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3

4 ***Stenogobius* (Teleostei: Gobioidi: Oxudercidae) from Indonesia**

5

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31

32 **Abstract**

33 Freshwater habitats in Indo-Pacific tropical islands are mainly inhabited by amphidromous
34 fish, which display a marine larval phase while the rest of their life cycle takes place in rivers.
35 Gobiiformes are the most diversified fish component in these ecosystems. In this study, we
36 focused on the status of the widespread *Stenogobius* genus (Gobioidei). This genus is
37 distributed from the Indian Ocean to French Polynesia. Recently, a first revision of
38 *Stenogobius* was undertaken leading to the redescription of *Stenogobius genivittatus*
39 (Valenciennes, 1837) and the placement of 12 species names as synonyms of *Stenogobius*
40 *genivittatus*. This paper focuses on the status of nine *Stenogobius* species supposedly existing
41 in Indonesia, a country well known as one of the freshwater hotspot of biodiversity. The
42 present study is based on 95 specimens, and includes morpho-meristic data and partial
43 mitochondrial *COI* sequences. Our results show that, at least, four species occur in Indonesia,
44 including the widespread species, *Stenogobius genivittatus*.

45

46 **French title**

47 *Stenogobius* (Teleostei : Gobioidei : Oxudercidae) d'Indonésie

48

49 **French abstract**

50 Les habitats dulçaquicoles dans les îles tropicales de l'Indo-Pacifique sont principalement
51 colonisés par des poissons amphidromes, qui présentent une phase larvaire marine alors que le
52 reste de leur cycle de vie se déroule au sein des rivières. Ces écosystèmes sont principalement
53 composés d'espèces appartenant au groupe des Gobiiformes. Dans cette étude, nous nous
54 intéressons au statut du genre *Stenogobius* (Gobioidei) à large répartition. Ce genre est
55 retrouvé de l'océan Indien à la Polynésie Française. Récemment, une première révision du
56 genre *Stenogobius* a été entreprise, conduisant à la redescription de *Stenogobius genivittatus*
57 (Valenciennes, 1837) et au placement de 12 noms d'espèces comme synonymes de
58 *Stenogobius genivittatus*. Cet article se concentre sur le statut de neuf espèces de *Stenogobius*
59 supposées présentes en Indonésie, archipel connu comme étant l'un des points chauds de la
60 biodiversité dulçaquicole. La présente étude est réalisée sur 95 spécimens, et se base sur des
61 données morpho-méristiques et sur le barcoding du gène mitochondrial *COI*. Nos résultats
62 montrent qu'au moins quatre espèces sont présentes en Indonésie, y compris l'espèce
63 largement répandue, *Stenogobius genivittatus*.

64

65 **Key words**

66 *Stenogobius*, Gobioidei, Integrative taxonomy, Barcode, Indo-Pacific area, Endemism,
67 Amphidromy

68

69

INTRODUCTION

70 Tropical aquatic biodiversity in the Indo-Pacific Ocean follows an East-West gradient
71 (Hubert *et al.*, 2012), peaking in the Indo-Australian archipelago, species richness is
72 exceptional in the coral triangle, a marine hotspot of biodiversity encompassing the
73 Philippines to New Caledonia, including Indonesia, Papua New Guinea, the Solomon Islands
74 and Vanuatu. The distribution of species richness in brackish environments follows this

75 general pattern and the highest diversity is located in Indonesia, Papua New Guinea and the
76 Solomon Islands. These regions are composed of numerous islands of volcanic or continental
77 origin, and are subject to extreme climatic and hydrological conditions. Terrestrial biota of the
78 region are also remarkable as pointed out by Myers *et al.* (2000), which identified several
79 biodiversity hotspots in South-East Asia (SEA) including Indo-Burma (Thailand, Cambodia,
80 Laos, Vietnam and Myanmar), Sundaland (Malaysia, Indonesia), Wallacea (Indonesia) and
81 Philippines. With nearly 1,200 native species recorded, the Indonesian ichthyofauna is one of
82 the most speciose in the world, with numerous species being described during the last decades
83 (Hubert *et al.*, 2015). Sundaland, in particular, is one of the richest biodiversity hotspot
84 worldwide in terms of species richness and endemism (Myers *et al.*, 2000; Lamoureux *et al.*,
85 2006).

86 A high majority of the freshwater organisms of the Indo-Australian archipelago have
87 an amphidromous life cycle, with larvae dispersing in the ocean and as such, enabling the
88 colonisation distant islands (McDowall, 2007, 2009; Keith *et al.*, 2015, 2020; Mennesson *et*
89 *al.*, 2015). The complete cycle includes adults spawning in freshwater; the eggs hatch in
90 rivers and free embryos drift downstream to the sea where they undergo a planktonic phase.
91 After a variable amount of time spent at sea, post-larvae return to rivers to grow and
92 reproduce (Keith, 2003; Watanabe *et al.*, 2014). This strategy is an adaptation to the
93 colonisation of new and remote islands (McDowall, 2009; Feutry *et al.*, 2013) and some
94 continental areas (Theusen *et al.*, 2011).

95 The fish group of Gobiiformes is the most represented in the Indo-Pacific Ocean, with
96 families (Gobiidae, Rhyacichthyidae, Odontobutidae, Milyeringidae, Eleotridae, Butidae and
97 Oxudercidae) and multiple subfamilies present such as the Sicydiinae (112 species) (Keith *et*
98 *al.*, 2015), Amblyopinae, Gobiinae and Gobionellinae. Among them, many include
99 amphidromous species. The genus *Stenogobius* (Bleeker, 1874), which belongs to the
100 subfamily Gobionellinae, is typically found in the lower reaches of streams less than 30 m to
101 a few kilometres from the sea, in clear rivers and small tributaries (Causse *et al.*, 2023). They
102 usually live in brackish waters or quiet rocky pools on fine sand bottoms protected from the
103 main current (Allen, 2004; Allen *et al.*, 2000; Keith *et al.*, 2013; Causse *et al.*, 2023). It has
104 been shown, and generally thought, that *Stenogobius* species are amphidromous (Radtke,
105 1988; Lindstrom, 1999; McDowald, 2008; Iida *et al.*, 2017). However, Heim-Ballew *et al.*
106 (2019) recently showed that a proportion of *Stenogobius hawaiiensis* (*i.e.* *S. genivittatus*
107 (Causse *et al.*, 2023)) populations in Hawaii (29%) seem to be landlocked.

108 Up-to-date, the *Stenogobius* genus was previously composed of 28 presumably valid
109 species names (Fricke *et al.*, 2022) with a wide distribution in Indo-Pacific tropical regions
110 from southern East Africa to Indonesia, and from West Pacific to Central Pacific. However,
111 Causse *et al.* (2023) revised the species *Stenogobius genivittatus* complex, redescribed it and
112 synonymized 12 nominal species names. They showed that this species, originally described
113 from Tahiti Island, presents a widespread distribution from Hawaii Islands and French
114 Polynesia to South Africa. Nevertheless, the Sundaland region was not included in the Causse
115 *et al.* (2023) study. In Indonesia and New Guinea nine species were described suggesting high
116 levels of endemism in this region. These species are as follows: *Gobius beauforti* Weber,
117 1907 (Northern New Guinea, Indonesia), *Gobius blokzeyli* Bleeker, 1860 (Bali, Indonesia),
118 *Stenogobius gymnopomus* (Bleeker, 1853) (Sumatra, Indonesia.), *Stenogobius lachneri* Allen,
119 1991 (West Papua), *Stenogobius laterisquamatus* (Weber, 1907) (West New Guinea,

120 Indonesia), *Stenogobius marinus* Watson, 1991 (Irian Jaya, Indonesia), *Stenogobius*
121 *ophthalmoporus* (Bleeker, 1853) (Ambon, Indonesia), *Stenogobius richardsonii* (Bleeker,
122 1853) (Sumatra, Indonesia) and *Gobius zurstrasseni* Popta, 1911 (Lombok, Indonesia). After
123 the work of Causse *et al.* (2023) on the wide distribution of *Stenogobius genivittatus*, a
124 revision of *Stenogobius* species in these regions is required.

125 The present study aims at revising *Stenogobius* in the Indonesian region, following an
126 “integrative taxonomy” approach *sensu* Padial *et al.* (2010). The principle of integrative
127 taxonomy is to combine findings from the evaluation of several independent characters
128 (morphological, genetic, ecological, biogeographical, etc.) to establish rigorous species
129 delimitations (Dayrat, (2005); Padial *et al.* (2010); Schlick-Steiner *et al.* (2010). This method
130 constitutes one of the best practices of modern taxonomy (Padial *et al.*, 2010; Schlick-Steiner
131 *et al.*, 2010; Teletchea, 2010).

