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# Five new ocellus-bearing species of the cusk-eel genus *Neobythites* (Ophidiidae, Ophidiiformes) from the West Pacific, with establishment of three new species groups

FRANZ UIBLEIN[1,2,3] & JØRGEN G. NIELSEN[4]
[1]*Institute of Marine Research, P.O. Box 1870 Nordnes, N-5817 Bergen, Norway. Corresponding author;*
*franz@imr.no; https://orcid.org/0000-0002-5642-0384*
[2] *National Research Foundation - South African Institute for Aquatic Biodiversity, Makhanda/Grahamstown, South Africa*
[3] *Vietnam National Museum of Nature, Hanoi, Vietnam*
[4] *Natural History Museum of Denmark, University of Copenhagen, Denmark*

## Abstract

Five new West Pacific species of the cusk-eel genus *Neobythites* (Ophidiidae) from the lower shelf and upper slope of the Solomon Sea, off Okinawa, Japan, and off Fiji are described. The descriptions are based on nine specimens from three fish collections and unvouchered fresh colour photographs showing three specimens taken shortly after being caught. The new species all bear at least one ocellus on the dorsal fin, a conspicuous colour pattern consisting of a dark spot surrounded by a contrasting white or pale ring. Fifteen ocellus-bearing congeners are rather similar with at least one of the new species, requiring detailed comparisons based on a large set of morphometric, meristic, colour and otolith-shape data from over 300 specimens. To facilitate the comparisons among the 20 *Neobythites* species in total and the preparation of identification keys, three new taxonomic species groups, the *australiensis*, *kenyaensis* and *longiventralis* groups, are established. Also, the *steatiticus* species group which had been previously established, is slightly updated. A key for identification of each of these four groups is prepared. The most important characters for distinction among groups are the presence and number of preopercular spines, the number and position of ocelli, and pelvic-fin length. For each of the three new groups, species accounts including new species descriptions, within-group comparisons, and identification keys are prepared. For the *steatiticus* group, only the description of the new species, *N. pako* **n. sp.**, and an updated account of the Atlantic *N. monocellatus* are provided, considering previously published accounts of the other seven species in comparisons with those two species and the identification key. The results are shortly discussed, emphasizing the finding of a unique ocellus structure in *N. superocellatus* **n. sp.** (*australiensis* species group) and the need for taxonomic studies of the remaining 10 ocellus-bearing species of *Neobythites* together with additional, non-ocellus-bearing congeners.

**Key words:** ocellus spot, meristics, morphometrics, otoliths, Solomon Sea, Fiji, Japan

## Introduction

The cusk-eel genus *Neobythites* (Ophidiidae) is one of the most diverse and colourful fish genera occurring on the deeper shelf and upper slope of tropical and subtropical oceans. Currently, 55 valid species of *Neobythites* are known which differ from each other in the combination of colour patterns, body-shape, meristic and otolith characters (Uiblein & Nielsen 2021, Nielsen & Uiblein 2022). In recent years, due to increased sampling and exploration of the typical habitats of this genus, and enhanced colour-pattern identification, several *Neobythites* species have been discovered, revised, and/or redescribed (Uiblein & Nielsen 2018, 2019, 2021; Uiblein *et al*. 2019).

Regarding diagnostically important colour patterns, 25 of the hitherto known *Neobythites* species bear at least one distinct eyespot or ocellus on the dorsal fin, i.e., a dark rounded spot surrounded by a contrasting pale ring. The ocellus spot covers several dorsal-fin rays and, in some species, also extends onto the body, covering one or several scale rows below the dorsal-fin base. The contrasting ring surrounds the spot forming a concentric pale area on the dorsal fin and sometimes also on the body below (Uiblein & Nielsen 2005, 2018, Nielsen *et al.* 2009).

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The form, placement, size, and number of ocelli varies among species and can be rather widely applied in species diagnosis, because the dark spot as well as the surrounding pale area are—in contrast to many other colour patterns (e.g., Uiblein *et al.* 2019)—mostly well retained after fixation and subsequent preservation (Uiblein & Nielsen 2005, 2018, 2021, Nielsen *et al.* 2009). Attention needs however to be paid to clearly distinguish ocelli from mere spots. Dark spots or blotches without contrasting rings may also occur on the dorsal fin and occasionally in addition to ocelli or other colour patterns (Uiblein & Nielsen 2005).

Among the 25 ocellus-bearing species, a taxonomic group of single-ocellus species, the so-called "*steatiticus*" group, was established by Uiblein & Nielsen (2018). The nine species previously included in this group share a single ocellus on the dorsal fin placed close to body midpoint ("central ocellus") and have no or only a single, poorly developed spine on the hind margin of the preopercle. By the combination of these two characteristics, the *steatiticus* species group can be distinguished from the 16 other species, which either have a single-ocellus and two preopercular spines or at least two dorsal-fin ocelli and zero, one, or two preopercular spines (Uiblein & Nielsen 2018).

During the current study, samples of several ocellus-bearing *Neobythites* specimens collected during cruises in the Solomon Sea (Uiblein & Nielsen 2021), off Okinawa, Japan, and off Fiji at depths between ca. 100 and 427 m were examined or re-examined with special attention paid to colour-pattern differences. Five new species were discovered which are described, diagnosed, and compared with the 15 most similar congeners that share important diagnostic characteristics with at least one of the five new species. For facilitating comparisons and preparing identification keys, three new taxonomic species groups are established and the *steatiticus* group slightly updated (see Table 1 for an overview).

In addition to the new species descriptions, taxonomic accounts are prepared for all member species of the three new groups and for the Atlantic *N. monocellatus* Nielsen, which had been included in the *steatiticus* species group before, but not considered in detail by Uiblein & Nielsen (2018). Identification keys to species groups and to species within each group are prepared. The results are discussed with emphasis on diversity in ocellus formation and unresolved challenges in *Neobythites* taxonomy.

## Material & methods

Meristic, morphometric, colour and/or otolith shape data from 339 specimens of 20 *Neobythites* species available from earlier studies or generated for the present study were considered in the preparation of species descriptions, accounts, comparisons, and identification keys. In addition, fresh colour photographs showing three specimens were considered. Radiographs were used for axial skeleton study. Methods for meristic counts, morphometric measurements, colour categorization, and description and otolith measurements follow Nielsen *et al.* (2009) and Uiblein & Nielsen (2005, 2018, 2019, 2021).

The following categorization of ocelli placed on the dorsal fin in the genus *Neobythites* was applied: central ocellus, anterior ocellus, incomplete ocellus, and posterior ocellus. "Central ocellus" is a dark rounded spot surrounded by a contrasting pale ring placed on dorsal fin close to body midpoint. "Anterior ocellus" is an ocellus placed close to dorsal-fin origin. Sometimes (e.g., *N. longiventralis* Nielsen, see below), the anterior portion of the dark ocellus spot covers the first rays of dorsal fin and hence the contrasting ring occurs only around the remaining part of this colour structure ("incomplete ocellus"). "Posterior ocellus" is an ocellus placed on the posterior half of the dorsal fin, well behind the position of the central ocellus. There may be up to three posterior ocelli which are termed first, second and third posterior ocellus, according to position (Nielsen *et al.* 2009).

Only material examined for the newly described species and a newly recorded *Neobythites unimaculatus* Smith & Radcliffe is specified in detail. Regarding all earlier described species considered in the four species groups see detailed material lists in Nielsen (2002) for *N. australiensis* Nielsen, *N. longipes* Smith & Radcliffe, *N. longiventralis, N. nigriventris* Nielsen and *N. unimaculatus*, Nielsen *et al.* (2009) for *N. monocellatus* and *N. ocellatus* Günther, Uiblein & Nielsen (2018) for *steatiticus*-group species (except for *N. monocellatus*), and Uiblein & Nielsen (2019) for *N. kenyaensis* Nielsen.

Illustrations focus primarily on new or newly recorded species involving preserved or fresh specimens and otoliths. In some cases, right-side photographs of specimens are used and they are shown in side-reversed mode for facilitating comparisons with the mostly left-side photographs. Similarly, one left-side otolith is shown in side-reversed mode together with the other five right-side otoliths.

Online screening of images of fresh fish shortly after being caught on three of four relevant cruises with R/V *Alis* in the Solomon Sea and off Fiji (Richer de Forges 1999, 2001, 2004, 2007) resulted in detection of three specimens of two of the newly described species. These photographs are the only available documentation of fresh colour in the new species.

Morphometric data are rounded to one decimal digit in numbers <10 and to whole numbers in higher values, except for one decimal digit in averages and two decimal digits in otolith ostium depth in % SL, a rather small value throughout. Abbreviations are as follows: HT = holotype, PT = paratype, SL = standard length, HL = head length, E = East, N = North, S = South, W = West. Institutional acronyms follow Sabaj (2020).

**TABLE 1.** Ocellus-bearing *Neobythites* species, with number and category of ocelli, preopercular spine number, and pelvic-fin length information.

| Species group | *Neobythites* species | Ocellus nr.; category | Preopercular spine(s) | Pelvic fin * |
|---|---|---|---|---|
| *australiensis* | *N. superocellatus* **n. sp.** | 1; c | 2 | short |
| | *N. australiensis* Nielsen | 1; c | 2 | short |
| | *N. nigriventris* Nielsen | 1; c | 2 | short |
| | *N. unimaculatus* Smith & Radcliffe | 1; c | 2 | short |
| *kenyaensis* | *N. japonicus* **n. sp.** | 2; a, c | 2 | short |
| | *N. kenyaensis* Nielsen | 2; a, c | 0 | short |
| | *N. ocellatus* Günther | 2; a, c | 0–1 (reduced) | short |
| *longiventralis* | *N. jonathan* **n. sp.** | 1; c | 2 | long |
| | *N. zora* **n. sp.** | 2; c, p1 | 2 | long |
| | *N. longiventralis* Nielsen | 2; a, c | 2 | long |
| | *N. longipes* Smith & Radcliffe ** | 1; c | 2 | long |
| *steatiticus* | *N. pako* **n. sp.** | 1; c | 1 | short |
| | *N. gloriae* Uiblein & Nielsen | 1; c | 0 | short |
| | *N. lombokensis* Uiblein & Nielsen | 1; c | 0 | short |
| | *N. malayanus* Weber | 1; c | 0 | short |
| | *N. malhaensis* Nielsen | 1; c | 1 (reduced) | short |
| | *N. meteori* Nielsen | 1; c | 1 (reduced) | short |
| | *N. monocellatus* Nielsen | 1; c | 0–1 (reduced) | short |
| | *N. steatiticus* Alcock | 1; c | 0–1 (reduced) | short |
| | *N. stefanovi* Nielsen & Uiblein | 1; c | 0 | short |
| ungrouped | *N. bimaculatus* Nielsen | 2; c, p1 | 2 | short |
| | *N. crosnieri* Nielsen | 2; p1, p2 | 2 | short |
| | *N. fasciatus* Smith & Radcliffe | 4; c, p1, p2, p3 | 2 | short |
| | *N. fijiensis* Nielsen | 3; c, p1, p2 | 2 | short |
| | *N. gilli* Goode & Bean | 2; c, p1 | 0–1 (reduced) | short |
| | *N. macrocelli* Nielsen | 2; c, p1 | 2 | short |
| | *N. macrops* Günther | 2 (3, 4); c, p1 (p2, p3) | 2 | short |
| | *N. marianaensis* Nielsen | 2; c, p1 | 2 | short |
| | *N. multiocellatus* Nielsen, Uiblein & Mincarone | 2; c, p1 | 0–1 (reduced) | short |
| | *N. stigmosus* Machida | 3; c, p1, p2 | 2 | short |

a = anterior ocellus; c = central ocellus; p1, p2, p3 = first, second, third posterior ocellus; * long/short: clearly extending/not extending beyond anus; ** formerly included in the *steatiticus* group (see Uiblein & Nielsen 2018).

## Taxonomy

### The four species groups of *Neobythites* (see also Table 1)

- *australiensis* group: species with a single ocellus, two pre-opercular spines, and pelvic fins not reaching anus. Four species belong to this group: *Neobythites superocellatus* **n. sp.**, *N. australiensis*, *N. nigriventris*, and *N. unimaculatus*.
- *kenyaensis* group: species with two ocelli, a central ocellus and an ocellus placed close to dorsal-fin origin, with zero, one, or two preopercular spines, and pelvic fins not reaching anus. Three species belong to this group: *Neobythites japonicus* **n. sp.**, *N. kenyaensis*, and *N. ocellatus*.
- *longiventralis* group: species with one or two ocelli on dorsal fin, zero, one, or two preopercular spines, and pelvic fins extending beyond anus. Four species belong to this group: *Neobythites jonathan* **n. sp.**, *N. zora* **n. sp.**, *N. longiventralis*, and *N. longipes*. The latter species was moved to this group after having originally been included in the *steatiticus* group (Uiblein & Nielsen 2018).
- *steatiticus* group: species with single ocellus, zero or one pre-opercular spine, and pelvic fins not reaching anus. This group includes nine species: *Neobythites pako* **n. sp.**, *N. gloriae* Uiblein & Nielsen, *N. lombokensis* Uiblein & Nielsen, *N. malayanus* Weber, *N. malhaensis* Nielsen, *N. meteori* Nielsen, *N. monocellatus*, *N. steatiticus* Alcock, and *N. stefanovi* Nielsen & Uiblein.

### Key to the four species groups

| | | |
|---|---|---|
| **1** | One or several ocelli on dorsal fin | 2 |
| - | No ocelli on dorsal fin | 30 non-ocellus bearing species (28 species listed in Uiblein & Nielsen 2005, plus *N. machidai* Ohashi, Nielsen & Yabe and *N. solomonensis* Uiblein & Nielsen) |
| **2** | A central ocellus with no posterior ocellus on dorsal fin or with a posterior ocellus and pelvic fins extending beyond anus | 3 |
| - | At least one posterior ocellus and pelvic fins not extending beyond anus | 10 ungrouped species (Table 1) |
| **3** | Pelvic fins not extending beyond anus | 4 |
| - | Pelvic fins extending beyond anus | *longiventralis* species group |
| **4** | A central ocellus and no anterior or posterior ocellus | 5 |
| - | A central ocellus and an anterior ocellus, no posterior ocellus | *kenyaensis* species group |
| **5** | 2 preopercular spines | *australiensis* species group |
| - | 0–1 preopercular spines | *steatiticus* species group |

## The *australiensis* species group

### *Neobythites superocellatus* n. sp.

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Figures 1–3, Tables 1–2

**Holotype.** MNHN 2021-0457, 95 mm SL, Solomon Sea, 9°48′6″S, 160°50′8″E, Salomon 1 cruise, R/V *Alis*, st. DW 1824, Waren dredge, 298–318 m depth, 4 Oct. 2001.

**Paratypes** (*n*=3, 79–98 mm SL)**.** MNHN 2002-3758, 2, 79–90 mm SL, same collecting data as for holotype; MNHN 2002-3654, 98 mm SL, Solomon Sea, 10°12′1″S, 161°19′3″E, Salomon 1 cruise, R/V *Alis*, st. CP 1831, beam trawl, 135–325 m depth, 5 Oct. 2001.

**Fresh colour photo** (Fig. 2). Two adult specimens (sample not retained, size not known) photographed together with entire beam-trawl catch, Solomon Sea, 07°44′S, 158°30′E, Salomon 2 cruise, R/V *Alis*, st. CP 2200, beam trawl, 325–331 m depth, 25 Oct. 2004 (see also Richer de Forges 2004).

**Diagnosis.** Hind margin of preopercle with two blunt spines; dorsal-fin rays 98–104; anal-fin rays 85–88; pectoral-fin rays 26–27; precaudal vertebrae 13; total vertebrae 58–60; pseudobranchial filaments 4; long rakers on anterior gill arch 14–15; head length 21–22% SL; pelvic-fin length 11–14% SL, fins not reaching anus; orbit length 4.6–5.1% SL and 22–24% HL; longest gill filament 0.8–1.4% SL and 3.7–6.6% HL; dorsal fin with large central ocellus placed well behind vertical line through anus, spot distance 51–54% SL and spot covers 15–17 dorsal-fin rays and extending ventrally to body covering 5 to 7 vertical-scale rows; dorsal half of ocellus in fresh specimens black, ventral half (extension to body) dark brown, connecting ventrally to brown vertical bar; dorsal fin and body anteriorly of ocellus two to three vertical bars, posteriorly more darkly pigmented; preserved specimens with dark-brown, ventrally less conspicuous ocellus, anterior part of lateral line brown, no vertical bars on body; otolith length 5.1–5.8% SL, sulcus length 3.6–4.7% SL, and ostium height 19–21% sulcus length and 28–30% ostium length.

