

Article

Who Is Who in *Rubricatochromis* Lamboj & Koblmüller, 2022 (Cichliformes, Cichlidae): Taxonomic Revision with Description of Four New Species and Revalidation of *R. fugax*

Anton Lamboj ^{1,*} and Stephan Koblmüller ^{2,*,†} 

¹ Division Integrative Zoology, Department of Evolutionary Biology, University of Vienna, Djerassiplatz 1, 1030 Vienna, Austria

² Institute of Biology, University of Graz, Universitätsplatz 2, 8010 Graz, Austria

* Correspondence: anton.lamboj@univie.ac.at (A.L.); stephan.koblmueeller@uni-graz.at (S.K.)

† ZooBank: LSID urn:lsid:zoobank.org:pub:C5F34CEE-D97F-4C03-87B1-CFEE682ECEAD.

Abstract

Cichlid fishes of the genus *Rubricatochromis* are widely distributed across western, central, and northern Africa, yet their taxonomy has long remained unstable because of overlapping morphological characters, variable coloration, and inconsistent use of species names. We present an integrative taxonomic revision of the genus based on mitochondrial DNA sequence data, molecular species delimitation analyses, morphometric and meristic analyses, qualitative assessment of live coloration, and a previously published multi-locus phylogeny. Phylogenetic analyses recovered several deeply divergent lineages, some of which had already been informally recognized in the aquarium trade. Although morphological overlap among species was substantial, several taxa could be diagnosed by combinations of morphometric traits and coloration patterns. We describe four new species, *Rubricatochromis gabonensis* sp. nov., *R. jebeli* sp. nov., *R. stephenthorntoni* sp. nov., and *R. vanheusdeni* sp. nov.; validate *R. fugax*; and synonymize *R. exsul*, *R. letourneuxi*, *R. paynei*, and *R. saharae* with *R. guttatus*, as well as *R. lifalili* with *R. stellifer*. Several newly recognized taxa appear to have highly restricted distributions and may qualify as threatened, emphasizing the conservation importance of West and Central African river systems and the urgent need for biodiversity assessments and habitat protection in these understudied regions.

Keywords: Africa; cichlid fish; Cichlidae; integrative taxonomy; jewel cichlids

Key Contribution: This study provides a taxonomic revision of the cichlid genus *Rubricatochromis* based on an integrative approach including genetic, morphometric, and meristic data, as well as body coloration.



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1. Introduction

African cichlid fishes (Actinopterygii, Cichlidae, Pseudocrenilabrinae) represent one of the most species-rich vertebrate lineages, yet scientific attention has been disproportionately focused on the spectacular adaptive radiations of the East African Great Lakes, which have become textbook examples for rapid speciation, sexual selection, and ecological diversification [1,2]. In contrast, the riverine cichlid faunas of Africa—although often older, taxonomically complex, and important for our general understanding of African cichlid evolution—remained, for a long time, comparatively understudied and largely

neglected [3,4]. These riverine and non-Great Lake lineages, however, have contributed a lot to our understanding of paleohydrological connections among African drainage systems, as their distributions and phylogenetic relationships often reflect historical river capture events, basin fragmentation, and climatic oscillations across the continent [5–9]. Among these riverine and non-Great Lake lacustrine taxa, the jewel cichlids of the genus *Rubricatochromis* stand out both for their wide distribution across West and Central Africa and for their prominence in the ornamental fish trade [10,11].

The genus *Rubricatochromis* Lamboj & Koblmüller was erected in 2022 following an integrative taxonomic revision of the genus *Hemichromis* Peters, 1858, based on the analysis of mitochondrial and nuclear DNA sequence data, morphometric and meristic data, and qualitative assessments of body coloration [12]. That study demonstrated that *Rubricatochromis* and *Hemichromis* diverged approximately 6–12 million years ago, supporting the recognition of two distinct evolutionary lineages. While the primary focus of that study was the genus *Hemichromis*, four well-supported clades were identified within *Rubricatochromis*, indicating substantial intrageneric structure and suggesting the presence of cryptic or previously unrecognized species diversity.

Based largely on the revision (primarily based on dentition, squamation patterns, and coloration) by Loiselle [10], eight described species are currently assigned to *Rubricatochromis*: *R. bimaculatus* (Gill, 1862), *R. cerasogaster* (Boulenger, 1898), *R. cristatus* (Loiselle, 1979), *R. guttatus* (Günther, 1862), *R. letourneuxi* (Sauvage, 1880), *R. lifalili* (Loiselle, 1979), *R. paynei* (Loiselle, 1979), and *R. stellifer* (Loiselle, 1979). A number of synonymies were proposed by this revision [10], treating *R. fugax* (Payne & Trewavas, 1976) as a junior synonym of *R. bimaculatus*, and *R. exsul* (Trewavas, 1933), *R. rolandi* (Sauvage, 1881), and *R. saharae* (Sauvage, 1880) as junior synonyms of *R. letourneuxi*. Several undescribed species have been recognized over the last decades, particularly from Upper Guinean drainages.

Despite its thoroughness, Loiselle's revision [10] has been inconsistently applied in subsequent literature. Species diagnoses have often been ignored or misinterpreted, particularly in studies based on preserved material, where coloration—a key diagnostic trait—cannot be adequately assessed. In the aquarist literature and in behavioral studies, misidentifications based solely on coloration are common, and the validity of several of Loiselle's synonymies has been repeatedly questioned [11,13]. This persistent confusion underscores the need for an integrative reassessment combining molecular and morphological evidence.

Species of *Rubricatochromis* are notably similar in overall morphology, rendering identification difficult in many cases. As in other cichlid lineages where coloration plays a major role in species recognition—such as the Lake Malawi cichlid genus *Diplotaxodon* [14] or the Lake Tanganyika genus *Tropheus* [15]—morphometric and meristic differences in *Rubricatochromis* are often subtle, and individual characters are often overlapping. Color patterns overlap extensively among some nominal species, most notably *R. guttatus* and *R. letourneuxi*. These two taxa cannot be reliably distinguished using available mitochondrial and nuclear DNA sequence data, nor by morphometric or meristic characters, casting serious doubt on their status as separate species [12]. In contrast, *R. cerasogaster* is readily distinguished from all congeners by the presence of two or three complete rows of teeth in each jaw and one incomplete inner row in one or both jaws in some specimens, compared to a single complete row of teeth and one incomplete inner row in one or both jaws in all other species [16].

The phylogenetic relationships and true species diversity within *Rubricatochromis* therefore remain incompletely understood. In a recently published molecular framework [12], several nominal species were not recovered as monophyletic. Two undescribed taxa, provisionally referred to as *R. sp.* ‘Guinea 1’ and *R. sp.* ‘Guinea 2’, formed a well-supported and distinct clade, underscoring the presence of previously unrecognized diversity within the genus.

In the present study, we provide a comprehensive revision of *Rubricatochromis*, building upon the molecular data (mitochondrial and nuclear sequence data) in [12], complemented by mitochondrial data for additional specimens, as well as detailed analyses of morphology and a qualitative assessment of body coloration. We provide revised diagnoses for all recognized species, describe four new species, and revalidate *R. fugax*. Finally, we include genetic data from populations established in thermal springs in Europe and North America, and also from India—originating from released aquarium specimens—to clarify their species identity.

2. Materials and Methods

2.1. Phylogenetic Analysis and Molecular Species Delimitation

The phylogenetic analyses are based on 159 *Rubricatochromis* samples collected by one of the authors (A.L.) between 1993 and 2023 under the respective permits (FD/PAO/9/V.6/337/93, Ministry of Agriculture, Fisheries Department, Accra, Ghana; 003/11-7/MRST/D00/D20, Ministère de la Recherche Scientifique et Technique, Yaounde, Cameroon; AR034/22/MESRITTCA/CENAREST/CG/CST/CSAR, Ministère de l’Enseignement supérieur de la Recherche Scientifique, du Transit des Technologies, de la Culture et des Arts, Centre National de la Recherche Scientifique et Technologique, Institut de Recherches Agronomiques et Forestières, Gabon). The fish were caught with hand nets or cast nets and euthanized with an overdose of MS222. Fin clips were immediately put in >95% undenatured ethanol; voucher specimens were preserved in either 70% denatured ethanol or 10% formaldehyde, unless imported alive for qualitative characterization of body coloration. Further samples were provided by A. Mansaray from Nyala University in Sierra Leone, T. Minesi and G. Bondoka-Akwalembale (Democratic Republic of the Congo), or obtained from museum collections (Table S1).

Extraction of whole genomic DNA from fin clips was done using a Chelex 100 method [17] or the Qiagen Blood & Tissue kit (Qiagen, Hilden, Germany) following the manufacturer’s instructions. PCR amplification and sequencing of partial mitochondrial cytochrome c oxidase subunit I (COI) gene fragments followed the protocol in [18], using the primers FishF1 and FishR2 [19]. PCR products were visualized on an ABI 3500 XL Genetic Analyzer (Thermo Fisher Scientific, Waltham, MA, USA). Sequence chromatograms were inspected and edited in MEGA11 [20]. In addition, DNA sequences from several previously published studies [12,21–25] and unpublished studies were downloaded from GenBank and BOLD, respectively, or were provided by J. Freyhof from the Museum für Naturkunde, Leibniz Institute for Evolution and Biodiversity Science, Berlin, Germany (Table S1).

Multiple sequence alignment was performed with MUSCLE [26]. Phylogenetic tree inference, using four species of the genus *Hemichromis* as outgroup, employed maximum likelihood (ML) and Bayesian inference (BI) in IQ-TREE 1.6.8 [27] and MrBayes 3.2.6 [28] plugins of the PhyloSuite 1.2.2 package [29]. The best-fitting model of sequence evolution was selected using ModelFinder [30] under the Bayesian Information Criterion (BIC). The ML analysis included 10,000 ultrafast bootstrap replicates to assess branch support. BI analyses consisted of two independent runs of 30 million generations each, with eight chains per run and sampling every 1000 generations. The first 25% of trees were discarded as burn-

in. Convergence was evaluated in MrBayes based on the average standard deviation of split frequencies (<0.01). Effective sample sizes (ESS) and parameter mixing were assessed in Tracer [31], with all parameters exceeding ESS values of 200, indicating adequate posterior sampling [32]. The two runs converged on similar posterior distributions, and trace plots showed no evidence of non-stationarity. Tree visualization was done in iTOL v.7 [33].

For molecular species delimitation, several methods were employed. The distance-based method ASAP [34] was used via iTaxonTools 1.0 [35]. Furthermore, two tree-based approaches, PTP [36] and GMYC [37], were applied. The PTP analysis was performed on the PTP web server (<http://species.h-its.org/ptp>, accessed on 16 February 2026) using default single-threshold settings and the ML tree as input. For the GMYC analysis, an ultrametric tree was inferred in BEAST 2.7.3 [38], employing model averaging with bModelTest, an optimized relaxed clock model, and, following the recommendations of [39], a birth–death tree prior. Three independent MCMC runs were conducted for 50 million generations each, sampling every 2000 generations. After examination of trace plots and confirmation that all relevant parameters achieved ESS values >200 in Tracer, the first 10% of trees were discarded as burn-in. A maximum clade credibility (MCC) tree was generated in TreeAnnotator (part of the BEAST 2 package) and used as input for single-threshold (sGMYC) analysis on the GMYC web server (<http://species.h-its.org/gmyc>, accessed on 5 March 2026).

2.2. Morphology and Live Coloration

A total of 413 specimens representing 10 species of *Rubricatochromis* from various museum collections were examined for morphological analyses. In total, 22 meristic characters and 25 morphometric measurements were recorded following [40]: upper lateral line scales, lower lateral line scales, scale rows between upper and lower lateral line, total scales of lateral line, scales on caudal fin, scales around caudal peduncle, scale rows between origin of pectoral and pelvic fin, scale rows on cheek, scale rows on opercle, spines in dorsal fin, rays in dorsal fin, spines in anal fin, rays in anal fin, rays in pectoral fin, spines in pelvic fin, rays in pelvic fin, gill rakers on first ceratobranchial, gill rakers on first epibranchial, gill rakers on first pharyngobranchial, gill rakers on first outer branch, tooth rows in upper jaw, tooth rows in lower jaw, standard length, body depth, head length, head depth, snout length, eye diameter, postorbital length, mouth width, interorbital width, length of dentigerous arm of premaxilla, lower jaw length, cheek depth, preorbital distance, caudal peduncle length, caudal peduncle depth, predorsal length, preanal length, prepectoral length, prepelvic length, dorsal fin base, anal fin base, longest dorsal fin ray, longest anal fin ray, longest pectoral fin ray, longest pelvic fin ray. All measurements were taken on the left side of each specimen using digital calipers to the nearest 0.03 mm. The morphometric and meristic raw data are available in Tables S2–S5.

To visualize patterns of morphological variation among individuals and putative species, Principal Component Analyses (PCA) were performed in PAST [41]. Analyses of meristic characters were based on the correlation matrix, whereas morphometric analyses were conducted on the covariance matrix of residuals obtained from regressions of log-transformed measurements on log-transformed standard length (SL), thereby minimizing allometric effects [42]. Morphological variation was explored using the first four principal components (PCs) for both meristic and morphometric datasets. Separate PCAs were done on the full morphometric and the full meristic dataset. Invariant meristic characters were excluded, as were specimens with missing values for any count or measurement. Permutational multivariate analyses of variance (PERMANOVA; 9999 permutations) were used to test for significant separation of species in morphospace. Separate PERMANOVAs were performed on the morphometric and meristic datasets. In addition, linear discriminant analyses (LDA), implemented in PAST, were applied to both datasets to evaluate the

morphological diagnosability of genetically distinct groups. Classification success was assessed using a jackknife (leave-one-out) cross-validation procedure.

Finally, live specimens collected by one of the authors (A.L.), obtained from collaborators in Africa, or imported through the ornamental fish trade were examined qualitatively to assess live coloration patterns. With the exception of specimens assigned to *R. sp. "neon"*, these individuals were not included in the genetic dataset. Aquarium specimens were excluded from morphometric analyses, as body proportions may be influenced by conditions in captivity (e.g., [43]).

Abbreviations used throughout the text are SL: standard length; HL: head length. Institutional abbreviations used are AMNH, American Museum of Natural History, New York; BMNH, British Museum (Natural History), London; MNHN, Muséum National d'Histoire Naturelle, Paris; MRAC, Musée Royal de l'Afrique Centrale, Tervuren; NMW, Naturhistorisches Museum, Wien; SAIAB, South African Institute for Aquatic Biodiversity, Grahamstown; USNM, Smithsonian Institution, National Museum of Natural History, Washington; UVZC, University Vienna Zoological Collection, Wien; ZMHU, Zoologisches Museum der Humboldt Universität Berlin, Berlin; ZSM, Zoologische Staatssammlung München, Munich.

3. Results

3.1. Phylogenetic Analysis and Molecular Species Delimitation

Phylogenetic inference using maximum likelihood (ML) and Bayesian inference (BI) yielded highly congruent tree topologies with strong support for most major clades (ML tree shown in Figure 1), corroborating the results of [12], which were based on two mitochondrial and two nuclear loci, but with more limited taxon sampling. Across numerous West and North African samples (*R. exsul*, *R. guttatus*, *R. letourneuxi*, *R. paynei*, *R. saharae*), only minimal genetic divergence was detected, with widespread haplotype sharing observed over large geographic distances, indicating very little phylogeographic structuring within this clade. In contrast, *R. bimaculatus*, *R. cristatus*, *R. fugax*, and three previously undescribed species from Guinea and Ghana—known in the aquarium trade as *R. sp. 'Guinea 1'*, *R. sp. 'Guinea 2'*, and *R. sp. 'Ankasa'*—were recovered as well-supported, distinct clades that are markedly divergent from other West African samples, suggesting a higher degree of lineage differentiation in this region than previously recognized. The Central African species *R. lifalili* and *R. stellifer* were recovered in two clades that are not reciprocally monophyletic. *Rubricatochromis cerasogaster* branched off first (albeit with low statistical support) in one of these clades.

Molecular species delimitation analyses using ASAP, PTP, and GMYC identified eight, 13, and nine molecular operational taxonomic units (MOTUs), respectively, highlighting considerable variation among methods (Figure 1). In general, results were consistent, but GMYC analysis further subdivided one of the Central African clades into two MOTUs, while PTP produced an even finer partitioning within the Central African clades, reflecting its tendency to delimit more narrowly defined lineages in single gene/DNA barcoding datasets (also see, e.g., [47,48]).

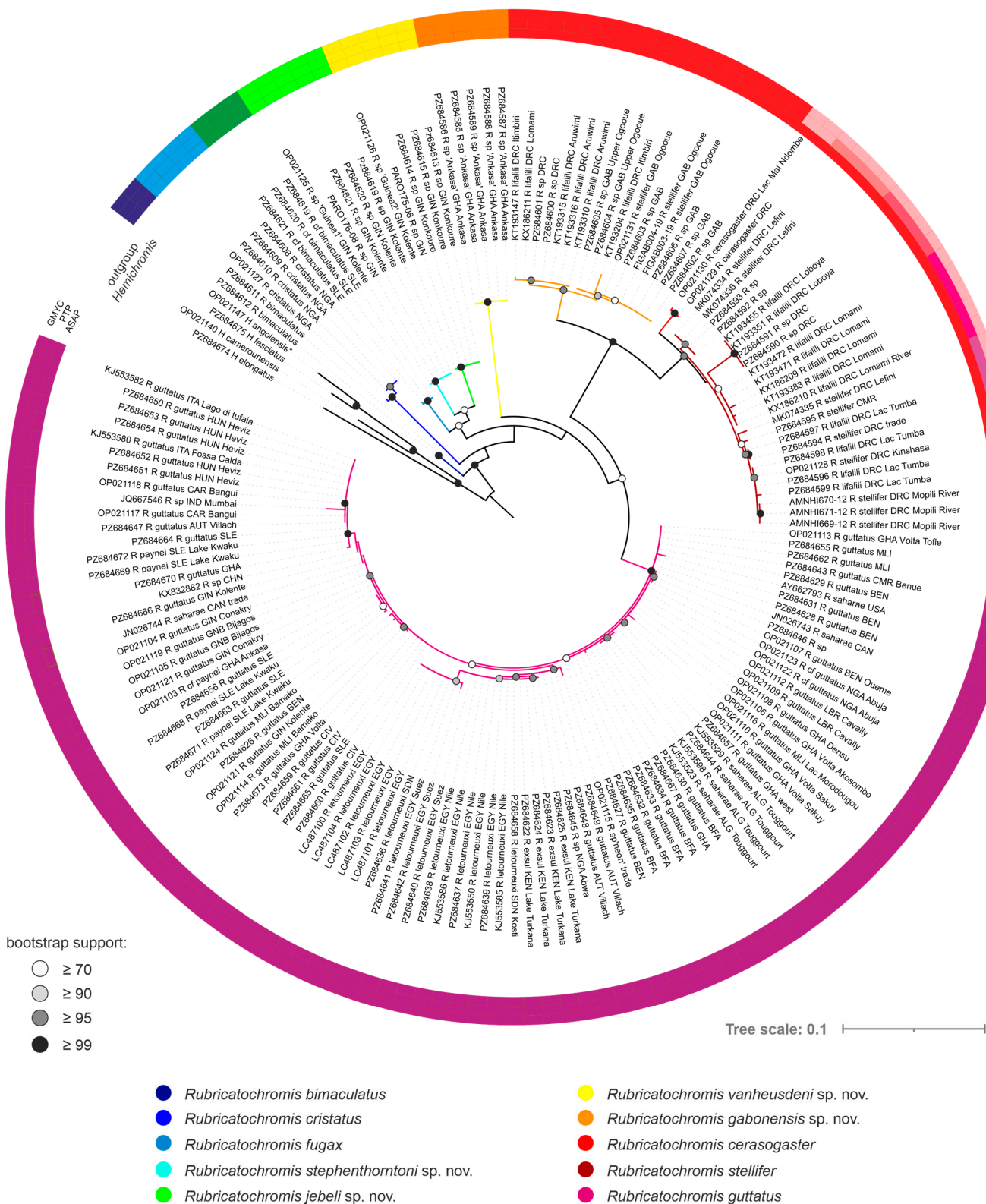


Figure 1. Maximum-likelihood (ML) phylogeny of *Rubricatochromis*, based on mitochondrial COI sequences. Molecular operational taxonomic units (MOTUs) inferred by different species delimitation methods (ASAP, PTP, GMYC) are indicated by different colors. Tree branches are colored according to final species assignment. Sample labels include GenBank accession number (or BOLD-ID), original species identification and, where available, country code and sampling locality or region. * For discussion on the validity of this species, see refs. [44–46].

