

Shallow-water zoantharians (Cnidaria, Hexacorallia) from the Central Indo-Pacific

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Abstract

Despite the Central Indo-Pacific (CIP) and the Indonesian Archipelago being a well-known region of coral reef biodiversity, particularly in the ‘Coral Triangle’, little published information is available on its zoantharians (Cnidaria: Hexacorallia: Zoantharia). In order to provide a basis for future research on the Indo-Pacific zoantharian fauna and facilitate comparisons between more well-studied regions such as Japan and the Great Barrier Reef, this report deals with CIP zoantharian specimens in the Naturalis collection in Leiden, the Netherlands; 106 specimens were placed into 24 morpho-species and were supplemented with 88 in situ photographic records from Indonesia, the Philippines, and Papua New Guinea. At least nine morpho-species are likely to be undescribed species, indicating that the region needs more research in order to properly understand zoantharian diversity within the CIP. The Naturalis’ zoantharian specimens are listed by species, as well as all relevant collection information, and in situ images are provided to aid in future studies on zoantharians in the CIP.

Keywords

Zoantharians, Indonesia, Indo-Pacific, biodiversity, coral reef, benthos

Introduction

Zoantharians (Cnidaria: Anthozoa: Hexacorallia: Zoantharia) are a common component of benthos in subtropical and tropical coral reef systems, with many zooxanthellate species found in shallow waters of both the Atlantic and Indo-Pacific Oceans. Nevertheless, common understanding of zoantharian species diversity is relatively poor when compared to the hard corals (Scleractinia). This lack of knowledge is due to a variety of reasons, including (1) high levels of intraspecific morphological variation hindering reliable identification (Burnett et al. 1997, Reimer et al. 2004), (2) problems in performing histological examinations owing to sand being incorporated in the body walls of many zoantharian species (Reimer et al. 2010), and (3) a confused taxonomic history as different researchers tried to properly classify and understand zoantharian diversity (Burnett et al. 1997, Reimer et al. 2004, Sinniger et al. 2005).

Despite these problems, an understanding of zoantharian diversity and their corresponding taxonomy have slowly become clearer as molecular techniques have been implemented into zoantharian research. The first molecular works of Burnett and co-workers (Burnett et al. 1994, 1995, 1997) combined with the ecological and descriptive works of Ryland (Ryland and Lancaster 2003, 2004) have led to more recent papers dealing with the molecular phylogeny of zoantharians (Reimer et al. 2004, 2012b, Sinniger et al. 2005, Swain 2010), resulting in a reassessment of zoantharian taxonomy (Fujii and Reimer 2011, 2013, Sinniger et al. 2013). Consequently, zoantharians are now perhaps the hexacorallian order for which the taxonomy most accurately reflects molecular phylogenetic understanding. However, whereas zoantharian supraspecific taxonomy and diversity is increasingly well understood, many problems remain at the species level (Reimer et al. 2007b), and total species diversity of zoantharians is still poorly known (Appeltans et al. 2012).

Recent work on zoantharians has focused on many regions of the Indo-Pacific, including Japan (Reimer 2010), Singapore (Reimer and Todd 2009), New Caledonia (Sinniger 2006), the Great Barrier Reef (Burnett et al. 1997, Reimer et al. 2011a) and Palau (Reimer et al. 2014a). In the center between these regions lies the central Indo-Pacific “Coral Triangle” (Hoeksema 2007), including parts or all of Malaysia, Indonesia, Brunei, the Philippines, and Papua New Guinea, the Solomons, and Timor Leste. This region is believed to harbor the highest species diversity in hard corals of the order Scleractinia (Hoeksema 2007, Veron et al. 2009, 2011), and it is believed that other coral reef organisms likely have similar diversity patterns (Roberts et al. 2002). Despite this, shallow-water zoantharian species within the Coral Triangle have only briefly been reported on in scientific literature and only a few publications exist (e.g. Den Hartog 1997, Sinniger et al. 2005, Di Camillo et al. 2010), and most information is made up of photographs in aquarium handbooks (Fosså and Nilsen 1998) and field guides (Colin and Arneson 1995, Gosliner et al. 1996, Erhardt and Knop 2005). Therefore, efforts to compare the regional zoantharian fauna of the Indo-Pacific are hampered by this almost complete lack of published scientific distribution information. Basic data on zoantharians from the Coral Triangle, such as species lists and

distribution records, are critical to achieve a comprehensive understanding of Indo-Pacific zoantharian diversity.