**TABLE 2.** Meristic, morphometric, quantitative colour, and otolith characters in *N. superocellatus* **n. sp.** types and the three other *australiensis* group species.

| | *N. superocellatus* **n. sp.** | | | | | | | | *N. australiensis* | | | | *N. nigriventris* | | | | *N. unimaculatus* | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Individual types | | | | All types | | | | NW Australia | | | | NE Australia | | | | Coral Sea | W Australia to Japan | | | |
| | HT | Paratypes | | | Min | Mean | Max | *n* | Min | Mean | Max | *n* | Min | Mean | Max | *n* | *n*=1 | Min | Mean | Max | *n* |
| SL (in mm) | 95 | 98 | 90 | 79 | 79 | 90.5 | 98 | 4 | 180 | 204.6 | 245 | 7 | 61 | 155.5 | 238 | 47 | 130 | 95 | 162.7 | 235 | 37 |
| Meristic characters | | | | | | | | | | | | | | | | | | | | | |
| Dorsal-fin rays | 103 | 104 | 98 | 102 | 98 | 101.8 | 104 | 4 | 88 | 90.6 | 92 | 7 | 90 | 92.7 | 95 | 37 | 92 | 90 | 93.5 | 99 | 35 |
| Caudal-fin rays | 8 | 8 | 8 | 8 | 8 | 8.0 | 8 | 4 | 8 | 8.0 | 8 | 7 | 8 | 8.0 | 8 | 29 | 8 | 8 | 8.0 | 8 | 32 |
| Anal-fin rays | 85 | 86 | 88 | 85 | 85 | 86.0 | 88 | 4 | 73 | 74.6 | 77 | 7 | 74 | 76.4 | 79 | 37 | 78 | 73 | 76.8 | 81 | 34 |
| Pectoral-fin rays | - | 26 | - | 27 | 26 | 26.5 | 27 | 2 | 26 | 26.6 | 27 | 5 | 23 | 24.7 | 26 | 26 | 28 | 27 | 27.9 | 30 | 27 |
| Precaudal vertebrae | 13 | 13 | - | 13 | 13 | 13.0 | 13 | 3 | 13 | 13.0 | 13 | 7 | 12 | 13.0 | 13 | 37 | 13 | 12 | 13.0 | 13 | 36 |
| Total vertebrae | 58 | 59 | - | 60 | 58 | 59.0 | 60 | 3 | 53 | 53.1 | 54 | 7 | 52 | 53.8 | 56 | 37 | 53 | 53 | 54.5 | 57 | 36 |
| Pseudobranchial filaments | 4 | 4 | 4 | 4 | 4 | 4.0 | 4 | 4 | 8 | 8.8 | 11 | 6 | 5 | 5.7 | 8 | 29 | 4 | 4 | 6.2 | 8 | 35 |
| Dorsal-fin origin above vertebra nr. | 5 | 6 | - | 5 | 5 | 5.3 | 6 | 3 | 5 | 5.3 | 6 | 7 | 4 | 5.0 | 6 | 37 | 5 | 4 | 5.1 | 6 | 32 |
| Anal-fin origin below dorsal fin ray nr. | 20 | 21 | 21 | 18 | 18 | 20.0 | 21 | 4 | 21 | 21.9 | 23 | 7 | 18 | 19.9 | 21 | 37 | 22 | 17 | 19.9 | 22 | 36 |
| Anal-fin origin below vertebra nr. | 15 | 15 | - | 14 | 14 | 14.7 | 15 | 3 | 15 | 16.1 | 17 | 7 | 14 | 14.8 | 15 | 37 | 16 | 13 | 15.2 | 16 | 36 |
| Developed gill rakers | 14 | 15 | 14 | 15 | 14 | 14.5 | 15 | 4 | 9 | 9.9 | 10 | 7 | 9 | 10.1 | 12 | 38 | 10 | 8 | 9.4 | 12 | 37 |
| Total gillrakers | 22 | 22 | 21 | 20 | 20 | 21.3 | 22 | 4 | 16 | 17.0 | 18 | 4 | 16 | 17.9 | 20 | 25 | 18 | 17 | 17.3 | 18 | 3 |
| Morphometric characters | | | | | | | | | | | | | | | | | | | | | |
| in % SL | | | | | | | | | | | | | | | | | | | | | |
| Head length | 21 | 22 | 21 | 21 | 21 | 21.0 | 22 | 4 | 23 | 24.1 | 25 | 7 | 21 | 22.3 | 24 | 44 | 23 | 21 | 22.6 | 25 | 37 |
| Body depth at anal-fin origin | 15 | 17 | 18 | 16 | 15 | 16.6 | 18 | 4 | 18 | 18.3 | 19 | 7 | 16 | 17.4 | 20 | 37 | 19 | 15 | 17.5 | 19 | 37 |
| Upper-jaw length | 11 | 10 | 11 | 10 | 10 | 10.7 | 11 | 4 | 12 | 12.7 | 13 | 7 | 11 | 11.6 | 12 | 25 | 12 | 11 | 11.6 | 13 | 34 |
| Orbit length | 5.1 | 4.8 | 4.8 | 4.6 | 4.6 | 4.8 | 5.1 | 4 | 4.2 | 4.5 | 4.7 | 7 | 4.0 | 4.7 | 5.5 | 24 | 4.5 | 4.0 | 4.6 | 5.4 | 37 |
| Preanal distance | 41 | 43 | 45 | 39 | 39 | 42.3 | 45 | 4 | 43 | 46.8 | 49 | 7 | 38 | 42.2 | 47 | 25 | 45 | 40 | 43.7 | 48 | 35 |
| Predorsal distance | 25 | 23 | 24 | 23 | 23 | 23.9 | 25 | 4 | 25 | 26.3 | 28 | 7 | 24 | 24.9 | 26 | 26 | 24 | 24 | 25.8 | 27 | 36 |
| Pelvic-fin to anal-fin origin distance | 26 | 27 | 26 | 25 | 25 | 26.2 | 27 | 4 | 25 | 27.8 | 29 | 7 | 22 | 25.8 | 30 | 37 | 27 | 23 | 27.0 | 32 | 35 |
| Pelvic-fin length | 14 | 12 | 12 | 11 | 11 | 12.2 | 14 | 4 | 14 | 15.9 | 19 | 7 | 16 | 20.3 | 24 | 36 | 18 | 12 | 16.7 | 20 | 36 |
| Gill-filament length | 1.4 | 1.2 | 1.2 | 0.8 | 0.8 | 1.1 | 1.4 | 4 | 1.6 | 1.7 | 1.8 | 7 | 1.4 | 1.6 | 1.9 | 30 | 1.2 | 1.2 | 1.8 | 2.2 | 30 |
| Postorbital distance | 13 | 13 | 11.0 | 12 | 11 | 12.4 | 13 | 4 | 14 | 14.6 | 15 | 7 | 12 | 13.4 | 14 | 24 | 13 | 13 | 13.7 | 15 | 33 |
| in % HL | | | | | | | | | | | | | | | | | | | | | |
| Upper-jaw length | 53 | 48 | 52 | 50 | 48 | 50.8 | 53 | 4 | 48 | 52.7 | 54 | 7 | 47 | 52.0 | 55 | 25 | 51 | 48 | 51.3 | 55 | 34 |
| Orbit length | 24 | 22 | 22.5 | 22 | 22 | 22.8 | 24 | 4 | 17 | 18.8 | 19 | 7 | 17 | 21.3 | 25 | 24 | 20 | 18 | 20.3 | 24 | 37 |
| Gill-filament length | 6.6 | 5.7 | 5.8 | 3.7 | 3.7 | 5.4 | 6.6 | 4 | 6.7 | 7.1 | 7.4 | 7 | 6.4 | 7.3 | 8.7 | 30 | 5.0 | 5.0 | 7.8 | 9.7 | 30 |
| Postorbital distance | 64 | 60 | 53 | 59 | 53 | 59.0 | 64 | 4 | 59 | 60.5 | 62 | 7 | 55 | 60.1 | 63 | 24 | 55 | 55 | 60.4 | 65 | 33 |
| Central ocellus characters | | | | | | | | | | | | | | | | | | | | | |
| Snout tip to ocellus spot distance % SL | 51 | 54 | 54 | 52 | 51 | 52.6 | 54 | 4 | 44 | 47.1 | 49 | 7 | 42 | 45.1 | 47 | 44 | 43 | 43 | 45.8 | 50 | 36 |
| Dorsal-fin rays covered by spot | 17 | 16 | 18 | 14 | 14 | 16.3 | 18 | 4 | 9 | 11.0 | 13 | 7 | 9 | 10.0 | 11 | 6 | 9 | 5 | 7.9 | 11 | 33 |
| First dorsal fin ray in spot | 25 | 30 | 25 | 29 | 25 | 27.3 | 30 | 4 | 21 | 22.1 | 23 | 7 | 21 | 21.8 | 23 | 5 | 22 | 19 | 22.1 | 26 | 27 |
| Central-most ray in spot | 33 | 38 | 34 | 36 | 33 | 35.3 | 38 | 4 | 25 | 27.4 | 29 | 7 | 25 | 26.8 | 28 | 5 | 26 | 23 | 25.8 | 29 | 27 |
| Vertical-scale rows covered by spot | 6 | 6 | 5 | 7 | 5 | 6.0 | 7 | 4 | 0 | 0.0 | 0 | 7 | 0 | 0.0 | 0 | 6 | 0 | 0 | 0.03 | 1 | 32 |
| Otolith characters | | | | | | | | | | | | | | | | | | | | | |
| in % SL | | | | | | | | | | | | | | | | | | | | | |
| Otolith length | 5.8 | 5.1 | 5.3 | 5.1 | 5.1 | 5.3 | 5.8 | 4 | 5.8 | 5.9 | 5.9 | 2 | 5.3 | 5.7 | 6.3 | 5 | 5.8 | 5.1 | 5.4 | 5.8 | 6 |
| Otolith height | 4.1 | 3.3 | 3.3 | 3.6 | 3.3 | 3.6 | 4.1 | 4 | 2.7 | 2.8 | 2.9 | 2 | 2.5 | 3.0 | 3.7 | 5 | 3.4 | 2.4 | 2.8 | 3.2 | 6 |
| Sulcus length | 4.7 | 3.9 | 3.7 | 3.6 | 3.6 | 4.0 | 4.7 | 4 | 4.7 | 4.7 | 4.8 | 2 | 4.5 | 4.8 | 5.3 | 5 | 4.6 | 3.9 | 4.3 | 4.7 | 6 |
| Ostium length | 3.5 | 2.7 | 2.6 | 2.5 | 2.5 | 2.8 | 3.5 | 4 | 3.1 | 3.2 | 3.3 | 2 | 2.9 | 3.2 | 3.4 | 5 | 3.2 | 2.7 | 3.0 | 3.2 | 6 |
| Ostium height | 1.01 | 0.82 | 0.72 | 0.71 | 0.71 | 0.81 | 1.01 | 4 | 0.63 | 0.63 | 0.64 | 2 | 0.59 | 0.63 | 0.71 | 5 | 0.72 | 0.56 | 0.64 | 0.73 | 6 |
| in % sulcus length | | | | | | | | | | | | | | | | | | | | | |
| Ostium length | 74 | 68 | 69 | 70 | 68 | 70.2 | 74 | 4 | 66 | 68.1 | 70 | 2 | 64 | 66.5 | 69 | 5 | 70 | 67 | 69.4 | 75 | 6 |
| Ostium height | 21 | 21 | 19 | 20 | 19 | 20.3 | 21 | 4 | 13 | 13.4 | 14 | 2 | 11 | 13.4 | 15 | 5 | 16 | 14 | 14.9 | 18 | 6 |
| in % ostium length | | | | | | | | | | | | | | | | | | | | | |
| Ostium height | 29 | 30 | 28 | 28 | 28 | 28.9 | 30 | 4 | 19 | 19.6 | 20 | 2 | 17 | 20.1 | 23 | 5 | 23 | 20 | 21.4 | 24 | 6 |

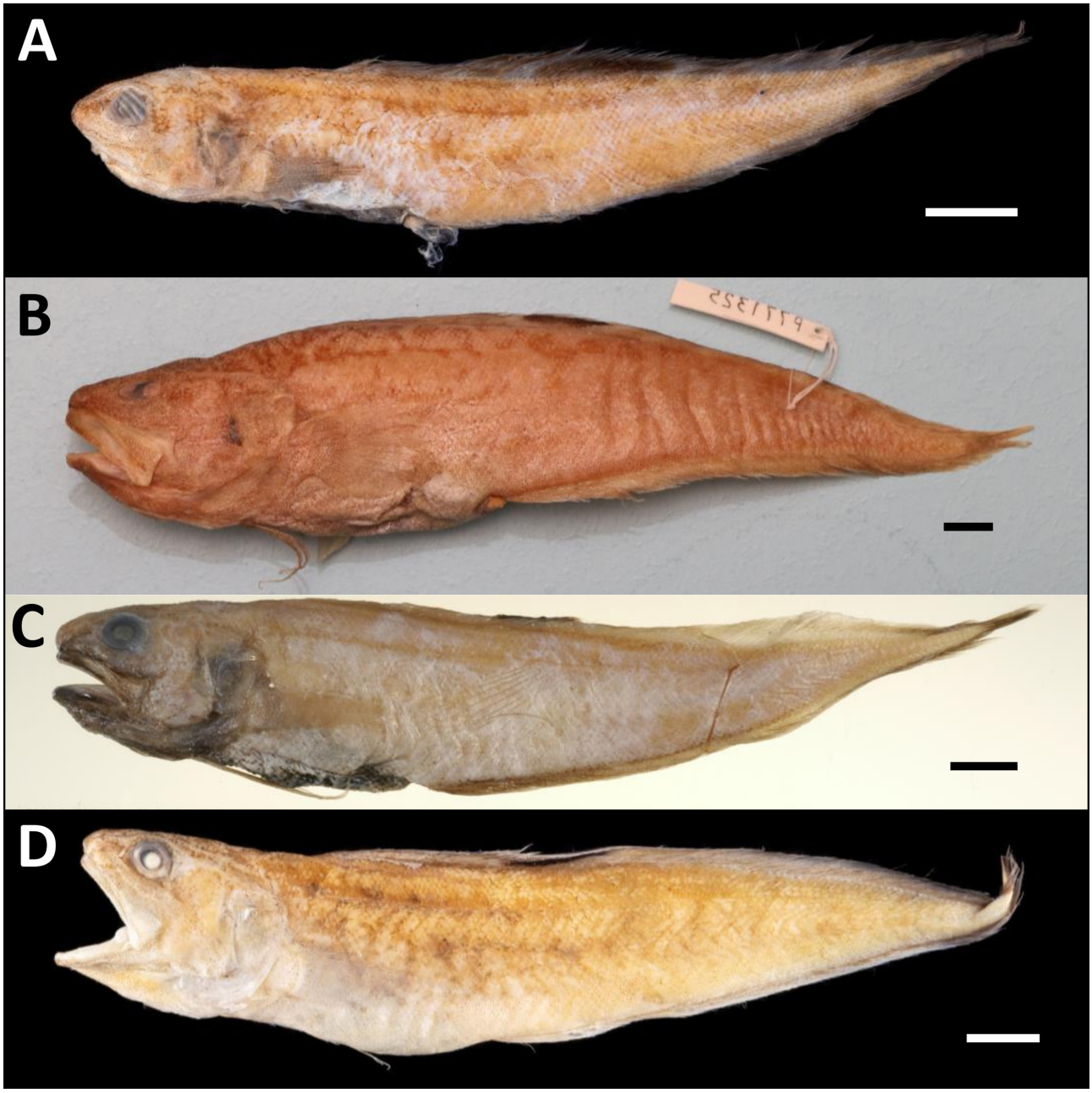


**FIGURE 1.** *S*pecies of the *australiensis* group. (A) *Neobythites superocellatus* **n. sp.**, HT, MNHN 2021-0457, 95 mm SL, Solomon Sea (M. Krag); (B) *N. australiensis*, PT, ZMUC P771325, 188 mm SL, W Australia (side-reversed; M. Krag); (C) *N. nigriventris*, HT, CSIRO H 2310-03 (side-reversed; H. O'Neill); (D) *N. unimaculatus*, MNHN 2005-3413, 130 mm SL, Coral Sea (M. Krag); with 10 mm scale bars.

**Description.** Principal meristic and morphometric characters are shown in Table 2. Morphological and preserved colour description based on HT, if not indicated otherwise. Elongate fish with tapering tail; head and body covered with deciduous scales; origin of dorsal fin above posterior half of pectoral fin; origin of anal fin well in front of midpoint of fish; protruding snout blunt, equal in length to diameter of eye; two blunt spines on posterior margin of preopercle (due to damage, lower spine missing on left side in holotype); opercular spine pointed; anterior gill arch on both sides with one short and four long rakers on upper branch, one long raker at angle and, nine long and six short rakers on lower branch; longest filaments on anterior gill arch 6.6 % HL; four small pseudobranchial filaments; longest gill raker on anterior gill arch 15 % HL.

