



## **Stenogobius (Teleostei : Gobioidae : Oxudercidae) from Indonesia**

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

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## 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*.

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## 46 **French title**

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

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## 49 **French abstract**

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

## Key words

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

## INTRODUCTION

Tropical aquatic biodiversity in the Indo-Pacific Ocean follows an East-West gradient (Hubert *et al.*, 2012), peaking in the Indo-Australian archipelago, species richness is exceptional in the coral triangle, a marine hotspot of biodiversity encompassing the Philippines to New Caledonia, including Indonesia, Papua New Guinea, the Solomon Islands 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,

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

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

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

## MATERIALS & METHODS

### Sample collections

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

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

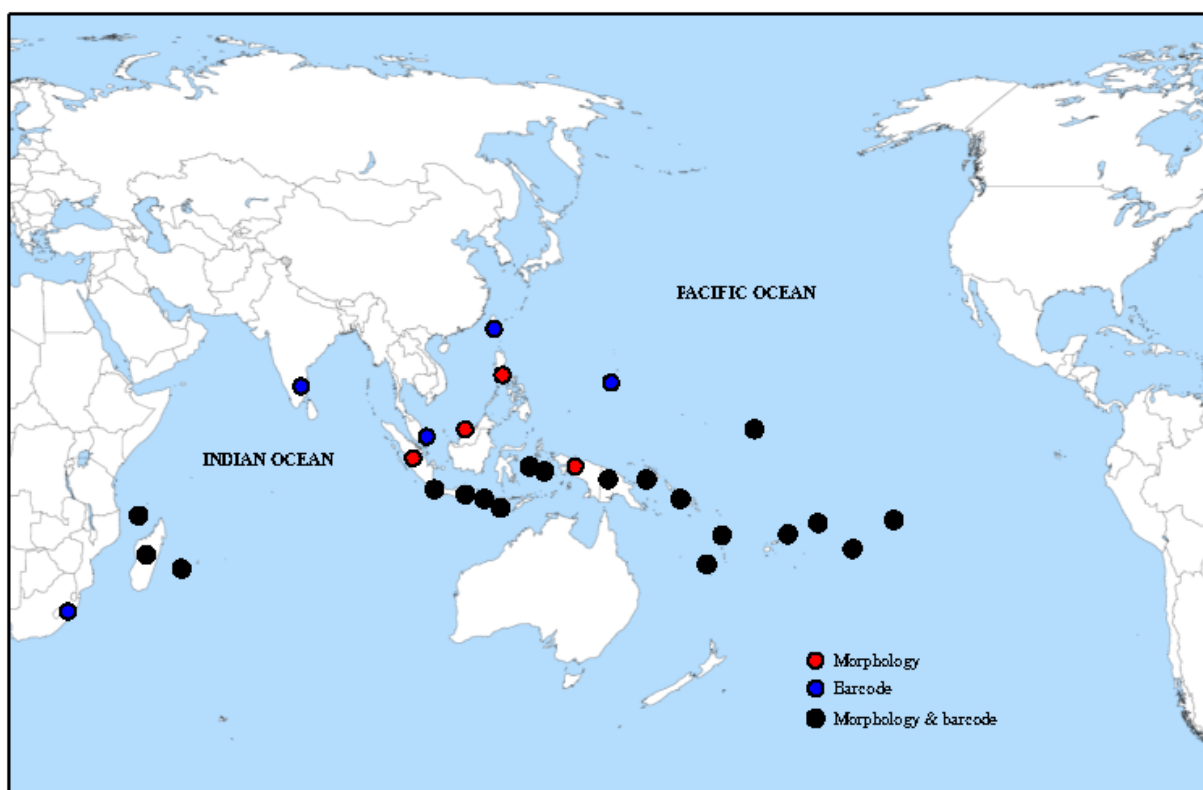


Figure 1. – Map of the Indo-Pacific showing sampling localities, and *Stenogobius* samples for which morphology, barcode and both morphology and barcode data was collected and analysed.

