeth procumbently implanted in lower jaw but only slightly so in upper jaw. Cusps well developed, particularly rostrally. Rostrally, upper and lower jaws with two inner rows of smaller teeth of the same morphology as those of outer rows. Total of three rows of teeth along rostral margin of both upper and lower jaws, tapering to a single row of teeth posteriorly. Dentition covers anterior half of dentary and nearly entire surface of premaxillary arcade. Uniquely with lachrymal bone on snout extending ventrally to cover a portion of upper lip, whereas in congeners the upper lip is fully exposed below lachrymal plate.

Lower pharyngeal jaw (LPJ) with a weakly interdigitating suture on posteroventral margin. Dentition on LPJ and upper pharyngeal toothplates (UPJ) composed of numerous, closely set, hooked, and bicuspid teeth. Medially on UPJ and posteromedially on LPJ, dentition becoming robust and molariform (fig. 12B). Four rows of hooked and bicuspid teeth on second pharyngobranchial toothplate. Three rows of teeth medially on "free" second epibranchial toothplate.

Lower limb rakers of first gill arch denticulate dorsomedially. Nine or ten (modally 10) triangular and somewhat elongate gill rakers (fig. 12C) arrayed along lower limb of first arch. Seven to nine epibranchial gill rakers. Rakers on remaining arches short, laterally expanded, and strongly denticulate. Teeth elongate and conical. Robust toothplates present on dorsal surface of fourth ceratobranchial bones; toothplates confluent with gill rakers of outer row of these elements. Teeth on fourth ceratobranchial toothplates unicuspid and conical laterally to hooked and bicuspid medially.

Body covered with large, regularly imbricate, weakly ctenoid scales from about level of midorbit to proximal portion of caudal fin. Scales above upper lateral line to about level of origin of soft dorsal fin cycloid. Scales on flanks becoming increasingly ctenoid posteriorly, but at most only weakly so. Scales on nape and head region cycloid. Four or five

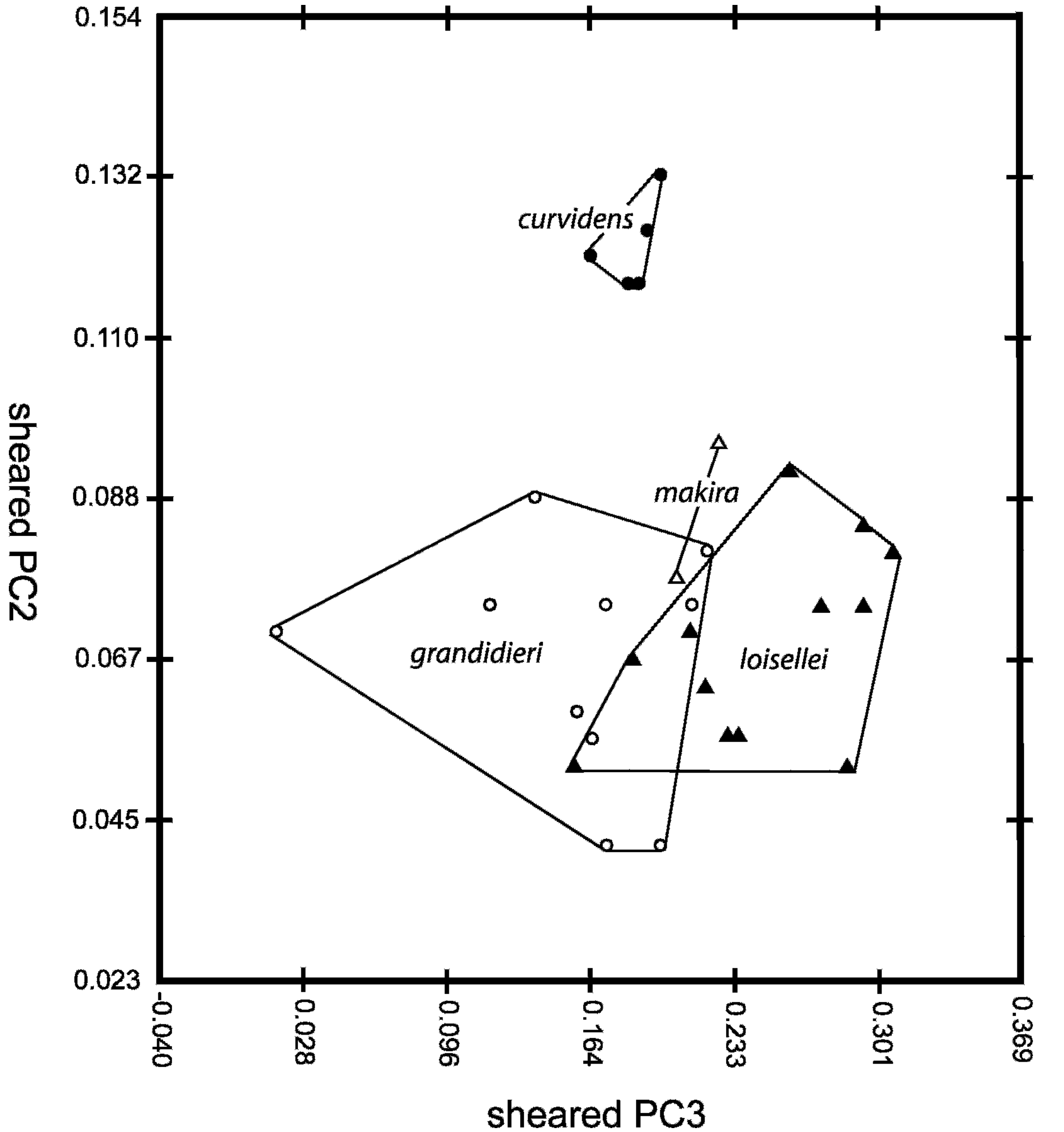

Fig. 10. Scatterplot of sheared second and third PC scores of 13 log-transformed morphometric variables for species of *Ptychochromis* exhibiting the eastern-type palatine configuration: *P. grandidieri* (open circles), *P. curvidens* (solid circles), *P. makira* (open triangles), and *P. loisellei* (solid triangles).

rows of cycloid scales on cheek. Scales on opercle and subopercle missing in all specimens. Anterior chest scales reduced in size and embedded. Scales on chest weakly ctenoid, except anteriorly where they are cycloid. Scales on belly cycloid. Snout, lachrymal, and anterior portion of interorbital region asquamate. Scales on caudal fin reduced in size. Lateral line scales 33 or 34. Five scales in diagonal from lateral line to dorsal-fin origin. Four or five scale rows between bases of pectoral and pelvic fins. No scale rows present along dorsal- and anal-fin bases.

Dorsal fin with XIII spines and 12 soft rays. Anal fin with III spines and eight or nine soft rays. First anal spine very short, second and third spines elongate and of similar length. All fins damaged, making determination of orig-

TABLE 3
Loadings of Morphometric Variables in Sheared Principal Components Analysis for Species of *Ptychochromis* Exhibiting the Eastern Type Palatine Configuration (figs. 6G, 10)

Variable	Sheared PC2	Sheared PC3
Standard length	0.082	0.059
Head length	0.115	−0.118
Body depth	0.082	0.232
Snout length	0.193	−0.264
Lower jaw length	0.193	−0.372
Upper jaw length	0.187	0.203
Interorbital width	0.155	0.462
Preorbital depth	0.153	−0.569
Caudal peduncle depth	0.096	0.227
Caudal peduncle length	0.105	0.262
Caudal peduncle width	−0.882	−0.023
Orbit diameter (horizontal)	0.129	0.140
Orbit depth	0.051	0.059

inal fin shape impossible. Pelvic fins short, extending at most to origin of anal fin.

MISCELLANEOUS OSTEOLOGY AND ANATOMY: Well-developed exoccipital foramina present on posterior of neurocranium. Paired anterior gas bladder extensions well developed but feeble, in contact with exoccipital region of neurocranium via connective tissue, but do not extend into exoccipital foramina. Infraorbital series composed of seven elements: lachrymal with four pores (fig. 12D), IO2 excluded from orbit by ventrally displaced IO3. Uncinate process and anterior arm of first epibranchial bone short and robust (fig. 12C). Well-developed process and deep indentation present on inner face of Cb4.

COLORATION IN LIFE: According to Kiener (1963) and Kiener and Maugé (1966), adults of this taxon were uniformly gray brown,

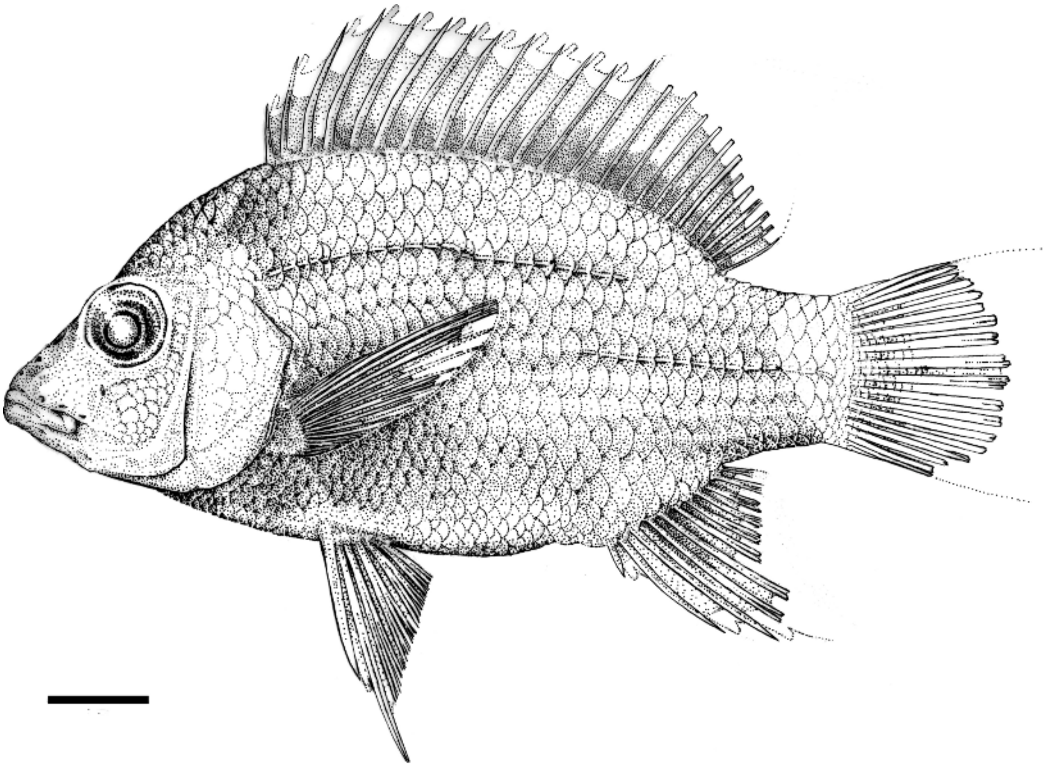

Fig. 11. *Ptychochromis onilahy*, new species, holotype, MNHN 1962-0201, 84.3 mm SL, southwestern Madagascar, Province of Tulear, Onilahy River. Scale bar = 1 cm. Drawing by Ian Hart.

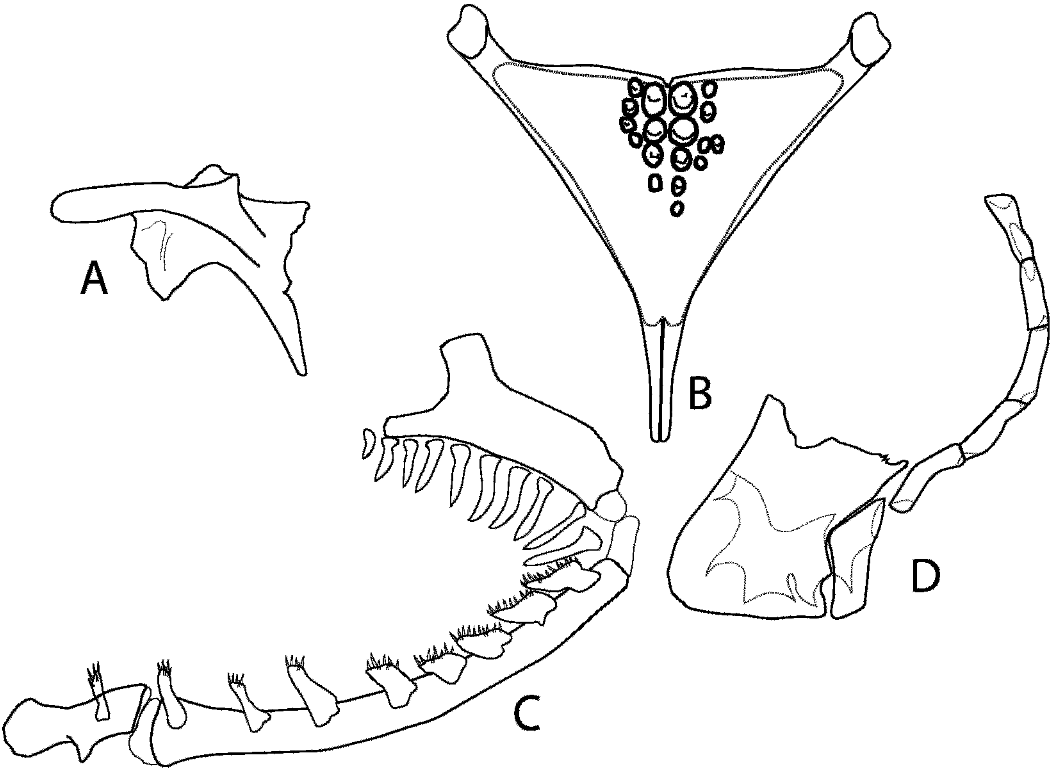

Fig. 12. *Ptychochromis onilahy*, new species, paratype, MNHN 2006-0780: (A) palatine, (B) LPJ, (C) first gill arch, and (D) infraorbital series.

paler ventrally and lacking any obvious body markings.

Coloration in Preservative: Ground coloration brownish to golden-brown, lighter ventrally. All fins brownish, pectoral fins lightest and somewhat hyaline.

All five specimens appear quite faded in preservation, although a faint banding pattern is discernable in most specimens, whereas in two specimens a faded series of midlateral blotches remains.

Distribution and Habitat: *Ptychochromis onilahy* is currently known only from the type series that was collected in the Onilahy River, a major westward flowing basin in southwestern Madagascar (fig. 1). Although detailed locality information is lacking, these specimens were collected by Kiener and almost certainly correspond to the "forme" of *P. oligacanthus* identified by Kiener and Maugé (1966) from the southwest of Madagascar. According to Kiener (1963) this taxon was particularly abundant in the Onilahy River to Ambohimahavelona (Lower Onilahy), and Kiener and Maugé (1966) indicate that it occurred, historically at least, from the Lower Onilahy River in the south, and northward in coastal basins to a little south of the Mangoky River.

Conservation Status: Despite a number of collecting expeditions to southwestern Madagascar in recent years, no additional specimens referable to *P. onilahy* have been collected and the species may be extinct. However, many areas of southwestern Madagascar have not been thoroughly surveyed for freshwater fishes, and the Onilahy River basin is a large drainage system, thus, the possibility exists that remnant populations of *P. onilahy* persist in more remote areas within the region.

Local Name: According to Kiener (1963), in the Onilahy region *P. onilahy* was referred to as *boramany*, whereas fishermen around Lake Ihotry referred to the species as *kotro*.

Etymology: The species is named after the basin in which the type, and only known,

TABLE 4
Morphometric and Meristic Data for *Ptychochromis onilahy*, new species
Values in parentheses indicate number of specimens examined with that count. (H) indicates count corresponding to holotype.

Character	N	Holotype	Range	Mean	SD
Standard length (mm)	5	84.3	66.4–85.8	78.0	
Percentage of SL					
Head length	5	33.6	32.8–34.7	33.9	0.72
Body depth	5	45.0	44.6–47.3	45.5	1.10
Predorsal length	5	32.5	30.7–36.0	33.6	2.21
Preanal length	5	72.2	72.2–75.3	74.2	1.21
Prepelvic length	5	38.8	38.7–42.3	40.4	1.65
Head width (max.)	5	15.1	13.9–15.7	15.1	0.75
Caudal peduncle length	5	14.4	14.1–15.4	14.5	0.50
Caudal peduncle width	5	3.4	3.2–3.6	3.4	0.16
Caudal peduncle depth	5	20.3	18.6–20.3	19.4	0.78
Pectoral-fin length	5	N.A.	N.A.	N.A.	N.A.
Pelvic-fin length	5	N.A.	N.A.	N.A.	N.A.
Percentage of HL					
Snout length	5	33.9	32.1–36.1	34.3	1.66
Orbit diameter	5	28.3	24.8–28.3	26.7	1.54
Upper jaw length	5	28.3	28.0–29.4	28.7	0.61
Lower jaw length	5	37.1	37.1–40.8	38.9	1.58
Interorbital width	5	30.4	28.4–32.7	30.3	1.52
Preorbital depth	5	25.8	22.9–27.6	25.0	1.85
Caudal peduncle length/depth	5	0.7	0.7–0.8	0.8	0.05
Caudal peduncle length/width	5	4.2	4.1–4.4	4.2	0.14
Scales in lateral line	5	33 (3), 34 (2) (H)			
Scales: lateral line to dorsal fin	5	5 (H)			
Scales: pectoral to pelvic bases	5	4 (1) (H), 5 (4)			
Gill rakers (lower limb)	5	9 (1), 10 (4) (H),			
Vertebrae (precaudal + caudal)	5	13 + 13 = 26 (1), 13 + 14 = 27 (4) (H)			
Dorsal fin	2	XIII 12 (H)			
Anal fin	2	III 8 (2) (H), III 9 (3)			

specimens were reportedly collected. Specific epithet used as a noun in apposition.

Discussion and Comparisons: In sharing the western-type palatine morphology (fig. 6F, *Character 14:1*), *Ptychochromis onilahy* is recovered in a "western clade" of *Ptychochromis* (fig. 2), whose members are restricted to western drainages (fig. 1). In overall appearance it is most similar to *P. oligacanthus* from which it is readily distinguished by lateral line scale count (33 or 34 vs. 29–31 in *P. oligacanthus*) and some proportional measurements (e.g., HL 32.8–34.7% SL vs. 35.9–40.0% SL in *P. oligacanthus*). Unfortunately, no suitable tissue sample is available for inclusion in molecular phylogenetic studies and morphological character data gathered to date are not informative at this level of analysis; therefore, the sister group to *P. onilahy* is not known.

***Ptychochromis makira*, new species**
Figures 13–14, Plate 2B, Table 5

Ptychochromis sp. "Makira": Sparks and Smith, 2004: fig. 1, table 1.

Holotype: AMNH 237131, adult, 146.2 mm SL; northeastern Madagascar, Toamasina Province, north of Maroansetra, near town of Marovonona, Antainambalana River, purchased from local fishermen by Augustin Sarovy, J. S. Sparks, W. L. Smith, and K. L. Tang, Nov. 2003.