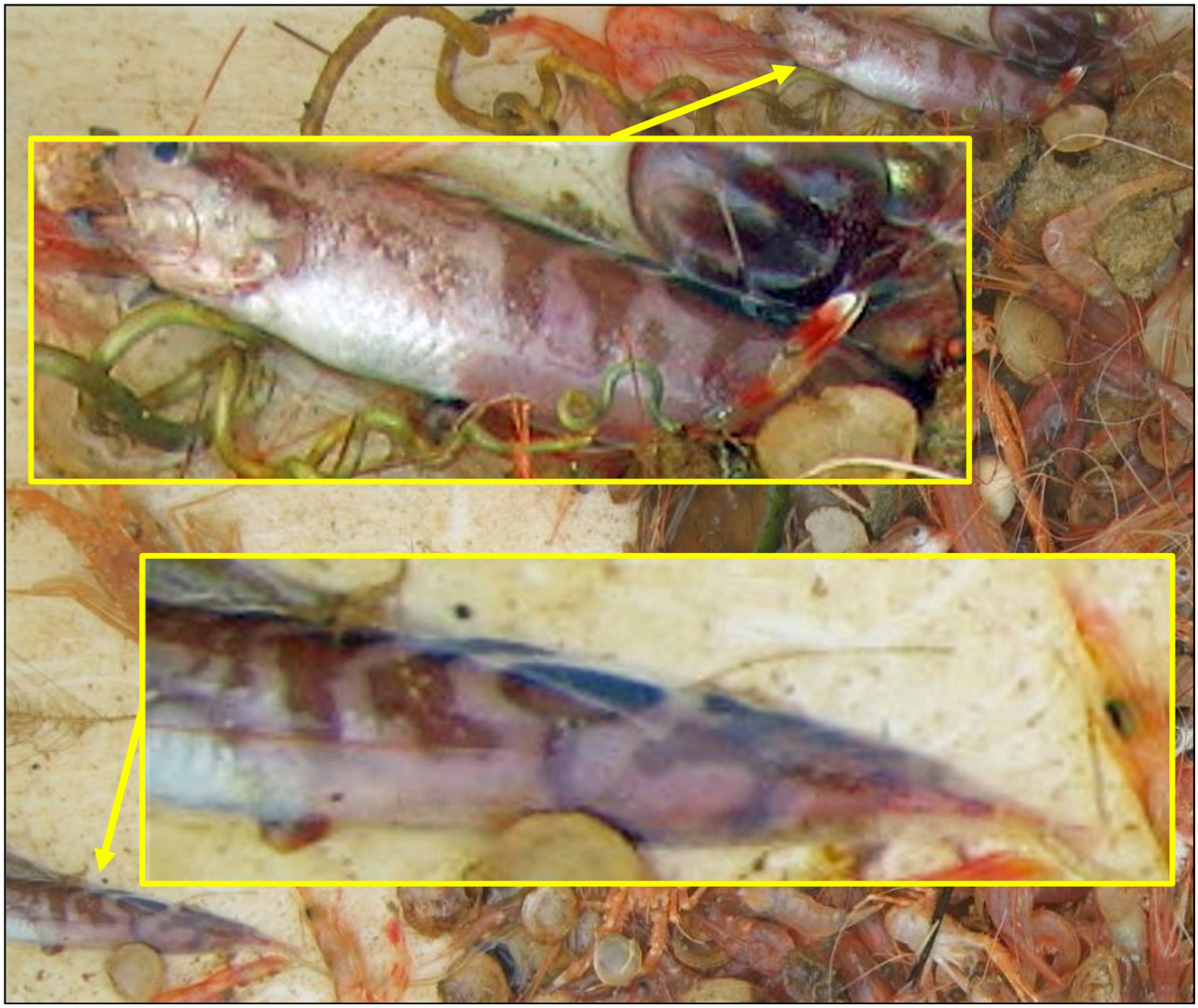

**FIGURE 2.** Two specimens of *Neobythites superocellatus* **n. sp.** photographed together with beam-trawl catch, Solomon Sea (Salomon 2 cruise participants; see also Richer de Forges 2004).

*Sagittal otolith* (Fig. 3A). Otolith slightly oval, almost rounded, its depth 1.4 times in its length; sulcus 1.2 times in otolith length; ostium 1.4 times in sulcus length; ostium depth 4.7 times in sulcus length and 3.4 times in ostium length.

*Dentition.* Premaxillaries, palatines, and dentaries with many small, pointed, close-set teeth in irregular rows; vomer boomerang-shaped with many small, pointed teeth; two median basibranchial tooth patches, anterior one long and narrow and posterior one small and circular.

*Axial skeleton*. Precaudal vertebrae 13, all with pointed tip; anterior neural spine almost half as long as second spine; spines on vertebrae 3–8 depressed; parapophyses present on vertebrae 7–13, pleural ribs on vertebrae 3–13, and epipleural ribs indistinct; bases of neural spines 3–13 enlarged.

*Colour.* Fresh fish (Fig. 2). Head and body with pale-pink background colour, belly white; head behind and above eye with two brown bands; central ocellus well behind vertical line through anus, ocellus spot surrounded almost entirely by a broad pale whitish-rose ring, spot diameter about three times orbit length, upper half of spot on dorsal fin black, its dark-brown lower half extending down to body, connected at ventral-spot margin with similarly coloured vertical bar which reaches ventral body margin; two to three crescent-shaped bars extending from dorsal fin to body anterior of ocellus, black on dorsal fin and becoming brown on body, the posterior-most bar bordering the central ocellus ring; dark spot on dorsal fin posterior to ocellus connecting to brown area behind and below on body, latter pigmentation along dorsal margin of body, reaching down towards ventral body margin in form of two brown bars, one anterior bar shorter and crescent shaped, bordering ocellus ring, posterior bar thinner and longer;

anal fin pale brown, becoming pale transparent towards posterior end; posterior end of dorsal fin and caudal fin pale transparent.

Preserved fish (Fig. 1A). Body and head mostly pale brown, head anterior and posterior of orbit with beige-brown pigmentation patches, lateral line beige-brown in its anterior half, belly whitish; central ocellus placed well behind vertical line through anus, ocellus spot diameter at least three times orbit length, spot covers 17 dorsal-fin rays (14–18 in PT's) and extends onto body, covering six horizontal scale rows (5–7 in PT's); dorsal part of ocellus spot on dorsal fin dark brown, ventral part on body pale brown, but shape of both ocellus spot and ring not fully retained; dorsal fin anterior and posterior of ocellus mostly brown or brown scattered with the pale-whitish ocellus ring well visible, while being inconspicuous on body; anal and caudal fins pale transparent; no vertical bars on body.

**Etymology.** The specific name refers to the large dorsal-fin ocellus.

**Distribution and size.** W Pacific, Central and SE Solomon Sea at 135–331 m depth. Known up to 98 mm SL.

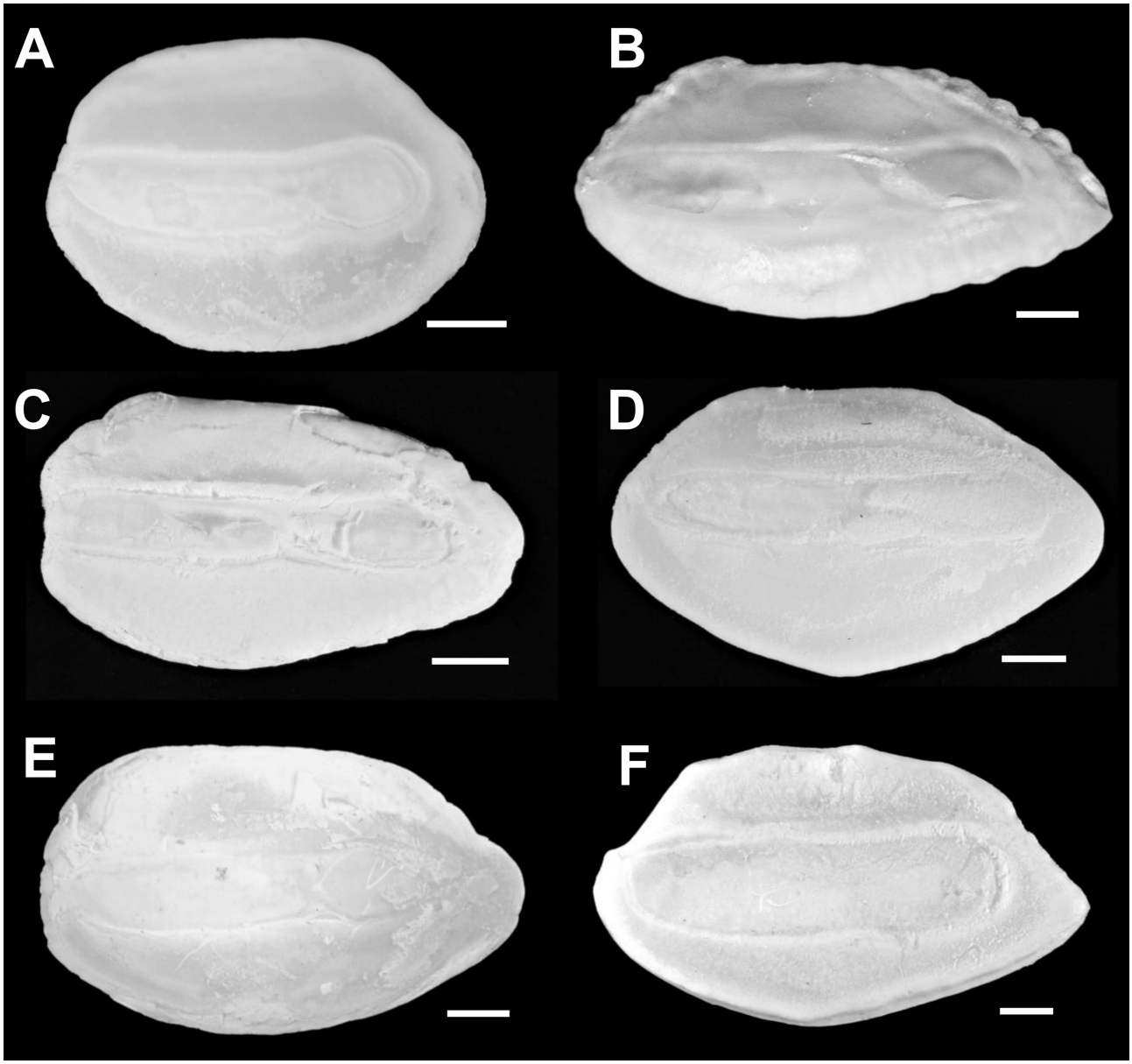


**FIGURE 3.** *Neobythites* otoliths. (A) *N. superocellatus* **n. sp.**, HT, MNHN 2021-0457, Solomon Sea (M. Krag). (B) *N. japonicus* **n. sp.**, HT, KAUM -I. 37071, off Okinawa (from left side of head, shown side-reversed; M. Krag); (C) *N. jonathan* **n. sp.**, HT, MNHN 2002-3883, Solomon Sea (C. Høegh-Guldberg); (D) *N. zora* **n. sp.**, HT, ZMUC P771324, Fiji (C. Høegh-Guldberg); (E) *N. pako* **n. sp.**, HT, MNHN 2006-0337, otolith number MNHN-ICOT-001969, Solomon Sea (M. Krag); (F) *N. malayanus,* ZMUC P77742, Lombok (C. Høegh-Guldberg); all otoliths from right side of head except for (B); with 1 mm scale bars.

### *Neobythites australiensis* Nielsen, 2002

Figure 1, Tables 1, 2

*Neobythites australiensis* Nielsen, 2002: 20, fig. 10 (Southwest of Rowley Shoals, 18°4.6′S, 118°22′E, Western Australia, 327–328 m; holotype: WAM P.28107-001).

**Diagnosis.** Hind margin of preopercle with two spines; dorsal-fin rays 88–92; anal-fin rays 73–77; pectoral-fin rays 26–27; precaudal vertebrae 13; total vertebrae 53–54; pseudobranchial filaments 8–11; long rakers on anterior gill arch 9–10; head length 23–25% SL; pelvic-fin length 14–19% SL, fins not reaching anus; orbit length 4.2–4.7% SL and 17–19% HL; longest gill filament 1.6–1.8% SL and 6.7–7.4% HL; dorsal fin with large ocellus placed slightly behind line through anus, spot distance 44–49% SL and spot covers 9–13 dorsal-fin rays, not extending ventrally onto body; preserved specimens with dark-brown ocellus spot; no vertical bars on body; otolith length 5.8–5.9% SL, sulcus length 4.7–4.8% SL, and ostium height 13–14% sulcus length and 19–20% ostium length.

**Distribution and size.** SE Indian Ocean, off NW Australia at 42–350 m depth. Known up to 245 mm SL.

### *Neobythites nigriventris* Nielsen, 2002

Figure 1, Tables 1, 2

*Neobythites nigriventris* Nielsen, 2002: 66, fig. 57 (Marion Plateau, Queensland, 22°53.3′S, 152°59.3′E, Australia, 325–338 m; holotype: CSIRO H 2310-03).

**Diagnosis.** Hind margin of preopercle with two spines; dorsal-fin rays 90–95; anal-fin rays 74–79; pectoral-fin rays 23–26; precaudal vertebrae 12–13; total vertebrae 52–56; pseudobranchial filaments 5–8; long rakers on anterior gill arch 9–12; head length 21–24% SL; pelvic-fin length 16–24% SL, fins not reaching beyond anus; orbit length 4.0–5.5% SL and 17–25% HL; longest gill filament 1.4–1.9% SL and 6.4–8.7% HL; dorsal fin with large ocellus placed slightly behind line through anus, the spot distance 42–47% SL and spot covers 9–11 dorsal-fin rays, not extending ventrally onto body; preserved specimens with black ocellus spot; no vertical bars on body; otolith length 5.3–6.3% SL, sulcus length 4.5–5.3% SL, and ostium height 11–15% sulcus length and 17–23% ostium length.

**Distribution and size.** SW Pacific, off Queensland and New South Wales at 67–357 m depth. Known up to 238 mm SL.

### *Neobythites unimaculatus* Smith & Radcliffe, 1913

Figure 1, Tables 1, 2

*Neobythites unimaculatus* Smith & Radcliffe *in* Radcliffe, 1913: 140, pl. 7 (fig. 2) (near Mabul Island, 4°10′50″N, 118°39′35″E, Borneo, 310 fathoms; holotype: USNM 74127).

*Neobythites nigromaculatus* Kamohara, 1938: 67, fig. 37 (type locality Mimase market, Japan).

**New material examined** (see Nielsen 2002 for all other material examined including types). MNHN 2005-3413, 130 mm SL, Coral Sea, 15°6′0″S, 156°57′0″E, Salomon 2 cruise, R/V *Alis*, st. CP 2317, beam trawl 215–300 m, 16 Nov. 2004.

**Diagnosis.** Hind margin of preopercle with two spines; dorsal-fin rays 90–99; anal-fin rays 73–81; pectoral-fin rays 27–30; precaudal vertebrae 12–13; total vertebrae 53–57; pseudobranchial filaments 4–8; long rakers on anterior gill arch 8–12; head length 21–25% SL; pelvic-fin length 12–20% SL, fins not reaching anus; orbit length 4.0–5.4% SL and 18–24% HL; longest gill filament 1.2–2.2% SL and 5.0–9.7% HL; dorsal fin with large ocellus placed slightly behind line through anus, spot distance 43–50% SL and spot covers 5–11 dorsal-fin rays, rarely extending ventrally onto body; preserved specimens with dark-brown ocellus spot; no vertical bars on body; otolith length 5.1–5.8% SL, sulcus length 3.9–4.7% SL, and ostium height 14–18% sulcus length and 20–24% ostium length.

**Distribution and size.** Japan to northwestern Australia and eastward to Fiji Islands at 146–567 m depth. New record for Coral Sea. Known up to 218 mm SL.

**Comparisons.** *Neobythites superocellatus* **n. sp.** differs from the three other *australiensis*-group species with a larger central ocellus which is positioned further posteriorly on the dorsal fin and the spot extending onto the body; it differs also in having more anal-fin rays, total vertebrae and gill rakers, and a higher otolith ostium height relative

to sulcus and ostium length; it differs from *N. australiensis* and *N. nigriventris* in having more dorsal-fin rays and from *N. australiensis* in having a shorter head and gill filaments; it differs from *N. nigriventris* in having shorter pelvic fins.

*Neobythites australiensis* differs from *N. nigriventris* in absence vs. presence of black-speckled pigment on abdomen, the combination of slightly more pectoral-fin rays and pseudobranchial filaments, slightly more dorsal-fin rays and vertebrae above anal-fin origin, and slightly longer postorbital; it differs from *N. unimaculatus* in the combination of slightly more pectoral-fin rays and pseudobranchial filaments, a slightly larger ocellus spot and slightly higher otolith ostium related to sulcus and ostium length.

*Neobythites nigriventris* differs from *N. unimaculatus* in presence vs. absence of black-speckled pigment on abdomen, more pectoral-fin rays, and slightly longer and higher ostium related to sulcus length.

**Remarks.** *Neobythites superocellatus* has the largest ocellus of all ocellus-bearing congeners and its ocellus is also unique in covering a large number of vertical scale rows on body and connecting to a vertical bar ventrally.

The specimen from Japan reported by Okamoto *et al.* (2011) as *N. australiensis* was found to be an undescribed species and is reported further below as part of the newly established *kenyaensis* species group. *Neobythites australiensis* has no anterior ocellus, but has spots in some specimens.

*Neobythites unimaculatus* requires a revision. The wide distribution of this species and the wide ranges of several counts and measurements deserve a detailed comparative study among the different populations, involving material from the distribution area of the putative junior synonym *N. nigromaculatus* (Japan to Taiwan)

**Key to the *australiensis* species group**

| | |
|---|---|
| **1** | Central ocellus placed at 42–50% SL, its spot covering 5–11 dorsal-fin rays and 0 or exceptionally 1 vertical scal rows on body below dorsal fin, anal-fin rays 73–81, vertebrae 52–57, and developed gill rakers 8–12 . . . . . 2 |
| - | Central ocellus placed at 51–54% SL, its spot covering 14–18 dorsal-fin rays and 5 to 7 vertical scale rows on body below dorsal fin, anal-fin rays 85–88, vertebrae 58–60, and developed gill rakers 14–15 . . . . . *N. superocellatus* |
| **2** | Abdomen with or without black-speckled pigmentation, dorsal-fin rays 90–99, pseudobranchial filaments 8–11, and dorsal-fin rays covered by central-ocellus spot 9–13 . . . . . 3 |
| - | Abdomen without black-speckled pigmentation, dorsal-fin rays 88–92, pseudobranchial filaments 4–8, and dorsal-fin rays covered by central-ocellus spot 5–11 . . . . . *N. australiensis* |
| **3** | Abdomen with black-speckled pigmentation, pectoral-fin rays 23–26, otolith ostium height 64–69% sulcus length, and 11–15 ostium length . . . . . *N. nigriventris* |
| - | Abdomen without black-speckled pigmentation, pectoral-fin rays 27–30, otolith ostium height 67–75% sulcus length and 14–18 ostium length . . . . . *N. unimaculatus* |

## The *kenyaensis* species group

### *Neobythites japonicus* n. sp.

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Figures 3–4, Tables 1, 3

*N. australiensis:* Okamoto *et al.* 2011

**Holotype.** KAUM -I. 37071, 167 mm SL, female, W Pacific, west of Okinawa Island, Japan, ca. 100 m depth, 16 May 1998.

**Diagnosis.** Hind margin of preopercle with two spines; dorsal-fin rays 91; anal-fin rays 75; pectoral-fin rays 26; precaudal vertebrae 13; total vertebrae 52; pseudobranchial filaments 6; long rakers on anterior gill arch 11; head length 23% SL; pelvic-fin length 16% SL, fins not reaching anus; orbit length 4.1% SL and 18% HL; longest gill filament 1.6% SL and 7.1% HL; dorsal fin with two ocelli, one smaller ocellus placed close to fin origin, spot distance 29% SL and spot covers 6 dorsal-fin rays, and a larger central ocellus placed behind line through anus, spot distance 46% SL and spot covers 9 dorsal-fin rays; both ocellus spots not extending ventrally onto body; preserved specimens with two dark-brown ocellus spots; no vertical bars on body; otolith length 5.3% SL, sulcus length 4.2% SL, and ostium height 15% sulcus length and 23% ostium length.