The present study addresses this lack of Central Indo-Pacific (CIP) zoantharian data via examinations of specimen collections housed in Naturalis Biodiversity Center, Leiden, the Netherlands: RMNH (the former Rijksmuseum van Natuurlijke Historie) and ZMA (the former Zoologisch Museum van Amsterdam). These zoantharian collections are partly based on specimens from numerous surveys in Indonesia dating from the Snellius Expedition (1929–1930) to a recent Marine Biodiversity Workshop in Lembeh Strait (2012), with the large majority of these specimens collected from coral reef environments. Despite the presence of these large and scientifically valuable collections, no previous effort has been made to comprehensively catalogue or examine these historical collections for over 80 years, which could also serve as base-line material for studies on biotic change (Hoeksema et al. 2011). Here, for the first time, we report on the zoantharian specimens from Indonesia housed at Naturalis, and list shallow water species of the CIP, including specimen collection information. Our records are further enhanced by numerous *in situ* images from more recent fieldwork in Indonesia taken by the last author starting with the Snellius–II Expedition (1984–1985). Finally, we discuss the shallow water zoantharian diversity of CIP in relation to information from surrounding regions, and make recommendations for future zoantharian research in the region.

Materials and methods

Specimen collection

Zoantharian specimens from the Naturalis collections in Leiden (RMNH + ZMA) were collected primarily from expeditions to the Indonesia region, starting with the Snellius Expedition (1929–1930). Our examinations showed 22 regions in which either specimens or photographic records were present. All specimen/record localities are shown in Figure 1 with location and reference details in Table 1.

Regions (numbers also referred to in species notes and in distributional maps, with names used hereafter in bold, and with representative publications included):

1. **West Sumatra**, Indonesia. Fieldwork by B.W. Hoeksema in collaboration with Dr. A. Kunzmann, Bung Hatta University, Padang, West Sumatra, in 1996–1997.
2. **Southwest Java**, Indonesia. Collections from Teluk Pelabuhan Ratu by Dr. P.H. van Doesburg, RMNH, in 1977.
3. Thousand Islands, off Jakarta, Java Sea, **northwest Java**, Indonesia. Expedition organized by the Research Center for Oceanography (RCO–LIPI) and Naturalis in 2005 (Tuti and Soemodihardjo 2006).
4. **West Bali**, Indonesia. Fieldwork by B.W. Hoeksema in collaboration with K.S. Putra of WWF Indonesia Marine Program in 1998 (Hoeksema and Putra 2000).

5. **East Bali** (including southeast Bali, Nusa Lembongan, Nusa Penida in Lombok Strait), Indonesia. Fieldwork by B.W. Hoeksema in collaboration with K.S. Putra of WWF in 1997 and 1998 (Hoeksema and Putra 2000). Expedition organized by the Research Center for Oceanography (RCO–LIPI), WWF Bali Indonesia Marine Program, and Naturalis in 2001 (Hoeksema and Tuti 2001).
6. **Northeast Sumba**, Indonesia. Indonesian – Dutch Snellius–II Expedition in 1984 (Van der Land and Sukarno 1986, Best et al. 1989).
7. **South Flores**, Indonesia. Snellius Expedition in 1929–1930 (Boschma 1936).
8. **Komodo Island**, Indonesia. Indonesian – Dutch Snellius–II Expedition (Van der Land and Sukarno 1986, Best et al. 1989).
9. **Spermonde Archipelago**, South Sulawesi, Indonesia. Snellius Expedition in 1929–1930 (Boschma 1936). Indonesian – Dutch Snellius–II Expedition in 1984 (Van der Land and Sukarno 1986, Best et al. 1989). Fieldwork by Dr. H. Moll in 1980 (Moll 1983). Fieldwork by B.W. Hoeksema around reefs along onshore-off-shore gradients in 1984–1987 (Hoeksema 2012a) and in 1993–1998 (Hoeksema and Crowther 2011).
10. **Salayer Island**, South Sulawesi, Indonesia. Indonesian – Dutch Snellius–II Expedition in 1984 (Van der Land and Sukarno 1986, Best et al. 1989).
11. **Taka Bone Rate** (Tiger Islands), Flores Sea, Indonesia. Indonesian – Dutch Snellius–II Expedition in 1984 (Van der Land and Sukarno 1986, Best et al. 1989).
12. **Tukang Besi Islands** (Wakatobi), Southeast Sulawesi, Indonesia. Indonesian – Dutch Snellius–II Expedition in 1984 (Van der Land and Sukarno 1986, Best et al. 1989). Rapid Ecological Assessment (REA) Wakatobi National Park in 2003 (Pet–Soede and Erdmann 2004).
13. **Maisel Islands**, Banda Sea, Indonesia. Indonesian – Dutch Snellius–II Expedition in 1984 (Van der Land and Sukarno 1986, Best et al. 1989).
14. Ambon and Haruku, **Moluccas**, Indonesia. Snellius Expedition in 1929–1930 (Boschma 1936). Indonesian – Dutch Snellius–II Expedition in 1984 (Van der Land and Sukarno 1986, Best et al. 1989). Rumphius Biohistorical Expedition to Ambon in 1990 (Strack 1993). Fauna Malesiana Marine Maluku Expedition in 1996 (Van der Land 1996).
15. **Bo Islands**, Halmahera Sea, Indonesia. Snellius Expedition in 1929–1930 (Boschma 1936).
16. **West Halmahera Sea**, Indonesia. Ekspedisi Widya Nusantara (E–Win): Ternate Expedition in 2009, involving reefs on volcanic slopes and reefs around sand-cays (Hoeksema and Van der Meij 2010; Gittenberger et al. 2014).
17. **Lembah Strait**, North Sulawesi, Indonesia. Fauna Malesiana Marine Sulawesi Expedition organized by Research Center for Oceanography (RCO–LIPI) and Naturalis in 1994. Marine Biodiversity Workshop North Sulawesi organized by Research Center for Oceanography (RCO–LIPI), Universitas Sam Ratulang and Naturalis in 2012.

