

***Vanneaugobius longignathus*, a new gobiid species  
from São Tomé Island (eastern tropical Atlantic),  
with a rediagnosis of the genera *Wheelerigobius* and *Vanneaugobius***

(Teleostei, Gobiiformes, Gobiidae)

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A new species of goby, *Vanneaugobius longignathus* sp. nov., is described from São Tomé Island, eastern tropical Atlantic. The new goby belongs to the *Gobius*-lineage (Teleostei, Gobioidae, Gobiidae). Examination of the two known specimens showed a unique combination of morphological characters. The new species differs from both other *Vanneaugobius* species by each of the following characters: head wide and depressed, anterior tip of the mouth above the level of the edge of the lower eye, posterior angle of jaw ending posteriorly below posterior iris, suborbital longitudinal row *b* anteriorly ending distally behind the vertical of the posterior edge of eye, no transverse rows *c* above or below row *b*, six suborbital transverse *c* rows of sensory papillae, suborbital longitudinal row *d* divided, anterior dorsal transverse row *o* distant at the dorsal midline from the equivalent row. The genera *Vanneaugobius* and *Wheelerigobius* are redescribed, and, based on molecular phylogenetic evidence and reassessment of morphological characters, *Vanneaugobius canariensis* is reassigned to the genus *Wheelerigobius*.

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## Introduction

The goby-like fishes of the suborder Gobioidae, one of three suborders in the order of Gobiiformes (sensu Near & Thacker 2024) represent almost two thousand five hundred species (Fricke et al. 2025). They are classified in a varying number of families and subfamilies, the number and composition depending on authors (e.g. Larson 2022 vs. Near & Thacker 2024). One of the groups alone, classified either as a family Gobiidae or a subfamily Gobiinae, with 201 new species described in the past decade, has the largest number of new species descriptions (Fricke et al. 2025). Recently, several new species and three new genera (Kovačić et al. 2019b, Iglésias et al. 2021, Schliewen et al. 2023, and references therein) have been described in the monophyletic Afro-European *Gobius*-lineage (sensu Agorreta et al. 2013), even though this lineage is mostly distributed in the well-studied European seas. However, a few of these new species have been found in the tropical eastern Atlantic (Kovačić et al. 2020, Schliewen et al. 2023 and references therein). In 2023 one of us (PW) collected two specimens of an apparently new species at the coast of São Tomé Island (Democratic Republic of São Tomé and Príncipe) showing similarities with the genera *Odondebuena* de Buen, 1930, *Vanneaugobius* Brownell, 1978 and *Wheelerigobius* Miller, 1981. Morphological examination of the specimen confirmed a unique combination of characters of the undescribed species. Molecular phylogenetic analysis based on a representative outgroup sampling of gobies related to the *Gobius*-lineage and *Gobius*-lineage specimens unambiguously placed the new species in the *Vanneaugobius* clade. The aim of the present study is to describe the new species from the tropical eastern Atlantic, to present the molecular phylogenetic results regarding the placement of the new species and to suggest taxonomical consequences based on these results, i.e. the redescription of the two genera *Vanneaugobius* and *Wheelerigobius*, as well as to reassign *V. canariensis* Van Tassell, Miller & Brito, 1988 to the genus *Wheelerigobius*.

## Materials and methods

Both specimens were collected in front of the village Água Izé, São Tomé Island (0.211°N, 6.740°E) on 29 January 2023. They were collected at 26 m depth from a rocky outcrop on sandy/silty bottom by SCUBA diving using the anesthetic Quinaldine, and subsequently fixed in 96 % ethanol under anaesthesia.

Morphometric methods, measurements, and definitions correspond to those used in Schliewen & Kovačić (2008). Measurements smaller than 20 mm were taken with interactively selected points in Olympus cellSens

Entry 2.2. software using a camera Olympus SC180 camera and an Olympus U-TV0.5XC-3 camera adapter on the stereomicroscope Olympus SZX10. The length of the specimens is presented as standard length + caudal-fin length. Standard length (SL) is measured from the median anterior point of the upper lip to the base of the caudal fin (posterior end of the hypural plate). Morphometric data are given as a ratio in the text and as percentages of SL in Table 1. Count of scales and fins follows Schliewen et al. (2018). Terminology of the lateral-line system follows Kovačić & Svensen (2024), for the head lateral line system (HLLS). For the trunk and caudal fin lateral line system (TCLS), we adopt the nomenclature and numbering of Ahnelt & Bohacek (2004), modified from Sanzo (1911); however, instead of using superscript numbering for the TCLS we use normal line typing in order to harmonize its use with the one for the HLLS in Kovačić & Svensen (2024). The term “ventrolateral head ridge” (Kovačić et al. 2019b) describes the ridge on the underside of the head formed by the ventral margin of the cheek, ending anteriorly below lips.

Meristic counts related to fin spines and rays and vertebrae, including first dorsal fin pterygiophore formula (Birdsong et al. 1988) are based on digital x-rays made with a Faxitron Ultrafocus X-ray cabinet at SNSB-ZSM.

The type material and the comparative material have been deposited in SNSB-ZSM – Bavarian State Collection of Zoology, Munich, Germany and in PMR – Natural History Museum, Rijeka, Croatia.

Molecular phylogenetic methods are based on partial mitochondrial DNA loci (12S and 16S rRNA, cytochrome oxidase subunit I (COI) and cytochrome b (CYTB) and on three partial nuclear protein coding genes (G protein-coupled receptor 85 (GPR85), recombination activating gene 1 (RAG1), and zinc finger protein zic1 (ZIC1)). The selection of loci is based on Agorreta et al. (2013), except for the barcoding fragment of COI. Comparative data were retrieved either from Genbank, or were generated de novo either by PCR amplification and Sanger sequencing (for most sequences of the single available sample of *Vanneaugobius pruvoti* (Fage, 1907)) or by genome skimming of whole genome sequencing (WGS) shotgun libraries sequenced from DNA-extracts by Biomarker Technologies GmbH (Münster, Germany). Genome skimming was performed on the adaptor trimmed and quality filtered (Phred Score >30) sequence reads using the “Medium-Low Sensitivity/Fast” option of the Geneious mapper as implemented Geneious Prime v. 2023.1.2 (Biomatters Ltd.). We used a minimum mapping quality of 30 against Genbank sequences of closely related Gobiidae-taxa, mostly from the study of Agorreta et al. (2013). Genbank and consensus sequences were aligned using MAFFT v7.490 (Katoh & Standley 2013) with default parameters as implemented in Geneious Prime and cut to equal length with a reading frame of 1<sup>st</sup>, 2<sup>nd</sup> and 3<sup>rd</sup> codon positions for protein coding genes. Since preliminary analyses revealed strong mito-nuclear discordance with regard to the phylogenetic placement of *Gymnesigobius medits* we performed separate maximum

likelihood (ML) and Bayesian inference (BI) phylogenetic analyses for the mitochondrial and nuclear DNA data set. ML inferences were conducted with W-IQ-TREE (Trifinopoulos et al. 2016) after selecting the best model and partition with ModelFinder and with 1000 ultrafast bootstrap replicates (as implemented in W-IQ-TREE based on Chernomor et al. (2016), Kalyaanamoorthy et al. (2017), Hoang et al. (2018)). BI were conducted with the Mr Bayes 3.2.6 (Huelsenbeck & Ronquist (2001) plugin in Geneious Prime under the General Time Reversible +  $\Gamma$  (GTR) model with five  $\Gamma$  categories, unconstrained branch lengths, 1100100 chain length and a burnin of 100000.

Comparative taxon sampling included one distant outgroup of the gobioid family Thalasseleotrididae, i.e. *Grahamichthys radiatus* (Valenciennes, 1837), and one or two representatives of each of the different Gobiidae lineages defined by Agorreta et al. (2013), i.e. *Glossogobius*-, *Asterropteryx*-, *Lophogobius*-, *Aphia*-, *Valenciennea*-, *Gobio*-, *Cryptocentrus*-, *Gunnellichthys*-, *Priolepis*- and *Gobiosomatini*-lineages (*Callogobius* and *Kraemeria*-lineage were not included), and representative members of all major *Gobius*-lineage clades as derived from Agorreta et al. (2013), Neilson & Stepien (2009), Thacker & Roje (2011), Kovačić et al. (2019a,b, 2021), Schliewen et al. (2023), all *Vanneaugobius*, *Odondenbuena* and *Wheelerigobius* species, *Gymnesigobius medits* Kovačić, Ordines, Ramirez-Amaro & Schliewen, 2019 and the new species. The final taxon sampling consisted of 54 taxa, and the length of the two final concatenated alignments of the four mitochondrial loci and of the three nuclear genes consisted of 3'525 bp and 3'288 bp, respectively. For voucher specimen information and Genbank accession numbers of published and newly generated sequences see Appendix 1.

# Results

## Genetics and phylogeny

Phylogenetic analysis of mitochondrial and nuclear DNA sequences clearly support (BS 100 % and 1.0 PP) the new species assignment, with *Vanneaugobius pruvoti* as the sister taxon and *Vanneaugobius dollfusi* Brownell, 1978 being the sister taxon of the taxon pair *V. longignathus* – *V. pruvoti* (Fig. 1). Both the mitochondrial and nuclear DNA analyses identified the monotypic genus *Odondenbuena* as the sister taxon to the three species *V. pruvoti*, *V. longignathus* and *V. dollfusi* (BS 100 % and 1.0 PP), whereas the only other *Vanneaugobius* species, *V. canariensis* is identified as the sistergroup of two *Wheele-*

**Table 1.** Morphometric characters (as proportional measurements in %) of *Vanneaugobius longignathus* sp. nov.

Specimen	ZSM48375 PMR VP6169	
	Holotype	Paratype
Sex	male	female
Standard length (SL) in mm	22.48	26.84
% of standard length		
1st spine length of first dorsal fin	33.5	12.3
2nd spine length of first dorsal fin	14.7	12.2
3rd spine length of first dorsal fin	12.5	12.1
Anal fin base	21.3	20.1
Anal fin spine length	8.0	7.3
Body depth at anal fin origin	14.1	15.3
Body depth at pelvic fin origin	14.4	15.2
Body width at anal fin origin	12.4	12.6
Body width at pelvic fin origin	19.8	20.6
Caudal fin length	27.0	25.1
Caudal peduncle depth	11.5	11.3
Caudal peduncle length	21.3	22.3
Eye diameter no ligaments	6.7	6.5
First dorsal fin base	13.9	12.7
Head depth at mideye	12.4	12.1
Head length	29.2	27.7
Head width at opercles	19.4	20.2
Interdorsal space	7.3	7.7
Pectoral fin length	23.0	23.3
Pelvic fin length	21.9	25.5
Pelvic spine length	5.3	5.9
Pelvic to anus	24.9	26.3
Second dorsal fin base	23.1	23.9
Second dorsal fin spine length	14.9	7.3
Snout to origin of first dorsal fin	31.1	29.6
Snout to origin of second dorsal fin	50.5	50.2
Snout to vertical of anal fin origin	55.6	58.7
Snout to vertical of anus	49.2	52.1
Snout to vertical of pelvic fin origin	23.0	25.1
The greatest body depth	15.5	15.7
% of caudal peduncle		
Caudal peduncle depth	54.2	50.6
% of head length		
Anterior upper lip width	7.8	8.3
Cheek depth	23.3	23.5
Eye diameter	23.0	23.4
Head depth	42.5	43.7
Head width	66.6	72.8
Lateral preorbital depth	6.9	6.3
Maximum lip width	7.2	8.3
Postorbital length	61.1	63.0
Snout length	25.2	24.9
Upper lip length	44.5	45.0
% of eye diameter		
Interorbital width	23.8	23.0
% of pelvic to anus		
Pelvic fin length	88.0	96.9

*rigobius* species (BS 100 % and 1.0 PP), i.e. *W. wirtzi* Miller, 1988 and *W. maltzani* (Steindachner, 1881) (BS  $\geq 94$  % and 1.0 PP in all analyses). Based on these analyses, *Vanneaugobius* is paraphyletic with respect to *Wheelerigobius*, as it had already been suggested by previous mtDNA-based analyses (Kovačić et al 2019b). *Gymnesigobius medits*, the only other putative member of the *Vanneaugobius*–*Odondebuenia*–*Wheelerigobius*-clade (i.e. the VOW-clade sensu Kovačić et al 2019b) is in the mtDNA phylogeny nested with strong statistical support within the VOW-clade as the sistergroup of *Odondebuenia* and *Vanneaugobius* without *V. canariensis* (BS 96 % and 1.0 PP); or it is placed in the nucDNA phylogeny outside of the strongly supported clade consisting of *Vanneaugobius*–*Odondebuenia*–*Wheelerigobius* (BS 100 % and 1.0 PP). In the nucDNA phylogeny, *G. medits* is grouped with rather weak statistical support (BS 82 % and 0.93 PP) as the sistergroup to a clade within the *Gobius*-lineage (BS 98 % and 1.0 PP), composed of *Gobius*, *Thorogobius*, *Neogobius*, *Ponticola*, *Proterorhinus* and *Benthophilus* species in our dataset. Thus, the phylogenetic position of *G. medits* is not consolidated with regard to its placement within the *Gobius*-lineage, as nuclear and mtDNA support alternative hypotheses. All other phylogenetic results of our dataset are generally in line with previous analyses (e.g. Agorreta et al. 2013, Kovačić et al. 2019a) and are not further presented here. For phylogenetic trees and all associated BS and PP supports based on ML and BI analyses of mitochondrial and nuclear loci refer to Figure 1.