**Description.** The principal meristic and morphometric characters are shown in Table 3. Body elongate with indistinct lateral line; body and head covered by deciduous cycloid scales; origin of dorsal-fin above middle of pectoral-fin; origin of anal fin slightly in front of midpoint of fish; snout slightly blunt, equal in length to diameter of eye window; two distinct spines on hind margin of preopercle; opercular spine short and pointed; anterior gill arch on

both sides with 5 short and 2 long rakers on upper branch, one long raker at angle, and 7–8 long and 6–7 short rakers on lower branch; longest filaments on anterior gill arch 7.1% HL; longest gill raker on anterior gill arch 13% HL.

**TABLE 3.** Meristic, morphometric, quantitative colour, and otolith characters in *Neobythites japonicus* **n. sp.** and the two other *kenyaensis* group species.

| | *N. japonicus* **n. sp.** | | *N. kenyaensis* | | | *N. ocellatus* | | | |
|---|---|---|---|---|---|---|---|---|---|
| | HT | Min | Mean | Max | *n* | Min | Mean | Max | *n* |
| SL (in mm) | 167 | 97 | 127.6 | 162 | 15 | 66 | 112.5 | 147 | 17 |
| Meristic characters | | | | | | | | | |
| Dorsal-fin rays | 91 | 97 | 98.8 | 102 | 13 | 95 | 98.0 | 100 | 18 |
| Caudal-fin rays | 8 | 7 | 7.7 | 8 | 10 | 7 | 7.9 | 8 | 14 |
| Anal-fin rays | 75 | 80 | 81.8 | 84 | 12 | 81 | 82.8 | 85 | 17 |
| Pectoral-fin rays | 26 | 26 | 28.4 | 32 | 14 | 24 | 25.5 | 27 | 17 |
| Precaudal vertebrae | 13 | 13 | 13.0 | 13 | 14 | 12 | 12.0 | 12 | 18 |
| Total vertebrae | 52 | 55 | 57.2 | 59 | 13 | 56 | 57.1 | 58 | 17 |
| Pseudobranchial filaments | 6 | 2 | 2.8 | 4 | 11 | 3 | 3.7 | 4 | 18 |
| Dorsal-fin origin above vertebra nr. | 5 | 4 | 4.5 | 5 | 14 | 5 | 5.1 | 6 | 18 |
| Anal-fin origin below dorsal fin ray nr. | 21 | 20 | 21.4 | 22 | 14 | 19 | 20.2 | 21 | 18 |
| Anal-fin origin below vertebra nr. | 15 | 14 | 15.4 | 16 | 14 | 14 | 14.4 | 15 | 18 |
| Developed gill rakers | 11 | 8 | 9.1 | 10 | 14 | 14 | 14.5 | 16 | 18 |
| Total gillrakers | 22 | 16 | 17.7 | 19 | 10 | 21 | 21.7 | 23 | 17 |
| Morphometric characters in % SL | | | | | | | | | |
| Head length | 23 | 20 | 20.2 | 21 | 14 | 21 | 22.4 | 24 | 17 |
| Body depth at anal-fin origin | 18 | 17 | 18.2 | 19 | 14 | 16 | 17.2 | 19 | 17 |
| Upper-jaw length | 11 | 9.1 | 9.7 | 10 | 14 | 11 | 11.6 | 13 | 17 |
| Orbit length | 4.1 | 4.3 | 5.0 | 5.3 | 12 | 5.3 | 5.6 | 6.1 | 17 |
| Preanal distance | 44 | 37 | 40.8 | 45 | 14 | 38 | 41.1 | 44 | 17 |
| Predorsal distance | 25 | 22 | 24.2 | 27 | 14 | 24 | 25.1 | 26 | 17 |
| Pelvic-fin to anal-fin origin distance | 27 | 24 | 26.7 | 29 | 13 | 22 | 24.1 | 26 | 17 |
| Pelvic-fin length | 16 | 10 | 10.8 | 12 | 13 | 16 | 18.9 | 22 | 16 |
| Gill-filament length | 1.6 | 1.4 | 1.8 | 2.4 | 14 | 1.7 | 1.8 | 2.6 | 16 |
| Postorbital distance | 14 | 11 | 11.8 | 13 | 14 | 12 | 12.9 | 14 | 16 |
| in % HL | | | | | | | | | |
| Upper-jaw length | 51 | 45 | 48.4 | 52 | 14 | 48 | 51.7 | 55 | 16 |
| Orbit length | 18 | 22 | 25.6 | 31 | 12 | 22 | 25.0 | 28 | 16 |
| Gill-filament length | 7.1 | 6.9 | 8.9 | 12 | 14 | 7.3 | 8.0 | 8.4 | 16 |
| Postorbital distance | 60 | 56 | 58.5 | 64 | 14 | 54 | 57.3 | 60 | 16 |
| Anterior ocellus characters | | | | | | | | | |
| Snout tip to ocellus spot distance % SL | 29 | 29 | 31.6 | 35 | 14 | 28 | 28.8 | 30 | 17 |
| Dorsal-fin rays covered by spot | 6 | 6 | 7.7 | 9 | 15 | 5 | 6.0 | 7 | 17 |
| First dorsal fin ray in spot | 4 | 7 | 10.6 | 14 | 14 | 4 | 5.5 | 7 | 17 |
| Central-most ray in spot | 6 | 11 | 14.2 | 17 | 14 | 6 | 7.6 | 9 | 17 |
| Vertical-scale rows covered by spot | 0 | 0 | 0.0 | 0 | 15 | 0 | 0 | 0 | 17 |
| Central ocellus characters | | | | | | | | | |
| Snout tip to ocellus spot distance % SL | 46 | 53 | 54.5 | 57 | 14 | 45 | 47.1 | 50 | 17 |
| Dorsal-fin rays covered by spot | 9 | 8 | 11.7 | 15 | 15 | 8 | 8.8 | 11 | 16 |
| First dorsal fin ray in spot | 23 | 33 | 34.7 | 37 | 14 | 23 | 24.7 | 27 | 16 |
| Central-most ray in spot | 27 | 39 | 40.3 | 43 | 14 | 27 | 28.6 | 31 | 16 |
| Vertical-scale rows covered by spot | 0 | 0 | 0.0 | 0 | 15 | 0 | 0 | 0 | 16 |
| Otolith characters in % SL | | | | | | | | | |
| Otolith length | 5.3 | 4.9 | 5.2 | 5.8 | 11 | 5.6 | 5.7 | 5.8 | 3 |
| Otolith height | 2.6 | 3.1 | 3.5 | 3.8 | 11 | 3.5 | 3.9 | 4.2 | 3 |
| Sulcus length | 4.2 | 3.4 | 3.8 | 4.7 | 11 | 4.0 | 4.1 | 4.3 | 3 |
| Ostium length | 2.9 | 2.1 | 2.5 | 2.9 | 11 | 2.5 | 2.6 | 2.9 | 3 |
| Ostium height | 0.65 | 0.67 | 0.84 | 1.08 | 11 | 0.71 | 0.79 | 0.83 | 3 |
| in % sulcus length | | | | | | | | | |
| Ostium length | 69 | 56 | 65.3 | 72 | 11 | 61 | 64.2 | 68 | 3 |
| Ostium height | 15 | 20 | 22.0 | 24 | 11 | 18 | 19.3 | 21 | 3 |
| in % ostium length | | | | | | | | | |
| Ostium height | 23 | 29 | 33.8 | 37 | 11 | 28 | 30.1 | 34 | 3 |

*Sagittal otolith* (Fig. 3B). Otolith oval, pointed at posterior end, its depth 2.0 times in its length; sulcus 1.3 times in otolith length; ostium 1.5 times in sulcus length; ostium depth 6.5 times in sulcus length and 4.4 times in ostium length.

*Dentition.* Premaxillaries, palatines, and dentaries with many small, pointed, close-set teeth in irregular rows; vomer boomerang-shaped with many small, pointed teeth; two median basibranchial tooth patches, anterior one long and narrow and posterior one small and circular.

*Axial skeleton*. Precaudal vertebrae 13, all with pointed tip; anterior neural spine about half as long as second spine; neural spines on vertebrae 3–10 depressed; parapophyses developed on vertebrae 8–13, pleural ribs on vertebrae 4–13, and epipleural ribs indistinct; bases of neural spines 3–13 enlarged.

*Colour.* Preserved fish (Fig. 4A). Body and head in preserved HT mostly pale brown and mottled, lateral line pale beige, mostly indistinct, belly whitish; two distinct ocelli, one anterior and central ocellus placed behind vertical line through anus, central-ocellus spot diameter about twice orbit length, covering 9 dorsal-fin rays, not extending ventrally onto body; contrasting pale whitish-grayish ring surrounds central-ocellus spot almost entirely; anterior ocellus placed closely behind dorsal-fin origin, its spot diameter about orbit length, covering 6 dorsal-fin rays, not extending onto body below; contrasting pale ring almost completely surrounds anterior ocellus spot; dorsal fin between ocelli and posterior of central ocellus pale brown ventrally, lighter dorsally and distally towards caudal fin, anal fin rather pale along first two-thirds, then slightly pale-brown, pigmented like dorsal and caudal fins in posterior tail region; no vertical bars.

**Etymology.** The species name refers to the type locality.

**Distribution and size.** Only known from HT (167 mm SL) caught west of Okinawa, Japan, at a depth of ca. 100 m.


**FIGURE 4.** Species of the *kenyaensis* group. (A) *Neobythites japonicus* **n. sp.**, HT, KAUM I.37071, 167 mm SL, off Okinawa (H. Motomura); (B) *N. kenyaensis*, SAIAB 82154, 136 mm SL, off S Mozambique (O. Alvheim); (C) *N. ocellatus*, MOVI 39146, 147 mm SL, off E Brazil (G. Brovad); with 10 mm scale bars.

### *Neobythites kenyaensis* Nielsen, 1995

Figure 4, Tables 1, 3

*Neobythites kenyaensis* Nielsen, 1995: 5, fig. 4 (off Ras Ngomeni, Kenya, western Indian Ocean, 02°50′S, 40°31′E, 275 m; holotype: SAIAB 13952).

**Diagnosis.** No spines on hind margin of preopercle; dorsal-fin rays 97–102; anal-fin rays 80–84; pectoral-fin rays 26–32; precaudal vertebrae 13; total vertebrae 55–59; pseudobranchial filaments 2–4; long rakers on anterior gill arch 8–10; head length 20–21% SL; pelvic-fin length 10–12% SL, fins not reaching anus; orbit length 4.3–5.3% SL

and 22–31% HL; longest gill filament 1.4–2.4% SL and 6.9–12% HL; dorsal fin with two ocelli, one slightly smaller ocellus placed closer to fin origin, spot distance 29–35% SL and spot covers 6–9 dorsal-fin rays, and slightly larger central ocellus placed well behind line through anus, spot distance 56–64% SL and spot covers 8–15 dorsal-fin rays; both ocellus spots not extending ventrally onto body; fresh and recently preserved specimens with two black ocellus spots and posterior part of dorsal fin and anal fin with a black stripe; no vertical bars on body; otolith length 5.9–5.8% SL, sulcus length 3.4–4.7% SL, and ostium height 20–24 % sulcus length and 29–37% ostium length.

**Distribution and size.** SW Indian Ocean: from Kenya, off Ras Ngomeni, to Tanzania, Mozambique, and off Durban, Natal (South Africa) at 238–457 m depth. Known up to 162 mm SL.

### *Neobythites ocellatus* Günther, 1887

Figure 4, Tables 1, 3

*Neobythites ocellatus* Günther, 1887: 103, pl. 21 (fig. B) (off Pernambuco, northeastern Brazil, 09°05′S, 34°50′W, 350 fathoms; holotype: BMNH 1887.12.7.43).

**Diagnosis.** No or one thin and flat spine on hind margin of preopercle; dorsal-fin rays 95–100; anal-fin rays 81–85; pectoral-fin rays 24–27; precaudal vertebrae 12; total vertebrae 56–58; pseudobranchial filaments 3–4; long rakers on anterior gill arch 14–16; head length 21–24% SL; pelvic-fin length 16–22% SL, fins not extending beyond anus; orbit length 5.3–6.1% SL and 22–28% HL; longest gill filament 1.7–2.6% SL and 7.3–8.4% HL; dorsal fin with two ocelli, one smaller ocellus placed closer to fin origin, spot distance 28–30% SL and spot covers 5–7 dorsal-fin rays, and slightly larger central ocellus placed behind line through anus, spot distance 45–50% SL and spot covers 8–11 dorsal-fin rays; both ocellus spots not extending ventrally onto body; preserved specimens with two black ocellus spots; no vertical bars on body; otolith length 5.6–5.8% SL, sulcus length 4.0–4.3% SL, and ostium height 18–21% sulcus length and 28–34% ostium length.

**Distribution and size.** SW Atlantic, off Bahia, E Brazil at 233–641 m depth. Known up to 148 mm SL.

**Comparisons.** *Neobythites japonicus* **n. sp.** differs from *N. kenyaensis* and *N. ocellatus* in having two vs. 0 or 1 reduced preopercular spines, fewer dorsal-fin rays, anal-fin rays, and vertebrae, more pseudobranchial filaments, smaller eyes, and shallower otolith ostium height; furthermore, it differs from *N. kenyaensis* in having both ocelli placed more anterior on the dorsal fin and longer head and pelvic fin; and it differs from *N. ocellatus* in having fewer gill rakers and shorter gill filaments.

*Neobythites kenyaensis* differs from *N. ocellatus* in having more precaudal vertebrae, fewer gill rakers, shorter upper jaw and pelvic fin, and more posteriorly placed ocelli.

**Remarks.** Okamoto *et al.* 2011 considered the colour structure close to the dorsal-fin origin to be merely a black blotch. However, our re-examination revealed a clear ring surrounding the spot (Fig. 4A).