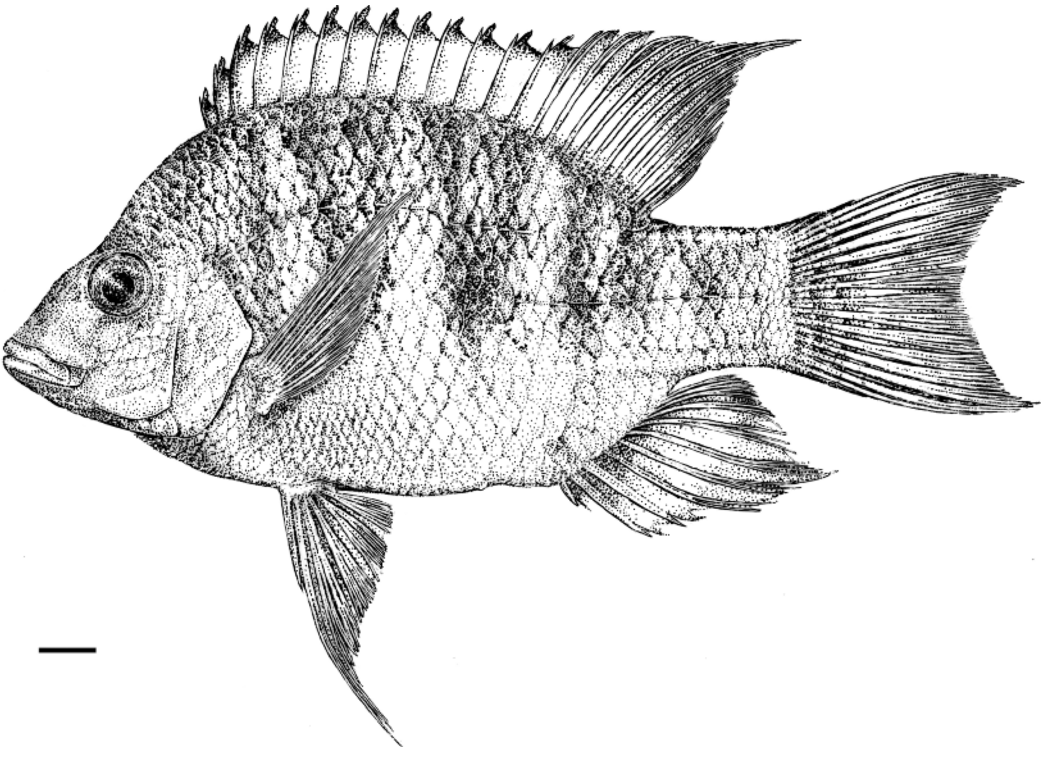

Fig. 13. *Ptychochromis makira*, new species, holotype, AMNH 237131, adult, 146.2 mm SL, northeastern Madagascar, Toamasina Province, north of Maroansetra, near town of Marovonona, Antainambalana River. Scale bar = 1 cm. Drawing by Ian Hart.

PARATYPE: AMNH 237132, 1 ex. (C&S in part), 112.5 mm SL; data as for holotype.

DIAGNOSIS: A *Ptychochromis* exhibiting the eastern-type palatine morphology (fig. 14A) and distinguished from all congeners by the presence of three (vs. four) laterosensory pore foramina on the lachrymal (the posteriormost [= third] foramen forms part of the marginal canal between the lachrymal and second infraorbital bone; fig. 14D) and a unique pigmentation pattern consisting of four distinctive V-shaped black bars on the flanks superimposed on an overall whitish base. *Ptychochromis makira* is further distinguished from all congeners, except *P. insolitus* (with five), in the possession of a total of six (rather than seven) infraorbital bones.

DESCRIPTION: Morphometric and meristic data presented in table 5. Morphological characteristics and general pigmentation pattern can be observed in figure 13 and plate 2B. Extremely deep-bodied and laterally compressed. Dorsal body profile strongly curved, particularly in holotype. Ventral body profile moderately convex in paratype and relatively straight in holotype. Lateral snout outline straight to mildly curved. Predorsal head profile moderately convex from midorbit to dorsal-fin origin. Supraoccipital crest prominent and deep in larger specimen. Caudal peduncle short, deep, and laterally compressed. Dorsal-fin origin located slightly anterior to vertical through pectoral-fin insertion. Pelvic-fin origin located well posterior to vertical through pectoral-fin insertion.

Total vertebral count 27, with a formula of 13 + 14 precaudal and caudal vertebrae, respectively.

Jaws isognathous. Oral dentition bilaterally symmetrical and bicuspid, with moderately to well-developed distally expanded and slightly recurved cusps. Outer row teeth of both jaws enlarged and graded in size laterally. Rostrally, outer row teeth procumbently im-

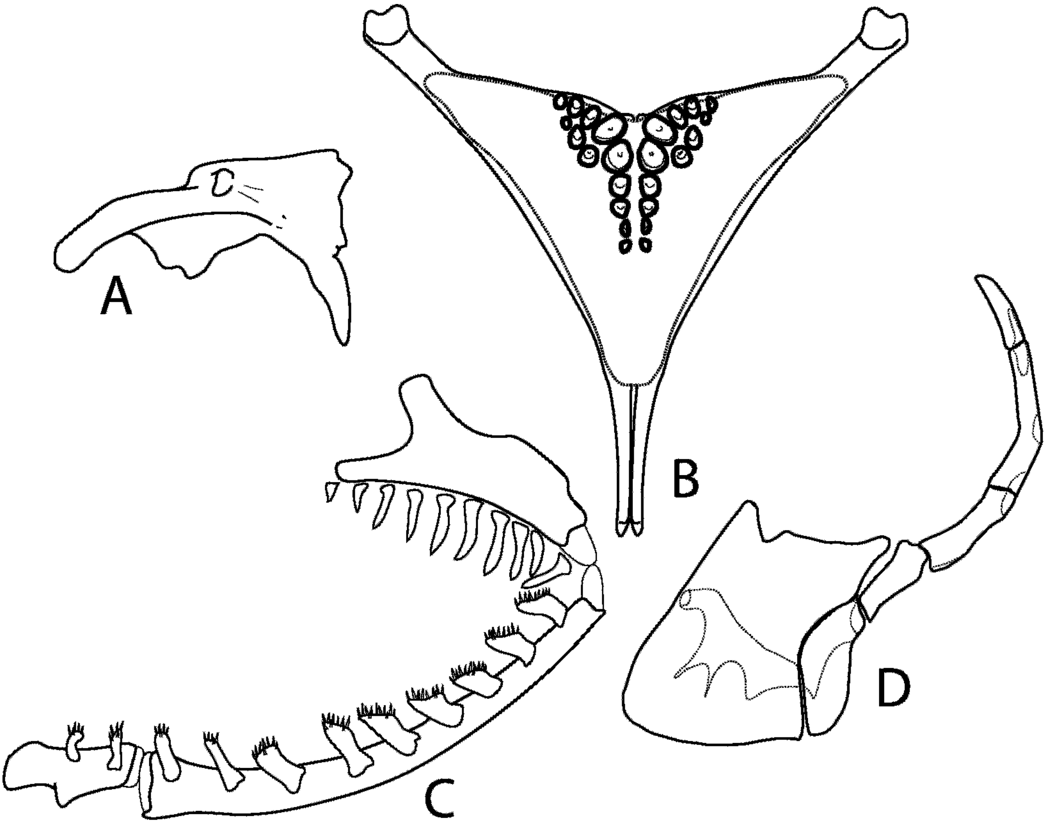

Fig. 14. *Ptychochromis makira*, new species, paratype, AMNH 237132: (A) palatine, (B) LPJ, (C) first gill arch, and (D) infraorbital series.

planted in lower jaw but only slightly so in upper jaw. Rostrally, both upper and lower jaws with three inner rows of smaller teeth of the same morphology as those of outer rows. Total of four rows of teeth along rostral margin of both upper and lower jaw, tapering to a single row of teeth posteriorly. Dentition covers anterior 2/3 of dentary and nearly entire surface of premaxillary arcade.

LPJ robust with weakly interdigitating suture on posteroventral margin. Dentition on LPJ and UPJ comprised of numerous, closely set, hooked, and bicuspid teeth. Cusps on LPJ better developed posteriorly. Medially on both LPJ and third pharyngobranchial, dentition robust and molariform (fig. 14B). Five or six rows of hooked and bicuspid teeth on expansive second pharyngobranchial toothplates. Three rows of teeth present medially on "free" second epibranchial toothplate. Robust, laterally expanded, toothplates cover majority of dorsal surface of fourth ceratobranchial bones; toothplates confluent with outer row gill rakers of these elements. Dentition on fourth ceratobranchial toothplates unicuspid (and generally conical) or weakly hooked and bicuspid laterally, hooked and bicuspid medially (similar to lateral LPJ dentition).

Lower limb rakers of first gill arch denticulate dorsomedially. Eleven somewhat elongate gill rakers arrayed along lower limb of first arch. Nine epibranchial gill rakers. Gill rakers on remaining arches short, laterally expanded, and strongly denticulate. Teeth elongate and conical, somewhat bulbous distally.

Body covered with large, regularly imbricate, weakly ctenoid scales. Ctenoid scales extend from just posterior to dorsal-fin origin above upper lateral line and slightly anterior to pectoral-fin base below upper lateral line, to proximal portion of caudal fin. Scales on nape

TABLE 5
Morphometric and Meristic Data for *Ptychochromis makira*, new species
Values in parentheses indicate number of specimens examined with that count. (H) indicates count corresponding to holotype.

Character	*N*	Holotype	Range	Mean	SD
Standard length (mm)	2	146.2	112.5–146.2	129.4	
Percentage of SL					
Head length	2	32.0	32.0–32.2	32.1	0.12
Body depth	2	48.9	48.1–48.9	48.5	0.58
Predorsal length	2	39.8	39.8–40.8	40.3	0.70
Preanal length	2	75.1	75.1	75.1	0.01
Prepelvic length	2	41.7	41.7–41.9	41.8	0.10
Head width (max.)	1	15.4	15.4	15.4	N.A.
Caudal peduncle length	2	14.0	14.0–14.2	14.1	0.14
Caudal peduncle width	2	4.9	4.9–5.0	5.0	0.04
Caudal peduncle depth	2	18.1	16.4–18.1	17.2	1.20
Pectoral-fin length	2	32.7	32.7–34.7	33.7	1.39
Pelvic-fin length	2	36.3	29.3–36.3	32.8	4.89
Percentage of HL					
Snout length	2	42.7	39.8–42.7	41.3	2.09
Orbit diameter	2	25.6	25.6–27.6	26.6	1.40
Upper jaw length	2	36.1	30.4–36.1	33.2	4.05
Lower jaw length	2	38.9	38.1–38.9	38.5	0.54
Interorbital width	2	33.8	32.0–33.8	32.0	1.21
Preorbital depth	2	25.6	25.6–26.5	26.1	0.62
Caudal peduncle length/depth	2	0.8	0.8–0.9	0.8	0.06
Caudal peduncle length/width	2	2.9	2.9	2.9	0.01
Scales in lateral line	2	33 (2) (H)			
Scales: lateral line to dorsal fin	2	5 (2) (H)			
Scales: pectoral to pelvic bases	2	4 (2) (H)			
Gill rakers (lower limb)	2	11 (2) (H)			
Vertebrae (precaudal + caudal)	2	13 + 14 = 27 (2) (H)			
Dorsal fin	2	XIII 12 (2) (H)			
Anal fin	2	III 8 (1) (H), III 9 (1)			

and head region cycloid. Scales on opercle and subopercle also cycloid. Cheek scales cycloid and comprising four rows. Anterior chest scales slightly reduced in size and embedded. Snout, lachrymal, and anterior portion of interorbital region to about level of midorbit asquamate. Scales on caudal fin reduced in size and ctenoid anteriorly, markedly smaller and cycloid posteriorly. Lateral line scales 33. Five scale rows between bases of pectoral and pelvic fins. Five scales in diagonal from lateral line to dorsal-fin origin. No scale rows present along dorsal- and anal-fin bases.

Dorsal fin with XIII spines and 12 soft rays. Anal fin with III spines and eight or nine soft rays. First anal spine very short, second and third spines elongate and similar in length. Caudal fin emarginate, trailing margins of upper and lower lobes slightly produced. Pectoral fin elongate and tapered distally. Distal margins of soft dorsal and anal fins produced and pointed in holotype (= larger specimen). Trailing margin of soft dorsal fin elongate and filamentous in holotype. Pelvic fin not extending to anal-fin origin in smaller specimen (= paratype), slightly beyond origin in holotype.

MISCELLANEOUS OSTEOLOGY AND ANATOMY: Well-developed exoccipital foramina present on posterior of neurocranium. Paired anterior gas bladder extensions in contact with exoccipital region of neurocranium via connective tissue, but do not extend into exoccipital foramina. Infraorbital series (fig. 14D) composed of six elements. Although infraorbital number is extremely variable within Cichlidae (see Stiassny, 1991; Kullander, 1998), a total of seven infraorbital elements is resolved as the plesiomorphic condition for Cichlidae and is most commonly encountered among ptychochromins. A reduction to six is interpreted as a derived condition within *Ptychochromis* (*Character 16*, fig. 2). Lachrymal deep, with only three pores (fig. 14D), IO2 excluded from orbit by ventrally displaced IO3. Uncinate process and anterior arm of first epibranchial bone short and robust (fig. 14C). Well-developed process and deep indentation present on inner face of Cb4.

COLORATION IN LIFE: Unknown. Coloration and pigmentation pattern notes were taken within a couple days of preservation (plate 2B) and live coloration is probably similar to that reported below for preserved state.

COLORATION IN PRESERVATIVE: Ground coloration pale creamy white to yellow. Four black V-shaped bands present on flanks, which extend ventrally to lateral midline. Body much lighter ventrally, and essentially uniform pale creamy yellow. Fins pale yellow to grayish; fin rays dark gray to black. Fins, excluding pectorals, blackish terminally. Pectoral fin olive proximally and mostly hyaline distally. Anterior interorbital region, snout, and lachrymal grayish-green. Lips light olive. Scales on chest and ventral flanks, primarily rostral of anal-fin origin, brown along exposed margins.

DISTRIBUTION AND HABITAT: *Ptychochromis makira* is known only from the type series, collected in the Antainambalana River just north of Maroansetra in northeastern Madagascar (fig. 1). The southern range limit of *P. makira* is not known with certainty, but it is possible that *P. makira* is conspecific with populations of similarly pigmented *Ptychochromis* reported by local fishermen to occur as far south as the coastal towns of Manompana and Mananara.

CONSERVATION STATUS: Although once common throughout the region, *P. makira* has suffered a severe decline in abundance in recent years, according to local fishermen. Little original riparian vegetation remains in the lower reaches of the Antainambalana River basin. Fishing pressure is high in the region surrounding Maroansetra and habitat degradation has been widespread throughout the Antainambalana basin. Local fishermen report that the species is now rare.

LOCAL NAME: *Saroy* is the Malagasy name used throughout eastern Madagascar to refer to species of *Ptychochromis*.

ETYMOLOGY: The species is named after the region in which the type specimens were collected. The specific epithet, *makira*, is used as a noun in apposition.

DISCUSSION AND COMPARISONS: In our phylogenetic analysis, *P. makira* is recovered in a polytomy and its immediate relationships remain unresolved (fig. 2). Although there is currently no unambiguous evidence for the monophyly of an assemblage comprising *P. makira*, *P. grandidieri*, *P. loisellei*, and *P. curvidens*, the shared possession of an eastern-type palatine morphology is unique to these four species and may indicate a close relationship among them. Molecular data analyzed alone indicates that *P. makira* is the sister taxon to the remaining species of *Ptychochromis* (Sparks and Smith, 2004). Regardless, morphometrically *P. makira* is most similar to *P. grandidieri* from which it is readily distinguished by pigmentation pattern and coloration, infraorbital morphology, and also in the possession of a considerably smaller LPJ with fewer and less well-developed molariform teeth (compare fig. 14B and fig. 24B).

Ptychochromis loisellei, new species
Figures 15–16, Plates 1C and 2C, Table 6

Ptychochromis sp. "nord-est": de Rham and Nourissat, 2002.
Ptychochromis n. sp. "green garaka": Sparks, 2003.
Ptychochromis nov. sp. "green garaka": Sparks and Stiassny, 2003.
Ptychochromis sp. "Garaka": Sparks and Smith, 2004: fig. 1, table 1.

HOLOTYPE: AMNH 232462, 99.5 mm SL, male; northeastern Madagascar, Antsiranana Province, north of Sambava, Mahanara River at Antsirabe-Nord, just upstream of bridge over route N-5 (13°58.49S; 49°57.81E), PVL-01-29, P.V. Loiselle and local fishermen, 1 Nov., 2001.

PARATYPES: AMNH 231249, 1 ex., 108.5 mm SL; northeastern Madagascar,

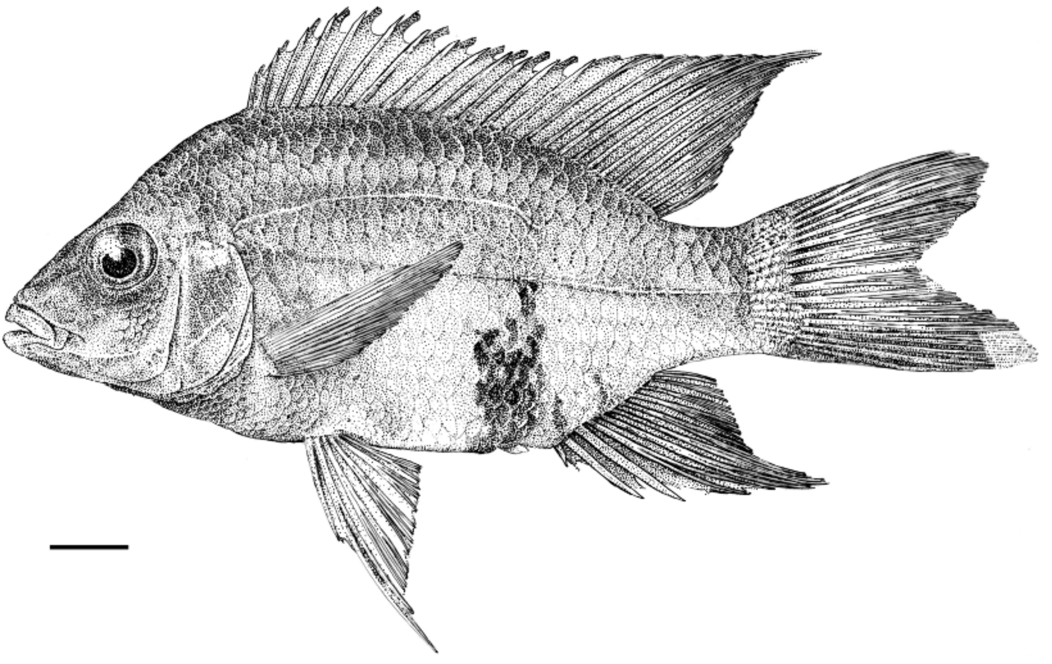

Fig. 15. *Ptychochromis loisellei*, new species, holotype, AMNH 232462, 99.5 mm SL, northeastern Madagascar, Antalaha Province, north of Sambava, Mahanara River at Antsirabe-Nord. Scale bar = 1 cm. Drawing by Ian Hart.

Antsiranana Province, main channel of the Mahanara River at Antsirabe-Nord, at bridge on Route N-5 (13°38.49S; 49°57.81E), PVL-00-07, P.V. Loiselle, 9 Oct. , 2000. AMNH 231258, 3 ex., 1 ex. C&S, 81.3–106.5 mm SL; northeastern Madagascar, Antsiranana Province, main channel of the Mahanara River at Antsirsabe-Nord, at bridge on Route N-5 (13°58.49S; 49°57.81E), PVL-00-12, P.V. Loiselle, 13 Oct., 2000. MNHN 2006-0781, 1 ex., 97.2 mm SL; data as for AMNH 231258; AMNH 232458, 1 ex., 118.6 mm SL; northeastern Madagascar, Antsiranana Province, Mahanara River, ca. 4 km northwest of Antsirabe-Nord (13°57.30S; 49°56.20E), PVL-01-27, P.V. Loiselle and local fishermen, 31 Oct., 2001. MHNG 2676.095, 1 ex., 109.2 mm SL; data as for AMNH 232458. AMNH 237135, 5 ex., 39.3–50.8 mm SL; data as for holotype.

Diagnosis: A *Ptychochromis* exhibiting the eastern-type palatine morphology (fig. 16A) and distinguished from all congeners by a unique pigmentation pattern and coloration comprising an expansive (generally vertically oriented) black band or blotched region of black pigment below the lateral midline and just anterior to origin of (and often extending over) the anal fin, and by an overall dark grayish-green body coloration. *Ptychochromis loisellei* is further diagnosed by an apomorphic lateral expansion of the LPJ toothplate anteriorly, which obscures the underlying bone in dorsal view (fig. 16B).