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 |             |             |
|         | <i>Stenogobius laterisquamatus</i> | <i>Stenogobius laterisquamatus</i> | WAM 29597-004      | 8      | X              |              |     |                      | Papua New Guinea |             | Ulieg Creek |
|         | <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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86

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## Morphomeristic analysis

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

## Material examined

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

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

## Type material

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

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

## **DNA barcoding**

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

Genomic DNA was extracted from the muscle tissue samples using a Qiagen DNeasy 96 tissue extraction kit following the manufacturer's instructions. A 652 bp segment from the 5' region of the cytochrome oxidase I gene (COI) was amplified using the primer cocktail C\_FishF1t1/C\_FishR1t1 (Ivanova *et al.*, 2007). PCR amplifications were done on a Veriti 96-well Fast thermocycler (ABI-Applied Biosystems) with a final volume of 10.0 µL containing 5.0 µL buffer 2X, 3.3 µL ultrapure water, 1.0 µL of each primer (10 µM), 0.2 µL enzyme Phire Hot Start II DNA polymerase (5U), and 0.5 µL of DNA template (~50 ng). The following thermocycler regime was used: initial denaturation at 98°C for 5 min followed by 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](https://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](https://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

## Morphomeristics

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

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

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

## Molecular analysis

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

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



Figure 2. – Maximum Likelihood tree of the *COI* DNA sequences for specimens of the *Stenogobius* genus. Number above branches represent bootstrap proportion, codes below represent Barcode Index Number in BOLD.

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

|   |                           | 1    | 2    | 3    | 4   | 5 |
|---|---------------------------|------|------|------|-----|---|
| 1 | <i>S. genivittatus</i>    |      |      |      |     |   |
| 2 | <i>S. laterisquamatus</i> | 11.6 |      |      |     |   |
| 3 | <i>S. gymnopus</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. gymnopus*,  
 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. gymnopus*; 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.

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

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

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

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

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

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 caudal peduncle 9; ZZ D2 base 9; head length between 24 to 26 (in % of SL); preanal length 54-55 (in % of SL); BDL 17-20 (in % of SL); BDM 20-23 (in % of SL); caudal peduncle length 11-15 (in % of SL); HD1 20 (female) to 23-27 (male) (in % of SL); jaw length 9-11 (in % of SL); anal length 45-47 (in % of SL); second dorsal 42-46 (male) (in % of SL); caudal peduncle depth 12-13 (in % of SL); space inter D1-D2 7 (female) to 8-9 (male) (in % of SL); eye diameter 4-7 (in % of SL); interorbital distance 3-4 (in % of SL); snout length 6-7 (in % of SL); interdorsal membrane distance 3 (female) to 1-5 (male) (in % of SL); pelvic length 18-24 (in % of SL); pectoral length 20-22 (in % of SL). Cheek naked, opercle naked; central pectoral base scaled or not; breast and belly naked or not; predorsal region naked or few scaled on the anterior part to the first dorsal fin; first dorsal fin with blackish marks on the posterior half of fin near base, marking darker posterior to fifth spine (Fig. 3). Pores and papillae are presented in Fig. 4.

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

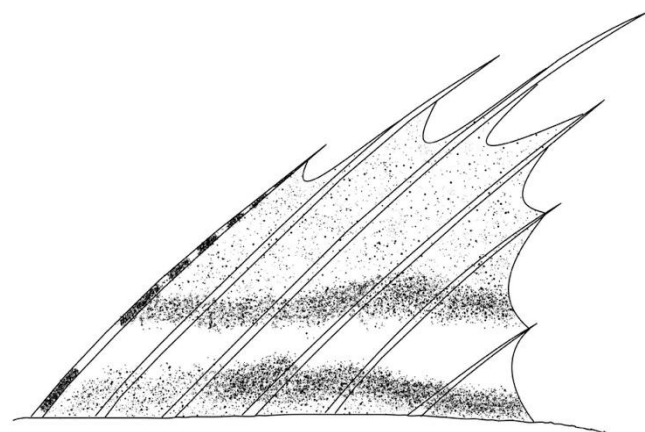


Figure 3. – Illustration of *Stenogobius gymnopomus* first dorsal fin.