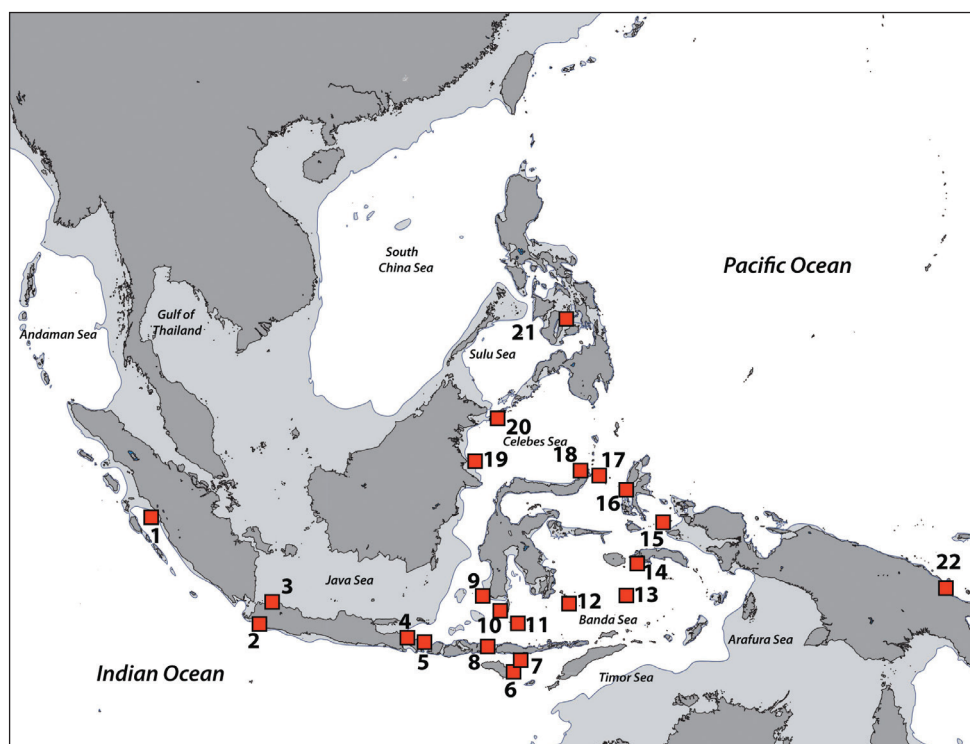


Figure 1. Sampling regions in this study. Note that the region numbers correspond with numbers given in text. **1** West Sumatra **2** Southwest Java **3** Thousand Islands, northwest Java, Java Sea **4** West Bali **5** East Bali **6** Northeast Sumba **7** South Flores **8** Komodo Island **9** Spermonde Archipelago, Southwest Sulawesi **10** Salayer Island, Southwest Sulawesi **11** Taka Bone Rate, Flores Sea **12** Tukang Besi Islands (Wakatobi), Southeast Sulawesi **13** Maisel Islands, Banda Sea **14** Ambon and Haruku, Moluccas **15** Bo Islands, Halmahera Sea **16** West Halmahera **17** Lembah Strait, North Sulawesi **18** Bunaken, North Sulawesi **19** Berau Islands, East Kalimantan **20** Sulu Islands, Philippines **21** Cebu, Philippines **22** Madang, Papua New Guinea. Regions with no country names are in Indonesia. Oceanic names in italics. Dark grey: land masses. Light grey: continental flats.

18. **Bunaken**, North Sulawesi, Indonesia. Fieldwork by B.W. Hoeksema in collaboration with Universitas Sam Ratulung, Manado, in 1994 and 1998.
19. **Berau Islands**, East Kalimantan, Indonesia. East Kalimantan Program in 2003 (Hoeksema 2004).
20. **Sulu Islands**, Philippines. Snellius Expedition in 1929–1930 (Boschma 1936).
21. **Cebu**, Philippines. Cebu Fieldwork by M. L. Esmeno in 1976. Strait Expedition organized by San Carlos University and National Museum of Natural History, Leiden in 1999.
22. **Madang**, Bismarck Sea, north coast of Papua New Guinea. Fieldwork by B.W. Hoeksema with Christensen Research Institute in 1992 (Hoeksema 1993).