3.2. Morphology

Both the morphometric and meristic PCAs based on the full dataset separated some species; however, all groups showed substantial overlap with *R. guttatus* (Figures 2 and 3).

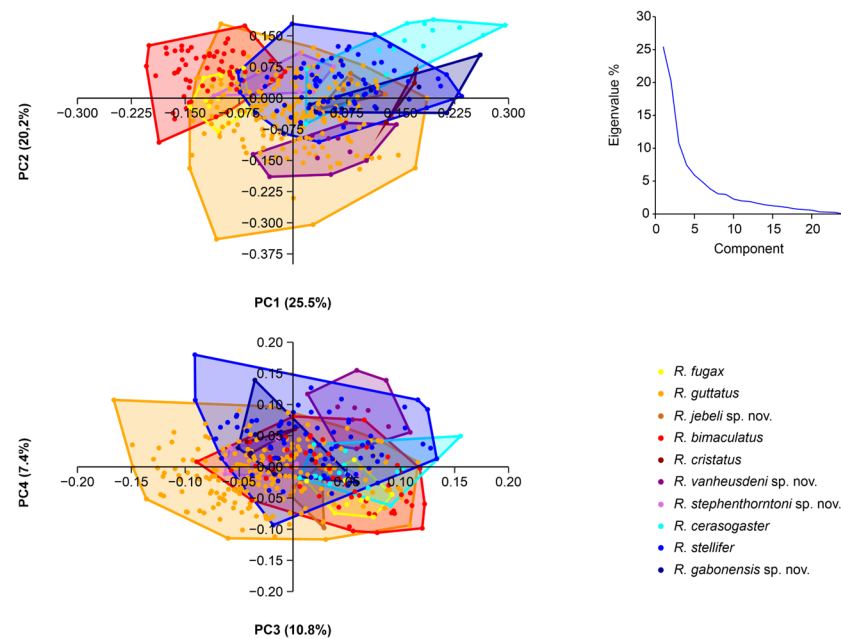


Figure 2. Scatterplots of the scores on the principal components based on the morphometric data of the entire dataset. The Scree plot (small inset to the **right**) shows how much of the total variation is explained by the different components.

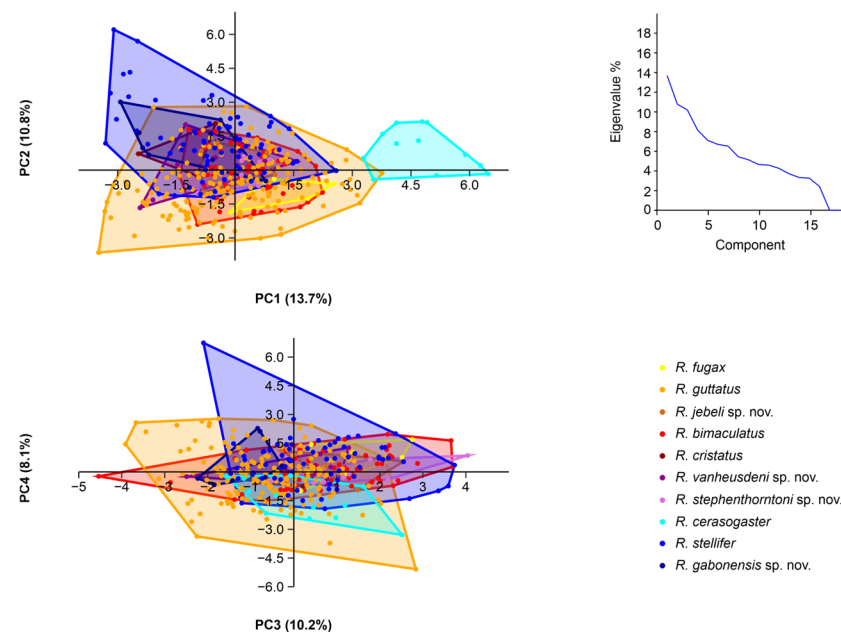


Figure 3. Scatterplots of the scores on the principal components based on the meristic data of the entire dataset. The Scree plot (small inset to the **right**) shows how much of the total variation is explained by the different components.

In the morphometric PCA, the first four principal components (PCs) explained 63.9% of the total variation (Figure 2; scree plot). PC1 accounted for 25.5% of the variation and was characterized by high positive loadings for the length of the longest dorsal, anal, and caudal fin rays. PC2 showed particularly high positive loadings for snout length, mouth width, and preorbital distance. PC3 had high positive loadings for preorbital distance

and caudal peduncle length, and a particularly strong negative loading for mouth width. PC4 was characterized by high positive loadings for snout length, preorbital distance, and body depth, and high negative loadings for the length of the dentigerous arm of the premaxilla, lower jaw length, and cheek depth, and a high negative loading for the length of the longest dorsal fin ray (Table S6). PERMANOVA indicated significant differences among species ($F = 18.06$; $p < 0.0001$), and, except for one, pairwise PERMANOVAs were also significant (Table S7). Linear discriminant analysis (LDA) based on the morphometric variables yielded a jackknifed classification accuracy of 82.25%; *R. cerasogaster*, *R. jebeli* sp. nov., and *R. vanheusdeni* sp. nov. were the only species of which all specimens were correctly classified.

In the meristic PCA, the first four PCs explained 44.8% of the total variation (Figure 3; scree plot). PC1 accounted for 13.7% of the variation and was characterized by high positive loadings for the number of gill rakers on the first ceratobranchial, gill rakers on the first outer branchial arch, and the number of tooth rows in the lower and upper jaws. PC2 showed high positive loadings for gill rakers on the first pharyngobranchial and high negative loadings for gill rakers on the first epibranchial. PC3 had high positive loadings for the number of lower lateral-line scales and dorsal-fin rays, and a high negative loading for the number of scale rows between the upper and lower lateral lines. PC4 was characterized by high positive loadings for total lateral-line scales, dorsal-fin spines, and gill rakers on the first pharyngobranchial (Table S8). PERMANOVA again revealed significant differences among species ($F = 8.39$; $p < 0.0001$), and most pairwise PERMANOVAs were significant (Table S9). LDA based on the meristic variables resulted in a jackknifed classification accuracy of 62.2%; *R. cerasogaster* was the only species for which all specimens were correctly classified.

Within *R. guttatus*, strong overlap among all previously recognized species (*R. exsul*, *R. guttatus*, *R. letourneuxi*, *R. paynei*, *R. saharae*) was observed in the PCA of both morphometric and meristic data, with the exception of the morphometric PCA, in which the two *R. saharae* individuals clustered together slightly apart from the remainder of the complex (Figure 4). In the morphometric PCA, the first four principal components (PCs) explained 59.5% of the total variation (Figure 4a; scree plot). PC1 accounted for 23.3% of the variation and was characterized by high positive loadings for the snout length and mouth width. PC2 showed high positive loadings for the length of the longest dorsal, pectoral, and ventral fin rays. PC3 had particularly high positive loadings for preorbital distance and caudal peduncle length. PC4 was characterized by high positive loadings for snout length and high negative loadings for snout length (Table S10). PERMANOVA indicated significant differences among species ($F = 5.03$; $p < 0.0001$), and pairwise PERMANOVAs were significant between the pairs *R. guttatus*/*R. paynei*, *R. guttatus*/*R. saharae*, *R. guttatus*/*R. letourneuxi*, *R. paynei*/*R. saharae* and *R. paynei*/*R. letourneuxi* (Table S11). LDA based on the morphometric variables yielded a jackknifed classification accuracy of 77.67%; *R. saharae* was the only species of which all specimens were correctly classified (only two specimens available).

In the meristic PCA, the first four PCs explained 45.3% of the total variation (Figure 4b; scree plot). PC1 accounted for 15.3% of the variation and was characterized by high positive loadings for gill rakers on the first ceratobranchial, gill rakers on the first pharyngobranchial, and gill rakers on the first outer branch, and high negative loadings for gill rakers on the first epibranchial. PC2 showed high positive loadings for upper lateral line scales, lower lateral line scales, and total scales of lateral line, and high negative loadings for scale rows between upper and lower lateral line. PC3 had high positive loadings for rays in the dorsal fin and rays in the anal fin, and high negative loadings for scale rows between upper and lower lateral line and the number of spines in the dorsal fin. PC4 had particularly

high positive loadings for total scales of the lateral line (Table S12). PERMANOVA again revealed significant differences among species ($F = 2.67$; $p = 0.0002$), and all pairwise tests were significant (Table S13). LDA based on the meristic variables resulted in a jackknifed classification accuracy of 59.8%; for none of the species were all specimens correctly classified. For *R. saharae*, no specimens with a sufficient number of usable meristic characters were available.

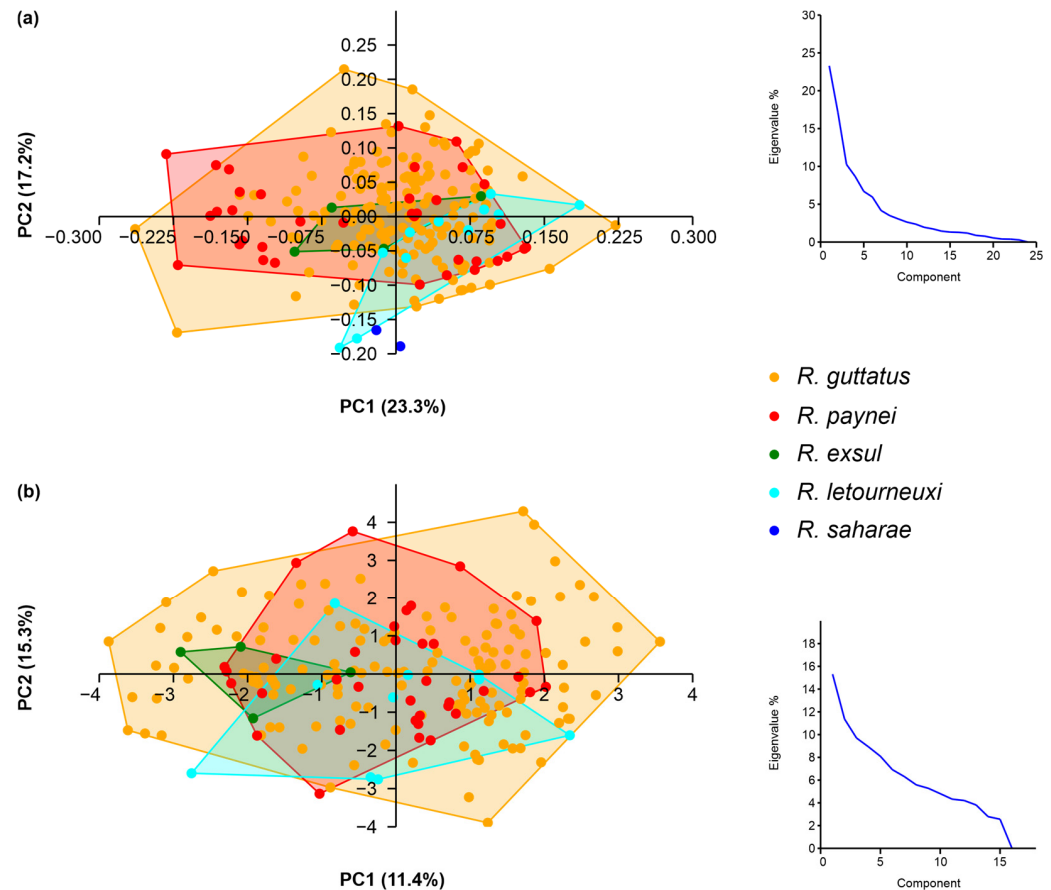


Figure 4. Scatterplots of the scores on the principal components based on the morphometric (a) and meristic data (b) of species that are synonymized with *R. guttatus* in the present study. The Scree plot (small inset to the right) shows how much of the total variation is explained by the different components.

In general, however, sample sizes per group were highly unbalanced (due to a lack of availability of specimens for some species), which likely affected our PERMANOVA results. Hence, significant PERMANOVA results should be regarded with caution.

Based on molecular phylogenetic analyses (also taking into account the combined mitochondrial and nuclear phylogenetic analysis by [12], morphological data, and coloration patterns in adult specimens, we recognize four new species herein. We revalidate *Rubricatichromis fugax* and synonymize *R. exsul*, *R. letourneuxi*, *R. paynei*, and *R. saharae* with *R. guttatus*, and *R. lifalili* with *R. stellifer*. Revised diagnoses are provided for all recognized species. Note: Previous genus-species combinations are listed under “Synonyms” where applicable.

Rubricatichromis gabonensis, new species

ZooBank: urn:lsid:zoobank.org:act:579372C8-45DA-4DC7-97B9-082F9E1085BE.

Holotype: MNHN 1906-227, Ogooué River at Ngomo; Gabon; Figure 5a.

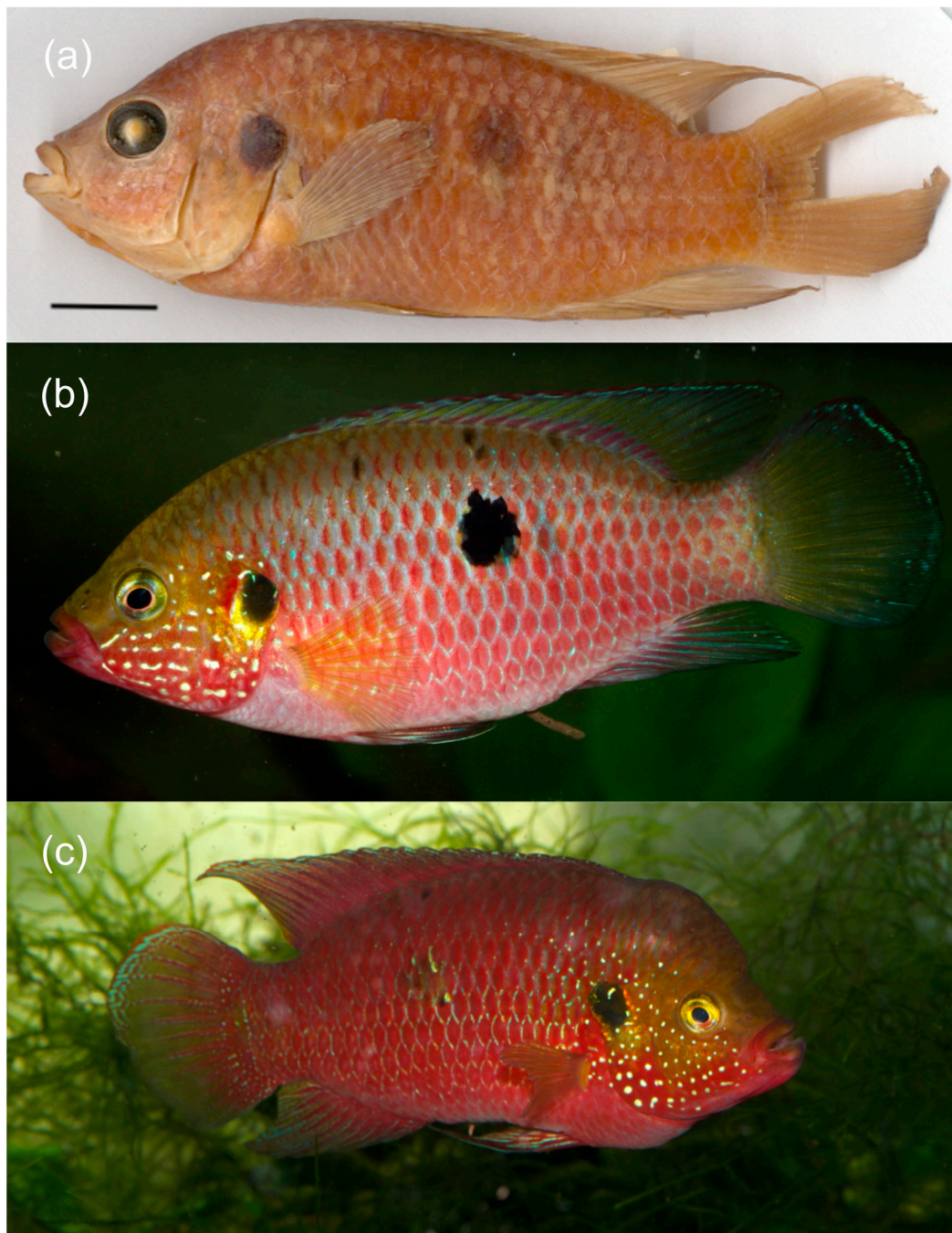


Figure 5. *Rubricatichromis gabonensis* sp. nov. (a) Holotype, MNHN 227, SL 79.9 mm, Gabon, Ogooué River at Ngomo, scale bar = 1 cm. (b) Semiadult male in an aquarium. Gabon, Menguengne (Ogooué River system), S 00°11.472', E 10°34.478'. (c) Adult, old male with a small hump on the forehead. Gabon, Fougamou (Nguinie, Ogooué River system). Both not preserved; not measured.

Paratypes: seven specimens, all Gabon; MNHN A-897, Ogooué River at Doumé; MNHN 1930-52, Ogooué River at Léconi.

All type specimens were previously included as paratypes of *H. stellifer* Loisel, 1979 (part, misidentification).

Diagnosis: The new species is distinguished from its congeners by a combination of morphometric characters and coloration patterns. It differs from *R. stellifer* by blue margins on body scales (vs. scales lacking margins but with blue centers) and in coloration of dominant or territorial individuals, which display red coloration over the en-

tire body (vs. reddish-orange ventrally and yellowish dorsally). It differs from *Rubricatichromis bimaculatus* by greater body depth (36.0–44.1% SL vs. 31.5–40.6% SL), longer dorsal-fin base (54.3–57.8% SL vs. 46.8–55.9% SL), shorter dentigerous arm of the premaxilla (19.9–28.7% HL vs. 27.4–35.0% HL), and shorter lower jaw (21.7–34.7% HL vs. 31.4–41.5% HL). From *R. cerasogaster* it differs by the presence of one complete inner tooth row in both jaws and one incomplete inner row in one or both jaws of some specimens (vs. two to three complete rows and one incomplete inner row), greater postorbital distance (42.4–48.2% HL vs. 39.4–43.6% HL), and the absence of black spots at the base of the dorsal fin. From *R. cristatus* it differs by a longer caudal peduncle (11.0–13.9% SL vs. 9.5–11.0% SL), shallower caudal peduncle (16.3–18.6% SL vs. 17.5–19.0% SL), shorter anal-fin base (18.6–21.2% SL vs. 21.8–23.2% SL), and a caudal peduncle length corresponding to 59.8–76.8% of its depth (vs. 53.4–57.9%). It further differs in lacking the pale or yellow ring surrounding the black lateral blotch and the yellowish midlateral band present in that species. It differs from *R. fugax* by greater body depth (36.0–44.1% SL vs. 31.0–37.5% SL), greater caudal peduncle depth (16.3–18.6% SL vs. 14.2–16.9% SL), longer anal-fin base (18.6–21.2% SL vs. 16.5–17.9% SL), greater head depth (55.1–69.6% HL vs. 51.3–58.2% HL), shorter dentigerous arm of the premaxilla (19.9–28.7% HL vs. 25.4–32.9% HL), and shorter lower jaw (21.7–34.7% HL vs. 37.5–41.9% HL). The caudal peduncle length corresponds to 59.8–76.8% of its depth (vs. 73.7–94.6%). It differs from *R. guttatus* in having blue margins on the body scales (vs. scales lacking margins but with blue centers). From *R. jebeli* sp. nov. it differs by greater predorsal distance (32.5–34.7% SL vs. 29.7–32.3% SL), greater prepectoral distance (37.0–42.1% SL vs. 36.8–38.3% SL), shorter dentigerous arm of the premaxilla (19.9–28.7% HL vs. 29.4–31.6% HL), and shorter lower jaw (21.7–34.7% HL vs. 36.3–39.6% HL). It differs from *R. stephenthorntoni* sp. nov. by a longer caudal peduncle (11.0–13.9% SL vs. 10.5–11.9% SL), shorter dentigerous arm of the premaxilla (19.9–28.7% HL vs. 27.1–30.7% HL), shorter lower jaw (21.7–34.7% HL vs. 34.6–38.8% HL), and by the absence of a black midlateral vertical bar extending into the dorsal fin. It differs from *R. vanheusdeni* sp. nov. by greater predorsal distance (32.5–34.7% SL vs. 28.6–32.4% SL) and a somewhat shorter lower jaw (21.7–34.7% HL vs. 32.4–36.4% HL).

Description: Measurements and meristic counts for the holotype and seven paratypes are presented in Table 1.