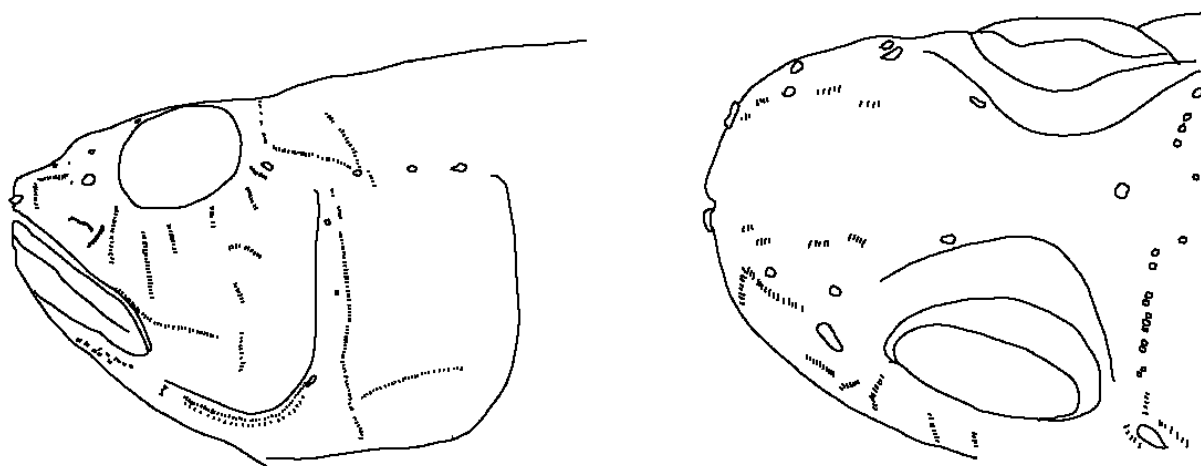


Figure 4. – Illustration of *Stenogobius gymnopomus* cephalic pores and papillae.

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

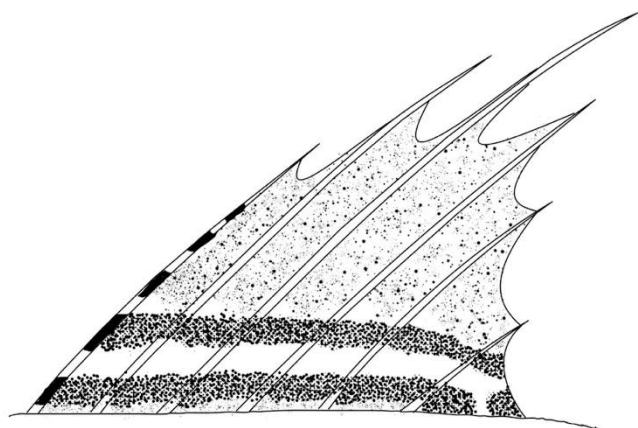
Twenty-seven specimens were analysed, including type specimens (ZMA116477), from New Guinea (Indonesia) and PNG.

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

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

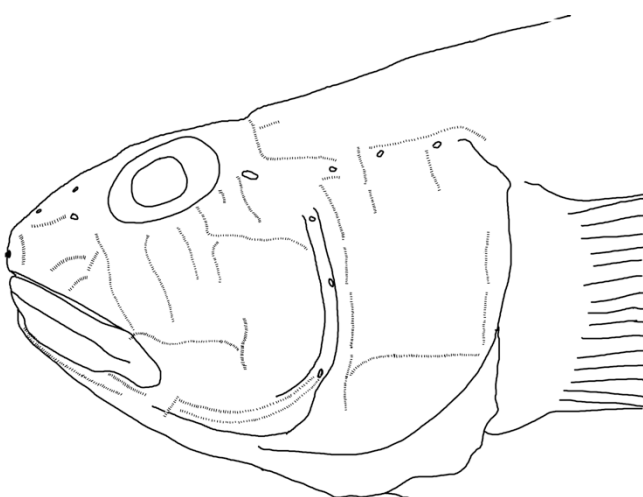
409



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

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

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

Besides, in addition to the conclusions of Causse *et al.* (2023), the genus *Stenogobius* presents a smaller species diversity than previously thought with 28 species initially described and 12 valid ones after this taxonomic revision. Indeed, 15 species names have been synonymized under the species name *genivittatus*: 12 in Causse *et al.*, (2023) and 3 in the 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.

