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Review of the *steatiticus*-species group of the cuskeel genus *Neobythites* (Ophidiidae) from the Indo-Pacific, with description of two new species

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Abstract

This review was motivated by the recent collection of a specimen of the specious cuskeel genus *Neobythites* (Ophidiidae) off Myanmar and difficulties to identify it based on the available literature. This specimen has an ocellus consisting of a dark oval spot and a concentric white ring placed on the dorsal fin at mid-body, typical for many *Neobythites* species. It belongs to a group of single-ocellus bearing species which have no or only one weakly developed, flat preopercular spine which we term here the "*steatiticus*-species group". Before this study, the *steatiticus* group consisted of six Indo-Pacific species, *N. longipes*, *N. malhaensis*, *N. malayanus*, *N. meteori*, *N. steatiticus*, and *N. stefanovi*, and the Atlantic *N. monocellatus*. From 136 specimens representing the six Indo-Pacific *steatiticus*-group species counts or measurements of 12 meristic, 14 body shape, five ocellus and six otolith characters were obtained and compared, revealing two undescribed species. We describe *N. gloriae* **n. sp**. from the Arabian Gulf and inner Gulf of Oman based on nine specimens that had been previously misidentified as *N. steatiticus* and *N. stefanovi*. The latter species differ from the new species and from each other in the combination of five characters, head length, orbit length, gill-filament length, ocellus-spot distance, and ocellus-spot size. The second new species described is *N. lombokensis* **n. sp**. which consists of a single specimen from off SE Lombok, southern Indonesia. It differs from all other *steatiticus*-group species in having a larger ocellus spot and in several meristic and morphometric characters. The specimen from off Myanmar, eastern Bay of Bengal, was found to belong to *N. steatiticus*, providing new information on distribution and colour. Diagnoses, updated distribution information, and a key for the eight Indo-Pacific *steatiticus*-group species are here presented. We discuss our findings with special emphasis on the variation and possible function of colour patterns in *Neobythites*, being important for understanding the ecology and evolution of this specious genus.

Key words: Teleostei, Ophidiidae, *Neobythites,* Indo-West Pacific, colour, ocellus size, depth distribution

Introduction

Neobythites is by far the species-richest genus among the family of cuskeels (Ophidiidae) with 52 valid species (Nielsen 2002, Nielsen *et al.* 2009, Ohashi *et al.* 2012). Important diagnostic characters for this genus are a tapering caudal part, median basibranchial tooth patches 2, pelvic rays 2, strong opercular spine, 0 to 3 preopercular spines, eye diameter 3.7 to 6.0 % SL, equal to or slightly shorter than snout, and occurrence of vertical bars, dark fin margins, dark spots, or so-called ocelli (Nielsen 2002; Uiblein & Nielsen 2005; Nielsen & Machida 2006).

Preopercular spines and ocelli are also important diagnostic characters for the identification of *Neobythites* species. Ocelli are defined as dark, oval spots that cover 5–14 dorsal-fin rays and are surrounded by a contrasting white ring (Uiblein & Nielsen 2005). Ocelli vary among species in number, size, and position. Ocellar spots are well-retained in preserved specimens. Among the 23 currently-known ocellus-bearing species there is a group of single ocellus-bearing species with the ocellus placed at mid-body and no or only one weakly developed, flat preopercular spine. This group, which we term the "*steatiticus*-species group", prior to this study consisted of the following seven species: *N. longipes* Smith & Radcliffe, 1913, *N. malhaensis* Nielsen, 1995, *N. malayanus* Weber,

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1913, *N. meteori* Nielsen, 1995, *N. steatiticus* (Alcock, 1894), *N. stefanovi* Nielsen & Uiblein, 1993 (all from the Indo-Pacific), and *N. monocellatus* Nielsen, 1999 (from the Atlantic).

During a recent cruise off Myanmar of the RV *Dr. Fridtjov Nansen*, a *Neobythites* specimen was collected and sent to us for further examination. During a preliminary check, we found it to belong to the *steatiticus*-species group, resembling *N. steatiticus* in several morphometric, meristic, and colour characters. However, it turned out to have a larger ocellus than all *N. steatiticus* specimens we had studied so far. Also, the comparative examination of this character and gill-filament length involving all Indo-Pacific *steatiticus*-group species, revealed the need to adopt a more detailed taxonomic approach.

In this review of *steatiticus*-species, we describe two new species and provide updated diagnoses and distribution information for all eight Indo-Pacific species as well as an identification key. We discuss these results with respect to the need of further sampling and taxonomic efforts. The variation and possible function of colour patterns in *Neobythites*, and the ecology and evolution of this specious genus are also discussed.

Material and methods

This review is based on 136 specimens from various museum collections and fresh colour photographs of five specimens from research cruises taken on board immediately after capture. Counts or measurements of 12 meristic, 14 body shape, five ocellus and six otolith characters were obtained and compared. Meristic characters, body-shape measurements, and qualitative morphological characters follow Nielsen *et al*. (1999) and Nielsen *et al.* (2009). Otolith measurements follow Uiblein *et al.* (2008) and description and analysis of colour patterns follow Uiblein & Nielsen (2005). If not otherwise indicated, all morphometric data are given as percentage of SL. Ranges of the resulting values below 10 were rounded to one decimal place and between 10 and below 50 to the nearest 0.5. The means of all measurements and counts were rounded to one decimal.

Ocellus characters for the *steatiticus*-species group are termed and defined as follows (slightly deviating terms used by Uiblein & Nielsen 2005 given in round brackets): "ocellus-spot distance" (= central ocellus-spot distance) is the distance between upper-jaw symphysis and the anterior edge of the ocellus spot and is a morphometric character to indicate ocellus-spot position in relation to body; "number of ocellus-spot rays" is the number of dorsal-fin rays in (= covered by) the ocellus spot and is a count referring to ocellus length and size; "first dorsal-fin ray in spot" is the anterior-most ray covered by the ocellus spot; "central-most ray in spot" (= position of the ocellus-spot central ray) is the ray closest to the middle of the ocellus spot and is, together with the before-mentioned, a meristic character to indicate ocellus-spot position in relation to dorsal fin; and "vertical scale rows covered by spot" is the number of pigmented scale rows just below the spot which contribute to form the ocellus spot.

For comparisons with the Atlantic *steatiticus*-group species *Neobythites monocellatus* and all other *Neobythites* species published data (e.g., Nielsen 1995, 1999, 2002; Uiblein & Nielsen 2005; Nielsen *et al*. 2009) were used. Institutional acronyms follow Fricke & Eschmeyer (2017). SL = standard length, HT = holotype, PT = paratype.

Taxonomy

Neobythites gloriae n. sp.

(Figures 1–3, Tables 1–3)

Neobythites steatiticus: Nielsen 1995 (in part, Arabian Gulf, Gulf of Oman).
Neobythites stefanovi: Nielsen & Uiblein 1993 and Nielsen 1995, 2002 (in part, Gulf of Oman).

Holotype. USNM 309008 (male, 158 mm SL), Gulf of Oman, NW Indian Ocean, 25°02' N, 56°52' E, RV *Anton Bruun,* cruise 4B, st. 264A, bottom trawl, 272–291 m depth, 2 Dec 1963.

Paratypes (n=8, 130–150 mm SL). BMNH 1904.5.25.1 (1 male, 150 mm SL), Gulf of Oman, 25°32' N, 57°47' E, 320 m depth; BMHN 1910.1.31.7–10 (3 females and 1 male, 132–145 mm SL), Gulf of Oman, 25°35' N, 57°47' E, 311 m depth; BMHN 1910.1.31.23 (1 female, 130 mm SL), Arabian Gulf, 10' W of Dubai, United Arab Emirates, 26 m depth; USNM 440378 (1 male, 140 mm SL), and ZMUC P771754 (1 female, 131 mm SL), same data as for the holotype.

Diagnosis. No spines on hind margin of preopercle; dorsal fin-rays 90–93; anal-fin rays 72–76; pectoral fin-rays 24–27; precaudal vertebrae 12; total vertebrae 54–56; pseudobranchial filaments 3–4; long gill rakers on anterior arch 11–13; head length 25.5–28.0 % SL; pelvic-fin length 13.5–17.0 % SL, pelvic fins not reaching beyond anus; orbit length 5.3–5.9 % SL, 19.5–23.5 % head length, and 2.0–2.2 times in upper-jaw length; longest gill filament 3.9–4.9 % SL and 15.5–19.0 % head length; ocellus spot placed well posterior to a vertical line through anus, the ocellus-spot distance being 49.0–51 % SL, and the spot covering 6–8 dorsal-fin rays; margins of posterior fifth to a quarter of dorsal fin and posterior half to two thirds of anal fin dark pigmented; no vertical bars on body; otolith length 4.8–5.0 % SL, sulcus length 3.4–3.7 % SL, and ostium height 21.0–26.5 % sulcus length.

Description (based on holotype, differences in paratypes mentioned in round brackets). Rather elongate fish with complete lateral line in preserved specimens; on the anterior half of body, the lateral line runs with 8–10 scale rows to dorsal edge, decreasing posteriorad; head and body fully covered with cycloid scales; origin of dorsal fin above hind margin of opercle; origin of anal fin slightly in front of midpoint of fish; tip of pectoral fins ending just above origin of anal fin; pelvic fins reaching almost to origin of anal fin; blunt snout slightly shorter than diameter of eye; upper jaw ending well behind eye; anterior nostril ending in a short tube and the larger posterior nostril in a mere hole; no spines on preopercle; strong opercular spine; anterior gill raker with 1–2 (2–3) blunt and 3–4 (2–3) long rakers on upper branch; one long raker in angle and lower branch with eight long and 6 (7) blunt rakers; gill filaments 1.5–3.0 (1–4) times as long as long rakers; distinct pseudobranchial filaments 3 (3–4).

Otolith. Otolith oval, its height 1.6 (1.5–1.7) times in its length; sulcus large, 1.3 (1.3–1.4) times in otolith length; ostium 1.5 times in sulcus length; ostium height 3.3 (2.6–3.3) times in ostium length.