132 Thus, the purpose of this paper is to review the *Stenogobius* species found in
133 Indonesia, using, when possible, genetic and morphometric approaches. This work will
134 complement that of Causse *et al.* (2023) and thus will provide a basis for determining the
135 species of the Pacific Ocean.

136

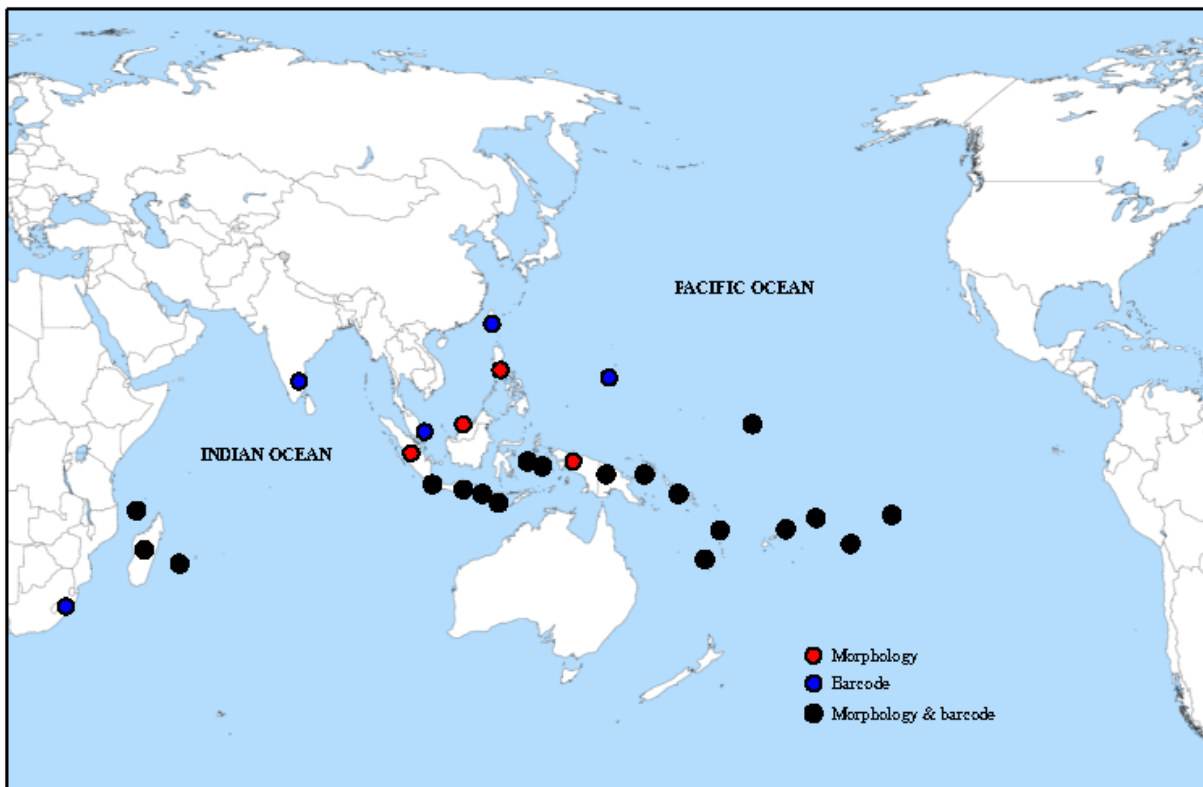
137

MATERIALS & METHODS

138 **Sample collections**

139 As this revision completes the study of Causse *et al.* (2023) where a total of 318
140 specimens were examined, we chose to only use 16 of them in order to represent at best the
141 widespread distribution of *Stenogobius genivittatus* outside of Indonesia. Seventeen locations
142 were studied for the Sundaland region, 44 specimens collected in Indonesia, four from the
143 Philippines and one from Malaysia. In addition to Sundaland, 28 specimens from Papua New
144 Guinea and 2 from India were added (Fig. 1; Table I).

145 All specimens were sampled using an electrofishing system or during snorkelling with
146 hand nets. Specimens were sampled in the lower parts of streams and rivers, in freshwater,
147 along sand banks and shores covered by plants. Fish were anesthetized using clove oil (10%),
148 a fin clip was taken, stored and preserved in 95% ethanol for molecular analysis, and fish
149 were euthanized with an overdose of clove oil (10%). Voucher specimens were stored and
150 preserved in 95% ethanol for morphomeristic analysis. No surgical procedures were
151 performed so fish weren't under any stress nor did they suffer. No experiment of any kind
152 was performed on the fish. The care and use of fish complied with the annex IV of the
153 directive 2010/63/EU animal welfare laws, guidelines and policies. Specimens and tissue
154 samples were collected under permits of sampling and euthanasia.
155



156
157 Figure 1. – Map of the Indo-Pacific showing sampling localities, and *Stenogobius* samples for which
158 morphology, barcode and both morphology and barcode data was collected and analysed.

159 Table I. – Details of specimens analysed and proposed synonymy.

| Status | Species name before studies | Species name after studies | Museum numbers | Number | Morphomeristic | Field number | COI | Genbank ID/Bold BINS | Country | Island | Locality |
|--------|-----------------------------------|---------------------------------|-------------------|--------|----------------|--------------|-----|----------------------|------------------|--------------|------------|
| | <i>Stenogobius genivittatus</i> * | <i>Stenogobius genivittatus</i> | | 1 | | | X | AF391349 | Guam Is. | | |
| | <i>Stenogobius genivittatus</i> * | <i>Stenogobius genivittatus</i> | Goby type2 #1_06 | 1 | | | X | DSLAF458-07 | South Africa | | |
| | <i>Stenogobius genivittatus</i> * | <i>Stenogobius genivittatus</i> | | 1 | | | X | KU944871 | Taiwan | | |
| | <i>Stenogobius genivittatus</i> * | <i>Stenogobius genivittatus</i> | MNHN-IC 2020-0446 | 1 | X | 19025 | X | | New Caledonia | | |
| | <i>Stenogobius genivittatus</i> * | <i>Stenogobius genivittatus</i> | MNHN-IC 2023-0186 | 1 | X | 19006 | X | | Samoa Is. | | |
| | <i>Stenogobius genivittatus</i> * | <i>Stenogobius genivittatus</i> | MNHN-IC 2020-0391 | 1 | X | 13513 | X | | Cook Is. | | |
| | <i>Stenogobius genivittatus</i> * | <i>Stenogobius genivittatus</i> | MNHN-IC 2020-0415 | 1 | X | 2810 | X | | Marquesas Is. | | |
| | <i>Stenogobius genivittatus</i> * | <i>Stenogobius genivittatus</i> | MNHN-IC 2020-0401 | 1 | X | 15364 | X | | Austral Is. | | |
| | <i>Stenogobius genivittatus</i> * | <i>Stenogobius genivittatus</i> | MNHN-IC 2020-0412 | 1 | X | 19017 | X | | Futuna Is. | | |
| | <i>Stenogobius genivittatus</i> * | <i>Stenogobius genivittatus</i> | MNHN-IC 2020-0436 | 1 | X | 17700 | X | | Papua New Guinea | New Britain | |
| | <i>Stenogobius genivittatus</i> * | <i>Stenogobius genivittatus</i> | MNHN-IC 2023-0188 | 1 | X | 13509 | X | | Solomon Is. | | |
| | <i>Stenogobius genivittatus</i> * | <i>Stenogobius genivittatus</i> | MNHN-IC 2023-0214 | 1 | X | 12958 | X | | Reunion Is. | | |
| | <i>Stenogobius genivittatus</i> * | <i>Stenogobius genivittatus</i> | MNHN-IC 2023-0215 | 1 | X | 2747 | X | | Tahiti Is. | | |
| | <i>Stenogobius genivittatus</i> * | <i>Stenogobius genivittatus</i> | MNHN-IC 2020-0413 | 1 | X | 15356 | X | | Madagascar | | |
| | <i>Stenogobius genivittatus</i> * | <i>Stenogobius genivittatus</i> | MNHN-IC 2020-0392 | 1 | X | 14015 | X | | Vanuatu | | |
| | <i>Stenogobius genivittatus</i> * | <i>Stenogobius genivittatus</i> | MNHN-IC 2020-0431 | 1 | X | 19013 | X | | Mayotte | | |
| | <i>Gobius blokzeyli</i> | <i>Stenogobius genivittatus</i> | MZB.26658 | 1 | X | BIF0227 | X | KU692898 | Indonesia | West Java | Ci Tiis |
| | <i>Stenogobius gymnopomus</i> | <i>Stenogobius gymnopomus</i> | MZB.26659 | 1 | X | BIF0231 | X | KU692905 | Indonesia | West Java | Ci Tiis |
| | <i>Gobius blokzeyli</i> | <i>Stenogobius genivittatus</i> | MZB.26660 | 1 | X | BIF0232 | X | KU692899 | Indonesia | West Java | Ci Tiis |
| | <i>Gobius blokzeyli</i> | <i>Stenogobius genivittatus</i> | MZB.26661 | 1 | X | BIF0233 | X | KU692900 | Indonesia | West Java | Ci Tiis |
| | <i>Gobius blokzeyli</i> | <i>Stenogobius genivittatus</i> | MZB.26662 | 1 | X | BIF0253 | X | KU692896 | Indonesia | West Java | Ci Tiis |
| | <i>Stenogobius gymnopomus</i> | <i>Stenogobius gymnopomus</i> | MZB.26663 | 1 | X | BIF0439 | X | KU692904 | Indonesia | West Java | Ci Haur |
| | <i>Gobius blokzeyli</i> | <i>Stenogobius genivittatus</i> | MZB.26664 | 1 | X | BIF2147 | X | KU692901 | Indonesia | East java | Mujur |
| | <i>Gobius blokzeyli</i> | <i>Stenogobius genivittatus</i> | MZB.26665 | 1 | X | BIF2803 | X | KU692903 | Indonesia | West Bali | Tukad Unda |
| | <i>Gobius blokzeyli</i> | <i>Stenogobius genivittatus</i> | MZB.26666 | 1 | X | BIF2804 | X | KU692895 | Indonesia | West Bali | Tukad Unda |
| | <i>Gobius blokzeyli</i> | <i>Stenogobius genivittatus</i> | MZB.26667 | 1 | X | BIF2805 | X | KU692897 | Indonesia | West Bali | Tukad Unda |
| | <i>Gobius blokzeyli</i> | <i>Stenogobius genivittatus</i> | MZB.26668 | 1 | | BIF2806 | X | KU692902 | Indonesia | West Bali | Tukad Unda |
| | <i>Gobius blokzeyli</i> | <i>Stenogobius genivittatus</i> | MZB.26669 | 1 | X | BIF3781 | X | | Indonesia | Lombok Utara | Sidutan |
| | <i>Gobius blokzeyli</i> | <i>Stenogobius genivittatus</i> | MZB.26670 | 1 | X | BIF3782 | X | | Indonesia | Lombok Utara | Sidutan |