Table 1. Overview of field surveys from which order Zoantharia specimens examined in this study were collected.

	Area	Year(s)	References	Remarks on locality and conditions of sample collecting
1	West Sumatra, Indonesia	1996	Jonker and Johan (1999; Figure 1)	Reefs off Padang and Siberut. Coral reef survey in collaboration with Bung Hatta University, Padang. Most reefs damaged, possibly as a result of blast fishing and red tide. Observer/collector: B.W. Hoeksema.
2	Southwest Java, Indonesia	1977	NA	Locality: Teluk Pelabuhan Ratu. Observer/collector: P.H. van Doesburg, RMNH.
3	Northwest Java, Indonesia	2005	Tuti and Soemodihardjo (2006); Annex 2 (157–161), Annex 5 (179)	Thousand Islands Expedition, off Jakarta, Java Sea. In collaboration with RCO–LIPI. Zoantharians were observed during a coral survey along an onshore-offshore gradient.
4	West Bali, Indonesia	1998	Hoeksema and Putra (2000; Figure 1)	Coral biodiversity survey in collaboration with WWF Indonesia Marine Program.
5	Eastern Bali, Indonesia	1997, 1998	Hoeksema and Putra (2000; Figure 1)	Includes southeast Bali and Lombok Strait. Coral biodiversity surveys in collaboration with RCO–LIPI and WWF Bali Indonesia Marine Program.
		2001	Hoeksema and Tuti (2001: 12–15)	Includes southeast Bali and Lombok Strait. Coral biodiversity surveys in collaboration with RCO–LIPI and WWF Bali Indonesia Marine Program.
6	Northeast Sumba, Indonesia	1984	Van der Land and Sukarno (1986: 2.4–2.6, 3.5), Best et al. (1989: 108)	Indonesian – Dutch Snellius–II Expedition.
7	South Flores, Indonesia	1930	Boschna (1936: 24)	Snellius Expedition.
8	Komodo Island, Indonesia	1984	Van der Land and Sukarno (1986: 2.6–2.9, 2.19–2.20, 3.6), Best et al. (1989: 108)	Indonesian – Dutch Snellius–II Expedition.
		1980	Moll (1983: 26)	Coral reef surveys on reefs along onshore-offshore gradients. Observer/collector: H. Moll
9	Spermonde Archipelago, South Sulawesi, Indonesia	1984	Van der Land and Sukarno (1986: 2.22, 3.10), Best et al. (1989: 108)	Indonesian – Dutch Snellius–II Expedition.
		1984–1987	Hoeksema (2012a: Figure 1)	Coral reef surveys on reefs along onshore-offshore gradients.
		1993–1998	Hoeksema and Crowther (2011: Figure 1)	Coral reef surveys on reefs along onshore-offshore gradients.
10	Salayer Island, S Sulawesi, Indonesia	1984	Van der Land and Sukarno (1986: 2.12–2.17, 3.9), Best et al. (1989: 108)	Indonesian – Dutch Snellius–II Expedition.
11	Taka Bone Rate (Tiger Is.), Indonesia	1984	Van der Land and Sukarno (1986: 2.11–2.12, 2.17–2.19, 3.8), Best et al. (1989: 108)	Indonesian – Dutch Snellius–II Expedition.
12	Tukang Besi Is. (Wakatobi), SE Sulawesi, Indonesia	1984	Van der Land and Sukarno (1986: 2.2–2.4, 3.4), Best et al. (1989: 108)	Indonesian – Dutch Snellius–II Expedition.
		2003	Pet-Soede and Erdmann (2004: 57, 117, 143)	Rapid Ecological Assessment (REA) Wakatobi National Park.

13	Maisel Is., Banda Sea, Indonesia	1984	Van der Land and Sukarno (1986: 2.2, 3.3), Best et al. (1989: 108)	Indonesian – Dutch Snellius-II Expedition.
14	Moluccas (Ambon, Haruku), Indonesia	1930	Boschma (1936: 19–20)	Snellius Expedition.
		1984	Van der Land and Sukarno (1986: 2.1–2.2), Best et al. (1989: 108)	Indonesian – Dutch Snellius-II Expedition.
		1990	Strack (1993: 16–42)	Rumphius Biohistorical Expedition to Ambon.
		1996	Van der Land (1996)	Fauna Malesiana Marine Maluku Expedition.
15	Bo Is., Halmahera Sea, Indonesia	1930	Boschma (1936: 23)	Snellius Expedition.
16	West Halmahera Sea, Indonesia	2009	Hoeksema and Van der Meij (2010: 80–85)	Ekspedisi Widya Nusantara (E-Win): Ternate Expedition. Coral biodiversity survey B.W. Hoeksema.
		2009	Gittenberger et al. (2014: Figure 1)	Ekspedisi Widya Nusantara (E-Win): Ternate Expedition. Coral biodiversity survey B.W. Hoeksema.
		1994	Van der Land (1994: 7–9)	Fauna Malesiana Marine Sulawesi Expedition in collaboration with RCO-LIPI.
		2012	NA	Marine Biodiversity Workshop North Sulawesi in collaboration with RCO-LIPI and Universitas Sam Ratulang. Observer/collector: B.W. Hoeksema.
18	Bunaken, North Sulawesi, Indonesia	1994, 1998	NA	Fieldwork in collaboration with Universitas Sam Ratulang, Manado. Observer/collector: B.W. Hoeksema.
19	Berau Islands, East Kalimantan, Indonesia	2003	Hoeksema (2004: 57–60, Figure 1)	East Kalimantan Program. Coral biodiversity survey B.W. Hoeksema.
20	Sulu Islands, Philippines	1929	Boschma (1936: 8–9)	Snellius Expedition.
21	Cebu, Bohol Philippines	1976	NA	Fieldwork by M.L. Esmeno.
		1999	NA	Coral biodiversity survey B.W. Hoeksema during Cebu Strait Expedition in collaboration with San Carlos University, Cebu City.
22	Madang, Bismarck Sea, Papua New Guinea	1992	Hoeksema (1993: Figures 1–2)	Coral biodiversity survey in collaboration with Christensen Research Institute.