*Neobythites ocellatus* only has posterior spots, but no posterior ocelli (Nielsen *et al.* 2009)

**Key to the *kenyaensis* species group**

| | |
|---|---|
| **1** | 0–1 preopercular spines, dorsal-fin rays 95–102, anal-fin rays 80–85, total vertebrae 55–59, pseudobranchial filaments 2–4, orbit length 4.3–6.1% SL and 22–31% HL . . . . . 2 |
| - | 2 preopercular spines, dorsal-fin rays 91, anal-fin rays 75, total vertebrae 52, pseudobranchial filaments 6, orbit length 4.1% SL and 18% HL . . . . . *N. japonicus* **n. sp.** |
| **2** | 0 preopercular spines, central ocellus distance 53–57% SL, precaudal vertebrae 13, developed gill rakers 8–10, pelvic-fin length 10–12% SL . . . . . *N. kenyaensis* |
| - | 1 preopercular spine, central ocellus distance 45–50% SL, precaudal vertebrae 12, developed gill rakers 14–16, pelvic-fin length 16–22% SL . . . . . *N. ocellatus* |

## The *longiventralis* species group

### *Neobythites jonathan* n. sp.

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Figures 3, 5, Tables 1, 4

**TABLE 4.** Meristic, morphometric, quantitative colour, and otolith characters in the individual types of *Neobythites jonathan* **n. sp.** and *N. zora* **n. sp.** and the two other species of the *longiventralis* group.

| | *N. jonathan* **n. sp.** | | *N. zora* **n. sp.** | *N. longiventralis* | | | | *N. longipes* | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | HT | PT | PT | Min | Mean | Max | *n* | Min | Mean | Max | *n* |
| SL (in mm) | 119 | 122 | 132 | 108 | 132.8 | 148 | 6 | 90 | 212.3 | 301 | 23 |
| Meristic characters | | | | | | | | | | | |
| Dorsal-fin rays | 91 | 92 | 91 | 90 | 91.7 | 94 | 6 | 96 | 100.5 | 103 | 23 |
| Caudal-fin rays | 8 | 8 | 0 | 8 | 8.0 | 8 | 6 | 8 | 8.0 | 8 | 22 |
| Anal-fin rays | 76 | 72 | 75 | 73 | 75.0 | 76 | 6 | 79 | 82.4 | 87 | 23 |
| Pectoral-fin rays | 28 | 29 | 27 | 25 | 25.8 | 27 | 6 | 27 | 28.5 | 30 | 17 |
| Precaudal vertebrae | 13 | 13 | 13 | 13 | 13.0 | 13 | 6 | 13 | 13.9 | 14 | 23 |
| Total vertebrae | 53 | 53 | 53 | 53 | 54.3 | 55 | 6 | 57 | 58.3 | 60 | 23 |
| Pseudobranchial filaments | 5 | 5 | 5 | 4 | 5.0 | 6 | 6 | 5 | 7.2 | 10 | 19 |
| Dorsal-fin origin above vertebra nr. | 6 | 6 | 5 | 5 | 5.0 | 5 | 6 | 5 | 5.0 | 6 | 22 |
| Anal-fin origin below dorsal fin ray nr. | 21 | 22 | 20 | 20 | 20.7 | 22 | 6 | 19 | 21.1 | 22 | 23 |
| Anal-fin origin below vertebra nr. | 16 | 16 | 15 | 15 | 15.3 | 16 | 6 | 15 | 16.0 | 17 | 23 |
| Developed gill rakers | 10 | 10 | 10 | 10 | 11.2 | 12 | 6 | 8 | 8.9 | 10 | 22 |
| Total gillrakers | 18 | 17 | 20 | 18 | 18.6 | 21 | 5 | 17 | 18.6 | 20 | 8 |
| Morphometric characters in % SL | | | | | | | | | | | |
| Head length | 24 | 24 | 23 | 22 | 23.3 | 24 | 6 | 22 | 23.5 | 25 | 23 |
| Body depth at anal-fin origin | 17 | 17 | 17 | 15 | 17.1 | 18 | 6 | 14 | 15.4 | 17 | 22 |
| Upper-jaw length | 13 | 12 | 11 | 11 | 12.0 | 12 | 6 | 12 | 12.5 | 13 | 23 |
| Orbit length | 5.2 | 5.1 | 5.5 | 4.7 | 4.9 | 5.1 | 6 | 3.9 | 4.4 | 5.0 | 23 |
| Preanal distance | 45 | 43 | 43 | 42 | 44.9 | 47 | 6 | 41 | 43.7 | 49 | 22 |
| Predorsal distance | 27 | 26 | 27 | 26 | 26.5 | 27 | 6 | 23 | 25.4 | 28 | 23 |
| Pelvic-fin to anal-fin origin distance | 26 | 24 | 23 | 24 | 24.9 | 26 | 6 | 23 | 26.1 | 30 | 23 |
| Pelvic-fin length | 32 | 29 | 34 | 32 | 33.2 | 34 | 4 | 28 | 36.5 | 54 | 23 |
| Gill-filament length | 1.8 | 1.7 | 1.3 | 1.3 | 1.7 | 1.9 | 6 | 1.3 | 1.8 | 2.7 | 22 |
| Postorbital distance | 14 | 15 | 13 | 13 | 13.8 | 15 | 6 | 13 | 13.7 | 16 | 22 |
| in % HL | | | | | | | | | | | |
| Upper-jaw length | 55 | 51 | 49 | 49 | 51.1 | 54 | 7 | 48 | 53.0 | 57 | 23 |
| Orbit length | 22 | 21 | 24 | 20 | 21.6 | 24 | 7 | 17 | 18.9 | 22 | 23 |
| Gill-filament length | 7.8 | 7.1 | 5.7 | 5.3 | 6.9 | 8.3 | 7 | 5.7 | 7.6 | 11 | 22 |
| Postorbital distance | 59 | 60 | 58 | 57 | 59.0 | 61 | 7 | 54 | 58.4 | 61 | 22 |
| Central ocellus characters | | | | | | | | | | | |
| Snout tip to ocellus spot distance % SL | 46 | 45 | 46 | 46 | 47.3 | 50 | 6 | 42 | 48.1 | 53 | 23 |
| Dorsal-fin rays covered by spot | 12 | 11 | 12 | 7 | 8.0 | 9 | 6 | 9 | 10.4 | 13 | 21 |
| First dorsal fin ray in spot | 20 | 21 | 21 | 24 | 24.3 | 25 | 6 | 21 | 25.0 | 28 | 21 |
| Central-most ray in spot | 25 | 26 | 27 | 28 | 28.2 | 29 | 6 | 27 | 30.1 | 33 | 21 |
| Vertical-scale rows covered by spot | 0 | 0 | 0 | 0 | 0.0 | 0 | 6 | 0 | 0.0 | 0 | 21 |
| Otolith characters in % SL | | | | | | | | | | | |
| Otolith length | 5.4 | 5.4 | 5.9 | 5.4 | 5.5 | 5.7 | 3 | 4.8 | 5.6 | 6.2 | 5 |
| Otolith height | 2.9 | 3.4 | 2.4 | 2.8 | 3.0 | 3.3 | 3 | 2.1 | 2.6 | 2.9 | 5 |
| Sulcus length | 4.6 | 4.8 | 4.8 | 4.3 | 4.4 | 4.6 | 3 | 4.3 | 4.5 | 4.9 | 5 |
| Ostium length | 3.2 | 3.2 | 3.5 | 2.5 | 2.8 | 3.1 | 3 | 2.7 | 3.0 | 3.4 | 5 |
| Ostium height | 0.71 | 0.83 | 0.79 | 0.64 | 0.75 | 0.82 | 3 | 0.54 | 0.61 | 0.73 | 5 |
| in % sulcus length | | | | | | | | | | | |
| Ostium length | 70 | 67 | 73 | 59 | 64.0 | 68 | 3 | 62 | 65.5 | 71 | 5 |
| Ostium height | 15 | 17 | 16 | 15 | 17.0 | 19 | 3 | 12 | 13.5 | 15 | 5 |
| in % ostium length | | | | | | | | | | | |
| Ostium height | 22 | 26 | 23 | 25 | 26.5 | 28 | 3 | 20 | 20.5 | 21 | 5 |

**Holotype.** MNHN 2002-3883, 119 mm SL, Solomon Sea, 9°31′S, 160°35′E, Salomon 1 cruise, R/V *Alis*, st. CP1802, 245–269 m, 2 Oct. 2001.

**Paratype. MNHN 2023-0262,** 122 mm, same collecting data as HT.

**Fresh colour photo** (Fig. 5B). One adult specimen (sample not retained, size not known) photographed shortly after being caught, Solomon Sea, 9°47′S, 160°53′E, Salomonboa cruise, st. CP 2854, beam trawl, 261–278 m depth, 25 Sep 2007 (see also Richer de Forges 2007).

**Diagnosis.** Hind margin of preopercle with two small but distinct spines; dorsal-fin rays 91–92; anal-fin rays 72–76; pectoral-fin rays 28–29; precaudal vertebrae 13; total vertebrae 53; pseudobranchial filaments 5; long rakers on anterior gill arch 10; head length 24% SL; pelvic-fin length 29–32% SL, fins extending beyond anus; orbit length 5.1–5.2% SL and 21–22% HL; longest gill filament 1.7–1.8% SL and 7.1–7.8% HL; dorsal fin with central ocellus, spot distance 45–46% SL and spot covers 11–12 dorsal-fin rays, placed just behind line through anus; ocellus spot black in fresh and preserved status, not extending ventrally onto body; when fresh, four pale brown vertical bars from dorsal fin down to body or anal fin; no bars in preserved specimens; otolith length 5.4% SL, sulcus length 4.6–4.8% SL, and ostium height 15–17% sulcus length and 22–26% ostium length.

**Description.** The principal meristic and morphometric characters are shown in Table 4. Morphological and preserved colour description based on HT, if not indicated otherwise. Fish elongate with indistinct lateral line; body and head covered by deciduous cycloid scales; origin of dorsal-fin above anterior third of pectoral fin; origin of anal fin slightly in front of midpoint of fish; snout slightly blunt, equal in length to diameter of eye window; two small but distinct spines on hind margin of preopercle; opercular spine pointed; anterior gill arch on both sides with 5 short and 2 long rakers on upper branch, one long raker at angle, and 7 long and 5 short rakers on lower branch; longest filaments on anterior gill arch 7.8% HL; longest gill raker on anterior gill arch 12% HL.

*Sagittal otolith* (Fig. 3C). Otolith oval, tapering in posterior half, its depth 1.8 times in its length; sulcus 1.2 times in otolith length; ostium 1.4 times in sulcus length; ostium depth 6.5 times in sulcus length and 4.6 times in ostium length.

*Dentition.* Premaxillaries, palatines, and dentaries with many pointed, close-set teeth in irregular rows; vomer boomerang-shaped with many small teeth; two median basibranchial tooth patches, anterior one long and narrow and posterior one small and rounded.

*Axial skeleton*. Characters from both HT and PT; precaudal vertebrae 13, all with pointed tips; anterior neural spine half the length of second spine; spines on vertebrae 2–8 depressed; parapophyses on vertebrae 8–13, pleural ribs on vertebrae 2–3 to 13, and epipleural ribs not observed; bases of vertebrae 3–4 to 11–12 enlarged.

*Colour.* Fresh fish (Fig. 5B). Head and body with pale-beige background colour, belly pale silvery-gray; dorsal half of head and body brown marbled, four irregularly shaped, vertical brown bars reaching from below dorsal fin to lower body half, posterior two bars ending at anal fin; a black central ocellus, spot not extending onto body below dorsal fin; ocellus ring only faintly visible along ventral side of ocellus spot due to tightly folded dorsal fin, dorsal fin behind ocellus partly dark-brown pigmented, connecting in part to posterior two vertical bars; anal fin hyaline apart from brown pigmentation areas connected to two posterior bars and along posterior margin of fin; pelvic fins hyaline.

Preserved fish (Fig. 5A). Body and head mostly pale brown, dorsal third of head and body with brownish lines or stripes of various length, one incomplete stripe along lateral line; abdomen anteriorly whitish, mingled with dark-gray patches which widen posteriorly; distinct central ocellus placed just behind vertical line through anus, dark-brown ocellus spot more than twice orbit length, covering 11 dorsal-fin rays and contrasting pale-whitish ring surrounding ocellus spot entirely, spot not extending onto body below dorsal fin; dorsal fin anterior and posterior of spot with weak pale gray pigmentation, becoming lighter posteriorly; anal, pelvic and caudal fin hyaline.

**Etymology.** The new species name "*jonathan*" is used as a noun in apposition and acknowledges Mr. Jonathan Pfliger, MNHN fish collection manager, for his invaluable assistance in our fish taxonomy research.

**Distribution and size**. W Pacific, Solomon Sea, at 245–269 m depth. At least up to 122 mm SL.

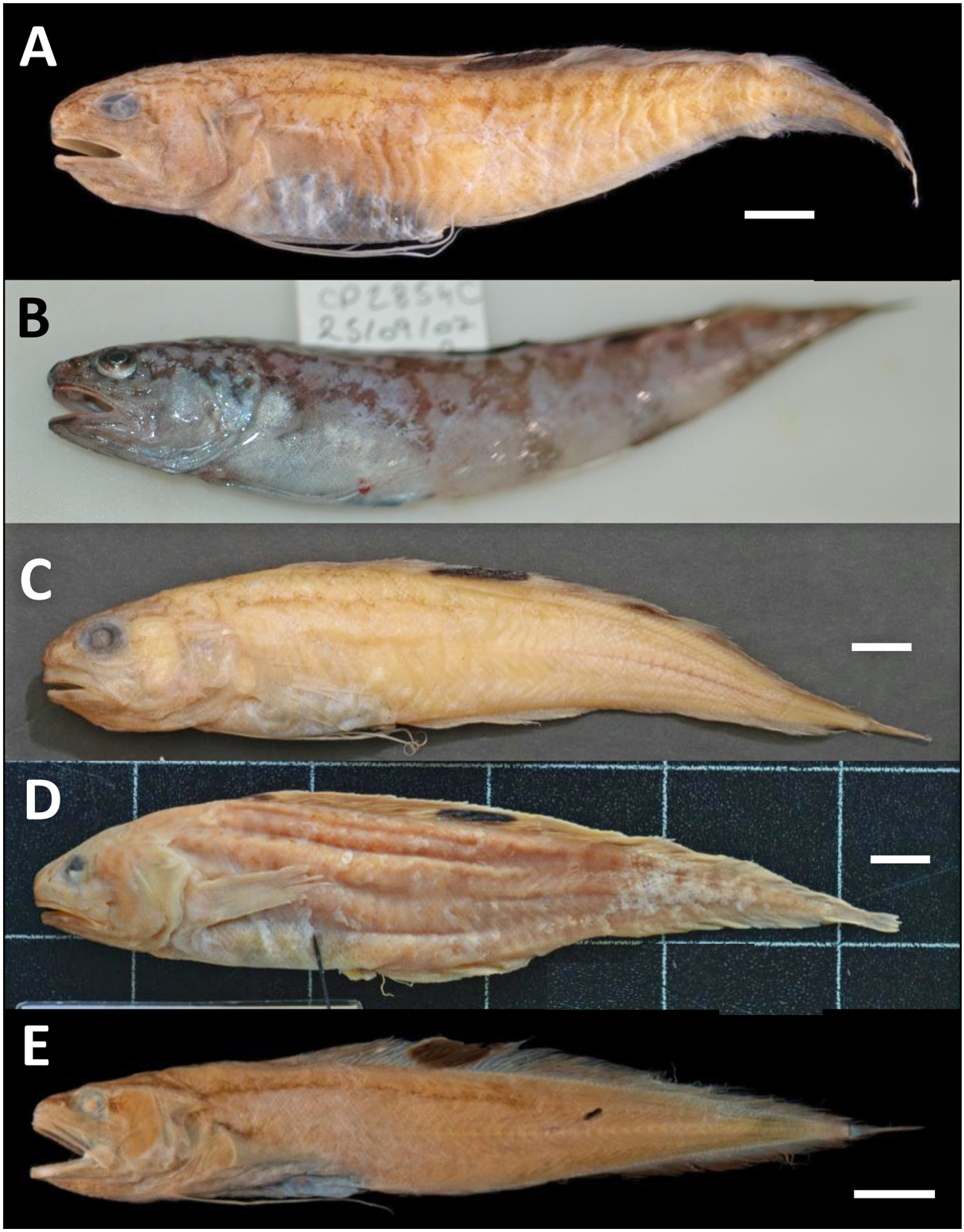


**FIGURE 5.** *S*pecies of the *longiventralis* group. (A) *Neobythites jonathan* **n. sp.**, HT MNHN 2002-3883, 119 mm SL, Solomon Sea (M. Krag); (B) *N. jonathan* **n. sp.**, photographed shortly after being caught by beam-trawl, Solomon Sea (Salomonboa cruise participants; see also Richer de Forges 2007); (C) *N. zora* **n. sp.**, HT, ZMUC P771324, Fiji (side-reversed; H. Carl); (D) *N. longiventralis*, MNHN HT 1994-0739, off New Caledonia (M. Krag); (E) *N. longipes*, ZMUC P77740, 98 mm SL, off Lombok (M. Krag); with 10 mm scale bars.

### *Neobythites zora* n. sp.

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Figures 3, 5, Tables 1, 4

*Neobythites longiventralis* Nielsen, 1997: Nielsen 2002

**Holotype.** ZMUC P771324, 132 mm SL, female, W Pacifc, off Lakeba, Fiji Is., 18°12′S, 178°36′W, Bordau 1 cruise, R/V *Alis*, st. CP 1467, beam trawl, 417–427 m depth, 6 Mar. 1999.

**Diagnosis.** Hind margin of preopercle with two small spines; dorsal-fin rays 91; anal-fin rays 75; pectoral-fin rays 27; precaudal vertebrae 13; total vertebrae 53; pseudobranchial filaments 5; long rakers on anterior gill arch 10; head length 23% SL; pelvic-fin length 34% SL, fins extending well beyond anus; orbit length 5.5% SL and 24% HL; longest gill filament 1.3% SL and 5.7% HL; dorsal fin with two ocelli, larger central ocellus placed just behind vertical line through anus, ocellus spot black, its distance 46% SL and spot covers 12 dorsal-fin rays, and smaller posterior ocellus placed just behind midpoint of dorsal fin, spot distance 69% SL and spot covers 7 dorsal-fin rays; both ocellus spots not extending ventrally onto body; no vertical bars on body; otolith length 5.9% SL, sulcus length 4.8% SL, and ostium height 16% sulcus length and 23% ostium length.

**Description.** The principal meristic and morphometric characters are shown in Table 4. Fish elongate with indistinct lateral line; body and head with deciduous cycloid scales; origin of dorsal fin above anterior third of pectoral fin; origin of anal fin slightly in front of midpoint of fish; snout rather blunt, equal in length to diameter of eye window; two small spines on hind margin of preopercle; opercular spine pointed; anterior gill arch (left side) with 5 short and 2 long rakers on upper branch, one long raker at angle, and 7 long and 5 short rakers on the lower branch; longest filaments on anterior gill arch 5.7% HL; longest gill raker on anterior gill arch 12% HL.

*Sagittal otolith* (Fig. 3D). Otolith oval, egg-shaped, with blunt angle ventrally, its depth 1.7 times in its length; sulcus large, 1.2 times in otolith length; ostium 1.4 times in sulcus length; ostium depth 6.1 times in sulcus length and 4.4 times in ostium length.

*Dentition.* Premaxillaries, palatines, and dentaries with many pointed, close-set teeth in irregular rows; vomer subtriangular with many small teeth; two median basibranchial tooth patches, anterior one long and narrow and posterior one small and rounded.

*Axial skeleton*. Precaudal vertebrae 13, all with pointed tips; anterior neural spine half length of second spine; spines on vertebrae 2–8 depressed; parapophyses on vertebrae 8–13, pleural ribs on vertebra 3–12, and no epipleural ribs observed; basis of vertebrae 4–13 enlarged.