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

## CONSERVATION

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

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

## CONCLUSION

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

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## REFERENCES

563 Abdou A., Lord C., Keith P. & Galzin R., 2019. – Phylogéographie de *Neritina stumpffi*  
 564 Boettger, 1890 et *Neritina canalis* Sowerby, 1825 (Gastropoda, Cycloneritida,

565 Neritidae). *Zoosystema*, 41(12): 237-248.  
 566 <https://doi.org/10.5252/zoosystema2019v41a12>

567 Allen G.R., Hortle K.G. & Renyaan S.J., 2000. – Freshwater Fishes of the Timika Region,  
 568 New Guinea. P.T. Freeport Indonesian Company, Timaka, Indonesia.

569 Allen G.R., 2004. – Two new species of gobiid fishes (*Lentipes* & *Stenogobius*) from  
 570 freshwaters of Papua New Guinea. *Fish. Sahul.*, 18(4): 73-95.

571 Brown W.M., George M. Jr & Wilson A.C., 1979. – Rapid evolution of animal mitochondrial  
 572 DNA. *Proc. Natl. Acad. Sci. USA*, 76(4): 1967-1971.  
 573 <https://doi.org/10.1073/pnas.76.4.1967>.

574 Castelin M., Feutry P., Hautecoeur M., Marquet G., Wowor D., Zimmermann G. & Keith P.,  
 575 2013. – New insight on population genetic connectivity of widespread amphidromous  
 576 prawn *Macrobrachium lar* (Fabricius, 1798) (Crustacea: Decapoda: Palaemonidae).  
 577 *Mar Biol.*, 160: 1395-1406. <https://doi.org/10.1007/s00227-013-2191-y>

578 Causse R., Mennesson M.I., Lord C. & Keith P., 2023. – *Stenogobius* (Teleostei: Gobioidi)  
 579 from the Indian-Pacific Island rivers. *Cybum*, 47(2): 141-165  
 580 <https://doi.org/10.26028/cybum/2023-011>.

581 Dayrat B., 2005. – Towards integrative taxonomy. *Biol. J. Linn. Soc.*, 85(3): 407-417.  
 582 <https://doi.org/10.1111/j.1095-8312.2005.00503.x>

583 Felsenstein J., 1981. – Evolutionary trees from DNA sequences: a maximum likelihood  
 584 approach. *J. Mol. Evol.*, 17: 368-376. <https://doi.org/10.1007/BF01734359>

585 Feutry P., Castelin M., Ovenden J., Dettai A., Robinet T., Cruaud C. & Keith P., 2013. –  
 586 Evolution of diadromous behaviour in fish species: insights from a tropical genus  
 587 (*Kuhlia* spp.). *Am. Nat.*, 181(1): 52-63. <https://doi.org/10.1086/668593>

588 Fricke R., Eschmeyer W.N. & Van Der Laan R. (eds), 2020. – Eschmeyer’s Catalog of  
589 Fishes: Genera, Species, References.  
590 (<http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp>).

591 Galtier N., Nabholz B., Glemin S. & Hurst G.D.D., 2009. – Mitochondrial DNA as a marker  
592 of molecular diversity: a reappraisal. *Mol. Ecol.*, 18(22): 4541-4550.  
593 <https://doi.org/10.1111/j.1365-294X.2009.04380.x>

594 Häy V., Menneson M.I., Lord C. & Keith P., 2023. – Why several when one can unite them  
595 all? Integrative taxonomic revision of Indo-Pacific freshwater pipefish (Nerophinae).  
596 *Zool. J. Linn. Soc.*, 198(4): 923-956. <https://doi.org/10.1093/zoolinnean/zlad007>

597 Hebert P.D.N., Dewaard J.R., Zakharov E.V., Prosser S.W.J., Sones J.E., Mckeown J.T.A.,  
598 Mantle B. & La Salle J., 2013. – A DNA ‘Barcode Blitz’: Rapid Digitization and  
599 Sequencing of a Natural History Collection. *PLOS ONE*, 8(7): e68535.  
600 <https://doi.org/10.1371/journal.pone.0068535>.