NA=not available.

Specimen registration and identification

Examination of the registered (n=52) and unregistered zoantharian specimens (n=570) of the Naturalis collection showed that of a total 622 specimens, 105 were from Indonesia, with an additional four from the Philippines. Of these 109 specimens, 106 form the basis of this research, as we excluded three specimens that could not be conclusively identified as zoantharians. 88 photographic records of zoantharians specimens were also examined.

Although most species are from depths in the range of SCUBA (<40 m), we also included all *Epizoanthus illorricatus* Tischbierck, 1930 specimens, as although some specimens were from >40 m (and down to 190 m), the range of this species does extend into shallower (<40 m) depths. Additionally, three specimens of *Parazoanthus* collected by rectangular dredge from depths of 50–100 m were included in analyses. In this study, these 106 zoantharian specimens are collectively referred to as “shallow-water zoantharians”.

All unregistered specimens were newly registered into the Naturalis collection in the course of our research. All specimens, newly registered or not, were re-identified by the first author. A list of specimens, their collection information, and Naturalis (RMNH Coel) registration numbers are given within each species’ section. Descriptions of each species are given to aid in field and specimen identification, and are not formal taxonomic redescriptions.

Most zoantharian specimens were easily identifiable to genus level without microscopic examination. Species determinations were made consulting previous literature (listed with each species). However, many specimens were only identified to “confers with” (cf.) or “affinity” (aff.) levels. Besides from a few species (e.g. *Palythoa heliodiscus*), very few records of zoantharians had previously been formally reported from the CIP/ Coral Triangle region. Given these reasons, we followed recent research (Burnett et al. 1994, 1995, 1997, Reimer et al. 2006a, 2007b, Sinniger 2006, Sinniger et al. 2010, Reimer and Todd 2009, Reimer 2010, Reimer et al. 2011a, Fujii and Reimer 2011) from neighboring regions and used *Zoanthus* and *Palythoa* species names for which numerous references, molecular data and/or accurate descriptions were available, unless specimens and/or images clearly did not match with previously published information.

Sizes of specimens are averages taken from measurements of 10 polyps per specimen, unless the specimen contained less than 10 polyps, in which case all non-damaged polyps were examined. For species’ dimensions, average dimensions were taken from the overall average of specimens, unless there were less than three specimens within a species. In such cases, dimensions are stated only as a range (minimum to maximum).

Results

From specimen examination, the 106 Indonesian zoantharian specimens in the Naturalis collection supplemented with images were placed into 24 morphospecies, detailed below. Locations are in Indonesia unless otherwise noted, and all photographic images

were taken by B.W. Hoeksema unless otherwise noted. Duplicate photographic images of the same species from the same site are counted as one record. Latitude and longitude are given when available.

Specimens and species

Abbreviations: NA=not available.