Body deep, ovoid, and laterally compressed; greatest body depth at midbody. Sexual dimorphism weakly expressed; females are approximately 10–15% smaller than males. The first pelvic-fin ray is usually the longest in both sexes. Snout short and moderately pointed (25.3–32.2% HL). Caudal fin rounded to moderately truncate. Caudal peduncle laterally compressed and shorter than deep (59.8–76.8% of caudal peduncle depth). Large males may develop a small nuchal hump.

Osteology and dentition: Infraorbital series complete, consisting of a plate-like first infraorbital followed by five tubular elements. Infraorbital series with four openings of the laterosensory canal. Outer tooth row complete in both jaws; inner row absent or incomplete, usually represented by a few teeth restricted to the anterior portion of the jaws. Anteriormost teeth of the premaxilla slightly enlarged.

Gill rakers on first gill arch: First gill arch with six pointed to moderately tuberculate rakers on the lower limb and 2–3 pointed rakers on the pharyngobranchial. Microbranchiospines absent.

Squamation: Scales cycloid. Cheek with three scale rows; opercle with four horizontal rows. Dark spot on the outer margin of the opercle, unscaled. 5–6 scales between the bases of the pelvic and pectoral fins. Upper lateral line separated from dorsal-fin base at its highest point (8th pored scale) by 2–2.5 scales, and by 1–2 scales at its posterior end. Distance between the end of the upper lateral line and the end of the lower lateral line:

0–4 scales. Caudal fin scaled basally for approximately one third to one half of its length; other fins unscaled.

Coloration in life (Figure 5b,c): Body pale brown with a rosy hue in juvenile or subdominant individuals. Dominant or territorial specimens exhibit intense red coloration over the body, with blue margins on the scales. Anterior part of head orange-brown to red; cheeks and opercles red with numerous blue spots. An ovoid to circular black lateral blotch present in most individuals and behavioral states. A vertically elongated to circular black blotch at the base of the caudal fin, often fading in large specimens. A black opercular spot present at the posterodorsal margin of the opercle. Fins pale yellowish to reddish, with stronger red coloration at the base of the unpaired fins. Dorsal fin and upper part of caudal fin with a thin red to orange marginal band followed by a blue submarginal band. Posterior margins of pelvic fins with bluish bands. Small black spots may occur on the dorsum in some individuals.

Table 1. Morphometrics and meristics of the holotype and the type series (holotype plus seven paratypes) of *Rubricatochromis gabonensis* sp. nov.

Morphometrics	Holotype	Mean	s.d.	Range
standard length (mm)	79.9	54.9		38.2–79.9
body depth ¹	39.3	40.1	2.4	36.0–44.1
head length ¹	36.6	36.9	1.1	35.4–38.5
caudal peduncle length ¹	13.9	12.4	0.9	11.0–13.9
caudal peduncle depth ¹	18.1	17.6	0.7	16.3–18.6
length of dorsal fin base ¹	56.7	56.2	1.1	54.3–57.8
length of anal fin base ¹	20.2	20.1	0.9	18.6–21.2
predorsal distance ¹	33.5	33.4	0.8	32.5–34.7
preanal distance ¹	69.2	69.6	2.4	68.0–75.2
prepectoral distance ¹	38.0	38.9	1.7	37.0–42.1
prepelvic distance ¹	43.3	42.0	1.2	40.9–43.7
head depth ²	65.0	61.0	4.7	55.1–69.6
snout length ²	32.2	27.7	2.4	25.3–32.2
eye diameter ²	22.2	25.3	2.4	22.2–29.8
postorbital distance ²	45.3	46.0	1.9	42.4–48.2
interorbital distance ²	29.6	25.5	2.7	21.3–29.6
cheek depth ²	28.3	25.4	1.9	22.6–28.3
premaxilla length ²	26.7	25.7	2.8	19.9–28.7
lower jaw length ²	33.9	30.2	4.3	21.7–34.7
preorbital distance ²	13.6	13.3	0.9	11.8–14.5
caudal peduncle length ³	76.8	70.5	5.7	59.8–76.8
Meristics	Holotype	Median		Range
upper lateral line scales	18	16		14–18
lower lateral line scales	8	8		6–9
total lateral line scales	27	26		26–27
circumpeduncular scales	16	16		16
dorsal fine spines	15	14		14–15
dorsal fin rays	10	11		10–11
anal fin spines	3	3		3
anal fin rays	8	8		7–9
pectoral fin rays	13	13		12–13
gill rakers on lower limb of first arch	6	6		6
total gill rakers on first arch	9	9		8–9

¹, % of standard length; ², % of head length; ³, % of caudal peduncle depth.

Coloration in preserved specimens (Figure 5a): Overall coloration brown to olive. Iridescent markings on head and body not visible. Opercular spot always present; caudal peduncle spot visible in some specimens.

Distribution. Known from the Ogooué River system in Gabon, where it appears to be widespread from the upper to lower reaches of the drainage, as well as (based on genetic data only) from the Itimbiri, Lomami, and the Aruwimi systems in the D.R. Congo.

Etymology. The species name refers to its apparently endemic occurrence in Gabon.

Reproductive behavior. The species is a biparental open substrate spawner with brood guarding behavior.

Remarks. Specimens of this species were included in the type series of *Rubricatochromis stellifer* by Loiselle [10]. Doubts regarding their conspecificity were later expressed by Lamboj [11], mainly based on differences in coloration. Coloration of the Congolese specimens of *R. gabonensis* sp. nov. included in the present study is currently unknown.

***Rubricatochromis jebeli*, new species**

Other names: *Hemichromis* sp. 'Guinea 2', *H.* sp. 'Simballa'.

ZooBank: urn:lsid:zoobank.org:act:33025924-7E1B-40C1-9210-79B5BC3132C.

Holotype: MRAC 2018-005-P-03; coll. M. Traore, Guinea, Samou River, Kindia region. 09°52.045' N, 13°05.2589' W, elev. 205 m, 03/2008 (Figure 6a).

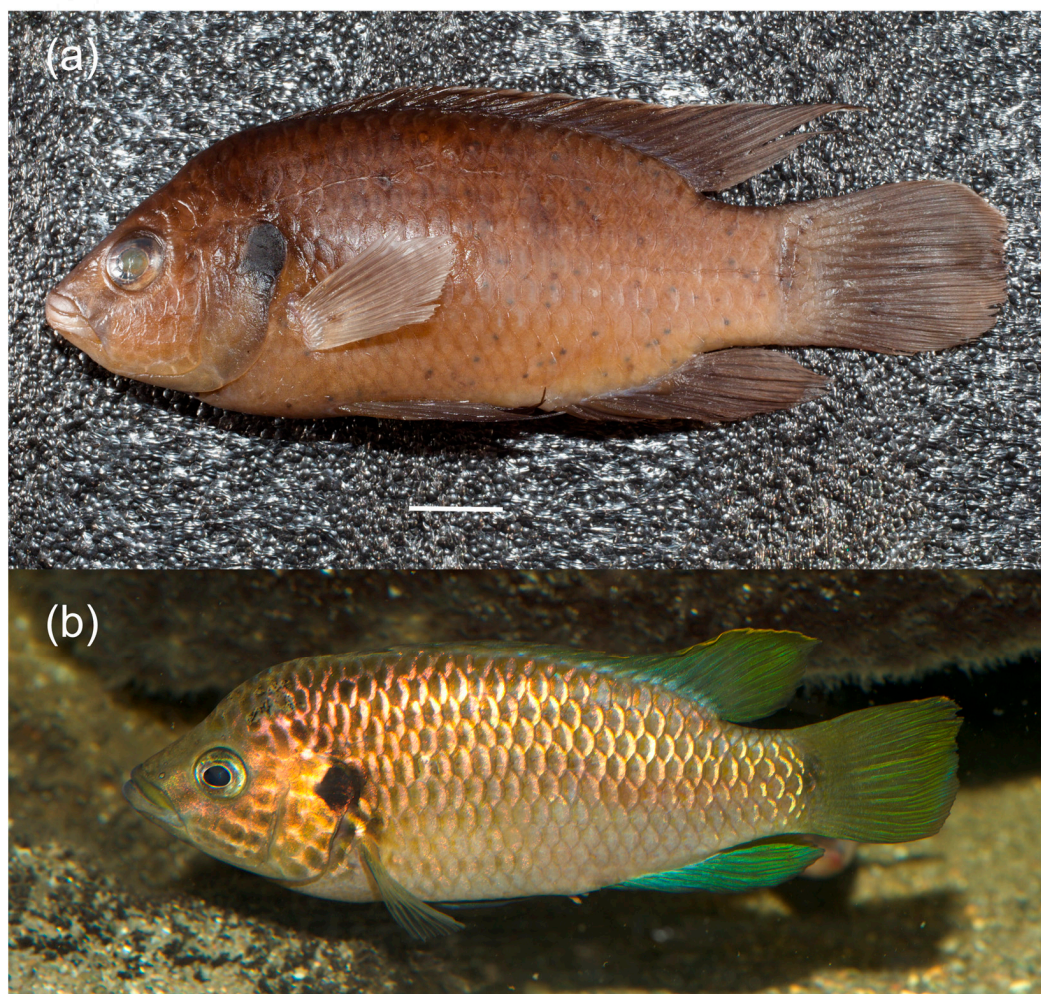


Figure 6. *Rubricatochromis jebeli* sp. nov. (a) Holotype, MRAC 2018-005-P-03, SL 85.2 mm, Guinea, Samou River, Kindia region, 09°52.045' N, 13°05.2589' W, scale bar = 1 cm. (b) Specimen of *R. jebeli* sp. nov. in an aquarium. Guinea, Samou River, not preserved, not measured.

Paratypes: four specimens, same data as holotype. AMNH 277412; BMNH 2024.1.31.10; MRAC 2018-005-P-0004; UVZC VZ5730.

Diagnosis: The new species is distinguished from all congeners by the complete absence of blue coloration on the head, body, and fins. It further differs from all congeners, except *R. gabonensis* sp. nov., in lacking red pigmentation on the body in both sexes and in having a vermiculate bronze-brown to golden pattern on the cheek and opercle (vs. blue patterns that are round, ovoid, or vermiculate in other species). From *R. bimaculatus* it differs by greater caudal peduncle depth (17.2–18.6% SL vs. 13.7–17.8% SL) and a caudal peduncle length corresponding to 56.6–71.5% of its depth (vs. 64.1–98.7%). It differs from *R. cerasogaster* by the presence of one complete tooth row in both jaws and one complete inner row in one or both jaws of some specimens (vs. two to three complete rows and one incomplete inner row), by a greater postorbital distance (42.4–48.2% HL vs. 39.4–43.6%) and the absence of black spots at the base of the dorsal fin. From *R. cristatus* it differs by lesser body depth (37.4–40.8% SL vs. 41.1–43.8% SL), longer dorsal-fin base (55.6–59.5% SL vs. 53.2–56.9% SL), shorter anal-fin base (19.4–21.5% SL vs. 21.8–23.2% SL), greater postorbital distance (44.3–46.5% HL vs. 43.0–43.9% HL), longer dentigerous arm of the premaxilla (29.4–31.6% HL vs. 24.2–27.4% HL), longer lower jaw (36.3–39.6% HL vs. 33.7–34.9% HL), greater cheek depth (26.4–30.7% HL vs. 20.4–22.7% HL), greater preorbital distance (13.6–15.2% HL vs. 11.8–13.5% HL), and a caudal peduncle length corresponding to 56.6–71.5% of its depth (vs. 53.5–57.9%). From *R. fugax* it differs by greater body depth (37.4–40.8% SL vs. 30.1–37.5% SL), longer dorsal-fin base (55.6–59.9% SL vs. 50.7–55.8% SL), longer anal-fin base (19.4–21.5% SL vs. 16.5–17.9% SL), shorter predorsal distance (29.7–32.3% SL vs. 32.1–36.1% SL), shorter prepelvic distance (36.8–38.3% SL vs. 37.9–43.9% SL), greater head depth (55.9–68.7% HL vs. 51.3–58.2% HL), greater cheek depth (26.4–30.7% HL vs. 22.0–27.1% HL), and a caudal peduncle length corresponding to 56.6–71.5% of its depth (vs. 73.7–94.6%). From *R. gabonensis* sp. nov. it differs by shorter predorsal distance (29.7–32.3% SL vs. 32.5–34.7% SL), shorter prepectoral distance (36.8–38.3% SL vs. 37.0–42.1% SL), longer dentigerous arm of the premaxilla (29.4–31.6% HL vs. 19.9–28.7% HL), and longer lower jaw (36.3–39.6% HL vs. 21.7–34.7% HL). From *R. stellifer*, it differs by a longer lower jaw (36.3–39.6% HL vs. 23.8–37.9% HL). From *R. stephenthorntoni* sp. nov. it differs by the absence of a black to dark bar or saddle on the dorsal body and dorsal fin, shorter predorsal distance (29.7–32.3% SL vs. 32.4–36.6% SL), shorter prepelvic distance (39.3–42.4% SL vs. 41.7–45.3% SL), longer dentigerous arm of the premaxilla (29.4–31.6% HL vs. 27.1–30.7% HL), and greater preorbital distance (13.6–15.2% HL vs. 12.7–14.3% HL). From *R. vanheusdeni* sp. nov. it differs by lesser body depth (37.4–40.8% SL vs. 40.5–43.9% SL), greater cheek depth (26.4–30.7% HL vs. 19.1–26.5% HL), longer dentigerous arm of the premaxilla (29.4–31.6% HL vs. 20.0–26.4% HL), and longer lower jaw (36.3–39.6% HL vs. 32.4–36.4% HL).

Description: Measurements and meristic counts for the holotype and four paratypes are provided in Table 2.

Body deep, ovoid, and laterally compressed, with greatest body depth at midbody. Sexual dimorphism weakly expressed; females approximately 10% smaller than males. The first pelvic-fin ray usually the longest in both sexes. Snout short and moderately pointed (27.2–29.6% HL). Caudal fin rounded to moderately truncate. Caudal peduncle laterally compressed and shorter than deep (56.6–71.5% of caudal peduncle depth).

Osteology and dentition: Infraorbital series complete, consisting of a plate-like first infraorbital followed by 3–5 tubular elements. Infraorbital series with four openings of the laterosensory canal. Outer tooth row complete in both jaws; inner row absent or incomplete and restricted to the anterior parts of the jaws. Anteriormost teeth of the premaxilla slightly enlarged.

Table 2. Morphometrics and meristics of the holotype and the type series (holotype plus four paratypes) of *Rubricatochromis jebeli* sp. nov.

Morphometrics	Holotype	Mean	s.d.	Range
standard length (mm)	85.2	77.1		65.1–85.2
body depth ¹	39.3	39.3	1.2	37.4–40.8
head length ¹	36.2	36.4	1.0	35.3–37.9
caudal peduncle length ¹	12.4	11.3	0.7	10.4–12.4
caudal peduncle depth ¹	17.3	17.9	0.7	17.2–18.6
length of dorsal fin base ¹	55.6	57.1	1.5	55.6–59.5
length of anal fin base ¹	19.4	20.3	0.9	19.4–21.5
predorsal distance ¹	30.3	31.2	1.2	29.7–32.3
preanal distance ¹	68.8	68.8	0.8	67.8–70.0
prepectoral distance ¹	36.8	37.3	0.7	36.8–38.3
prepelvic distance ¹	41.8	41.5	1.3	39.3–42.4
head depth ²	64.2	62.0	4.9	55.9–68.7
snout length ²	27.2	28.5	0.9	27.2–29.6
eye diameter ²	26.3	26.1	1.1	25.0–27.6
postorbital distance ²	46.5	45.4	1.0	44.3–46.5
interorbital distance ²	24.0	24.1	0.5	23.7–25.0
cheek depth ²	30.2	28.4	1.9	26.4–30.7
premaxilla length ²	31.6	30.3	1.1	29.4–31.6
lower jaw length ²	39.6	37.5	1.4	36.3–39.6
preorbital distance ²	14.4	14.6	0.7	13.6–15.2
caudal peduncle length ³	71.5	63.1	5.8	56.6–71.5
Meristics	Holotype	Median		Range
upper lateral line scales	16	17		16–17
lower lateral line scales	10	9		9–10
total lateral line scales	26	26		26–27
circumpeduncular scales	16	16		16
dorsal fin spines	14	14		14–15
dorsal fin rays	10	11		10–12
anal fin spines	3	3		3
anal fin rays	9	8		8–9
pectoral fin rays	14	14		14
gill rakers on lower limb of first arch	6	5		5–6
total gill rakers on first arch	8	8		8–9

¹, % of standard length; ², % of head length; ³, % of caudal peduncle depth.

Gill rakers on first gill arch: First gill arch with 5–6 pointed to moderately tuberculate rakers on the lower limb and 2–3 pointed rakers on the pharyngobranchial. Microbranchiospines absent.

Squamation: Scales cycloid. Cheek with 3–4 scale rows; opercle with four horizontal rows. Dark spot on outer margin of opercle unscaled. Five scales between bases of pelvic and pectoral fins. Upper lateral line separated from dorsal-fin base at its highest point (8th pored scale) by about 2.5 scales and at its posterior end by about 1.5 scales. Posterior end of upper lateral line and start of lower lateral line separated by 0–1 scale. Caudal fin scaled basally for approximately one third to one half of its length; other fins unscaled.

Coloration in life (Figure 6b): Body pale brown to bright bronze or golden brown in dominant or territorial individuals. Red pigmentation on body absent in both sexes. Lateral scales on the middle body and caudal peduncle with iridescent bronze to golden posterior halves, anterior halves dark brown. Iridescent coloration is weaker on ventral body parts and absent on most dorsal scales, which often show dark to black margins. An ovoid to circular black midlateral blotch present in smaller specimens (<50 mm SL) but often faint

or absent in adults. A vertically elongated to circular black blotch present at the caudal-fin base, usually fading in large individuals. Head brown with bronze to golden spots and interrupted vermiculate markings on the lower parts. Black opercular spot present at the posterodorsal margin of the opercle. Fins pale yellowish to greenish or turquoise. Dorsal and upper caudal fins with a very thin red to orange marginal band in life. Anal and pelvic fins with faint dark marginal bands posteriorly.

Coloration in preserved specimens (Figure 6a): Overall coloration brown to olive. No iridescent markings on head and body. Opercular spot always present; caudal peduncle spot visible in some specimens.

Distribution: Known only from the Kindia Region of Guinea, where it occurs in the Jaré and Samou rivers.

Etymology: Named after the company JBL (Germany) in recognition of its long-standing support for research on West and Central African fishes through the provision of equipment and water-testing materials. The spelling with two “e” facilitates pronunciation. The name is treated as a noun in apposition.

Reproductive behavior: *Rubricatochromis jebeli* sp. nov. is a biparental open substrate spawner with brood guarding behavior.

***Rubricatochromis stephenthorntoni*, new species**

Other names: *Hemichromis* sp. ‘Guinea 1’, *H.* sp. ‘Lim bun’.

ZooBank: urn:lsid:zoobank.org:act:694E2FE3-5431-48E8-91B9-D297C086E21.

Holotype: MRAC 2018-005-P-01; coll. M. Traore & O. Lucanus, Guinea, Limbun River, Kolente River system. 10°18.355' N, 12°28.725' W, elev. 465 m, 03/2008. Figure 7a.

Paratypes: Seven specimens, MRAC 2018-005-P-02, 1 spec.; AMNH 277412, 4 spec.; UVZC VZ5729, 2 spec.; same data as holotype.