601 Heim-Ballew H., Moody K.N., Blum M.J., McIntyre P.B. & Hogan J.D., 2019. – Migratory  
602 flexibility in native Hawai’ian amphidromous fishes. *J. Fish Biol.*, 96: 456-468.  
603 <https://doi.org/10.1111/jfb.14224>

604 Hubert N., Meyer C.P., Bruggemann H.J., Guerin F., Komeno R.J.L., Espiau B., Causse R.,  
605 Williams J.T. & Planes S., 2012. —Cryptic diversity in Indo-Pacific coral-reef fishes  
606 revealed by DNA-Barcoding provides new support to the centre-of-overlap  
607 hypothesis. *PLOS ONE*, 7(3): e28987. <https://doi.org/10.1371/journal.pone.0028987>

608 Iida M., Kondo M., Tabouret H., Maeda K., Pecheyran C., Hagiwara A., Keith P. &  
609 Tachihara K., 2017. – Specific gravity and migratory patterns of amphidromous  
610 gobioid fish from Okinawa Island, Japan. *J. Exp. Mar. Biol. Ecol.*, 486: 160-169.  
611 <https://doi.org/10.1016/j.jembe.2016.09.011>

612 Ivanova N.V., Zemlak T.S., Hanner R.H. & Hebert P.D.N., 2007. – Universal primer  
613 cocktails for fish DNA barcoding. *Mol. Ecol. Resour.*, 7(4): 544-548.  
614 <https://doi.org/10.1111/j.1471-8286.2007.01748.x>

615 Kalvaanamoorthy S., Minh B.Q., Wong T.K.F., Von Haeseler A. & Jermiin L.S., 2017. –  
616 ModelFinder: fast model selection for accurate phylogenetic estimates. *Nat. Methods*,  
617 14: 587-589. <https://doi.org/10.1038/nmeth.4285>

618 Katoh K., Rozewicki J. & Yamada K.D., 2019. – Access the recommendation on F1000  
619 MAFFT online service: multiple sequence alignment, interactive sequence choice and  
620 visualization. *Brief. Bioinform.*, 20: 1160-1166. <https://doi.org/10.1093/bib/bbx108>

621 Kearse M., Moir R., Wilson A., Stones-Havas S., Cheung M., Sturrock S., Buxton S., Cooper  
622 A., Markowitz S., Duran C., Thierer T., Ashton B., Meintjes P. & Drummond A.,  
623 2018. – Geneious Basic: an integrated and extendable desktop software platform for  
624 the organization and analysis of sequence data. *Bioinformatics*, 28(12): 1647-1649.  
625 <https://doi.org/10.1093/bioinformatics/bts199>

626 Keith P., 2003. – Biology and ecology of amphidromous Gobiidae in the Indo-Pacific and the  
627 Caribbean regions. *J. Fish Biol.*, 63: 831-847. <https://doi.org/10.1046/j.1095-8649.2003.00197.x>

628

629 Keith P. & Mennesson M.I., 2020. – Review of *Giuris* (Teleostei: Eleotridae) from Indo-  
630 Pacific islands, with description of three species. *Cybium*, 44(4): 331-349.  
631 <https://doi.org/10.26028/cybium/2020-444-004>

632 Keith P., Marquet G., Gerbeaux P., Lord C. & Vigneux E., 2013. – Polynesian Freshwater  
633 Fish and Crustaceans: Taxonomy, Ecology, Biology and Management. Société  
634 Française d'Ichtyologie, Paris: 282 p.

635 Keith P., Lord C. & Maeda K., 2015. – Indo-Pacific Sicydiine Gobies: Biodiversity, Life  
636 Traits and Conservation. Société Française d'Ichtyologie, Paris: 256 p.