Order Zoantharia Gray, 1832

Suborder Brachyncnemina Haddon & Shackleton, 1891a

Family Zoanthidae Rafinesque, 1815

Genus *Acrozoanthus* Saville-Kent, 1893

1. *Acrozoanthus australiae* Saville-Kent, 1893

Figures 2A, 3

Specimens examined (n=16). RMNH Coel 23405, Tg. Bengteng (=Galghoek), Ambon, Moluccas, depth = 3 to 4 m, collected November 10, 1990 by J.C. den Hartog; RMNH Coel 23406, outer bay, Ruhmatiga, Hitu, Ambon, Moluccas, depth = approx. 3 m, collected December 3, 1990 by J.C. den Hartog; RMNH Coel 23407, station 17, southeast side of Pombo Island, Ambon, Moluccas, depth = 6 m, collected November 17, 1994 by J.C. den Hartog; RMNH Coel 23408, west-northwest of Barrang Lompo, Spermonde Archipelago, South Sulawesi, depth = 1.5 to 4 m, collected December 23, 1994 by J.C. den Hartog; RMNH Coel 23409, entrance of harbor near light beacon, northwest of Gusung, Spermonde Archipelago, South Sulawesi, depth = 5 to 7 m, collected October 7, 1990 by J.C. den Hartog; RMNH Coel 23410, 7.5 km west of Makassar, Spermonde Archipelago, South Sulawesi (05°07'S, 119°20'E), depth = NA, collected May 31, 1994 by J.C. den Hartog; RMNH Coel 23411, west of Gusung (=Lae-Lae Keke) (=1 km northwest of Makassar), Spermonde Archipelago, South Sulawesi (05°07.5'S, 119°23'E), depth = NA, collected May 31, 1994 by J.C. den Hartog; RMNH Coel 24100, station MAL04, south coast northeast of Cape Hahurong, Ambon, Moluccas (03°47'S, 128°06'E), depth = 2 to 28 m, collected June 6, 1996 by J.C. den Hartog; RMNH Coel 40361, NNM-LIPI-WWF Expedition station BAL.16, southeast side of Pulau Serangan, Bali (08°44'48"S, 115°14'26"E), depth = to 10 m, collected April 6, 2001 by J. Goud; RMNH Coel 40549, Snellius-II Expedition station 4.011, reef edge west of Mai, Maisel Islands, Banda Sea (05°28'S, 127°31'E), depth = 1 to 30 m, collected September 7, 1984; RMNH Coel 40550, Snellius-II Expedition station 4.001, near Tawiri, Ambon Bay, Moluccas (03°42'S, 128°07'E), depth = approx. 1.5 to 8 m, collected September 4, 1984; RMNH Coel 40554, Snellius-II Expedition station 4.006, near Eri, Ambon Bay, Moluccas (03°45'S, 128°8'E), depth = approx. 1.5 to 5 m, collected September 4, 1984; RMNH Coel 40556, Snellius-II Expedition station 4.006, near Eri, Ambon Bay, Moluccas (03°45'S, 128°8'E), depth

= approx. 1.5 to 5 m, collected August 29, 1984; RMNH Coel 40558, Snellius–II Expedition station 4.030, west coast of Binongko, Tukang Besi Islands, Banda Sea (05°55'S, 123°59'E), depth = approx. 3 to 4 m, collected September 10, 1984 by M. Slierings; RMNH Coel 40566, west side of Pulau Samalona, 7.5 km west of Makassar, Spermonde Archipelago, South Sulawesi (05°07'S, 119°20'E), depth = NA, collected February 18, 1994 by B.W. Hoeksema; RMNH Coel 40569, Fauna Malesiana Marine Sulawesi Expedition station SUL.06, Pantai Parigi, Pulau Lembah, Selat Lembah, North Sulawesi (01°28'N, 125°14'E), depth = 0 to 6 m, collected October 15, 1994 by M. Slierings.

Photographic records (n=6). West side of Pulau Lae–Lae (05°08'05"S, 119°23'15"E), South Sulawesi, May 24, 1997; station MAL.19 (03°43'S, 128°03'E), Tanjune Batu Dua, east of Hatu, north coast of Ambon Bay, Moluccas, November 19, 1996; station MAL.22 (03°48'S, 128°06'E), southwest coast, east of Tunjung Nusanive, Ambon Bay, Moluccas, November 21, 1996; Nusa Penida, Lombok Strait, east Bali, May 26, 1998 (08°40'56"S, 115°28'56"E); northwest Pulau Samalona, Spermonde Archipelago, South Sulawesi (05°07'25"S, 119°20'10"E), January 12, 1997; western slope of Bone Lola shoal, Spermonde Archipelago, South Sulawesi (05°03'15"S, 119°21'15"E), April 22, 1998.

Description. Non-incrusted zooxanthellate zoantharian that inhabits the outside of eunicid worm tubes (Haddon 1895), with a unique asexual form of “budding” (Ryland 1997). Easily recognizable as it is an epibiont on outside surface of eunicid worm tube, and has a reduced stoloniferous coenenchyme, long pale yellow-green or pale purple tentacles (n=approx. 40–50) with occasional fluorescent green markings and black tips, and light brown/purple to white ectoderm with similarly colored oral disks (Figure 2A). Preserved specimens in this study had polyps of average 6.0 mm in height (range 2.5–14 mm), 3.2 mm in width (range 2–5 mm) (n=8 specimens examined [RMNH Coel 40361, 40549, 40550, 40554, 40556, 40558, 40566, 40569], 10 polyps/specimen), and oral disks approximately 6 mm in diameter when expanded in situ (partially adapted from Reimer et al. 2011b). Specimen RMNH Coel 40566 had much larger polyps than other specimens (average height 10.6 mm, average width 4.3 mm), but this may be due to preservation in formalin as opposed to ethanol than to any phenotypic difference.