Dentition. Premaxillaries and dentaries with small, pointed teeth in 3–4 irregular rows anteriorly, decreasing to 1–2 rows posteriorad. Teeth in outer rows somewhat longer. Vomer triangular with many small, close-set teeth. Palatines with several rows of small, close-set teeth. Two median basibranchial tooth patches, the anterior elongate and the posterior much smaller and circular.

Axial skeleton (from radiographs). Precaudal vertebrae 12 and caudal vertebrae 42 (42–45) and all neural and haemal spines pointed; first neural spine one third length of second spine, that is longer than the following spines; bases of neural spines more or less enlarged; parapophyses present on posterior 7–8 precaudal vertebrae; pleural ribs on vertebrae 3–11 (3–4 to 10–12); epipleural ribs on vertebrae 3–8.

Colour. Preserved fish (holotype [Figure 1A] and paratypes). Body mottled brown, abdomen silvery bluish, lateral line pale brown, rather indistinct; head pale brown with brown preopercular area behind eye, gill cover transparent, eyes bluish; ocellus spot dark brown, its horizontal diameter about orbit length, placed well behind a vertical line through anal-fin origin; dorsal and anal fins with pale- to dark-brown distal margins along posterior fifth to quarter of dorsal fin and posterior half to two-thirds of anal fin; margins becoming darker towards dark caudal-fin tip.

Etymology. The new species name honors the wife of the first author, Gloria Jansen Echevarria.

Distribution. Inner Gulf of Oman, NW Indian Ocean, at 272–320 m depth, and southern Arabian Gulf, United Arab Emirates, at 26 m depth.

Comparisons. *Neobythites gloriae* **n. sp**. differs from all congeners by the following combination of characters: a single ocellus placed on dorsal fin at mid-body, preopercular spines lacking, 11–13 developed gill rakers, head length 25.5–28.0 % SL, gill filament length 3.9–4.9 % SL, orbit length 19.5–23.5 % head length and 45–50 % upper-jaw length, and otolith sulcus length 3.4–3.7 % SL.

Neobythites gloriae **n. sp**. is most similar to *N. stefanovi*, sharing the following characters: dorsal fin with one ocellus, preopercular spine absent, pelvic fins ending anterior to anus, similar number of long rakers on anterior gill arch, eyes five times or less in head length, and similar otolith sulcus length. *Neobythites gloriae* differs from *N. stefanovi* having longer gill filaments (3.9–4.9 *vs.* 1.4–3.7 % SL) and a slightly smaller ocellus spot (spot covering 6–8 *vs*. 8–12 dorsal-fin rays). These two characters in combination with head length, orbit length, and ocellus-spot distance best distinguish *N. gloriae* from *N. steatiticus* and *N. steatiticus* from *N. stefanovi* (Figure 3; Tables 1–3).

Remarks. The description of *Neobythites gloriae* **n. sp**. is based on three former *N. stefanovi* paratypes from the inner Gulf of Oman (Nielsen & Uiblein 1993) and six specimens previously identified as *N. steatiticus* (Nielsen 1995). Apart from this earlier misidentified material, no additional specimens and no photographs of fresh fish were available for our study. The depth of 26 m reported for the single Arabian Gulf specimen (BMHN 1910.1.31.23), indicated as questionable by Nielsen (1995), is here confirmed based on original data recordings available from NHM.

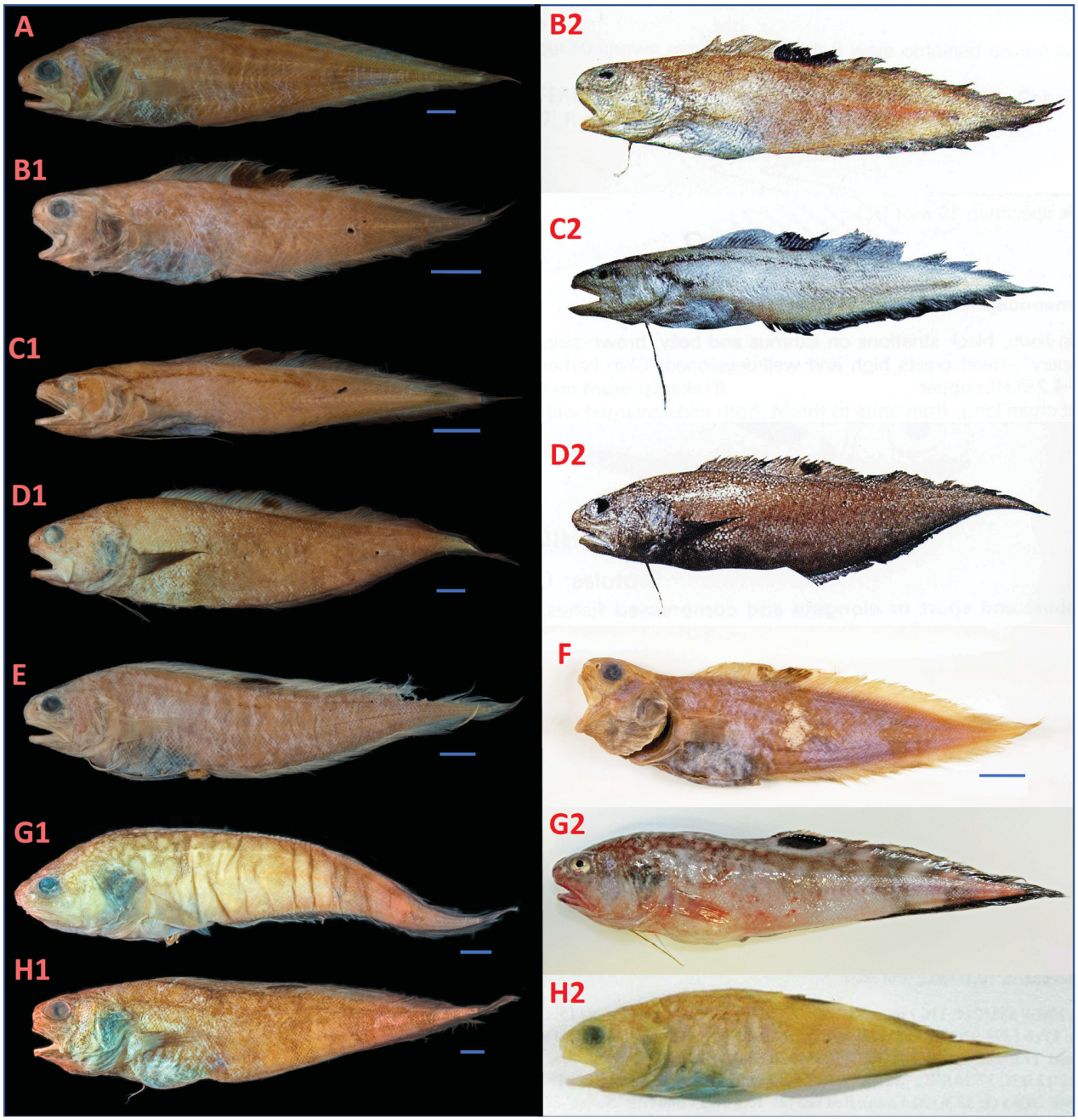

FIGURE 1. Indo-Pacific *Neobythites steatiticus* species group. All photographs at left side and F show preserved fishes; the remaining five photographs at right side show fresh fishes, photographed on board immediately after capture. A) *Neobythites gloriae* **n. sp**. USNM 309008, HT, 158 mm SL, inner Gulf of Oman; B) *N. lombokensis*, ZMUC P 77744, HT, 93 mm SL, SE off Lombok, preserved (B1) and fresh (B2; side reversed); C) *N. longipes*, ZMUC P77740, 98 mm SL, SE off Lombok, preserved (C1) and fresh (C2); D) *N. malayanus,* ZMUC P77742, 138 mm SL, SE off Lombok, preserved (D1) and fresh (D2); E) *N. malhaensis,* ZMUC P77840, PT, 135 mm SL, Saya de Malha bank, preserved; F) *N. meteori*, ZMH 5621, HT, 102 mm SL, off Sokotra, preserved; G) *N. steatiticus*, ZMUC P771752, 162 mm SL, off Myanmar, preserved (G1) and fresh (G2); H1) *N. stefanovi*, ZMUC P77841, PT, 198 mm SL, Gulf of Aden, preserved; H2) *N. stefanovi*, SMF 26785, 111 mm SL, Red Sea, fresh. Photographers: Oddgeir Alvheim (G2), Thomas Gloerfelt-Tarp (B2, C2, D2), Marcus Krag (A, B1, C1, D1, E, G1, H1), Ralph Thiel (F), Michael Türkay (H2). The blue bars indicate 1 cm length for the respective specimen.

Neobythites lombokensis n. sp.

(Figures 1–2, Tables 1, 3)

Neobythites meteori: Nielsen 2002: 57, fig. 47.
Neobythites sp. 2: Gloerfelt-Tarp & Kailola 1984: 88–89 (colour photo).

Holotype. ZMUC P77744 (93 mm SL), SE of Lombok Island, Indonesia, Eastern Indian Ocean, 8°58'S, 116°34' E, JETINDOFISH, sta. TGT 1717, bottom trawl, 150–280 m depth, July 1981.

Diagnosis. No spines on hind margin of preopercle; dorsal fin-rays 91; anal-fin rays 72; pectoral fin-rays 29; precaudal vertebrae 13; total vertebrae 53; pseudobranchial filaments 3; long gill rakers on anterior arch 7; head length 23.0 % SL; pelvic-fin length 13.0 % SL, pelvic fins not reaching beyond anus; orbit length 5.2 % SL, 22.5 % head length, and 53 % upper-jaw length; longest gill filament 2.2 % SL and 9.4 % head length; ocellus spot originating just behind at a vertical line through anus, the ocellus-spot distance being 43.0 % SL, and the spot covering 14 dorsal-fin rays; dorsal and anal fins not or only patchily pigmented; no vertical bars on body; otolith length 4.8 % SL, sulcus length 3.2 % SL, and ostium height 26.0 % sulcus length.