637 Keith P., Mennesson M.I., Sauri S., Busson F., Delrieu-Trottin E., Limmon G., Nurjirana,  
 638 Dahrudin H. & Hubert N., 2020. – *Giuris* (Teleostei: Eleotridae) from Indonesia,  
 639 with description of a new species. *Cybium*, 44(4): 317-329.  
 640 <https://doi.org/10.26028/cybium/2020-444-003>  
 641 Lamoureux J.F., Morrison J.C., Ricketts T.H., Olson D.M., Dinerstein E. & McKnight M.,  
 642 2006. – Global tests of biodiversity concordance and the importance of endemism.  
 643 *Nature*, 440: 212-214. <https://doi.org/10.1038/nature04291>  
 644 Kuraku S., Zmasek C.M., Nishimura O. & Katoh K., 2013. – aLeaves facilitates on-demand  
 645 exploration of metazoan gene family trees on MAFFT sequence alignment server with  
 646 enhanced interactivity. *Nucleic Acids Res.*, 41: W22-W28.  
 647 <https://doi.org/10.1093/nar/gkt389>  
 648 Lanfear R., Calcott B., Ho S.Y.W. & Guideron S., 2012. – PartitionFinder: combined selection  
 649 of partitioning schemes and substitution models for phylogenetic analyses. *Mol. Biol.*  
 650 *Evol.*, 29: 1695-1701. <https://doi.org/10.1093/molbev/mss020>  
 651 Lord C., Lorion J., Dettai A., Watanabe S., Tsukamoto K., Cruaud C. & Keith P., 2012. –  
 652 From endemism to widespread distribution: phylogeography of three amphidromous  
 653 *Sicyopterus* species (Teleostei: Gobioidae: Sicydiinae). *Mar. Ecol. Prog. Ser.*, 455:  
 654 269-285. <https://doi.org/10.3354/meps09617>  
 655 Lindstrom D.P., 1999. – Molecular species identification of newlyhatched Hawaiian  
 656 amphidromous gobioid larvae. *Mar. Biotechnol.*, 1: 167-174.  
 657 <https://doi.org/10.1007/PL00011764>  
 658 McDowall R.M., 2007. – On amphidromy, a distinct form of diadromy in aquatic organism.  
 659 *Fish Fish.*, 8:1-13. <https://doi.org/10.1111/j.1467-2979.2007.00232.x>  
 660 McDowall R.M., 2008. – Diadromy, history and ecology: a question of scale. *Hydrobiologia*,  
 661 602: 5-14. <https://doi.org/10.1007/s10750-008-9290-7>

662 McDowall R.M., 2009. – Early hatch: a strategy for safe down-stream larval transport in  
 663 amphidromous gobies. *Rev. Fish Biol. Fish.*, 19: 1-8. [https://doi.org/10.1007/s11160-](https://doi.org/10.1007/s11160-008-9085-y)  
 664 008-9085-y  
 665 De Mazancourt V.C., Klotz W., Marquet G. & Keith P., 2018. – Integrative taxonomy helps  
 666 separate four species of freshwater shrimps commonly overlooked as *Caridina*  
 667 *longirostris* (Crustacea: Decapoda: Atyidae) on Indo-West Pacific islands. *Invertebr.*  
 668 *Syst.*, 32: 1422-1447. <https://doi.org/10.1071/IS18034>  
 669 Mennesson M.I. & Keith P., 2020. – *Eleotris* (Teleostei: Eleotridae) of the Indian Ocean: an  
 670 overview with the description of three new species. *Cybium*, 44(3): 185-203.  
 671 <https://doi.org/10.26028/cybium/2020-443-002>  
 672 Mennesson M.I., Tabouret H., Peycheran C. & Keith P., 2015. – Amphidromous life cycle of  
 673 *Eleotris fusca* (Teleostei: Gobioidae: Eleotridae) a widespread species from the Indo-  
 674 Pacific studied by otolith analyses. *Cybium*, 39(4): 249-260.  
 675 <https://doi.org/10.26028/cybium/2015-394-002>  
 676 Mennesson M.I., Bonillo C., Feunteun E. & Keith P., 2018. – Phylogeography of *Eleotris*  
 677 *fusca* (Teleostei: Gobioidae: Eleotridae) in the Indo-Pacific area reveals a cryptic  
 678 species in the Indian Ocean. *Conserv. Genet.*, 19: 1025-1038.  
 679 <https://doi.org/10.1007/s10592-018-1063-x>.  
 680 Mennesson M.I., Maeda K. & Keith P., 2019. – Evolutionary aspects of cephalic sensory  
 681 papillae of the Indo-Pacific of *Eleotris* (Teleostei: Eleotridae). *Zool. Scripta*, 48(5):  
 682 557-689. <https://doi.org/10.1111/zsc.12366>  
 683 Myers N., Mittermeier R.A., Mittermeier C.G., Da Fonseca G.A.B. & Kent J., 2000. –  
 684 Biodiversity hotspots for conservation priorities. *Nature*, 403: 853-858.  
 685 <https://doi.org/10.1038/35002501>