Distribution. Regions recorded in this study (Figure 3). East coast of Bali (5), Spermonde Archipelago (9), Tukang Besi Islands (12), Maisel Islands (13), Moluccas (14), Lembah Strait (17).

Previous records. Originally described from Australia, where it has been reported from both the coast of northern Queensland, and the region around Darwin in the Northern Territory. Subsequent records reported from North Sulawesi, Indonesia (Siniger et al. 2005, Reimer et al. 2011b), and photographic records from Mactan Island, Philippines (Reimer et al. 2011b). Also reported from southern Taiwan (Reimer et al. 2011b) and at Ningaloo, Western Australia (Y. Irei and J.D. Reimer, unpubl. data).

Remarks. This genus is positioned within the genus *Zoanthus* based on phylogenetic analyses (Reimer et al. 2011b).

Genus *Zoanthus* Lamarck, 1801

2. *Zoanthus sansibaricus* Carlgren, 1900

Figures 2B, 3

Specimens examined (n=1). RMNH Coel 40476, Rumphius Biohistorical Expedition station 27, Leitimur, south coast, Hutumuri, Ambon, Moluccas, depth = intertidal, collected November 26, 1990 by M.S.S. Lavaleye.

Photographic records (n=9). Southeast Siberut, West Sumatra (01°44'S, 99°15'E), December 15, 1996; east Menjangan Island, West Bali (08°05'25"S, 114°31'40"E), May 21, 1998; west Pulau Lumu Lumu, Spermonde Archipelago, South Sulawesi (04°58'30"S, 119°12'30"E), October 8, 1997; west Pulau Kudingareng Keke, Spermonde Archipelago, South Sulawesi (05°06'20"S, 119°17'03"E), May 29, 1997; northwest Pulau Barang Lompo, Spermonde Archipelago, South Sulawesi (05°02'35"S, 119°19'10"E), July 21, 1998; south Pulau Samalona, Spermonde Archipelago, South Sulawesi (05°07'45"S, 119°20'25"E), October 27, 1997; west Pulau Lae Lae Besar, Spermonde Archipelago, South Sulawesi (05°08'15"S, 119°23'10"E), November 12, 1997; northwest Pulau Lae Lae Keke, Spermonde Archipelago, South Sulawesi (05°07'10"S, 119°23'25"E), October 11, 1997; Station BER.26, northeast Buliulin (south of Samama Island), Berau Islands, East Kalimantan, (02°07'07"N, 118°20'32"E), October 15, 2003.

Description. Can form colonies of up to 1 m², but often forming much smaller colonies in cracks and small overhangs in intertidal and shallow waters (<5 m). with polyps well clear and free of the coenenchyme ("liberae") (Pax 1910, Reimer et al. 2006b). Adult polyps 2–12 mm in diameter when open, up to 20 mm in length but usually shorter, particularly in locations with strong currents or waves. The sole specimen (RMNH Coel 40476) in this study has small polyps (height average 2.8 mm, range 2–5 mm; width average 2.4 mm, range 1.5–4 mm) within the reported range of this species. External polyp surface generally uniform, light to dark gray-blue with no significant markings or patterns. Tentacles 40–58, mesenteries 48–54. Wide variation in oral disk colors, patterns, and in colors of tentacles (Figure 2B) (Reimer et al. 2004, 2006a) (partially adapted from Reimer and Hickman 2009).

Distribution. Regions recorded in this study (Figure 3). West Sumatra (1), West Bali (4), Spermonde Archipelago (9), Moluccas (14), Berau Islands (19).

Previous records. This species has previously been reported from Zanzibar (type locality), Singapore (Reimer and Todd 2009), Taiwan (Reimer et al. 2011c, 2013a), Palau (Reimer et al. 2014a), southern Japan (Reimer et al. 2004, 2006a, Kamezaki et al. 2013), and is considered to have a very wide Indo-Pacific distribution.

Remarks. Based on its wide Indo-Pacific distribution, it is very likely that this zooxanthellate species is much more common within the CIP than reported here. One possible reason for the lack of records from the CIP is that this species is most commonly found in the intertidal zone, which is under-sampled during SCUBA surveys. However, this species is also found to depths of 52 m (Kamezaki et al. 2013), although below the shallow littoral zone it rarely forms colonies >100 polyps.

Additionally, as preserved specimens of *Zoanthus* are notoriously hard to identify to species level, the large number of unidentified *Zoanthus* specimens in this study undoubtedly include some *Z. sansibaricus* colonies. This is also likely one important reason explaining the presence of comparatively more photographic records of this species in this study, as *in situ* identification of colonies with expanded oral polyps is easier than preserved specimen identification.