Description: Morphometric and meristic data presented in table 6. Morphological characteristics and general pigmentation pattern can be observed in figure 15 and plates 1C and 2C. Moderately deep-bodied and laterally compressed. Snout markedly acute and pointed. Lateral snout outline straight to moderately curved. Dorsal body profile moderately curved posterior to dorsal-fin origin. Ventral body profile straight. Predorsal head profile moderately convex from midorbit to dorsal-fin origin. Caudal peduncle short, deep, and laterally compressed. Dorsal-fin origin located anterior to vertical through pectoral-fin insertion. Pelvic-fin origin located well posterior to vertical through pectoral-fin insertion.

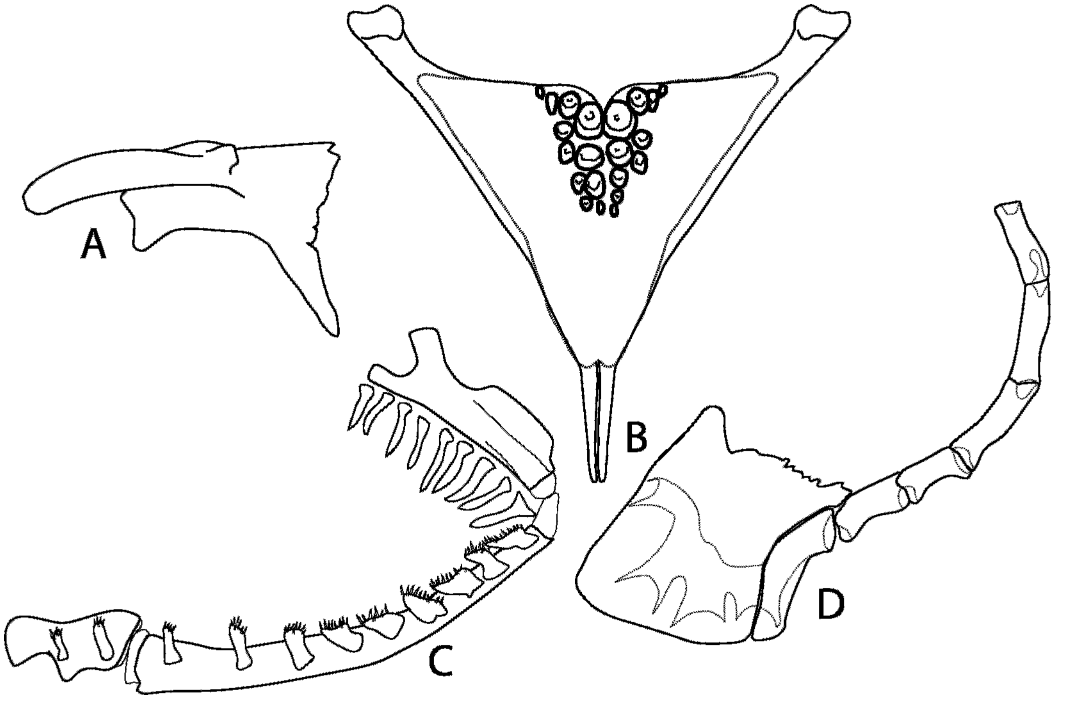

Fig. 16. *Ptychochromis loisellei*, new species, paratype, AMNH 231258: (A) palatine, (B) LPJ, (C) first gill arch, and (D) infraorbital series.

Total vertebral count 27 or 28, with a formula of 14 + 13 or 14 + 14 precaudal and caudal vertebrae, respectively.

Jaws isognathous or with lower jaw slightly prognathous. Oral dentition bilaterally symmetrical and bicuspid, with well-developed distally expanded and slightly recurved cusps. Outer row teeth in both jaws enlarged and graded in size laterally. Rostrally, outer row teeth procumbently implanted in lower jaw but only slightly so in upper jaw. Two to four inner rows of teeth in upper jaw, and two to three inner rows in lower jaw. Inner row teeth smaller than those of outer row but of similar morphology. Total of three to five rows of teeth along rostral margin of upper jaw and three or four in lower jaw, tapering to a single row of teeth posteriorly. Dentition covers anterior half of dentary and nearly entire surface of premaxillary arcade.

LPJ well sutured on posteroventral margin. Dentition on LPJ and UPJ comprised of numerous, closely set, hooked, and bicuspid teeth. Medially on both LPJ and UPJ dentition robust and becoming strongly molariform. The LPJ toothplate is markedly laterally expanded rostrally, and obscures the underlying bone when viewed from above (fig. 16B). Three to six rows of hooked and bicuspid teeth on second pharyngobranchial toothplates. Three rows of teeth medially on "free" second epibranchial toothplate. Robust toothplates covering majority of dorsal surface of fourth ceratobranchial bones; toothplates confluent with outer row gill rakers of these elements. Teeth on fourth ceratobranchial toothplates unicuspid and conical laterally to hooked and bicuspid medially.

Lower limb rakers of first gill arch denticulate dorsomedially. Usually with 10 or 11 (modally 10; one individual with 8) triangular and somewhat elongate gill rakers arrayed along lower limb of first arch. Seven to nine epibranchial gill rakers. Gill rakers on remaining arches short, laterally expanded, and strongly denticulate. Teeth elongate and conical.

Body covered with large, regularly imbricate, ctenoid scales, including region above upper lateral line, from posterior of nape to

TABLE 6
Morphometric and Meristic Data for *Ptychochromis loisellei*, new species
Values in parentheses indicate number of specimens examined with that count. (H) indicates count corresponding to holotype.

Character	*N*	Holotype	Range	Mean	SD
Standard length (mm)	13	99.5	39.3–118.6	80.6	
Percentage of SL					
Head length	13	34.0	34.0–37.4	35.0	1.17
Body depth	13	44.9	36.9–48.5	42.8	3.13
Predorsal length	13	28.3	28.3–43.9	33.7	4.14
Preanal length	13	72.1	50.2–77.9	70.5	8.91
Prepelvic length	13	40.1	38.4–45.5	41.6	1.94
Head width (max.)	13	16.5	15.0–17.2	16.1	0.83
Caudal peduncle length	13	14.5	11.2–15.6	13.4	1.11
Caudal peduncle width	13	3.1	2.5–5.0	3.7	0.70
Caudal peduncle depth	13	17.7	10.1–19.1	17.7	1.22
Pectoral-fin length	13	31.7	25.4–34.7	30.1	2.73
Pelvic-fin length	13	32.1	27.0–36.1	31.3	3.38
Percentage of HL					
Snout length	13	40.2	28.9–42.9	36.6	5.21
Orbit diameter	13	28.7	25.7–29.1	27.8	1.73
Upper jaw length	13	28.1	20.0–32.7	27.6	3.34
Lower jaw length	13	36.7	34.0–40.9	37.2	1.92
Interorbital width	13	29.9	24.1–31.5	28.1	2.59
Preorbital depth	13	22.8	16.7–26.6	21.9	3.00
Caudal peduncle length/depth	13	0.8	0.7–1.1	0.8	0.08
Caudal peduncle length/width	13	4.7	2.7–4.8	3.8	0.76
Scales in lateral line	13	28 (4), 29 (2), 31 (6) (H), 32 (1)			
Scales: lateral line to dorsal fin	13	5 (11), 6 (2) (H)			
Scales: pectoral to pelvic bases	12	5 (1), 6 (6), 7 (5) (H)			
Gill rakers (lower limb)	13	8 (1), 10 (14), 11 (7) (H)			
Vertebrae (precaudal + caudal)	13	14 + 13 = 27 (11) (H), 14 + 14 = 28 (2)			
Dorsal fin	13	XIII 12 (4) (H), XIII 13 (3), XIV 12 (6)			
Anal fin	13	III 8 (8) (H), III 9 (5)			

proximal portion of caudal fin. Scales on flanks becoming slightly more ctenoid posteriorly, but not strongly so. Most of scales on nape ctenoid. Scales on anterior of nape, most of head region, and cheek cycloid. Three or four rows of scales on cheek. Anterior chest and belly scales cycloid; posterior chest scales ctenoid. Scales on opercle and subopercle cycloid or weakly ctenoid. Anterior chest scales reduced in size and embedded. Snout, lachrymal, and anterior portion of interorbital region asquamate. Scales on caudal fin reduced in size; ctenoid anteriorly and much smaller and cycloid posteriorly. Lateral line scales 28–32. Five scales in diagonal from lateral line to dorsal-fin origin. Five to seven scales in oblique series between bases of pectoral and pelvic fins. No scale rows present along dorsal- and anal-fin bases.

Dorsal fin with XIII or XIV spines and 12 or 13 soft rays. Anal fin with III spines and eight or nine soft rays. First anal spine very short, second and third spines elongate and similar in length. Caudal fin emarginate, trailing margins of upper and lower lobes quite produced. Pectoral fin elongate, tapered distally. Distal margins of soft dorsal and anal fins produced and markedly pointed in larger specimens. Trailing margin of soft dorsal fin elongate and filamentous. Pelvic fin extending just past anal-fin origin in smaller specimens, well beyond origin in larger individuals.

MISCELLANEOUS OSTEOLOGY AND ANATOMY: Well-developed exoccipital foramina present on posterior of neurocranium. Paired anterior gas bladder extensions well developed, in contact with exoccipital region of neurocranium via connective tissue, but do not extend into exoccipital foramina. Infraorbital series (fig. 16D) composed of seven elements. Lachrymal deep, with four pores (fig. 16D). IO2 notably narrow and elongate, excluded from orbit by slightly ventrally displaced IO3. Uncinate process and anterior arm of first epibranchial bone short and robust (fig. 16C). Well-developed process and deep indentation present on inner face of Cb4.

COLORATION IN LIFE (plate 1C): Sexually active individuals exhibit an intense copper-orange wash on the flanks and an orange spot in the center of each scale of the middle four or five rows around the lateral line. A dusky, wedge-shaped bar extends from a point immediately anterior to the origin of the anal fin dorsad to the base of the dorsal fin. As it approaches the dorsum, the bar tapers to a point. Soft dorsal, anal, lower lobe of the caudal and pelvic fins dusky black. Spinous dorsal fin edged in yellowish-white. Caudal with an intense red distal margin. Iris of the eye marked with orange-red.

COLORATION IN PRESERVATIVE: Ground coloration dark grayish-green or green. Large irregular black band, bands, or blotched region just anterior to and extending above anal-fin base (i.e., posterior region of flank). Black pigment mainly concentrated below lateral midline, but may extend dorsally onto dorsal-fin membrane. Some individuals with irregular black blotching on flanks. Some specimens with blue-gray spangling on flanks, particularly below lateral midline. Chest, belly, opercular region, and ventral flanks golden in some individuals, dark blackish-gray in others. Base body coloration slightly lighter ventrally. Upper lip medium to dark gray, lower lip pale yellow to golden. Dorsal and anal fins dark gray to blackish, anal fin lighter distally. Pectoral fins light gray and hyaline. Gular region blackish. Snout, lachrymal, and interorbital region dark gray.

DISTRIBUTION AND HABITAT: *Ptychochromis loisellei* is currently known only from the Mahanara River and its tributaries in northeastern coastal Madagascar near the town of Antsirabe-Nord (fig. 1).

CONSERVATION STATUS: According to local fishermen, *P. loisellei* is still relatively common throughout its limited range within the Mahanara River basin.

LOCAL NAME: *Garaka* is the local Malagasy name used to refer to the species of *Ptychochromis* of this region.

ETYMOLOGY: Named for our colleague Paul V. Loiselle, who collected the type series, in recognition of his many contributions to the understanding and conservation of Madagascar's freshwater fishes.

DISCUSSION AND COMPARISONS: In our phylogenetic analysis, *P. loisellei* is recovered in a polytomy and its immediate relationships remain unresolved (fig. 2). Although there is currently no unambiguous evidence for the monophyly of an assemblage comprising *P. loisellei*, *P. grandidieri*, *P. makira*, and *P. curvidens*, the shared possession of an eastern-type palatine morphology is unique to these four species and may indicate a close relationship among them. An indepenedent analysis of nucleotide characters also was unable to resolve the intrageneric placement of *P. loisellei* (Sparks and Smith, 2004: fig. 1). Morphometrically *P. loisellei* is most similar to *P. grandidieri* from which it is readily distinguished by pigmentation pattern and coloration, infraorbital morphology, and also in the possession of a considerably smaller LPJ with fewer and less well-developed molariform teeth (compare fig. 16B with fig. 24B).

Ptychochromis curvidens, new species
Figures 17–18, Plates 1B and 2D, Table 7

Ptychochromis sp. "vert-ouest de la Montagne d'Ambre": de Rham and Nourissat, 2002.

Ptychochromis n. sp. "montagne d'ambre" Sparks, 2003.

HOLOTYPE: MHNG 2623.82, 127.6 mm SL; northern Madagascar, Antsiranana (Diego Suarez) Province, Andranfanjava, Andranofanjava-Sandriapiana River system, P. de Rham and J.-C. Nourissat, 9 Oct., 1999.

PARATYPES: MHNG 2676.096, 2 ex., 92.8–146.8 mm SL, data as for holotype. AMNH 237133, 2 ex., 1 ex. C&S, 92.3–105.1 mm SL, data as for holotype. MHNG 2623.84, 1 ex.,

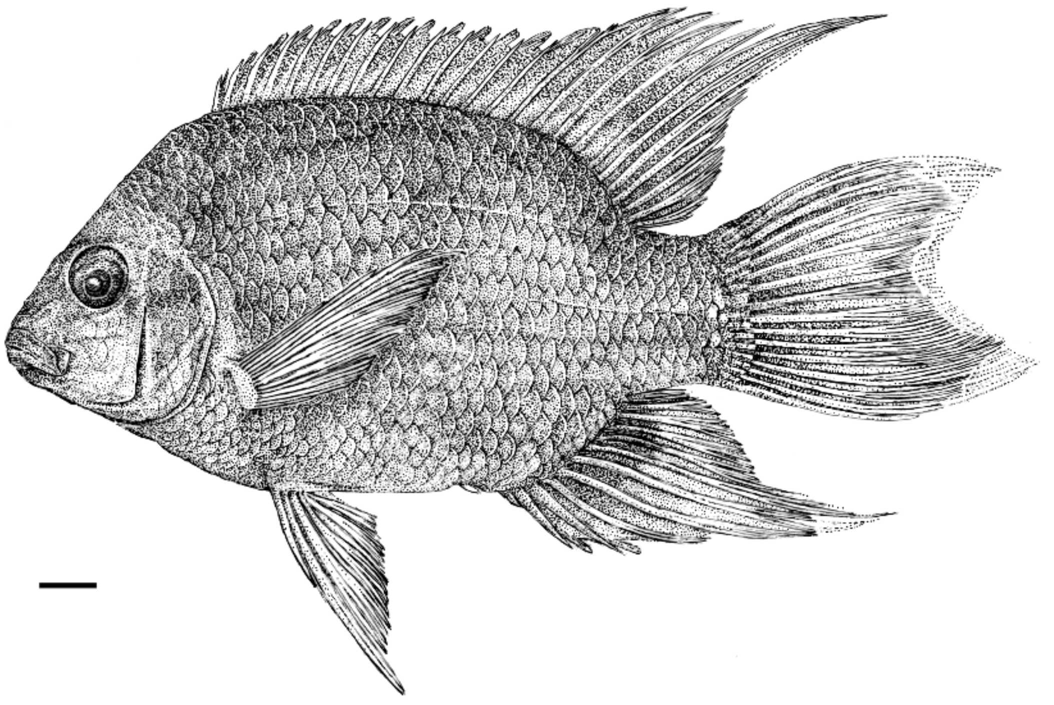

Fig. 17. *Ptychochromis curvidens*, new species, holotype, MHNG 2623.82, 127.6 mm SL, northern Madagascar; Diego Suarez Province, Andranofanjava, Andranofanjava-Sandriapiana River system. Scale bar = 1 cm. Drawing by Ian Hart.

90.2 mm SL; northern Madagascar, Antsiranana (Diego Suarez) Province, Mirosolava, P. de Rham and J.-C. Nourissat, 10 Oct., 1999.

DIAGNOSIS: A *Ptychochromis* exhibiting the eastern-type palatine morphology (fig. 18A) and distinguished from all congeners by the presence of a characteristically robust and strongly recurved oral dentition (fig. 18E). *Ptychochromis curvidens* is further distinguished by the possession of a feeble LPJ with only weakly molariform posteromedian dentition (fig. 18B), and a characteristic iridescent golden-green coloration in life.

DESCRIPTION: Morphometric and meristic data presented in table 7. Morphological characteristics and general pigmentation pattern can be observed in figure 17 and plates 1B and 2D. An extremely deep-bodied and robust species, rather less laterally compressed than other members of the genus. Head rather small (HL 30.4–31.7% SL), snout rounded, and ventral body outline convex and rounded. Lateral snout outline straight. Predorsal head profile straight from midorbit to dorsal-fin origin. Dorsal body profile relatively straight posterior to dorsal-fin origin, and strongly curved caudally. Ventral body profile moderately to strongly curved caudally. Caudal peduncle short, deep, and laterally compressed. Dorsal-fin origin located at about level of, to slightly posterior of, vertical through pectoral-fin insertion. Pelvic-fin origin located well posterior to vertical through pectoral-fin insertion.

Total vertebral count 27 or 28, with a formula of 13 + 14 or 13 + 15 precaudal and caudal vertebrae, respectively.

Jaws isognathous. Oral dentition bilaterally symmetrical and bicuspid. Teeth extremely robust particularly rostrally, with notably recurved cusps (fig. 18E) that are L-shaped in lateral view. Outer row teeth enlarged and graded in size laterally. Rostrally, outer row teeth procumbently implanted in lower jaw. Rostrally, upper jaw with three to four and lower jaw with two to three inner rows of smaller teeth of similar shape to those of outer rows although with less markedly recurved

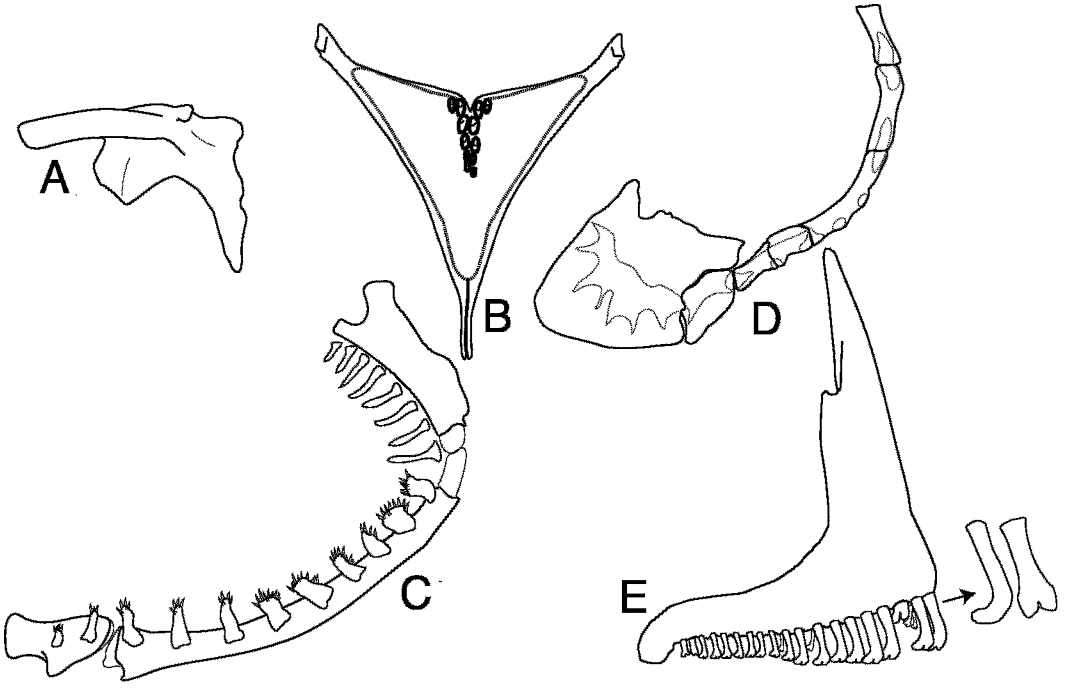

Fig. 18. *Ptychochromis curvidens*, new species, paratype, AMNH 237133: (A) palatine, (B) LPJ, (C) first gill arch, (D) infraorbital series, and (E) premaxilla.

cusps. Total of three to five rows of teeth along rostral margin of upper jaw and three or four in lower jaw, tapering to a single row of teeth posteriorly in both. Dentition covers anterior 2/3–3/4 of dentary and nearly entire surface of premaxillary arcade.