Description. Body rather elongate; complete lateral line running close to dorsal edge; head and body covered with cycloid scales; origin of dorsal fin well behind opercle; origin of anal fin slightly anterior to midpoint of fish; tip of pectoral fin well in front of anal fin origin; pelvic fins reaching halfway to origin of anal fin; blunt snout shorter than diameter of eye; upper jaw ends below posterior half of eye; anterior nostril with low rim and larger posterior nostril a mere hole; spine absent on posterior margin of preopercle; opercular spine strong and straight; anterior gill arch with 2–3 short and 1 long raker on upper branch, 1 long raker in angle and lower branch with 5 long and 6 short rakers; gill filaments twice the length of the long rakers; three distinct pseudobranchial filaments.

Otolith (Nielsen 2002, fig. 48B). Otolith oval, its height 1.5 times in its length; sulcus large, 1.5 times in otolith length; ostium length 1.7 times in sulcus length; ostium height 2.3 in ostium length.

Dentition. Premaxillaries and dentaries with irregular tooth rows, teeth on outer rows needle-like. Blunt teeth on subtriangular vomer and palatines. Two median basibranchial tooth patches, the anterior oblong and posterior smaller and circular.

Axial skeleton (from radiograph). Precaudal 13 and caudal vertebrae 40; tip of all neural and haemal spines thin and pointed; first neural spine half length of second spine; vertebrae 3–5 with slightly depressed neural spines; bases of vertebral spines 5–8 enlarged; parapophyses present on posterior seven precaudal vertebrae; pleural ribs on vertebrae 3–13; epipleural ribs not observed.

Colour (fresh fish; Figure 1B2). Body mottled pale-brown to brown, becoming paler posteriorly, abdomen whitish blue, lateral line indistinct; head brown dorsally and pale brown below and behind eye, gill cover pale; ocellus with large black spot, its horizontal diameter more than twice of orbit length, placed above anterior part of anal fin; posterior parts of dorsal fin and nearly entire anal fin patchily covered with pale-brown or brown pigment; no margin or band on anal fin.

Colour (preserved fish; holotype after 36 years of preservation, Figure 1B1). Body and head mottled brown, abdomen and eyes bluish, lateral line indistinct; gill cover transparent, inside of peritoneum with many black spots of various sizes; ocellus spot dark-brown; patchily distributed traces of brown pigmentation on dorsal and anal fins.

Etymology. Named after the type locality, SE off Lombok Island, southern Indonesia.

Distribution. Single type specimen trawled SE of Lombok Island, Indonesia, Eastern Indian Ocean, at 150–280 m depth.

Biology. The holotype is an unripe female caught between the lower shelf and upper continental slope. Its intestinal contents were unidentifiable except for parts of a small bivalve, suggesting a benthic lifestyle.

Comparisons. *Neobythites lombokensis* **n. sp**. differs from all congeners in the following combination of characters: a single ocellus placed on dorsal fin at mid-body, no preopercular spines, 7 developed gill rakers, head length 23.0 % SL, gill filament length 2.2 % SL, orbit length 22.5 % head length and 1.9 times in upper-jaw length, and otolith sulcus length 3.2 % SL.

Neobythites lombokensis seems most similar to *N. meteori*, sharing the following characters: dorsal fin with one ocellus, preopercular spine absent, pelvic fins ending anterior to anus, teeth needle-like and less than eight long rakers on anterior gill arch. *Neobythites lombokensis* differs from *N. meteori* in having a larger ocellus spot (spot covering 14 *vs.* 9 dorsal-fin rays), the ocellus placed above anterior part of anal fin (*vs.* above anus), and shorter gill filaments (9.4 *vs.*13.0 % head length), respectively.

Remarks. In a review of the genus *Neobythites* from the Western Indian Ocean, Nielsen (1995) described seven new species. One of these, *N. meteori*, was based on a specimen from off Socotra Is. Furthermore, a specimen from off Lombok was referred to *N. meteori* but not designated as a paratype because of a number of differences from the Socotra specimen. Subsequent examination of the Lombok specimen showed that it represented an undescribed species of *Neobythites*, which is herein described.

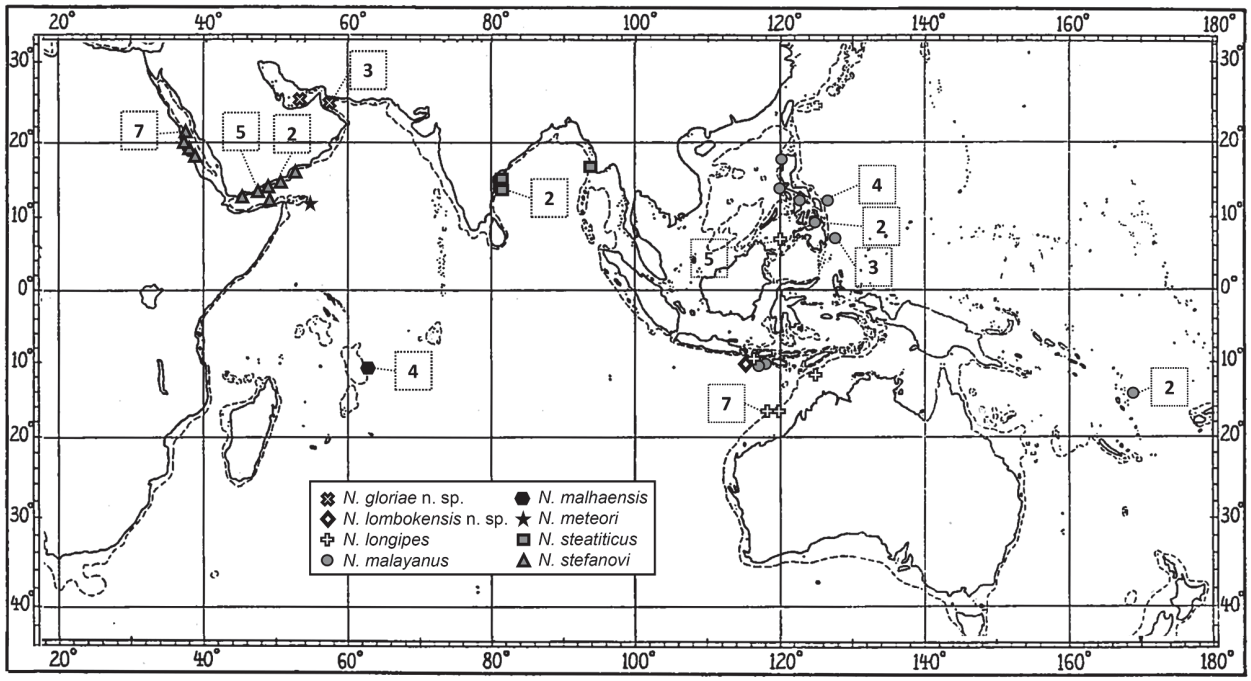

FIGURE 2. Distribution of studied specimens of *Neobythites*, with numbers indicating multiple sampling events.

Neobythites longipes Smith & Radcliffe, 1913

(Figures 1–2, Tables 1, 3)

Neobythites longipes: Nielsen 2002: 38, fig. 9.

Holotype. USNM 74126 (female, 276 mm SL), off Jolo Island, Philippines, Western Pacific, 06°02'00" N, 120°44'40" E, RV *Albatross*, st. 5550, bottom trawl, 472 m depth, 17 Sep. 1909.

Paratypes (n = 4, 90–207 mm SL). USNM 99070 (2 females, 165–242 mm SL), Philippines, 05°50' N, 120°31' E, RV *Albatross*, st. 5564, dredge, 432 m depth, 21 Sep. 1909; USNM 99073 (female, 90 mm SL), off Borneo, 04°52'45" N, 119°06'45" E, RV *Albatros*s, st. 5580, trawl, 296 m depth, 25 Sep. 1909; USNM 99091 (male, 207 mm SL), off Jolo, Philippines, 06°01'15" N, 120°44'20" E, RV *Albatross* st. 5549, trawl, 481 m depth, 17 Sep. 1909.

Non-types (n = 18, 98–301 mm SL). AMS I.22808-019 (female, 204 mm SL), 220 km N of Port Hedland, Western Australia, 17°59' S 118°17' E, RV *Soela*, st. SO 2/82/17–18, Engel trawl, 404–420 m depth, 3 Apr. 1982; AMS 1.22821-027 (female and male, 165–180 mm SL), 190 km northwest of Port Hedland, 18°16' S 118°12' E, RV *Soela*, st. SO 2/82/36–38, Engel trawl, 298–320 m depth, 10 Apr. 1982; AMS 1.23425-007 (2 males, 240–242 mm SL), northwest shelf, Western Australia, 18°46' S 117°00" E, RV *Soela*, st. SO 4/82/leg l, bottom trawl, 400 m depth, 1 Aug. 1982; CSIRO CA3916–19 (2 females and 2 males, 212–301 mm SL), off Port Hedland, Western Australia, 17°45.1' S 118°30.4' E, RV *Soela*, st. SO 183170, 442–460 m depth, 5 Feb. 1983; NTM S.12588-020 (female, 194 mm SL), off Rowley Shoals, Western Australia, 17°22' S 118°38' E, RV *Comac Endeavour*, st. WH 85-15, 430 m depth, 2 Nov. 1985; NTM S.12631-005 (female and 2 males, SL 226–264 mm SL), off Rowley Shoals, Western Australia, 17°37' S 118°40' E, RV *Comac Endeavour*, st. YW 85-21, 400 m depth, 4 Nov. 1985; NTM S.14378-001 (male, 245 mm SL), off Cartier Reef, Timor Sea, 13°7.89' S 123°12.65' E, RV *Lady Basten*, st. RW 96-30, 420 m, 19 June 1996; WAM P.28081-001 (female, 230 mm SL), 45 km northeast of Rowley Shoals, Western Australia, 17°44' S 120°5' E, 431–433 m depth, 20 Aug. 1983; WAM P.29125-001 (female, 163 mm SL), Rowley Shoals, Western Australia, 17°27' S 119°44' E, RV *Umitaka Maru*, trawl, 20 Dec. 1969; ZMUC P779 (female, 195 mm SL), off Jolo, Philippines, trawl, 463 m depth, 27 Mar. 1914; ZMUC P77740 (male, 98 mm SL), SE of Lombok, Indonesia, 8°58' S 116°34' E, JETINDOFISH TGT 1718, trawl, 150–280 m depth, July 1981.