### Taxonomy

Our molecular phylogenetic results revealed a close relationship between the new species and the two *Vanneaugobius* species, *V. dollfusi*, the type species of *Vanneaugobius*, and *V. pruvoti*. The strong support for paraphyly of *Vanneaugobius* with respect to *Wheelerigobius* (i.e. the placement of *V. canariensis*) and divergent morphological characters of the new species made a reevaluation of diagnostic morphological characters for *Vanneaugobius* and *Wheelerigobius* necessary. This evaluation supported the reassignment of *V. canariensis* to *Wheelerigobius*, and made a re-diagnosis of the genera *Vanneaugobius* and *Wheelerigobius* necessary.

#### *Wheelerigobius* Miller, 1981

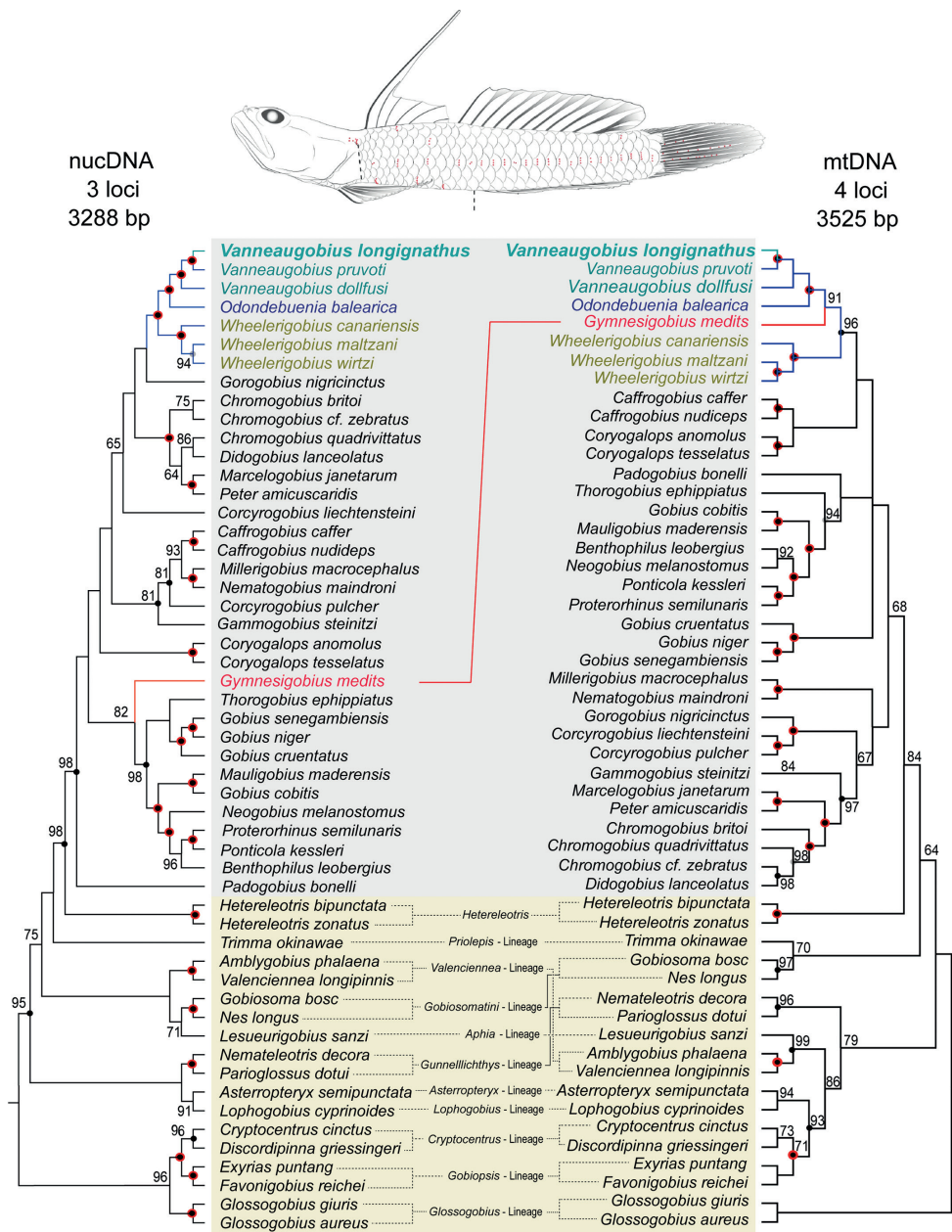
**Diagnosis.** (1) Anterior nostril tubular, not reaching upper lip and without process from rim; (2) posterior nostril flat pore; (3) chin without fold or

barbels; (4) mouth with anterior tip below horizontal level of lower eye edge; (5) pelvic fins divided, only low dermal ridge present between left and right fin; (6) pelvic fin anterior membrane (frenum) absent; (7) predorsal area naked, first dorsal fin base scaled; (8) uppermost and lowermost scales on base of caudal fin with enlarged ctenii; (9) head with anterior and posterior oculoscapular and preopercular canals, with pores  $\sigma$ ,  $\lambda$ ,  $\kappa$ ,  $\omega$ ,  $\alpha$ ,  $\beta$ ,  $\rho$ ,  $\theta$ ,  $\tau$  and  $\gamma$ ,  $\delta$ ,  $\epsilon$  respectively; (10) pores of head canals not enlarged, e.g. pores  $\alpha$  and  $\rho$  half of size or less as their interspaces to pore  $\beta$ ; (11) four anterior transverse suborbital *c* rows continuous, the fifth *c* row divided, one or two posteriormost *c* rows just with upper parts; (12) transverse suborbital row *c*5 divided in three parts.

This diagnosis is the combination of the selected important characters that distinguish *Wheelerigobius* from the other 27 genera presently assigned to the “*Gobius*-lineage” based on genetics (Neilson & Stepien 2009, Thacker & Roje 2011, Agorreta et al. 2013, Kovačić et al. 2019a, 2021, Schliewen et al. 2023, and the results of the phylogenetic analysis in the present study (Appendix 1, Fig. 1). A selected character was considered diagnostic for the newly defined *Wheelerigobius*, if it was not variable among species of any compared genus, i.e. if it differentiates trenchantly between the newly defined genus *Wheelerigobius* and each of the species of a compared genus; the only exception is a single *Coryogalops* species which differs from other congeners by separate pelvic fins, *Coryogalops anomolus* Smith, 1958, but which is nevertheless placed in the same genus. The different genera of the “*Gobius*-lineage” sensu Agorreta et al. (2013) differ by 4–8 out of twelve characters from the different genera of the “*Gobius*-lineage” (Table 2).

### Description

Body moderately elongate, laterally more compressed towards caudal peduncle, height gently decreasing from the trunk posterior end of trunk backwards. Caudal peduncle strong. Head of moderate size, subcylindrical. Snout oblique, with convex profile, much shorter to shorter than eye. Anterior nostril tubular, not reaching upper lip and without process from rim; posterior nostril flat pore. Eyes large, dorsolateral, elevated or slightly elevated above dorsal profile. Eye diameter about one third of the distance between mouth tip and preopercular edge. Interorbital space very narrow. Mouth terminal, lower and upper jaws ending anteriorly at about the same vertical level, gently oblique to oblique, with anterior tip below level of lower eye edge. Mouth moderately large, posterior angle of jaws end-



**Fig. 1.** Bayesian Inference (BI) phylogeny phylogenetic tree topology based on three concatenated nuclear loci (partial *zic1*, *rag1*, *gpr85* genes) (left) or four concatenated mitochondrial loci (partial 12s rRNA, 16s rRNA, COI and CYTB genes). Numbers on branches are ultrafast bootstrap support (BS) values >60 and <100 for the Maximum Likelihood (ML) analysis in IQtree; black dots a nodes indicate posterior probabilities (PP) 1.0, grey dots PP 0.99 values of the BI analysis, red circles indicated BS values of 100. Taxon names of members of the VOW-clade and *Gymnesigobius medits* are differentially coloured according to genus. The red connecting line highlights the mito-nuclear discordant phylogenetic placement of *Gymnesigobius medits*. Taxon names of *Gobius*-lineage members sensu Agorreta et al. (2013) are shaded light grey, those of other Gobiidae-lineages greenish. The trees are rooted with the Thalasseleotrididae outgroup *Grahamichthys radiatus* (not shown). Inserted: Drawing of holotype of *V. longignathus* sp. nov. Drawing: R. Böhmer.

**Table 2.** Comparison of the twelve diagnostic characters of *Vanneaugobius* with other genera of the “Gobius-lineage” sensu Agorretta et al. (2013), with additional genera included to “Gobius-lineage” based on Neilson & Stepien 2009, Thacker & Roje 2011, Kovačić et al. 2019a,b, 2021, Schliewen et al. 2023, and the results of the phylogenetic analysis in the present paper (Appendix 1, Fig. 2). The characters are based on the data in the cited references in the table and on the studied type material of the new species and comparative material of other species, see Comparative material examined for details. 1, Anterior nostril; 2, Posterior nostril; 3, Chin; 4, Mouth anterior tip position; 5, Pelvic fin anterior membrane; 6, Connection of pelvic rays; 7, Predorsal and first dorsal fin base squamation; 8, Uppermost and lowermost scales on base of caudal fin; 9, Posterior oculoscapular canal; 10, The size of pores; 11, Number of continuous rows + upper/lower parts of divided and partial suborbital transversal *c* rows; 12, Suborbital transversal row *c*5.

Genus	Source of data (*studied material)	1	2	3	4	5
<i>Vanneaugobius</i> Brownell, 1978	Brownell 1978, Van Tassell et al. 1988, Kovačić 2008	long tube overlap- ping lip and no process from rim	short tube	without fold or barbels	in the level of lower eye edge or above	missing
<i>Babka</i> Iljin, 1927	Miller 2003	short tube	flat pore	without fold or barbels	below level of lower eye edge	present
<i>Benthophilus</i> Eichwald, 1831	Miller 2004	short tube	flat pore	fold and barbels present	variable, above or below level of lower eye edge	present
<i>Caffrogobius</i> Smitt, 1900	Goren 1996	tube not reaching lip and without process from rim	pore with slightly raised edges	without barbels, mental flap from broad and short to indistinctive	below level of lower eye edge, in the level in <i>C. agullhensis</i>	present
<i>Caspiosoma</i> Iljin, 1927	Miller 2004	tube with process from rim	flat pore	without fold or barbels	below level of lower eye edge	present
<i>Chromogobius</i> de Buen, 1930	Miller 1971, Van Tassell 2001	long tube overlap- ping lip, no pro- cess from rim	short tube	without fold or barbels	variable, below or above	present
<i>Corcyrogobius</i> Miller 1972	Miller 1972, Miller 1988	tube not reaching lip and without process from rim	flat pore	without fold or barbels	below level of lower eye edge	present
<i>Coryogalops</i> Smith, 1959	Kovačić et al. 2014, Kovačić et al. 2016	tube with or with- out process from rim	short tube to slightly raised or flat pore	without fold or barbels	below level of lower eye edge	present, except in <i>C. anomolus</i>
<i>Didogobius</i> Miller, 1966	Van Tassell 1988, Miller 1993, Schliewen et al. 2023	tube overlapping or just reaching upper lip, no pro- cess from rim	short tube to flat pore	without fold or barbels	below level of lower eye edge	present
<i>Gammogobius</i> Bath, 1971	Bath 1971	tube not reaching lip and without process from rim	short tube	without fold or barbels	below level of lower eye edge	present
<i>Gobius</i> Linneaus, 1758	Miller 1986, Kovačić 1995, Kovačić & Miller 2000, Miller 2004	tube with process from rim or no process from rim	flat pore	without fold or barbels	below level of lower eye edge	present
<i>Gorogobius</i> Miller, 1978	Kovačić & Schliewen 2008	tube not reaching lip and without process from rim	pore with slightly raised edges	without fold or barbels	below or at level of lower eye edge	present

ing posteriorly from below mid or rear pupil. Chin without fold or barbels. Branchiostegal membrane attached posteriorly to immediately before pectoral lobe. Cranial roof completely covered by dorsal axial musculature anteriorly to posterior eye edge. No spines on preopercle. Two dorsal fins, first dorsal fin with VI spines, second dorsal and anal fins with

moderate number of rays (second dorsal fin I+9-11 and anal fin I+9). The second or third spine of the first dorsal fin longest. The second spine in *W. wirtzi* and third and fourth spines in *W. canariensis* elongated and filamentous in males. Pectoral girdle without flaps on anterior edge. Uppermost rays of pectoral fin not free from membrane. Pelvic fins divided,