LPJ with a few weakly interdigitating sutures on posteroventral margin. Lower pharyngeal toothplates markedly smaller and less robust compared to those of similarly sized congeners. Dentition on LPJ and UPJ comprised of numerous, closely set, weakly hooked, and bicuspid teeth. Medially on UPJ and posteromedially on LPJ dentition becoming progressively robust, but only weakly so, and teeth are enlarged but rarely molariform. Three rows of hooked and bicuspid teeth on second pharyngobranchial toothplates. Two rows of teeth on "free" toothplate associated with second epibranchial bone. Robust, laterally expanded toothplates cover majority of dorsal surface of fourth ceratobranchial bones. Toothplates confluent with outer-row gill rakers of these elements. Dentition on fourth ceratobranchial toothplates unicuspid laterally, weakly to moderately hooked and bicuspid medially.

Lower limb rakers of first gill arch denticulate dorsomedially. Ten or eleven (modally 11) triangular and somewhat elongate gill rakers arrayed along lower limb of first arch. Eight or nine epibranchial gill rakers. Gill rakers on remaining arches laterally expanded, and strongly denticulate. Gill raker teeth on remaining arches elongate and conical.

Flanks covered with large, regularly imbricate, weakly ctenoid scales from posterior of nape to base of caudal fin. Scales on flanks becoming increasingly ctenoid posteriorly, but never strongly so. Scales on head, anterior portion of nape, and cheek cycloid. Three or four rows of scales on cheek. Scales on opercle and subopercle cycloid. Chest scales weakly ctenoid, except anteriorly. Scales on belly and anterior of chest cycloid, somewhat reduced in size and embedded. Snout, lachrymal, and anterior portion of interorbital region to about midorbit asquamate. Scales on caudal fin reduced in size, increasingly so posteriorly; ctenoid anteriorly and cycloid posteriorly.

TABLE 7
Morphometric and Meristic Data for *Ptychochromis curvidens*, new species
Values in parentheses indicate number of specimens examined with that count. (H) indicates count corresponding to holotype.

Character	*N*	Holotype	Range	Mean	SD
Standard length (mm)	6	127.6	90.2–146.8	109.7	
Percentage of SL					
Head length	6	31.7	30.4–31.7	31.2	0.62
Body depth	6	52.0	45.9–52.8	49.7	3.07
Predorsal length	6	30.1	27.5–42.0	31.3	5.39
Preanal length	6	68.3	68.3–73.7	70.7	2.15
Prepelvic length	5	38.2	35.7–38.2	37.2	0.96
Head width (max.)	5	18.2	15.4–18.7	17.3	1.40
Caudal peduncle length	6	13.0	12.6–14.5	13.4	0.67
Caudal peduncle width	5	5.6	5.0–5.7	5.4	0.29
Caudal peduncle depth	6	20.9	17.5–20.9	19.3	1.11
Pectoral-fin length	5	32.9	31.0–33.7	32.3	1.07
Pelvic-fin length	5	37.6	31.9–37.6	35.5	2.14
Percentage of HL					
Snout length	6	42.6	37.4–44.4	40.1	2.74
Orbit diameter	6	29.0	26.6–31.4	29.0	1.52
Upper jaw length	6	32.9	28.4–36.6	32.5	2.68
Lower jaw length	6	32.9	31.4–35.6	33.0	1.54
Interorbital width	6	38.1	33.2–39.6	36.6	2.18
Preorbital depth	6	22.8	20.4–23.1	22.0	1.08
Caudal peduncle length/depth	6	0.6	0.6–0.8	0.7	0.06
Caudal peduncle length/width	5	2.3	2.3–2.9	2.5	0.25
Scales in lateral line	6	30 (1), 31 (1), 32 (4) (H)			
Scales: lateral line to dorsal fin	6	5 (3) (H), 5.5 (2), 6.5 (1)			
Scales: pectoral to pelvic bases	5	5 (3), 6 (2) (H)			
Gill rakers (lower limb)	6	10 (1), 11 (5) (H)			
Vertebrae (precaudal + caudal)	6	13 + 14 = 27 (5) (H), 13 + 15 = 28 (1)			
Dorsal fin	6	XIV 11 (3), XIV 12 (3) (H)			
Anal fin	6	III 9 (6) (H)			

Lateral line scales 30–32. Five-and-a-half to 6 1/2 scales in diagonal from lateral line to dorsal-fin origin. Five or six scales in oblique row between bases of pectoral and pelvic fins. No scale rows present along dorsal- and anal-fin bases.

Trailing margin of soft dorsal fin elongate and filamentous, particularly in larger specimens; trailing margin of anal fin elongate and filamentous, but to lesser degree than dorsal filament. Dorsal fin tall, with XIV spines and 11 or 12 soft rays. Anal fin with III spines and nine soft rays. First anal spine short, second and third spines elongate, although second spine noticeably shorter than third. Caudal fin very large and fanlike, weakly emarginate. Pectoral fin somewhat elongate, tapered distally. Pelvic fin extending to about level of anal-fin origin or slightly beyond when adducted.

MISCELLANEOUS OSTEOLOGY AND ANATOMY: Well-developed exoccipital foramina present on posterior of neurocranium. Paired anterior gas bladder extensions in contact with exoccipital region of neurocranium via connective tissue, but do not extend into exoccipital foramina. Infraorbital series (fig. 18D) composed of seven elements. Lachrymal rather shallow, with four pores (fig. 18D). IO2 broad and platelike, excluded from orbit by ventrally displaced IO3. Uncinate process of first epibranchial roughly twice diameter of anterior arm (fig. 18C). Well-developed process and deep indentation present on inner face of Cb4. Preopercular and mandibular canals markedly enlarged and pores expanded.

COLORATION IN LIFE (plate 1B): Base body coloration iridescent golden-green. Body dark golden-green dorsal of midline, and bright, iridescent golden below. Opercular region bright golden, except dorsally which is greenish. No distinctive lateral markings. Snout, lachrymal, interorbital region, gular region, and lips dusky charcoal gray. Belly charcoal gray. Unpaired fins dusky charcoal gray, membranes grayish to hyaline. Pelvic fins hyaline proximal to base, blackish distally. Pectoral fins bright yellowish-orange.

COLORATION IN PRESERVATIVE: Ground coloration dark brownish-green. Body darker dorsally. Smaller specimens yellowish to golden ventrally. No distinct lateral markings. Larger specimens with some light grayish spangling/spotting posteriorly on flanks, for the most part restricted ventral of lateral midline. Opercular and preopercular region golden. Gular region, lower lip, belly, and chest yellowish to golden in smaller individuals. Gular region and lower lip in larger specimens dark brownish-gray. Interorbital region, lachrymal, snout, and upper lip dark brownish-gray.

DISTRIBUTION AND HABITAT: Currently known only from a few westward flowing rivers draining the western flank of Montagne d'Ambre in extreme northern Madagascar. Most specimens are from the Andranofanjava-Sandriapiana River system, located southwest of the town of Antsiranana, but a single specimen purportedly collected from the Mirosolava River (Sahinana-Sampiena system) is included here in the type series. However, we note that although this single specimen (MHNG 2623.84) is labelled as coming from "northern Madagascar; Antsiranana (Diego Suarez) Province, Mirosolava, P. de Rham and J.-C. Nourissat," Patrick de Rham (in litt.), does not recall preserving any specimen of this species from Mirosolava, and, therefore, some doubt as to the exact provenance of this specimen persists. De Rham (in litt.) has expressed reservations as to whether the Andranofanjava and Sahinana river populations are conspecific, nevertheless our examination supports the presence of a single species in the far north of the island.

CONSERVATION STATUS: According to Patrick de Rham (in litt.), the conservation status of *P. curvidens* is difficult to assess. The species is not abundant anywhere within its range and exotic fishes, especially *Oreochromis* sp., are present in the region. However, several other native species persist in reasonable numbers and exotic species are not abundant, suggesting that the ecosystem remains relatively healthy. This is further indicated by a diverse aquatic flora recorded at many sample sites, where endemic plant species such as *Aponogeton* cf. *bovinianus* remain plentiful. Human populations in these remote and poorly accessible regions remain small, and fishing pressure is consequently also low.

LOCAL NAME: *Ptychochromis curvidens* is referred to locally as *garaka*, a name that is used throughout much of northeastern and northern Madagascar to refer to species of *Ptychochromis*.

ETYMOLOGY: From the Latin, *curvus*, a "curve", and *dens*, a "tooth", in reference to the apomorphically recurved oral jaw dentition characteristic of this species.

DISCUSSION AND COMPARISONS: Although *P. curvidens* occurs in westward flowing basins in far northern Madagascar, the species exhibits the eastern-type palatine morphology (fig. 18A) otherwise found only in members of the genus restricted to eastern basins: *P. grandidieri*, *P. makira*, and *P. loisellei*. As such, *P. curvidens* represents the only species of *Ptychochromis* occurring in a western drainage with the eastern-type palatine configuration. Regrettably, no tissue sample suitable for molecular studies was available from specimens of *P. curvidens*, and the species could not be included in molecular phylogenetic analyses (Sparks and Smith, 2004). In our phylogenetic analysis, *P. curvidens* is recovered in a polytomy and its intrageneric relationships remain unresolved (fig. 2).

Ptychochromis insolitus, new species
Figures 19–20, Plates 1D and 2E, Table 8

Ptychochromis oligacanthus, race géographique "region de Mandritsara": Kiener and Maugé, 1966.

Ptychochromis sp. "Mangarahara ou Mandritsara": de Rham and Nourissat, 2002.

Ptychochromis n. sp. "sofia": Sparks, 2003.

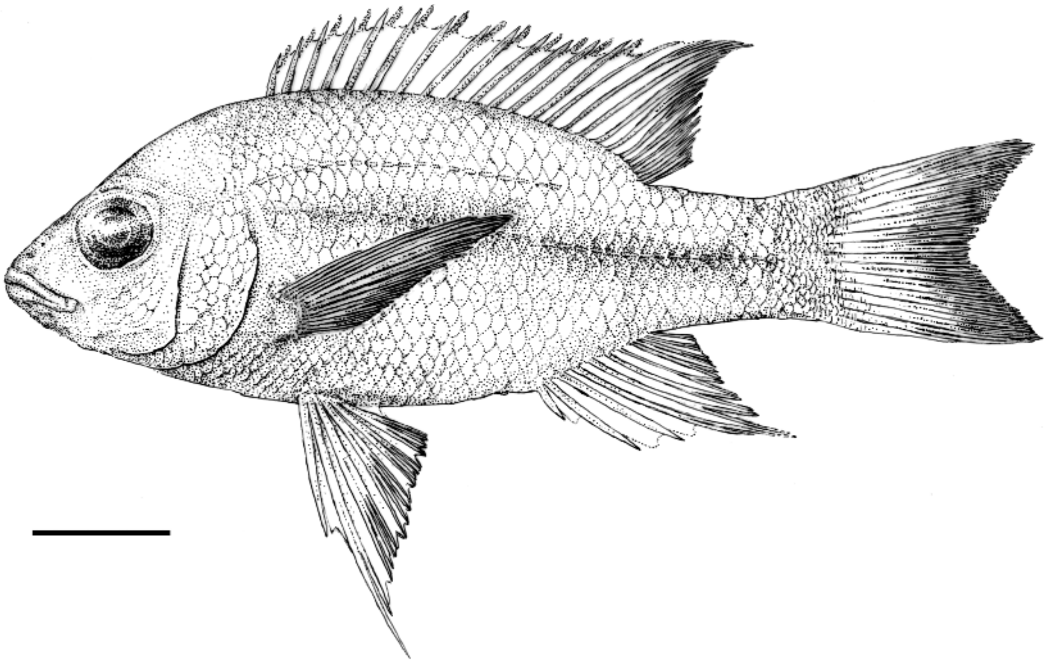

Fig. 19. *Ptychochromis insolitus*, new species, holotype, UMMZ 237066, juvenile, 54.8 mm SL, northeastern Madagascar, Antalaha Province, near town of Mandritsara, Sofia drainage basin, Amboaboa River. Scale bar = 1 cm. Drawing by Ian Hart.

Ptychochromis nov. sp. "sofia": Sparks and Stiassny, 2003: table 9.1.
Ptychochromis sp. "Sofia": Sparks and Smith, 2004: fig. 1, table 1.

HOLOTYPE: UMMZ 237066, 54.8 mm SL, juvenile; northeastern Madagascar, Mahajanga Province, near town of Mandritsara, Sofia drainage basin, Amboaboa (= Ambomboa) River (15°50′1″S; 48°42′51″E), J. S. Sparks and K. J. Riseng, 10 July 1996.

DIAGNOSIS: A *Ptychochromis* exhibiting the western-type palatine morphology (fig. 20A) and distinguished from congeners by a reduced number of precaudal vertebrae (12 vs. 13–14 in congeners) and a reduced number of infraorbital elements (five vs. six or seven in congeners). *Ptychochromis insolitus* is further distinguished from congeners by the presence (most obvious in preservation) of a faint midlateral stripe, beginning just posterior to the dorsocaudal margin of the opercle and extending to caudal-fin origin. *Ptychochromis insolitus* and *P. inornatus* are distinguished from the remaining species of *Ptychochromis* by the presence of strongly ctenoid scales, with the entire caudal scale margin bearing well-developed cteni (vs. weakly ctenoid scales, with only the central portion of the caudal margin bearing weak cteni).

DESCRIPTION: Morphometric and meristic data for the holotype presented in table 8. Morphological characteristics and general pigmentation pattern can be observed in figure 19 and plates 1D and 2E. The following description is based on the holotype, a wild caught specimen from the region of Mandritsara within the Sofia River drainage. However, a number of field photographs of additional specimens from the region have been made available to us and these are incorporated into the color description for the species. Additionally, a number of aquarium-raised specimens (purportedly F2) are available for examination; however, some morphological anomalies were noted in these individuals (see discussion below) and for that reason they have not been formally included within the type series.

A comparatively shallow bodied and laterally compressed *Ptychochromis*. Lateral snout

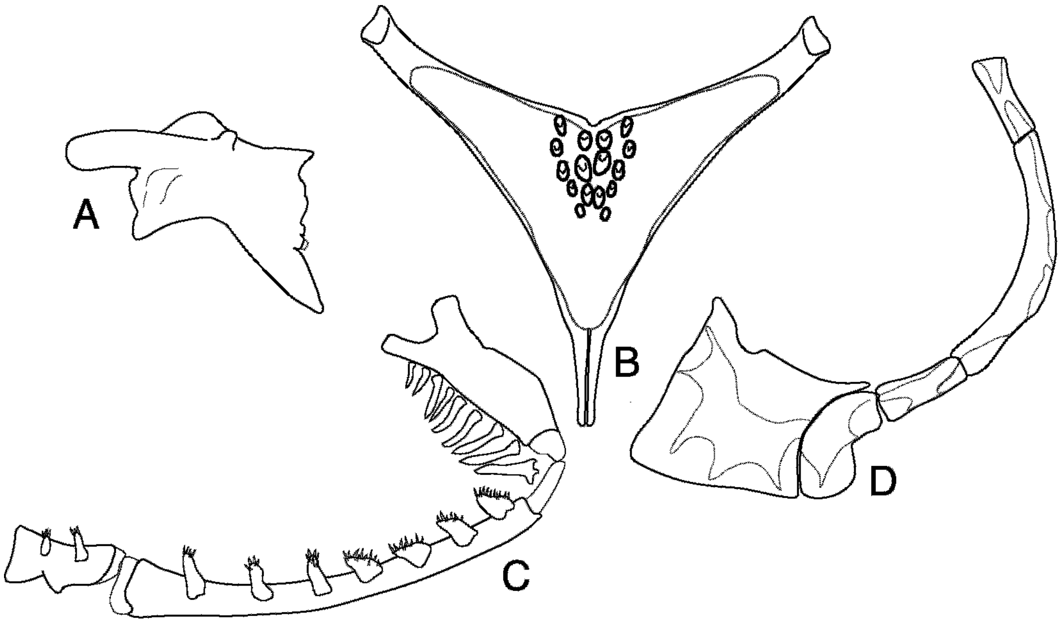

Fig. 20. *Ptychochromis insolitus*, new species, holotype, UMMZ 237066: (A) palatine, (B) LPJ, (C) first gill arch, and (D) infraorbital series.

outline straight to somewhat convex. Predorsal head profile mildly convex from midorbit to dorsal-fin origin. Dorsal body profile relatively straight posterior of dorsal-fin origin. Ventral body profile relatively straight. Caudal peduncle comparatively elongate and laterally compressed. Dorsal-fin origin located slightly anterior to vertical through pectoral-fin insertion. Pelvic-fin origin located well posterior to vertical through pectoral-fin insertion.

Total vertebral count 27, with a formula of 12 + 15 precaudal and caudal vertebrae, respectively.

Jaws isognathous. Oral dentition bilaterally symmetrical and bicuspid, cusps expanded distally. Outer row teeth in both jaws enlarged and graded in size laterally. Rostrally, outer row teeth somewhat recurved. Teeth procumbently implanted in lower jaw, only slightly so in upper jaw. Rostrally, upper and lower jaws with three inner rows of smaller teeth of the same morphology as in outer rows; inner teeth tapering to a single row of teeth posteriorly in both jaws. Dentition covers anterior 2/3 of dentary and nearly entire surface of premaxillary arcade.

LPJ well sutured, with few weakly interdigitating sutures on posteroventral margin. Dentition on LPJ and UPJ comprised of numerous, closely set, hooked, and bicuspid teeth. Medially on both LPJ and UPJ dentition robust, but not molariform (fig. 20B). Three rows of hooked and bicuspid teeth on second pharyngobranchial toothplates. Two rows of teeth on "free" toothplate associated with second epibranchial bone. Robust, laterally expanded, toothplates cover most of dorsal surface of fourth ceratobranchial bones. Dentition on fourth ceratobranchial toothplates unicuspid or weakly hooked and bicuspid laterally, hooked and bicuspid medially.

Lower limb rakers of first gill arch denticulate dorsomedially. Nine triangular and somewhat elongate gill rakers arrayed along lower limb of first arch. Eight or nine epibranchial gill rakers. Gill rakers on remaining arches laterally expanded and strongly denticulate; teeth elongate and conical.

Body covered with large, regularly imbricate, strongly ctenoid scales from nape to proximal portion of caudal fin. Entire caudal margin of most scales with well-developed cteni. Scales on flanks becoming increasingly

TABLE 8
Morphometric and Meristic Data for Holotype of *Ptychochromis insolitus*, new species

Standard length (mm)	54.8
Percentage of SL	
Head length	33.4
Body depth	38.7
Predorsal length	41.2
Preanal length	70.4
Prepelvic length	42.2
Head width (max.)	17.5
Caudal peduncle length	17.2
Caudal peduncle width	6.6
Caudal peduncle depth	15.3
Pectoral-fin length	29.6
Pelvic-fin length	30.1
Percentage of HL	
Snout length	28.4
Orbit diameter	37.2
Upper jaw length	32.2
Lower jaw length	42.1
Interorbital width	27.9
Preorbital depth	17.5
Caudal peduncle length/depth	1.1
Caudal peduncle length/width	2.6
Scales in lateral line	34
Scales: lateral line to dorsal fin	6
Scales: pectoral to pelvic bases	5
Gill rakers (lower limb)	9
Vertebrae (precaudal + caudal)	12 + 15 = 27
Dorsal fin	XIII 11
Anal fin	III 8

ctenoid posteriorly. Scales on head and anterior portion of nape cycloid; posterior nape scales ctenoid. Scales on opercle and subopercle cycloid. Belly scales cycloid and chest scales weakly to moderately ctenoid, both somewhat reduced in size and embedded. Four rows of cycloid scales on cheek. Snout, lachrymal, and anterior portion of interorbital region asquamate. Scales on caudal fin reduced in size; ctenoid anteriorly and cycloid posteriorly. Lateral line with 34 scales. Seven scales in diagonal from lateral line to dorsal-fin origin. Five scale rows between bases of pectoral and pelvic fins. No scale rows present along dorsal- and anal-fin bases.