Diagnosis. No spines on hind margin of preopercle; Dorsal fin-rays 96–103; anal-fin rays 72–76; pectoral fin-rays 27–30; precaudal vertebrae 13–14 (mostly 14); total vertebrae 57–60; pseudobranchial filaments 5–10; long

gill rakers on anterior arch 8–10; head length 22.5–25.5 % SL; pelvic-fin length 28.5–54 % SL, pelvic fins reaching well beyond anus; orbit length 3.9–5.0 % SL, 17.0–21.5 % head length, and 2.4–3.2 times in upper-jaw length; longest gill filament 1.3–2.7 % SL and 5.7–11.0 % head length; ocellus spot placed behind a vertical line through anus, the ocellus-spot distance being 42.0–53 % SL, and the spot covering 9–13 dorsal-fin rays; margins of posterior third of dorsal fin and posterior two thirds of anal fin dark pigmented; no vertical bars on body; otolith length 4.8–6.2 % SL, sulcus length 4.3–4.9 % SL, and ostium height 12.5–15.0 % sulcus length.

Distribution. From NW Australia to Philippines, at 150–481 m depth.

Remarks. The photograph of the fresh specimen (Figure 1C2) shows that the anterior two thirds of the lateral line and the entire margin of the anal fin to be black pigmented. The pigmentation of the dorsal fin as revealed by examination of the preserved specimen is however not evident in the fresh photograph. The overall bluish colour of the fresh specimen appears to us as artifact.

Neobythites malayanus Weber, 1913

(Figures 1–2, Tables 1, 3)

Neobythites malayanus: Nielsen 2002: 48, fig. 39.

Lectotype. ZMA 110.841 (male, 137 mm SL), off Sumbawa, Indonesia, Western Pacific, 8°19' S 117°41' E, RV *Siboga*, st. 312, trawl, 274 m depth, 14 Feb. 1900.

Paralectotypes. ZMA 110.841 (3 females and 1 male, 87–148 mm SL), same data as for the lectotype.

Non-types (n = 39, 76–199 mm SL). CAS 33088, male, 140 mm SL, Luzon Is., Philippines, 220–238 m depth, 19 Jul. 1966; CAS 56373 (male), 140 mm SL, southeast of Salomague Is., Philippines, 287–313 m depth, 20 Oct. 1960; MNHN 1995-915 (3 females, 84–159 mm SL), Vanuatu, West Pacific, 15°7'1" S, 166°55'12" E, MUSORSTOM 8, st. CP 1123, trawl, 262–352 m depth, 9 Oct. 1994; MNHN 1995-918 (female, 119 mm SL), and MNHN 1995-921 (male, 88 mm SL), Vanuatu, West Pacific, 15°6'58" S, 166°53'25" E, MUSORSTOM 8, st. CP 1121, trawl, 315–360 m depth, 9 Oct. 1994; USNM 99054 (6 females and 1 male, 114–129 mm SL), and ZMUC P771288–90 (3 females, 95–112 mm SL), Uanivan Is., Philippines, 6°50'45" N, 126°14'38" E, RV *Albatross*, st. 5241, trawl, 393 m depth, 14 May 1908; USNM 99127 (male, 199 mm SL), Bongo Is., Philippines, 7°21'45" N, 124°7'15" E, RV *Albatross*, st. 5256, trawl, 289 m depth, 22 May 1908; USNM 99128 (female and male, 76–128 mm SL), between Leyte and Cebu, Philippines, 11°10' N, 124°17'15" E, RV *Albatross*, st. 5403, trawl, 333 m depth, 16 Mar. 1909; USNM 99129 (2 females, 133–143 mm SL), between Cebu and Leyte, Philippines, 10°40'15" N, 124°15' E, RV *Albatross*, st. 5408, trawl, 291 m depth, 18 Mar. 1909; USNM 99130 (2 females, 2 males and 1 unsexed, 85–161 mm SL), Uanivan Is., Philippines, 6°50'55" N, 126°14'35" E, RV *Albatross*, st. 5243, trawl, 399 m depth, 14 Mar. 1908; USNM 99131 (female and male, 141–153 mm SL), Verde Is., Philippines, 13°44'36" N, 120°59'15" E, RV *Albatross*, st. 5266, trawl, 183 m depth, 8 June 1908; USNM 99132 (female and male, 132–143 mm SL), Pescador Is., Philippines, 9°44' N, 123°14'20" E, RV *Albatross*, st. 5188, trawl, 549 m, 1 Apr. 1908; USNM 99133 (2 females and 3 males, 131–173 mm SL), Pescadore Is., Philippines, 9°56'30" N, 123°15' E, RV *Albatross*, st. 5189, trawl, 549 m depth, 1 Apr. 1908; USNM 99138 (female, 154 mm SL), off Leyte, Philippines, 10°50' N, 124°26'18" E, RV *Albatross*, st. 5404, trawl, 348 m depth, 17 Mar. 1909; USNM 99150 (female and male, 119+–129 mm SL), between Leyte and Cebu, Philippines, 11°11'45" N, 124°15'45" E, RV *Albatross*, st. 5402, trawl, 344 m depth, 16 Mar. 1909; ZMUC P77741–42 (female and male, 138–171+ mm SL), Saleh Bay, SE of Lombok, 8°58’ S 116°34’ E, JETINDOFISH, st. TGT 1897, bottom trawl, 180–300 m depth, Jul. 1981.

Diagnosis. Indistinct or flat spine on hind margin of preopercle; dorsal fin-rays 90–96; anal-fin rays 74–79; pectoral fin-rays 26–28; precaudal vertebrae 12–13 (mostly 13); total vertebrae 54–57; pseudobranchial filaments 2–4; long gill rakers on anterior arch 8–11; head length 21.5–28.0 % SL; pelvic-fin length 13.5–20.0 % SL, pelvic fins not reaching anus; orbit length 4.2–5.6 % SL, 16.0–23.5 % head length, and 2.2–2.7 times in upper-jaw length; longest gill filament 1.3–3.8 % SL and 5.2–13.5 % head length; ocellus spot placed behind a vertical line through anus, the ocellus-spot distance being 42.5–52 % SL, and the spot covering 6–10 dorsal-fin rays; margins of posterior quarter of dorsal fin and posterior two thirds of anal fin dark pigmented; no vertical bars on body; otolith length 5.1–5.3 % SL, sulcus length 3.3–4.1 % SL, and ostium height 21.0–25.5 % sulcus length.

Distribution. Indonesia, Philippines, and Vanuatu, at 180–549 m depth.

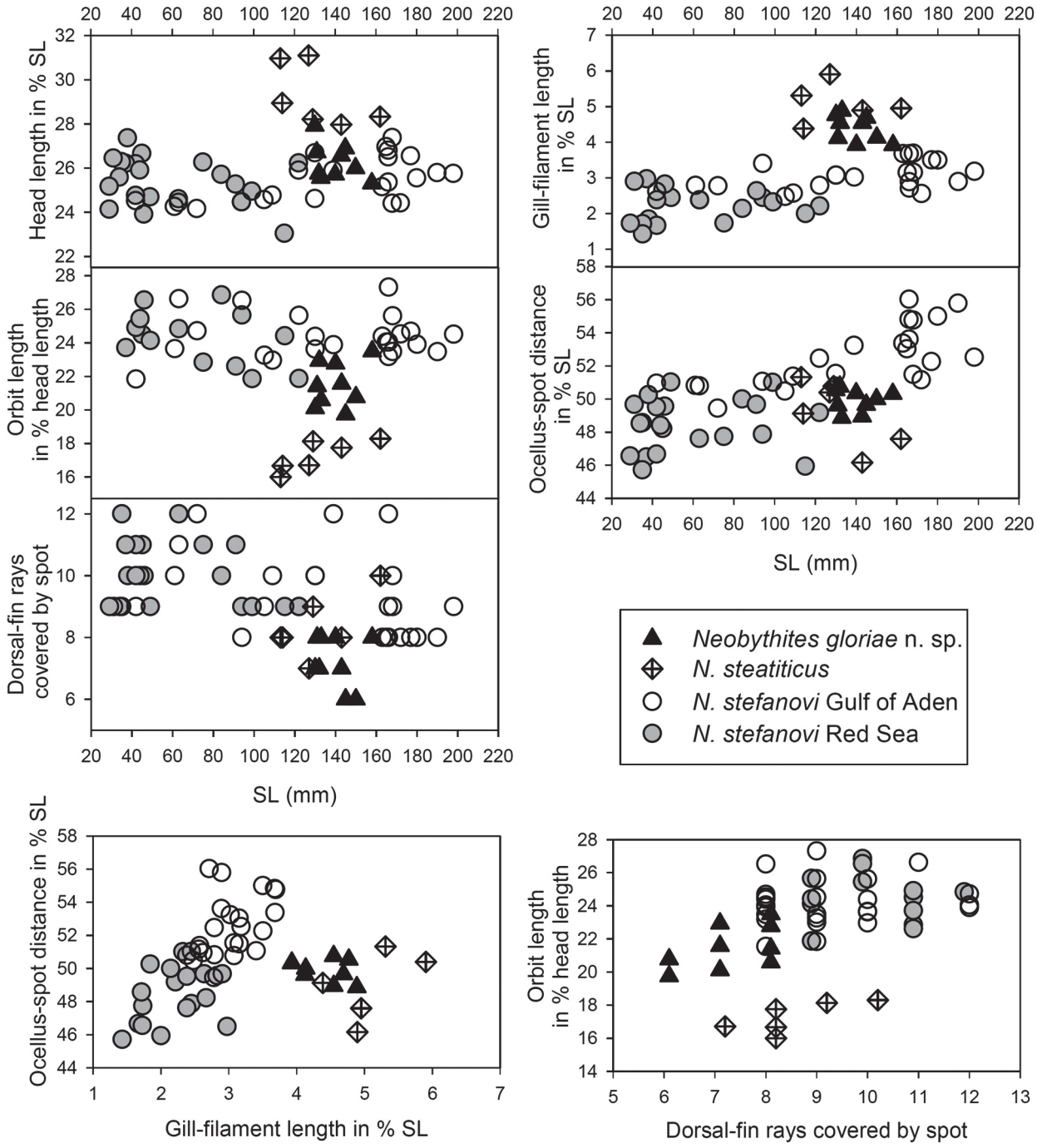

FIGURE 3. Relationships between SL, morphometric body-shape characters, and number of dorsal-fin rays covered by ocellus spot in *Neobythites gloriae* **n. sp.**, *N. steatiticus*, and two populations of *N. stefanovi*.