6	7	8	9	10	11	12
only low dermal ridge between pelvic rays 5 origin	predorsal naked, the first dorsal fin base scaled	with elongate ctenii	absent	pores small e.g. pores $\alpha$ , $\beta$ , $\rho$ clearly smaller than their interspaces	4+2/1 or 4+3/1	divided in three parts
connected by the well developed membrane	predorsal partially scaled, the first dorsal fin scaled	with no enlarged ctenii	with pores $\theta$ , $\tau$	pores small e.g. pores $\alpha$ , $\beta$ , $\rho$ clearly smaller than their interspaces	4+3/2	—
connected by the well developed membrane	predorsal and the first dorsal fin base naked	with no enlarged ctenii	absent	pores small e.g. pores $\alpha$ , $\beta$ , $\rho$ clearly smaller than their interspaces	4+2/2	divided in two parts
connected by the well developed membrane	predorsal variably scaled and the first dorsal fin base scaled	with no enlarged ctenii	with pores $\theta$ , $\tau$	pores small e.g. pores $\alpha$ , $\beta$ , $\rho$ clearly smaller than their interspaces	4+2/2	divided in two parts
connected by the well developed membrane	predorsal and the first dorsal fin base naked	with no enlarged ctenii	absent	no pores	4+2/2	divided in two parts
connected by the well developed membrane	predorsal variably scaled and the first dorsal fin base scaled	with no enlarged ctenii	absent	pores small e.g. pores $\alpha$ , $\beta$ , $\rho$ clearly smaller than their interspaces	4+3/1	single
connected by the well developed membrane	predorsal naked and the first dorsal fin base variably scaled	with no enlarged ctenii	absent	pores small e.g. pores $\alpha$ , $\beta$ , $\rho$ clearly smaller than their interspaces	4+2/0	single
connected by the well developed membrane, except in <i>C. anomolus</i>	predorsal naked and the first dorsal fin base variably scaled	with no enlarged ctenii	with pores $\theta$ , $\tau$	pores small e.g. pores $\alpha$ , $\beta$ , $\rho$ clearly smaller than their interspaces	variable	single
connected by the well developed membrane	predorsal variably scaled posteriorly or naked, and the first dorsal fin base scaled	with no enlarged ctenii	absent	pores small e.g. pores $\alpha$ , $\beta$ , $\rho$ clearly smaller than their interspaces	4+2/1 or 4+3/1	single
connected by the well developed membrane	predorsal variably scaled and the first dorsal fin base scaled	with no enlarged ctenii	absent	pores small e.g. pores $\alpha$ , $\beta$ , $\rho$ clearly smaller than their interspaces	4+3/1	divided in two parts
connected by the well developed membrane	predorsal variably scaled and the first dorsal fin base scaled	with no enlarged ctenii	with pores $\theta$ , $\tau$	pores small e.g. pores $\alpha$ , $\beta$ , $\rho$ clearly smaller than their interspaces	4+2/2 and 4+3/2	divided in two parts
connected by the well developed membrane	predorsal and the first dorsal fin base scaled	with no enlarged ctenii	absent	pores small e.g. pores $\alpha$ , $\beta$ , $\rho$ clearly smaller than their interspaces	4+2/0	single

Table 2. Continued.

Genus	Source of data (* studied material)	1	2	3	4	5
<i>Gymnesigobius</i> Kovačić, Ordines, Ramirez-Amaro & Schliewen, 2019	Kovačić et al. 2019a	long tube overlap- ping lip, no pro- cess from rim	short tube	without fold or barbels	“terminal, lips end frontally equal, mouth oblique, with an- terior tip above horizontal level of lower eye edge”	present
<i>Marcelogobius</i> Schliewen, 2023	Ahnelt & Patzner 1995, Van Tassell & Kramer 2014, Schliewen et al. 2018	tube reaching or overlapping up- per lip, no process from rim	pore with slightly raised edges to short tube	without fold or barbels	variable, below or above	present
<i>Mauligobius</i> Miller, 1984	Miller 1984	tube with process from rim	flat pore	without fold or barbels	below level of lower eye edge	present
<i>Mesogobius</i> Bleeker, 1874	Miller 2004	short tube	flat pore	without fold or barbels	far below level of lower eye edge	present
<i>Millerigobius</i> Bath, 1973	Bath 1973	long tube overlap- ping lip, no pro- cess from rim	short tube	without barbels	below level of lower eye edge	present
<i>Nematogobius</i> Boulenger, 1910	Harrison 1990	tube with long digitate process reaching upper lip (*ZSM 35478)	flat pore or short tube (*ZSM 35478)	with fold and two barbels (*ZSM 35478)	below level of lower eye edge (*ZSM 35478)	present (*ZSM 35478)
<i>Neogobius</i> Iljin, 1927	Miller 2003	short tube	flat pore	without fold or barbels	below or far below level of lower eye edge	present
<i>Odondebuena</i> de Buen, 1930	Miller & Tortonese 1968	tube not reaching lip and without process from rim	short tube	without fold or barbels	terminal, below level of lower eye edge	missing
<i>Padogobius</i> Iljin, 1933	Miller 2004	tube with process from rim	flat to raised pore	without fold or barbels	below level of lower eye edge	present
<i>Peter</i> Schliewen, 2023	Schliewen & Kovačić 2008	tube barely reach- ing upper lip, no process from rim	pore with slightly raised edges	without fold or barbels	variable, below or reaching	present
<i>Ponticola</i> Iljin, 1927	Miller 2003	short tube	flat pore	without fold or barbels	below level of lower eye edge	present
<i>Proterorhinus</i> Smitt, 1900	Miller 2004	long tube overlap- ping lip, no pro- cess from rim	flat pore	without fold or barbels	below level of lower eye edge	present

6	7	8	9	10	11	12
connected by the well developed membrane	predorsal and the first dorsal fin base naked	unknown, scales lost	absent	large e.g. pores $\alpha$ , $\beta$ , $\rho$ larger or about same size as their interspaces	4+2/1	divided in three parts
connected by the well developed membrane	predorsal naked or partially scaled and the first dorsal fin base scaled	with no enlarged ctenii	absent or present	pores, if present, small e.g. pores $\alpha$ , $\beta$ , $\rho$ clearly smaller than their interspaces	4+2/1	divided in two parts
connected by the well developed membrane	predorsal and the first dorsal fin base scaled	with no enlarged ctenii	with pores $\theta$ , $\tau$	pores small e.g. pores $\alpha$ , $\beta$ , $\rho$ clearly smaller than their interspaces	4+3/2	divided in two parts
connected by the well developed membrane	predorsal partially scaled, the first dorsal fin scaled	with no enlarged ctenii	with pores $\theta$ , $\tau$	pores small e.g. pores $\alpha$ , $\beta$ , $\rho$ clearly smaller than their interspaces	5-7+3/3	continuous
connected by the well developed membrane	predorsal naked, the first dorsal fin base scaled	with no enlarged ctenii	absent	pores small e.g. pores $\alpha$ , $\beta$ , $\rho$ clearly smaller than their interspaces	4+3/2	divided in two parts
connected by the well developed membrane (*ZSM 35478)	predorsal scaled (*ZSM 42325) or posteriorly scaled (*ZSM 35478) and the first dorsal fin base scaled	with no enlarged ctenii	with pores $\theta$ , $\tau$ (*ZSM 35478)	pores small e.g. pores $\alpha$ , $\beta$ , $\rho$ clearly smaller than their interspaces (*ZSM 42325 and ZSM 35478)	4+3/2 (*ZSM 35478)	divided in two parts (*ZSM 35478)
connected by the well developed membrane	predorsal and the first dorsal fin base scaled	with no enlarged ctenii	with pores $\theta$ , $\tau$	pores small e.g. pores $\alpha$ , $\beta$ , $\rho$ clearly smaller than their interspaces	4+3/2	divided in two parts (*ZSM 47256)
only low dermal ridge between pelvic rays 5 origin	predorsal naked, the first dorsal fin base scaled	elongate, with lateral ctenii greatly enlarged	absent	pores small e.g. pores $\alpha$ , $\beta$ , $\rho$ clearly smaller than their interspaces	4+2/0	divided in two parts
connected by the well developed membrane	predorsal and the first dorsal fin base scaled or naked	with no enlarged ctenii	with pores $\theta$ , $\tau$ or absent	pores small e.g. pores $\alpha$ , $\beta$ , $\rho$ clearly smaller than their interspaces or absent	4+3/2 and 4+3/1	divided in two parts
connected by the well developed membrane	predorsal naked and the first dorsal fin base scaled	with no enlarged ctenii	absent	pores small e.g. pores $\alpha$ , $\beta$ , $\rho$ clearly smaller than their interspaces	4+2/1	divided in two parts
connected by the well developed membrane	predorsal and the first dorsal fin base scaled	with no enlarged ctenii	with pores $\theta$ , $\tau$	pores small e.g. pores $\alpha$ , $\beta$ , $\rho$ clearly smaller than their interspaces	4+3/2	divided in two parts
connected by the well developed membrane	predorsal and the first dorsal fin base scaled	with no enlarged ctenii	with pores $\theta$ , $\tau$	pores small e.g. pores $\alpha$ , $\beta$ , $\rho$ clearly smaller than their interspaces or no pores	4+3/2	divided in two parts

Table 2. Continued.

Genus	Source of data (* studied material)	1	2	3	4	5
<i>Sufflogobius</i> Smith, 1956	Hoese 1986	tube not reaching lip and without process from rim* (*ZSM 35520)	flat pore (*ZSM 35520)	fold with two lateral barbels present on chin (*ZSM 35520)	terminal, lower lip anteriorly slightly in front of upper lip, mouth oblique, with anterior tip above horizontal of lower eye edge	present
<i>Thorogobius</i> Miller, 1969	Miller 1969, 1988, Sauberer et al. 2018	tube not reaching lip and without process from rim	flat pore	without fold or barbels	below level of lower eye edge	present
<i>Wheelerigobius</i> Miller, 1981	Miller 1981, Miller 1988, Van Tassell et al. 1988	tube not reaching lip and without process from rim	flat pore	without fold or barbels	below level of lower eye edge	missing
<i>Zebrus</i> de Buen, 1930	Miller 1977	tube with tentacle on posterior rim	short tube	without barbels	below level of lower eye edge	present

with fourth ray longest and only low dermal ridge present between left and right fin. Anterior pelvic membrane (frenum) absent. Caudal fin truncate to rounded, from slightly shorter than head, to longer than head, at least in male. Body scaled with ctenoid scales. Head with cheek and opercle naked. Predorsal area naked. First dorsal-fin base scaled. Prepectoral naked, breast and belly scaled. Low count of scales in lateral series, 25–30. Dorsal and ventral posterior-most scales on base of caudal fin with little to clearly enlarged lateral ctenii. Head with anterior and posterior oculoscapular and preopercular canals, with pores  $\sigma$ ,  $\lambda$ ,  $\kappa$ ,  $\omega$ ,  $\alpha$ ,  $\beta$ ,  $\rho$ ,  $\theta$ ,  $\tau$  and  $\gamma$ ,  $\delta$ ,  $\varepsilon$  respectively. Pores of head canals not enlarged, e.g. pores  $\alpha$  and  $\rho$  half of size or less as their interspaces to pore  $\beta$ . *Preorbital* rows with four median rows. Longitudinal row *r* anteriorly beginning at horizontal level and medially to pore  $\sigma$ ; row *sa* below pore  $\sigma$ ; row *sb* medially to anterior nostril; row *sc* is the anterior-most preorbital row above upper lip. Four lateral *preorbital* rows, row *ja* between anterior and posterior nostrils and laterally to it; row *jb* below and close to anterior nostril; superior row *jc* and inferior row *jd*, above upper posterior lip row *jd* entering the space between upper lip and anterior eye. *Suborbital* rows without longitudinal row *a*. Suborbital longitudinal row *b* short and anteriorly ending at vertical to eye posterior edge. Six (*W. maltzani*) or seven (*W. wirtzi*

and *W. canariensis*) transverse suborbital rows of sensory papillae, four anterior suborbital rows continuous, in front of row *b*, fifth divided but in front of row *b*, sixth just as superior part, seventh row, if present, near pore  $\alpha$ . The length of suborbital transverse rows *c2*, *c3* and *c4* more than half of the distance from eye to row *d*, placed distantly both from lower eye edge and row *d*, or with rows *c3* and *c4* close to eye (*W. canariensis*). Suborbital transverse row *c5* divided in three parts. Longitudinal row *d* extending from above upper lip backwards along lower cheek, divided on cheek below rows *c3* and *c4*, reaching to vertical of posterior eye edge or behind. *Preoperculo-mandibular* rows with divided external row *e* and internal row *i*, row *i* parallel to row *e*, both ending anteriorly at chin before frontal part of jaw and posteriorly at preopercular ventral margin. Mental row *f* near chin tip. *Opercular* rows with transverse row *ot* on anterior part of operculum; superior longitudinal row *os* on upper part of operculum; inferior longitudinal row *oi* on lower part of operculum. *Oculoscapular* rows with anterior longitudinal row *xa* anteriorly beginning above posterior edge of preopercle. Posterior longitudinal row *xb* above posterior edge of operculum. Transverse row *z* approximately in area of upper edge of preopercle. Row *q* behind pore  $\rho$ ; row *u* as two papillae between row *q* and posterior oculoscapular canal. Transverse