Diagnosis: The new species is distinguished from most congeners by the absence of red pigmentation on the body in both sexes (shared only with *R. jebeli* sp. nov.). It is further characterized by an intensive vermiculate blue pattern on the opercle (vs. a dotted blue pattern in *R. guttatus* and *R. cristatus*, and absence of blue pattern in *R. jebeli* sp. nov.). In specimens larger than 50 mm SL, a midlateral dark bar is present, most prominent above the anterior portion of the lateral line and extending into the dorsal fin (vs. a circular to ovoid midlateral blotch that does not extend into the dorsal fin in *R. bimaculatus*, *R. cristatus*, *R. fugax*, *R. gabonensis* sp. nov., *R. guttatus*, *R. stellifer*, and *R. vanheusdeni* sp. nov.). From *R. bimaculatus* it differs by greater body depth (36.6–44.9% SL vs. 31.5–40.6% SL) and greater caudal peduncle depth (16.8–18.5% SL vs. 13.7–17.8% SL). From *R. cerasogaster* it differs by the presence of a midlateral dark gray bar (vs. absent), the presence of one complete tooth row in both jaws and one incomplete row in one or both jaws in some specimens (vs. two to three complete rows and one incomplete inner row), and greater postorbital distance (43.3–47.7% HL vs. 39.4–43.6% HL). From *R. cristatus* it differs by a longer dorsal-fin base (55.4–58.9% SL vs. 53.2–56.9% SL), shorter anal-fin base (18.7–22.0% SL vs. 21.8–23.2% SL), longer dentigerous arm of the premaxilla (27.1–30.7% HL vs. 24.2–27.4% HL), longer lower jaw (34.6–38.8% HL vs. 33.7–34.9% HL), greater cheek depth (23.5–29.9% HL vs. 20.4–22.7% HL), and a caudal peduncle length corresponding to 58.5–70.5% of its depth (vs. 53.5–57.9%). From *R. fugax* it differs by greater body depth (36.6–44.9% SL vs. 31.0–37.5% SL), shorter caudal peduncle (10.5–11.9% SL vs. 11.3–14.1% SL), greater caudal peduncle depth (16.8–18.5% SL vs. 14.2–16.9% SL), longer dorsal-fin base (55.4–58.9% SL vs. 50.7–55.8% SL), longer anal-fin base (18.7–22.0% SL vs. 16.5–17.9% SL), greater head depth (54.2–68.6% HL vs. 51.3–58.2% HL), and shorter lower jaw (34.6–38.8% HL vs. 37.5–41.9% HL). From *R. gabonensis* sp. nov., it differs by a shorter caudal peduncle (10.5–11.9% SL vs. 11.0–13.9% SL), longer dentigerous arm of the premaxilla (27.1–30.7% HL vs. 19.9–28.7% HL), and longer lower jaw (34.6–38.8% HL vs. 21.7–34.7% HL). From *R. guttatus*, it differs

in having, on average, greater body depth (36.6–44.9% SL vs. 30.7–42.3% SL). From *R. jebeli* sp. nov. it differs by greater predorsal distance (32.4–36.6% SL vs. 29.7–32.3% SL), greater prepelvic distance (41.7–45.3% SL vs. 39.3–42.4% SL), shorter dentigerous arm of the premaxilla (27.1–30.7% HL vs. 29.4–31.6% HL), and shorter preorbital distance (12.7–14.3% HL vs. 13.6–15.2% HL). From *R. stellifer*, it differs by the absence of thin vertical bars in adults (vs. 7–10 bars visible in various behavioral situations).

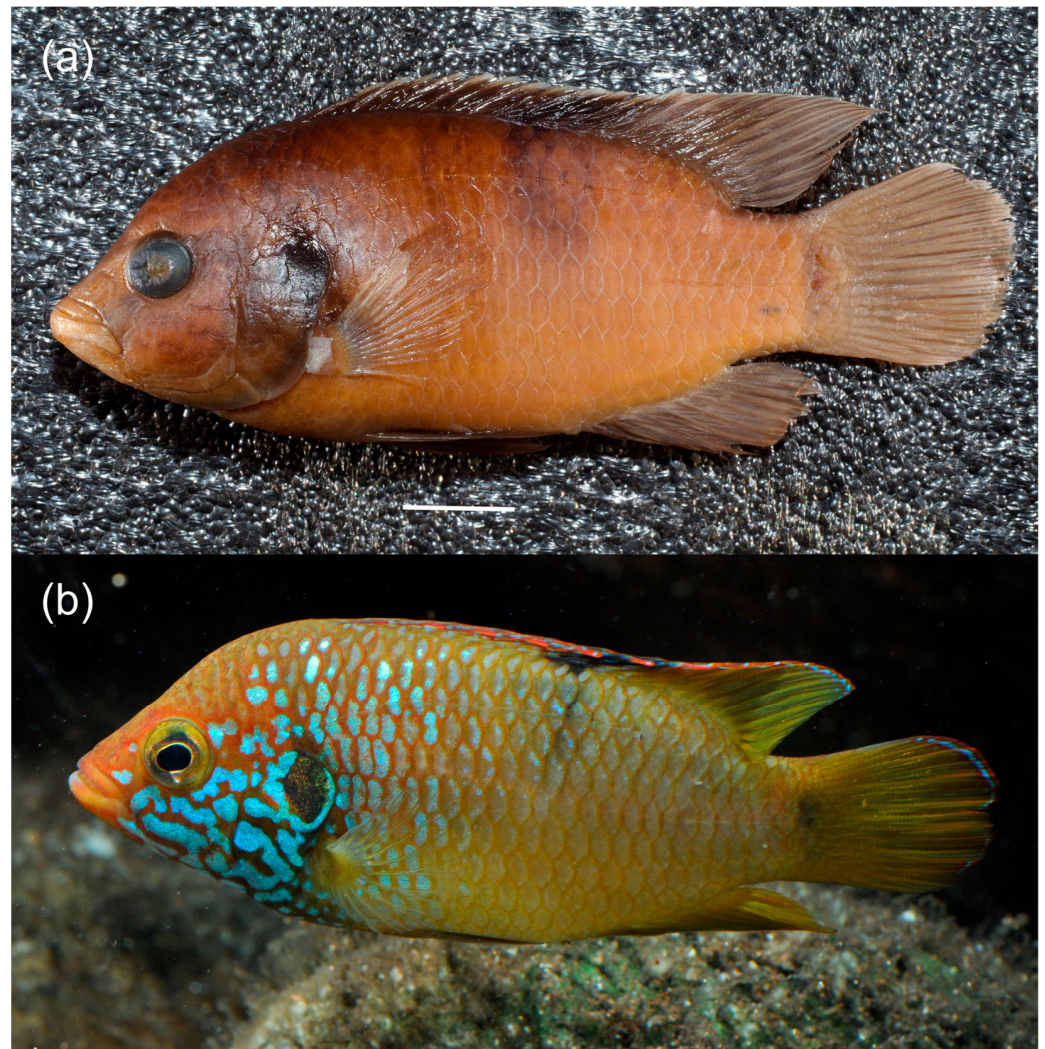


Figure 7. *Rubricatichromis stephenthorntoni* sp. nov. (a) Holotype, MRAC 2018-005-P-01, SL 70.3 mm. Guinea, Limbun River, Kolente River system, 10°18.355' N, 12°28.725', scale bar = 1 cm. (b) Specimen of *R. stephenthorntoni* sp. nov. in an aquarium, Guinea, Kolente River drainage, not preserved, not measured.

Description: Measurements and meristic counts for the holotype and seven paratypes are provided in Table 3.

Body deep, ovoid, and laterally compressed, with greatest body depth at midbody. Sexual dimorphism weakly expressed; females approximately 10% smaller than males. The first pelvic-fin ray usually the longest in both sexes. Snout short and moderately pointed (25.1–31.8% HL). Caudal fin rounded to moderately truncate. Caudal peduncle laterally compressed and shorter than deep (58.5–70.5% of caudal peduncle depth).

Table 3. Morphometrics and meristics of the holotype and the type series (holotype plus seven paratypes) of *Rubricatochromis stephenthorntoni* sp. nov.

Morphometrics	Holotype	Mean	s.d.	Range
standard length (mm)	70.3	59.7		45.7–70.6
body depth ¹	42.3	41.4	2.3	36.6–44.9
head length ¹	37.6	38.0	1.0	36.5–39.8
caudal peduncle length ¹	10.9	11.1	0.4	10.5–11.9
caudal peduncle depth ¹	18.5	17.7	0.5	16.8–18.5
length of dorsal fin base ¹	58.7	57.1	1.2	55.4–58.9
length of anal fin base ¹	22.0	20.1	1.0	18.7–22.0
predorsal distance ¹	32.4	34.1	1.3	32.4–36.6
preanal distance ¹	69.2	70.1	2.7	66.9–75.9
prepectoral distance ¹	37.1	38.3	1.4	36.5–41.0
prepelvic distance ¹	43.7	43.1	1.3	41.7–45.3
head depth ²	67.2	62.1	5.2	54.2–68.6
snout length ²	29.2	28.5	2.1	25.1–31.8
eye diameter ²	24.4	26.0	1.8	24.4–29.3
postorbital distance ²	46.4	45.5	1.5	43.3–47.7
interorbital distance ²	25.5	22.5	1.7	20.2–25.5
cheek depth ²	29.6	23.5	2.6	23.5–29.9
premaxilla length ²	30.7	28.8	1.5	27.1–30.7
lower jaw length ²	37.4	36.1	1.5	34.6–38.8
preorbital distance ²	14.3	13.7	0.5	12.7–14.3
caudal peduncle length ³	58.6	62.9	3.8	58.5–70.5
Meristics	Holotype	Median		Range
upper lateral line scales	17	17		17–18
lower lateral line scales	9	9		8–10
total lateral line scales	25	26		25–26
circumpeduncular scales	16	16		16
dorsal fin spines	14	14		14
dorsal fin rays	11	11		11
anal fin spines	3	3		3
anal fin rays	8	8		8
pectoral fin rays	14	13		13–14
gill rakers on lower limb of first arch	6	6		5–6
total gill rakers on first arch	9	9		8–10

¹, % of standard length; ², % of head length; ³, % of caudal peduncle depth.

Osteology and dentition: Infraorbital series complete, consisting of a plate-like first infraorbital followed by three–five tubular elements. Infraorbital series with four openings of the laterosensory canal. Outer tooth row complete in both jaws; inner row absent or incomplete and restricted to the anterior portions of the jaws. Anteriormost teeth of the premaxilla slightly enlarged.

Gill rakers on first gill arch: First gill arch with 5–6 pointed to moderately tuberculate rakers on the lower limb and 2–3 pointed rakers on the pharyngobranchial. Microbranchiospines absent.

Squamation: Scales cycloid. Cheek with 3–4 scale rows; opercle with four horizontal rows. Dark spot on outer margin of opercle unscaled. Five–six scales between bases of pelvic and pectoral fins. Upper lateral line separated from dorsal-fin base at its highest point (8th pored scale) by 2–2.5 scales and by 1–1.5 scales at its posterior end. Posterior end of upper lateral line separated from lower lateral line by one scale or overlapping with the anterior portion of the lower lateral line by up to two scales. Caudal fin scaled basally for approximately one third to one half of its length; other fins unscaled.

Coloration in life (Figure 7b): Body brown to olive. Red pigmentation absent from body in both sexes, although orange coloration may appear on the head, breast, and immediately behind the posterior margin of the opercle in larger or dominant individuals. Lateral scales with circular to vertically elongated iridescent blue spots, decreasing in size and intensity toward the caudal peduncle. Specimens < 50 mm SL show an ovoid midlateral blotch without a pale border, crossed by a broad dark bar that extends into the dorsal fin. In larger specimens, the blotch and bar are reduced or usually absent. Remnants of the bar form a V-shaped saddle on the upper back, most prominent in the dorsal fin. Six to ten faint dark vertical bars are present in specimens < 50 mm SL, extending ventrally to about midbody. A vertically elongated black blotch is present at the caudal-fin base, usually disappearing in larger specimens. Head brown with blue iridescent spots and vermiculate markings on the lower parts. Black opercular spot present at the posterodorsal margin of the opercle. Predorsal scales and those on the upper head lack blue iridescent spots. Dorsal fin and upper part of caudal fin with thin red marginal and white submarginal bands. Anal and pelvic fins hyaline with faint dark posterior margins.

Coloration in preserved specimens (Figure 7a): Overall coloration brown to olive. Iridescent markings not visible. Six–ten faint vertical bars visible in most specimens. Opercular spot always present; caudal peduncle spot visible in some specimens.

Distribution: Known only from the Kolenté River system in Guinea.

Etymology: Named in honor of Stephen Thornton (USA) in recognition of his long-standing support for research on the fishes of West and Central Africa.

Reproductive behavior: *Rubricatochromis stephenthorntoni* sp. nov. is a biparental open substrate spawner with brood guarding behavior.

***Rubricatochromis vanheusdeni*, new species**

Other names: *Hemichromis* sp. 'Ankasa'.

ZooBank: urn:lsid:zoobank.org:act:E1CC95F7-ECEA-4C47-8218-A550191654F.

Holotype: MRAC 2018-005-P-0006; coll. H. van Heusden, Ghana, Western Province, Ankasa River at the entrance of Ankasa National Park, 03/2004. 05°13.026' N, 02°39.115' W. Figure 8a.

Paratypes: Six specimens. MRAC 2018-005-P-0007–0008; UVZC VZ5731, same data as holotype.

Diagnosis: Can be distinguished from congeners by a combination of morphometric characters and coloration patterns. It differs from *R. bimaculatus* by greater body depth (40.5–43.9% SL vs. 31.5–40.6% SL), shorter predorsal distance (28.6–32.4% SL vs. 32.5–39.3% SL), and shorter dentigerous arm of the premaxilla (20.0–26.4% HL vs. 27.4–35.0% HL). From *R. cerasogaster* it differs by a single complete tooth row in both jaws and one incomplete inner row in one or both jaws (vs. two to three complete rows and one incomplete inner row), shorter head length (32.6–37.6% SL vs. 36.6–39.6% SL), shorter snout (20.7–28.8% HL vs. 27.3–34.9% HL), greater postorbital distance (42.7–46.4% HL vs. 39.4–43.6% HL), shorter dentigerous arm of the premaxilla (20.0–26.4% HL vs. 24.9–29.6% HL), and absence of black spots on the dorsum or dorsal fin. From *R. cristatus* it differs by longer caudal peduncle (11.4–12.1% SL vs. 9.5–11.0% SL), shallower caudal peduncle depth (16.1–17.7% SL vs. 17.5–19.0% SL), shorter anal-fin base (19.6–21.1% SL vs. 21.8–23.2% SL), shorter predorsal distance (28.6–32.4% SL vs. 31.7–35.5% SL), and a caudal peduncle length corresponding to 65.8–74.9% of its depth (vs. 53.4–57.9%). It further differs by lacking the pale or yellow ring around the black lateral blotch and the yellowish midlateral band present in that species. It differs from *R. fugax* by greater body depth (40.5–43.9% SL vs. 31.0–37.5% SL), greater caudal peduncle depth (16.1–17.7% SL vs. 14.2–16.9% SL), longer anal-fin base (19.6–21.1% SL vs. 16.5–17.9% SL), shorter predorsal distance (28.6–32.4% SL vs. 32.1–36.7% SL), shorter dentigerous arm of the premaxilla (20.0–26.4% HL vs.

25.4–32.9% HL), and shorter lower jaw (32.4–36.4% HL vs. 37.5–41.9% HL). It differs from *R. gabonensis* sp. nov. by shorter predorsal distance (28.6–32.4% SL vs. 32.5–34.7% SL). It differs from *R. guttatus* by blue margins on the body scales (vs. scales lacking margins but with blue centers). It differs from *R. jebeli* sp. nov. by greater body depth (40.5–43.9% SL vs. 37.4–40.8% SL), shallower caudal peduncle depth (16.1–17.7% SL vs. 17.2–18.6% SL), shallower cheek depth (19.1–26.5% HL vs. 26.4–30.7% HL), shorter dentigerous arm of the premaxilla (20.0–26.4% HL vs. 29.4–31.6% HL), and shorter lower jaw (32.4–36.4% HL vs. 36.3–39.6% HL). It differs from *R. stellifer* by blue margins on the body scales (vs. scales lacking margins but with blue centers), absence of dark vertical bands on the body, and shorter predorsal distance (28.6–32.4% SL vs. 30.0–38.0% SL). It differs from *R. stephenthorntoni* sp. nov. by shorter head length (32.6–37.6% SL vs. 36.5–39.8% SL), longer caudal peduncle (11.4–12.1% SL vs. 10.5–11.9% SL), shorter predorsal distance (28.6–32.4% SL vs. 32.4–36.6% SL), greater interorbital distance (23.2–29.8% HL vs. 20.2–25.5% HL), shorter dentigerous arm of the premaxilla (20.0–26.4% HL vs. 27.1–30.7% HL), and shorter lower jaw (32.4–36.4% HL vs. 34.6–38.8% HL).

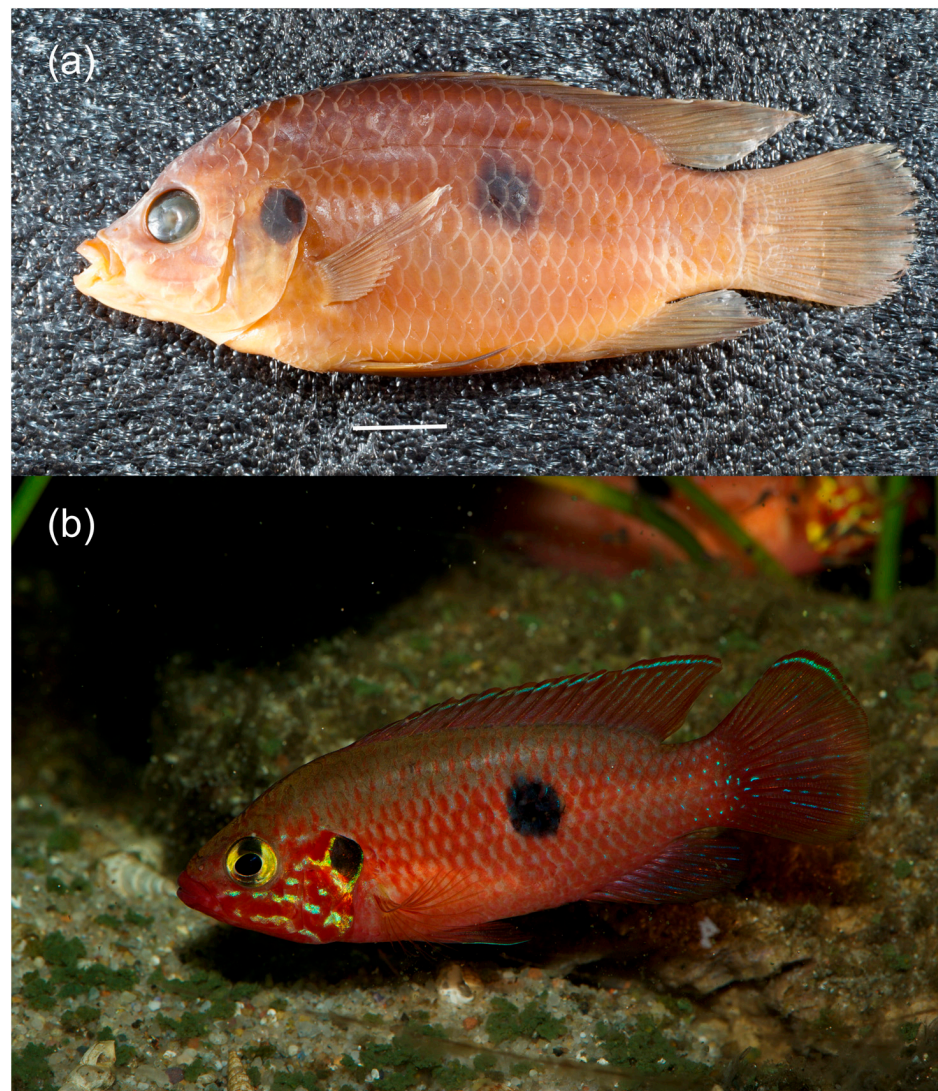


Figure 8. *Rubricatichromis vanheusdeni* sp. nov. (a) Holotype, MRAC 2018-005-P-0006, SL 74.1 mm, Ghana, Western Province, Ankasa River at entrance of Ankasa National Park, 05°13.026' N, 02°39.115' W, scale bar = 1 cm. (b) Adult female in an aquarium, Ghana, creek close to village of Ojamadjin, 05°04.465' N, 02°38.988' W, not preserved, not measured.

Description: Measurements and meristic counts for the holotype and six paratypes are given in Table 4.

Table 4. Morphometrics and meristics of the holotype and the type series (holotype plus six paratypes) of *Rubricatochromis vanheusdeni* sp. nov.