Neobythites malhaensis Nielsen, 1995

(Figures 1–2, Tables 1, 3)

Neobythites malhaensis Nielsen, 1995: 6, fig. 5a.

Holotype. ZM MGU P-18915 (male, 123 mm SL), Saya de Malha Bank, Western Indian Ocean, 11°02' S, 62°15' E, 250 m depth (probably same cruise as paratypes).

Paratypes (*n* = 3; 117–135 mm SL). Saya de Malha Bank, Western Indian Ocean: ZM MGU P-18916 (female,

117 mm SL), 11°08' S, 62°16' E, RV *Professor Mesiatzev*, trawl 476, 235–239 m depth, 7 Oct 1977; ZM MGU P-18917 (female, 132 mm SL), 11°06' S, 62°19' E, RV *Professor Mesiatzev*, trawl 478, 240 m depth, 7 Oct 1977; ZMUC P77840 (female, 135 mm SL), RV *Fiolent*, 1973 (no other data).

Diagnosis. Indistinct or flat spine on hind margin of preopercle; dorsal fin-rays 99–103; anal-fin rays 78–82; pectoral fin-rays 30; precaudal vertebrae 13; total vertebrae 57–59; pseudobranchial filaments 3–4; long gill rakers on anterior arch 12–13; head length 21.0–21.5 % SL; pelvic-fin length 12.5–13.0 % SL, pelvic fins not reaching anus; orbit length 4.1–4.9 % SL, 19.5–23.0 % head length, and 2.2–2.4 times in upper-jaw length; longest gill filament 1.6–1.9 % SL and 7.5–8.9 % head length; ocellus spot placed behind a vertical line through anus, the ocellus-spot distance being 42.5–45.5 % SL, and the spot covering 13 dorsal-fin rays; dorsal and anal fins not pigmented; one vertical, dark bar on body below ocellus spot; otolith length 5.2 % SL, sulcus length 3.8 % SL, and ostium height 21.5 % sulcus length.

Distribution. Saya de Malha Bank, off SE Seychelles, Western Indian Ocean, at 235–250 m depth.

Neobythites meteori Nielsen, 1995

(Figures 1–2, Tables 1, 3)

Neobythites meteori Nielsen,1995: 7, fig. 6a.
Neobythites unimaculatus: Kotthaus 1979: 13, fig. 462.

Holotype. ZMH 5621 (female, 102 mm SL), off southwestern Socotra Island, Yemen, NW Indian Ocean, 11°33.9' N, 52°54' E; RV *Meteor*, st. 102, Agassiz trawl; 175–337 m depth; 20 Dec. 1964.

Diagnosis. Flat process on hind margin of preopercle; dorsal fin-rays 91; anal-fin rays 75; pectoral fin-rays 27; precaudal vertebrae 13; total vertebrae 53; pseudobranchial filaments 3; long gill rakers on anterior arch 6; head length 22.0 % SL; pelvic-fin length 11.0 % SL, pelvic fins not reaching anus; orbit length 4.1–4.9 % SL, 22.0 % head length, and and 2.0 times in upper-jaw length; longest gill filament 2.8 % SL and 13.0 % head length; ocellus spot placed above anus, the ocellus-spot distance being 39.0 % SL, and the spot covering 9 dorsal-fin rays; dorsal and anal fins not pigmented; no vertical bars on body; otolith length 4.6 % SL.

Distribution. Off Sokotra Island, NW Indian Ocean, at 175–337 m depth.

Remarks. In his review, Nielsen (1995: 8) included a second specimen (from off Lombok) as *Neobythites meteori* without designated it as paratype. This specimen is described as *N. lombokensis* **n. sp**. in the current paper. A photo of the freshly caught specimen, later to become the holotype of *N. meteori*, shows no dark margins or bands on dorsal and anal fins (*cf*. Kotthaus 1979). Also, the otolith of the holotype of *N. meteori* turned out to be in bad condition allowing us only to measure otolith length and height.

Neobythites steatiticus Alcock, 1894

(Figures 1–3, Tables 1–3)

Neobythites steatiticus Alcock, 1894: 181, pl. IX
Neobythites steatiticus: Norman 1939: 76 (non *steatiticus*); Nielsen 1995: 11 and 2002: 84 (in part); Jawad 2014: 1(non *steatiticus).*

Holotype. ZSI 13435 (female, 129 mm SL), Bay of Bengal, NE Indian Ocean, 15°4'7" N, 80°25'7" E, RV *Investigator*, st. 137, Agassiz trawl, 234 m depth, 3 Mar. 1893.

Non-types (*n* = 5, 113–162 mm SL). BMNH 1895.1.3.3 (former ZSI 13477), (female, 143 mm SL), Bay of Bengal, 13°1'6" N, 80°36'56" E, RV *Investigator*, st. 170, Agassiz trawl, 193 m depth, 16 Feb. 1894; USNM 46756 (former ZSI 13475), (female, 113 mm SL), USNM 256238 (former ZSI 13474), (female, 127 mm SL), and BMNH 1895.1.3.4 (female, 114 mm SL), Bay of Bengal, 13°51'12" N, 80°28'12" E, RV *Investiga*tor, st. 162, Agassiz trawl, 261–450 m depth, 30 Jan. 1894; ZMUC P 771752 (unripe, 162 mm SL), off Myanmar, 16°27' N 93°57' E, RV *Dr. Fridtjof Nansen*, st. 42, bottom trawl, 274–277 m depth, 6 May 2015.

TABLE 1. Meristic, morphometric, and quantitative ocellus and otolith characters in eight *steatiticus*-group species. Clear differences from *Neobythites gloriae* n. sp. are indicated by bold italics.

	Neobythites gloriae n. sp.					*N. lombokensis* n. sp.		*N. longipes*			*N. malayanus*				*N. malhaensis*				*N. meteori*	*N. steatiticus*				*N. stefanovi*			
	HT	Min	Mean	Max	*n*	HT	Min	Mean	Max	*n*	Min	Mean	Max	*n*	Min	Mean	Max	*n*	HT	Min	Mean	Max	*n*	Min	Mean	Max	*n*
Standard length (SL, in mm)	158	130	140.2	158	9	93	90	212.3	301	23	76	128.1	199	43	117	126.8	135	4	102	113	131.3	162	6	29	98.3	198	45
Meristic characters																											
Dorsal-fin rays	93	90	91.2	93	9	91	***96***	***100.5***	***103***	23	90	93.2	96	23	***99***	***101.0***	***103***	4	91	88	91.2	94	6	89	91.6	95	39
Caudal-fin rays	8	8	8.0	8	6	***7***	8	8.0	8	22	8	8.0	8	20	8	8.0	8	4	***7***	8	8.0	8	5	8	8.0	8	28
Anal-fin rays	76	72	74.6	76	9	72	***79***	***82.4***	***87***	23	74	76.1	79	23	***78***	***79.8***	***82***	4	75	73	75.2	77	6	73	74.9	78	40
Pectoral-fin rays	25	24	25.7	27	9	***29***	27	28.5	30	17	26	26.8	28	13	***30***	***30.0***	***30***	4	27	24	25.7	27	6	24	24.9	26	31
Precaudal vertebrae	12	12	12.0	12	9	***13***	***13***	***13.9***	***14***	23	12	12.9	13	23	***13***	***13.0***	***13***	4	***13***	12	12.0	12	5	12	12.0	12	48
Total vertebrae	54	54	54.2	56	9	***53***	***57***	***58.3***	***60***	23	54	55.5	57	23	***57***	***57.8***	***59***	4	53	53	54.2	57	5	52	53.9	56	40
Pseudobranch filaments	3	3	3.2	4	9	3	***5***	***7.2***	***10***	19	2	2.9	4	34	3	3.3	4	4	3	2	2.7	3	6	2	4.1	6	29
Dorsal-fin origin above vertebra no.	4	4	4.4	5	9	5	5	5.0	6	22	5	5.5	6	23	***2***	***2.3***	***3***	4	5	4	4.4	5	5	4	4.3	5	47
Anal-fin origin below dorsal fin ray no.	19	18	19.3	21	9	21	19	21.1	22	23	17	19.2	21	23	***23***	***24.3***	***25***	4	20	19	20.2	21	5	17	19.3	21	44
Anal-fin origin below vertebra no.	15	15	15.0	15	9	***16***	15	16.0	17	23	15	15.1	16	23	15	15.0	15	4	15	14	14.8	15	5	14	14.5	16	46
Developed gill rakers	12	11	12.1	13	9	***7***	***8***	***8.9***	***10***	22	8	9.8	11	42	12	12.5	13	4	***6***	11	12.5	14	6	10	11.8	13	44
Total gill rakers	20	20	21.0	22	9	***15***	17	18.6	20	8	17	18.0	20	18	21	21.5	22	4	***12***	21	22.5	24	6	18	20.7	24	30
Morphometric characters (in % SL)																											
Head length (HL)	25.5	25.5	26.3	28.0	9	***23.0***	22.5	23.5	25.5	23	21.5	24.3	28.5	43	***21.0***	***21.4***	***21.5***	4	***22.0***	***28.0***	***29.3***	***31.0***	6	23.0	25.4	27.5	45
Body depth at anal-fin origin	20.5	17.5	19.0	20.5	9	19.0	***14.0***	***15.4***	***17.5***	22	16.5	18.9	20.0	21	17.0	17.7	19.0	4	19.0	17.5	18.4	20.5	6	15.5	18.8	22.0	45
Upper-jaw length	12.0	11.5	11.9	12.0	9	***9.7***	12.0	12.5	13.5	23	11.0	11.7	12.5	20	11.0	10.8	11.0	2	***9.8***	12.0	12.8	13.5	5	11.0	11.9	13.5	37
Orbit length	5.9	5.3	5.6	5.9	9	***5.2***	***3.9***	***4.4***	***5.0***	23	4.2	4.8	5.6	36	***4.1***	***4.5***	***4.9***	4	***4.9***	***4.8***	***5.0***	***5.2***	6	5.4	6.2	6.9	37
Preanal distance	38.5	38.5	40.9	42.0	8	***44.5***	41.0	43.7	48.5	22	39.0	42.9	47.0	20	36.5	38.3	40.0	4	***45.0***	40.0	42.9	46.0	6	37.5	41.1	45.0	38
Predorsal distance	25.5	24.5	25.7	27.0	8	26.0	23.0	25.4	28.5	23	24.0	26.7	29.5	42	20.0	20.4	20.5	4	24.5	24.5	26.9	28.5	6	24.0	26.3	28.5	38
Pelvic-fin to anal-fin origin distance	25.0	22.5	25.4	26.5	9	***30.0***	23.5	26.1	30.5	23	22.0	25.3	30.0	19	21.0	24.6	27.5	4	***26.5***	24.0	26.6	29.0	5	21.0	25.1	28.5	37