*Colour.* Preserved fish (Fig. 5C). Body and head of preserved HT rather uniformly pale brown, dorsal third of head and body with some weakly indicated brownish patches of stripes, one incompletely follows lateral line in anterior half of body; abdomen similar pale brown colour as entire body; two distinct ocelli, central ocellus placed at midpoint of fish just behind anus and posterior ocellus placed just behind midpoint of dorsal fin; central-ocellus spot about twice orbit length, covering 12 dorsal-fin rays, not extending onto body below, posterior ocellus spot about orbit length, covering 7 dorsal-fin rays, not extending onto body below fin; contrasting pale rings surrounding both ocellus spots distinct, becoming particularly well visible when erecting dorsal fin; latter with pale brown pigmentation in between ocelli and behind posterior ocellus; pelvic, pectoral, and anal fins hyaline, caudal fin weakly pigmented.

**Etymology.** The new species name "*zora*" is used as a noun in apposition and acknowledges Mrs. Zouhaira "Zora" Harakati Gabsi, MNHN fish collection manager, for her invaluable assistance in our fish taxonomy research.

**Distribution and size**. Only known from HT (132 mm SL), W Pacific, off Fiji, at 417–427 m depth.

### *Neobythites longiventralis* Nielsen, 1997

Figure 5, Tables 1, 4

*Neobythites longiventralis* Nielsen, 1997: 66, fig. 13 (New Caledonia, 18°59.3′S, 163°25′E, 320 m; holotype: MNHN 1994-0739).

*Neobythites longiventralis*: Nielsen 2002: 42, fig. 33, in part.

**Diagnosis.** Hind margin of preopercle with two spines; dorsal-fin rays 90–94; anal-fin rays 73–76; pectoral-fin rays 25–27; precaudal vertebrae 13; total vertebrae 53–55; pseudobranchial filaments 4–6; long rakers on anterior gill

arch 10–12; head length 22–24% SL; pelvic-fin length 32–34% SL, fins reaching well beyond anus; orbit length 4.7–5.1% SL and 20–24% HL; longest gill filament 1.3–1.9% SL and 5.3–8.3% HL; dorsal fin with two ocelli, one small ocellus with incomplete contrasting ring (ring missing anteriorly) placed at fin origin, spot distance 26–27% SL and spot covers 2–4 dorsal-fin rays, and large central ocellus placed well behind vertical line through anus, spot distance 46–50% SL and spot covers 7–9 dorsal-fin rays; both ocellus spots not extending ventrally onto body; no vertical bars on body; otolith length 5.4–5.7% SL, sulcus length 4.3–4.6% SL, and ostium height 15–19% sulcus length and 25–28% ostium length.

**Distribution and size.** W Pacific, off Philippines to Caledonia and Fiji, at 219–427 m depth. Known up to 148 mm SL.

### *Neobythites longipes* Smith & Radcliffe, 1913

Figure 5, Tables 1, 4

*Neobythites longipes* Smith & Radcliffe in Radcliffe, 1913: 139, pl. 7 (fig. 1) (off Jolo Island, 06°02′00″N, 120°44′40″E, Philippines, 258 fathoms; holotype: USNM 74126).

**Diagnosis.** Hind margin of preopercle with single spine; dorsal-fin rays 96–103; anal-fin rays 79–87; pectoral-fin rays 27–30; precaudal vertebrae 13–14; total vertebrae 57–60; pseudobranchial filaments 5–10; long rakers on anterior gill arch 8–10; head length 22–25% SL; pelvic-fin length 28–54% SL, fins reaching well beyond anus; orbit length 3.9–5.0% SL and 17–22% HL; longest gill filament 1.3–2.7% SL and 5.7–11% HL; dorsal fin with a central ocellus, placed behind vertical line through anus, the spot distance being 42–53% SL and the spot covering 9–13 dorsal-fin rays; ocellus spot not extending ventrally to body; no vertical bars on body in preserved and fresh specimens (see also Uiblein & Nielsen 2018); otolith length 4.8–6.2% SL, sulcus length 4.3–4.9% SL, and ostium height 12–15% sulcus length and 20–21% ostium length.

**Distribution and size.** W Pacific, off Philippines to Western Australia, at 150–481 m depth. Known up to 301 mm SL.

**Comparisons.** *Neobythites jonathan* **n. sp.** differs from *N. zora* in having only a single ocellus vs. two ocelli, longer upper jaw and gill filaments, smaller eyes, shorter pelvic fins; it differs from *N. longiventralis* in having only a single ocellus vs. two ocelli, a smaller central-ocellus spot and more pectoral-fin rays; and, together with *N. zora* **n. sp.**, it differs from *N. longipes* in having fewer dorsal-fin rays, anal-fin rays, and total vertebrae.

*Neobythites zora* **n. sp.** differs from the three other species in having a posterior ocellus vs. none; it differs from *N. longiventralis* in having a larger central-ocellus spot and from both *N. longiventralis* and *N. longipes* in having a larger orbit length in % SL.

*Neobythites longiventralis* differs from the other three species in having an anterior ocellus vs. none; it differs from *N. longipes* in having fewer dorsal- and anal-fin rays, fewer vertebrae, and a slightly smaller central-ocellus spot.

**Remarks**. *Neobythites longipes* was placed in the *steatiticus* species group by Uiblein & Nielsen (2018), but is now included in the newly established *longiventralis* group.

**Key to the *longiventralis*-species group**

| | |
|---|---|
| **1** | A central and no posterior ocellus, orbit length 3.9–5.2% SL and 17–24% HL, gill-filament length 1.3–2.7% SL, otolith ostium length 2.5–3.4% SL and 59–71% sulcus length . . . . . 2 |
| **-** | A central and one posterior ocellus placed just behind midpoint of dorsal fin, orbit length 5.5% SL and 24% HL, gill-filament length 1.3% SL, otolith ostium length 3.5% SL and 73% sulcus length . . . . . *N. zora* **n. sp.** |
| **2** | A central ocellus and no anterior ocellus, pectoral-fin rays 27–30, central-ocellus spot covering 9–13 dorsal-fin rays . . . . . 3 |
| **-** | An anterior and a central ocellus, pectoral-fin rays 25–27, central-ocellus spot covering 7–9 dorsal-fin rays . . . . . *N. longiventralis* |
| **3** | Dorsal-fin rays 96–103, anal-fin rays 79–87, total vertebrae 57–60 . . . . . *N. longipes* |
| **-** | Dorsal-fin rays 91–92, anal-fin rays 72–76, total vertebrae 53 . . . . . *N. jonathan* **n. sp.** |

**The *steatiticus* species group**

***Neobythites pako* n. sp.**
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Figures 3, 6, 7; Tables 1, 5, 6

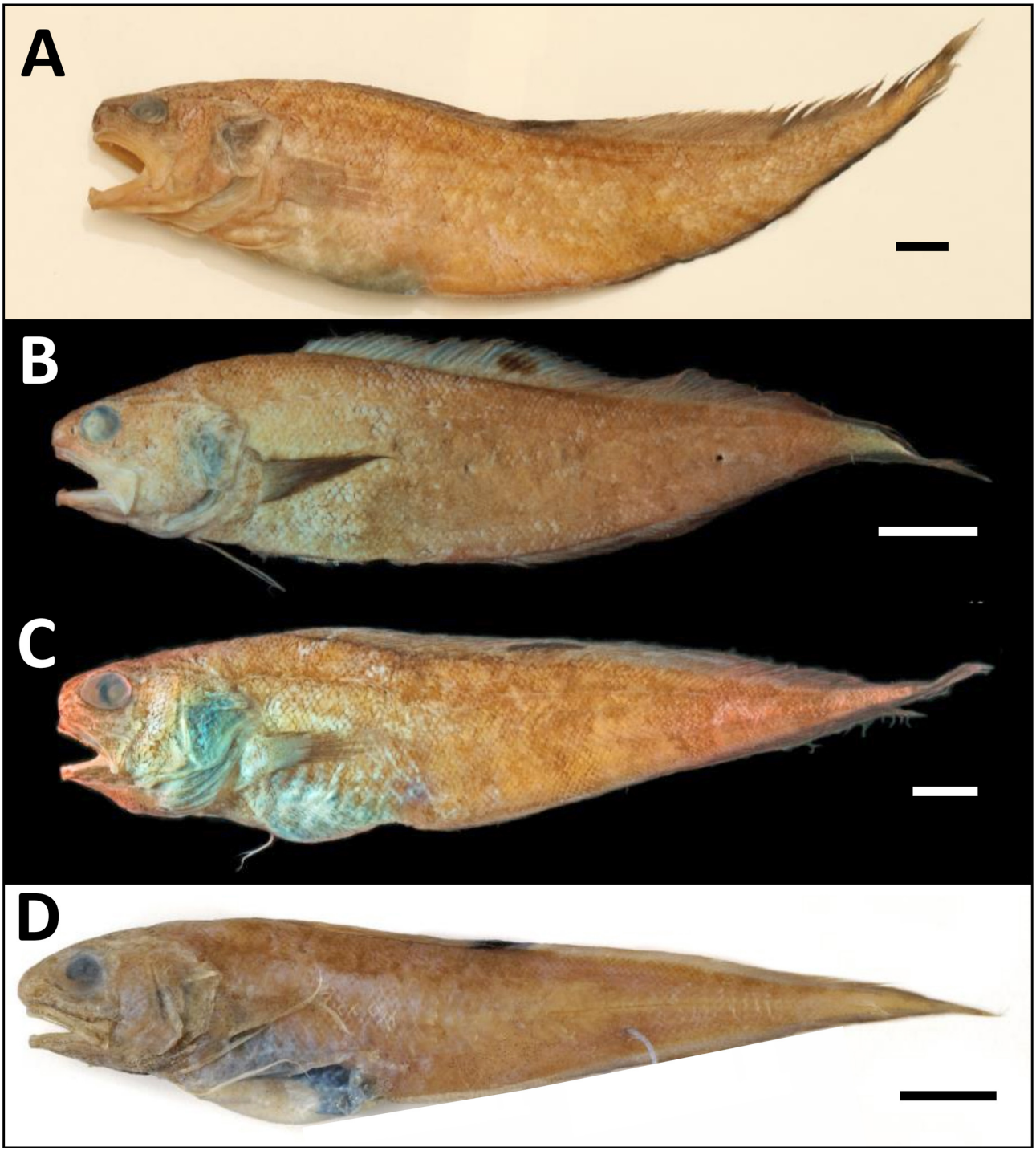


**FIGURE 6.** Four species of the *steatiticus* group. (A) *Neobythites pako* **n. sp.**, HT, MNHN 2006-0337, SL 165 mm, Solomon Sea (side-reversed; M. Krag), (B) *N. malayanus* ZMUC P77742, 138 mm SL, off Lombok (listed in Uiblein & Nielsen 2018; M. Krag); (C) *N. stefanovi*, ZMUC P77841, PT, 198 mm SL, Gulf of Aden (listed in Uiblein & Nielsen 2018; M. Krag); (D) *N. monocellatus*, MOVI 39139, 97 mm SL, off E Brazil (listed in Nielsen *et al*. 2009; G. Brovad); with 10 mm scale bars.

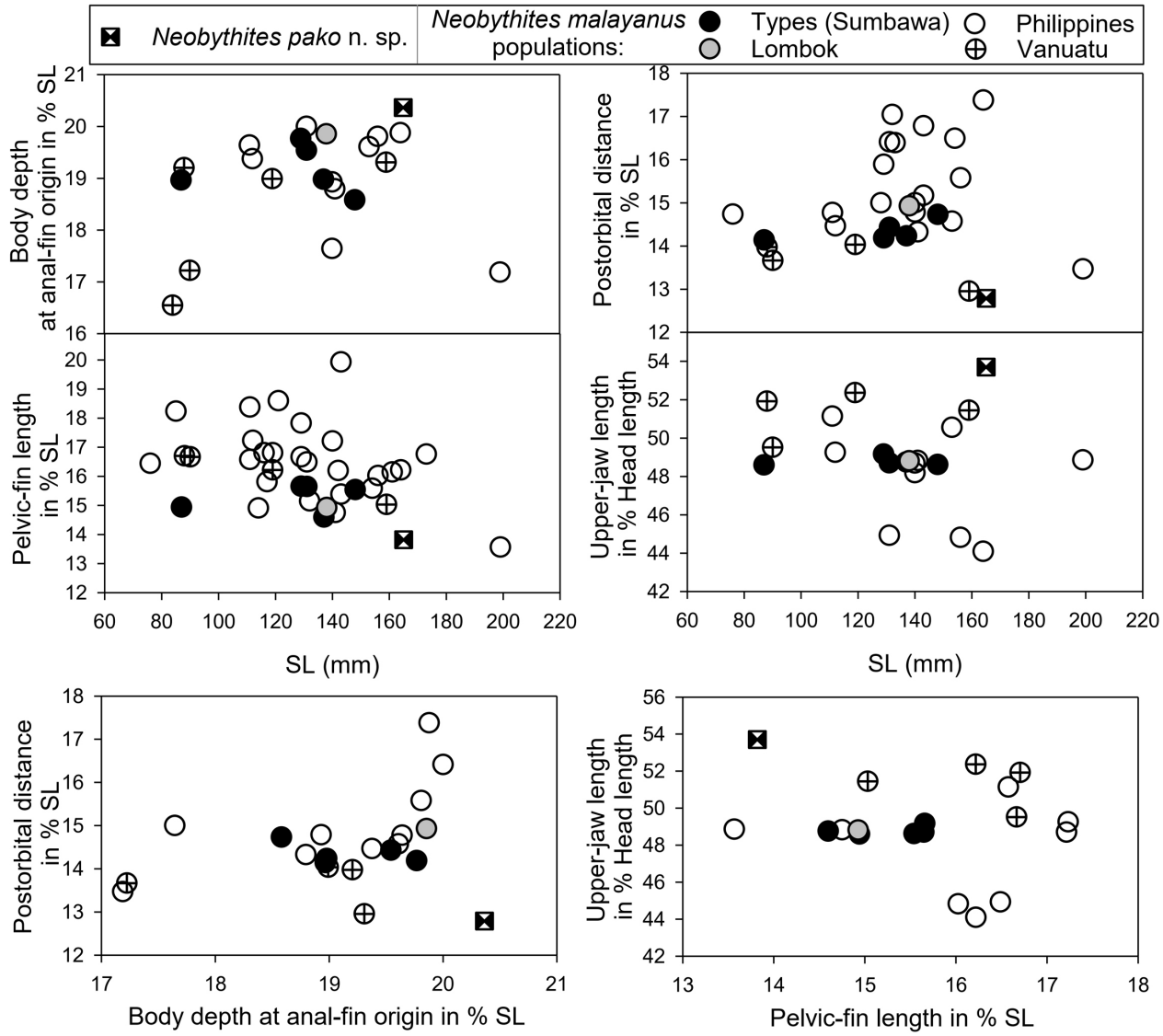


**FIGURE 7.** Plots of four morphometric characters and SL for visual comparisons between *N. pako* **n. sp.** and *N. malayanus* (the latter separated into 4 populations).

**Holotype.** MNHN 2006-0337, 165 mm SL, Solomon Sea, 8°6′25.2″S, 157°23′2.4″E, Salomon 2 cruise, R/V *Alis*, st. CP 2286, 248–253 m depth, 6 Nov. 2004.

**Diagnosis.** Hind margin of preopercle with very short spine; dorsal-fin rays 92; anal-fin rays 77; pectoral-fin rays 28; precaudal vertebrae 13; total vertebrae 56; pseudobranchial filaments 2; long rakers on anterior gill arch 10; head length 22% SL; pelvic-fin length 14% SL, fins not reaching anus; orbit length 4.5% SL and 21% HL; longest gill filament 1.9% SL and 8.8% HL; dorsal fin with central ocellus placed well behind vertical line through anus, spot distance 46% SL and spot covers 7 dorsal-fin rays, not extending ventrally onto body; ocellus spot dark brown; posterior two-thirds of anal fin black; no vertical bars on body; otolith length 4.8% SL, sulcus length 3.8% SL, and ostium height 17% sulcus length and 25% ostium length.

**Description.** The principal meristic and morphometric characters are shown in Table 5. Elongate fish with complete lateral line; head and body covered by deciduous, cycloid scales; origin of dorsal fin above middle of pectoral fin; origin of anal fin slightly in front of midpoint of fish; snout blunt and equal in length to diameter of eye window; very short spine on hind margin of preopercle; opercular spine short and pointed; anterior gill arch on both sides with 4 short and 2 long rakers on upper branch, one long raker at angle, and 7 long and 6–8 short rakers on lower branch; longest filaments on anterior gill arch 8.8% HL and longest raker on anterior gill arch 10% HL.