Morphometrics	Holotype	Mean	s.d.	Range
standard length (mm)	74.1	42.4		30.2–74.1
body depth ¹	43.2	41.9	1.4	40.5–43.9
head length ¹	35.2	35.9	1.6	32.6–37.6
caudal peduncle length ¹	12.1	11.8	0.2	11.4–12.1
caudal peduncle depth ¹	17.1	17.1	0.6	16.1–17.7
length of dorsal fin base ¹	58.4	56.1	1.9	53.6–58.7
length of anal fin base ¹	21.1	20.4	0.6	19.6–21.1
predorsal distance ¹	29.4	31.0	1.5	28.6–32.4
preanal distance ¹	69.8	68.3	1.4	66.9–70.3
prepectoral distance ¹	35.0	37.0	1.7	35.0–39.9
prepelvic distance ¹	40.3	40.9	1.3	39.1–43.3
head depth ²	63.7	57.0	4.1	54.1–63.7
snout length ²	28.8	23.6	2.5	20.7–28.8
eye diameter ²	26.2	32.1	2.9	26.2–34.3
postorbital distance ²	45.0	44.3	1.3	42.7–46.4
interorbital distance ²	27.1	26.1	2.1	23.2–29.8
cheek depth ²	24.9	25.4	2.7	19.1–26.5
premaxilla length ²	25.1	22.2	2.5	20.0–26.4
lower jaw length ²	32.4	34.0	1.3	32.4–36.4
preorbital distance ²	15.9	13.4	1.6	11.6–15.9
caudal peduncle length ³	70.5	69.2	3.2	65.8–74.9
Meristics	Holotype	Median		Range
upper lateral line scales	17	17		16–17
lower lateral line scales	8	8		8–9
total lateral line scales	27	26		25–27
circumpeduncular scales	16	16		16
dorsal fine spines	14	14		14
dorsal fin rays	11	11		10–11
anal fin spines	3	3		3
anal fin rays	8	8		7–8
pectoral fin rays	13	13		12–13
gill rakers on lower limb of first arch	5	5		5–6
total gill rakers on first arch	8	9		8–10

¹, % of standard length; ², % of head length; ³, % of caudal peduncle depth.

Deep-bodied species, egg-shaped and laterally compressed. Greatest body depth at mid-body. Sexual dimorphism weakly expressed; females approximately 10–15% smaller than males. Large adult males may develop a small nuchal hump. The first pelvic-fin ray is usually the longest in both sexes. Snout short and moderately pointed (20.7–28.8% HL). Caudal fin rounded to moderately truncate. Caudal peduncle laterally compressed and shorter than deep (65.8–74.9% of CPD).

Osteology and dentition: Infraorbital series complete, consisting of a plate-like first infraorbital followed by three–five tubular elements. Infraorbital series with four openings of the laterosensory canal. Outer tooth row of both jaws complete; second row absent or incomplete and restricted to the anterior part of the jaws. Anteriormost teeth of the premaxilla slightly enlarged.

Gill rakers on first gill arch: Lower limb with 5–6 pointed to moderately tuberculate rakers; 2–3 pointed rakers on pharyngobranchial. Microbranchospines absent.

Squamation: Scales cycloid. Cheek covered with 3–4 scale rows; opercle with four horizontal scale rows. Dark spot on outer edge of opercle unscaled. Five–seven scales between bases of pelvic and pectoral fins. Upper lateral line separated from dorsal-fin base at its highest point (8th pored scale) by 2–2.5 scales and at the last pored scale by 1–1.5 scales. Posterior end of upper lateral line and anterior end of lower lateral line separated by 0–2 scales.

Cycloid, cheek covered with 3–4 scale rows, four horizontal scale rows on opercle. Dark spot on outer edge of opercle unscaled. Five–seven scales between the base of pelvic and pectoral fins. Upper lateral line is separated from dorsal-fin base at its highest point (8th pored scale) by 2–2.5 scales, at last pored scale by 1–1.5 scales. The end of the upper lateral line is separated by 0–2 scales from the lower lateral line. Caudal fin basally scaled for approximately one third to one half of its length; other fins unscaled.

Coloration in life (Figure 8b): Body pale brown to rosy brown in juveniles or submissive individuals, bright red on head and body in dominant or territorial specimens. In dominant individuals, body scales from head to caudal peduncle often show blue iridescent margins, which may disappear or be reduced to small blue dots. Dorsal body scales with a greenish hue. Round black lateral blotch usually present but occasionally fading; caudal peduncle blotch often absent in adults. Head mostly red with greenish to green-brown upper areas and golden to greenish vermiculate iridescent stripes on cheek and opercle. Black opercular spot present at posterodorsal corner of opercular margin, framed with a thin golden to greenish iridescent margin. Fins pale yellowish to greenish or turquoise. Dorsal and upper caudal fins with a very thin red margin and a blue submarginal band. Anal and pelvic fins posteriorly with faint dark marginal bands. Unpaired fins often with very fine blue dots or lines. Pectoral fins hyaline.

Coloration in preserved specimens (Figure 8a): Overall coloration brown to olive. Iridescent markings usually not visible. Opercular spot and caudal peduncle spot present.

Distribution: Known from coastal creeks in western parts of Ghana and eastern parts of Ivory Coast. Seems to prefer forested areas.

Etymology: Named in honor of Hans van Heusden, collector of the type material.

Reproductive behavior: *Rubricatochromis vanheusdeni* sp. nov. is a biparental open substrate spawner with brood guarding behavior.

Remarks: This species was first documented by Wilkerling [49] from Ivory Coast, approximately 60 km north of Abidjan near the town of Agboville. The author illustrated a single specimen and attempted breeding with a female of *R. guttatus*, but the eggs failed to develop. He therefore suggested that the specimen might represent a distinct species. Subsequently, no further records from Ivory Coast were documented. Approximately 20 years later, the Dutch aquarist Hans van Heusden collected the species in Ghana, in the Ankasa National Park region. Since then, it has been collected there several times, including by one of the authors (L.A.), but it has not yet been recorded from other regions of Ghana.

***Rubricatochromis bimaculatus* (Gill, 1862)**

Synonyms: *Hemichromis bimaculatus* Gill, 1862.

Material: Sixty-three specimens, all Liberia; AMNH 263182, Sinoe, 5°4'9" N, 08°29'56" W, F. L. Pezold et al., 4 February 2014; AMNH 263208, Sinoe, 05°08'09" N, 8°29'56" W, F. L. Pezold et al., 7 February 2014; AMNH 263212, Sinoe, 05°06'51" N, 8°39'26" W, F. L. Pezold et al., 6 February 2014; 263216, Sinoe, 05°06'30" N, 08°29'11" W, F. L. Pezold et al., 7 February 2014; AMNH 263220, Sinoe, 05°06'08" N, 08°29'32" W, F. L. Pezold et al., 7 February 2014; AMNH 263222, Sinoe, 05°06'52" N, 08°29'56" W, F. L. Pezold et al., 7 February 2014; AMNH 263229, Sinoe, 05°05'14" N, 08°31'52" W,

F. L. Pezold et al., 7 February 2014; AMNH 263242, Sinoe, 05°06'27'' N, 08°32'12'' W, F. L. Pezold et al., 11 February 2014, AMNH 263261, Sinoe, 05°07'37'' N, 08°30'23'' W, F. L. Pezold et al., 15 February 2014; AMNH 263265, Sinoe, 05°07'18'' N, 08°30'04'' W, F. L. Pezold et al., 7 February 2014; MRAC 73-27-P-1158-159, Bong County, W. G. Johnson, November 1972–April 1973; MRAC 73-27-P-1160-174, Joe Town, Bong County, W. G. Johnson, 10 November 1972; MRAC 73-27-P-1237-1238, Yanokala, Bong County, W.G. Johnson, 9 September 1972; MRAC 73-27-P-1283-1294, Sanoyah, Bong County, W. G. Johnson, 14 April 1973; USNM 4907 (holotype, Figure 9a).

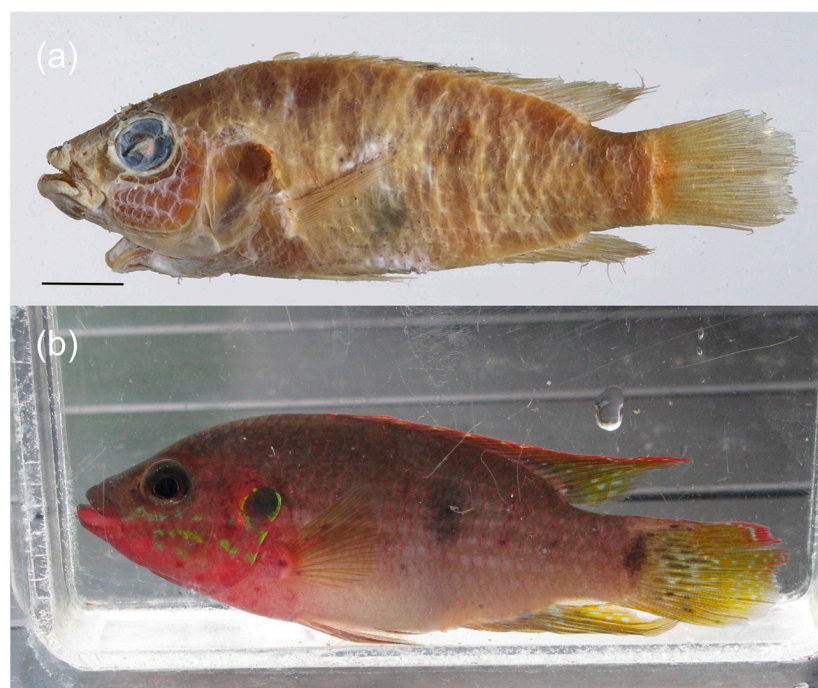


Figure 9. *Rubricatichromis bimaculatus*. (a) Holotype, USNM 4907, SL 78.0 mm. Liberia, scale bar = 1 cm, Photo: Smithsonian Museum of Natural History. (b) *Rubricatichromis bimaculatus* immediately after being caught, Liberia, photo R. Schmidt, not measured.

Diagnosis. The species can be distinguished from congeners by a combination of morphometric characters and coloration patterns. It differs from *R. cerasogaster* by a single complete tooth row in both jaws and one incomplete row in one or both jaws in some specimens (vs. two to three complete rows and one incomplete inner row), greater predorsal distance (32.5–39.3% SL vs. 30.8–35.8% SL), shorter dorsal-fin base (46.8–55.9% SL vs. 52.2–59.6% SL), longer dentigerous arm of the premaxilla (27.4–35.0% HL vs. 24.9–29.4% HL), and longer lower jaw (31.4–41.5% HL vs. 23.9–37.5% HL). It differs from *R. cristatus* by shallower body (31.5–40.6% SL vs. 41.1–43.8% SL), longer caudal peduncle (10.4–14.3% SL vs. 9.5–11.0% SL), shallower caudal peduncle depth (13.7–17.8% SL vs. 17.5–19.0% SL), and shorter anal-fin base (15.2–20.4% SL vs. 21.8–23.2% SL). It differs from *R. fugax* in the structure of the lateral blotch, which consists of scales entirely black (vs. scales darkest at their posterior margins and paler at their bases in *R. fugax*), and by a slightly greater head length (35.3–40.1% SL vs. 33.5–38.6% SL). It differs from *R. gabonensis* sp. nov. by a shallower body (31.5–40.6% SL vs. 36.0–44.1% SL), shorter dorsal-fin base (46.8–55.9% SL vs. 54.3–57.8% SL), longer dentigerous arm of the premaxilla (27.4–35.0% HL vs. 19.9–28.7% HL), and longer lower jaw (31.4–41.5% HL vs. 21.7–34.7% HL). It differs from *R. guttatus* in having a slightly shorter dorsal-fin base (46.8–55.9% SL vs. 48.4–60.0% SL), a greater average length of the dentigerous arm of the premaxilla (27.4–35.0% HL, mean 30.0% vs. 20.5–34.1% HL, mean 27.8%), and a greater average lower jaw length (31.4–41.5% HL, mean

38.2% vs. 22.9–41.7% HL, mean 32.4%). It differs from *R. jebeli* sp. nov. by shallower caudal peduncle depth (13.7–17.8% SL vs. 17.2–18.6% SL) and shorter caudal peduncle relative to its depth (56.6–71.5% vs. 64.1–98.7%). It differs from *R. stephenthorntoni* sp. nov. by a shallower body (31.5–40.6% SL vs. 36.6–44.9% SL) and a shallower caudal peduncle depth (13.7–17.8% SL vs. 16.8–18.5% SL). It differs from *R. stellifer* by a somewhat shallower body (31.5–40.6% SL vs. 34.3–44.7% SL), a slightly shorter dorsal-fin base (46.8–55.9% SL vs. 48.3–62.0% SL), a slightly shorter anal-fin base (15.2–20.4% SL vs. 18.3–23.0% SL), and a caudal peduncle length corresponding to 64.1–98.7% of its depth (vs. 54.3–85.3%). It differs from *R. vanheusdeni* sp. nov. by a shallower body (31.5–40.6% SL vs. 40.5–43.9% SL), greater predorsal distance (32.5–39.3% SL vs. 28.6–32.4% SL), and a longer dentigerous arm of the premaxilla (27.4–35.0% HL vs. 20.0–26.4% HL).

Coloration in life (Figure 9b): Ground coloration is pale brown, sometimes with a rosy hue. During territorial, aggressive, or reproductive behavior, the entire body becomes bright red, usually with the belly lighter than the dorsum. Iridiophores on head and body are sparse and often entirely absent, occasionally present in small numbers on the head and unpaired fins. Some specimens show a few greenish to yellowish vermiculate lines on the head. Black spots usually present on the mid-body and caudal peduncle but may occasionally disappear. The midlateral blotch is oval to round and lacks a surrounding pale ring. The scales forming the blotch are completely black, distinguishing this species from *R. fugax*. Some males display small pale bluish to greenish dots and faint dark markings on the soft portions of the dorsal and anal fins and on the anterior part of the caudal fin.

Coloration in preserved specimens (Figure 9a): Body overall brown, with narrow, faint dark vertical bars restricted mainly to the dorsal portion of the flanks. A distinct dark spot is present on the opercle, and the midlateral and caudal peduncle spots are clearly visible. The subdued coloration of the holotype is likely attributable to prolonged preservation in alcohol.

Distribution: Probably restricted to inland waters of Liberia, where the species appears to be relatively widespread in several regions of the country. Seems to prefer forested areas.

Remarks: The original description [50] does not explicitly state the country of origin of the holotype. However, according to Loiselle [10] and our interpretation, the specimen most likely originated from Liberia. The author of the original description wrote: “A single specimen is in the collection of the Smithsonian Institution. . . There is no indication of locality, but it is probable that it was sent from Liberia.” The color description provided by Gill also matches the characteristics of *R. bimaculatus*. The morphology of the holotype, particularly the relatively long snout, corresponds well with specimens collected in Liberia and Sierra Leone. Our genetic data indicate clear differences between recently collected long-snouted populations from Liberia and those from Sierra Leone. Because *R. fugax* was originally described from Sierra Leone, we revalidate that taxon and separate it from *R. bimaculatus*.

***Rubricatochromis cerasogaster* (Boulenger, 1898)**

Synonyms: *Hemichromis cerasogaster* (Boulenger, 1898), *Paratilapia cerasogaster* Boulenger, 1898.

Material: Fifteen specimens, all Democratic Republic of the Congo; MRAC 1050, Utanda, Boulenger, 1899 (syntype); MRAC 1053, Utanda, M. Delhez, 1899 (syntype, Figure 10a); MRAC 1055, Utanda, M. Delhez, 1899 (syntype); ZSM 29694, Lac Mai Ndombe, Bandudu Province, U. K. Schliewen, 29 August–4 September 2002.

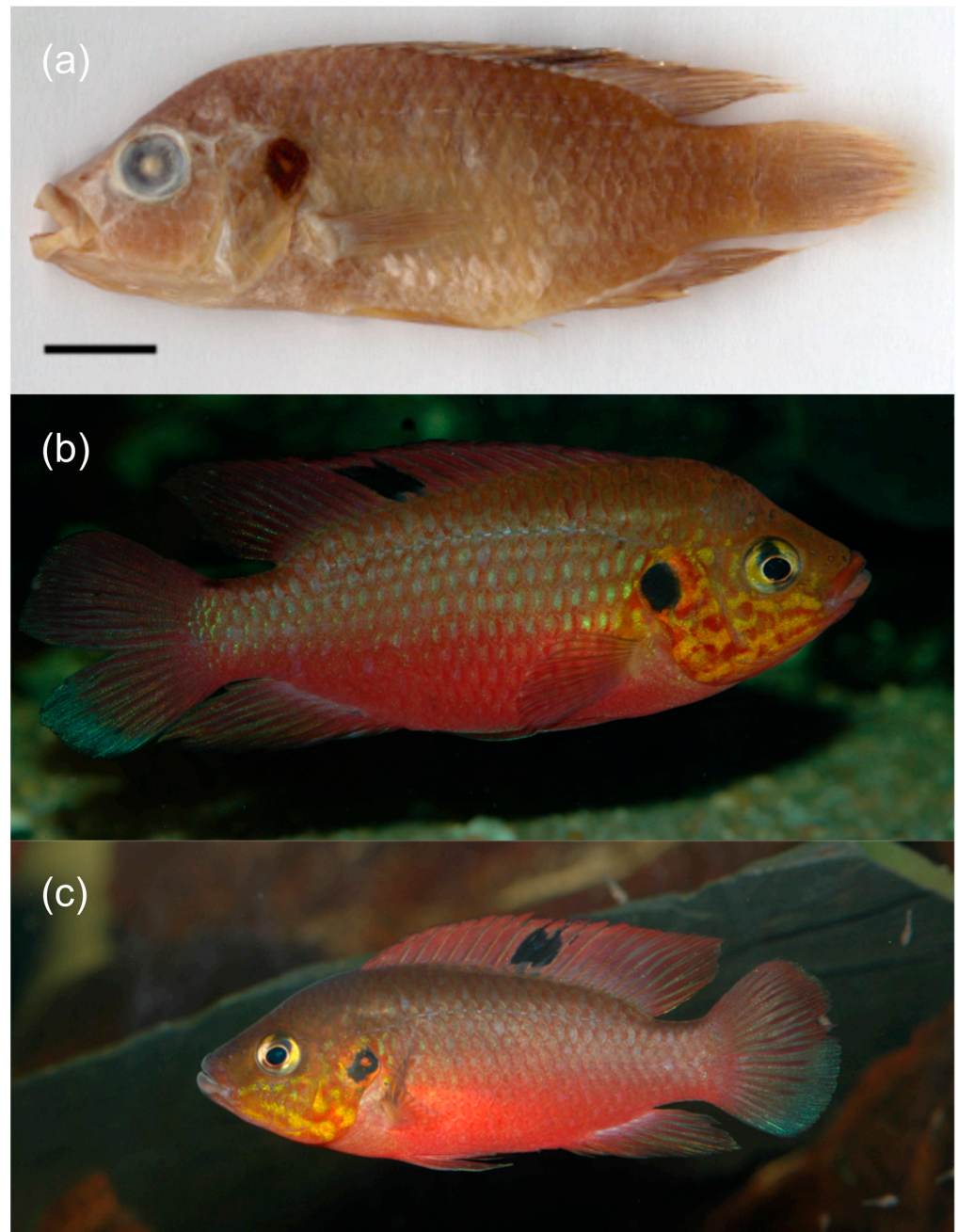


Figure 10. *Rubricatichromis cerasogaster* (a) Syntype, MRAC 1053, SL 62.3 mm Democratic Republic of the Congo, Lac Mai Ndombe, Utanda, scale bar = 1 cm. (b) Male and (c) female in the aquarium, not preserved, not measured.

Diagnosis: The species is distinguished from all congeners by two to three complete tooth rows in both jaws and one incomplete inner row in both jaws (vs. one complete row and one incomplete inner row in bone or both jaws in some specimens in all other species). It differs from *Rubricatichromis bimaculatus* by a shorter predorsal distance (30.8–35.8% SL vs. 32.5–39.3%), longer dorsal-fin base (52.2–59.6% SL vs. 46.8–55.9%), shorter dentigerous arm of the premaxilla (24.9–29.4% HL vs. 27.4–35.0%), and shorter lower jaw (23.9–37.5% HL vs. 31.4–41.5%). It differs from *Rubricatichromis cristatus* by a shorter anal-fin base (16.6–21.0% SL vs. 21.8–23.2%), greater head depth (57.0–67.0% HL vs. 52.5–59.1%), and greater cheek depth (23.9–29.6% HL vs. 20.4–22.7%). It differs from *Rubricatichromis fugax* by a longer dorsal-fin base (52.2–59.6% SL vs. 50.7–55.8%), greater head depth (57.0–67.0% HL vs. 51.3–58.2%), lesser postorbital distance (39.4–43.6% HL vs. 42.9–46.9%), shorter

lower jaw (23.9–37.5% HL vs. 37.5–41.9%), and a caudal peduncle length corresponding to 60.1–75.1% of its depth (vs. 73.7–94.6%). It differs from *Rubricatochromis gabonensis* sp. nov. by a shorter postorbital distance (39.4–43.6% HL vs. 42.4–48.2%) and the presence of black spots on the base of the dorsal fin. It differs from *Rubricatochromis guttatus* by a longer preorbital distance (12.6–17.3% HL, mean 15.2%, vs. 8.0–16.9%, mean 12.5%). It differs from *Rubricatochromis jebeli* sp. nov. by a greater head length (36.6–39.6% SL vs. 35.3–37.9%), shorter postorbital distance (39.4–43.6% HL vs. 44.3–46.5%), shorter dentigerous arm of the premaxilla (24.9–29.4% HL vs. 29.4–31.6%), shorter lower jaw (23.9–37.5% HL vs. 36.3–39.6%), and shorter anal-fin base (16.6–21.0% SL vs. 19.4–21.5%). It differs from *Rubricatochromis stephenthorntoni* sp. nov. by the absence of a midlateral dark bar (vs. presence) and shorter postorbital distance (39.4–43.6% HL vs. 43.3–47.7%). It differs from *Rubricatochromis stellifer* by a longer snout (27.3–34.9% HL vs. 20.5–32.8%) and shorter anal fin base (16.6–21.0% SL vs. 18.4–23.0%). It differs from *Rubricatochromis vanheusdeni* sp. nov. by a longer head length (36.6–39.6% SL vs. 32.6–37.6%), longer snout (27.3–34.9% HL vs. 20.7–28.8%), shorter postorbital distance (39.4–43.6% HL vs. 42.7–46.4%), greater dentigerous arm of the premaxilla length (24.9–29.4% HL vs. 20.0–26.4%), and black spots on the dorsum or dorsal fin.