6	7	8	9	10	11	12
connected by the well developed membrane	predorsal and the first dorsal fin base scaled	with no enlarged ctenii (*ZSM 35520)	with pores $\theta, \tau$ (*ZSM 35520)	pores small e.g. pores $\alpha, \beta, \rho$ clearly smaller than their interspaces (*ZSM 35520)	5+3-4/2 (*ZSM 35520)	single (*ZSM 35520)
connected by the well developed membrane	predorsal variably scaled and the first dorsal fin base variably scaled	with no enlarged ctenii	with pores $\theta, \tau$	pores small e.g. pores $\alpha, \beta, \rho$ clearly smaller than their interspaces except <i>T. rofeni</i> with large e.g. pores $\alpha, \beta, \rho$ larger or about same size as their interspaces	4+3/2	divided in two parts
only low dermal ridge between pelvic rays 5 origin	predorsal naked, the first dorsal fin base scaled	with lateral ctenii little to clearly enlarged	with pores $\theta, \tau$	pores small e.g. pores $\alpha, \beta, \rho$ clearly smaller than their interspaces	4+2/1 or 4+3/1	divided in three parts
connected by the well developed membrane	predorsal naked, the first dorsal fin base scaled	with no enlarged ctenii	with pores $\theta, \tau$	pores small e.g. pores $\alpha, \beta, \rho$ clearly smaller than their interspaces	4+3/2	divided in two parts

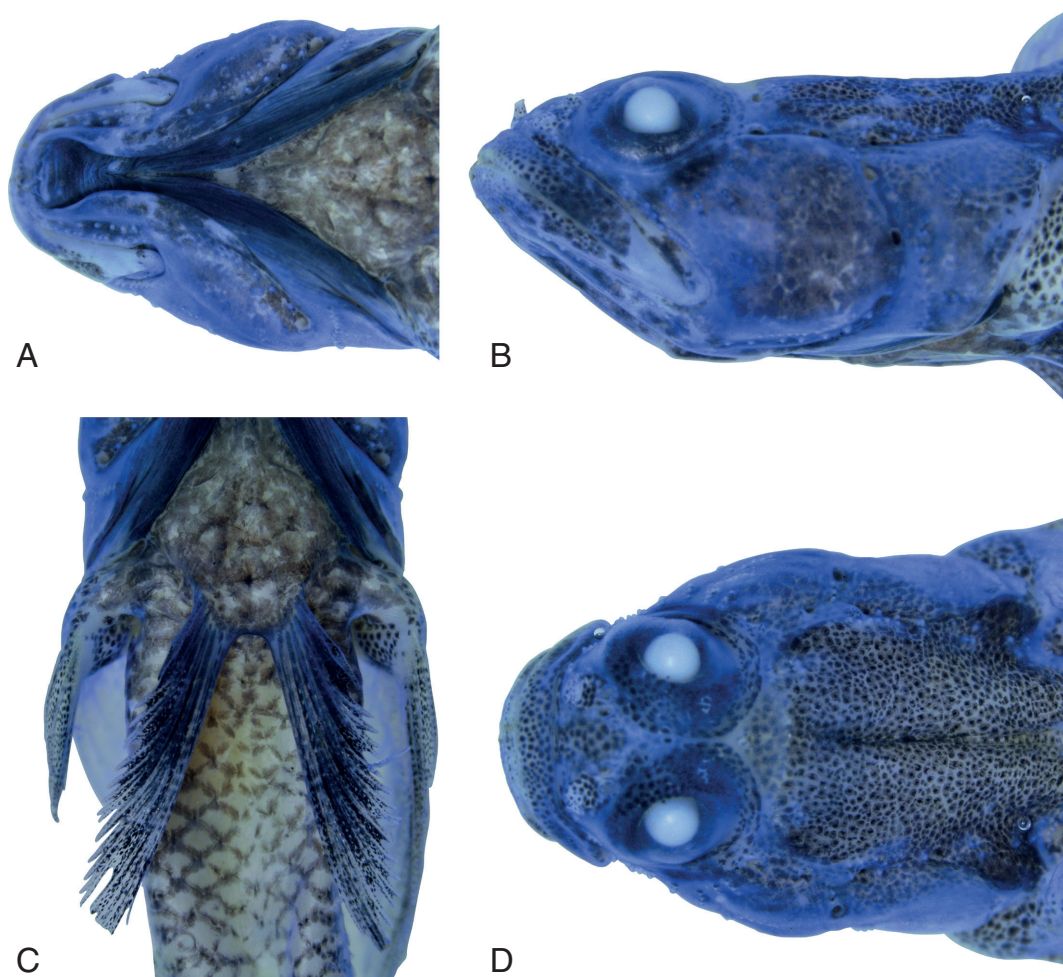
row *y* just below row *xb*. Transverse axillary rows *ka*, *kb* and *kc* radiating from upper pectoral fin base; longitudinal axillary rows *la* and *lb* just above them. Anterior dorsal rows with transverse row *n* on anterior nape behind eye and pore  $\omega$ . Transverse rows *o* roughly vertical to preopercular edge. Anterior dorsal transverse row *o* divided from the equivalent row of the other lateral side and distant at the dorsal midline from the equivalent row of the other lateral side. Longitudinal row *g* not reaching anteriorly to transverse row *o* (*W. maltzani* and *W. canariensis*) or reaching it (*W. wirtzi*). Longitudinal row *m* below horizontal level of row *g* and below of vertical of its posterior edge. Longitudinal row *h* continuous or divided, near dorsal midline in front of first dorsal fin origin. Interorbital rows absent. 10 precaudal and 18 caudal vertebrae (including urostyle), total count: 28. Pty 3-22110; two pterygiophores anterior to the first haemal spine.

#### *Vanneaugobius* Brownell, 1978

**Diagnosis.** (1) Anterior nostril long tube overlapping lip with no process from rim; (2) posterior nostril is a short tube; (3) chin without fold or barbels (Fig. 2A); (4) mouth with anterior tip at or above horizontal level of lower eye edge (Fig. 2B); (5) pelvic

fins divided, only low dermal ridge present between left and right fin (Fig. 2C); (6) pelvic fin anterior membrane (frenum) absent (Fig. 2C); (7) predorsal area naked, first dorsal fin base scaled (Fig. 2D); (8) uppermost and lowermost scales on base of caudal fin with enlarged ctenii; (9) head with anterior oculoscapular and preopercular canals, with pores  $\sigma, \lambda, \kappa, \omega, \alpha, \beta, \rho$  and  $\gamma, \delta, \varepsilon$  respectively, posterior oculoscapular canal absent (Fig. 3); (10) pores of head canals not enlarged, e.g. pores  $\alpha$  and  $\rho$  half of size or less as their interspaces to pore  $\beta$  (Fig. 3); (11) four anterior transverse suborbital *c* rows continuous, the fifth *c* row divided, one or two posteriormost *c* rows just with upper parts (Fig. 3); (12) transverse suborbital row *c*5 divided in three parts (Fig. 3).

This diagnosis is the combination of the selected cardinal characters that distinguish *Vanneaugobius* from the other 27 genera currently assigned to the “*Gobius*-lineage” based on phylogenetics (Neilson & Stepien 2009, Thacker & Roje 2011, Agorreta et al. 2013, Kovačić et al. 2019a, 2021, Schliewen et al. 2023, and the results of the phylogenetic analysis in the present paper (Appendix 1, Fig. 1). A character was considered as differential only if it was monomorphic within a given genus and it was considered different between a given genus and all species of a compared genus. The combination of twelve characters provides differences in three



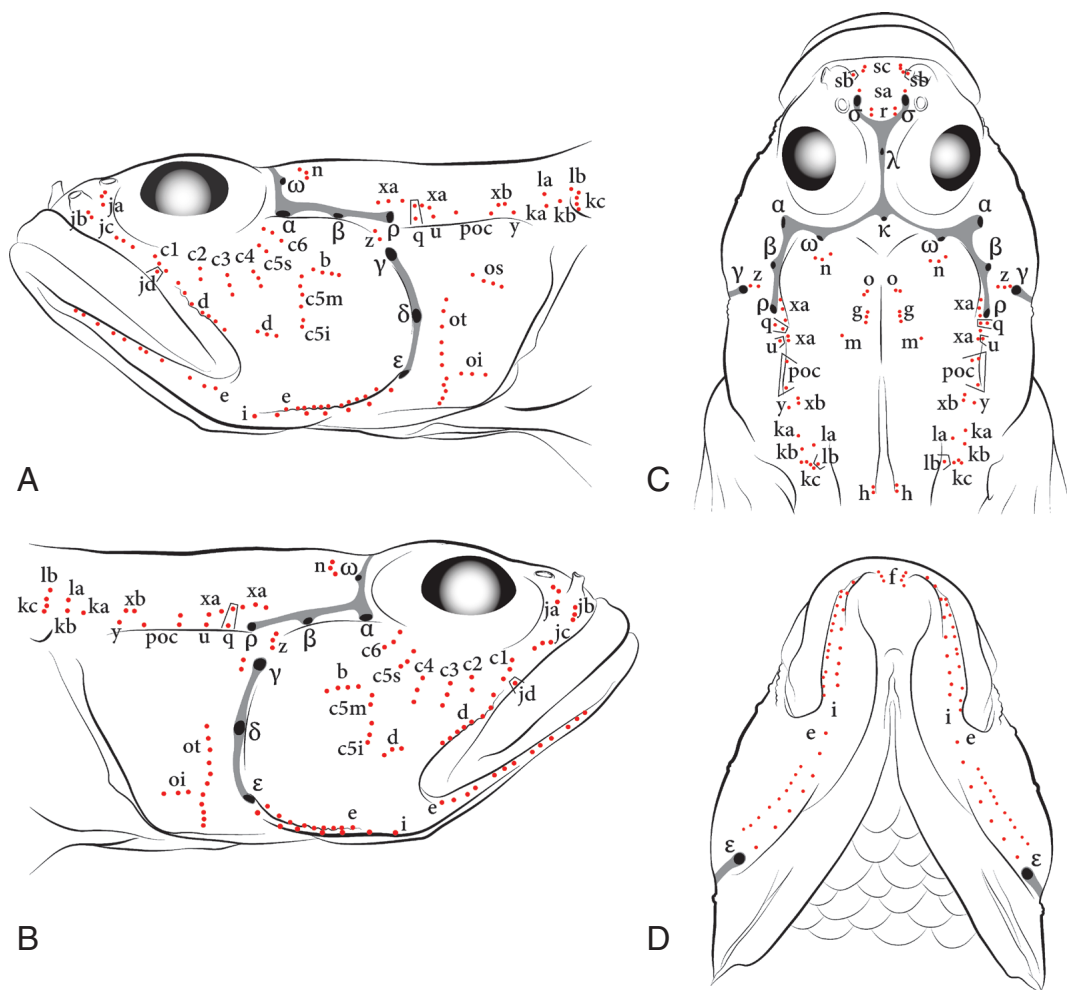
**Fig 2.** *Vanneaugobius longignathus* sp. nov., ZSM 48375, holotype, male, 26.84 + 6.75 mm, off Água Izé, São Tomé Island: **A.** Head ventral side. **B.** Mouth gently superior with jaws subequal, lower jaw ending anteriorly in front of upper jaw, strongly oblique, with anterior tip above horizontal level of lower eye edge. **C.** Pelvic fins divided with low dermal ridge present between left and right fin and pelvic fin anterior membrane (frenum) absent. **D.** Predorsal area naked, first dorsal fin base scaled. Photos by Robin Böhmer.

to ten characters when compared to the remaining genera within the “Gobius-lineage” sensu Agorreta et al. (2013) (Table 2).