686 Nguyen L.T., Schmidt H.A., Von Haeseler A. & Minh B.Q., 2015. – IQ-TREE: a fast and  
 687 effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Mol.*  
 688 *Biol. Evol.*, 32: 268-274. <https://doi.org/10.1093/molbev/msu300>  
 689 Padial J.M., Miralles A., De La Riva, I. & Vences M., 2010. – The integrative future of  
 690 taxonomy. *Front Zool.*, 7: 16. <https://doi.org/10.1186/1742-9994-7-16>  
 691 Radtke R.L., Kinzie R.A. III & Folstom S.D., 1988. – Age at recruitment of Hawaiian  
 692 freshwater Gobies. *Environ. Biol. Fish.*, 23: 205-213.  
 693 <https://doi.org/10.1007/BF00004911>  
 694 Rambaut A., 2007. - FigTree v1.3.1. Available at <http://tree.bio.ed.ac.uk/software/figtree/>  
 695 Rambaut A. & Drummond A.J., 2007. - Tracer v1.4, Available at  
 696 <http://beast.bio.ed.ac.uk/Tracer>  
 697 Ratnasingham S. & Hebert P.D.N., 2013. – A DNA-based registry for all animal species: the  
 698 Barcode Index Number (BIN) system. *PLOS ONE* 8(7): e66213.  
 699 <https://doi.org/10.1371/journal.pone.0066213>.  
 700 Schlick-Steiner B.C., Steiner F.M., Seifert B., Stauffer C., Christian E. & Crozier R.H., 2010.  
 701 – Integrative taxonomy: a multisource approach to exploring biodiversity. *Ann. Rev.*  
 702 *Entomol.* 55(1): 421-438. <https://doi.org/10.1146/annurev-ento-112408-085432>  
 703 Tavaré S., 1986. – Some probabilistic and statistical problems in the analysis of DNA  
 704 sequences. Lectures on Mathematics in the Life Sciences. Vol. 17.  
 705 Teletchea F., 2010. – After 7 years and 1000 citations: comparative assessment of the DNA  
 706 barcoding and the DNA taxonomy proposals for taxonomists and non-taxonomists.  
 707 *Mitochondrial DNA*, 21: 206-226. <https://doi.org/10.3109/19401736.2010.532212>  
 708 Thuesen P., Ebner B., Larson H., Keith P., Silcock R., Prince J. & Russell D.J., 2011. –  
 709 Amphidromy links a newly documented fish community of continental Australian

- streams, to oceanic islands of the West Pacific. *PLOS ONE*, 6(10): e26685.  
<https://doi.org/10.1371/journal.pone.0026685>
- Trifinopoulos J., Nguyen L.T., Von Haeseler A. & Minh B.Q., 2016. – W-IQ-TREE: a fast  
 online phylogenetic tool for maximum likelihood analysis. *Nucleic Acids Res.*, 44:  
 W232-5. <https://doi.org/10.1093/nar/gkw256>
- Vawter L. & Brown W.M., 1986. – Nuclear and mitochondrial DNA comparisons reveal  
 extreme rate variation in the molecular clock. *Science*, 234(4773): 194-196.  
<https://doi.org/10.1126/science.301893>
- Watanabe S., Iida M., Lord C., Keith P. & Tsukamoto K., 2014. – Tropical and temperate  
 freshwater amphidromy: a comparison between life history characteristics of  
 Sicydiinae, ayu, sculpins and galaxiids. *Rev. Fish Biol. Fish.*, 24: 1-14.  
<https://doi.org/10.1007/s11160-013-9316-8>
- Watson R.E., 1991. – A provisional review of the genus *Stenogobius* with descriptions of a  
 new subgenus and thirteen new species (Pisces, Teleostei, Gobiidae). *Rec. West. Mus.*,  
 15(3): 571-654.
- Watson R.E. & Lachner E.A., 1985. – A new species of *Psilogobius* from the Indo-Pacific  
 with a redescription of *Psilogobius mainlandi* (Pisces: Gobiidae). *Proc. Biol. Soc.*  
*Washington*, 98(3): 644-654.
- Yamasaki N., Kondo M., Maeda K. & Tachihara K., 2011. – Reproductive biology of three  
 ampidromous gobies, *Sicyopterus japonicus*, *Awaous melanocephalus*, and  
*Stenogobius sp.*, on Okinawa Island. *Cybiu*, 35(4): 345-359.

## **Supplementary data**

Morphomeristic data of *Stenogobius* specimens.