| Status | Species name before studies | Species name after studies | Museum numbers | Number | Morphomeristic | Field number | COI | Genbank ID/Bold BINS | Country | Island | Locality |
|----------|------------------------------------|------------------------------------|-----------------|--------|----------------|--------------|-----|----------------------|------------------|---------------------|----------------------|
| | <i>Gobius blokzeyli</i> | <i>Stenogobius genivittatus</i> | MZB.26671 | 1 | X | BIF3941 | X | | Indonesia | Lombok Utara | Kali muntur |
| | <i>Gobius blokzeyli</i> | <i>Stenogobius genivittatus</i> | MZB.26672 | 1 | | BIF3942 | X | | Indonesia | Lombok Utara | Kali muntur |
| | <i>Gobius blokzeyli</i> | <i>Stenogobius genivittatus</i> | MZB.26673 | 1 | X | BIF3943 | X | | Indonesia | Lombok Utara | Kali muntur |
| | <i>Gobius blokzeyli</i> | <i>Stenogobius genivittatus</i> | MZB.26674 | 1 | X | BIF4025 | X | | Indonesia | Lombok Utara | Kali Sidutan |
| | <i>Stenogobius sp.</i> | <i>Stenogobius genivittatus</i> | MZB.26675 | 1 | X | BIF5151 | X | | Indonesia | Ambon | Solepai River Mamala |
| | <i>Stenogobius sp.</i> | <i>Stenogobius genivittatus</i> | MZB.26676 | 1 | X | BIF5152 | X | | Indonesia | Ambon | Solepai River Mamala |
| | <i>Stenogobius sp.</i> | <i>Stenogobius genivittatus</i> | MZB.26677 | 1 | X | BIF5153 | X | | Indonesia | Ambon | Solepai River Mamala |
| | <i>Stenogobius sp.</i> | <i>Stenogobius genivittatus</i> | MZB.26678 | 1 | X | BIF5224 | X | | Indonesia | Ambon | Waai Tasoi River |
| | <i>Stenogobius laterisquamatus</i> | <i>Stenogobius laterisquamatus</i> | MZB_KL88 | 1 | | KL88 | X | BIFZ037-17 | Indonesia | New Guinea | |
| Paratype | <i>Stenogobius marinus</i> | <i>Stenogobius genivittatus</i> | MZB_5649 | 1 | X | | | | Indonesia | Papua | |
| Holotype | <i>Stenogobius gymnopomus</i> | <i>Stenogobius gymnopomus</i> | RMNH 4552 | 1 | X | | | | Indonesia | Sumatra | |
| | <i>Stenogobius gymnopomus</i> | <i>Stenogobius gymnopomus</i> | RMNH 4552 | 3 | X | | | | Indonesia | Sumatra | |
| Syntype | <i>Gobius beauforti</i> | <i>Stenogobius genivittatus</i> | RMNH.14357 | 1 | X | | | | Indonesia | West New Guinea | Tanah Merah Creek |
| Holotype | <i>Gobius richardsonii</i> | <i>Gobius rischardsoni</i> | RMNH.4990 | 1 | X | | | | Indonesia | Sumatra | |
| Holotype | <i>Stenogobius marinus</i> | <i>Stenogobius genivittatus</i> | USNM 274586 | 1 | X | | | | Indonesia | Papua | |
| | <i>Stenogobius ophthalmoporus</i> | <i>Stenogobius ophthalmoporus</i> | ZMA 111557 | 2 | X | | | | Indonesia | Molucca | |
| | <i>Stenogobius ophthalmoporus</i> | <i>Stenogobius ophthalmoporus</i> | ZMA 113656 | 1 | X | | | | Indonesia | Molucca | |
| | <i>Stenogobius ophthalmoporus</i> | <i>Stenogobius ophthalmoporus</i> | ZMA 113657 | 1 | X | | | | Indonesia | Molucca | |
| Paratype | <i>Stenogobius marinus</i> | <i>Stenogobius genivittatus</i> | ZMA 113659 | 2 | X | | | | Indonesia | Java Island | |
| Syntype | <i>Stenogobius ophthalmoporus</i> | <i>Stenogobius ophthalmoporus</i> | ZMA 4510 | 3 | X | | | | Indonesia | Ambon | |
| Syntype | <i>Gobius beauforti</i> | <i>Stenogobius genivittatus</i> | ZMA.1109443 | 1 | X | | | | Indonesia | West New Guinea | Tanah Merah Creek |
| Syntype | <i>Stenogobius laterisquamatus</i> | <i>Stenogobius laterisquamatus</i> | ZMA116477 | 2 | X | | | | Indonesia | Northern New Guinea | |
| Syntype | <i>Gobius beauforti</i> | <i>Stenogobius genivittatus</i> | ZMZA.1109944 | 2 | X | | | | Indonesia | West New Guinea | Tanah Merah Creek |
| | <i>Stenogobius marinus</i> | <i>Stenogobius genivittatus</i> | NTM S.16645-001 | 1 | | | X | GOBY167-09 | Papua New Guinea | | |
| | <i>Stenogobius laterisquamatus</i> | <i>Stenogobius laterisquamatus</i> | NTM S.16647-001 | 1 | X | HKL-G159 | X | GOBY160-09 | Papua New Guinea | Sepik River | Angoram |
| | <i>Stenogobius laterisquamatus</i> | <i>Stenogobius laterisquamatus</i> | AMS 24632-001 | 1 | X | | | | Papua New Guinea | Sepik River | |
| | <i>Stenogobius laterisquamatus</i> | <i>Stenogobius laterisquamatus</i> | NTM S.16647-002 | 1 | X | | | | Papua New Guinea | Sepik River | Angoram |
| | <i>Stenogobius laterisquamatus</i> | <i>Stenogobius laterisquamatus</i> | NTM S.16647-003 | 1 | X | | | | Papua New Guinea | Sepik River | Angoram |
| | <i>Stenogobius laterisquamatus</i> | <i>Stenogobius sp.</i> | NTM S.16647-004 | 1 | X | | | | Papua New Guinea | Sepik River | Angoram |
| | <i>Stenogobius laterisquamatus</i> | <i>Stenogobius laterisquamatus</i> | NTM S.16647-005 | 1 | X | | | | Papua New Guinea | Sepik River | Angoram |
| | <i>Gobius blokzeyli</i> | <i>Stenogobius genivittatus</i> | USNM 270373 | 1 | X | | | | Papua New Guinea | National District | |