### Description

Body moderately elongate to elongate, laterally more compressed towards caudal peduncle. Caudal peduncle strong, height gently decreasing backward from the trunk posterior end. Head of moderate size, wide and depressed in *Vanneaugobius longignathus* sp. nov., not markedly depressed, subcylindrical in *V. dollfusi* and *V. pruvoti*. Snout oblique, with slightly

convex profile, longer than eye (no data for *V. pruvoti*). Anterior nostril long, tubular, overlapping lip and without process from rim; posterior nostril is a short tube. Eyes large, dorsolateral, elevated or slightly elevated above dorsal profile. Eye diameter about one third of the distance between mouth tip and preopercular edge. Interorbital space narrow. Mouth slightly superior with jaws subequal, lower jaw ending anteriorly in front of upper jaw, gently oblique, with anterior tip above or in the level of horizontal level of lower eye edge. Mouth large, posterior angle of jaws ending posteriorly from below pupil midpoint to below posterior iris. Chin



**Fig 3.** *Vanneaugobius longignathus* sp. nov., ZSM 48375, holotype, male, 26.84 + 6.75 mm, off Água Izé, São Tomé Island. Head lateral line sensory papillae and canal pores. **A.** Left lateral view. **B.** Right lateral view. **C.** Dorsal view. **D.** Ventral view. Terminology in text. Drawing by Robin Böhmer.

without fold or barbels. Branchiostegal membrane attached posteriorly just to behind midpoint between posterior edge of opercle and posterior edge of preopercle or attached to immediately before pectoral lobe. Cranial roof completely covered by dorsal axial musculature anteriorly to posterior eye edge. No spines on preopercle. Two dorsal fins, first dorsal fin with VI spines, second dorsal and anal fins with moderate number of rays (second dorsal fin I+10–11 and anal fin I+9–10). The first spine of the first dorsal fin longest, only in females of *V. dollfusi* first and second spine about equal. The first spine elongated and filamentous in males of *V. dollfusi*

and *V. longignathus* sp. nov. Pectoral girdle without flaps on anterior edge. Uppermost rays of pectoral fin not free from membrane. Pelvic fins divided, with fourth ray longest and only low dermal ridge present between left and right fin. Anterior pelvic membrane (frenum) absent. Caudal fin rounded and short, shorter than head length. Body scaled with ctenoid scales. Head with cheek and opercle naked. Predorsal area naked. First dorsal-fin base scaled. Prepectoral naked, breast and belly scaled. Low count of scales in lateral series, 26–29. Dorsal and ventral posteriormost scales on base of caudal fin with elongate ctenii. Head with anterior oculoscapu-

lar and preopercular canals, with pores  $\sigma$ ,  $\lambda$ ,  $\kappa$ ,  $\omega$ ,  $\alpha$ ,  $\beta$ ,  $\rho$  and  $\gamma$ ,  $\delta$ ,  $\varepsilon$  respectively, posterior oculoscapular canal absent. Pores of head canals not enlarged, e.g. pores  $\alpha$  and  $\rho$  half of size or less as their interspaces to pore  $\beta$ . Suborbital rows of sensory papillae with low number of papillae in rows. *Preorbital* rows with four median rows. Longitudinal row *r* anteriorly beginning at horizontal level or above and medially to pore  $\sigma$  (no data for *V. pruvoti*); row *sa* below pore  $\sigma$ , no data for *V. pruvoti*; row *sb* medially to anterior nostril; row *sc* is the anteriormost preorbital row above upper lip. Five lateral *preorbital* rows, row *ja* as two rows between anterior and posterior nostrils and laterally to it; row *jb* below and close to anterior nostril; superior row *jc* and inferior row *jd*, above upper posterior lip, both or just row *jd* entering the space between upper lip and anterior eye. *Suborbital* rows without longitudinal row *a*. Suborbital longitudinal row *b* short and anteriorly ending at vertical to eye posterior edge or distant behind the vertical to the posterior edge of eye. Six (*V. longignathus* sp. nov.) or seven (*V. dollfusi* and *V. pruvoti*) transverse suborbital rows of sensory papillae, four anterior suborbital rows continuous, fifth divided in three parts but in front of row *b*, sixth just as superior part, seventh row, if present, near pore  $\alpha$ . Suborbital transverse rows short, the lengths of rows *c2*, *c3* and *c4* about 1/3 of the distance from eye to row *d*, placed distantly both from lower eye edge and row *d*. Suborbital transverse row *c5* divided in three parts. Longitudinal row *d* extending from above upper lip backwards along lower cheek, continuous or divided on cheek, reaching to vertical of posterior eye edge. *Preoperculo-mandibular* rows with external row *e* and internal row *i* divided, row *i* parallel to row *e*, both ending anteriorly at chin before frontal part of jaw and posteriorly at preopercular ventral margin. Mental row *f* longitudinal near chin tip. *Opercular* rows with transverse row *ot* on anterior part of operculum; superior longitudinal row *os* on upper part of operculum; inferior longitudinal row *oi* on lower part of operculum. *Oculoscapular* rows with anterior longitudinal row *xa* anteriorly beginning above posterior edge of preopercle. Posterior longitudinal row *xb* above posterior edge of operculum. Transverse row *z* approximately in area of upper edge of preopercle. Row *q* behind pore  $\rho$ ; row *u* as one or two comparatively large papillae between row *q* and row *poc*. One or two large *poc* papillae on the place of missing posterior oculoscapular canal. Transverse row *y* just below row *xb*. Transverse axillary rows *ka*, *kb* and *kc* radiating from upper pectoral fin base; longitudinal axillary rows *la* and *lb* just above them. *Anterior dorsal* rows with transverse row *n* on anterior nape behind eye. Transverse rows *o* roughly vertical to preopercular edge. Anterior dorsal transverse

row *o* divided from the equivalent row of the other lateral side, distant at the dorsal midline from the equivalent row of the other lateral side in *V. longignathus* sp. nov., close to it in *V. dollfusi* and *V. pruvoti*. Longitudinal row *g* not reaching anteriorly to transverse row *o*. Longitudinal row *m* below horizontal level of row *g* and behind of vertical of its posterior edge. Longitudinal row *h* continuous, near dorsal midline in front of first dorsal fin origin. *Interorbital* rows absent. 10 precaudal and 18 caudal vertebrae (including urostyle), total count: 28. Pty 3-22110; two pterygiophores anterior to the first haemal spine.

***Vanneaugobius longignathus*  
Kovačić, Schliewen & Böhmer sp. nov.**

**Holotype** (Figs 4A, 4C and 5A). Male, 22.48 + 6.08 mm, ZSM 48375, off Água Izé, São Tomé Island (0.211°N, 6.740°E), 26 m depth, 29 January 2023, Peter Wirtz.

**Paratype** (Fig. 4B and 5B). Female, 26.84 + 6.75 mm, PMR VP6169, same data as holotype.

**Diagnosis.** *V. longignathus* sp. nov. is distinguished from the other two *Vanneaugobius* species by the following character combination: (1) head wide and depressed (Fig. 2) (vs. not markedly depressed in *V. dollfusi* and *V. pruvoti*); (2) mouth anterior tip above level of lower eye edge (vs. in the level in *V. dollfusi* and *V. pruvoti*) (Fig. 2B); (3) posterior angle of jaw ending posteriorly below posterior iris (Fig. 2B) (vs. below pupil in *V. dollfusi* and *V. pruvoti*); (4) suborbital longitudinal row *b* anteriorly ending distant behind the vertical to the posterior edge of eye (Fig. 3) (vs. ending at vertical to eye posterior edge in *V. dollfusi* and *V. pruvoti*); (5) no transverse rows *c* above or below row *b* (Fig. 3) (vs. one or two transverse rows *c* above row *b* in *V. dollfusi* and *V. pruvoti*); (6) six suborbital transverse *c* rows of sensory papillae (Fig. 3) (vs. seven rows in *V. dollfusi* and *V. pruvoti*); (7) suborbital longitudinal row *d* divided (Fig. 3) (vs. continuous in *V. dollfusi* and *V. pruvoti*); (8) anterior dorsal transverse row *o* distant at the dorsal midline from the equivalent row (Fig. 3) (vs. close to it in *V. dollfusi* and *V. pruvoti*).

## Description

(all morphometric and meristic values in the text are presented as holotype first and paratype, if different, in parentheses).

**General morphology** (Figs 4 and 5). Body proportions are given in Table 1. Body elongate, laterally more compressed towards caudal peduncle, height gently decreasing from the trunk posterior end of

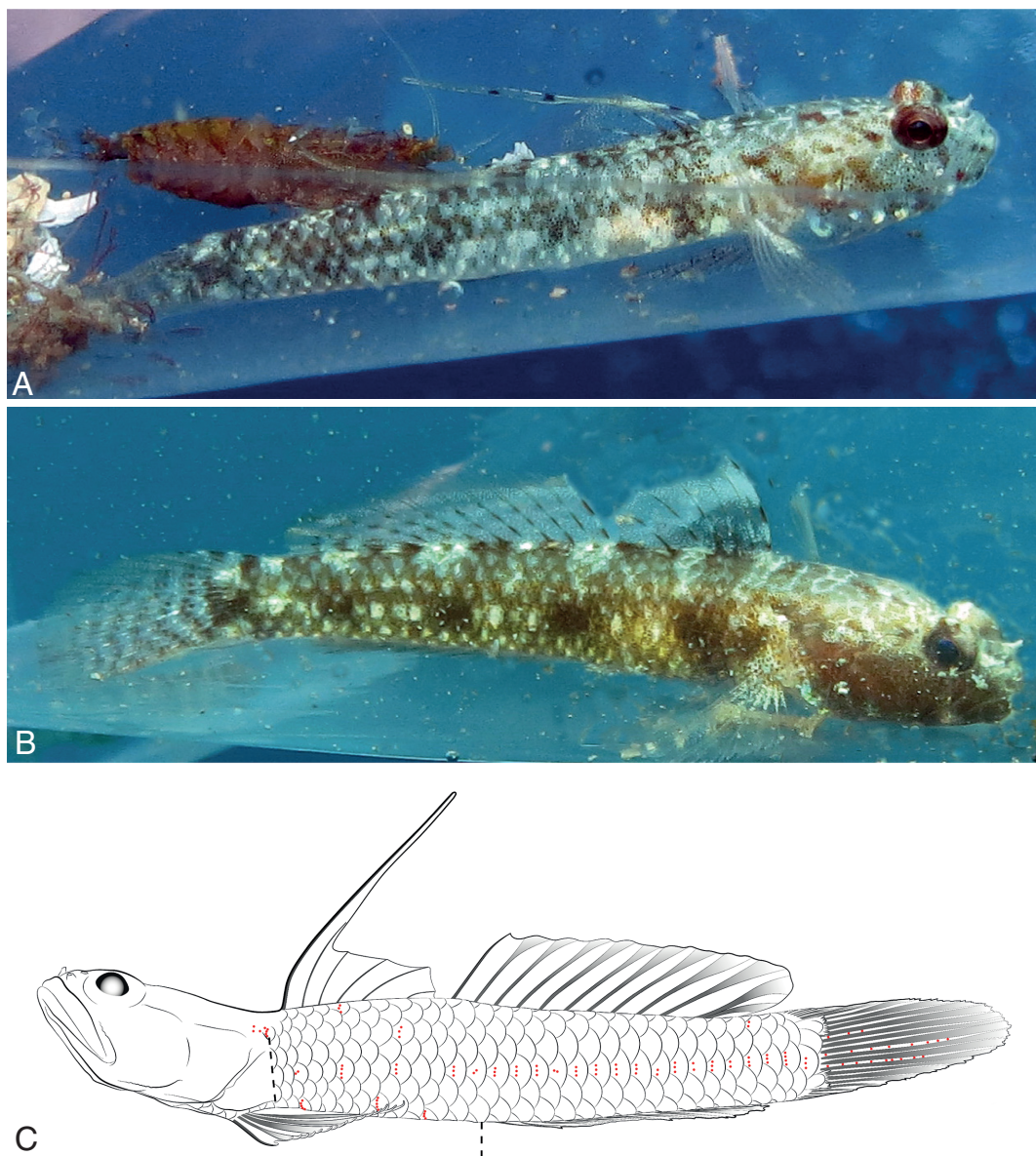
trunk backwards. Caudal peduncle strong. Head of moderate size, wide and depressed, head depth 64 % (60 %) of head width. Snout gently oblique, slightly longer than eye diameter, snout length 109 % (106 %) of eye diameter. Anterior nostril long, tubular, without process from rim; posterior nostril is a short tube. Eyes large, eye diameter about one third length distance between mouth tip and preopercular edge. Eye dorsolateral, slightly elevated above dorsal profile. Interorbital space narrow. Mouth slightly superior with jaws subequal, lower jaw ending anteriorly in front of upper jaw, gently oblique, with anterior tip above horizontal level of lower eye edge. Posterior angle of jaws terminating behind posterior edge of iris. Upper lip width more or less uniform. Cheek deep, distance between eye and posterior angle large. Chin without fold or barbels. Ventrolateral head ridge broad, but distant at the ventral midline from its counterpart of the other lateral side, also no anterior connection between ventrolateral head ridges. Branchiostegal membrane attached along entire lateral margin of isthmus, posteriorly to immediately before pectoral lobe. Predorsal area about horizontal. Cranial roof completely covered by dorsal axial musculature anteriorly to posterior eye edge. No spines on preopercle. The membranous edge of opercle extends over upper pectoral base. Pectoral girdle without dermal flaps on anterior edge. Tongue well developed, anteriorly rounded. Teeth in upper and lower jaws large, erect, curved backwards, caniniform. Lower jaw with outer and inner rows of teeth and the intermediate smaller teeth. Upper jaw with only outer and inner rows of teeth visible.