Coloration in life (Figure 10b): Body generally yellowish brown, with the belly region pale rosy. Cheek and opercle usually with bluish vermiculated lines and small dots; several rows of iridescent blue dots present on the body, more pronounced in males than in females. A dark opercular spot typically present and usually surrounded by a reddish area. Adults lack black spots on the flanks and caudal peduncle. One or two small black spots may occur in the central part of the dorsal fin in some individuals. Dark vertical bars may appear in certain behavioral situations. In territorial, aggressive, or breeding individuals, the lower parts of the body, dorsal fin, and anal fin become intensely red, while the body scales show blue dots in their central parts.

Coloration in preserved specimens (Figure 10a): Body uniformly brown; fins hyaline. A distinct dark spot is present on the opercle, and a conspicuous black spot is visible in the dorsal fin.

Distribution: Endemic to Lake Mai-Ndombe and surrounding regions in the Democratic Republic of the Congo.

Remarks: Although morphological differences between species of *Rubricatochromis* are often subtle, *R. cerasogaster* can be readily distinguished by its dentition. Adults consistently have 2–3 fully developed outer tooth rows and one incomplete inner row in both jaws, whereas all other congeners have only one complete row; when a second row is present in those species, it usually consists of only a few (approximately 5–6) widely spaced teeth.

Rubricatochromis cristatus (Loiselle, 1979)

Synonyms: *Hemichromis cristatus* Loiselle, 1979.

Material: Three specimens, all from Nigeria; BMNH 1969.3.26.76 (holotype, Figure 11a), Ogba River, R. A. Whitehead, 24 July 1959; ZSM 26860, Niger River delta, T. R. Roberts, 6 September 1987.

Diagnosis: The species can be distinguished from congeners by a combination of morphometric characters and coloration patterns. It is the smallest species of the genus, not exceeding 67 mm SL (vs. 70.1–95 mm SL in all congeners). It further differs from most congeners, except some specimens of *R. guttatus* and *R. stellifer*, by the presence of a black midlateral blotch surrounded by a conspicuous pale or yellow ring that often extends anteriorly and posteriorly as a yellowish band along the mid-body. It differs from *R. bimaculatus* by greater body depth (41.1–43.8% SL vs. 31.5–40.6% SL), shorter caudal peduncle length (9.5–11.0% SL vs. 10.4–14.3% SL), greater caudal peduncle depth (17.5–19.0% SL vs. 13.7–17.8% SL), and longer anal-fin base (21.8–23.2% SL vs. 15.2–20.4%

SL). It differs from *R. cerasogaster* by having one complete inner tooth row in both jaws (vs. two to three complete rows and one incomplete inner row incomplete row), by a longer anal-fin base (21.8–23.2% SL vs. 16.6–21.0% SL), lesser head depth (52.5–59.1% HL vs. 57.0–67.0% HL), and lesser cheek depth (20.4–22.7% HL vs. 23.9–29.6% HL). It differs from *R. gabonensis* sp. nov. by a shorter caudal peduncle (9.5–11.0% SL vs. 11.0–13.9% SL), greater caudal peduncle depth (17.5–19.0% SL vs. 16.3–18.6% SL), longer anal-fin base (21.8–23.2% SL vs. 18.6–21.2% SL), and a caudal peduncle length corresponding to 53.4–57.9% of its depth (vs. 59.8–76.8%). It further differs by the presence of a pale or yellow ring around the black lateral blotch and a yellowish band along the mid-body. It differs from *R. fugax* by greater body depth (41.1–43.8% SL vs. 30.1–37.5% SL), shorter caudal peduncle length (9.5–11.0% SL vs. 11.3–14.1% SL), greater caudal peduncle depth (17.5–19.0% SL vs. 14.2–16.9% SL), longer anal-fin base (21.8–23.2% SL vs. 16.5–17.9% SL), shorter dentigerous arm of the premaxilla (24.2–27.4% HL vs. 25.4–32.9% HL), shorter lower jaw (33.7–34.1% HL vs. 37.5–41.9% HL), and lesser cheek depth (20.4–22.7% HL vs. 22.1–27.5% HL). In addition, the caudal peduncle length corresponds to 53.5–57.9% of its depth (vs. 73.7–94.6%). It differs from *R. guttatus* by a deeper body on average (41.1–43.8% SL, mean 42.0% vs. 30.7–42.3% SL, mean 36.9%) and by a longer anal-fin base (21.8–23.2% SL vs. 15.0–22.6% SL). It differs from *R. jebeli* sp. nov. by greater body depth (41.1–43.8% SL vs. 37.4–40.8% SL), shorter dorsal-fin base (53.2–56.9% SL vs. 55.6–59.5% SL), longer anal-fin base (21.8–23.2% SL vs. 19.4–21.5% SL), shorter postorbital distance (43.0–43.9% HL vs. 44.3–46.5% HL), shorter dentigerous arm of the premaxilla (24.2–27.4% HL vs. 29.4–31.6% HL), shorter lower jaw (33.7–34.9% HL vs. 36.3–39.6% HL), lesser cheek depth (20.4–22.7% HL vs. 26.4–30.7% HL), shorter preorbital distance (11.8–13.5% HL vs. 13.6–15.2% HL), and by a caudal peduncle length corresponding to 53.5–57.9% of its depth (vs. 56.6–71.5%). It differs from *R. stephenthorntoni* sp. nov. by a shorter dorsal-fin base (53.2–56.9% SL vs. 55.4–58.9% SL), longer anal-fin base (21.8–23.2% SL vs. 18.7–22.0% SL), shorter dentigerous arm of the premaxilla (24.2–27.4% HL vs. 27.1–30.7% HL), shorter lower jaw (33.7–34.9% HL vs. 34.6–38.8% HL), lesser cheek depth (20.4–22.7% HL vs. 23.5–29.9% HL), and by a caudal peduncle length corresponding to 53.5–57.9% of its depth (vs. 58.5–70.5%). It differs from *R. stellifer* by greater caudal peduncle depth (17.5–19.0% SL vs. 14.3–18.6% SL). It differs from *R. vanheusdeni* sp. nov. by a shorter caudal peduncle (9.5–11.0% SL vs. 11.4–12.1% SL), greater caudal peduncle depth (17.5–19.0% SL vs. 16.1–17.7% SL), longer anal-fin base (21.8–23.2% SL vs. 19.6–21.1% SL), greater predorsal distance (31.7–35.5% SL vs. 28.6–32.4% SL), and by a caudal peduncle length corresponding to 53.4–57.9% of its depth (vs. 65.8–74.9%). It further differs by the presence of a pale or yellow ring around the black lateral blotch and a yellowish band along the mid-body.

Coloration in life (Figure 11b): When not territorial, breeding, or aggressive, brownish body with a well-developed black mid-lateral spot surrounded by a prominent pale yellowish ring, which often extends anteriorly and posteriorly to a yellowish band in the middle of the body that can reach anterior to the black opercular spot and caudal to the end of the caudal peduncle. A small dark spot on the caudal peduncle is always present. Some dark vertical bars reaching from the dorsum to about the middle of the body are visible during most behavioral situations. Iridiophores on the body, head, and fins are always present, although their numbers vary individually. Cheeks, opercles, and throat are yellowish. When aggressive, territorial, or breeding, most body parts turn intensely red, except for those that were formerly yellowish; they turn bright yellow, as does the zone surrounding the mid-lateral spot. No sexual differences, but males seem to tend to have a higher number of iridiophores.

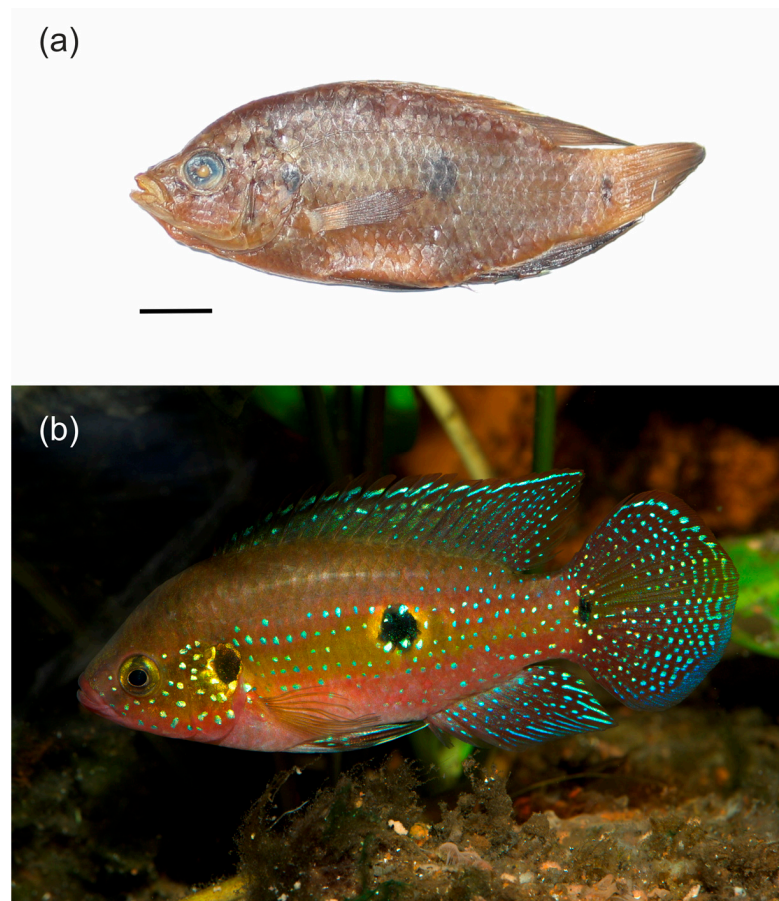


Figure 11. *Rubricatichromis cristatus*. (a) Holotype, BMNH-3-26-76, SL 67 mm. Nigeria, Ogba River, scale bar = 1 cm. (b) Male in an aquarium, not preserved, not measured.

Coloration in preserved specimens (Figure 11a): Body uniformly brown; fins hyaline. A distinct dark spot is present on the opercle, and the midlateral and caudal peduncle spots are clearly visible.

Distribution: Contrary to the distribution reported by Loiselle (1979) [10], the species appears to be restricted to southern Nigeria, particularly the Niger River delta region. Specimens reported from other parts of West Africa represent misidentifications of *R. guttatus*.

Remarks: Loiselle [10] reported a much wider distribution for this species in West Africa, ranging from Guinea to Nigeria. This likely resulted from the considerable variation in coloration as well as head and snout morphology observed in *R. guttatus*. Some individuals of *R. guttatus* can closely resemble *R. cristatus*, although they usually attain substantially larger sizes. Molecular data obtained in [12] and the present study clearly separate specimens from southern Nigeria from those collected elsewhere in West Africa, the latter consistently clustering with *R. guttatus*.

Rubricatichromis fugax (Payne & Trewavas, 1976)

Original combination: *Hemichromis fugax* Payne & Trewavas, 1976.

Material: Nine specimens; BMNH 1976.1.28.1 (holotype, Figure 12a), 72 mm SL, I. Payne, Sierra Leone, forest stream, Kasewe Forest Reserve, 1976; BMNH 2024.1.31.1-5, A. Lamboj et al., Sierra Leone, restwater ponds of river Wehba near Moyamba Junction, 08°14.744' N, 12°13.793' W, elevation 94 m; UVZC VZ5734, A. Lamboj et al., Sierra Leone, restwater ponds of river Wehba near Moyamba Junction, 08°14.744' N, 12°13.793' W, elevation 94 m.

Diagnosis: The species can be distinguished from congeners by a combination of morphometric characters and coloration patterns. It differs from *R. bimaculatus* in the structure of the lateral blotch, which is formed by scales darkest along their posterior margins and paler at their centers (vs. scales entirely black in *R. bimaculatus*). It differs from *R. cerasogaster* by having one complete tooth row in both jaws and one incomplete inner row in one or both jaws of some specimens (vs. two to three complete and on incomplete inner row), a shorter dorsal-fin base (50.7–55.8% SL vs. 52.2–59.6% SL), lesser head depth (51.3–58.2% HL vs. 57.0–67.0% HL), greater postorbital distance (42.9–46.9% HL vs. 39.4–43.6% HL), greater lower jaw length (37.5–41.9% HL vs. 23.9–37.5% HL), and a caudal peduncle length corresponding to 73.7–94.6% of its depth (vs. 60.1–75.1%). It differs from *R. cristatus* by shallower body depth (31.0–37.5% SL vs. 41.1–43.8% SL), longer caudal peduncle (11.3–14.1% SL vs. 9.5–11.0% SL), shallower caudal peduncle depth (14.2–16.9% SL vs. 17.5–19.0% SL), shorter anal-fin base (16.5–17.9% SL vs. 21.8–23.2% SL), longer dentigerous arm of the premaxilla (25.4–32.9% HL vs. 24.2–27.4% HL), longer lower jaw (37.5–41.9% HL vs. 33.7–34.1% HL), greater cheek depth (22.1–27.1% HL vs. 20.4–22.7% HL), and a caudal peduncle length corresponding to 73.7–94.9% of its depth (vs. 53.5–57.9%). It differs from *R. gabonensis* sp. nov. by a shallower body (31.0–37.1% SL vs. 36.0–44.1% SL), shallower caudal peduncle depth (13.7–15.6% SL vs. 16.3–18.6% SL), shorter anal-fin base (14.2–16.9% SL vs. 18.6–21.2% SL), lesser head depth (51.3–58.2% HL vs. 55.1–69.6% HL), longer dentigerous arm of the premaxilla (25.4–32.9% HL vs. 19.9–28.7% HL), longer lower jaw (37.5–41.9% HL vs. 21.7–34.7% HL), and a caudal peduncle length corresponding to 73.7–94.6% of its depth (vs. 59.8–76.8%). It differs from *R. guttatus* by having a slightly shallower body on average (31.0–37.5% SL, mean 34.1% vs. 30.7–42.3% SL, mean 36.9%) and a slightly shallower head on average (51.3–58.2% HL, mean 53.9% vs. 48.5–69.4% HL, mean 59.3%). It differs from *R. jebeli* sp. nov. by a shallower body (31.0–37.5% SL vs. 37.4–40.8% SL), shorter dorsal-fin base (50.1–55.8% SL vs. 55.6–59.9% SL), shorter anal-fin base (16.5–17.9% SL vs. 19.4–21.5% SL), longer predorsal distance (32.1–36.2% SL vs. 29.7–32.3% SL), longer prepelvic distance (37.9–43.9% SL vs. 36.8–38.3% SL), lesser head depth (51.3–58.2% HL vs. 55.9–68.7% HL), lesser cheek depth (22.1–27.1% HL vs. 26.4–30.7% HL), and a caudal peduncle length corresponding to 73.7–94.6% of its depth (vs. 56.6–71.5%). It differs from *R. stephenthorntoni* sp. nov. by a shallower body (31.0–37.5% SL vs. 36.6–44.9% SL), longer caudal peduncle (11.3–14.1% SL vs. 10.5–11.9% SL), shallower caudal peduncle depth (14.2–16.9% SL vs. 16.8–18.5% SL), shorter dorsal-fin base (50.1–55.8% SL vs. 55.4–58.9% SL), shorter anal-fin base (16.5–17.9% SL vs. 18.7–22.0% SL), lesser head depth (51.3–58.2% HL vs. 54.2–68.6% HL), and longer lower jaw (37.5–41.9% HL vs. 34.6–38.8% HL). It differs from *R. stellifer* by a shallower caudal peduncle depth (14.2–16.9% SL vs. 14.3–18.6% SL). It differs from *R. vanheusdeni* sp. nov. by a shallower body (31.0–37.5% SL vs. 40.5–43.9% SL), shallower caudal peduncle depth (14.2–16.9% SL vs. 16.1–17.7% SL), shorter anal-fin base (16.5–17.9% SL vs. 19.6–21.1% SL), greater predorsal distance (32.1–36.1% SL vs. 28.6–32.4% SL), longer dentigerous arm of the premaxilla (25.4–32.9% HL vs. 20.0–26.4% HL), and longer lower jaw (37.5–41.9% HL vs. 32.4–36.4% HL).

Coloration in life (Figure 12b): On the head, greenish to golden vermiculate lines and small dots are visible. In juvenile to semiadult specimens, blue dots may occur on the body scales but often disappear in adults. The midlateral blotch is situated at mid-body, oval to round in shape, and lacks a surrounding pale ring. The scales forming this blotch are not entirely black; the pigmentation is darkest along the posterior margins of the scales and paler or absent in their centers, distinguishing this species from *R. bimaculatus*. A black spot on the caudal peduncle may be present but can disappear in adults. The normal ground coloration is pale brown, sometimes with a rosy hue. During territorial, aggressive, or breeding behavior, the entire body becomes bright red, usually with a greenish-brown

hue on the dorsum. Some males display small pale bluish to greenish dots and faint dark markings on the soft portions of the dorsal and anal fins and on the anterior part of the caudal fin.

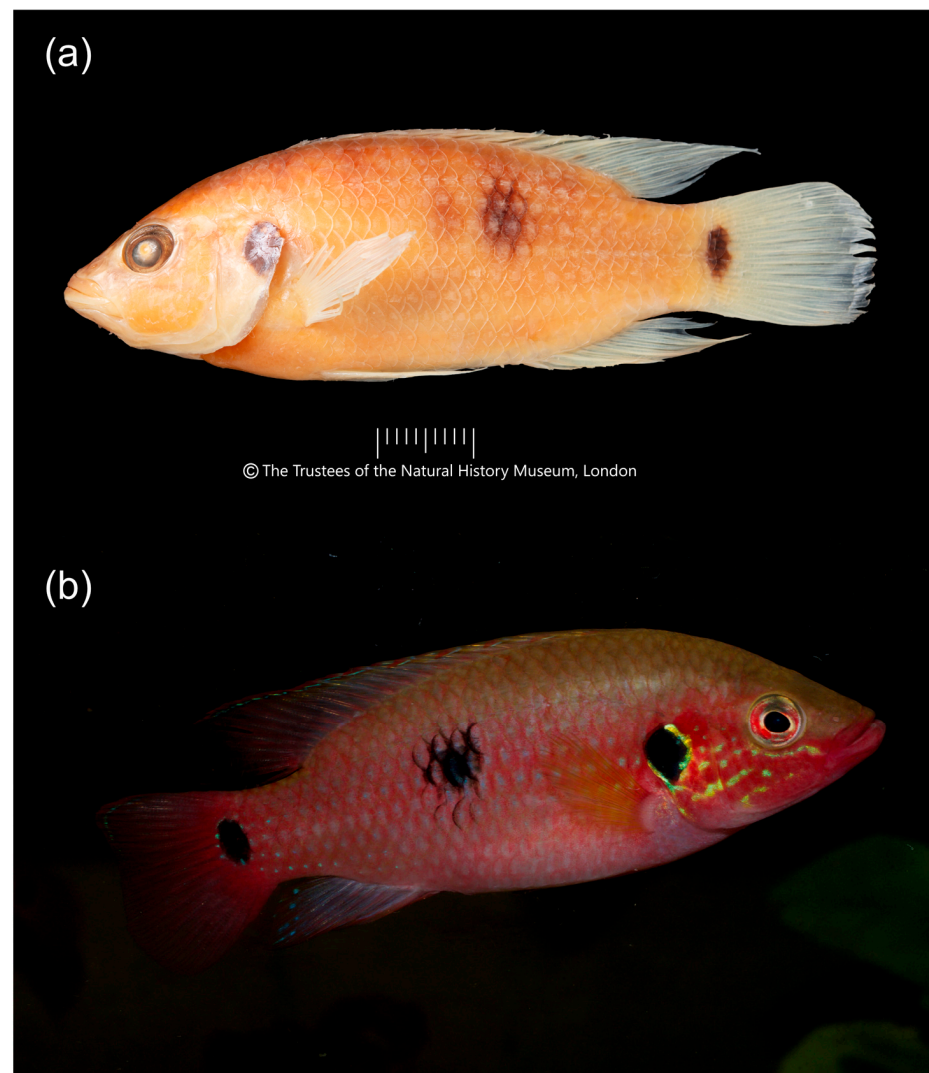


Figure 12. *Rubricatichromis fugax*. (a) Holotype, BMNH 1976.1.28.1, SL 72 mm, Sierra Leone, forest stream, Kasewe forest reserve, Photo BMNH, scale bar = 1 cm. (b) Female in an aquarium, Sierra Leone, Kasewe, 08°29.887' N, 12°08.319' W, not preserved, not measured.