... ...continued on the next page

TABLE 1. (Continued)

	Neobythites gloriae n. sp.					*N. lombokensis* n. sp.	*N. longipes*				*N. malayanus*				*N. malhaensis*				*N. meteori*	*N. steatiticus*				*N. stefanovi*			
	HT	Min	Mean	Max	*n*	HT	Min	Mean	Max	*n*	Min	Mean	Max	*n*	Min	Mean	Max	*n*	HT	Min	Mean	Max	*n*	Min	Mean	Max	*n*
Pelvic-fin length	15.0	13.5	15.3	17.0	8	***13.0***	***28.5***	***36.5***	***54***	23	13.5	16.3	20.0	35	12.5	12.9	13.0	4	11.0	14.0	14.6	15.0	6	14.5	17.2	20.5	38
Gill-filament length	3.9	3.9	4.4	4.9	9	***2.2***	***1.3***	***1.8***	***2.7***	22	***1.3***	***2.1***	***3.8***	43	***1.6***	***1.7***	***1.9***	4	***2.8***	4.4	5.1	5.9	5	***1.4***	***2.7***	***3.7***	42
Ocellus-spot distance	50	49.0	49.9	51	9	***43.0***	42.0	48.1	53	23	42.5	47.9	52	42	***42.5***	***43.8***	***45.5***	4	***39.0***	46.0	49.2	51	6	45.5	50.6	56	44
Postorbital distance	16.0	15.0	16.3	17.5	9	***14.0***	12.5	13.7	15.5	22	13.0	15.0	17.5	28		***13.0***		1	***14.0***	17.0	18.5	19.0	4	13.5	15.4	17.5	37
Morphometric characters (in % HL)																											
Upper-jaw length	47.5	42.5	45.2	47.5	9	42.5	***48.0***	***53.0***	***57***	23	44.0	48.9	52	20	***50***	***50.6***	***51***	2	44.5	42.5	44.2	47.5	5	40.5	47.0	55	37
Orbit length	23.5	19.5	21.5	23.5	9	22.5	17.0	18.9	21.5	23	16.0	20.1	23.5	36	19.5	21.0	23.0	4	22.0	***16.0***	***17.3***	***18.5***	6	21.5	24.2	27.5	40
Gill-filament length	15.5	15.5	16.7	19.0	9	***9.4***	***5.7***	***7.6***	***11.0***	22	***5.2***	***8.6***	***13.5***	43	***7.5***	***8.1***	***8.9***	4	13.0	15.0	17.3	19.0	5	***5.4***	***10.7***	***16.0***	45
Postorbital distance	63	59	61.9	65	9	62	54	58.4	61	22	56	60.8	66	28		60		1	63	60	65.1	68	4	57	60.7	66	37
Ocellus meristic characters																											
Number of ocellus-spot rays	8	6	7.2	8	9	***14***	***9***	***10.4***	***13***	21	6	7.1	10	19		*13*		1	***9***	7	8.3	10	6	***8***	***9.6***	***12***	47
First dorsal-fin ray in spot	29	24	27,0	30	9	***18***	21	25,0	28	21	20	22,7	27	19		*23*		1	***17***	21	24,0	27	6	22	25,3	30	47
Central-most ray in spot	33	27	30.4	34	9	***25***	27	30.1	33	21	24	26.1	30	19		29		1	***21***	25	28.0	31	6	26	29.9	34	47
Vertical-scale rows covered by spot	1	0	0.3	1	9	0	0	0.0	0	21	0	0.0	0	19		1		1	0	0	0.0	0	4	0	1.2	4	38
Otolith characters (in % SL)																											
Otolith length	4.9	4.8	4.9	5.0	4	4.8	4.8	5.6	6.2	5	***5.1***	***5.2***	***5.3***	6		***5.2***		1	*4.6*	5.0	5.1	5.2	2	4.6	5.0	5.2	5
Otolith height	3.1	3.0	3.1	3.3	4	3.1	***2.1***	***2.6***	***2.9***	5	3.0	3.2	3.4	6		3.3		1	***2.6***	3.0	3.2	3.4	2	2.9	3.1	3.3	5
Sulcus length	3.7	3.4	3.5	3.7	4	3.2	***4.3***	***4.5***	***4.9***	5	3.3	3.7	4.1	6		***3.8***		1	-	3.6	3.7	3.7	2	3.4	3.7	4.1	5
Ostium length	2.5	2.3	2.4	2.5	4	***1.9***	***2.7***	***3.0***	***3.4***	5	2.1	2.4	2.7	6		2.5		1	-	2.3	2.4	2.5	2	2.3	2.5	2.6	5
Ostium height	0.8	0.7	0.8	0.9	4	0.8	0.5	0.6	0.7	5	0.8	0.8	0.9	6		0.8		1	-	0.8	0.8	0.9	2	0.7	0.9	1.1	5
Otolith characters (in % Sulcus Length)																											
Ostium height	21.0	21.0	22.5	26.5	4	26.0	***12.5***	***13.5***	***15.0***	5	21.0	22.7	25.5	6		21.5		1	-	21.0	22.8	24.5	2	20.0	23.4	28.5	6

TABLE 2. Meristic, morphometric, and quantitative ocellus characters in populations of *Neobythites steatiticus* and *N. stefanovi.*

	Neobythites steatiticus					*N. stefanovi*							
	Eastern Bay of Bengal	Western Bay of Bengal				Gulf of Aden				Red Sea			
		Min	Mean	Max	*n*	Min	Mean	Max	*n*	Min	Mean	Max	*n*
Standard Length (SL, in mm)	162	113	125.2	143	5	42	136.8	198	23	29	58.1	122	22
Meristic characters													
Dorsal-fin rays	94	88	90.6	93	5	89	91.7	94	23	89	91.4	95	16
Caudal-fin rays	8	8	8.0	8	4	8	8.0	8	18	8	8.0	8	10
Anal-fin rays	77	73	74.8	76	5	73	74.7	78	23	73	75.2	77	17
Pectoral-fin rays	25	24	25.8	27	5	24	24.7	26	22	25	25.4	26	9
Precaudal vertebrae	12	12	12.0	12	4	12	12.0	12	26	12	12.0	12	22
Total vertebrae	54	53	54.3	57	4	52	53.9	55	23	53	53.9	56	17
Pseudobranch filaments	3	2	2.6	3	5	3	4.2	6	21	2	3.9	5	8
Dorsal-fin origin above vertebra no.	4	4	4.5	5	4	4	4.3	5	26	4	4.2	5	21
Anal-fin origin below dorsal fin ray no.	21	19	20.0	21	4	17	19.7	21	26	18	18.8	20	18
Anal-fin origin below vertebra no.	15	14	14.8	15	4	14	14.8	16	26	14	14.1	15	20
Developed gill rakers	14	11	12.2	13	5	10	12.0	13	26	10	11.4	13	18
Total gill rakers	22	21	22.6	24	5	19	21.0	24	23	18	19.6	21	7
Morphometric characters (in % SL)													
Head length (HL)	28.5	28.0	29.4	31.0	5	24.0	25.4	27.5	23	23.0	25.5	27.5	22
Body depth at anal-fin origin	18.5	17.5	18.3	20.5	5	16.5	20.1	22.0	23	15.5	17.6	20.5	22
Upper-jaw length	13.5	12.0	12.6	13.5	4	11.0	11.6	12.5	22	11.0	12.4	13.5	15
Orbit length	5.2	4.8	5.0	5.2	5	5.4	6.2	6.9	23	5.5	6.1	6.9	14
Preanal distance	41.5	40.0	43.2	46.0	5	38.5	41.7	45.0	23	37.5	40.2	43.5	15
Predorsal distance	28.5	24.5	26.6	28.0	5	24.5	26.4	28.5	23	24.0	26.3	28.5	15
Pelvic-fin to anal-fin origin distance	25.0	24.0	27.0	29.0	4	23.5	25.4	27.5	22	21.0	24.7	28.5	15
Pelvic-fin length	15.0	14.0	14.6	15.0	5	14.5	17.1	20.0	22	15.0	17.3	20.5	16
Gill-filament length	5.0	4.4	5.1	5.9	4	2.4	3.0	3.7	23	1.4	2.2	3.0	19
Ocellus-spot distance	47.5	46.0	49.6	51	5	49.5	52.5	56	23	45.5	48.5	51	21
Postorbital distance	19.0	17.0	18.4	19.0	3	14.5	15.4	17.0	22	13.5	15.4	17.5	15
Morphometric characters (in % HL)													
Upper-jaw length	47.5	42.5	43.4	44.5	4	40.5	45.8	50	22	44.0	48.9	55	15
Orbit length	18.5	16.0	17.1	18.0	5	21.5	24.2	27.5	26	22.0	24.3	27.0	14
Gill-filament length	17.5	15.0	17.2	19.0	4	9.7	12.1	16.0	26	5.4	8.8	12.0	19
Postorbital distance	66	60	64.6	68	3	57	60.8	63	22	57	60.5	66	15
Ocellus meristic characters													
Number of ocellus-spot rays	10	7	8.0	9	5	8	9.3	12	26	9	10.0	12	21
First dorsal-fin ray in spot	22	21	24.4	27	5	23	26.5	30	26	22	23.9	27	21
Central-most ray in spot	27	25	28.2	31	5	27	31.0	34	26	26	28.5	31	21
Vertical-scale rows covered by spot	0	0	0.0	0	3	0	0.5	3	23	0	2.3	4	15

Tentatively referred. Tuticorin Research Center, Tamil Nadu, India, 2, 178–180 mm SL, Gulf of Manar, 8°44'46" N, 78°37'24" E, bottom trawl, 200–250 m depth, 22 Feb. 2010.