**Fins.** First dorsal fin VI; second dorsal fin I/10; anal fin I/9; caudal fin with 32(31) total rays, of which 15 segmented, 14(15) of them branched, inserting in parhypural and hypuralia 1–5, 8(7) upper and 7 lower precurent rays; pectoral fin 16(17), only left side, right fin cut; pelvic fin I/5 + 5/I. Fin morphometrics in proportion to standard body length given in Table 1. The first spine of the first dorsal fin elongated and filamentous in male; male spines V and VI also reaching the second dorsal fin spine. In female, among the first dorsal fin spines, only spine VI nearly reaching second dorsal fin spine when depressed. Interdorsal space membranous with a very small gap between the end of the first dorsal fin membrane and the origin of the second dorsal fin spine. Second dorsal fin originates above urogenital papilla, the longest second dorsal fin rays reaching base of uppermost caudal-fin rays in males, nearly reaching in females. Anal fin originates at vertical through the first or the second soft ray of the second dorsal fin. Anal fin with last ray origin below penultimate ray of the second dorsal fin or the third ray counted from posterior end of the second dorsal

fin. The longest anal rays nearly reaching base of uppermost caudal-fin rays in males, ending before uppermost caudal-fin rays in females. Pectoral fin posteriorly barely reaching vertical of the second dorsal fin base anterior beginning. Uppermost rays of pectoral fin not free from membrane. Pectoral fin rays branched, except for two unbranched uppermost rays. Pelvic fins divided, only low dermal ridge present between left and right fin. The fifth ray unbranched, other rays branched. Pelvic fourth ray the longest, longer than fifth ray, with fifth ray long as about the shortest branch of the fourth ray. Pelvic fin anterior membrane (frenum) absent. Pelvic fin short, shorter in male, clearly not reaching anus, in female nearly reaching it. Caudal fin rounded and short, shorter than head, caudal fin length 93 % (91 %) of head length.

**Scales.** Body scaled with ctenoid scales. Head with cheek and opercle naked. Predorsal area naked. First dorsal-fin base scaled. The upper edge of scaled area extending from above pectoral fin base backwards and up to the anterior part of the first dorsal fin base. Prepectoral naked, breast and belly scaled. Dorsal and ventral posteriormost basicaudal scales modified with elongate ctenii. Scales in lateral series 28 and 28 (29 and 28), left and right side, with one more row of small scale over caudal fin ray origins; in transverse series 7 and 7 (8 and 8), left and right side; circumpeduncular scales 12 (12).

**Lateral line system** (Fig. 3). Head with anterior oculoscapular and preopercular canals, with pores  $\sigma$ ,  $\lambda$ ,  $\kappa$ ,  $\omega$ ,  $\alpha$ ,  $\beta$ ,  $\rho$  and  $\gamma$ ,  $\delta$ ,  $\epsilon$  respectively; posterior oculoscapular canal absent. Pores of head canals not enlarged, e.g. pores  $\alpha$  and  $\rho$  half of size or less as their interspaces to pore  $\beta$ . Rows of sensory papillae with low count of papillae compared to other *Gobi*-lineage species, some rows just as single or double papilla (Fig. 3). Rows with range of number of sensory papillae in parentheses, counted on both sides of holotype and left side of paratype, if different: (holotype left, right and paratype left, right). (1) *preorbital*: with four median preorbital series and lateral series in four parts, row *r* (2) above and medially to pore  $\sigma$ , row *sa* single papilla below pore  $\sigma$ , row *sb* close to anterior nostril (1, 2 and 1), row *sc* (2 and 2) more medially above upper lip. Lateral series *j* in four parts: superior *ja* (2 + 1 and 2 + 1, 2 + 2) as two rows laterally to nostrils and middle *jb* (2, 3 and 2, 1) below anterior nostril; inferior rows: upper horizontal *jc* (3) above upper lip and lower horizontal *jd* (1, 1 and 2, 1) between upper lip and row 1. (2) *suborbital*: row *a* absent. Longitudinal row *b* (4) short, anteriorly ending distant from vertical to the posterior edge of eye and posterior to row *c5*. Six transverse suborbital rows of sensory papillae (*c1*: 3 and 4, 3, *c2*: 2 and 2, 3, *c3*: 3 and 2, 3, *c4*: 3, *c5*: 2 + 4 + 2,



**Fig. 4.** *Vanneaugobius longignathus* sp. nov. **A.** ZSM 48375, holotype, male, 22.48+6.08 mm, off Água Izé, São Tomé Island. **B.** PMR VP 6169, paratype, female, 26.84+6.75 mm, off Água Izé, São Tomé Island. Living specimens. Photos by Peter Wirtz. **C.** Drawing of holotype ZSM 48375, with trunk neuromast pattern (red dots), and position of anus (dotted line) inserted. Drawing by Robin Böhmer. Please note, that the upwardly angled head position of both specimens is a preservation artifact.

3+2+3 and 3+3+4, 2+3+4,  $c_6$ : 3). Four transverse suborbital rows continuous in front of row *b*, fifth transverse row divided in three parts, all in front of row *b*, sixth transverse row just as superior part also in front of vertical of row *b* and below pore *a* and eye, no transverse rows above or below row *b*.

Suborbital transverse rows short, distant from eye and from row *d*, the lengths of rows *c*<sub>2</sub>, *c*<sub>3</sub> and *c*<sub>4</sub> about 1/3 of the distance from eye to row *d*. Suborbital transverse row *c*<sub>5</sub> divided in three parts, lowermost segment of row *c*<sub>5</sub> nearly reaching downwards the level of row *d*. A single papilla visible inside pore *a*



**Fig. 5.** *Vanneaugobius longignathus* sp. nov. **A.** ZSM 48375, holotype, male, 22.48+6.08 mm, off Águia Izé, São Tomé Island. **B.** PMR VP 6169, paratype, female, 26.84+6.75 mm, off Águia Izé, São Tomé Island. Preserved specimens. Each type photo is composite of two photos under stereomicroscope, due to the size limits of the stereomicroscope photos. Photos by Robin Böhmer. Please note, that the upwardly angled head position of both specimens is a preservation artifact

in paratype female. Longitudinal row *d* (7+3, 8+3 and 9+5, 10+4) divided with the gap between supralabial and posterior part placed below row *c*3. (3) *preoperculo-mandibular*: external row *e* (11+11, 13+9 and 12+11, 13+11) and internal row *i* (9+7, 8+7 and 9+7) uniserial rows, divided into anterior and posterior sections; longitudinal row *f* present in mental area (4, 3 and 3). (4) *oculoscapular*: anterior longitudinal row *xa* (3+2 and 3+2, 4+2) as two parts, first above pore *p*, and second more posteriorly; posterior longitudinal row *xb* (2) above posterior operculum; row *z* (2, 3 and 3), (4) above pore *γ*, row *q* (2 and 2, 1) transversal behind pore *p*, row *u* as single larger papilla behind row *q* and below *xa*; two or three more larger *poc* papillae backwards from row *u* on the place of the missing posterior oculoscapular canal tentatively; transversal row *y* single papilla slightly behind vertical to posterior papilla of row *xb* (holotype) or below row *xb* (paratype). Axillary vertical rows *ka* (1 and 1), *kb* (1 and 1) and *kc* (4, 3 and 3) above pectoral fin base, row *la* (1 and 1, 2) and row *lb* as single papilla above *k* rows. (5) *opercular*: transverse row *ot* (12 (only 11 visible on lateral view in Figs 3A and 3B) and 15); superior longitudinal row *os* (4, missing on the right side of the holotype and 5); and inferior longitudinal row *oi* (3 and 4); right side of the holotype with two papillae as aberration near pore *γ*. (6) *anterior dorsal*: anterior transverse row *n* (3 and 4) behind pore *ω*, transverse row *o* (2 and 1) distant at the dorsal midline from the equivalent row of the other lateral side; longitudinal row *g* (3 and 2)

short, posterior and distant from row *o*, longitudinal row *m* single papilla posterior and distant to row *g*, longitudinal row *h* (2). Interorbital papillae absent. (7) *trunk*: (counted on left and right side of holotype and paratype) *ld* series as three (holotype) or two (paratype) widely spaced transverse rows, i.e. *ld*1 directly below first dorsal fin spine IV (3), *ld*2 below first dorsal fin spine VI (3,1; missing on both sides of paratype) and *ld*3 after D2 fin base on caudal peduncle (2); *lm* series in 22 (holotype) or 23 rows, i.e. paratype with one extra row (1) on both sides between rows *lm*3 and *lm*4; *lm* rows predominantly transverse along midline from behind pectoral fin origin to before caudal fin origin, *lm*1, *lm*5 and *lm*9 (holotype) or only *lm*1 longitudinal; *lm* neuromast counts (starting anteriorly): *lm*1 (2 and 3,2), *lm*2 (4 and 5), *lm*3 (3,4 and 4,3), *lm*4 (3 and 3), *lm*5 (2,1 and 3), *lm*6 (3 and 1), *lm*7 (3 and 2,3), *lm*8 (3 and 3), *lm*9 (2 and 3), *lm*10 (3 and 1,3), *lm*11 (3), *lm*12 (3), *lm*13 (3), *lm*14 (2,3 and 3), *lm*15 (3), *lm*16 (2,3 and 3,1), *lm*17 (3 and 3,2), *lm*18 (2,3 and 3), *lm*19 (3), *lm*20 (3 and 2,3), *lm*21 (4,3), *lm*22 (3,2 and 3,5); *lv* series in three transverse rows: *lv*1 (5 and 5,4), *lv*2 (5,4 and 6,5) and *lv*3 (4,4 and 5,4). (8) *caudal fin*: three longitudinal rows *lc* on caudal fin: *lcd* (3,4 and 5,4), *lcm* (8,4 and 5,3); *lcv* (9,8 and 7,5); no unambiguously discernable transversal row *lct* present.

**Osteology.** Vertebral column and pterygiophore insertion pattern (pty) (Fig. 6). 10 precaudal and 18 caudal vertebrae (including urostyle), total count: 28. Pty 3-22110; two pterygiophores anterior to the first haemal spine.

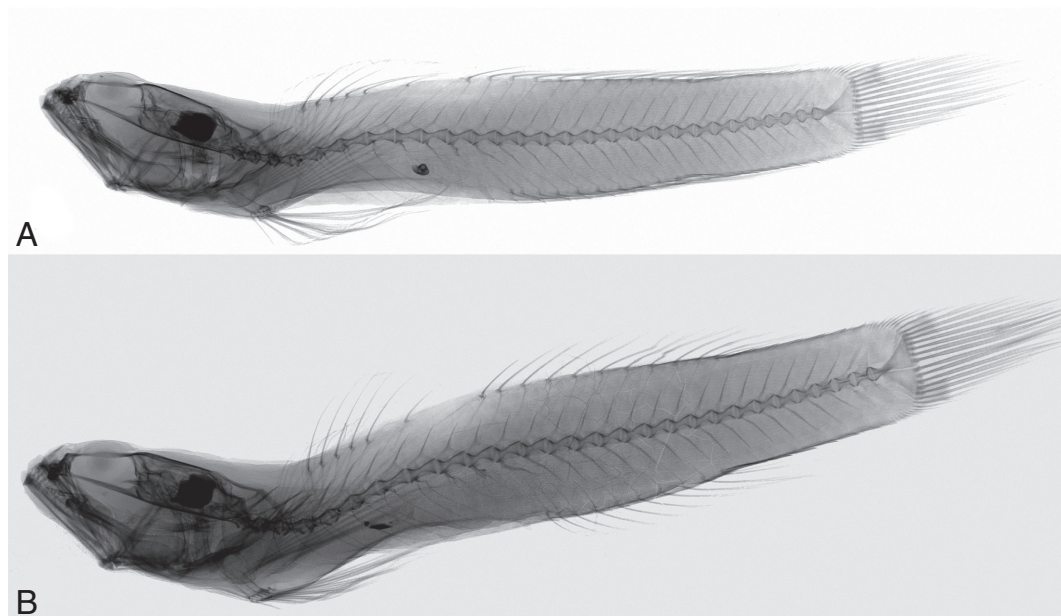
**Colouration.** Colour of specimens collected alive from photographs (Fig. 4). Male holotype (Fig. 4a) whitish with scattered brown dots. The melanophores shape the brown marks on body, the pattern that outline scales, and also the individual dark brown dots randomly distributed like peppered ash on body. The four dark brown midlateral brown blotches along lateral side present below first dorsal fin, origin of the second dorsal fin, posterior half of the second dorsal fin and the last one at anterior caudal peduncle. The fifth dark brown midlateral blotch present at caudal fin base. From the midlateral blotches the poorly visible broad zigzag brownish pattern extends upwards to dorsal fins and caudal peduncle top. Head whitish, with irregular brown marks roughly organized in several oblique bands going up and back from the lips and from the cheek bottom to eyes and nape. The iris brown, three brown transverse stripes visible on dorsal side from iris to iris, pupil with blue dark reflection. The elongated first spine of the first dorsal fin with four dark vertical dashes, the two similar marks visible on other spines. The other fins poorly pigmented, anal fin not visible (Fig. 5a). Female paratype (Fig. 4b) with darker body than male, body and head mostly brown with pale areas. The melanophores shaping brown area on body, also pattern outlining scales, while the individual dark brown dots randomly distributed like peppered ash on body were less prominent on more dark background. The four dark brown midlateral brown blotches along lateral side present below first dorsal fin, anterior and posterior of the second dorsal fin and the last one at anterior caudal peduncle. The fifth dark brown midlateral blotch present at caudal fin base, extending on caudal fin rays origin. From the midlateral blotches the broad zigzag brownish pattern extends upwards to dorsal fins and caudal peduncle top, leaving whitish areas mostly as saddles on back and as marks in between midlateral blotches. Head brown up to the level of eyes and to upper opercular edge. Upper snout and nape with irregular brown marks. The iris brown, pupil with blue dark reflection. The dorsal fins with dark vertical dashes on spines. Caudal fin with dark spots visible on spines, roughly shaping bars. Anal fin uniformly pigmented. Pectoral fin with whitish mark on the proximal third of rays. Pelvic fin not visible.