| Status | Species name before studies | Species name after studies | Museum numbers | Number | Morphomeristic | Field number | COI | Genbank ID/Bold BINS | Country | Island | Locality |
|---------|------------------------------------|------------------------------------|--------------------|--------|----------------|--------------|-----|----------------------|------------------|-------------|-------------|
| | <i>Stenogobius laterisquamatus</i> | <i>Stenogobius laterisquamatus</i> | WAM 28206,02 | 1 | X | | | | Papua New Guinea | | Ulieg Creek |
| | <i>Stenogobius laterisquamatus</i> | <i>Stenogobius laterisquamatus</i> | WAM 29597-004 | 8 | X | | | | Papua New Guinea | | |
| | <i>Stenogobius laterisquamatus</i> | <i>Stenogobius laterisquamatus</i> | WAM 29606,07 | 2 | X | | | | Papua New Guinea | | |
| | <i>Stenogobius laterisquamatus</i> | <i>Stenogobius laterisquamatus</i> | WAM 29608,05 | 1 | X | | | | Papua New Guinea | | |
| | <i>Stenogobius laterisquamatus</i> | <i>Stenogobius laterisquamatus</i> | WAM 29609,02 | 8 | X | | | | Papua New Guinea | | |
| | <i>Stenogobius gymnopomus</i> | <i>Stenogobius gymnopomus</i> | BMNH 1906.10.29.32 | 1 | X | | | | Malaysia | Sibu Island | |
| Syntype | <i>Gobius lacrymosus</i> | <i>Stenogobius ophthalmoporus</i> | MNHN-IC 0000-6159 | 2 | X | | | | Philippines | Luzon | Quingoa |
| Syntype | <i>Gobius lacrymosus</i> | <i>Stenogobius ophthalmoporus</i> | NHMUK 1868,7,10,10 | 1 | X | | | | Philippines | Luzon | Quingoa |
| Syntype | <i>Gobius lacrymosus</i> | <i>Stenogobius ophthalmoporus</i> | NHMUK 1868,7,10,11 | 1 | X | | | | Philippines | Luzon | Quingoa |
| | <i>Stenogobius gymnopomus</i> | <i>Stenogobius gymnopomus</i> | NBFR:10A2 | 1 | | | X | MT758489 | India | | |
| | <i>Stenogobius gymnopomus</i> | <i>Stenogobius gymnopomus</i> | NBFR:10A3 | 1 | | | X | MT758490 | India | | |

* Specimens from Causse *et al.* (2023)

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161 **Morphomeristic analysis**

162 Abbreviations for institutions and collections cited follow [https://asih.org/standard-](https://asih.org/standard-symbolic-codes)
163 symbolic-codes. Methods follow Watson and Lachner (1985), Watson (1991) and Causse *et*
164 *al.* (2023). Measurements of specimens were taken with a dial calliper to the nearest tenth of a
165 millimetre. All counts were taken from the left side. The size is given as standard length (SL).

166

167 ***Material examined***

168 Eighty-six specimens were examined in morphomeristic analyses including 19 type
169 specimens and 67 non-type specimens, representing 7 of the 9 nominal species reported from
170 Indonesia (Table I). Among these 86 specimens, 13 specimens of *S. genivittatus* from Causse
171 *et al.* (2023) and 73 specimens from Indonesia, PNG, Philippines and Malaysia. Thirty-three,
172 specimens, among the 86 fishes, were examined using both molecular and morphomeristic
173 datasets (Table I).

174 Institution acronyms: MNHN-IC: Collection of ichthyology, Muséum National
175 d'Histoire Naturelle, Paris; USNM: Smithsonian National Museum of Natural History,
176 Washington; MZB: Museum of Zoology of Bogore; RMNH: National Museum of Natural
177 History, Leiden; ZMA: Zoological Museum of Amsterdam (currently RMNH Leiden).

178

179 ***Type material***

180 In addition to studied types from Causse *et al.* (2023), we analysed *Stenogobius marinus*
181 Watson, 1991: 1 holotype (male) from Irian Jaya, New Guinea, Indonesia (USNM 274586), 1
182 paratype (male) same origin (MZB 5649); 2 paratypes (male and female) from Java Island,
183 Indonesia (ZMA 113659). *Stenogobius ophthalmoporus* Bleeker, 1853: 3 syntypes (2 males, 1
184 female) from Ambon Is., Molucca Islands, Indonesia (ZMA 4510); *Stenogobius*

185 *laterisquamatus* (Weber, 1907): 2 syntypes (males) from Mosso River, tributary of Tami
186 River, North New Guinea (ZMA 116477); *Gobius richardsonii* Bleeker, 1854: 1 holotype
187 (male) from Padang, Sumatra, Indonesia (RMNH 4990); *Stenogobius gymnopomus* (Bleeker,
188 1853): holotype (male) from Priaman, Sumatra, Indonesia (RMNH 4552 (1)); *Gobius*
189 *beauforti* Weber, 1097: 4 syntypes (females) from Kiplong River and Mamapiri Creek,
190 northern New Guinea, Indonesia (RMNHN 14357 (1); ZMA 110943 (1); ZMA 110944 (2));
191 *Gobius lacrymosus* Peters, 1868: 4 syntypes from Luzon, Philippines: 2 males (NHMUK
192 1868,7, 10, 10 & NHMUK 1868, 7, 10, 11) and 2 females (MNHN 6159). Types of
193 *Stenogobius lachneri*, *Gobius zurstrasseni* and *Gobius blokzeyli* could not be consulted.

194

195 *Non-type material (names given here are according to their labels in the different collections)*

196 *Stenogobius 'blokzeyli'* Bleeker, 1860: 1 (female) from National District, Papua New
197 Guinea (USNM 270373); 4 (females) from West Java, Indonesia (MZB.26658, MZB.26660,
198 MZB.26661, MZB.26662); 1 (female) from East Java, Indonesia (MZB.26664); 4 from West
199 Bali, Indonesia: 2 females (MZB.26665 & MZB.26667) and 1 male (MZB.26666) ; 6 from
200 Lombok, Indonesia: 3 males (MZB.26669,72 and 74) and 3 females (MZB.26670, 71 and 73).
201 *Stenogobius 'gymnopomus'* Bleeker, 1853: 1 (female) from Sibiu, Sarawak, Malaysia (BMNH
202 1906.10.29.32); 2 from Java, Indonesia: 1 female (MZB.26659) & 1 male (MZB.26663); 3
203 (males) from Sumatra, Indonesia (RMNH 4552). *Stenogobius 'laterisquamatus'* Weber, 1907:
204 12 from Papua New Guinea (PNG) (WAM 29606.07 (1 male and 1 female); 29608.05 (1
205 male); 28206.02 (1 female); 29609.02 (1 male and 7 females); 29597-004 (1 male and 6
206 females); AMS 24632-001 (1 male); NTM S.16647 (5 females)). *Stenogobius* sp.: 4 from
207 Ambon Island, Indonesia (MZB.26675 to MZB.26678). *Stenogobius 'ophthalmoporus'*
208 Bleeker, 1853: 4 males from Molucca, Indonesia; 111557 (2); 113656 (1); 113657 (1)).
209 *Stenogobius genivittatus* Valenciennes, 1837: 1 from New Caledonia (MNHN-IC 2020-0446);

210 1 from Samoa Is. (MNHN-IC 2023-0186); 1 (male) from Cook Is. (MNHN-IC 2020-0391); 1
211 from Marquesas Arch. (MNHN-IC 2020-0415); 1 (female) from Austral Is. (MNHN-IC 2020-
212 0401); 1 from Futuna Is. (MNHN-IC 2020-0412); 1 from New Britain (PNG) (MNHN-IC
213 2020-0436); 1 from Solomon Is. (MNHN-IC 2023-0188); 1 from Reunion Is. (MNHN-IC
214 2023-0214); 1 from Tahiti Is. (MNHN-IC 2023-0215); 1 from Madagascar (MNHN-IC 2020-
215 0413); 1 (male) from Vanuatu (MNHN-IC 2020-0392) and 1 from Mayotte (MNHN-IC 2020-
216 0431).

217

218 **DNA barcoding**

219 Among the 42 specimens used for the molecular analysis (Table I), 22 specimens from
220 Indonesia were sequenced for this study and 13 have been sequenced from our previous study
221 on the *Stenogobius genivittatus* (Causse *et al.*, 2023). In addition, seven sequences were taken
222 from GenBank or BOLD (<http://www.boldsystems.org/>) (Table I) to complete our data (*i.e.*,
223 Guam Islands, South Africa, Taiwan, Papua New Guinea and India). Two specimens of
224 *Awaous grammepomus* (KU692317 and KU692306) from Indonesia and two specimens of
225 *Awaous ocellaris* (JX983227 and JX983228) from India were used as outgroups.