Diagnosis. (Tentatively referred specimens from Gulf of Mannar not included). 0–1 weak spine on hind margin of preopercle; dorsal fin-rays 88–94; anal-fin rays 73–77; pectoral fin-rays 24–27; precaudal vertebrae 12; total vertebrae 53–57; pseudobranchial filaments 2–3; long gill rakers on anterior arch 11–14; head length 28.0–31.0 % SL; pelvic-fin length 14.0–15.0 % SL, pelvic fins not reaching anus; orbit length 4.8–5.2 % SL, 16.0–18.5 % head length, and 2.3–2.8 times in upper-jaw length; longest gill filament 4.4–5.9 % SL and 15.0–19.0 % head length; ocellus spot placed well behind a vertical line through anus, the ocellus-spot distance being 46.0–51.5 % SL, and the spot covering 7–10 dorsal-fin rays; median part of anal-fin dark and distal and proximal parts light; dorsal fin mostly unpigmented; up to 6 broad, rather distinct dark vertical bars on body; otolith length 5.0–5.2 % SL, sulcus length 3.6–3.7 % SL, and ostium height 21.0–24.5 % sulcus length.

Distribution. Known from both sides of the Bay of Bengal, NE Indian Ocean, at 193–450 m depth.

Remarks. According to Alcock (1899) ZSI held the holotype and eight additional specimens, five of which are here examined. Kannan *et al.* (2013:1) published the first record in Indian waters of *Neobythites stefanovi.* However, the illustration shows more resemblance to *N. steatiticus* so we treat it here as tentatively referred to *N. steatiticus.* Some specimens that in earlier literature were referred to *N. steatiticus* are now transferred to other *Neobythites* species: Norman (1939: 76) referred three specimens to *N. steatiticus*. Two of these from the Gulf of Aden have been transferred to *N. stefanovi* and one from off Zanzibar to *N. kenyaensis* Nielsen, 1995. Nielsen (1995: 11 and 2002: 84) mentioned six specimens caught in the Gulf of Oman (all from BMNH) which now are referred to *N. gloriae* **n. sp**.

The specimen collected during the RV *Dr. Fridtjov Nansen* cruise off Myanmar represents the first record from the eastern Bay of Bengal. The photo taken on board immediately after capture is the first to document fresh colour of the species (Figure 1G2). It reveals considerable similarity with ocellus, fin and body colour patterns shown in two different drawings of *N. steatiticus* provided by Alcock (1893, 1898) based on shortly preserved specimens. The slightly larger ocellus of the specimen from off Myanmar (10 *vs.* 7–9 dorsal-fin rays covered by the spot) contributes to the distinction of *N. steatiticus* from *N. gloriae* **n. sp**. (Figure 3, Tables 2–3).

Jawad (2014) reported *N. steatiticus* from the Arabian Gulf off Iraq. However, judging from the dark blotch near the origin of the dorsal fin (*vs.* no anterior blotch), the position of the mid-body ocellus above or in front of anus (*vs.* well behind anus), and head length (21.5 *vs.* 28.0–31.0 % SL) this is neither a *N. steatiticus* nor a member of the *steatiticus* species group.

Neobythites stefanovi Nielsen & Uiblein, 1993

(Figures 1–3, Tables 1–3)

Neobythites stefanovi Nielsen & Uiblein, 1993: 110.

Neobythites stefanovi: Nielsen 1995: page 15; Nielsen 2002: 86 (in part); Kannan *et al.* 2013: 1 (here tentatively referred to *N. steatiticus*).

Holotype. ZM MGU P18923 (male, 166 mm SL), Gulf of Aden, NW Indian Ocean, 14°48.8' N, 51°16.1' E, RV *Dmitry Stefanov* cr. 3*,* trawl 91, 245–335 m depth; 5 Jan. 1989.

Paratypes (*n* = 25, 42–195+ mm SL). BMHN 1939.5.24.1437 (female, 195+ mm SL), Gulf of Aden, 13°14.4' N, 46°14.2' E, RV *John Murray,* st. 35, otter trawl, 457–549 m depth, 16 Oct. 1933; SMF 26427–29 (2 females, 2 males, and 4 unsexed; 42–122 mm SL), Gulf of Aden, 12°16' N, 44°09.5' E, RV *Meteor*, MeS-287, beam-trawl; 472–479 m depth, 16 Mar. 1987; USNM 302930, female, 179 + mm SL, Gulf of Aden, 11°10.6'N, 48°11.2'E, RV *Beinta,* cr. 19, haul 32, 351–384 m depth, 19 Feb. 1987; ZM MGU P-18924 (female, 139 mm SL), Gulf of Aden, 13°15.5' N, 46°14.3' E, RV *Akademik Petrovsky* cr. 14, st. 34, 250–300 m depth, 26 Sep. 1983; ZM MGU P-18925 (male*,* 130 mm SL), Gulf of Aden, 15°59.8' N, 52°23.9' E, RV *Dmitry Stefanov* cr.3, trawl 9, 80–110 m depth, 19 Nov. 1988; ZM MGU P-18926 (female, 162+ mm SL), Gulf of Aden 14°49.2' N, 50°35.1' E, RV *Dmitry Stefanov,* trawl 78, 375 m depth, 3 Feb. 1989; ZM MGU P-18927 (female, 168 mm SL), same data as holotype; ZM MGU P-18928 (female, 180 mm SL), Gulf of Aden, 13°13.7' N, 45°41.8' E, RV *Dmitry Stefanov,* cr.5, trawl 48, 355–365 m depth, 22 Nov. 1989; ZM MGU P-18929 (female, 190 mm SL), and ZMUC P77841 (female, 198 mm SL), Gulf of Aden, 13°09' N, 45°41' E, RV *Dmitry Stefanov,* trawl 51; 460 m; 24 Nov. 1989; ZM MGU P-18930 (female and

male, 165–179 mm SL), and ZMUC P77842 (male, 168 mm SL), Gulf of Aden, 13°25.1' N 47°14.S' E, RV *Dmitry Stefanov,* trawl 68, 367 m depth, 28 Nov. 1989; ZM MGU P 18931 (female, male, and unsexed, 130–172 mm SL), and ZMUC P77843–44 (male and female, 163–166 mm SL), Gulf of Aden, RV *Dmitry Stefanov,* 1989.

Non-types (*n* = 22, 29–122 mm SL). SMF 26430 (female, 122 mm SL), Red Sea, 18°35.3' N, 39°03.5' E, RV *Meteor,* MeS-171, beam trawl, 434–469 m depth, 23 Feb. 1987; SMF 26431 and 26434 (3 unsexed, 45–94 mm SL), Red Sea, 19°18.2' N, 38°15.5' E, RV *Meteor,* MeS-194, beam trawl, 537–681 m depth, 28 Feb. 1987; SMF 26432 (2 unsexed, 75–84 mm SL), Red Sea, 22°05' N, 37°09.3' E, RV *Meteor,* MeS-96, beam trawl, 600 m depth, 9 Feb. 1987; SMF 26433 (2 unsexed, 44–99 mm SL), Red Sea, 19°44.5' N, 37°40.2' E, RV *Meteor,* MeS-148, beam trawl, 517–583 m depth, 20 Feb. 1987; SMF 26435 and 26440 (2 unsexed, 49–31 mm SL), Red Sea, 21°28.97' N, 38°15.55' E, RV *Valdivia,* st. 111 TA, closing trawl, 740–785 m depth, 12 Apr. 1979; SMF 26436 and 26441 (3 unsexed, 29–46 mm SL), Red Sea, 21°26.5' N, 38°38.3' E, RV *Valdivia,* st. 121 TA, closing trawl, 779–801 m depth, 15 Apr. 1979; SMF 26437 and 26785 (2 unsexed, 63–115 mm SL), Red Sea, 20°94.9' N, 37°26.1' E; RV *Sonne* 35 TA, c1osing trawl, 490–588 m, 17 Oct. 1977; SMF 26438 (42 mm SL), Red Sea, 21°10.8' N, 37°34.0' E, RV *Sonne* 27 TA, closing trawl, 733–757 m depth, 16 Oct. 1977; SMF 26439 (38 mm SL), Red Sea, 21°12.0' N, 37°26.8' E, RV *Sonne*, 25 TA, closing trawl, 724–747 m depth, 15 Oct. 1977; SMF 26442 (5 unsexed, 29–42 mm SL), Red Sea, 21°33' N, 38°21' E, RV *Valdivia*, 99 TA, closing trawl, 753–804 m depth, 9 Apr. 1979.