Colour of preserved specimens in alcohol (Fig. 5). Body yellowish white, with scattered dark dots. The dark dotted pattern follows posterior edges of scales, both on the upper and lower part of body along body and tail from behind pectoral axilla to caudal peduncle. The four dark brown midlateral blotches along lateral side present below first dorsal fin, origin of the second dorsal fin, posterior half of the second dorsal fin and the last one below posterior end of the

second dorsal fin and anterior caudal peduncle. The fifth dark brown midlateral blotch present at caudal fin base, extending on the caudal fin rays origin. Head dark brown, slightly darker in male. Upper head with snout, upper iris, nape and predorsal area similar, densely dotted with melanophores. Head lateral side with upper lip, cheek, preopercle and opercle almost uniformly brown, only upper opercle dotted. The iris brown to bronze brown, pupil whitish. The last third of lips and angle of jaw whitish. The posterior opercle edge with opercle partially whitish, more in female. Underside of head black over mental and gular regions and over anterior isthmus and branchiostegal membranes in male. The ventrolateral head ridge dark brown with whitish areas. The posterior isthmus and prepelvic area greyish brown. Female with mental region dark, gular region and anterior isthmus whitish, branchiostegal membranes dark and posterior isthmus and prepelvic greyish brown with whitish areas. The rest of the ventral side of body from belly to the caudal peduncle with the dark dotted pattern following posterior edges of scales in both sexes, same as on the lateral side. The elongated first spine of the first dorsal fin with five black spots in male, the two lowermost spots extend backwards into two greyish oblique bands over other spines. Male with the second dorsal fin and caudal fin uniformly pigmented with grey dark dots, except for the dark brown blotch present at the caudal fin rays origin. Pectoral fin uniformly pigmented with grey dark dots, except for the dark brown blotch present at the upper pectoral fin rays origin. Anal fin and pelvic fin uniformly pigmented with black dots in male. Female with two greyish oblique band over other spines on the first dorsal fin. The second dorsal fin and caudal fin unevenly dotted, but without clearly recognizable pattern in female. Anal fin and pelvic fin uniformly dark greyish, pigmented with dark dots in female. Female with pectoral fin uniformly pigmented with grey dots, except for the dark brown blotch present at the upper pectoral fin rays origin.

**Etymology.** The specific name *longignathus* is formed from the Latin word *longus* (long) and Greek word *gnáthos* (jaw).

**Distribution and ecology.** Currently, the species is only known from the collection site in 26 m depth off Água Izé, São Tomé Island. There were numerous rocky outcrops, varying in size from a few to many square meters on a sandy/muddy bottom. The rocky outcrops were covered with corals like *Schizoculina africana* and *Siderastrea radians*, various gorgonian species (*Muriceopsis* and *Leptogorgia* spp.) and whip coral (*Stichopathes* sp.). The goby *Wheelerigobius wirtzi* was also common in the same area, as well as the



**Fig. 6.** *Vanneaugobius longignathus* sp. nov. **A.** ZSM 48375, holotype, male, 22.48 + 6.08 mm, off Águia Izé, São Tomé Island. **B.** PMR VP 6169, paratype, female, 26.84 + 6.75 mm, off Águia Izé, São Tomé Island. (X-rays: Ulrich Schliewen). Please note, that the upwardly angled head position of both specimens is a preservation artifact.

small scorpionfish *Scorpaenodes africanus*. The female specimen of *Vanneaugobius longignathus* was collected from rocky substrate, while the much lighter male specimen was collected on sand directly next to the same rocky substrate.

## Discussion

Molecular phylogenetic evidence based on a comparatively large dataset of nuclear and mitochondrial genetic data confirmed the monophyly of the *Vanneaugobius*–*Odondebuena*–*Wheelerigobius* (VOW) clade, but made *Wheelerigobius* paraphyletic with respect to *Vanneaugobius*. In addition, strong mitochondrial discordance with regard to the phylogenetic placement of *Gymnesigobius medits* puts doubts on the inclusion of the recently described monotypic genus *Gymnesigobius* into the VOW-clade as suggested by Kovačić et al. (2019b). Whereas reevaluation of morphological characters supported the reassignment of *W. canariensis* to the genus *Vanneaugobius*, the phylogenetic placement of *Gymnesigobius* as a member of the VOW-clade, as indicated by the mitochondrial DNA phylogeny remained contentious, because the nuclear DNA-based phylogeny (Fig. 1) placed it with moderately high support (BS 82 %) as the sister-taxon to a large and well-supported

clade including the genera *Gobius*, *Mauligobius*, *Proterorhinus*, *Neogobius*, *Benthophilus* and *Thorogobius*. The few known specimens of *Gymnesigobius* are partially damaged due to dredge-sampling, which caused one character supporting the monophyly of the VOW-clade unscorable for this taxon, the presence of highly modified basicaudal scales (Kovačić et al. 2019b) (Table 2). Furthermore, among the genera of the *Gobius*-lineage (Agorreta et al. 2013) (Table 2), *Vanneaugobius* shares with *Wheelerigobius* and *Odondebuena* the synomorphy of divided pelvic fins, with only a low dermal ridge present between left and right fin and the anterior pelvic membrane (frenum) absent (Table 2). In contrast, *Gymnesigobius*, has its pelvic fins not divided and the anterior pelvic membrane (frenum) is well-developed (Kovačić et al. 2019b). Thus, from the morphological perspective, *Gymnesigobius*, falls outside of the VOW-clade, hereby rather supporting the nuclear DNA-based hypothesis. Nevertheless, the statistically well supported placement of *Gymnesigobius* within the VOW-clade based on mtDNA alone indicates either ancient incomplete lineage sorting of mtDNA-haplotypes or ancient gene flow between the VOW-clade and *Gymnesigobius*. Since the statistical support based on nuclear DNA is not overwhelming both for the placement of *Gymnesigobius* and for other basal lineages within the *Gobius*-lineage (see Fig. 1), additional

genomic data are necessary to clarify the apparently complex phylogenetic history of *Gymnesigobius*.

In contrast to pelvic fin shape, the new *Vanneaugobius* species shares, among closely related genera, one other character with *Gymnesigobius*, i.e. the position of the anterior tip of the mouth, which is above the edge of the lower eye. In the other *Vanneaugobius* species, this character appears to be present only in some individuals of *Vanneaugobius dollfusi* Brownell, 1978, (figure 2 in Brownell 1978 compared to figure 1 in Kovačić 2008). Finally, the new species shows also several morphometric autapomorphies in the head region, i.e. head proportions being unique within the *Vanneaugobius*–*Odondebuenia*–*Wheelerigobius*-clade and within the genus *Vanneaugobius*. Their evolutionary origin appears to be caused by its peculiar head shape transformation, which, in comparison with congeners, shifted the lower posterior head part backwards as the mouth gape extends backwards with its posterior jaw angle ending posteriorly below the posterior part of the iris. Seemingly as a consequence of that morphometric shift, the posterior suborbital rows terminate more backwards, e.g. row *b* ends anteriorly distantly from the vertical to eye posterior edge, row *c5i* is also behind eye, and the posterior part of row *d* is below the eye posterior edge. Their shifted positions produced some of the lateral line system character states that were used in the species diagnosis.

Among the genera of the *Gobius*-lineage (Agorreta et al. 2013) (Table 2), ten genera are present in the tropical West Africa (Schliewen 2011, Kovačić et al. 2020, Schliewen et al. 2023). Six genera among them reach out into the warm temperate Atlantic or/and Mediterranean (*Corcyrogobius* Miller, 1972, *Marcelogobius* Schliewen et al., 2023, *Mauligobius* Miller, 1981, *Peter* Schliewen et al., 2023, *Vanneaugobius*, *Wheelerigobius*); and two additional genera, *Gobius* Linnaeus, 1758 and *Thorogobius* Miller, 1969, extend their distribution even further north, to the cold temperate Atlantic (Kovačić et al. 2020), having broad Eastern Atlantic and Mediterranean presence, while only *Gorogobius* Miller, 1978 and *Nematogobius* Boulenger, 1910 are restricted to the tropical West Africa (Schliewen 2011). Nevertheless, even for these two last mentioned genera, their phylogenetic relationships indicate a closer relationship with some non-tropical taxa such as *Millerigobius* and *Odondebuenia* (Fig. 1; Agorreta et al. 2013).

The discovery of a morphologically aberrant new *Vanneaugobius* species in the tropical eastern Atlantic highlights, that the cryptobenthic fish fauna of that region has remained poorly studied up to today and that even morphologically divergent taxa of the highly distinctive *Gobius*-lineage remain to be discovered.

## Comparative material examined

*Benthophilus persicus* Kovačić, Esmaeili, Zarei, Abbasi & Schliewen, 2021: PMR VP4679, paratype male, 43.3+10.0 mm; PMR VP4680, paratype male, 47.0+8.6 mm; PMR VP4681, paratype male, 35.1+8.5 mm; PMR VP4682, paratype female, 30.4+7.4 mm; PMR VP4683, paratype female, 34.2 mm. *Chromogobius zebratus* (Kolombatović, 1891): PMR VP2757, 2 males, 33.9+8.4 mm and 34.1+7.5 mm; PMR VP2788, 1 female, 30.3+7.3 mm and 1 juvenile of unidentified sex, 22.4+5.5 mm. *Corcyrogobius liechtensteini* (Kolombatović, 1891): PMR VP2753, one juvenile of unidentified sex, 7.5+2.0 mm; PMR VP2790, 1 juvenile of unidentified sex, 8.7+2.1 mm. *Corygogobius anomalus* Smith, 1958: PMR VP3050, 1 female, 24.9+6.3 mm; PMR VP3051, 1 female, 25.8+6.1 mm; PMR VP3052, 1 male, 24.3+6.2 mm. *Marcelogobius splechnai* (Ahneft & Patzner, 1995): PMR VP2783, 1 female, 16.6+4.4 mm. *Gammogobius steinitzi* Bath, 1971: 2 females, 26.2+5.2 mm and 24.8+5.0 mm. *Gobius auratus* Risso, 1810: PMR VP3367, 2 males, 40.9+9.2 mm and 49.0+11.3 mm, 5 females, 33.0+8.8–40.6+9.9 mm. *Gobius incognitus* Kovačić & Šanda, 2016: PMR VP 2963, 2 females, 76.1+17.7 mm and 65.2+15.6 mm; PMR VP 2962, male, 46.6+11.5 mm; PMR VP 2961, female, 40.4+10.4 mm. *Gymnesigobius medits* Kovačić, Ordines, Ramirez-Amaro & Schliewen, 2019: PMR VP4649, holotype male, 42.6+11.1 mm. *Millerigobius macrocephalus* (Kolombatović, 1891): PMR VP3354, male, 34.5+8.0 mm; PMR VP3355, female, 24.6+5.9 mm; PMR VP3356, female, 26.8+6.1 mm. *Nematogobius brachynemus* (Pfaff, 1933): ZSM 35478. *Neogobius caspius* (Eichwald, 1831): ZSM 47256. *Odondebuenia balearica* (Pellegrin & Fage, 1907): PMR VP4140, 1 male, 19.2+4.3 mm. *Ponticola rizensis* (Kovačić & Engin, 2008): PMR VP1456, 1 paratype male, 104.1+21.2 mm. *Sufflogobius bibarbatus* (von Bonde, 1923): ZSM 35520. *Thorogobius ephippiatus* (Lowe, 1839): PMR VP3518, 2 females, 60.8+13.9 mm and 48.7 mm with damaged caudal fin, 1 juvenile female 28.4+7.5 mm. *Vanneaugobius dollfusi* Brownell, 1978: PMR VP3857, female, 22.2+5.9 mm; PMR VP3865, male, 32.0+8.1 mm. *Zebrus zebrus* (Risso, 1827): juvenile of unidentified sex, PMR VP2878, 10.0+2.2 mm, juvenile of unidentified sex, PMR VP2882, 9.4+2.3 mm.