**TABLE 5.** Meristic, morphometric, quantitative colour, and otolith characters in *Neobythites pako* **n. sp.** and the eight other *steatiticus* group species.

| | *N. pako* **n. sp.** | *N. gloriae* | | *N. lombokensis* | *N. malayanus* | | *N. malhaensis* | | *N. meteori* | *N. steatiticus* | | *N. stefanovi* | | *N. monocellatus* | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | HT | range | *n* | HT | range | *n* | range | *n* | HT | range | *n* | range | *n* | range | *n* |
| SL (in mm) | 165 | 130–158 | 9 | 93 | 76–199 | 44 | 117–135 | 4 | 102 | 113–162 | 6 | 29–198 | 45 | 36–154 | 67 |
| Meristic Characters | | | | | | | | | | | | | | | |
| Dorsal-fin rays | 92 | 90–93 | 9 | 91 | 90–96 | 23 | 99–103 | 4 | 91 | 88–94 | 6 | 89–95 | 39 | 93–99 | 65 |
| Caudal-fin rays | 8 | 8–8 | 6 | 7 | 8–8 | 23 | 8–8 | 4 | 7 | 8–8 | 5 | 8–8 | 28 | 8–8 | 61 |
| Anal-fin rays | 77 | 72–76 | 9 | 72 | 74–79 | 20 | 78–82 | 4 | 75 | 73–77 | 6 | 73–78 | 40 | 78–83 | 66 |
| Pectoral-fin rays | 28 | 24–27 | 9 | 29 | 26–28 | 13 | 30–30 | 4 | 27 | 24–24 | 6 | 24–26 | 31 | 24–27 | 49 |
| Precaudal vertebrae | 13 | 12–12 | 9 | 13 | 12–13 | 23 | 13–13 | 4 | 13 | 12–12 | 5 | 12–12 | 48 | 12–13 | 67 |
| Total vertebrae | 56 | 54–56 | 9 | 53 | 54–57 | 23 | 57–59 | 4 | 53 | 53–57 | 5 | 52–56 | 40 | 54–58 | 67 |
| Pseudobranchial filaments | 2 | 3–4 | 9 | 3 | 2–4 | 35 | 3–4 | 4 | 3 | 2–3 | 6 | 2–6 | 29 | 4–6 | 60 |
| Dorsal-fin origin above vertebra nr. | 6 | 4–5 | 9 | 5 | 5–6 | 24 | 2–3 | 4 | 5 | 4–5 | 5 | 4–5 | 47 | 5–6 | 66 |
| Anal-fin origin below dorsal fin ray nr. | 21 | 18–21 | 9 | 21 | 17–21 | 24 | 23–25 | 4 | 20 | 19–21 | 5 | 17–21 | 44 | 17–21 | 66 |
| Anal-fin origin below vertebra nr. | 15 | 15–15 | 9 | 16 | 15–16 | 24 | 15–15 | 4 | 15 | 14–15 | 5 | 14–16 | 46 | 14–15 | 66 |
| Developed gill rakers | 10 | 11–13 | 9 | 7 | 8–11 | 43 | 12–13 | 4 | 6 | 11–14 | 6 | 10–13 | 44 | 13–15 | 63 |
| Total gillrakers | 19 | 20–22 | 9 | 15 | 17–20 | 19 | 21–22 | 4 | 12 | 21–24 | 6 | 18–24 | 30 | 19–24 | 63 |
| Morphometric characters in % SL | | | | | | | | | | | | | | | |
| Head length | 22 | 25–28 | 9 | 23 | 21–28 | 43 | 21–22 | 4 | 22 | 28–31 | 6 | 23–27 | 45 | 21–24 | 67 |
| Body depth at anal-fin origin | 20 | 18–21 | 9 | 19 | 17–20 | 21 | 17–19 | 4 | 19 | 17–20 | 6 | 15–22 | 45 | 15–19 | 64 |
| Upper-jaw length | 12 | 12–12 | 9 | 9.7 | 11–12 | 20 | 11–11 | 2 | 9.8 | 12–14 | 5 | 11–14 | 37 | 10–13 | 61 |
| Orbit length | 4.5 | 5.3–5.9 | 9 | 5.2 | 4.2–5.6 | 36 | 4.1–4.9 | 4 | 4.9 | 4.8–5.2 | 6 | 5.4–6.9 | 37 | 4.9–7.0 | 61 |
| Preanal distance | 41 | 38–42 | 8 | 44 | 39–47 | 20 | 36–40 | 4 | 45 | 40–46 | 6 | 38–45 | 38 | 36–43 | 64 |
| Predorsal distance | 25 | 25–27 | 8 | 26 | 24–29 | 42 | 20–21 | 4 | 24 | 24–28 | 6 | 24–28 | 38 | 20–27 | 64 |
| Pelvic-fin to anal-fin origin distance | 25 | 22–27 | 9 | 30 | 22–30 | 19 | 21–27 | 4 | 27 | 24–29 | 5 | 21–29 | 37 | 20–27 | 62 |
| Pelvic-fin length | 14 | 14–17 | 8 | 13 | 14–20 | 35 | 13–13 | 4 | 11 | 14–15 | 6 | 14–20 | 38 | 17–23 | 62 |
| Gill-filament length | 1.9 | 3.9–4.9 | 9 | 2.2 | 1.3–3.8 | 43 | 1.6–1.9 | 4 | 2.8 | 4.4–5.9 | 5 | 1.4–3.7 | 42 | 1.4–2.0 | 62 |
| Postorbital distance | 13 | 15–18 | 9 | 14 | 13–17 | 28 | 13 | 1 | 14 | 17–19 | 4 | 14–17 | 37 | 11–14 | 16 |
| in % HL | | | | | | | | | | | | | | | |
| Upper-jaw length | 54 | 43–48 | 9 | 42 | 44–52 | 21 | 50–51 | 2 | 44 | 43–47 | 5 | 41–55 | 37 | 49–56 | 61 |
| Orbit length | 21 | 20–24 | 9 | 23 | 16–23 | 37 | 19–23 | 4 | 22 | 16–18 | 6 | 22–27 | 40 | 22–30 | 61 |
| Gill-filament length | 8.8 | 15–19 | 9 | 9.4 | 5.2–14 | 44 | 7.5–8.9 | 4 | 13 | 15–19 | 5 | 5.4–16 | 45 | 6.2–9.0 | 62 |
| Postorbital distance | 58 | 59–65 | 9 | 62 | 56–66 | 29 | 60 | 1 | 63 | 60–68 | 4 | 57–66 | 37 | 48–63 | 16 |
| Central ocellus characters | | | | | | | | | | | | | | | |
| Snout tip to ocellus spot distance % SL | 46 | 49–51 | 9 | 43 | 43–52 | 42 | 42–46 | 4 | 39 | 46–51 | 6 | 46–56 | 44 | 41–51 | 67 |
| Dorsal-fin rays covered by spot | 7 | 6–8 | 9 | 14 | 6–10 | 20 | 13 | 1 | 9 | 7–10 | 6 | 8–12 | 47 | 6–7 | 9 |
| First dorsal fin ray in spot | 22 | 24–30 | 9 | 18 | 20–27 | 20 | 23 | 1 | 17 | 21–27 | 6 | 22–30 | 47 | 22–28 | 9 |
| Central-most ray in spot | 25 | 27–34 | 9 | 25 | 24–30 | 20 | 29 | 1 | 21 | 25–31 | 6 | 26–34 | 47 | 25–31 | 9 |
| Vertical-scale rows covered by spot | 0 | 0–1 | 9 | 0 | 0–0 | 20 | 1 | 1 | 0 | 0–0 | 4 | 0–4 | 38 | 0–0 | 9 |
| Otolith characters in % SL | | | | | | | | | | | | | | | |
| Otolith length | 4.8 | 4.8–5.0 | 4 | 4.8 | 5.1–5.6 | 6 | 5.2 | 1 | 4.6 | 5.0–5.2 | 2 | 4.6–5.2 | 5 | 5.0–5.8 | 8 |
| Otolith height | 2.8 | 3.0–3.3 | 4 | 3.1 | 3.0–3.4 | 6 | 3.3 | 1 | 2.6 | 3.0–3.4 | 2 | 2.9–3.3 | 5 | 2.9–3.7 | 8 |
| Sulcus length | 3.8 | 3.4–3.7 | 4 | 3.2 | 3.3–4.1 | 6 | 3.8 | 1 | – | 3.6–3.7 | 2 | 3.4–4.1 | 5 | 4.0–4.7 | 8 |
| Ostium length | 2.6 | 2.3–2.5 | 4 | 1.9 | 2.1–2.7 | 6 | 2.5 | 1 | – | 2.3–2.5 | 2 | 2.3–2.6 | 5 | 2.5–2.9 | 8 |
| Ostium height | 0.71 | 0.73–0.89 | 4 | 0.84 | 0.77–0.94 | 6 | 0.80 | 1 | – | 0.77–0.89 | 2 | 0.74–1.05 | 5 | 0.70–0.89 | 8 |
| in % sulcus length | | | | | | | | | | | | | | | |
| Ostium length | 68 | 67–68 | 4 | 59 | 61–72 | 7 | 67 | 1 | – | 65–67 | 2 | 63–70 | 6 | 59–64 | 8 |
| Ostium height | 19 | 21–26 | 4 | 26 | 21–25 | 7 | 21 | 1 | – | 21–25 | 2 | 20–29 | 6 | 18–22 | 8 |
| in % ostium length | | | | | | | | | | | | | | | |
| Ostium height | 27 | 31–39 | 4 | 44 | 32–38 | 7 | 32 | 1 | – | 31–38 | 2 | 30–41 | 6 | 28–34 | 8 |

**TABLE 6.** Meristic, morphometric, quantitative colour, and otolith characters in *Neobythites pako* **n. sp.** and *N. malayanus*.

| | *N. pako* **n. sp.** | *N. malayanus* | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Solomon Sea | Types, (Sumbawa) | | | | Lombok | Philippines | | | | Vanuatu | | | | all | | | |
| | HT | Min | Mean | Max | *n* | *n*=2 | Min | Mean | Max | *n* | Min | Mean | Max | *n* | Min | Mean | Max | *n* |
| SL (in mm) | 165 | 87 | 126.4 | 148 | 5 | 138–171+ | 76 | 131.2 | 199 | 32 | 84 | 108.0 | 159 | 5 | 76 | 128.1 | 199 | 44 |
| Meristic characters | | | | | | | | | | | | | | | | | | |
| Dorsal-fin rays | 92 | 90 | 91.6 | 93 | 5 | 93 | 92 | 93.8 | 96 | 12 | 92 | 93.6 | 96 | 5 | 90 | 93.2 | 96 | 23 |
| Caudal-fin rays | 8 | 8 | 8.0 | 8 | 4 | – | 8 | 8.0 | 8 | 11 | 8 | 8.0 | 8 | 5 | 8 | 8.0 | 8 | 20 |
| Anal-fin rays | 77 | 74 | 74.8 | 76 | 5 | 74 | 74 | 76.7 | 79 | 12 | 75 | 76.4 | 77 | 5 | 74 | 76.1 | 79 | 23 |
| Pectoral-fin rays | 28 | 27 | 27.0 | 27 | 4 | 27 | 26 | 26.7 | 28 | 6 | 27 | 27.0 | 27 | 2 | 26 | 26.8 | 28 | 13 |
| Precaudal vertebrae | 13 | 12 | 12.8 | 13 | 5 | 13–13 | 12 | 12.9 | 13 | 12 | 13 | 13.0 | 13 | 5 | 12 | 12.9 | 13 | 24 |
| Total vertebrae | 56 | 54 | 54.6 | 55 | 5 | 55 | 54 | 55.7 | 57 | 12 | 56 | 56.0 | 56 | 5 | 54 | 55.5 | 57 | 23 |
| Pseudobranchial filaments | 2 | 3 | 3.3 | 4 | 3 | 3–3 | 3 | 3.0 | 3 | 26 | 2 | 2.4 | 3 | 5 | 2 | 2.9 | 4 | 35 |
| Dorsal-fin origin above vertebra nr. | 6 | 5 | 5.6 | 6 | 5 | 5–6 | 5 | 5.3 | 6 | 12 | 5 | 5.8 | 6 | 5 | 5 | 5.5 | 6 | 24 |
| Anal-fin origin below dorsal fin ray nr. | 21 | 19 | 19.4 | 20 | 5 | 20–20 | 17 | 19.2 | 21 | 12 | 18 | 19.0 | 20 | 5 | 17 | 19.2 | 21 | 24 |
| Anal-fin origin below vertebra nr. | 15 | 15 | 15.0 | 15 | 5 | 15–15 | 15 | 15.1 | 16 | 12 | 15 | 15.4 | 16 | 5 | 15 | 15.1 | 16 | 24 |
| Developed gill rakers | 10 | 10 | 10.0 | 10 | 5 | 9–10 | 8 | 9.8 | 11 | 31 | 8 | 9.6 | 10 | 5 | 8 | 9.8 | 11 | 43 |
| Total gillrakers | 20 | 17 | 18.0 | 19 | 5 | 18–18 | 17 | 18.1 | 20 | 10 | 17 | 17.5 | 18 | 2 | 17 | 18.0 | 20 | 19 |
| Morphometric characters | | | | | | | | | | | | | | | | | | |
| in % SL | | | | | | | | | | | | | | | | | | |
| Head length | 22 | 23 | 23.8 | 25 | 5 | 24 | 22 | 24.7 | 28 | 32 | 21 | 22.6 | 24 | 5 | 21 | 24.3 | 28 | 43 |
| Body depth at anal-fin origin | 20 | 19 | 19.2 | 20 | 5 | 20 | 17 | 19.1 | 20 | 10 | 17 | 18.3 | 19 | 5 | 17 | 18.9 | 20 | 21 |
| Upper-jaw length | 12 | 11 | 11.6 | 12 | 5 | 12 | 11 | 11.7 | 12 | 10 | 11 | 11.8 | 12 | 4 | 11 | 11.7 | 12 | 20 |
| Orbit length | 4.5 | 4.7 | 4.9 | 5.0 | 4 | 5.1 | 4.2 | 4.8 | 5.6 | 27 | 4.8 | 5.1 | 5.3 | 4 | 4.2 | 4.8 | 5.6 | 36 |
| Preanal distance | 41 | 44 | 45.5 | 47 | 5 | 45 | 39 | 42.2 | 46 | 10 | 39 | 40.8 | 43 | 4 | 39 | 42.9 | 47 | 20 |
| Predorsal distance | 25 | 26 | 26.4 | 28 | 5 | 27 | 24 | 26.9 | 29 | 31 | 25 | 26.0 | 27 | 5 | 24 | 26.7 | 29 | 42 |
| Pelvic-fin to anal-fin origin distance | 25 | 25 | 25.9 | 27 | 5 | 27 | 22 | 24.8 | 30 | 9 | 24 | 25.3 | 27 | 4 | 22 | 25.3 | 30 | 19 |
| Pelvic-fin length | 14 | 15 | 15.3 | 16 | 5 | 15 | 14 | 16.5 | 20 | 25 | 15 | 16.2 | 17 | 4 | 14 | 16.3 | 20 | 35 |
| Gill-filament length | 1.9 | 1.9 | 2.0 | 2.1 | 5 | 2.0 | 1.3 | 2.2 | 3.8 | 32 | 1.4 | 1.5 | 1.7 | 5 | 1.3 | 2.1 | 3.8 | 43 |
| Postorbital distance | 13 | 14 | 14.3 | 15 | 5 | 15 | 13 | 15.5 | 17 | 18 | 13 | 13.7 | 14 | 4 | 13 | 15.0 | 17 | 28 |
| in % HL | | | | | | | | | | | | | | | | | | |
| Upper-jaw length | 54 | 49 | 48.8 | 49 | 5 | 49–50 | 44 | 47.9 | 51 | 10 | 50 | 51.3 | 52 | 4 | 44 | 48.9 | 52 | 21 |
| Orbit length | 21 | 20 | 20.7 | 21 | 4 | 20–21 | 16 | 19.7 | 23 | 27 | 21 | 22.1 | 23 | 4 | 16 | 20.1 | 23 | 37 |
| Gill-filament length | 8.8 | 8.0 | 8.5 | 9.1 | 5 | 8.0–8.2 | 5.2 | 8.9 | 14 | 32 | 6.3 | 6.8 | 7.3 | 5 | 5.2 | 8.6 | 14 | 44 |
| Postorbital distance | 58 | 57 | 60.2 | 61 | 5 | 60–61 | 56 | 61.2 | 66 | 18 | 59 | 59.6 | 61 | 4 | 56 | 60.8 | 66 | 29 |
| Central ocellus characters | | | | | | | | | | | | | | | | | | |
| Snout tip to ocellus spot distance % SL | 46 | 47 | 47.8 | 49 | 5 | 48 | 44 | 48.2 | 52 | 31 | 43 | 46.0 | 48 | 5 | 43 | 47.9 | 52 | 42 |
| Dorsal-fin rays covered by spot | 7 | 6 | 6.8 | 8 | 5 | 6–6 | 6 | 7.1 | 10 | 10 | 7 | 8.0 | 9 | 3 | 6 | 7.1 | 10 | 20 |
| First dorsal fin ray in spot | 22 | 21 | 22.4 | 23 | 5 | 21–23 | 20 | 23.6 | 27 | 10 | 20 | 21.0 | 22 | 3 | 20 | 22.7 | 27 | 20 |
| Central-most ray in spot | 25 | 24 | 25.6 | 26 | 5 | 24–26 | 25 | 26.9 | 30 | 10 | 24 | 24.7 | 25 | 3 | 24 | 26.1 | 30 | 20 |
| Vertical-scale rows covered by spot | 0 | 0 | 0.0 | 0 | 5 | 0–0 | 0 | 0.0 | 0 | 10 | 0 | 0.0 | 0 | 3 | 0 | 0.0 | 0 | 20 |
| Otolith characters | | | | | | | | | | | | | | | | | | |
| in % SL | | | | | | | | | | | | | | | | | | |
| Otolith length | 4.8 | | - | | | 5.6 | 5.3 | 5.3 | 5.3 | 2 | 5.1 | 5.2 | 5.3 | 4 | 5.1 | 5.2 | 5.3 | 6 |
| Otolith height | 2.8 | | - | | | 3.1 | 3.1 | 3.2 | 3.3 | 2 | 3.0 | 3.2 | 3.4 | 4 | 3.0 | 3.2 | 3.4 | 6 |
| Sulcus length | 3.8 | | - | | | 3.9 | 4.0 | 4.0 | 4.1 | 2 | 3.3 | 3.5 | 3.7 | 4 | 3.3 | 3.7 | 4.1 | 6 |
| Ostium length | 2.7 | | - | | | 2.6 | 2.6 | 2.6 | 2.7 | 2 | 2.1 | 2.3 | 2.5 | 4 | 2.1 | 2.4 | 2.7 | 6 |
| Ostium height | 0.65 | | - | | | 0.94 | 0.86 | 0.90 | 0.93 | 2 | 0.77 | 0.80 | 0.83 | 4 | 0.77 | 0.84 | 0.93 | 6 |
| in % sulcus length | | | | | | | | | | | | | | | | | | |
| Ostium length | 71 | | - | | | 66–72 | 65 | 65.4 | 66 | 2 | 61 | 65.6 | 68 | 4 | 61 | 65.5 | 68 | 7 |
| Ostium height | 17 | | - | | | 24–25 | 21 | 22.2 | 23 | 2 | 21 | 22.9 | 25 | 4 | 21 | 22.7 | 25 | 7 |
| in % ostium length | | | | | | | | | | | | | | | | | | |
| Ostium height | 25 | | - | | | 35–36 | 32 | 34.0 | 36 | 2 | 32 | 35.0 | 38 | 4 | 32 | 34.7 | 38 | 7 |

+ tail broken, only data for anterior body part and measurements not related to Sl available for larger specimen.