Trailing margin of soft dorsal fin somewhat elongate. Dorsal fin with XIII spines and 11 soft rays. Anal fin with III spines and eight soft rays. First anal spine very short, second and third spines elongate and similar in length. Caudal fin emarginate. Pectoral fin elongate, tapered distally. Pelvic fin extending well beyond anal-fin origin when adducted.

MISCELLANEOUS OSTEOLOGY AND ANATOMY: Well-developed exoccipital foramina present on posterior of neurocranium. Paired anterior gas bladder extensions in contact with exoccipital region of neurocranium via connective tissue, but do not extend into exoccipital foramina. Infraorbital series (fig. 20D) composed of five elements. As noted previously, although infraorbital number is extremely variable within Cichlidae, a total of seven infraorbital elements is resolved as the plesiomorphic number for Cichlidae and is the number most often encountered among ptychochromins. A reduction to five is interpreted as a derived condition within *Ptychochromis* (*Character 16(2)*, fig. 2). Lachrymal shallow, with four pores (fig. 20D). IO2 only marginally excluded from orbit by ventrally displaced IO3. Uncinate process and anterior arm of first epibranchial bone short and robust (fig. 20C). Well-developed process and deep indentation present on inner face of Cb4.

COLORATION IN LIFE (plate 1D): Based on photos of freshly captured specimens in de Rham and Nourissat (2002) and from the photo collection of de Rham. Base body coloration silvery to silvery-golden, particularly below lateral midline. Cheek and opercular series silvery. Body golden with blackish speckles and blotches above midline, including nape, top of head, and infraorbital series. Snout, interorbital region, and area dorsal to orbit gray to dark gray-green. Unpaired fins reddish, particularly distally, or dark gray. Caudal fin dark gray to black proximal to base, reddish distally. Thin, golden midlateral stripe; caudally stripe along lower lateral line particularly prominent in juveniles. Another thin, dark brown to blackish stripe paralleling dorsal-fin base. Pectoral fins pale and reddish. Pelvic fins pale reddish and may exhibit some black pigmentation along caudal margin. Some photographed, freshly captured specimens exhibit faint vertical barring on dorsal flanks.

COLORATION IN PRESERVATIVE: Ground coloration pale yellowish-olive. Faint dark stripe present along lateral midline, more pro-

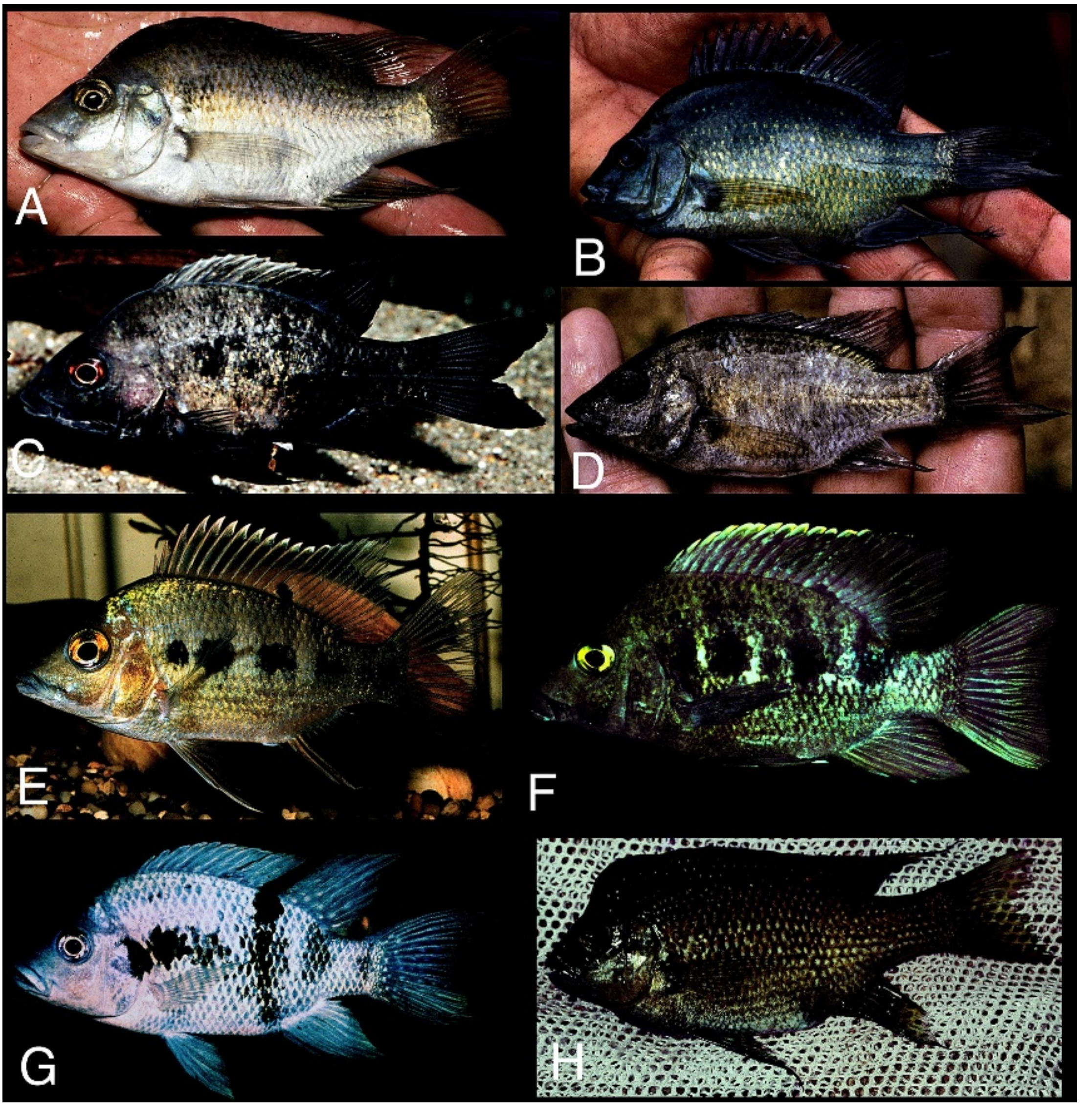

Plate 1. *Ptychochromis* live coloration: (A) *Ptychochromis inornatus*, northwestern Madagascar, Anterano River. Photo by Patrick de Rham. (B) *Ptychochromis curvidens*, new species, northern Madagascar, Andranofanjava-Sandriapiana River system. Photo by Patrick de Rham. (C) *Ptychochromis loisellei*, new species, northeastern Madagascar, Mahanara River. Photo by Paul Loiselle. (D) *Ptychochromis insolitus*, new species, northeastern Madagascar, Amboaboa River. Photo by Patrick de Rham. (E) *Ptychochromis grandidieri*, male, eastern Madagascar, Lake Salehy. Photo by Paul Loiselle. (F) *Ptychochromis grandidieri*, female, eastern Madagascar, Ambila Lemaitso. Photo by Paul Loiselle. (G) *Ptychochromis oligacanthus*, male, northwestern Madagascar, Nosy Be, Lake Bemapaza. Photo by Paul Loiselle. (H) *Katria katria*, eastern Madagascar, Nosivolo River. Photo by M. Stiassny,

nounced posteriorly. No additional lateral markings evident. Body slightly lighter posterolaterally. Fins hyaline to pale yellowish-olive. Black pigment distally on dorsal fin. Caudal and anal fins dusky gray distally. Small, brownish spot present near base of anterior portion of soft dorsal fin, near margin of spinous and soft dorsal.

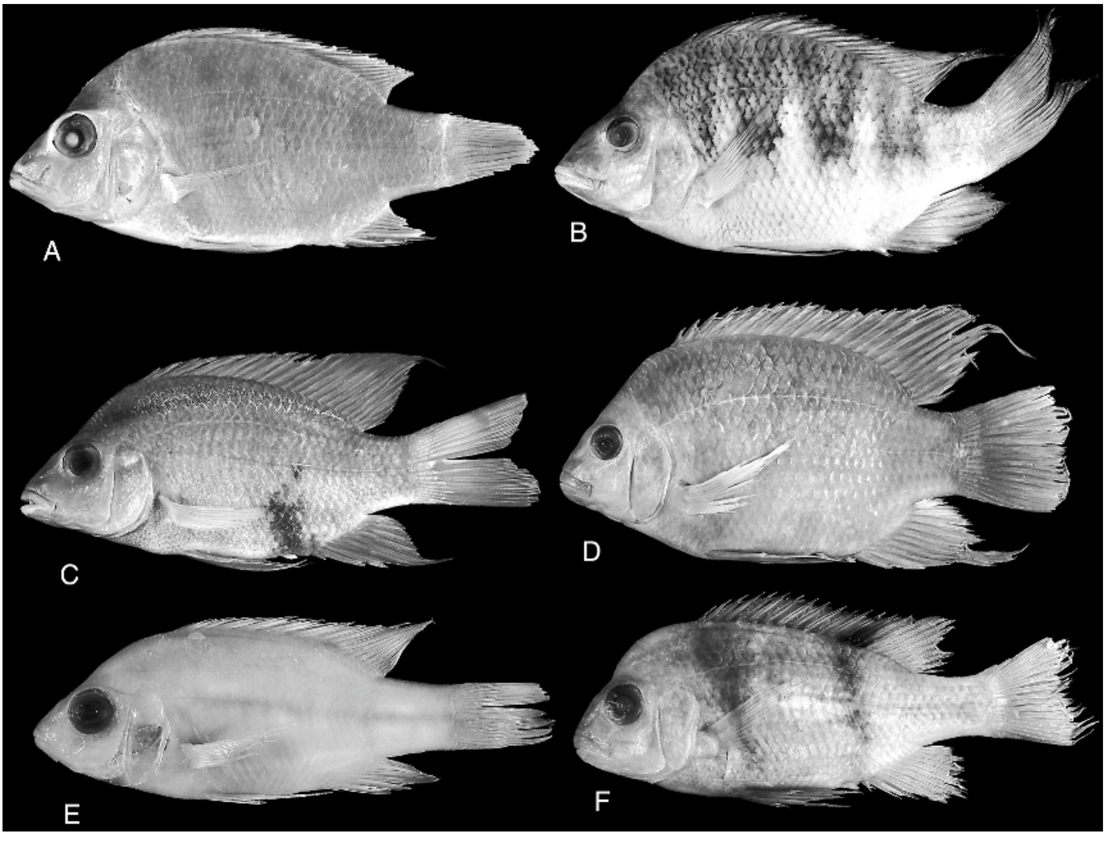

Plate 2. *Ptychochromis* in preservative: (A) *Ptychochromis onilahy*, new species, holotype, MNHN 1962-0201, 84.3 mm SL. (B) *Ptychochromis makira* new species, holotype, AMNH 237131, 151.0 mm SL. (C) *Ptychochromis loisellei*, new species, holotype, AMNH 232462, 99.5 mm SL. (D) *Ptychochromis curvidens*, new species, holotype, MHNG 2623.82, 127.6 mm SL. (E) *Ptychochromis insolitus*, new species, holotype, UMMZ 237066, 54.8 mm SL. (F) *Katria katria*, holotype, AMNH 217739, 105.2 mm SL.

DISTRIBUTION AND HABITAT: *Ptychochromis insolitus* is known only from tributaries of the Sofia River (viz., Mangarahara and Amboaboa rivers near the town of Mandritsara), a westward flowing basin in northeastern Madagascar (fig. 1). Habitat at type locality mostly sand and rock substrate. Deeper pools present in sheltered areas. Water clear, shallow and current swift.

CONSERVATION STATUS: *Ptychochromis insolitus* appears to be rare throughout its limited range, and few specimens have been collected despite sizeable collections of other species having been made in this region, including other cichlids (viz., *Paretroplus nourissati* and *P.* cf. *kieneri*).

LOCAL NAME: *Joba* or *Juba* is the Malagasy name used throughout much of northwestern Madagascar to refer to species of *Ptychochromis*, including *P. insolitus*.

ETYMOLOGY: From the Latin, *insolitus*, meaning "unusual, odd, queer". In reference to the somewhat atypical appearance of the species and the anomalous morphology of the aquarium raised specimens examined in our study.

DISCUSSION AND COMPARISONS: In addition to the holotype, two aquarium-raised specimens (AMNH 237134, 68.5–68.7 mm SL) have been examined. These two individuals are purportedly the offspring of specimens collected in the Mangarahara River within the Sofia River drainage basin (Loiselle, personal commun.). Whereas the specimens accord well with the holotype of *Ptychochromis insolitus* in their overall gracile appearance and in general morphometrics and meristics (including a reduced number of 12 precaudal vertebrae), they lack the presence of a ''free'' second epibranchial toothplate, a feature diagnostic of *Ptychochromis*. Additionally, these specimens lack a deeply rounded indentation and process on the inner margin of Cb4, a feature uniting *Katria* and *Ptychochromis*. Furthermore, although both specimens have a lachrymal and IO2 morphology very similar to that of the holotype of *P. insolitus*, their infraorbital series are composed of seven elements, not five as in the holotype. These anatomical anomalies may reflect epigenetic changes aquired in captivity or they may be the result of an unrecorded hybridization event. The possibility that a second ptychochromin taxon inhabits the Sofia drainage remains an alternative explanation. Whatever the identity of these specimens, we have opted to exclude them from the type series and base the following remarks on morphological and molecular analysis of the holotype.

Based on the current analysis of nucleotide and morphological characters, the holotype of *Ptychochromis insolitus* belongs to a ''western clade'' (i.e., occurring in westward-draining basins) of *Ptychochromis* and is recovered as the sister taxon to *P. inornatus* (fig. 2). Morphologically, *P. insolitus* and *P. inornatus* are distinguished from the remaining species of *Ptychochromis* by the presence of strongly ctenoid scales, with the entire caudal scale margin bearing well-developed cteni (vs. weakly ctenoid scales, with only the central portion of the caudal margin bearing weak cteni). *Ptychochromis insolitus* can readily be distinguished from *P. inornatus* by pigmentation pattern, the number of rows of second pharyngobranchial teeth (three in *P. insolitus* vs. two in *P. inornatus*), and by the number of precaudal vertebrae and infraorbital elements.

Ptychochromis inornatus Sparks, 2002
Figures 21–22, Plate 1A, Table 9

HOLOTYPE: UMMZ 237492, 115.3 mm SL, adult female, northwestern Madagascar, Mahajanga Province, northeast of Antsohihy, Ankofia drainage, Anjingo River (14°50′41.0″S; 48°14′38.3″E), JSS 94-19, J. S. Sparks, K. J. Riseng, and local Malagasy guides, 28 July 1994.

PARATYPES: UMMZ 237063, 5 ex., 1 ex. C&S, 85.1–122.3 mm SL; data as for holotype. AMNH 230746, 2 ex., 90.8–93.1 mm SL; data as for holotype. UMMZ 237064, 5 ex., 2 ex. C&S, 74.6–93.0 mm SL, northwestern Madagascar, Mahajanga Province, northeast of Antsohihy, Ankofia drainage, Bora Special Reserve, Bemahavony River (tributary of Anjingo River) (14°52′20.4″S; 48°14′52.2″E), JSS 94-20, 31 July 1994; AMNH 230747, 2 ex., 77.1–82.2 mm SL; data as for UMMZ 237064. UMMZ 237065, 1 ex., 97.4 mm SL, northwestern Madagascar, Mahajanga Province, northeast of Antsohihy, Ankofia drainage, Lake Andrapongy (14°41′49.3″S; 48°07′54.3″E), JSS 94-21, 2 August 1994. UMMZ 237067, 7 ex., 21.0–35.7 mm SL, northwestern Madagascar, Mahajanga Province, northeast of Antsohihy, Ankofia drainage, Anjingo River (14°50′39.7″S; 48°14′39.5″E), JSS 94-54, 15 November 1994.

DIAGNOSIS: A *Ptychochromis* exhibiting the western-type palatine morphology (fig. 22A) and distinguished from all congeners by the possession of two rows of teeth on the second pharyngobranchial toothplate (vs. 3–7), and the presence of ctenoid scales on the opercle (and occasionally also the cheek).

DESCRIPTION: Morphometric and meristic data presented in table 9. Morphological characteristics and general pigmentation pattern can be observed in figure 21 and plate 1A. Body deep, laterally compressed, and robust. Lateral snout outline slightly convex. Predorsal head profile curved in smaller individuals to strongly curved in large adults (Sparks, 2002: fig. 3), from approximately level of midorbit to dorsal fin origin. Larger individuals of both sexes exhibit a weak but distinctive occipital hump. Caudal peduncle relatively short and deep in adults. Dorsal-fin origin located slightly anterior of vertical through pectoral-fin insertion. Pelvic-fin origin located well posterior to vertical through pectoral-fin insertion.

Total vertebrae count 26 or 27, 13 +14, 13 + 13, 12 + 15 precaudal and caudal vertebrae, respectively.

Jaws isognathous or slightly retrognathous. Oral dentition bilaterally symmetrical and bicuspid, cusps well developed. Upper and lower jaws with two to three inner rows of much

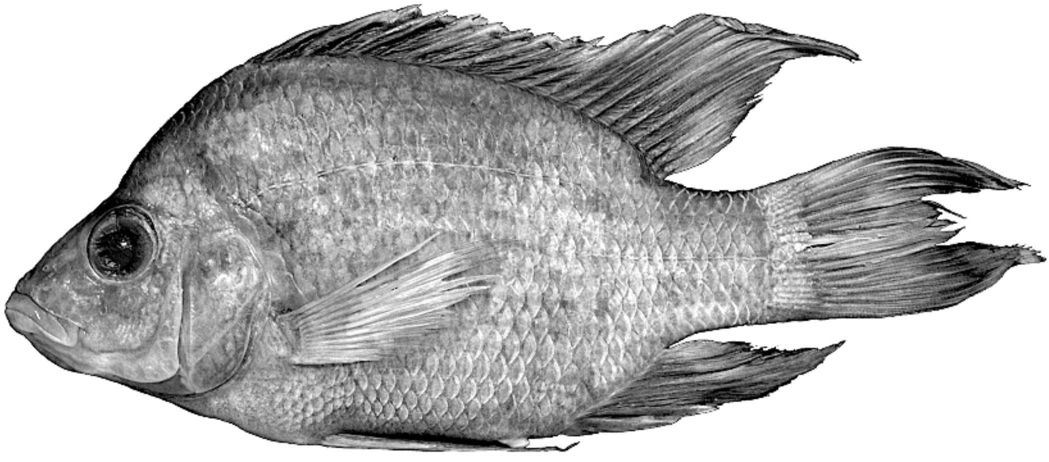

Fig. 21. *Ptychochromis inornatus*, holotype, UMMZ 237492, adult female, 115.3 mm SL, northwestern Madagascar, Mahajanga Province, northeast of Antsohihy, Ankofia drainage, Anjingo River.

smaller, bilaterally symmetrical bicuspid teeth of same morphology as those of outer rows. Posterior teeth in outer rows on both jaws widely set and highly variable in size. Dentition covers anterior 3/4 of dentary and nearly entire surface of premaxillary arcade.