Coloration preserved specimens (Figure 12a): Body overall pale brown. Opercular, midlateral, and caudal peduncle spots distinct and conspicuous. Several faint vertical dark bars present on the dorsal parts of the flanks.

Distribution: Possibly restricted to a small region of Sierra Leone around Kasewe and Moyamba, where the species appears to prefer forested habitats. Records from Liberia likely represent misidentifications of *R. bimaculatus*, as specimens from that country are genetically distinct.

Rubricatichromis guttatus (Günther, 1862)

Synonyms: *Hemichromis guttatus* Günther, 1862, *Rubricatichromis letourneauxi* (Sauvage, 1858), *Hemichromis letourneauxi* Sauvage, 1858, *Rubricatichromis saharae* (Sauvage, 1880), *Hemichromis saharae* (Sauvage, 1880), *Hemichromis rolandi* Sauvage, 1881, *Rubricatichromis exsul* (Trewavas, 1933), *Hemichromis exsul* (Trewavas, 1933), *Pelmatichromis exsul* Trewavas, 1933, *Rubricatichromis paynei* (Loiselle, 1979), *Hemichromis paynei* (Loiselle, 1979).

Material: A total of 223 specimens; AMNH 12318, Liberia, stream near Kaleata, G. W. Harley, February 1932; AMNH 242899, Guinea, N'Bagou River, 11°42' N, 12°20' W, B. Samoura et al., 2 April 2003; AMNH 242900, Guinea, Boke, Rio Nunez, rice field near Kamsar, 10°38'20" N, 14°29'27" W, F. Pezold et al., 8 January 2003; AMNH 242901, Guinea, Gaoual, Labiko River, 11°35' N, 13°21' W, B. Samoura et al., 29 March 2003; AMNH 242902, Guinea, Labe, Komba River, 11°39' N, 12°17' W, B. Samoura et al., 2 April 2003; AMNH 242906, Guinea, Boke, Singuilal River, Sikouya, 10°39' N, 14°24' W, B. Samoura et al., 23 March 2003; AMNH 242909, Guinea, Mamou, Bafing River, Sokotoro, 10°39'42" N, 11°45'04" W, F. Pezold et al., 14 March 2003; AMNH 242910, Guinea, Kankan, Kouroussa, Niandan River, 10°23'56" N, 9°44'24" W, F. Pezold et al., 18 May 2003; AMNH 242914, Guinea, Kindia, Badi River, F. Pezold et al., 21 January 2003; AMNH 242918, Guinea, Boke, Kitali River, 10°33'03" N, 14°24'22" W, F. Pezold et al., 6 January 2003; AMNH 242920, Guinea, Faranah, Niger River, 10°35'42" N, 9°57'21" W, F. Pezold et al., 17 May 2003; AMNH 242921, Guinea, Gaoual, Kabili River, 11°21'00" N, 13°13'48" W, B. Samoura et al., 29 March 2003; AMNH 242922, Guinea, Boffa, Sagna River, 10°17' N, 14°03' W, B. Samoura et al., 23 March 2003; AMNH 242931, Guinea, Boke, Thangui River, 11°15' N, 14°04' W, F. Pezold et al., 27 March 2003; MNHN A-5250 (syntypes of *R. letourneuxi*), Egypt, Lake Mareotis, M. Letourneaux; BMNH 1860.4.19.3-4 (syntypes; Figure 13), "Cape of Ceylon", possibly Sierra Leone; BMNH 1898.2.1.15.1 (syntype of *R. letourneuxi*), Egypt, Lake Mareotis, M. Letourneaux; BMNH 1933.2.23.134-136 (syntypes of *R. exsul*), Kenia, Lake Rudolf (Lake Turkana), E. B. Worthington, 1930; BMNH 1950.9.22.50 (holotype of *R. paynei*), Sierra Leone, Lake Kwarko, T. S. Jones, 1950; BMNH 1950.9.22.51-56+57-70, Sierra Leone, Lake Kwarko, T. S. Jones, 1950; BMNH 2024.1.13.6-9, Sierra Leone, Moa River, 08°02.989' N, 10°57.887' W, A. Lamboj & A. Mansaray, 7 February 2020; MNHN A-2618 (holotype of *R. saharae*), Algeria, Toggourt; MNHN 3794 (syntypes of *R. rolandi*), Algeria, Zibans, G. Roland; MRAC 76-1-P-387-392, Cameroon; MRAC 93-106-P-0017-19, Gambia, Marakissa, trous eau pour le bétail, 13° 13' N, 16° 39' W, O. Pauwels, 15 July 1993; MRAC 87-18_9-4947-949, Cote d'Ivoire; MRAC 73-10-P-5609-614, Sierra Leone; MRAC 73-10-P-5615-621, Sierra Leone, Rokupi, bras de la Great Scarcies River, T. van den Audenaerde, 6 April 1969; MRAC 73-10-P-5566-575, Cote d'Ivoire, Riv. Cavally, Sahibly, T. van den Audenaerde, 18–19 March 1969; MRAC 80-36-P-3159, Liberia, Duzeim Cetso bekken, M. Louette & P. Rigaux, 28 February 1980; MRAC 153996-153999, Rep. du Tchad, Riv. Mandoul, A. Sutter, March 1965; MRAC 73-10-P-5743-5752, Liberia, Hartford, Ri. St. John, T. van den Audenaerde, 17 May 1969; MRAC 2018-005-P-003, Ghana; SAIAB 75240, Benin, Province Atlantic area, Ouidah River, Mangrove swamps near Ouidah, 6°20'08" N, 02°05'16" E, 7 November 2003; SAIAB 75330, Mali, Senegal River system, River Faleme, Island site, 13°04'04" N, 11°25'52" W, 10 August 2004; SAIAB 75388, Mali, Senegal River system, River Faleme, most upstream site, 13°07'14" N, 11°21'25" W, 8 August 2004; UVZC VZ5732, Egypt, Riv. Nile, A. Oberleuthner, June 2003; UVZC VZ5733, Ghana, Western Region, small creek south of Ankasa NP, 05°11,267' N, 02° 11,873' W, A. Lamboj, 13 February 2018; UVZC VZ5735, Sierra Leone Moa River, N 08°02.989', W 10°57.887', A. Lamboj & A. Mansaray, 7 February 2020; UVZC VZ5736, Sierra Leone, Lake Kwarko, A. Mansaray, 22 March 2023; UVZC VZ5738, Kenia, Lake Turkana, Central Island, N 3°29.8742' E 36°1.4552', Blažek, 5 November 2010; UVZC VZ5739, Senegal, River Niokolo Koba, Lengekountou (tributary of Gambia River), N 13°01.938' W 13°04.898', Reichard & Vošlajerová, 23 March 2006; UVZC VZ5740, Benin, Oueme River system, 07°00'42" N, 02°39' 46" E, col. A. Lamboj, 15 November 2003; UVCZ VZ5741, Senegal, River Koulountou, Gué de Sambailo (tributary of Gambia River), N 12°39.478' W 13°19.852', River Koulountou, Gué de Sambailo (tributary of Gambia River), N 12°39.478' W 13°19.852', Reichard & Vošlajerová, 5 March 2007; UVCZ VZ5741, Senegal, River Niokolo Koba, Passage Koba (tributary of Gambia River), N 13°03.928' W 13°10.144',

Reichard et. Vošlajerová, 3 March 2007, ZSM 26860, Nigeria, Niger Delta, Riv. Sombreiro, about 6 km east of Omoku, T. R. Roberts, 6 September 1987; ZSM 26920, Central African Republic, Chad Basin, Riviere Gounda (near Chad border), T. R. Roberts, August 1988; ZSM 23698, Nigeria, Shonga, Zwilling, April 1951; ZSM 27409, Cote d' Ivoire, Cavally River, Bridge at Sahibly on road from Guilo to Toulepleu, H. Linke, March 1988; ZSM 35695, Ghana, Oda River, restwater pond and small stream at bridge on road Bekwai—Awiankwata, Ashanti Province, Pra River system, D. Neumann, K. Mensah, 30 October–2 November 2002; ZSM 35696, Ghana, Oda River, restwater pond and small stream at bridge on road Bekwai—Awiankwata, Ashanti Province, Pra River system, D. Neumann, K. Mensah, 2 November 2002.



Figure 13. *Rubricatochromis guttatus*. Holotype, BMHN 1860-4-19-3; SL 91.0 mm, scale bar = 1 cm.

Diagnosis: The species can be distinguished from congeners by a combination of often overlapping morphometric and coloration characters. It differs from most congeners except *R. cristatus* and some specimens of *R. stellifer* by a black mid-lateral spot surrounded by a prominent yellow ring, which in parts of specimens can extend anteriorly and posteriorly into a yellow band in the middle of the body that can reach anterior to the black opercular spot and caudal to the end of the caudal peduncle. Differs from *R. bimaculatus* in slightly longer dorsal-fin base (48.4–60.0% SL vs. 46.8–55.9% SL), slightly shorter dentigerous arm of premaxilla (20.5–34.1%, mean 27.8% HL vs. 27.4–35.0%, mean 30.0% HL) and mostly shorter lower jaw (22.9–41.7%, mean 32.4% HL vs. 31.4–41.5%, mean 38.2% HL). It differs from *R. cerasogaster* in having one complete tooth row in both jaws and one incomplete inner row in one or both jaws in some specimens (vs. two to three complete rows and one incomplete inner row) and shorter preorbital distance (8.0–16.9% HL with a mean of 12.5% vs. 12.6–17.3% HL with a mean of 15.2%). It differs from *R. cristatus* in lower body depth (30.7–42.3% SL with a mean of 36.9% vs. 41.1–43.8% SL with a mean of 42.0%) and shorter anal-fin base (15.0–22.6% SL vs. 21.8–23.2% SL). It differs from *R. fugax* in average greater body depth (30.7–42.3% SL with mean of 36.9% vs. 31.0–37.5% SL with mean of 34.1%) and average greater head depth (48.5–69.4% SL with mean of 59.3% vs. 51.3–58.2% SL with mean of 53.9%). It differs from *R. gabonensis* sp. nov. and *R. vanheusdeni* sp. nov. in blue centers of body scales vs. blue margins on body scales. It differs from *R. jebeli* sp. nov. by blue coloration on head, body and fins and red pigment on the body in both sexes vs. vermiculate bronze-brown to golden pattern on cheek and opercle and golden-brown body coloration. It differs from *R. stephenthorntoni* sp. nov. by red pigment on the body in both sexes vs. absence and by dotted blue pattern on opercle vs. vermiculate intense blue pattern on opercle. It differs from *R. stellifer* in somewhat lesser body depth (30.7–42.6% SL vs. 34.0–44.7% SL).

Coloration in life (Figures 14 and 15): Species with the highest variability within the genus. Basic body coloration for smaller or submissive specimens is brownish to rosy-brown. A black mid-lateral spot often, but not always, surrounded by a pale zone. When dominant or breeding, coloration can vary extremely. Individuals may become

completely red on head and body, or red only on the upper or lower half of the body while the remaining parts remain brownish or yellowish. The black mid-lateral spot can be surrounded by a bright yellow ring but may also lack this ring, and the spot may occasionally disappear completely. Blue dots and iridiophores can occur on the head and body in varying numbers but may also be absent in single specimens, and usually in the population of Lake Turkana (originally described as *Hemichromis exsul*). A black spot on the caudal peduncle may be visible or may disappear. All variations in coloration can occur within a single population, but sometimes populations show only one or a few of the possible coloration patterns (e.g., Lake Turkana). Body shape can vary from rounded head and snout to more pointed forms, and body from moderately ovoid and elongated to relatively deep-bodied. Usually variation within populations is higher than variation between populations (see Figures 14 and 15).

Coloration in preserved specimens (Figure 13): Body overall pale brown. Opercular spot consistently present and conspicuous. Midlateral and caudal peduncle spots usually visible, although one or both may be completely absent in some specimens. A few faint dark vertical bars may be present on the dorsal parts of the flanks.

Distribution: Widely distributed in North and West Africa: Egypt, Tunisia, Senegal, Gambia, Guinea-Bissau, Guinea, Sierra Leone, Liberia, Côte d'Ivoire, Ghana, Togo, Benin, Nigeria, Cameroon, Mali, Burkina Faso, Niger, Chad and Kenya (Lake Turkana).

Remarks: Due to the high variability in coloration and body shape, this species is the one within the genus that has caused the most confusion in the past. This variability led to numerous synonymizations and to the description of several populations as separate species. Genetic data of ref. [12] and the present study clearly show that these populations do not differ sufficiently to justify recognition as separate species. However, we cannot exclude the possibility that additional species may be detected in the future with more extensive sampling or more detailed genetic analyses, especially in regions that are still poorly explored.

***Rubricatichromis stellifer* (Loiselle, 1979)**

Synonyms: *Hemichromis stellifer* Loiselle, 1979, *Rubricatichromis lifalili* (Loiselle, 1979), *Hemichromis lifalili* Loiselle, 1979.

Material: Seventy-two specimens; MRAC 68036 (holotype, 16a), Democratic Republic of the Congo, Malembo (Stanley Pool); MRAC 58810-815, Democratic Republic of the Congo, Yakoma-Ubangi, Rosy, 1959; MRAC 37877-37881, Democratic Republic of the Congo, Leopoldville, env. Rivieres et moiss., Dr. Vineke, 1932; MRAC 100834-100838, Democratic Republic of the Congo, Lac Tumba, G. Marlier, 29–30 September 1955; MRAC 76-1-OP-730-732, Democratic Republic of the Congo, Bena Tshadi, Lukibu, Kananga, Mishombiatoka, T. S. Roberts, October 1975; MRAC 100839 (holotype of *R. lifalili*), Democratic Republic of the Congo, Lac Tumba, G. Marlier, 1955; MRAC 100840-842, Democratic Republic of the Congo, Lac Tumba, G. Marlier, 29–30 September 1955; MRAC 22948-22950, Democratic Republic of the Congo, Ruki River, Eala, Dr. van Oyl, 1 February 1923; MRAC 2018-0005-P-0009–0010; AMNH 238578, Democratic Republic of the Congo, Bandundu, Kasai River, 3°9'28" S, 17°9'44" E, Schelly et al., 19 September 2002; MNHN 1926-312-319, Democratic Republic of the Congo, Schouteden; MNHN 1958-131, Democratic Republic of the Congo, Malembo Pool, Poll et al.; MNHN 1962-421, Republic of the Congo, Bozouango, Likouala system, Stauch; MNHN 1962-422, Republic of the Congo, Lokakoua, Kouyou, Stacu; MNHN 1962-423, Republic of the Congo, Likouala River at Mossaka, Stauch; UVZC VZ5737, Democratic Republic of the Congo, Lac Tumba, G. A. Bondoka, 26 July 2023; ZSM 29607, Democratic Republic of the Congo, small stream approx. 500 m west of Semendua, Prov. Bandundu, U. Schliewen, 29 August–4 September 2002; ZSM 29612, Democratic Republic of the Congo, stream at Lompolé, Prov. Bandundu, U. K. Schliewen, 28–29 August 2002; ZSM 29727,

Democratic Republic of the Congo, streams and small rivers around Lui Kotale, Prov. Bandundu, U. Schliwen, 23–27 August 2002; ZSM 29630, Democratic Republic of the Congo, Riv. Lokoro, close to Lui Kotale, Prov. Bandundu, U. K. Schliwen, 23–27 August 2002; ZSM 29631, Democratic Republic of the Congo, Riv. Lokoro, close to Lui Kotale, Prov. Bandundu, U. K. Schliwen, 23–7 August 2002; ZSM 29651, Democratic Republic of the Congo, Riv. Lokoro, close to Lui Kotale, Prov. Bandundu, U. K. Schliwen, 23–27 August 2002.

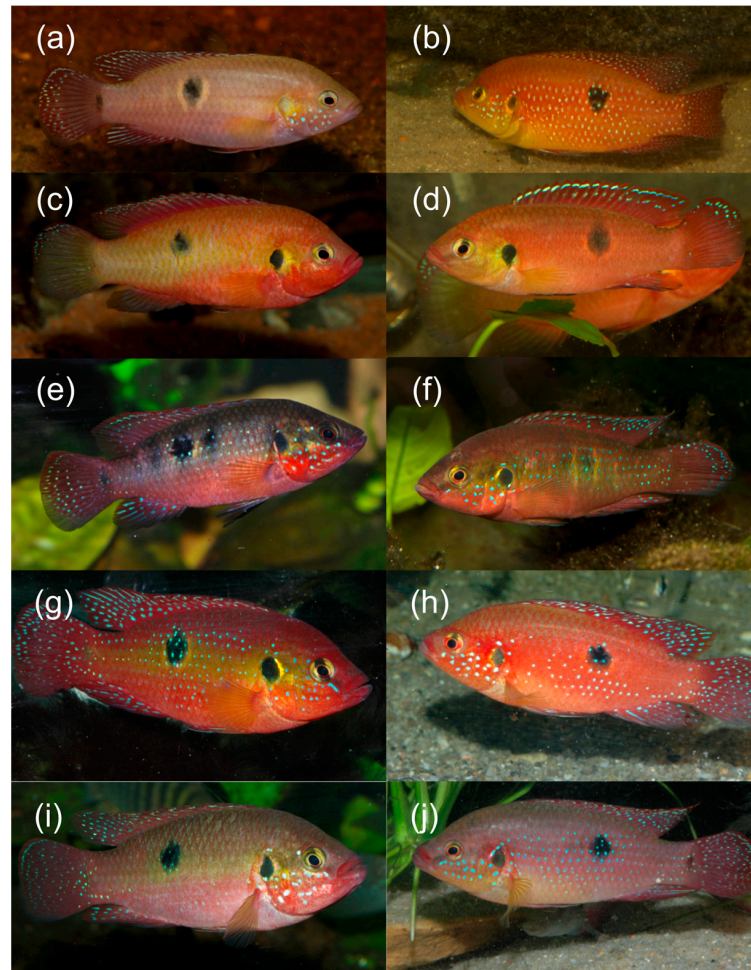


Figure 14. Specimens of *Rubricatichromis guttatus* in an aquarium, to show intraspecific variability in body coloration, both within and among localities. All not preserved, not measured. (a) Guinea-Bissau, Bijagos Island, (b) Guinea, Kolente River, (c,d) Mali, Niger River, (e) Liberia, St. Pauls River, (f) Benin, Natitingou, (g–j) Benin, Ouème River system, 07°10'15" N, 02°39'53" E.

Diagnosis: The species can be distinguished from congeners by a combination of often overlapping morphometric and coloration characters. Differs from *R. bimaculatus* in somewhat greater body depth (34.3–44.7% SL vs. 31.5–40.6%), slightly longer dorsal-fin base (48.3–62.0% SL vs. 46.8–55.9%), longer anal-fin base (18.3–23.0% SL vs. 15.2–20.4%) and a caudal peduncle length of 54.3–85.3% of caudal peduncle depth vs. 64.1–98.7%. It differs from *R. cerasogaster* in having one complete tooth row in both jaws and one incomplete inner row in one or both jaws in some specimens (vs. two to three complete rows and one incomplete inner row), shorter snout length (20.5–32.8% HL vs. 27.3–34.9%), and longer anal-fin base (18.4–23.0% SL vs. 16.7–21.0%). It differs from *R. cristatus* in shallower caudal peduncle depth (14.3–18.6% SL vs. 17.5–19.0%). Differs from *R. fugax* in greater caudal peduncle depth (14.3–18.6% SL vs. 14.2–16.9%). Differs from *R. gabonensis* sp. nov. in blue centers of body scales vs. blue margins

on body scales. Differs from *R. guttatus* in somewhat greater body depth (34.0–44.7% SL vs. 30.7–42.6%). Differs from *R. jebeli* sp. nov. by red pigmentation on head and body vs. absence, by blue coloration markings on head, body and fins vs. absence, and by blue patterns on cheek and opercle (round, ovoid or vermiculate) vs. absence. Differs from *R. stephenthorntoni* sp. nov. by a dotted blue pattern on the opercle vs. vermiculate, intensive patterns and by a rounded or ovoid mid-lateral blotch vs. a mid-lateral bar most prominent above the anterior lateral line and extending into the dorsal fin in specimens larger than 40 mm SL. Differs from *R. vanheusdeni* sp. nov. in lacking blue margins on body scales but having blue centers of scales and dark vertical bars on the body vs. absence, and in shorter predorsal distance (28.6–32.4% SL vs. 30.0–38.0%).