*Sagittal otolith* (Fig. 3E). Otolith peanut-shaped, ventrally rounded, dorsally and anteriorly flattened, posteriorly blunt, its depth 1.7 times in its length; sulcus large, 1.3 times in otolith length; ostium 1.5 times in sulcus length; ostium depth 5.4 times in sulcus length and 3.6 times in ostium length.

*Dentition.* Premaxillaries, palatines, and dentaries with many small, pointed, close-set teeth in irregular rows; vomer boomerang-shaped with many, pointed teeth; two median basibranchial tooth patches, anterior one long and narrow and posterior one small and circular.

*Axial skeleton*. Precaudal vertebrae 13, all with pointed tip; anterior neural spine almost half length of second spine; neural spines on vertebrae 1–9 somewhat depressed, parapophyses present on vertebrae 8–13, pleural ribs on vertebrae 3–13 and epipleural ribs indistinct; basis of neural spines 4–13 enlarged.

*Colour.* Preserved fish (Fig. 6A). Body and head of preserved HT rather uniformly pale brown, slightly darker dorsally and in snout region, gill cover anteriorly gray brown, posteriorly pale, lateral line indistinct, abdomen pale gray anterior of anus; single ocellus placed well behind vertical line through anus at body midpoint, central-ocellus spot dark brown, slightly larger than orbit diameter, covering 7 dorsal-fin rays, not extending onto body below dorsal fin, ocellus ring pale, rather indistinct on folded fin, becoming more distinct when fin is raised; dorsal fin anterior and behind ocellus pale gray brownish, pigmentation becoming somewhat more intense on posterior third towards caudal fin; anal fin almost entirely covered with continuous dark brown stripe behind vertical line through posterior ocellus spot edge; pelvic and pectoral fins hyaline.

**Etymology.** The new species name "*pako*" is used as a noun in apposition and honours the son of the first author, Francisco "Pako" Uiblein.

**Distribution and size.** Only known from the HT (165 mm SL), caught in bottom trawl in eastern Solomon Sea at 248–253 m depth.

### *Neobythites monocellatus* Nielsen, 1999

Figure 6; Tables 1, 5

*Neobythites monocellatus* Nielsen, 1999: 351, figs. 8–9 (off Venezuela, 09°53′N, 59°53′W, 229 m; holotype: USNM 309234).

**Diagnosis.** Spine on hind margin of preopercle absent or thin and flat; dorsal-fin rays 93–99; anal-fin rays 78–83; pectoral-fin rays 24–27; precaudal vertebrae 12–13; total vertebrae 54–58; pseudobranchial filaments 4–6; long rakers on anterior gill arch 13–15; head length 21–24% SL; pelvic-fin length 17–23% SL, fins not extending beyond anus; orbit length 4.9–7.0% SL and 22–30% HL; longest gill filament 1.4–2.0% SL and 6.2–9.0% HL; dorsal fin with central ocellus with black spot placed well behind vertical line through anus, the ocellus spot distance being 41–51% SL and the spot covering 6–7 dorsal-fin rays, not extending ventrally to body; no vertical bars on body; otolith length 5.0–5.8% SL, sulcus length 4.0–4.7% SL, and ostium height 18–22% sulcus length and 28–34% ostium length.

**Distribution and size.** Found in the tropical W and SW Atlantic from off Honduras and along the north coast of South America to French Guiana and off Bahia, E Brazil, on the continental shelf and upper slope (117–439 m). Max. size 154 mm SL.

**Comparisons.** *Neobythites pako* **n. sp.** differs clearly from all other *steatiticus* species in having a very short but distinct single preopercular spine vs. none or only a very weakly formed, flat, or indistinct spine, and in the combination of several colour, meristic, morphometric, and otolith characters (Table 5). It is most similar to *N. malayanus* and *N. stefanovi*. From *N. malayanus*, it differs in longer upper jaw relative to head length in combination with slightly deeper body, shorter pelvic fins and postorbital distance (Fig. 7), and it differs in several otolith characters including shorter and shallower otolith, and shallower ostium relative to SL, sulcus, and ostium length (Table 5; Fig. 3E, F). It differs from the Indonesian population (type locality) of *N. malayanus* in having more anal-fin rays, fewer pseudobranchial filaments, and shorter preanal distance, from the Vanuatu population in having in longer gill-filaments and from the Philippine population (which is most similar) in having fewer pseudobranchial filaments (Table 6). It differs from *N. stefanovi* in its absence of dark dorsal-fin margin, higher number of precaudal vertebrae, vertebrae number below dorsal-fin origin, smaller ocellus spot, and shallower otolith ostium (Table 5).

For further comparisons among all other *steatiticus* group members except for the W Atlantic *N. monocellatus*, see Uiblein & Nielsen (2018). *Neobythites monocellatus* differs from *N. pako* **n. sp.** in lack of dark stripe along anal fin, more dorsal-, anal- and pectoral fin rays, more pseudobranchial filaments, more developed gill rakers, and

longer pelvic fins; *N. monocellatus* is most similar to six *steaticus* group species, *N. gloriae*, *N. lombokensis*, *N. malayanus*, *N. meteori*, *N. steatiticus* and *N. stefanovi*, from which it differs in having a combination of relatively high number of dorsal- and anal-fin rays and gill rakers, relatively longer pelvic fins, shorter postorbital distance, and smaller-sized ocellus spot; from the remaining species, *N. malhaensis*, it differs in fewer pectoral-fin rays, more pseudobranchial filaments, longer pelvic fins, and smaller ocellus spot.

**Remarks.** One *Neobythites malayanus* specimen (length 171+ mm) from off Lombok could not be studied in detail due to missing its tail (Table 6). Like *N. unimaculatus*, *N. malayanus* should be studied in more detail regarding geographic differentiation (Table 6, Fig. 7).

**Key to the *steatiticus* species group**

**1** Anterior gill arch with 6–7 long rakers; anal fin without dark margin or band . . . . . 2
**-** Anterior gill arch with 8–15 long rakers; anal fin with or without dark margin or band . . . . . 3
**2** Ocellus short, placed above anus with ocellus spot covering 9 dorsal-fin rays; longest gill filament 13.0% HL . . . . . *N. meteori* (off Sokotra Island, NW Indian Ocean)
**-** Ocellus long, placed above anterior part of anal fin with ocellus spot covering 14 dorsal-fin rays; longest gill filament 9.4% HL . . . . . *N. lombokensis* (off Lombok, E Indian Ocean)
**4** Vertical, dark bar below ocellus spot; dorsal and anal fins without dark margin or band, dorsal-fin rays 99–103, dorsal-fin origin above vertebrae number 2–3, anal-fin origin below dorsal-fin ray number 23–25 . . . . . *N. malhaensis* (Saya de Malha Bank, W Indian Ocean)
**-** None to a few indistinct, vertical, dark bars on body; dorsal and/or anal fin with dark margin or band, dorsal-fin rays 88–99, dorsal-fin origin above vertebrae number 4–6, anal-fin origin below dorsal-fin ray number 17–21 . . . . . 4
**4** Median part of anal fin dark, and distal and proximal parts light; head length 28–31% SL; longest gill filament 4.4–5.9% SL . . . . . *N. steatiticus* (Bay of Bengal, NE Indian Ocean)
**-** Distal part of dorsal and anal fins dark and proximal part light; head length 21–28% SL; longest gill filament 1.3–4.9% SL . . . . . 5
**5** Developed gill rakers 8–11 (mostly 9 or 10); orbit length 4.2–5.6% SL and 37–46% upper-jaw length; precaudal vertebrae 13 (rarely 12) . . . . . 6
**-** Developed gill rakers 10–15 (mostly 11–15); orbit length 4.9–7.0% SL and 42–59% times in upper-jaw length; precaudal vertebrae 12 (rarely 13) . . . . . 7
**6** Preopercular spine indistinct or a flat process, upper-jaw length 44–52% HL, ostium height 0.77–0.93% SL, 21–25% sulcus length and 32–38% ostium length . . . . . *N. malayanus* (Indonesia, Philippines, Vanuatu)
**-** Preopercular spine very short but distinct, upper-jaw length 54% HL, ostium height 0.65% SL, 17% sulcus length and 25% ostium length . . . . . *N. pako* **n. sp.** (Solomon Sea)
**7** Dorsal-fin rays 93–99, anal-fin rays 78–83, developed gill rakers 13–15, head length 21–24% SL, postorbital distance 11–14% SL, sulcus length 4.0–4.7% SL and ostium length 59–64% sulcus length . . . . . *N. monocellatus* (Honduras to off Bahia, E Brazil, W and SW Atlantic)
**-** Dorsal-fin rays 89–95, anal-fin rays 72–78, developed gill rakers 10–13, head length 23–28% SL, postorbital distance 14–18% SL, sulcus length 3.4–4.1% SL, and ostium length 63–70% sulcus length . . . . . 8
**8** Longest gill filaments 1.4–3.7% SL; dorsal-fin rays in ocellus spot 8–12 . . . . . *N. stefanovi* (Red Sea and Gulf of Aden, NW Indian Ocean)
**-** Longest gill filaments 3.9–4.9% SL; dorsal-fin rays in ocellus spot 6–8 . . . . . *N. gloriae* (Arabian Gulf and inner Gulf of Oman, NW Indian Ocean)

## Discussion

Half of the now 60 valid species of the genus *Neobythites* bear ocelli. The continuing description of ocellus-bearing species (eight of ten new species described since 2009) suggests that that ocelli may be an even more dominating colour character in *Neobythites* than earlier assumed (Uiblein & Nielsen 2005) and the evolution of ocelli may have triggered a considerable portion of the diversity in this genus, which is, by far, the most species-rich of the entire family.

Ocelli may have various biological functions, including predator avoidance or deterrence and social signaling or recognition (Uiblein & Nielsen 2005). These conspicuous structures vary considerably among species and hence may reveal species-specific adaptations to various ecological constraints in light-reduced marine habitats of the deeper shelf and upper slope (Uiblein *et al.* 1994, 2010; Uiblein 1995, 1996; Uiblein & Nielsen 2005). Of considerable importance in this respect is the size of the central ocellus which differentiates several of the 20 *Neobythites* species considered in the current study (Fig. 8).

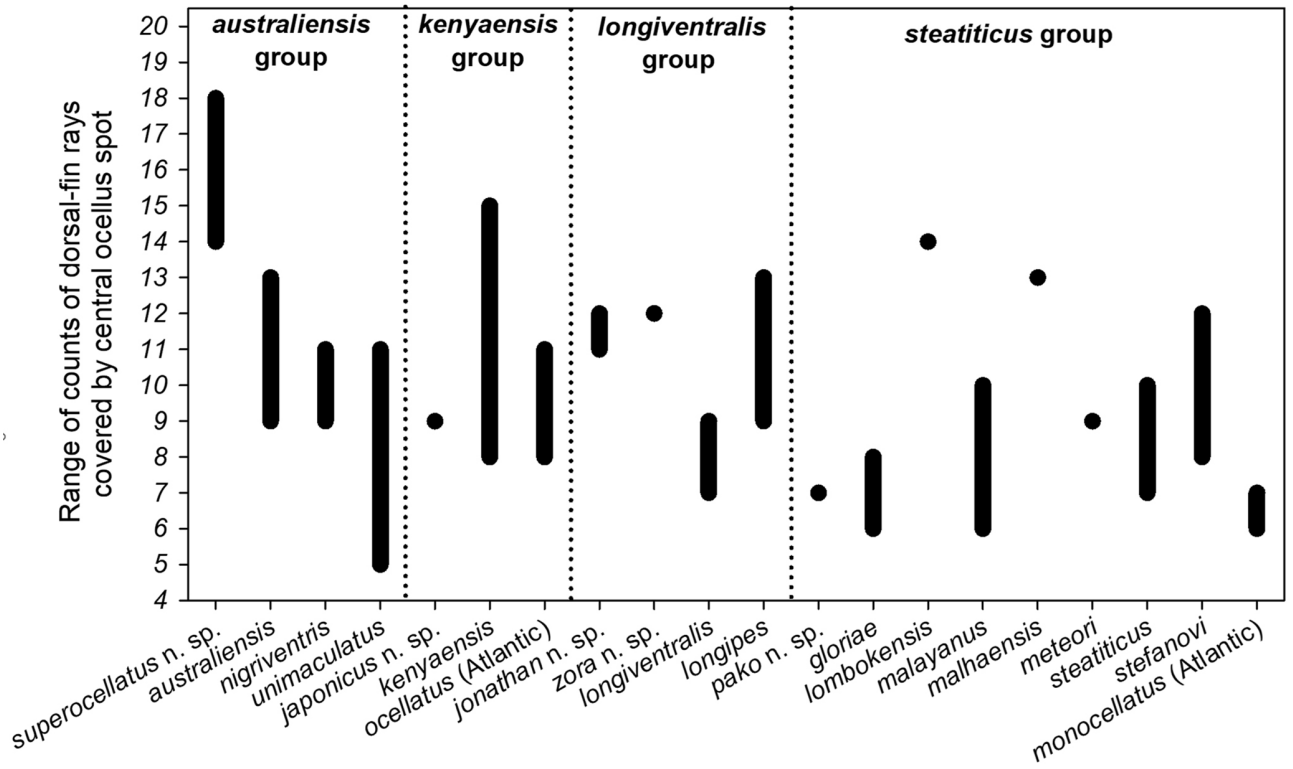


**FIGURE 8.** Ocellus size expressed in number of dorsal-fin rays covered by dark ocellus spot in 20 *Neobythites* species belonging to four species groups.

Although species differences in size, position, and number of ocelli have been rather well known from earlier studies of *Neobythites* (see Uiblein & Nielsen 2005, for a review), the particularly far-reaching extension of the dorsal-fin ocellus onto the body below the fin, as it occurs in the six specimens of *Neobythites superocellatus* **n. sp.** (four preserved specimens studied plus fresh colour documentation in two additional, photographed specimens; Table 1; Figs. 1, 2), is a new finding. So far, the coverage of up to four horizontal scale rows by the central ocellus spot was observed in a single species, *N. stefanovi* (Table 5). However, considerable variation among individuals occured, four horizontal scale rows being covered only in a single individual, whereas not a single scale row was covered in 14 of the 32 studied specimens (Uiblein 1995). However, there was a significant geographic difference between the populations of *N. stefanovi* from the Red Sea and the Gulf of Aden, with the majority of Red Sea specimens (8 of 15) showing a vertically enlarged ocellus spot covering three scale rows vs. 16 of the 17 specimens from the adjacent Gulf of Aden having no ($n$=12) or only one ($n$=4) scale row covered (Uiblein 1995, 1996).

Increasing the size of a conspicuous colour structure like an ocellus should enhance its signaling function. However, this process may be restricted by physical limitations, such as the space available on the dorsal fin in *Neobythites*. Therefore, the only option when further increasing the size beyond the space available on the fin is to extend the spot onto the body below the fin, which has been realized in *N. superocellatus*. We are not aware of any other examples in fishes where a similar structure exists. What is also puzzling is the connection of the ocellus with a vertical bar as well as the supporting crescent-shaped bars reaching down from the dorsal fin to the body in front and behind the ocellus (Fig. 2). These additional colour structures render the ocellus in *N. superocellatus* a rather unique, highly conspicuous feature that also requires further attention from an evolutionary-ecology point of view.

The separation into four taxonomic groups has facilitated making identification keys for the five new species described and can be used—in combination with the initially presented key to the groups—for identifying all 20 species considered. Ten additional ocellus-bearing, yet ungrouped, species remain (Table 1), which deserve additional studies. From the cruises in the Solomon Sea, for instance, several specimens of a species with at least two ocelli have become available which require a detailed comparative study that also involves additional species which have no ocelli, but just dark spots on the dorsal fin. Therefore, it will probably be necessary to consider non-ocellus-bearing species in this ongoing study (Uiblein & Nielsen, unpublished data).

In summary, while having contributed to more insights into the still largely hidden diversity of deep-shelf and upper-slope dwelling fishes, there is obvious need to further investigate this diversity from taxonomic, ecological, and evolutionary viewpoints. In a time of considerable changes due to manifold human-derived pressures on marine ecosystems, it appears more than appropriate to further try achieving a good understanding of the overall status of marine fish resources, including essential information required for monitoring, conservation, and sustainable management of yet insufficiently explored ecosystems.

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