LPJ with a few weakly interdigitating sutures on posteroventral margin. Dentition on LPJ and UPJ consists of numerous closely set, hooked, and bicuspid teeth. Dentition robust medially, but not molariform on LPJ or UPJ. Two rows of well developed, widely set, hooked, and bicuspid teeth on second pharyngobranchial toothplate. Two rows of teeth medially on "free" toothplate associated with second epibranchial bone. Robust, laterally expanded toothplates cover most of dorsal surface of Cb4. Toothplates confluent with

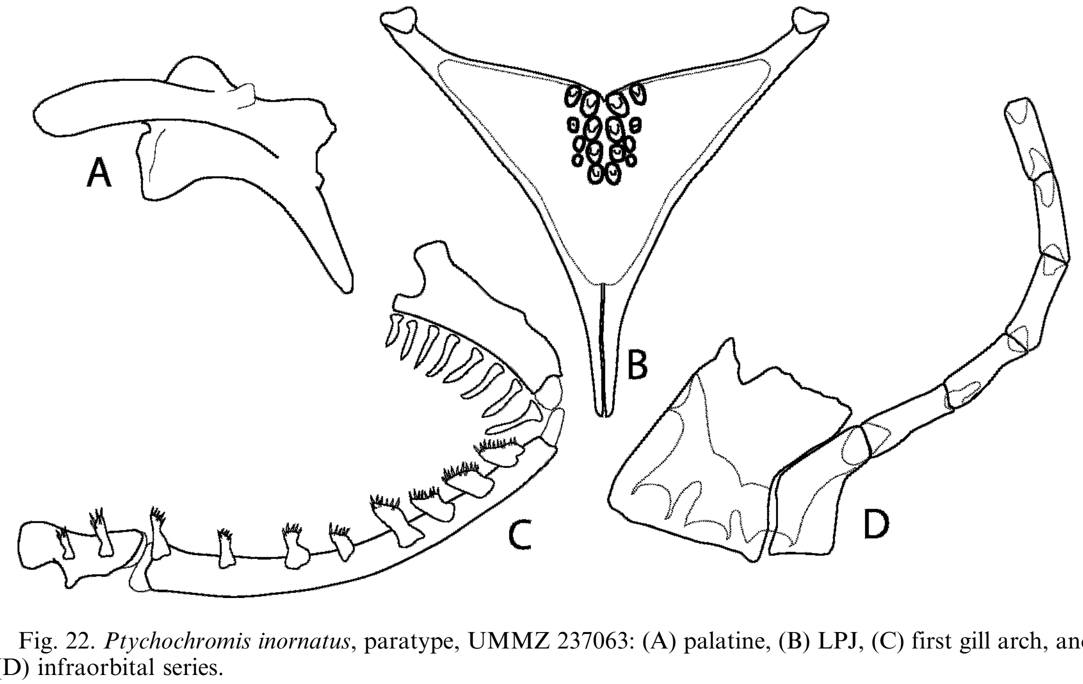

Fig. 22. *Ptychochromis inornatus*, paratype, UMMZ 237063: (A) palatine, (B) LPJ, (C) first gill arch, and (D) infraorbital series.

TABLE 9
Morphometric and Meristic Data for *Ptychochromis inornatus*
Values in parentheses indicate number of specimens examined with that count. (H) indicates count corresponding to holotype.

Character	*N*	Holotype	Range	Mean	SD
Standard length (mm)	20	115.3	25.9–122.3	80.6	
Percentage of SL					
Head length	20	35.5	34.2–37.7	35.6	0.99
Body depth	20	50.0	36.3–54.5	45.7	4.80
Predorsal length	20	43.3	41.4–45.8	43.5	1.09
Preanal length	20	73.6	67.3–74.5	71.5	1.62
Prepelvic length	20	43.5	40.3–47.2	42.9	1.63
Head width (max.)	20	18.6	17.4–19.4	18.3	0.60
Caudal peduncle length	20	13.9	12.4–16.6	13.9	0.93
Caudal peduncle width	20	6.8	4.2–8.2	6.1	1.12
Caudal peduncle depth	20	17.4	12.0–18.9	16.4	1.64
Pectoral-fin length	20	33.1	23.6–35.6	30.3	2.98
Pelvic-fin length	19	36.5	26.7–40.0	34.4	3.48
Percentage of HL					
Snout length	20	40.8	29.8–41.9	37.8	3.06
Orbit diameter	20	29.8	28.4–39.4	32.6	3.02
Upper jaw length	20	34.5	26.0–35.3	31.4	2.23
Lower jaw length	20	39.6	35.5–42.7	39.2	1.76
Interorbital width	20	28.9	23.1–31.0	27.3	1.90
Preorbital depth	20	24.9	19.8–25.6	23.0	1.59
Caudal peduncle length/depth	20	0.8	0.7–1.3	0.9	0.14
Caudal peduncle length/width	20	2.1	1.5–3.4	2.4	0.53
Scales in lateral line	19	31 (2), 32 (7), 33 (10) (H)			
Scales: lateral line to dorsal fin	20	6 (13) (H), 7 (7)			
Gill rakers (lower limb)	20	9 (2), 10 (13), 11 (5) (H)			
Vertebrae (precaudal + caudal)	20	13 + 13 = 26 (2), 12 + 15 = 27 (1), 13 + 14 = 27 (17) (H)			
Dorsal fin	20	XIII 11 (4), XIV 9 (1), XIV 10 (13) (H), XIV 11 (2)			
Anal fin	20	III 8 (9) (H), III 9 (11)			

outer-row gill rakers of these elements. Dentition on Cb4 toothplates unicuspid laterally, moderately hooked and bicuspid medially.

Lower limb rakers on first gill arch denticulate medially and dorsally. Eight to 10 (modally nine) robust and short gill rakers arrayed along lower limb of first arch. Seven or eight epibranchial gill rakers, most dorsal raker feeble and reduced in size. Gill rakers on remaining arches expanded, strongly denticulate, with well-developed elongate and conical teeth dorsally.

Flanks covered with large, regularly imbricate strongly ctenoid scales, with the entire caudal margin of each scale with well-developed cteni. Scales on flanks becoming increasingly ctenoid posteriorly. Scales on nape and most of head region also ctenoid. Scales on cheek and anterior chest cycloid, although small proportion of cheek scales also frequently ctenoid; posterior chest scales ctenoid. Scales on opercle and subopercle mostly cycloid to primarily ctenoid, and both scale morphologies always present in region. Anterior chest scales markedly reduced in size and embedded. Scales on caudal-fin base reduced in size and mostly ctenoid (a few cycloid scales present terminally). Lateral line scales 31–33. Six or seven scales in diagonal series from lateral line to dorsal-fin origin. No scale rows along dorsal- and anal-fin bases.

Trailing margins of segmented dorsal- and anal-fin rays produced, extend well posterior to origin of caudal fin and frequently to midcaudal in large adults. Dorsal fin with XIII–XIV spines and 9–11 soft rays. Anal fin with III spines and eight or nine soft rays. First anal spine short, second and third spines elongate and of similar size. Caudal fin emarginate, dorsal and ventral lobes somewhat produced, especially in larger individuals. Pectoral fins elongate, extending posterior to vertical through anal-fin insertion in larger individuals when adducted. Pelvic fins elongate, trailing filaments extend well beyond anal-fin origin when adducted.

MISCELLANEOUS OSTEOLOGY AND ANATOMY: Well-developed exoccipital foramina on posterior of neurocranium. Paired anterior gas bladder extensions contact exoccipital region of neurocranium, but do not extend into exoccipital foramina. Infraorbital series (fig. 22D) composed of seven elements. Lachrymal deep, with four pores. IO2 excluded from orbit, although IO3 not markedly ventrally displaced. Uncinate process of first epibranchial bone expanded, at least twice diameter of anterior arm (fig. 22C). Supraoccipital crest truncate and rounded at postero-dorsal margin. Prominent concavity present in lateral view at margin of supraoccipital and frontal bones. Well-developed process and deep indentation present on inner face of Cb4. Cephalic laterosensory canals well developed and enlarged.

COLORATION IN LIFE (plate 1A): Ground coloration iridescent silvery-green, olive, or copper dorsal of midline; light silver to silvery-green below midline. Some individuals much lighter ventrally, approaching silvery-white. Faint speckled patch immediately posterior to opercle and below lateral line present in some specimens, faded or absent in larger individuals. Opercle opalescent blue-green to copper. Copper or rust patches sometimes present on snout and dorsal to orbit. Body peppered to varying degree with small bluish and white iridescent spots/spangling. Dorsal fin black proximal to base and orange to deep red distally. Trailing margin of dorsal fin gold in some individuals. Anal fin either mostly hyaline with deep reddish rays, deep red overall, or primarily black with some golden coloration terminally. Caudal fin deep red to gray, golden terminally in some specimens. Pectoral fins hyaline with red rays, to reddish overall. Pelvic fins with white leading edge and red rays, grayish-red to grayish-black in overall coloration. Body with speckled appearance owing to scale coloration.

COLORATION IN PRESERVATIVE: Ground coloration olive to grayish-olive. Pigmentation dark along dorsal midline and also along dorsal-fin base, becoming lighter ventrally. Throat, ventral chest, and belly light olive to yellowish-white. A series of dark, faint, and narrow horizontal stripes along flanks, lending the body an alternating light and dark striping pattern. No other distinguishing marks present on body, except dark horizontal stripe on upper half of opercle, and very faint spotted or speckled region immediately posterior to opercle and below lateral line in some larger specimens. Snout, lachrymal, and interorbital region dark gray. Golden-olive coloration present on cheek, opercle, and immediately posterior to and somewhat dorsal of orbit. Anterior region of chest silvery. Dorsal, anal, and caudal fins grayish-black proximally, followed by light gray band medially, and varying amounts of black pigmentation terminally. Pelvic fins olive proximally, dark gray to black distally. Pectoral fins mostly hyaline, and faint black terminally.

DISTRIBUTION AND HABITAT: Known only from the Ankofia drainage basin and its tributaries, including the Anjingo River and Lake Andrapongy, in northwestern Madagascar (fig. 1). The Anjingo and Ankofia rivers and their tributaries are generally shallow, clear, moderate to swift flowing, and subject to vast seasonal fluctuation in water level and flow rate. Smaller tributaries (e.g., the Bemahavony River within Bora Special Reserve) experience periods of very reduced flow to near complete desiccation during the dry season, extending approximately from July to November. Individuals were collected from deeper pools or from under overhanging banks and vegetation in less disturbed areas, and seldom from shallow swift flowing regions of the larger rivers. Lake Andrapongy is a large, very shallow, and highly turbid lake characteristic of northwestern Madagascar.

CONSERVATION STATUS: Nowhere is *P. inornatus* abundant within its restricted range. The Ankofia and Anjingo river basins are

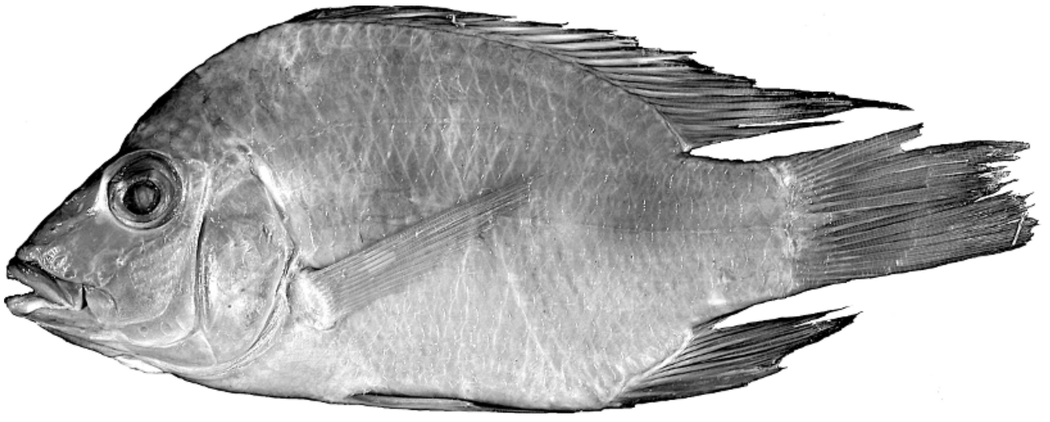

Fig. 23. *Ptychochromis grandidieri*, holotype, MNHN A.4147, 118.4 mm SL; Madagascar; region of high forests; Humblot and Grandidier.

moderately to highly disturbed and degraded throughout much of their course, with little original forest remaining. The small Bora Special Reserve represents the last remaining forested area in the immediate region. *Ptychochromis inornatus* was found to be relatively more common in the small Bemahavony River within the forested reserve than in the surrounding larger river channels. Lake Andrapongy is subject to high fishing pressure, agricultural conversion of a significant portion of the basin for rice cultivation, and the impact of several nearby villages.

LOCAL NAME: The local Malagasy name for *P. inornatus* is *juba*. *Ptychochromis oligacanthus* is known throughout most of its range as *tsipoy*, and infrequently also as *juba*.

ETYMOLOGY: The specific epithet, *inornatus*, is a Latin adjective meaning "plain or unadorned", in reference to the lack of lateral spotting or barring and overall plain appearance of the species.

DISCUSSION AND COMPARISONS: In sharing the western-type palatine morphology, *Ptychochromis inornatus* is placed in a "western clade" (i.e., restricted to western basins) of *Ptychochromis*, also comprising *P. oligacanthus*, *P. insolitus*, and *P. onilahy*, where it is resolved as the sister taxon of *P. insolitus* (fig. 2). Morphologically, *P. insolitus* and *P. inornatus* are united by the presence of strongly ctenoid scales, with the entire caudal scale margin bearing well-developed cteni (vs. weakly ctenoid scales, with only the central portion of the caudal margin bearing weak cteni in congeners). These two species, however, are readily distinguished on the basis of the number of tooth rows on Pb2 (two in *P. inornatus* vs. three in *P. insolitus*) and by a number of nonoverlapping meristic and morphometric measurements (compare tables 8 and 9).

Ptychochromis grandidieri Sauvage, 1882
Figures 23–24, Plates 1E and 1F, Table 10

Ptychochromis madagascariensis: Sauvage, 1891.
Ptychochromis oligacanthus (in part): Pellegrin, 1904.
Ptychochromis sp. "Ambila Lemaitso": de Rham and Nourissat, 2002.
Ptychochromis sp. "côte est Gold": de Rham and Nourissat, 2002.
Ptychochromis nov. sp. "black saroy": Sparks and Stiassny, 2003: table 9.1.

HOLOTYPE: MNHN A.4147, 118.4 mm SL; Madagascar, region of high forests, Humblot and Grandidier. See discussion in Sparks (2003) regarding the locality of the holotype.

ADDITIONAL MATERIAL EXAMINED: MNHN A.310, 1 ex., rivers that cross the eastern slope, Lantz. AMNH 88018, 56 ex., 1 ex., C&S, southeastern Madagascar, Mananjary, estuary of Mananjary River, 21°05′S 48°27′E. AMNH 88053, 2 ex., southeastern Madagascar, Mananjary, estuary of Mananjary River, 21°05′S 48°27′E. AMNH 88076, 2 ex., eastern Madagascar, Vatomandry, 19°20′S 49°00′E. AMNH 88090, 3 ex., eastern Madagascar, Mahanoro, 19°55′S 48°50′E. AMNH 88092, 17 ex., eastern

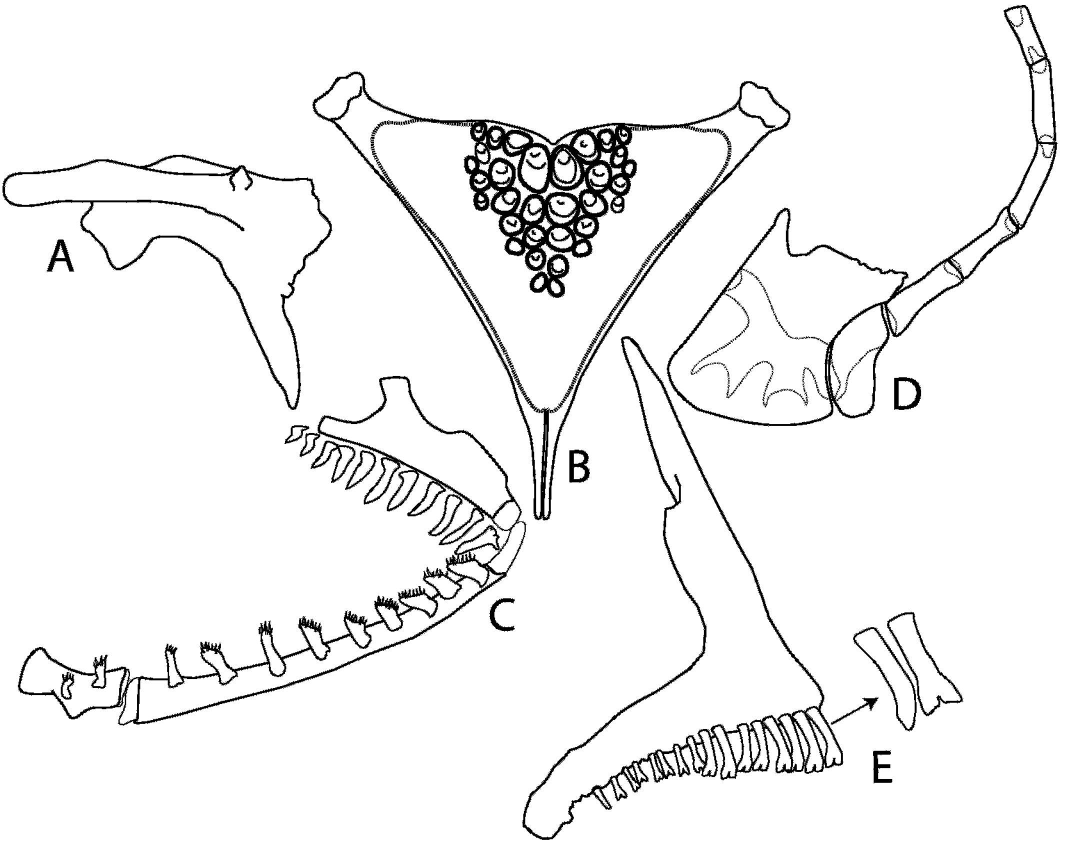

Fig. 24. *Ptychochromis grandidieri*, AMNH 88018: (A) palatine, (B) LPJ, (C) first gill arch, (D) infraorbital series, and (E) premaxilla.

Madagascar, Mahanoro, Pangalanes canal north of Mangoro River. AMNH 88102, 36 ex., 14 ex. C&S, eastern Madagascar, bay lake behind dunes, ca. 100 m from sea. AMNH 88117, 18 ex., eastern Madagascar, Tamatave market, 18°10′S 49°25′E. AMNH 88140, 1 ex., eastern Madagascar, 25 km north of Tamatave, Pangalanes canal, 18°00′S 49°25′E. AMNH 88153, 11 ex., eastern Madagascar, between Fenerive and Tamatave, Pangalanes canal, 18°00′S 49°25′E. AMNH 96999, 52 ex., 2 ex. C&S, eastern Madagascar, Tamatave Province, Mangoro River near mouth. AMNH 97008, 185 ex., eastern Madagascar, Salehy village, 1 km south of turnoff from Marolambo-Mananjary road, 19°55′S 48°50′E. AMNH 97012, 12 ex., eastern Madagascar, Mahanoro market. AMNH 97028, 7 ex., 3 ex. C&S, eastern Madagascar, Tamatave Province, bay lake behind first dune ca. 100 m from sea, east of road by Sahey Village, 1 km south of turnoff from Marolambo-Manajary Road. AMNH 97057, 1 ex., eastern Madagascar, Ambodisovoka village, Savalany River. AMNH 228067, 3 ex., southeastern Madagascar, Lopary, Mananizo River. AMNH 228072, 6 ex., southeastern Madagascar, Ampataka village, Sahambavy River. AMNH 228074, 3 ex., southeastern Madagascar, 12 km north of Farafangana, Manampatrona River, 22°43′47″S 47°47′25″E. AMNH 231347, 1 ex., southeastern Madagascar, Ampataka village, Sahambavy River, 23°21′04″S 47°28′18″E. AMNH 231352, 4 ex., southeastern Madagascar, Manombo Special Reserve, Takoandra River, 23°01′27″S 47°43′16″E. MNHN A.7896, 2 ex., central Madagascar to the west of Antananarivo, Lac Itasy(?). MNHN 1901-0020, 1 ex., eastern Madagascar, Tamatave. MNHN 1901-0021, 1 ex., eastern Madagascar, Tamatave. MNHN 1932-0082, 1 ex., eastern Madagascar, Manompana. MNHN 1932-0083, 13 ex., eastern Madagascar, Manompana. MNHN 1935-0007, 1 ex., eastern Madagascar, Mananara. UMMZ 233524, 17 ex., 2 ex. C&S, Madagascar, southeastern coastal region. UMMZ 237311, 22 ex., southeastern Madagascar, Mananjary. UMMZ

TABLE 10
Morphometric and Meristic Data for *Ptychochromis grandidieri*
Values in parentheses indicate number of specimens examined with that count. (H) indicates count corresponding to holotype.