226 Genomic DNA was extracted from the muscle tissue samples using a Qiagen DNeasy
227 96 tissue extraction kit following the manufacturer's instructions. A 652 bp segment from the
228 5' region of the cytochrome oxidase I gene (COI) was amplified using the primer cocktail
229 C_FishF1t1/C_FishR1t1 (Ivanova *et al.*, 2007). PCR amplifications were done on a Veriti 96-
230 well Fast thermocycler (ABI-Applied Biosystems) with a final volume of 10.0 μ L containing
231 5.0 μ L buffer 2X, 3.3 μ L ultrapure water, 1.0 μ L of each primer (10 μ M), 0.2 μ L enzyme
232 Phire Hot Start II DNA polymerase (5U), and 0.5 μ L of DNA template (~50 ng). The
233 following thermocycler regime was used: initial denaturation at 98°C for 5 min followed by
234 30 cycles denaturation at 98°C for 5 s, annealing at 56°C for 20 s, and extension at 72°C for

235 30 s, followed by a final extension step at 72°C for 5 min. PCR products were purified with
236 ExoSap-IT (USB Corporation, Cleveland, OH, USA) and sequenced in both directions.
237 Sequencing reactions were performed at the Centre for Biodiversity Genomics, University of
238 Guelph, Canada, using the BigDye Terminator v3.1 Cycle Sequencing Ready Reaction kit
239 following standard protocols described in (Hebert *et al.*, 2013). Sequencing was performed on
240 an ABI 3730xl capillary sequencer (Applied Biosystems). Sequences and collateral
241 information were deposited on BOLD and are available as a public data set
242 (dx.doi.org/10.5883/DS-BARBONYM, Table S1). All the sequences were aligned with
243 MAFFT Alignment (Kuraku *et al.*, 2013; Katoh *et al.*, 2019).

244 The translation into amino acids was checked for the partial fragment of *COI* gene,
245 using the vertebrate mitochondrial genetic code. After translation, one or two bases were
246 discarded at the beginning and at the end of the sequences and as a result all the sequences in
247 the alignment started and ended with a codon. All the sequences have been deposited in
248 BOLD and are available as a public data set (dx.doi.org/XX.XXXX/DS-STENO) as well as
249 GenBank (accession numbers accessible through BOLD).

250 We reconstructed a maximum likelihood (ML) tree for the former using IQ-TREE
251 (Nguyen *et al.*, 2015) with the most-likely substitution model according to ModelFinder
252 following the Bayesian information Criterion (BIC) (Kalyaanamoorthy *et al.*, 2017) available
253 at <http://iqtree.cibiv.univie.ac.at> (Trifinopoulos *et al.*, 2016). The robustness of the
254 phylogenetic inference was examined with 1000 replicates of ultrafast bootstrap as
255 implemented in IQ-TREE. Species delimitation analysis was performed using the RESL
256 algorithm, as implemented in BOLD, as used to produce Barcode Index Numbers
257 (Ratnasingham and Hebert, 2013).

258

259

RESULTS

260 **Morphomeristics**

261 After the morphomeristic analyses and the measurements (suppl. data) of the 86
262 specimens (including type specimens), four species were identified: (i) *S. genivittatus*
263 (Valenciennes, 1837) according to the work of Causse *et al.* (2023); (ii) *Stenogobius*
264 *gymnopomus* (Bleeker, 1853); (iii) *Stenogobius laterisquamatus* (Weber, 1907); and (iv)
265 *Stenogobius ophthalmoporus* (Bleeker, 1853). *Stenogobius genivittatus* specimens exist from
266 Papua, Java, Lombok, Bali and Ambon Islands; *S. gymnopomus* was observed in Sumatra
267 (type locality), Sibu Islands and West Java Is. (Indonesia); *S. laterisquamatus* in Papua (type
268 locality) and Papua New Guinea (PNG); *S. ophthalmoporus* in Ambon Is. and Molucca Is.
269 (Philippines) (type locality).

270 According to the examination of specimens (Suppl. data), the following three species,
271 *Gobius beauforti* Weber, 1907, *G. blokzeyli* Bleeker, 1860 and *S. marinus* Watson, 1991 are
272 not different from *S. genivittatus* and are here considered as synonyms of *S. genivittatus*.
273 Concerning the status of *S. lachneri* Watson, 1991, *G. zurstrasseni* Popta, 1911,
274 *G. lacrymosus* Peters, 1868 and *G. richardsonii* Bleeker, 1854, we cannot conclude at this
275 stage due to the lack of data.

276 NB: Watson (1991) placed *G. richardsonii* as a synonym of *S. gymnopomus*. But the
277 holotype of *G. richardsonii* (RMNH 4990) differs in having 15 caudal branched rays, instead
278 13-14* (* types specimens). Also, he designated *G. lacrymosus* as a synonym of
279 *S. ophthalmoporus*. However, pelvic fin length and the second dorsal fin length are shorter
280 compared to *S. ophthalmoporus* (17-22 vs. 19-29 in % SL, respectively for pelvic fin length;
281 36-47 vs. 36-56 in % SL; respectively for the second dorsal fin). At this stage, we cannot
282 conclude about the status of *G. lacrymosus*. Further analyses will be achieved to address these
283 validity issues.