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**Appendix 1.** Previous pages. Genbank numbers for published and newly generated nuclear and mitochondrial DNA loci as well as voucher-deposition information. ▷

Abbreviations: BLIH – Biological Laboratory Imperial Household, Tokyo, Japan; NMBE – Naturhistorisches Museum der Bürgergemeinde Bern, Bern, Switzerland; ZSM-PIS – Ichthyological Collection of the SNSB-Bavarian State Collection of Zoology, Munich, Germany; AMNH – American Museum of Natural History, New York, USA; NEFC – North East Fisheries Research Center, Woodshole, USA; OCF – Okinawa Institute of Science and Technology, Onna, Japan; IBS – Research Collection of the Incheon National University, Incheon, South Korea; USNM-FISH – Ichthyological Collection of the United States National Museum of Natural History, Washington, USA; TORI – Taiwan Ocean Research Institute, Kaoshiung, Taiwan; GOU – College of Fisheries Guangdong Ocean University, Zhanjiang, China; SAIAB – South African Institute of Aquatic Biodiversity, Makhanda, South Africa; MABIK – National Marine Biodiversity Institute of Korea, Chungcheongnam-do, Korea; MBA – Marine Biological Association, Plymouth, UK; PMR – Natural History Museum, Rijeka, Croatia.

Species (alphabetical order)	Nuclear Loci		
	gpr85	rag1	zic1
<i>Amblygobius phalaena</i> (Valenciennes, 1837)	KF416109	KF415693	KF415897
<i>Asterropteryx semipunctata</i> Rüppell, 1830	KF416117	KF415701	KF415906
<i>Benthophilus leobergius</i> Berg, 1949	PV768710	PV768742	PV768774
<i>Caffrogobius caffer</i> (Günther, 1874)	PV768711	PV768743	PV768775
<i>Caffrogobius nudiceps</i> (Valenciennes, 1837)	PV768712	PV768744	PV768776
<i>Chromogobius britoi</i> Van Tassell, 2001	PV768713	PV768745	PV768777
<i>Chromogobius quadrivittatus</i> (Steindachner, 1863)	PV768714	PV768746	PV768778
<i>Chromogobius zebratus</i> (Kolombatović, 1891)	PV768715	PV768747	PV768779
<i>Corcyrogobius liechtensteini</i> (Kolombatović, 1891)	PV768716	PV768748	PV768780
<i>Corcyrogobius pulcher</i> Kovačić, Wirtz & Schliewen, 2020	PV768717	PV768749	PV768781
<i>Coryogalops anomolus</i> Smith, 1958	PV768718	PV768750	PV768782
<i>Coryogalops tessellatus</i> Randall, 1994	PV768719	PV768751	PV768783
<i>Cryptocentrus cinctus</i> (Herre, 1936)	KF416150	no data	KF415940
<i>Didogobius lanceolatus</i> Schliewen, Knorn & Böhmer, 2023	PV768720	PV768752	PV768784
<i>Discordipinna griessingeri</i> Hoese & Fourmanoir, 1978	KF416155	KF415737	KF415945
<i>Exyrias puntang</i> (Bleeker, 1851)	KF416176	KF415758	KF415964
<i>Favonigobius reichei</i> (Bleeker, 1854)	KF416178	KF415760	KF415966
<i>Gammogobius steinitzi</i> Bath, 1971	PV768721	PV768753	PV768785
<i>Glossogobius aureus</i> Akihito & Meguro, 1975	KF416184	KF415766	KF415971
<i>Glossogobius giuris</i> (Hamilton, 1822)	KF416185	KF415767	KF415972
<i>Gobiosoma bosc</i> (Lacepède, 1800)	KF416199	KF415782	KF415986
<i>Gobius cobitis</i> Pallas, 1814	PV768722	PV768754	PV768786
<i>Gobius cruentatus</i> Gmelin, 1789	PV768723	PV768755	PV768787
<i>Mauligobius maderensis</i> (Valenciennes, 1837)	PV768724	PV768756	PV768788
<i>Gobius niger</i> Linnaeus, 1758	OX637619	OX637619	OX637619
<i>Gobius senegambiensis</i> Metzelaar, 1919	PV768725	PV768757	PV768789
<i>Gorogobius nigricinctus</i> (Delais, 1951)	PV768726	PV768758	PV768790
<i>Grahamichthys radiatus</i> (Valenciennes, 1837)	PV768727	PV768759	PV768791
<i>Gymnesigobius medits</i> Kovačić, Ordines, Ramirez-Amaro & Schliewen, 2019	PV768728	PV768760	PV768792
<i>Heteroleotris bipunctata</i> Tortonese, 1976	PV768729	PV768761	PV768793
<i>Heteroleotris zonata</i> (Fowler, 1934)	PV768730	PV768762	PV768794
<i>Lesueurigobius sanzi</i> (de Buen, 1918)	GCA_900303255	GCA_900303255	GCA_900303255
<i>Lophogobius cyprinoides</i> (Pallas, 1770)	KF416228	KF415812	KF416016
<i>Marcelogobius janetorum</i> (Schliewen, Wirtz & Kovačić, 2018)	PV768731	PV768763	PV768795
<i>Millerigobius macrocephalus</i> (Kolombatović, 1891)	PV768732	PV768764	PV768796
<i>Nemateleotris decora</i> Randall & Allen, 1973	KF416240	KF415821	KF416025
<i>Nematogobius maindroni</i> (Sauvage, 1880)	PV768733	PV768765	PV768797
<i>Neogobius melanostomus</i> (Pallas, 1814)	OM736846	OM736846	OM736846
<i>Nes longus</i> (Nichols, 1914)	KF416241	KF415822	KF416026
<i>Odondebuena balearica</i> (Pellegrin & Fage, 1907)	KF416242	KF415823	no data
<i>Padogobius bonelli</i> (Bonaparte, 1846)	PV768734	PV768766	PV768798
<i>Parioglossus dotui</i> Tomiyama, 1958	KF416257	no data	KF416042
<i>Peter amicuscaridis</i> (Schliewen & Kovačić, 2008)	PV768735	PV768767	PV768799
<i>Ponticola kessleri</i> (Günther, 1861)	PV768736	PV768768	PV768800
<i>Proterorhinus semilunaris</i> (Heckel, 1837)	KF416267	415845	KF416052
<i>Thorogobius ephippiatus</i> (Lowe, 1839)	PV768737	PV768769	PV768801
<i>Trimma okinawae</i> (Aoyagi, 1949)	KF416304	KF415880	KF416090
<i>Valenciennea longipinnis</i> (Lay & Bennett, 1839)	KF416308	KF415884	KF416094
<i>Vanneaugobius longignathus</i> sp. nov.	PV768738	PV768770	PV768802
<i>Vanneaugobius pruvoti</i> (Fage, 1907)	PV768739	PV768771	PV768803
<i>Vanneaugobius dollfusi</i> Brownell, 1978	PV768740	PV768772	PV768804
<i>Wheelerigobius canariensis</i> (Van Tassell, Miller & Brito, 1988)	KF416311	KF415887	KF416097
<i>Wheelerigobius maltzani</i> (Steindachner, 1881)	PV768741	PV768773	PV768805
<i>Wheelerigobius wirtzi</i> Miller, 1988	KF416312	KF415888	KF416098

Mitochondrial Loci				Voucher-ID
12s	16s	COI	Cytb	
AP019316	AP019316	AP019316	AP019316	NMBE 1066574 / OCF-P-4014
AP019329	AP019329	AP019329	AP019329	NMBE 1066527 / OCF-P-4008
PV843802	PV843330	PV843420	PV768680	ZSM-PIS-GO1182
PV843803	PV843331	PV843421	PV768681	ZSM-PIS_GO0155
PV843804	PV843332	PV843422	PV768682	ZSM-PIS-GO0147
PV843805	PV843333	PV843423	PV768683	ZSM-PIS-GO0164
PV843807	PV843335	PV843425	PV768684	ZSM-PIS-GO_britmad_XL10
PV843806	PV843334	PV843424	PV768685	ZSM-PIS-GO2050
PV843808	PV843336	PV843426	PV768686	ZSM-PIS-GO1184
PV843809	PV843337	PV843427	PV768687	ZSM-PIS-GO1799
PV843810	PV843338	PV843428	PV768688	ZSM-PIS-GO0671
PV843811	PV843339	PV843429	PV768689	ZSM-PIS-GO (84_Uli7)
MT199211	MT199211	MT199211	MT199211	NMBE 1066498 / IBS 2013-gobiidae007
PV843812	PV843340	PV843430	no data	ZSM-PIS-GO2348
OP035087	OP035087	OP035087	OP035087	BLIH 20103042 / USNM:FISH:446369
KU674801	KU674801	KU674801	KU674801	NMBE 1066509 / TORI
MN617828	MN617828	MN617828	MN617828	NMBE 1066511 / GOU103108
PV843813	PV843341	PV843431	PV768690	ZSM-PIS-GO0163
MT968499	MT968499	MT968499	MT968499	NMBE 1066514 / MABIK GR00004011 IFW11
MG680939	MG680939	MG680939	MG680939	SAIAB 73863 / not specified
OP057012	OP057012	OP057012	OP057012	AMNH 233154 / USNM:FISH:422185
PV843814	PV843342	PV843432	PV768691	ZSM-PIS-GO1500
PV843815	PV843343	PV843433	PV768692	ZSM-PIS-GO1182
PV843821	PV843351	PV843441	PV768693	ZSM-PIS-GO2205
OX637619	OX637619	OX637619	OX637619	MBA-210921-051A
PV843816	PV843344	PV843434	PV768694	ZSM-PIS-GO2405
PV843818	PV843345	PV843435	PV768695	ZSM-PIS-GO1742
PV843817	PV843346	PV843436	PV768696	ZSM-PIS-GO2080
PV843818	PV843347	PV843437	PV768697	PMR VP4963
PV843819	PV843348	PV843438	PV768698	ZSM-PIS-GO0747
PV843820	PV843349	PV843439	PV768699	ZSM-PIS-GO0026
GCA_900303255	GCA_900303255	GCA_900303255	GCA_900303255	see NCBI SRA: SAMEA4028816
OP056984	OP056984	OP056984	OP056984	NMBE 1066490 / USNM:FISH:415455
PV843822	PV843350	PV843440	no data	ZSM-PIS-GO0176
PV843823	PV843352	PV843442	PV768700	ZSM-PIS-GO1157
KT284932	KT284932	KT284932	KT284932	NMBE 1066445 / TORI
PV843824	PV843353	PV843443	PV768701	ZSM-PIS-GO (99 Uli6)
OM736846	OM736846	OM736846	OM736846	NEFC_F19-169
OP056846	OP056846	OP056846	OP056846	AMNH 233172/ USNM:FISH:415085
KF415421	KF415421	no data	no data	NMBE 1066446
PV843825	PV843354	PV843444	PV768702	ZSM-PIS-GO72_Uli8
AP019332	AP019332	AP019332	AP019332	NMBE 1066456 / OCF-P-4016
PV843826	PV843355	PV843445	PV768703	ZSM-PIS-GO2133
PV843827	PV843356	PV843446	PV768704	ZSM-PIS-GO 292 / NkeAGV3
MW856852	MW856852	MW856852	MW856852	NMBE 1066463 / NEFC_F18-153
PV843828	PV843357	PV843447	PV768705	ZSM-PIS-GO0156
AP019345	AP019345	AP019345	AP019345	NMBE 1066437 / OCF-P-4008 OCF-P-3851
AP019327	AP019327	AP019327	AP019327	NMBE 1066405 / OCF-P-4006
PV843830	PV843359	PV843449	PV768706	ZSM-PIS- 48375
PV843831	PV843360	PV843450	PV768707	AMNH 233178 (GO84)
PV843829	PV843358	PV843448	PV768708	ZSM-PIS-GO1096
AF491119	AF491119	no data	KF415681	AMNH 233177
PV843832	PV843361	PV843451	PV768709	ZSM-PIS-GO1925
KF415490	KF415490	MK628521	KF415682	NMBE 1066407