Character	*N*	Holotype	Range	Mean	SD
Standard length (mm)	25	118.4	19.0–177.2	91.3	
Percentage of SL					
Head length	25	35.4	33.5–39.6	35.5	1.51
Body depth	25	48.8	36.5–52.2	45.2	3.64
Predorsal length	25	46.0	42.2–49.7	44.9	1.73
Preanal length	25	76.9	66.8–79.1	73.8	2.46
Prepelvic length	25	42.8	36.8–45.2	41.9	1.98
Head width (max.)	25	16.1	14.4–18.5	16.4	1.03
Caudal peduncle length	25	12.6	12.1–17.3	13.8	1.45
Caudal peduncle width	25	6.25	3.0–8.6	5.6	1.30
Caudal peduncle depth	25	17.3	13.4–20.1	17.0	1.73
Pectoral-fin length	25	34.3	25.9–36.2	31.2	2.82
Pelvic-fin length	25	32.8	24.4–46.7	32.4	5.30
Percentage of HL					
Snout length	25	43.2	25.0–49.5	25.0	6.99
Orbit diameter	25	29.6	23.2–45.8	31.0	4.91
Upper jaw length	25	32.5	25.1–34.7	29.3	3.22
Lower jaw length	25	37.2	31.6–43.1	37.5	2.21
Interorbital width	25	30.8	13.9–35.0	27.4	4.63
Preorbital depth	25	29.8	17.5–32.2	25.0	4.59
Caudal peduncle length/depth	25	0.7	0.7–1.3	0.8	0.15
Caudal peduncle length/width	25	2.0	1.4–5.8	2.7	1.03
Scales in lateral line	24	30 (1), 32 (8), 33 (9), 34 (6) (H)			
Scales: lateral line to dorsal fin	24	5 (9), 5.5 (5), 6 (9) (H), 7 (1)			
Scales: pectoral to pelvic bases	16	5 (7), 6 (6), 7 (2) (H)			
Gill rakers (lower limb)	24	9 (1), 10 (2), 11 (19), 12 (2) (H)			
Vertebrae (precaudal + caudal)	21	13 + 14 = 27 (9), 14 + 13 = 27 (10) (H), 14 + 14 = 28 (2)			
Dorsal fin	22	XII 12 (1), XIII 11 (3), XIII 12 (7), XIII 13 (3), XIV 11 (5) (H), XIV 12 (3)			
Anal fin	20	III 8 (16) (H), III 9 (4)			

237312, 3 ex., 1 ex. C&S, southeastern Madagascar, Manombo Special Reserve. UMMZ 237495, 5 ex., southeastern Madagascar, 6 km north of Karianga at Mahavelo, Rienana drainage, Andriambondro River, 22°21′47″S 47°22′05″E. UMMZ 238453, 2 ex., southeastern Madagascar, near Manombo Special Reserve. UMMZ 238471, 1 ex., southeastern Madagascar, Mananjary port. UMMZ 238472, 11 ex., 2 ex. C&S, southeastern Madagascar, Farafangana market. UMMZ 238476, 7 ex., Madagascar, southeastern coastal region.

DIAGNOSIS: A *Ptychochromis* exhibiting the eastern-type palatine morphology (fig. 24A) and distinguished from all congeners by a unique adult pigmentation pattern and coloration consisting of a predominently golden-yellowish or greenish base without distinct iridescence encircling scale margins, and a horizontal series of four well-defined black spots or blotches restricted midlaterally on the flanks, with no opercular blotch or bar, and rarely with a fifth blotch near the caudal-fin base. *Ptychochromis grandidieri* is further distinguished from all cogeners in the possession of a robust and strongly molariform LPJ dentition, even at small sizes.

DESCRIPTION: Morphometric and meristic data presented in table 10. Morphological characteristics and general pigmentation pattern can be observed in figure 23 and plate 1E and F. Relatively deep-bodied and laterally compressed with dorsal body profile moderately curved, particularly so anteriorly. Ventral body profile moderately convex and rounded in smaller specimens and relatively straight in larger individuals. Lateral snout profile usually straight. Predorsal head profile moderately to strongly convex from midorbit to dorsal-fin origin, supraoccipital crest prominent in larger specimens. Caudal peduncle short, relatively deep and laterally compressed. Dorsal-fin origin located slightly anterior to vertical through pectoral-fin insertion. Pelvic-fin origin located well posterior to vertical through pectoral-fin insertion.

Total vertebral count 27 or 28, with a formula of 13 + 14, 14 + 13, and 14 + 14 precaudal and caudal vertebrae, respectively.

Jaws isognathous. Oral dentition bilaterally symmetrical and bicuspid, expanded distally with moderately to well-developed cusps (fig. 24E). Rostrally, outer row teeth procumbently implanted in both upper and lower jaws. Rostrally, upper and lower jaws with two to four inner rows of smaller teeth of the same morphology as those of outer rows; inner rows tapering posteriorly to a single row. Cusps of posterior teeth in outer row of both jaws weakly developed, often with some unicuspid teeth present. Dentition covers anterior 2/3 of dentary and nearly entire surface of premaxillary arcade.

LPJ with strongly interdigitating sutures on postero-ventral margin. LPJ generally more robust than that of similarly sized congeners. Dentition of LPJ and UPJ anteriorly and laterally comprised of numerous, very closely set, hooked, and bicuspid teeth. Teeth becoming markedly more robust posteromedially (fig. 24B). Medially on UPJ and posteromedially on LPJ dentition is enlarged and fully molariform. Four to seven rows of hooked and bicuspid teeth on expansive second pharyngobranchial toothplates. Two or three rows of teeth present medially on "free" toothplate associated with second epibranchial bone. Robust, laterally expanded toothplates cover most of dorsal surface of fourth ceratobranchial bones; Cb4 toothplates confluent with outer-row gill rakers. Dentition on Cb4 toothplates generally conical or weakly hooked and bicuspid laterally, hooked and bicuspid medially.

Lower limb rakers of first gill arch denticulate dorsomedially. Nine to twelve (modally 11) triangular and somewhat elongate gill rakers arrayed along lower limb of first gill arch. Nine or ten elongate epibranchial gill rakers. Gill rakers on remaining arches short, laterally expanded, and strongly denticulate.

Flanks covered with large, regularly imbricate, very weakly ctenoid scales, from about 1/3 to midpoint of spiny dorsal fin above upper lateral line and from pectoral base below upper lateral line to proximal portion of caudal fin. Scales on nape, head region, opercle and subopercle cycloid. Three or four rows of cycloid cheek scales. Scales on anterior chest and belly cycloid; posterior chest scales weakly ctenoid. Belly and anterior chest scales slightly reduced in size and embedded. Snout, lachrymal, and anterior portion of interorbital region to about level of midorbit asquamate. Scales on caudal fin base reduced in size and primarily cycloid. Lateral line scales 30–34. Five to seven scale rows between bases of pectoral and pelvic fins. Five to seven scales in diagonal from lateral line to dorsal-fin origin. No scale rows present along dorsal- and anal-fin bases.

Distal margins of soft dorsal and anal fins produced and pointed, particularly in large specimens where the dorsal fin is often markedly elongate and filamentous in males. Dorsal fin with XII–XIV spines and 11–13 soft rays. Anal fin with III spines and 8 or 9 soft rays. First anal spine very short, second and third spines elongate and of similar length. Caudal fin emarginate and trailing margins of upper and lower lobes slightly produced. Pectoral fin elongate and tapered distally. Adducted pelvic fin extending to about anal-fin origin in smaller specimens, and well beyond origin in larger individuals.

MISCELLANEOUS OSTEOLOGY AND ANATOMY: Well-developed exoccipital foramina present on posterior of neurocranium. Paired anterior gas bladder extensions in contact with exoccipital region of neurocranium via connective tissue, but do not extend into exoccipital foramina. Infraorbital series (fig. 24D) composed of seven elements. Lachrymal deep, with four pores. IO2 excluded from orbit by ventrally displaced IO3. Uncinate process and anterior arm of first epibranchial bone short and robust (fig. 24C). Well-developed process and deep indentation present on inner face of Cb4.

COLORATION IN LIFE (plate 1E and F): Although there is some variation in overall pigmentation pattern and coloration, particularly of juveniles, among populations considered here to be conspecifics (de Rham and Nourissat, 2002), nonetheless, certain aspects of pigmentation patterning are intraspecifically invariable. *Ptychochromis grandidieri* generally exhibits a golden-yellowish or greenish base coloration (although certain northern populations are frequently darker overall in coloration, contrast plate 1F and 1E), and the flank scales lack the distinct iridescence encircling scale margins that are prominent in *P. oligacanthus*. Body is somewhat darker dorsally, whereas the belly, chest, and gular region are often paler and silvery. Cheek and opercular region are iridescent gold. Snout, lachrymal, interorbital region, and upper lip are dusky gray-brown. All fins are hyaline to sooty gray, and the dorsal fin often has pale yellow or whitish lappets. No iridescent maculae present in caudal- or dorsal-fin membranes. Horizontal series of four well-defined black blotches present and restricted midlaterally on flanks; rarely with a fifth blotch near caudal-fin base. Loiselle (in litt.) notes that *P. grandidieri* displays latitudinal variation with respect to several elements of pigmentation pattern and coloration, with the color of adult specimens becoming progressively darker from the region of the Masihanaka River northward to the Ivoloina. Similarly the amount of orange-red in the vertical fins increases in populations south of the Mangoro River to the Masihanaka. In populations from the region around the Masihanaka River the caudal fin is also heavily suffused with orange-red.

COLORATION IN PRESERVATIVE: Ground coloration pale yellow, olive, or golden-brown. Four prominent, and more or less rounded, black blotches arrayed in horizontal series along the midflank. In older, or poorly preserved, specimens these midlateral spots and blotches are frequently faded (fig. 23), yet their traces can almost always be discerned with careful examination. Body slightly lighter ventrally, and essentially uniform pale yellow to silver. Head region more or less uniformly brown. Unpaired fins brownish. Dorsal and anal fins becoming charcoal to blackish terminally, trailing margins of soft dorsal and anal fins blackish. Pectoral fins hyaline to pale uniform olive or brown. Pelvic fins brownish, becoming charcoal to blackish distally. Anterior interorbital region, snout, and lachrymal dark brown. Lower lip lighter brown to olive.

DISTRIBUTION AND HABITAT: *Ptychochromis grandidieri* is restricted to eastern drainages and is most commonly found at low elevations in coastal regions, although it is frequently also collected in the submontane forest zone where the species may be encountered up to 100 km upstream from the sea (de Rham and Nourissat, 2002). Uniquely among *Ptychochromis* this species is apparently salt tolerant and occurs in brackish, as well as fresh, waters along much of the east and southeastern coastal regions (fig. 1). The precise geographical range of *P. grandidieri* is currently unclear and its northern limit may extend to the southern Makira region; however, collecting in this region has been limited. De Rham and Nourissat (2002) considered that the populations from around the mouth of the Rianila River to a little north of Tamatave (*Ptychochromis* "Ambila Lemaitso" of de Rham and Nourissat, 2002), which are generally darker in coloration than the more southerly populations, may represent a distinct and undescribed species. Our own examination of specimens from this region (as far north as Mahanara), as well as those of Sparks (2003), finds no evidence to support that supposition, and they are included here within our concept of *P. grandidieri*. At the southern end of the range the picture is less clear. Specimens from as far as a little south of Vangaindrano are *P. grandidieri*, however, de Rham and Nourissat (2002) have illustrated specimens from two "populations" from the region of Manantenina south to just beyond Fort Dauphin (*Ptychochromis* sp. "Tarantsy" and *Ptychochromis* sp. "Manampanihy") in extreme southeastern Madagascar. Unfortunately, we have been unable to obtain any specimens from these southernmost regions for inclusion in morphological or molecular analyses, and the identity of these fishes remains to be resolved.

Conservation Status: As currently recognized *P. grandidieri* has a widespread distribution throughout eastern lowland coastal regions. Environmental degradation is pervasive throughout much of its range, yet the species remains abundant in many areas. The salt tolerance of many populations suggests that its persistence throughout the Pangalanes canal system is likely; however, highland populations appear to have undergone severe attrition.

Local Name: *Saroy* is the Malagasy name most commonly used throughout eastern Madagascar to refer to species of *Ptychochromis*, including *P. grandidieri*.

Etymology: Named for the French naturalist and explorer Alfred Grandidier (1836–1921), who along with Humblot collected the holotype.

Discussion and Comparisons: In our phylogenetic analysis, *P. grandidieri* is placed among an unresolved group of *Ptychochromis* including *P. makira*, *P. loisellei*, and *P. curvidens* (fig. 2). In the analysis, *P. grandidieri* is recovered in a polytomy and its immediate relationships remain unresolved. Although there is currently no unambiguous evidence for the monophyly of an assemblage comprising *P. grandidieri*, *P. loisellei*, *P. makira*, and *P. curvidens*, the shared possession of an eastern-type palatine morphology is unique to these four species and may indicate a close relationship among them. An independent analysis of nucleotide characters also was unable to resolve the intrageneric placement of *P. grandidieri*, although it was united in a clade also comprising *P. loisellei* and a clade of *Ptychochromis* with western-type palatine morphology (Sparks and Smith, 2004: fig. 1). Morphometrically, *P. grandidieri* is most similar to *P. makira* from which it is readily distinguished by pigmentation pattern and coloration, infraorbital morphology, and also in the possession of a considerably larger LPJ with more numerous and well-developed molariform teeth (compare fig. 24B and fig. 14B).

Ptychochromis oligacanthus (Bleeker, 1868)

Figures 25–26, Plate 1G, Table 11

Tilapia oligacanthus var. *nossibeënsis*: Bleeker, 1868.

Ptychochromis nov. sp. "nossibeensis": Sparks and Stiassny, 2003: table 9.1.

Lectotype: RMNH 3.936, "Madagascar, in flumine Samberano, Nossibé, in lacu Pambilao", 66.9 mm SL, Pollen and van Dam.

Note: Of the six specimens cited by Bleeker, 1868 in his original description of *Tilapia oligacanthus*, only two putative syntypes have been located. According to records at the Natural History Museum, Leiden, these are RMNH 3.936, a well-pigmented individual of 66.9 mm SL (ca. 85 mm TL), and a juvenile of 35.3 mm SL (ca. 42.5 mm TL), which is lacking all trace of flank pigmentation. However, Bleeker (1868) gives a size range for the six type specimens of 50–103 mm (presumably TL), a range that clearly excludes the smaller of the two putative syntypes. Consequently, we find no justification for the inclusion of the 35.3 mm SL specimen in the syntypical series and believe that it was included with RMNH 3.936 in error at some time after 1868. To avoid further confusion, we select the larger specimen, which conforms well with Bleeker's original description, as the lectotype of *Ptychochromis oligacanthus*. There remains a question as to the precise provenance of the lectotype given that Bleeker's original type series was an amalgam of specimens from "in flumine Samberano" (the Sambirano River on mainland Madagascar) and specimens from "Nossibé; in lacu Pambilao" (Lake Ampombilava, on the Island of Nosy Be). Bleeker (1868) alludes to a stronger pigmentation and more generally colorful aspect of the Nosy Be specimens, and whereas the lectotpe is rather strongly pigmented (fig. 25A), with only a single specimen we have no comparative basis upon which to make a determination. Furthermore, the locality data currently associated with RMNH 3.936 is "Madagascar, Ambastuano", an apparent variant of the contemporary "Ambazoana", a tributary situated some 45 km north of the main channel of the Sambirano River on the mainland, suggesting that the lectotype is most probably part of the "in flumine Samberano" sample studied by Bleeker.

Additional Material Examined: AMNH 18841, 1 ex., Madagascar (probably mainland,

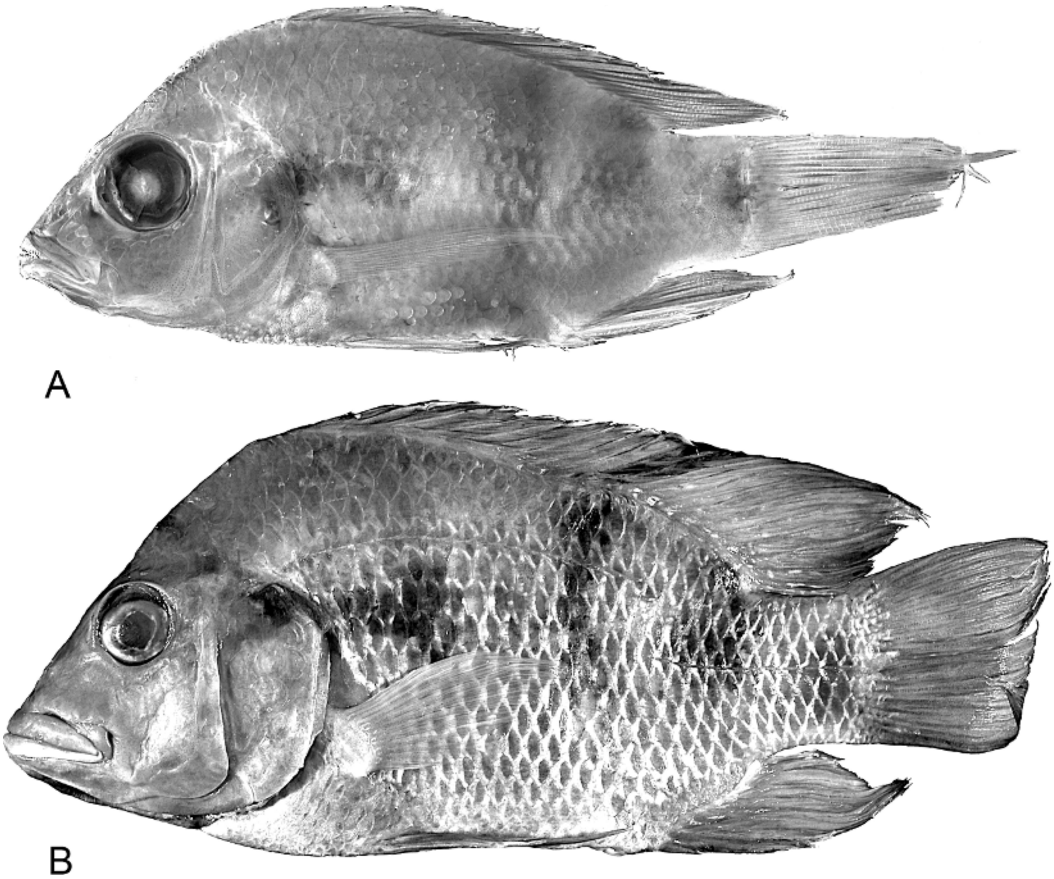

Fig. 25. *Ptychochromis oligacanthus*, (A) lectotype, RMNH 3.936, 66.9 mm SL; northwestern Madagascar, most likely Sambirano River (see text). (B) AMNH 215522, adult, 145.8 mm SL; Nosy Be, Lake Bempazava.