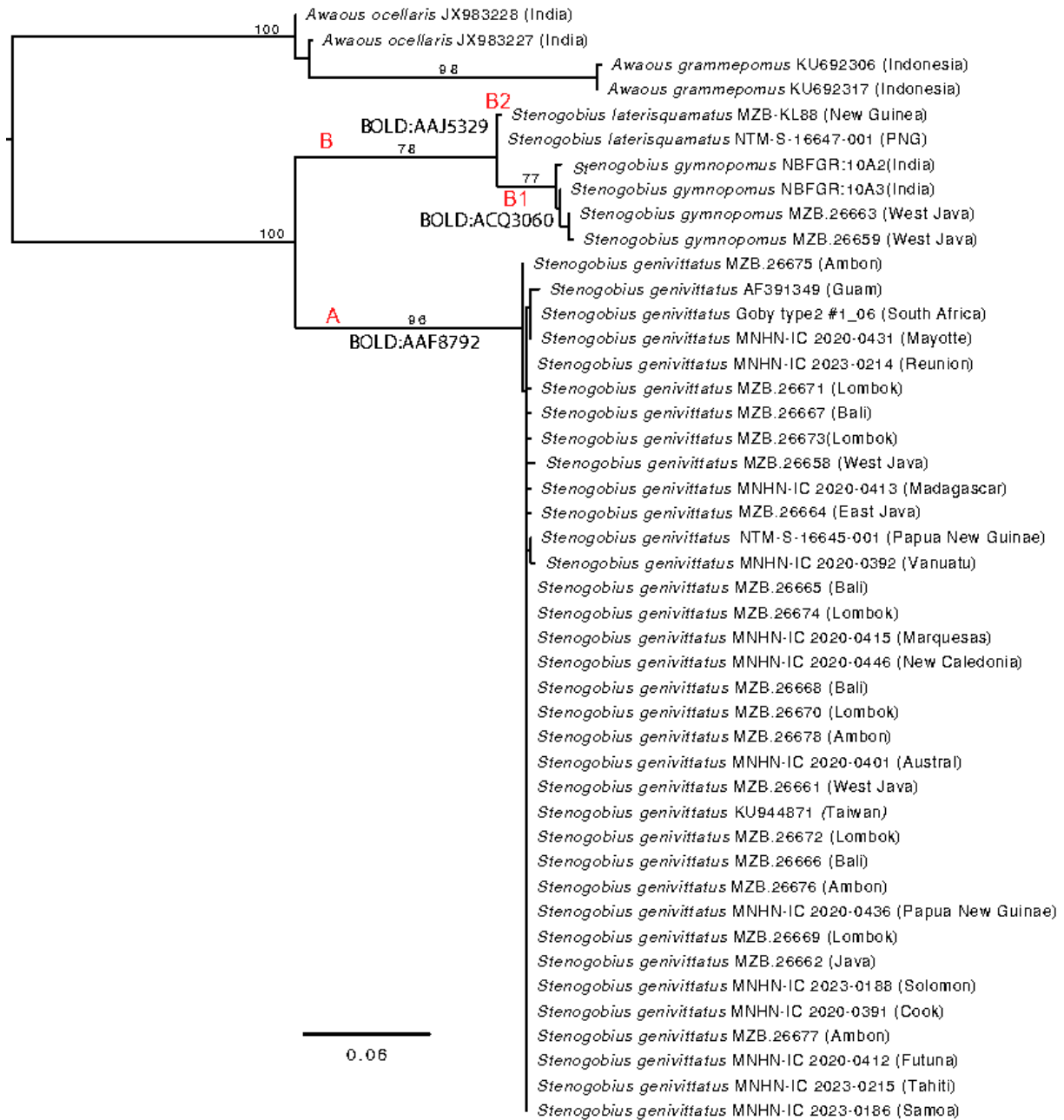
284

285 **Molecular analysis**

286 The partial *COI* sequences were obtained for 42 specimens. A 516 bp alignment was
287 constructed with the 42 specimens composed by 16 selected *S. genivittatus* *COI* sequences
288 (Austral Is., Guam Is., Mayotte, Madagascar, Vanuatu, Marquesas Arch., New Caledonia,
289 Futuna Is., Samoa Is., Cook Is., Taiwan, Tahiti Is., Solomon Is., PNG, Reunion Is., South
290 Africa) from Causse *et al.* (2023), two from India, two from PNG, 22 from Indonesia. Four
291 outgroup sequences (Table I) were added to the 42 specimens sequenced. The most likely
292 model according to the Bayesian Information Criterion is HKY+F+G4. The ML phylogenetic
293 reconstruction undertaken on the final 42 sequences alignment points to two well supported
294 clades (Fig. 2). The first clade (A) includes *S. genivittatus* (Valenciennes, 1837) specimens
295 (35 specimens from 5 different regions, including different localities of Indonesia and
296 specimens from South Africa, Taiwan, Papua New Guinea and Society Islands). In this clade,
297 the genetic analyses on specimens caught on type localities (Watson, 1991) (Table I; Fig. 2),
298 confirm results provided with the morphology, specifically from Bali with *G. blokzeyli* and
299 Papua with *S. marinus*. Our genetic results show no difference between all the specimens
300 cited above and confirm that they all correspond to the widespread species
301 *Stenogobius genivittatus*. The second clade (B) includes *Stenogobius gymnopomus* from West
302 Java (Indonesia) (B1) and *Stenogobius laterisquamatus* from Papua (B2).

303 The mean HKY+F+G4 genetic distance among the 35 specimens of *S. genivittatus* is
304 0.18 %, a value that is similar among *S. laterisquamatus* (0.2 %) specimens while it is higher
305 among *S. gymnopomus* (0.56%) specimens. The mean interspecific HKY+F+G4 genetic
306 distance is 11.6 % between *S. genivittatus* and *S. laterisquamatus*; 3.3 % between
307 *S. gymnopomus* and *S. laterisquamatus* and 12 % between *S. genivittatus* and *S. gymnopomus*
308 (Table II).

309



310

311 Figure 2. – Maximum Likelihood tree of the *COI* DNA sequences for specimens of the *Stenogobius*

312 genus. Number above branches represent bootstrap proportion, codes below represent Barcode Index

313 Number in BOLD.

314

315 Table II. – Mean percentage of divergence between outgroup species and *Stenogobius genivittatus*,
 316 *S. gymnopomus* and *S. laterisquamatus*.

| | 1 | 2 | 3 | 4 | 5 |
|-----------------------------|-------------|------------|------|-----|---|
| 1 <i>S. genivittatus</i> | | | | | |
| 2 <i>S. laterisquamatus</i> | 11.6 | | | | |
| 3 <i>S. gymnopomus</i> | 12 | 3.3 | | | |
| 4 <i>A. grammepomus</i> | 15.3 | 13.6 | 13.5 | | |
| 5 <i>A. ocellaris</i> | 15.1 | 15.1 | 15 | 9.1 | |

317

318 **Comparison within the Indonesian species**

319 *Stenogobius genivittatus* differs from the other Asian species (*S. gymnopomus*,
 320 *S. laterisquamatus* and *S. ophthalmoporus* in having more second dorsal and anal rays (I-11
 321 instead of I-10); pectoral rays usually 15, instead of 15 to 17; predorsal scales usually 12-23,
 322 instead of to 18-26 for *S. laterisquamatus* and 0-2 for *S. gymnopomus*; lateral scale series
 323 from **45 to 52** instead of 50-58 for *S. laterisquamatus*; scales on preopercle, opercle, pectoral
 324 fin base are more often absent, whereas always or at least more often present
 325 *S. laterisquamatus*, *S. ophthalmoporus* (suppl. Data). Preanal length (% in SL) usually from
 326 50 to 60, instead of *S. laterisquamatus* (35-58); snout length (% in SL): varied from 5 to 11;
 327 zigzag peduncle scales 9 instead of 10-11 for *S. laterisquamatus*. Head length (% in SL) is
 328 usually between 25 and 32 (with a maximum value of 19-39) instead of 23-26 for
 329 *S. ophthalmoporus*.

330

331 *Stenogobius* from Indonesia

332 ***Stenogobius genivittatus* (Valenciennes, 1837)**

333 Specimens analysed here from various localities (13 specimens coming from Causse *et*
 334 *al.*, 2023; 2 specimens from PNG and 25 from Ambon Is., West Java Is., East Java, West Bali
 335 Is., Lombok Is., West New Guinea) confirm the widespread presence of *Stenogobius*
 336 *genivittatus* in Indonesia.

337 Originally supposed to be endemic to French Polynesia and then reported from South
338 Africa to Hawaii, these occurrences extend the distribution of *S. genivittatus* in almost all
339 tropical Indo-Pacific regions. The morphomeristic analysis also showed that there are no
340 differences between the specimens originating from various localities sampled. These
341 congruent datasets allowed synonymising three species with *S. genivittatus* (Valenciennes,
342 1837): *G. blokzeyli* Bleeker, 1860, *G. beauforti* Weber, 1907 and *S. marinus* Watson, 1991,
343 which were previously supposed to be endemic to Indonesia.

344 The main morphomeristic characters of *S. genivittatus* are given by Causse *et al.*
345 (2023): D VI-I, 10-12 (mainly 11); A I-10/12 (mainly 11); C 11-15 (mainly 13); P 14-16
346 (mainly 15); PD 12-23; TRB 9-13; TRF 12-18; LS 45-52; ZZ caudal branched peduncle 8-9
347 (mainly 9); ZZ D2 base 7-10; predorsal length 30-52 (lengths in % of SL); head length
348 between 19-39 (in % of SL); preanal length 49-77 (in % of SL); BDL 15-30 (in % of SL);
349 BDM 15-29 (in % of SL); caudal peduncle length 7-17 (in % of SL); HD1 18-27 (female) to
350 18-31 (male) (in % of SL); jaw length 6-17 (in % of SL); anal length 31-55 (in % of SL);
351 second dorsal 35-56 (female) 37-63 (male) (in % of SL); caudal peduncle depth 8-14 (in % of
352 SL); space inter D1-D2 4-15 (in % of SL); eye diameter 2-10 v; interorbital distance 2-6 (in %
353 of SL); snout length 5-11 (in % of SL); interdorsal membrane distance 1-7 (in % of SL);
354 pelvic length 14-33 (in % of SL); pectoral length 13-33 (in % of SL). Cheek mainly naked,
355 opercle scaled or not; central pectoral base scaled or not; breast and belly mainly scaled;
356 predorsal region fully scaled on the anterior part to the first dorsal fin; first dorsal fin and
357 pores and papillae are presented in Causse *et al.* (2023).

358

359 ***Stenogobius gymnopomus* (Bleeker, 1853)**

360 Seven specimens were studied, including Holotype (RMNH 4552), from Sumatra
361 Island, West Java Island and Malaysia.

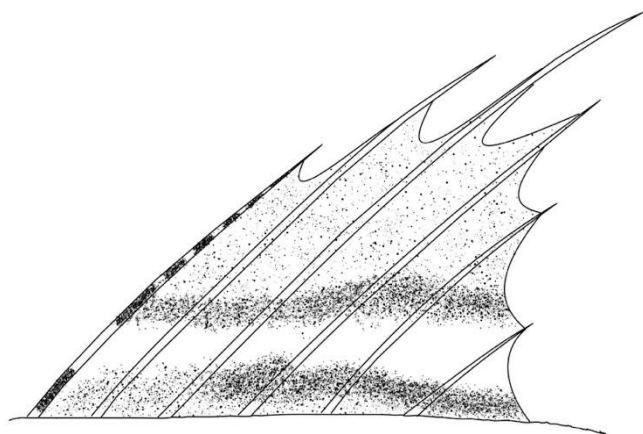
362 Described originally from Sumatra Island (Indonesia), this species was cited from
363 various other locations like India, Andaman Islands and Sumbawa Islands (Indonesia)
364 (Watson, 1991). The main morphomeristic characters are given below.