Figure 15. Specimens of *Rubricatichromis guttatus* in an aquarium, to show intraspecific variability in body coloration, both within and among localities. All not preserved, not measured. (a) Kenya, Lake Turkana; (b–d) Ghana, Volta River 05°59.572' N, 00°34.960' E; (e–g) Sierra Leone, little creek near village of Moyowa, 07°38.112' N, 12°07.225' W; (h–j) Egypt, Lake Maryut.

Coloration in life (Figure 16b): Basic body coloration pale yellowish-brown, dorsum somewhat darker. Cheeks and opercles golden to yellow. Ten to twelve dark vertical bars often present on the body, reaching from the dorsum to near the belly. Small dark blotches often present on dorsal parts of the body and on unpaired fins. Iridiophores may occur on all parts of the body but are usually concentrated on the head, dorsal fin, and caudal fin. Most body scales have a blue spot in their center. Head brownish with blue iridescent spots and interrupted vermiculate stripes on lower parts of cheeks and opercles. When dominant, lower parts of head and body are orange to red. A rounded lateral spot situated somewhat above the center of the body, in parts of specimens surrounded by a thin pale zone. A dark spot on the caudal peduncle may be present or absent depending on behavioral context.

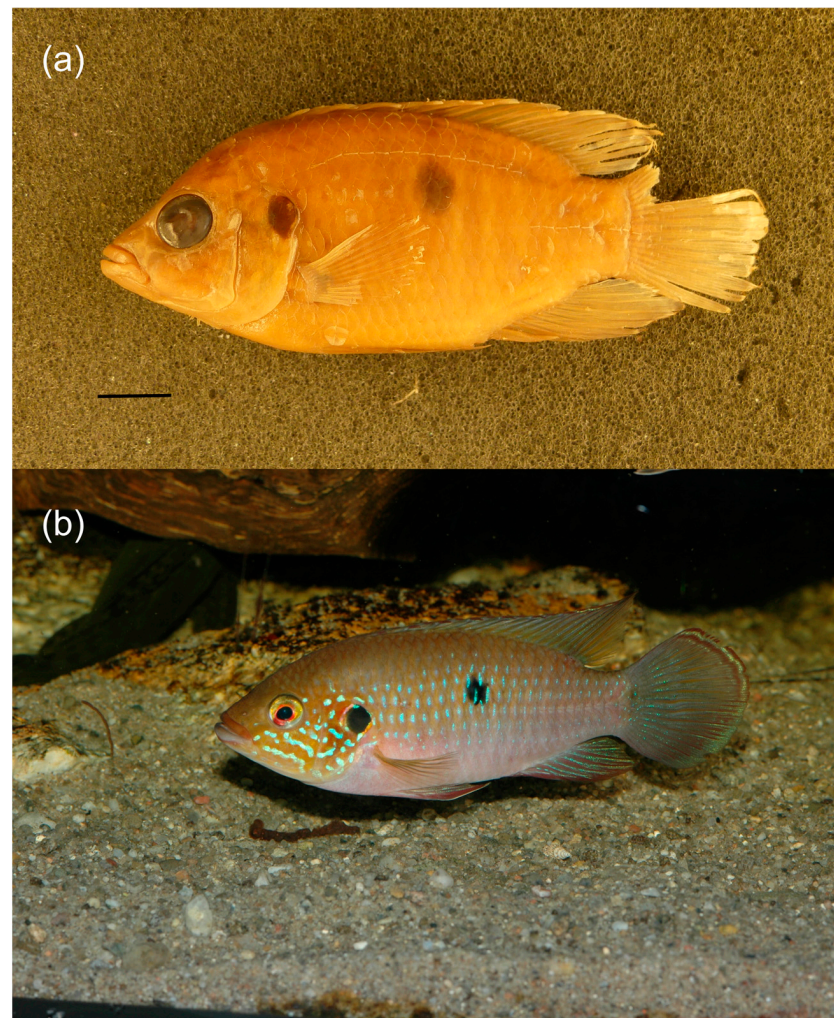


Figure 16. *Rubricatochromis stellifer*. (a) Holotype, MRAC 68036, SL 70.5 mm. Democratic Republic of the Congo, Stanley Pool, Scale bar = 1 cm, Photo: MRAC. (b) Male in an aquarium, Democratic Republic of the Congo, Stanley Pool, not preserved, not measured.

Coloration in preserved specimens (Figure 16a). Body coloration pale brown. Opercular spot consistently present and conspicuous. Midlateral spot present in most specimens; caudal peduncle spot absent in most specimens. Ten to twelve faint dark vertical bars may be visible in some individuals.

Distribution. Democratic Republic of the Congo, Republic of the Congo and Cameroon; Congo River system. Possibly also occurring in the Central African Republic.

Remarks. Loiselle [10] designated a specimen from Lake Tumba as the holotype of *Rubricatochromis lifalili*. Based on DNA data, morphology, and coloration, specimens

collected in Lake Tumba in 2023 cluster with *Rubricatochromis stellifer* from other parts of the Congo River system. *Rubricatochromis lifalili* is therefore considered herein a junior synonym of *R. stellifer*. As *R. stellifer* was described earlier in [10] (p. 81) than *R. lifalili* (p. 113), the former name has priority.

4. Discussion

The integrative phylogenetic framework established by Lamboj & Koblmüller [12] provided the first robust hypothesis of relationships within *Rubricatochromis* and demonstrated its clear separation from *Hemichromis*, with an estimated divergence time of approximately 6–12 million years. The recovery of four principal clades in ref. [12] already indicated substantial intrageneric differentiation with a pronounced geographic signal, separating northern (Nilo-Sudanian and Upper Guinean) from southern (Lower Guinean/Congo) lineages. The present revision, based on expanded sampling and additional molecular and morphological data, refines this framework, resulting in the description of four new species and the revalidation of *R. fugax*, while clarifying the status of several historically controversial taxa.

The overall distribution of *Rubricatochromis* corresponds to a “type 1” Afrotropical distribution sensu Lévêque [51] (Figure 17), a pattern also documented in several other freshwater fish species and genera that show various degrees of geographic structure across their distribution range (e.g., [52–54]). The genus’ distribution ranges from the lower and upper reaches of the Nile River, including the Lake Turkana basin, westward to the Senegal River and Gambia River systems, and southward into the Congo River drainage. This extensive distribution corresponds broadly to the Nilo-Sudanian ichthyogeographic province and reflects former hydrographic connectivity across northern tropical Africa. The northern representatives of the genus display a classical Nilo-Sudanian distribution pattern [55]. The occurrence of *Rubricatochromis* in isolated oases of Tunisia and Algeria is most plausibly explained by Pleistocene climatic oscillations. During pluvial phases, extensive lacustrine and fluvial systems developed across what is today the Sahara, facilitating dispersal of freshwater fishes through hydrological corridors that no longer exist. It has been proposed that during the last major pluvial period, hydrographic connections linked the Nile with the Lake Turkana basin as well as the Niger and Chad systems, and possibly also established temporary links between the Nile and Chad basins [55]. Additional connections between central Saharan massifs and the Senegal, Niger, and Chad drainages would account for the present-day distribution of *R. guttatus*, which represents the most widespread species of the genus. In addition, as popular aquarium fish, *Rubricatochromis*, and in particular *R. guttatus*, have established populations outside their natural distribution range in Asia, Europe, and the Americas (e.g., [56–63]). Indeed, all specimens originating from outside the native range of *Rubricatochromis* (including established populations in thermal springs in Europe) included in our study clustered unambiguously within the *R. guttatus* clade.

Ecologically, *R. guttatus* appears to be the most adaptable member of *Rubricatochromis*, particularly in West Africa. In contrast, congeners such as *R. vanheusdeni* sp. nov. in Ghana, *R. bimaculatus* in Liberia, and *R. fugax* in Sierra Leone seem to be more closely associated with forested habitats and are restricted to comparatively small areas that likely retained forest cover during late Quaternary arid phases. Although *R. guttatus* may occur in close geographic proximity to these taxa, it is typically found in more open habitats, including savanna regions or water bodies with reduced canopy cover. A striking characteristic of *R. guttatus* is its pronounced color polymorphism. Some populations exhibit extensive sympatric color variation, whereas others display only one or two morphs; however, these morphs recur across widely separated localities. In general, phenotypic variation within populations often exceeds variation between populations. The mechanisms underlying this

pattern remain unclear, but the shallow genetic differentiation observed among populations throughout the species' broad range strongly supports their conspecific status. On this basis, *R. exsul*, *R. letourneuxi*, *R. paynei*, and *R. saharae* are here regarded as junior synonyms of *R. guttatus*.

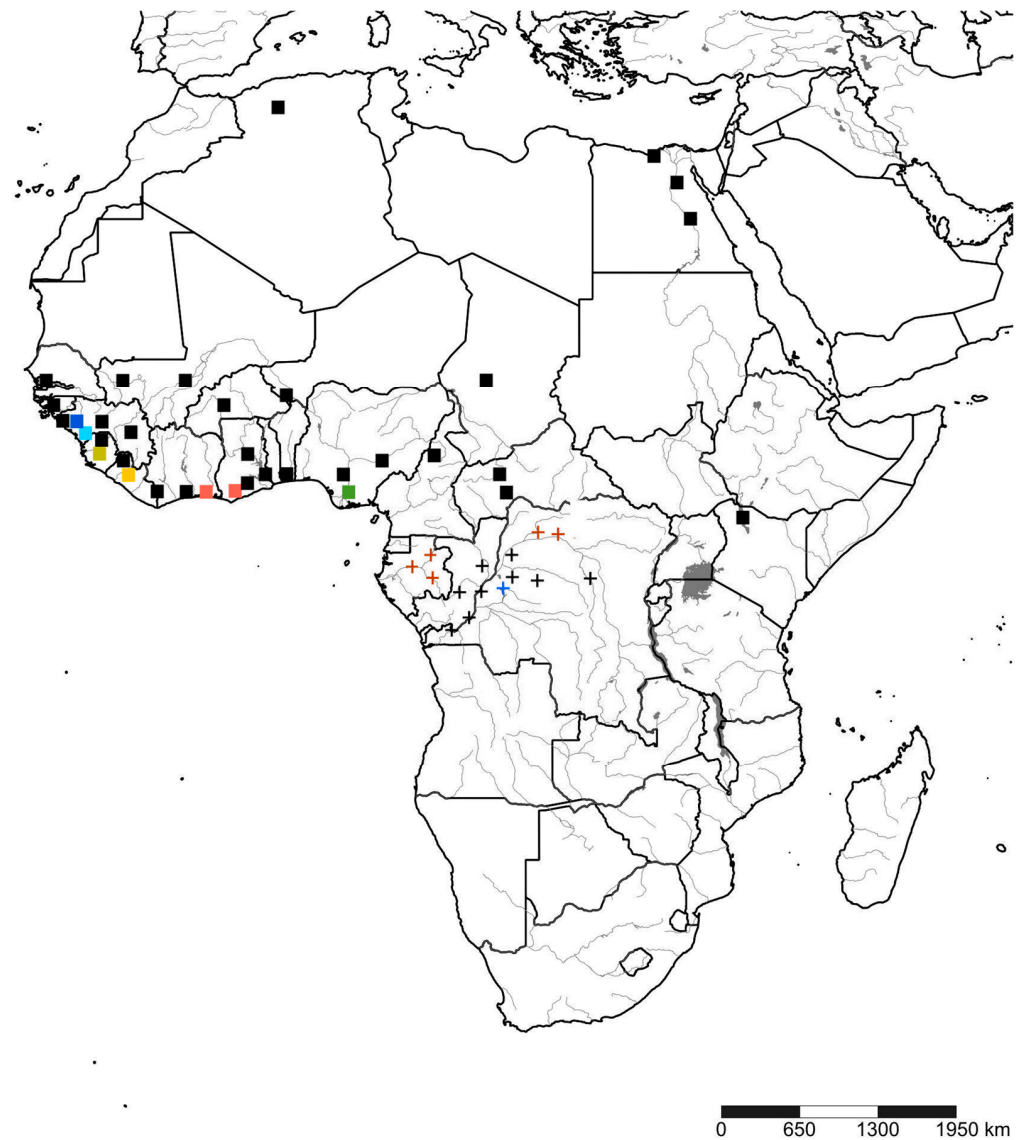


Figure 17. Distribution/occurrence records of *Rubricatichromis* species based on specimens/sequences with coordinates. Northern species are indicated by squares: black, *R. guttatus*; dark blue, *R. jebeli* sp. nov.; light blue, *R. stephenthorntoni* sp. nov.; olive green, *R. fugax*; yellow, *R. bimaculatus*; red, *R. vanheusdeni* sp. nov.; green, *R. cristatus*. Southern species are indicated by crosses: black, *R. stellifer*; brown, *R. gabonensis* sp. nov.; blue, *R. cerasogaster*. Map created using Natural Earth geographic data (public domain).

In contrast to the broad Nilo-Sudanian distribution of northern taxa, the southern representatives of *Rubricatichromis* show a more geographically structured pattern, as has already been noted by [19]. *Rubricatichromis gabonensis* sp. nov. occurs in the Ogooué River system in Gabon and a relatively small region in the upper Congo River basin in the Democratic Republic of the Congo, whereas *R. cerasogaster* and *R. stellifer* occur within the Congo River basin. Among these, *R. cerasogaster* seems confined to the Lake Mai-Ndombe region. Genetic data from topotypical material of *R. lifalili* clearly assign this taxon to *R. stellifer*, supporting its synonymization. Preliminary molecular evidence suggests that some

R. stellifer populations (e.g., Loboya) may represent distinct evolutionary lineages, with levels of divergence comparable to those separating *R. cerasogaster* and *R. stellifer*. Pending the availability of additional material—particularly data on live coloration, morphometrics, and meristics—we provisionally treat these populations as *R. stellifer*.

Morphological differentiation within *Rubricatochromis* is generally subtle and complicated by extensive character overlap. Despite statistically significant differences between species in the multivariate morphospace, diagnostic morphological characters are largely absent. Most morphometric characters show broad and overlapping ranges, especially in the two most widely distributed taxa, *R. guttatus* and *R. stellifer*. Both species display considerable phenotypic plasticity, which reduces the diagnostic value of body proportions. Only *R. fugax* and *R. bimaculatus* consistently exhibit a more elongate body form, a distinction also reflected in multivariate analyses. Meristic characters are highly conserved across the genus, with the notable exception of *R. cerasogaster*, which possesses a higher number of complete tooth rows in both upper and lower jaws than its congeners. In the absence of stable diagnostic morphological traits, species delimitation in the present revision relies primarily on molecular evidence.

The partial incongruence among the applied molecular species delimitation approaches highlights the methodological challenges associated with delimiting recently diverged lineages. Distance-based and tree-based methods differ fundamentally in their assumptions regarding branching processes, coalescent dynamics, rates of lineage diversification, and thresholds of lineage divergence. Single-locus approaches are known to be sensitive to population structure, uneven sampling, and recent divergence, which may result in either taxonomic inflation or underestimation of species boundaries depending on the demographic history of the taxa involved and the particular algorithm applied [64,65]. The comparatively finer partitioning recovered by PTP in the present study is not unexpected and likely reflects the tendency of this method to delimit narrowly defined lineages in DNA barcoding datasets. In addition, our dataset is not ideally suited for character-based molecular species delimitation, as sample sizes for several taxa are small, in some cases consisting of only two sequences. Restricted intraspecific sampling can substantially reduce the reliability of DNA-based species delimitation by failing to adequately capture within-species genetic variation and geographic structure [66]. Consequently, the robust identification of fixed diagnostic molecular characters that might be included in species diagnoses (as, e.g., in [67–69]) is currently not possible for several taxa within the genus, because apparently unique nucleotide substitutions may in part simply reflect insufficient sampling rather than true species-specific character states.

The synonymizations proposed herein should be regarded as hypotheses based on the currently available evidence, including the present morphometric, meristic, and single-locus dataset, and the multilocus framework of [12], which was based on two mitochondrial and two nuclear genes. Future studies employing genomic-scale datasets (e.g., RADseq, UCEs, or whole-genome data) are likely to provide substantially higher phylogenetic resolution and greater power to disentangle recent speciation events, introgression, and incomplete lineage sorting than single-locus or few-locus approaches, particularly in recently diverged taxa. Genome-wide datasets have repeatedly been shown to improve species delimitation and phylogenetic inference in systems characterized by shallow divergence and gene-tree discordance arising from incomplete lineage sorting and/or hybridization [70,71]. Consequently, some of the taxonomic decisions proposed here may require reevaluation as more comprehensive genomic evidence becomes available.

The systematics of *Rubricatochromis* has long been characterized by taxonomic instability [10]. For instance, Loiselles [10] proposed several synonymies, including *R. fugax* with *R. bimaculatus*, *R. rolandi* and *R. saharae* with *R. letourneuxi*, and *R. exsul* with *R. guttatus*,

and suggested groupings of West and Central African taxa based on squamation patterns, dentition, and coloration, particularly the position of the mid-lateral blotch. Subsequent authors did not consistently accept these synonymies, and species numbers were often reduced because of the practical difficulty of distinguishing taxa based on overlapping morphological characters. Conversely, some species were later recognized as valid by aquarists or individual researchers without comprehensive published revisions. As a result, the taxonomy of the genus remained unsettled for decades. The present revision sought to resolve these longstanding ambiguities by integrating broad geographic sampling with molecular data, thereby providing a (hopefully) more stable and evolutionarily informed taxonomic framework for *Rubricatochromis*.

Beyond their taxonomic significance, the results of the present revision also have important conservation implications. Several of the newly recognized and confirmed taxa appear, based on current knowledge, to have highly restricted distribution ranges and pronounced habitat specificity. They are currently known only from comparatively small forest-associated drainage systems. Given the ongoing anthropogenic pressure on West and Central African freshwater ecosystems, formal conservation assessments following IUCN Red List criteria appear urgently needed for several *Rubricatochromis* species, especially those apparently confined to single drainage systems or isolated forest refugia. At the same time, the widespread use of *Rubricatochromis* in the aquarium trade and the documented establishment of *R. guttatus* outside its native range indicate a potential risk of further introductions into suitable habitats. Accurate species identification will be important for assessing the origin and potential ecological significance of such introductions and for informing appropriate management responses. Additional field surveys will furthermore be essential to better assess the species' true distribution ranges, population sizes, and potential conservation threats.

Supplementary Materials: The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/fishes11090531/s1>: Table S1: Sample list with Genbank accession number or BOLD-ID, original species-ID, new species assignment according to the revision of *Rubricatochromis*, and, if available, country of origin; Table S2: Morphometric raw data (measurements in mm) for the entire dataset; Table S3: Meristic data for the entire dataset; Table S4: Morphometric raw data for the species herein synonymized with *R. guttatus*; Table S5: Meristic raw data for the species herein synonymized with *R. guttatus*; Table S6: PC loadings of the morphometric characters (whole dataset); Table S7: Results (*p*-values) of pairwise PERMANOVAs for the morphometric data of all *Rubricatochromis* species; Table S8: PC loadings of the meristic characters (whole dataset); Table S9: Results (*p*-values) of pairwise PERMANOVAs for the meristic data of all *Rubricatochromis* species; Table S10: PC loadings of the morphometric characters (for species now synonymized with *R. guttatus*); Table S11: Results (*p*-values) of pairwise PERMANOVAs for the morphometric data of previously recognized species now synonymized with *R. guttatus*; Table S12: PC loadings of the meristic characters (for species now synonymized with *R. guttatus*); Table S13: Results (*p*-values) of pairwise PERMANOVAs for the meristic data of previously recognized species now synonymized with *R. guttatus*.

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Informed Consent Statement: Not applicable.

Data Availability Statement: DNA sequence data generated in this study are available from GenBank under the accession numbers PZ684585, PZ684675; information on previously published DNA sequence data used in the present study is available in Table S1. The morphometric and meristic raw data are available in Tables S2–S5.

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