Sambirano region). AMNH 58491, 9 ex., northwestern Madagascar, Lake Amparihibe, at the mouth of the inflowing small stream from Lake Antsidihy, Nosy Be. AMNH 215522, 4 ex., northwestern Madagascar, Lake Bempazava, Nosy Be. AMNH 215523, 15 ex., northwestern Madagascar, Lakes Djabala and Ampombilava, Nosy Be. AMNH 230699, 3 ex., northwestern Madagascar, Lake Andjavibe, Nosy Be. AMNH 232399, 2 ex., northwestern Madagascar, Lake Ampombilava, Nosy Be. AMNH 232415, 3 ex., northwestern Madagascar, Lake Djabala, Nosy Be. MNHN 1962-322, 1 ex., northwestern Madagascar, Sambirano River. UMMZ 236591, 26 ex., 4 ex. C&S, northwestern Madagascar, Lake Ampombilava, Nosy Be. UMMZ 237498, 22 ex., 2 ex. C&S, northwestern Madagascar, Lake Djabala, Nosy Be. UMMZ 237493, 3 ex., northwestern Madagascar, Lac de Deux Soeurs, Nosy Be. UMMZ 237494, 1 ex., northwestern Madagascar, Lake Amparihibe, Nosy Be. UMMZ 237496, 6 ex., northwestern Madagascar, Lake Bempazava, Nosy Be. UMMZ 237497, 8 ex., northwestern Madagascar, Lake Anjavibe, Nosy Be. UMMZ 237499, 11 ex., 1 ex. C&S, northwestern Madagascar, Mananjeba drainage, Andranomaloto River, northeast of town of Ambanja.

Diagnosis: A *Ptychochromis* exhibiting the western-type palatine morphology and distinguished from congeners by the presence of a distinctive black blotch or bar covering the dorsoposterior margin of the opercle. The opercular blotch is usually contiguous with the first midlateral blotch on the anterior flank. Further distinguished from all congeners by the combination of iridescent maculae along the dorsal-, anal-, and caudal-fin bases, distinctive

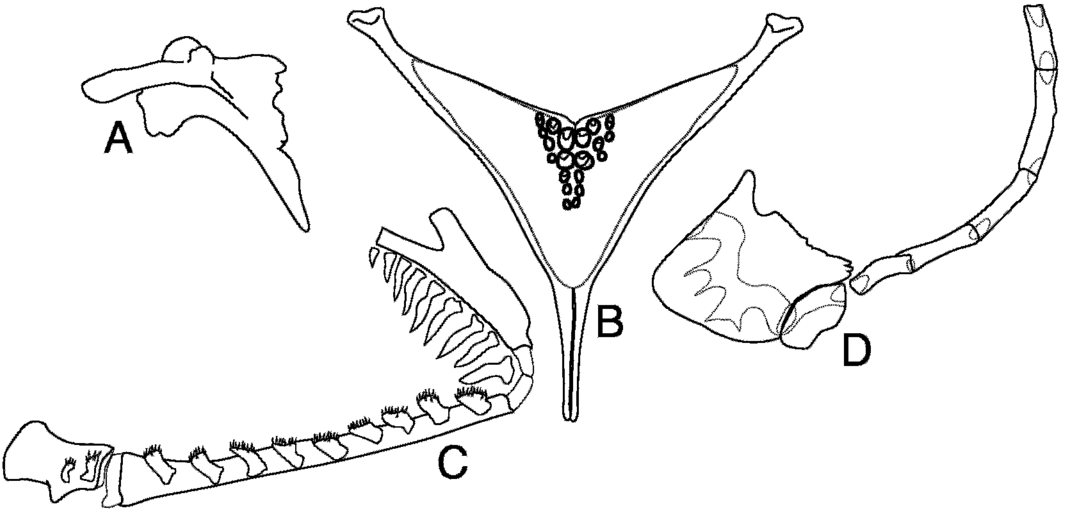

Fig. 26. *Ptychochromis oligacanthus*, AMNH 215523: (A) palatine, (B) LPJ, (C) first gill arch, and (D) infraorbital series.

pale iridescence encircling scale margins over much of the body, and a series of five or six prominent midlateral blotches or bars on the flanks and caudal peduncle. The third flank blotch or bar frequently extends dorsally onto the dorsal-fin membrane at the junction of spinous and soft rays. Anatomically, *Ptychochromis oligacanthus* is distinguished from all congeners, except *P. onilahy*, by the presence of only two rows of inner teeth in both upper and lower jaws, and cycloid scales above the upper lateral line on the flanks.

DESCRIPTION: Morphometric and meristic data presented in table 11. Morphological characteristics and general pigmentation pattern can be observed in figure 25 and plate 1G. Deep-bodied and laterally compressed. Dorsal body profile moderately to strongly curved, particularly anteriorly. Ventral body profile usually straight. Lateral snout outline straight to mildly convex, due to protuberance of premaxillary pedicels. Predorsal head profile convex posterior of orbit to dorsal-fin origin, and supraoccipital crest prominent. Caudal peduncle short, deep and laterally compressed. Dorsal-fin origin located well anterior to vertical through pectoral-fin insertion, except very large specimens where dorsal-fin origin is located only slightly anterior to vertical through pectoral-fin insertion. Pelvic-fin origin located well posterior to vertical through pectoral-fin insertion.

Total vertebral count 26 or 27 (modally 27) with a formula of 13 + 13, 14 + 12, 13 + 14, and 14 + 13 precaudal and caudal vertebrae, respectively.

Jaws isognathous, except in very large specimens where the lower jaws become slightly prognathous. Oral dentition bilaterally symmetrical and bicuspid, with cusps moderately to well developed. Outer row teeth enlarged and graded in size laterally. Rostrally, outer row teeth somewhat procumbently implanted in lower jaw and teeth slightly recurved. Rostrally, upper and lower jaws with two inner rows of smaller teeth of similar morphology to those of the outer rows. Laterally, inner rows of teeth taper to a single row, and posteriorly only the outer row teeth are present in both upper and lower jaws. Cusps of posterior teeth often only weakly developed. Dentition covers anterior 2/3 of dentary and nearly entire surface of premaxillary arcade.

LPJ rather gracile with a few weakly interdigitating sutures on posteroventral margin. Dentition on LPJ and UPJ comprised of numerous, closely set, hooked, and bicuspid teeth. Posteromedially on LPJ, dentition becoming somewhat more robust but still

TABLE 11
Morphometric and Meristic Data for *Ptychochromis oligacanthus*
Values in parentheses indicate number of specimens examined with that count. (L) indicates counts corresponding to lectotype.

Character	*N*	lectotype	Range	Mean	SD
Standard length (mm)	20	66.9	35.3–145.8	70.2	
Percentage of SL					
Head length	20	36.8	35.9–40.0	37.9	1.10
Body depth	20	45.0	37.9–51.0	44.2	3.66
Predorsal length	20	45.6	23.9–46.9	40.7	5.85
Preanal length	20	73.7	57.5–77.6	72.2	3.93
Prepelvic length	20	43.4	29.1–46.5	42.6	3.57
Head width (max.)	20	18.2	14.7–19.2	17.4	1.32
Caudal peduncle length	20	12.4	11.3–14.6	13.0	0.93
Caudal peduncle width	20	3.6	2.5–4.9	4.1	0.68
Caudal peduncle depth	20	16.6	12.8–19.3	16.1	1.80
Pectoral-fin length	20	32.9	22.6–44.9	31.7	6.20
Pelvic-fin length	20	35.1	23.9–35.5	28.7	3.46
Percentage of HL					
Snout length	20	35.8	27.7–39.0	34.8	3.22
Orbit diameter	20	37.4	23.8–38.9	32.1	4.95
Upper jaw length	20	32.5	25.8–34.3	30.6	2.65
Lower jaw length	20	40.7	35.6–42.2	39.1	1.71
Interorbital width	20	29.3	24.5–30.1	27.3	1.68
Preorbital depth	20	22.8	14.9–25.9	20.0	2.94
Caudal peduncle length/depth	20	0.8	0.7–1.1	0.8	0.11
Caudal peduncle length/width	20	3.5	2.6–5.1	3.3	0.65
Scales in lateral line	20	29 (3), 30 (9) (L), 31 (8)			
Scales: lateral line to dorsal fin	20	4 (8), 4.5 (2), 5 (7) (L), 5.5 (1), 6 (2)			
Scales: pectoral to pelvic bases	20	4 (10), 5 (10) (L)			
Gill rakers (lower limb)	20	11 (2) (L), 12 (9), 13 (9)			
Vertebrae (precaudal + caudal)	31	13 + 13 = 26 (1), 14 + 12 = 26 (1), 13 + 14 = 27 (20), 14 + 13 = 27 (9) (L)			
Dorsal fin	31	XII 13 (2), XIII 11 (5) (L), XIII 12 (24)			
Anal fin	31	III 7 (2), III 8 (24) (L), III 9 (5)			

retaining an apical cusp. Three or four rows of hooked and bicuspid teeth on second pharyngobranchial toothplates. Two rows of teeth present on "free" toothplate associated with second epibranchial bone. Robust, laterally expanded toothplates cover most of dorsal surface of Cb4; toothplates confluent with outer-row gill rakers. Dentition on fourth ceratobranchial toothplates generally conical or weakly hooked and bicuspid laterally, hooked and bicuspid medially.

Lower limb rakers of first gill arch denticulate dorsomedially. Eleven to 13 gill rakers arrayed along lower limb of first arch. Eight somewhat elongate epibranchial gill rakers. Gill rakers on remaining arches short, laterally expanded, and strongly denticulate.

Flanks covered with large, regularly imbricate, cycloid to weakly ctenoid scales. Scales dorsal to upper lateral line normally cycloid, those below upper lateral line weakly ctenoid from about level of pectoral-fin origin to proximal portion of caudal fin. Scales on nape, head, opercle and subopercle large and cycloid. Cheek scales cycloid and comprising three or four rows. Anterior chest scales hardly reduced in size and at most only weakly embedded. Snout, lachrymal, and anterior portion of interorbital region to about level of midorbit asquamate. Scales on caudal fin reduced in size, generally weakly ctenoid anteriorly, considerably smaller and cycloid posteriorly. Lateral line scales 29–31 (mode 30). Four to six scales in diagonal from lateral line to dorsal-fin origin. No scale rows present along dorsal- and anal-fin bases.

Distal margins of soft dorsal and anal fins produced and pointed in larger specimens. Dorsal fin with XII or XIII spines and 11–13 soft rays. Anal fin with III spines and seven to nine soft rays. First anal spine very short, second and third spines elongate and of similar length. Caudal fin weakly to moderately emarginate, trailing margins of upper and lower lobes somewhat produced. Pectoral fin elongate and tapered distally. Pelvic fins variable in length, extend to about level of, or slightly beyond, anal-fin origin when adducted (in largest specimens examined, pelvic fins do not extend to anal-fin origin).

MISCELLANEOUS OSTEOLOGY AND ANATOMY: Well-developed exoccipital excavations present on posterior of neurocranium. Paired anterior gas bladder extensions in contact with exoccipital region of neurocranium via connective tissue, but do not extend into exoccipital foramina. Infraorbital series (fig. 26D) composed of seven elements. Lachrymal rather shallow, with four pores. IO2 short and excluded from orbit by ventrally displaced IO3. Uncinate process of first epibranchial less than twice diameter of anterior arm (fig. 26C). Well-developed process and deep indentation present on inner face of Cb4.

COLORATION IN LIFE: Base body coloration somewhat variable, usually blue or gold, but often silvery, particularly in juveniles. Most body scales ringed with iridescent silver or gold. Mainland populations tend to be somewhat less colorful, but also with iridescent encircling scale margins over much of body. Uniquely among *Ptychochromis*, a dark blotch or bar covers much of dorsoposterior margin of opercle. This opercular blotch usually contiguous with first midlateral blotch on anterior flank. Usually a series of five or six prominent midlateral blotches or bars present on flanks and caudal peduncle. Third flank blotch or bar frequently extended dorsally onto dorsal-fin membrane at junction of spinous and soft rays. Iridescent blue, golden or silvery maculae usually present along dorsal-, anal-, and caudal-fin bases. Maculae particularly prominent in adults of both sexes of the Nosy Be populations, whereas in mainland populations the maculae remain prominent in females but are somewhat less distinct in large males.

COLORATION IN PRESERVATIVE: Larger individuals with silvery iridescence around scale margins over much of body, particularly ventrally. Scale centers darker and lacking iridescence. Ground coloration ranges from brownish and somewhat golden to dark grayish-brown and green. Dark blotch or bar covers much of dorsoposterior margin of opercle, and usually contiguous with first midlateral blotch on anterior flank. Five or six black blotches or bands (variably developed) present on flanks and caudal peduncle. These markings usually extend ventrally to below lateral midline and dorsally to dorsal-fin base, or may extend completely across dorsal fin. Body somewhat lighter ventrally, golden-brown to grayish-brown. Head and dorsum brown to dark grayish-brown, gular region black in larger specimens. Anterior interorbital region, snout, and lachrymal grayish-green. Lips light olive. Fins pale yellow to grayish; fin rays dark gray to black. Traces of maculae usually evident along dorsal-, anal-, and caudal-fin bases. Fins, excluding pectorals, blackish terminally. Pectoral fin olive proximally and mostly hyaline distally.

DISTRIBUTION AND HABITAT: Restricted to freshwater habitats of northwestern Madagascar, from the Sambirano River northward to the Mananjeba drainage (= Andranomaloto River), and including the crater lakes of Nosy Be (fig. 1). The southern limit of the species range has yet to be determined, and more collections between the Sambirano and Ankofia drainages will be necessary to resolve this issue.

CONSERVATION STATUS: Whereas populations on Nosy Be appear to be stable for the time being (Loiselle, 2005), mainland populations are threatened by rampant deforestation and habitat degradation or destruction throughout their range. Diversion of water for large-scale irrigation projects poses a particular threat to the populations of this species in the basins of the Mananjeba and the Mahavavy du Nord (Loiselle in litt.).

LOCAL NAME: *Ptychochromis oligacanthus* is commonly referred to by the Malagasy names *tsipoy* and *saroy*, the latter of which is also widely used throughout (primarily eastern) Madagascar to refer to species of *Ptychochromis*.

ETYMOLOGY: The Latin *oligacanthus*, "few spines", refers to the reduced number of dorsal-fin spines of the species (originally described as a *Tilapia*) when compared with most other nominal *Tilapia* known at the time of Bleeker's description.

DISCUSSION AND COMPARISONS: In our phylogenetic analysis, *P. oligacanthus* is recovered in a "western clade" of *Ptychochromis*, also including *P. onilahy*, *P. insolitus*, and *P. inornatus*, all with distributions confined to western drainages (fig. 2). Morphologically, these species share the western-type palatine morphology. Within the "western clade", current data do not allow us to further resolve the placement of *P. oligacanthus*, which is recovered in a polytomy. In overall appearance *P. oligacanthus* is most similar to *P. onilahy* from which it is readily distinguished by lateral line scale count (29–31 vs. 33–34 in *P. onilahy*), some proportional measurements (e.g., HL 35.9–40.0% SL vs. 32.8–34.7% SL in *P. onilahy*), and details of pigmentation pattern and coloration.

Katria, new genus

DIAGNOSIS: A ptychochromin genus diagnosed by a unique pigmentation and coloration pattern consisting of two prominent black vertical bars on an iridescent golden background (plate 1H and 2F), the presence of reduced anterior gas bladder horns that do not approach or contact the exoccipital region of the neurocranium (*Character 17: 0*, fig. 3A), a reduced number of gill rakers on the lower limb of the first gill arch (8–9 [mode 8] vs. 8–12 [mode 10] in other ptychochromins), an elevated vertebral count (29–30 [mode 30] vs. 26–28 [mode 27] in *Ptychochromis*), and a more slender caudal peduncle (length to depth ratio modally 1.4 vs. 0.6–1.2 in *Ptychochromis* and *Ptychochromoides*). *Katria* is readily differentiated from *Ptychochromoides* by the presence of two toothrows (fig. 7B) on Pb2 (vs. 1; *Character 19:1*), and from *Ptychochromis* by the absence (fig. 7B) of a "free" toothplate associated with Ep2 (vs. presence of "free" Ep2 toothplate; *Character 10:1*, Fig 7A).

TYPE SPECIES: *Katria katria* (Reinthal and Stiassny, 1997); by monotypy.

REMARKS: At the time of its original description, Reinthal and Stiassny (1997) were unable to provide unambiguous morphological support for their placement of *katria* in the genus *Ptychochromoides*. They proposed that the presence of a pronounced nuchal hump in adult *katria* and in *Ptychochromoides*, and the possession of an elevated vertebral count (relative to that of *Ptychochromis*) were suggestive of relationship, but cautioned that "further systematic analysis may necessitate an eventual reassignment and generic reorganization". The molecular analyses of Sparks (2004) and Sparks and Smith (2004) provide strong support for the placement of *Ptychochromoides katria* as the sister taxon to a monophyletic *Ptychochromis* (e.g., in the study of Sparks and Smith [2004], which comprised fragments of two mitochondrial and two nuclear genes, this sister group relationship is robustly supported [Bremer support: 11; jackknife 100%]). The current study corroborates that placement and, consequently, we remove *katria* from *Ptychochromoides* and place it in *Katria* new genus. Uniquely among ptychochromins, *Katria* shares with *Ptychochromis* the following synapomorphic features: Cb4 bears a characteristically elongate process and deeply rounded indentation on its inner margin (fig. 4C; *Character 6:1*); hypertrophy of the laterosensory canal system of the neurocranium, preopercle, mandible, and infraorbital series (*Character 7:1*, fig. 8E); two supraneural elements located anterior to the first neural spine (fig. 3A; *Character 8:1*); and a well-developed, expansive and dorsally elevated lateral ethmoid process on the dorsal margin of the palatine head (fig. 6E; *Character 9:1*). *Katria* lacks the four apomorphic features identified herein as diagnostic of its sister taxon, *Ptychochromis* (i.e., presence of a "free" toothplate associated with Ep2, *Character 10:1*; IO2 excluded from the orbit by IO3, *Character 11:1*; presence of a palatine groove, *Character 12:1*; ventral displacement of the palato-palatine ligament insertion, *Character 13:1*).

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APPENDIX 1

Collection Localities, Original Source/Citation, and GenBank Accession Numbers for Taxa Included in This Study

Species	Original source	16S	COI	Tmo-4C4	Histone H3
Etroplinae					
Paretroplus damii	Sparks, 2004	AY263827	AY263856	AY662820	AY662894
Ptychochrominae					
Katria katria	Sparks, 2004	AY263814	AY263880	AY662840	AY662915
Oxylapia polli	Sparks, 2004	AY263817	AY263881	AY662832	AY662907
Paratilapia polleni "Lake Ravelobe"	Sparks & Smith, 2004	AY662720	AY662772	AY662835	AY662910
Ptychochromoides betsileanus	Sparks, 2004	AY263815	AY263882	AY662838	AY662913
Ptychochromoides vondrozo	Sparks, 2004	AY263816	AY263883	AY662839	AY662914
Ptychochromis grandidieri	Sparks, 2004	AY263811	AY263878	AY662841	AY662916
Ptychochromis inornatus	Sparks, 2004	AY263812	AY263875	AY662842	AY662917
Ptychochromis oligacanthus "Nosy Be"	Sparks, 2004	AY263813	AY263873	AY662843	AY662918
Ptychochromis loisellei n. sp.	Sparks & Smith, 2004	AY662723	AY662776	AY662845	AY662920
Ptychochromis makira n. sp.	Sparks & Smith, 2004	AY662724	AY662775	AY662846	AY662921
Ptychochromis insolitus n. sp.	Sparks & Smith, 2004	AY662725	AY662777	AY662847	AY662922
Cichlinae					
Retroculus xinguensis	Aquarium Trade	AY662733	AY662784	AY662857	AY662934
Pseudocrenilabrinae					
Heterochromis multidens	Farias et al., 1999, 2000	AF048996	Unavailable	AF113060	Unavailable

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