365 D VI-I, 10; A I-10/11; C 13-14; P 16; PD 0-2; TRB 10-12; TRF 16; LS 49-52; ZZ
366 caudal peduncle 9; ZZ D2 base 9; head length between 24 to 26 (in % of SL); preanal length
367 54-55 (in % of SL); BDL 17-20 (in % of SL); BDM 20-23 (in % of SL); caudal peduncle
368 length 11-15 (in % of SL); HD1 20 (female) to 23-27 (male) (in % of SL); jaw length 9-11 (in
369 % of SL); anal length 45-47 (in % of SL); second dorsal 42-46 (male) (in % of SL); caudal
370 peduncle depth 12-13 (in % of SL); space inter D1-D2 7 (female) to 8-9 (male) (in % of SL);
371 eye diameter 4-7 (in % of SL); interorbital distance 3-4 (in % of SL); snout length 6-7 (in %
372 of SL); interdorsal membrane distance 3 (female) to 1-5 (male) (in % of SL); pelvic length
373 18-24 (in % of SL); pectoral length 20-22 (in % of SL). Cheek naked, opercle naked; central
374 pectoral base scaled or not; breast and belly naked or not; predorsal region naked or few
375 scaled on the anterior part to the first dorsal fin; first dorsal fin with blackish marks on the
376 posterior half of fin near base, marking darker posterior to fifth spine (Fig. 3). Pores and
377 papillae are presented in Fig. 4.

378 According to the restricted number of studied specimens, we couldn't test a possible
379 sexual dimorphism.

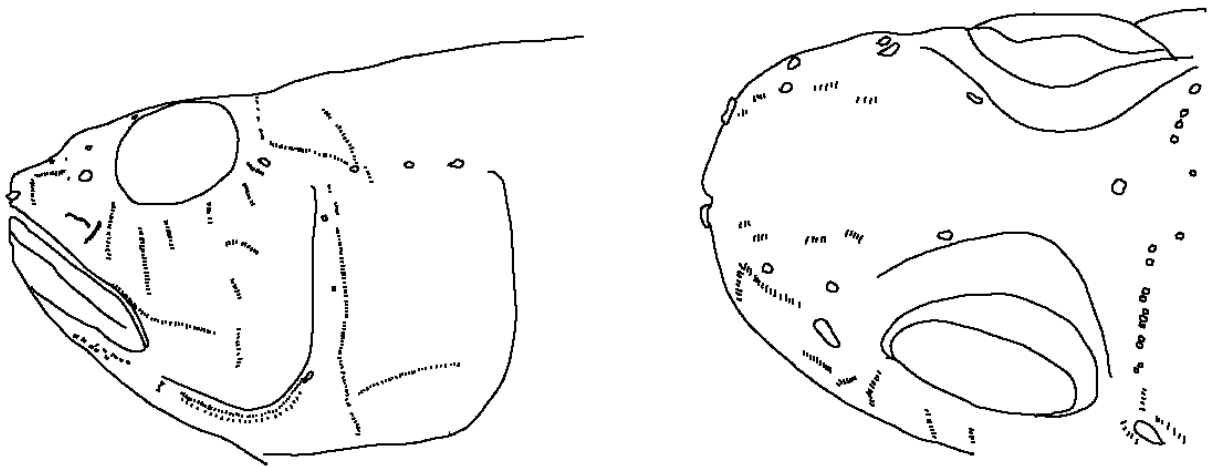
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381



382 Figure 3. – Illustration of *Stenogobius gymnopomus* first dorsal fin.

383



384

385 Figure 4. – Illustration of *Stenogobius gymnopomus* cephalic pores and papillae.

386

387 ***Stenogobius laterisquamatus* (Weber, 1908)**

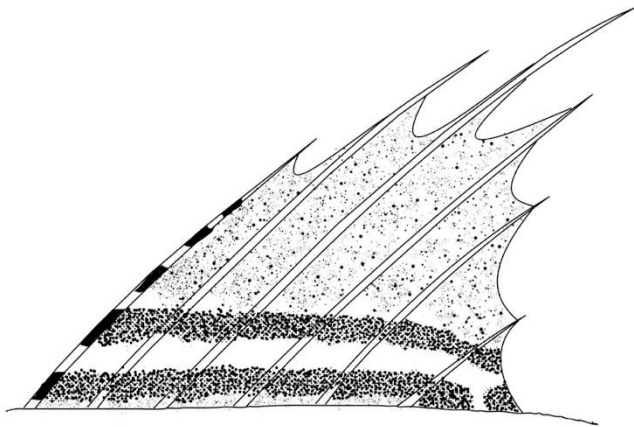
388 Twenty-seven specimens were analysed, including type specimens (ZMA116477),
389 from New Guinea (Indonesia) and PNG.

390 The species was described on the base of two specimens from a location in Northern
391 Papua, Moso River, tributary of Tami River by Beaufort and Weber. The type locality is close
392 to the frontier between Indonesia and PNG. The main morphomeric characters are given
393 below.

394 D VI-I, 10; A I-10; C 13-15; P 15-17 (mainly 16); PD 17-26; TRB 10-14; TRF 15-20;
395 LS 50-64; ZZ caudal peduncle 9-11; ZZ D2 base 9-11; head length between 24 to 26 (in % of
396 SL); preanal length 53-58 (in % of SL) (except for one specimen with 35); BDL 16-25 (in %
397 of SL); BDM 15-26 (in % of SL); caudal peduncle length 8-17 (in % of SL); HD1 18-30
398 (female) to 25-35 (male) (in % of SL); jaw length 6-9 (in % of SL); anal length 33-47 (in % of
399 SL); second dorsal 33-42 (except for one specimen with 63) (female) to 41-53 (male) (in % of
400 SL); caudal peduncle depth 9-12 (in % of SL); space inter D1-D2 7-10 (female) to 6-10
401 (male) (in % of SL); eye diameter 4-7 (in % of SL); interorbital distance 4-7 (in % of SL);

402 snout length 5-9 (in % of SL); interdorsal membrane distance 1-4 (female) to 1-6 (male) (in %
403 of SL); pelvic length 17-25 (in % of SL); pectoral length 16-23 (in % of SL). Cheek scaled,
404 opercle scaled; central pectoral base scaled; breast and belly scaled; predorsal region fully
405 scaled on the anterior part to the first dorsal fin; first dorsal fin with four to six spaced black
406 marks along the first dorsal spine, a black band all along the fin base, more pronounced on the
407 anterior part of each membrane between spines, a medial black band from the first spine to the
408 posterior part of the fin (Fig. 5). Pores and papillae are presented in Fig. 6.

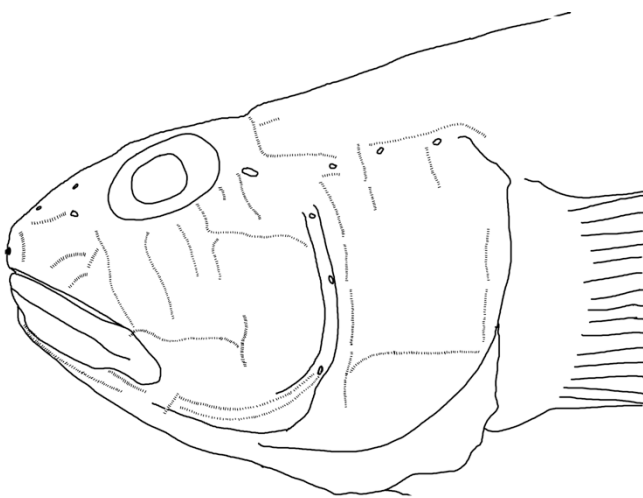
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410

411 Figure 5. – Illustration of *Stenogobius laterisquamatus* first dorsal fin.

412



413

414 Figure 6. – Illustration of *Stenogobius laterisquamatus* cephalic pores and papillae.

415

416 ***Stenogobius ophthalmoporus* (Bleeker, 1853)**

417 Eleven specimens, including syntypes (ZMA 4510), were examined from Molucca
418 Islands (Indonesia) and Luzon (Philippines). The main morphomeristic characters are given
419 below.