Diagnosis. No spines on hind margin of preopercle; dorsal fin-rays 89–95; anal-fin rays 73–78; pectoral fin-rays 24–26; precaudal vertebrae 12; total vertebrae 52–56; pseudobranchial filaments 2–6; long gill rakers on anterior arch 10–13; head length 23.0–27.5 % SL; pelvic-fin length 14.5–20.5 % SL, pelvic fins not reaching anus; orbit length 5.4–6.9 % SL, 21.5–27.5 % head length, and 1.7–2.3 times in upper-jaw length; longest gill filament 1.4–3.7 % SL and 5.4–16.0 % head length; ocellus spot placed well behind a vertical line through anus, the ocellus-spot distance being 45.5–56 % SL, and the spot covering 8–12 dorsal-fin rays; dorsal and anal fins with dark margins throughout; no vertical bars on body; otolith length 4.6–5.2 % SL, sulcus length 3.4–4.1 % SL, and ostium height 20.0–28.5 % sulcus length.

Distribution. Gulf of Aden, NW Indian Ocean, at 80-549 m depth and Red Sea, 434–804 m depth.

Remarks. Kannan *et al*. (2013) reported on two specimens of *N. stefanovi* from Gulf of Manar, Tamil Nadu (NW Indian Ocean). After inspection of the photo and some of the data provided by Kannan *et al.* (2013), we assume that these specimens should be treated as tentatively referred to *N. steatiticus.*

Uiblein (1995) reported considerable differences between the populations of the Red Sea and the Gulf of Aden based on quantitative studies of meristic, morphometric and ocellus characters. Those differences were however only statistically detectable and did not support the erection of a distinct taxon in the Red Sea. We have reconsidered these earlier findings when examining the differentiation degree among the three rather similar species *N. gloriae* **n. sp.**, *N. steatiticus*, and *N. stefanovi*. While these species can be well separated by five diagnostic characters (singly or in combination), the two *N. stefanovi* populations clearly overlap with each other in those as well as in all other characters studied (Figure 3, Tables 2–3).

TABLE 3. Distribution of selected meristic characters in the *steatiticus*-species group, with data for the two populations of *Neobythites stefanovi*.

	Pectoral-fin rays							Pre-caudal vertebrae		
Species or population	24	25	26	27	28	29	30	12	13	14
N. gloriae n. sp.	1	3	3	2				9		
N. lombokensis n. sp.						1			1	
N. longipes				2	7	6	2		3	20
N. malayanus			3	9	1			2	21	
N. malhaensis							4		4	
N. meteori				1					1	
N. steatiticus	1	1	3	1				5		
N. stefanovi, Gulf of Aden	9	10	3					26		
N. stefanovi, Red Sea		5	4					22		

TABLE 3. (Continued)

Species or population	Developed gill rakers									Number of ocellus-spot rays								
	6	7	8	9	10	11	12	13	14	6	7	8	9	10	11	12	13	14
N. gloriae n. sp.						2	4	3		2	3	4						
N. lombokensis n. sp.		1																1
N. longipes			3	18	1								5	9	1	5	1	
N. malayanus			2	10	25	5				6	8	3	1	1				
N. malhaensis							2	2									1	
N. meteori	1												1					
N. steatiticus						1	2	2	1		1	3	1	1				
N. stefanovi, Gulf of Aden					1	5	13	7				9	7	6	1	3		
N. stefanovi, Red Sea					1	9	7	1					9	5	5	2		

Key to the Indo-Pacific *Neobythites steatiticus*-group species

1a Pelvic fins reach beyond anus, orbit length 31.5–41.5 % upper-jaw length . . . . . *Neobythites longipes* (Philippines to NW Australia)

1b Pelvic fins not reaching beyond anus, orbit length 35.5–59 % upper-jaw length 2

2a Anterior gill arch with 6–7 long rakers; anal fin without dark margin or band 3

2b Anterior gill arch with 8–15 long rakers; anal fin with or without dark margin or band 4

3a Ocellus short, placed above anus with ocellus spot covering 9 dorsal-fin rays; longest gill filament 13.0 % head length . . . . . *N. meteori* (off Sokotra Id, NW Indian Ocean)

3b Ocellus long, placed above anterior part of anal fin with ocellus spot covering 14 dorsal-fin rays; longest gill filament 9.4 % head length . . . . . *N. lombokensis* **n. sp**. (off Lombok, Eastern Indian Ocean)

4a Vertical, dark bar below ocellus spot; dorsal and anal fins without dark margin or band, head length 21.0–21.5 % SL . . . . . *N. malhaensis* (Saya de Malha Bank, Western Indian Ocean)

4b None to a few indistinct, vertical, dark bars on body; dorsal and/or anal fin with dark margin or band, head length 21.5–31.0 % SL 5

5a Median part of anal fin dark and distal and proximal parts light; head length 28.0–31.0 % SL; longest gill filament 4.4–5.9 % SL . . . . . *N. steatiticus* (Bay of Bengal, NE Indian Ocean)

5b Distal part of dorsal and anal fins dark and proximal part light; head length 21.5–28.5 % SL; longest gill filament 1.3–4.9 % SL 6

6a Developed gill rakers 8–11 (mostly 9 or 10); orbit length 4.2–5.6 % SL and 37.0–45.5% upper-jaw length; precaudal vertebrae 13 (rarely 12). . . . . *N. malayanus* (Philippines, Indonesia)

6b Developed gill rakers 10–13 (mostly 11–13); orbit length 5.3–6.9 % SL and 43.5–59 % times in upper jaw length; precaudal vertebrae 12 7

7a 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)

7b Longest gill filaments 3.9–4.9 % SL; dorsal-fin rays in ocellus spot 6–8 . . . . . *N. gloriae* **n. sp**. (Arabian Gulf and inner Gulf of Oman, NW Indian Ocean)

Discussion

Neobythites consists now of 54 valid species, 38 of which have been described since 1990. Most of the recent descriptions were published in the revision of Indo-Pacific *Neobythites* species by Nielsen (2002) or in the decade before, and only four new species have been described after 2002. The current review was strongly motivated by the recent collection of a *N. steatiticus* specimen in a previously unreported area (Eastern Bay of Bengal), which showed slight deviations in several characters and hence required detailed taxonomic study. Similarly, the collection of several *Neobythites* specimens off the Brazilian slope resulted in a regional review of ocellus-bearing species of the West Atlantic with description of a new species (Nielsen *et al.* 2009). With more *Neobythites* specimens becoming available through sampling efforts in yet insufficiently explored areas, discovery of additional new species or new distribution records (e.g., Nielsen & Uiblein 2014) can be expected.

Much of the diversity among *Neobythites* spp. is related to colour patterns, in particular in the form of ocelli on the dorsal fin (Uiblein & Nielsen 2005). There are now 25 ocellus-bearing species in this genus, of which 12 species have a single ocellus, nine of them belonging to the *steatiticus* spp. group. Apart from the ocellus-bearing species, there are nine other species which have spots, but without the contrasting white ring on the dorsal fin and many of the ocellus- and spot-bearing species have vertical bars on the body (Uiblein & Nielsen 2005). Several of the species with or without ocelli or spots have dark margins or bands on the dorsal and anal fins (Uiblein & Nielsen 2005). These patterns are not always well documented and some of the very few available photographs of fresh specimens are of rather poor quality. Additional colour patterns may exist that have yet remained undetected. For many *Neobythites* species only specimens in preserved condition have been available so far. Clearly, more detailed documentation and associated research of the colour of fresh *Neobythites* species is required. The same is required for *N. gloriae* **n. sp**.

Ocelli in *Neobythites* species are usually well retained in preserved specimens. The size and form of the ocellus spot does not considerably change in preservative, thus allowing to study all available museum specimens comparatively regarding ocellus variation and related questions. In a comprehensive study of colour pattern in *Neobythites* species with special focus on ocellus variation and function we found that species with ocelli tend to occur shallower than species without ocelli and singe-ocellus bearing species occur particularly shallow (Uiblein & Nielsen 2005). Further evidence for the latter finding is the very shallow occurrence of N. gloriae n. sp. at 26 m depth in the Arabian Gulf which we have reconfirmed in the present study. This is the new minimum depth record for the entire genus. So far, the minimum verified depth reported for any *Neobythites* species was 67 m for *N. nigriventris* Nielsen, 2002, a single-ocellus bearing species from New South Wales (Uiblein & Nielsen 2005).

Another important finding of our earlier study was that co-occurring, ocellus-bearing *Neobythites* species often show divergence in size, position or number of ocelli (Uiblein & Nielsen 2005). The three *steatiticus*-group species *N. lombokensis* **n. sp**., *N. longipes*, and *N. malayanus* occur in sympatry off SE Lombok where they have been collected during the JETINDOFISH cruise within the same area (Gloerfelt-Tarpa & Kailola 1984). Figure 1B–D shows photographs of these specimens taken immediately after capture and in preserved condition 36 years after collection. Irrespective of being fresh or preserved, the considerable difference in ocellus size among these specimens can be clearly recognized, providing additional evidence to the findings on ocellus feature divergence in sympatry.

According to Uiblein & Nielsen (2005) the shallow occurrence of single-ocellus bearing species and the divergence in ocellus characteristics in sympatry point to two possible ecological functions of ocelli, i.e. antipredator function and species recognition. Predation risk increases at shallower depths and single ocellus-bearing species may be able to better cope with this risk than species with more or no ocelli. Sudden presentation of a large single eye-resembling ocellus by e.g. erecting the dorsal fin during encounters with visually hunting predators may serve to deter the latter or to divert their attacks to less vital part of the body such as the dorsal fin (instead of e.g. the head). The other function of conspicuous ocelli may be to signal con- or heterospecificity during encounters facilitating avoidance of interspecific interactions and thus contributing to save energy and reduce hybridization risk. Certainly, an increase of the number of ocelli as realized by several *Neobythites* may be particularly effective for species recognition, but would probably not contribute to deter or distract predators the same way as single large eye mimicry would do. Another possible option realized in this genus is to have no ocelli at all. This may contribute to increase overall crypticity especially at greater depths under reduced light conditions. The occurrence of bars and dark fin margins in several species may reflect still other adaptations. We are only at the very start of trying to understand the ecological backgrounds and evolutionary pathways towards the stunning diversity of *Neobythites*.

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