420 D VI-I, 10; A I-9/10 (mainly 10); C 13; P 16-17 (mainly 16); PD 13-20; TRB 10-11;
421 TRF 14-16; LS 46-52; ZZ caudal peduncle 9; ZZ D2 base 9-10; head length between 23 to 26
422 (in % of SL); preanal length 50-56 (in % of SL); predorsal 30-34 (in % of SL); BDL 16-22 (in
423 % of SL); BDM 19-24 (in % of SL); caudal peduncle length 13-16 (in % of SL); HD1 21-35
424 (in % of SL); jaw length 8-9 (in % of SL); anal length 40-52 (in % of SL); second dorsal 36-
425 56 (in % of SL); caudal peduncle depth 12-14 (in % of SL); space inter D1-D2 8-10 (in % of
426 SL); eye diameter 5-7 (in % of SL); interorbital distance 5-6 (in % of SL); snout length 6-7 (in
427 % of SL); interdorsal membrane distance 2-5 (in % of SL); pelvic length 19-26 (in % of SL);
428 pectoral length 18-21 (in % of SL). Cheek scaled, opercle scaled; central pectoral base scaled;
429 breast and belly scaled; predorsal region scaled on the anterior part to the first dorsal fin;
430 according to Watson, 1991, first dorsal fin with blackish marks on the posterior half of fin
431 near base, marking darker posterior to fifth spine. Coloration of type first dorsal fin could not
432 be analysed due to their bad state.

433 The morphomeristic analysis also showed that there are no differences between the
434 specimens originating from various localities sampled. These congruent datasets allowed
435 synonymising the species *G. lacrymosus* Peters, 1868 with *S. ophthalmoporus* (Bleeker,
436 1853), which was previously supposed to be endemic to Luzon.

437 According to the restricted number of studied specimens, we couldn't test a possible
438 sexual dimorphism.

439

440

DISCUSSION

441

442 Causse *et al.* (2023) showed that *S. genivittatus* is a widespread species distributed in
443 the entire Indo-Pacific Ocean, from South Africa in the Western part to Hawaii and French
444 Polynesia in the Eastern part. The present study aimed at analysing its distribution in areas
445 like Indonesia, the northern part of the Indian Ocean (India, Sri Lanka), the Andaman Islands
446 and the Indochinese Peninsula. It shows the presence of this species in different islands of the
447 Indonesian Archipelago: firstly, in the Lesser Sunda Islands, including Java, Bali and Lombok
448 islands, and secondly in Moluccas Archipelago with Ambon Island. Contiguously, the
449 presence of *S. genivittatus* in the National Central District in Papua New Guinea is also
450 indicated. All these new occurrences are, after all, consistent with the results provided by
451 Causse *et al.* (2023), in which it was demonstrated that this species has a large-scale
452 distribution in the Indo Pacific Ocean.

453 Up-to-date, there is only a restricted number of amphidromous species presenting a
454 large distribution in the Indo-Pacific; Among fishes, there are the species *Sicyopterus*
455 *lagocephalus* (Pallas, 1770) (Lord *et al.*, 2012), *Eleotris fusca* Bloch & Schneider, 1801
456 (Mennesson *et al.*, 2018), *Microphis brachyurus* (Häy *et al.*, 2023) (Häy *et al.*, 2023) and
457 *Giuris viator* Keith, Mennesson, Lord & Hubert, 2020. There are also the crustaceans
458 *Caridina typus* Edwards, 1837 (De Mazancourt *et al.*, 2020) and *Macrobrachium lar*
459 (Fabricius, 1798) (Castelin *et al.*, 2013) or the mollusc *Neritina stumpffi* Boettger, 1890
460 (Abdou *et al.*, 2018).

461 Besides, in addition to the conclusions of Causse *et al.* (2023), the genus *Stenogobius*
462 presents a smaller species diversity than previously thought with 28 species initially described
463 and 12 valid ones after this taxonomic revision. Indeed, 15 species names have been
464 synonymized under the species name *genivittatus*: 12 in Causse *et al.*, (2023) and 3 in the
465 present work (*S. marinus*, *G. beauforti* and *G. blokzeyli*). Three other species were recognized

466 in our study: *Stenogobius laterisquamatus* in New Guinea, *S. gymnopomus* in West Bali,
467 and *S. ophthalmoporus* in Moluccas Archipelago. The species *G. lacrymosus* Peters, 1868 is
468 synonymized with *S. ophthalmoporus* (Bleeker, 1853). According to the number of samples
469 we have (both in *COI* Barcoding and morphology), these three species seem restricted to
470 specific areas. This taxonomic work allowed to identify that even if the Indonesian
471 Archipelago is well known for its freshwater ichthyofauna, with about 1200 native species
472 (Hubert et al., 2015), in which a high endemism is present, only 4 *Stenogobius* species are
473 identified in the archipelago at this stage: a large-scale *S. genivittatus* species and the three
474 species with a restricted geographic distribution, *S. laterisquamatus*, *S. gymnopomus* and
475 *S. ophthalmoporus*. This low specific diversity was also demonstrated in Causse *et al.* (2023)
476 concerning other areas of the Indo Pacific. For example, the Marquesas Archipelago, in which
477 high levels of endemism are usually observed in amphidromous fishes, and especially gobies
478 (*Lentipes rubrofasciatus* Maugé *et al.*, 1992; *Sicyopterus marquesensis* Fowler, 1932;
479 *Smilosicyopus bitaeniatus* (Maugé *et al.*, 1992); *Stiphodon oatea* Keith *et al.*, 2010; *Stiphodon*
480 *tuivi* Watson, 1995) (Keith *et al.*, 2013), only present the widespread species *S. genivittatus*.

481 The distribution of *S. genivittatus* in the entire Indo Pacific region and the low number
482 of species in the *Stenogobius* genus is the result of the combination between the complex
483 biogeography of tropical islands (changes in the marine connections between the Indian and
484 Pacific Oceans throughout time, island emergence...), the biology of the species (life history
485 traits, pelagic larval duration, oceanic migration during the larval phase...) and evolutionary
486 processes (genetic variation, gene flow between populations...). Further studies on the life
487 history traits of *Stenogobius* species are needed (estimation of pelagic larval duration as a
488 proxy for dispersal capacities, population structure studies...) in order to understand the
489 evolutionary processes, which have shaped this surprising distribution, as opposed to many
490 other amphidromous species, which usually have a more restricted distribution.

491 Indonesia is located in the Indo-pacific Barrier (IPB), which is composed of the three
492 regions of Indo-Burma in the northern, Sundaland on the western part and Wallacea in the
493 South. In the south-eastern, between New Guinea and Australia is present the Torres Strait
494 Barrier in the Sahul Shelf and endly, in the eastern, the Philippines region. The IPB
495 topography changed during history with huge oceanic level variations depending to Ice Ages
496 and Interglacial Periods (mainly the Pleistocene period). This period was described as the
497 most important and the most explanatory for actual and amphidromic species distribution.
498 Concerning *S. genivittatus*, the IPB history seems not impact his distribution, in the contrary
499 to *S. laterisquamatus* and *ophthalmoporus*. Indeed, these two species are restricted to small
500 regions along the IPB. Concerning *S. gymnopomus*, the confirmed presence in India allowed
501 to think a possible passage through the Sunda region.

502 CONSERVATION

503 As all tropical insular amphidromic species, the *Stenogobius* species are submitted to
504 multiples threat. Up-to-date, *Stenogobius* species are labelled as Least Concern (LC) (for *S.*
505 *ophthalmoporus*, *S. laterisquamatus* and *S. genivittatus*) or Data Deficient (DD) (for *S.*
506 *genivitattus*) in IUCN Red List categories with very few available data on the geographic
507 ranges and population dynamics (population trends, habitat fragmentation...). Indeed, insular
508 rivers are more and more impacted by series of anthropic activities, such as deforestation,
509 water pollution by domestic discharges and chemicals, water-flow impediments and global
510 change. Excepted few isolated studies for Hawaii Islands (Heim-Ballew *et al.*, 2019 and
511 Radkte *et al.*, 1988) and Okinawa (Yamazaki *et al.*, 2011), no other comprehensive works
512 were focused on their life cycles: *S. genivitattus* large-scale Indo-Pacific distribution shows
513 migrations ways between islands, continents and sometimes a resident way of life (Heim-
514 Ballew *et al.*, 2019). In the contrary, the three other species in this paper present more
515 restricted areas. These conclusions tend to enhance a better understanding of taxonomic and

516 ecologic of the Oxudercidae genera, especially in Indonesia, well known for endemism to
517 upgrade efficient management and conservation measures.

518

519

CONCLUSION

520 The present study improves our knowledge of the genus *Stenogobius* in Indonesia. It
521 confirmed the presence of endemic *Stenogobius* species in several locations (Moluccas, West
522 Bali, Northern New Guinea) and the presence of the widespread *Stenogobius genivittatus*. As
523 oceanographic topographies of each Indonesian coasts are known to impact river biodiversity
524 in Indonesia, it is important that a sampling effort be undertaken in more localities in order to
525 check whether there are more *Stenogobius* species in this area of the Indo Pacific.

526

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731

732 **Supplementary data**

733 Morphometric data of *Stenogobius* specimens.