This species may be the same as *Zoanthus coppingeri* Haddon & Shackleton, 1891b from the Great Barrier Reef, Australia, based on molecular data (Reimer, data not shown), which has been reported to be a senior synonym of *Z. jukesii* Haddon & Shackleton, 1891b, *Z. macgillivrayi* Haddon & Shackleton, 1891b, *Z. annae* Carlgren, 1937, *Z. mantoni* Carlgren, 1937, *Z. fraseri* Carlgren, 1937, all described from the Great Barrier Reef based on nematocyst data (Burnett et al. 1997).

3. *Zoanthus* sp.

Figures 2C, D, 3

Specimens examined (n=10). RMNH Coel 40360, NNM–LIPI–WWF Expedition station BAL.03, south of tidal channel, Palung Semawang, off Kesumasari Beach, Sanur, Bali (08°42'39"S, 115°16'09"E), depth to 5 m, collected by L. P. van Ofwegen and M. Slierings on March 31, 2001; RMNH Coel 40457, piers of harbor, Cebu City, Cebu, Philippines by M. L. Esmeno in 1976 (original label "specimen 196"); RMNH Coel 40516, Snellius–II Expedition station 27, west side of Bone Tambung, South Sulawesi (05°03'00"S, 119°15'45"E), depth = 1 m, collected October 23, 1980 by H. Moll; RMNH Coel 40537, Snellius–II Expedition station 4.139, reef flat edge south of Tarupa Kecil, northeast Taka Bone Rate (06°30'S, 121°08'E), depth = 30 m, collected September 25, 1984; RMNH Coel 40539, Snellius–II Expedition station 4.011, reef edge west of Mai, Maisel Islands, Banda Sea (05°28'S, 127°31'E), depth 1 to 30 m, collected September 7, 1984; RMNH Coel 40542, Snellius–II Expedition station 4.084, Selat Linta, east of Komodo I. (08°35'S, 119°34'E), depth = approx. 3 m, collected September 18, 1984; RMNH Coel 40551, Snellius–II Expedition station 4.079, Selat Linta, east of Komodo I. (08°35'S, 119°34.2'E), collected September 10, 1984; RMNH Coel 40560, Snellius–II Expedition station 4.096, northeast cape of Komodo I. (08°29'S, 119°34.1'E), from "shallow water", collected September 20, 1984; RMNH Coel 40564, Fauna Malesiana Marine Sulawesi Expedition station SUL.08, channels between lava outflows, south of Tanjung Batu Angus, Selat Lembeh, North Sulawesi (01°30'N, 125°15'E), depth 5 to 10 m, collected by M. Slierings on October 16 or 25, 1994; RMNH Coel 40565, Fauna Malesiana Marine Sulawesi Expedition station SUL.08, channels between lava outflows, south of Tanjung Batu Angus, Selat Lembeh, North Sulawesi (01°30'N, 125°15'E), depth to 10 m, collected on October 16 or 25, 1994.

Photographic records (n=3). West side of Pulau Lae–Lae, Spermonde Archipelago, South Sulawesi (05°08'05"S, 119°23'15"E), September 16, 1997; west side of Pu-

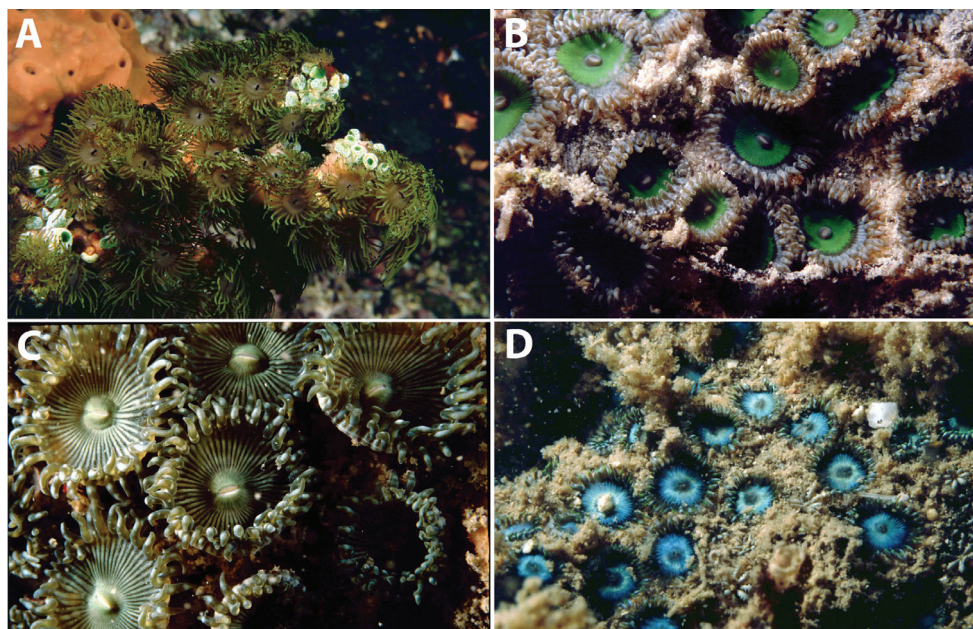


Figure 2. Images of *Acrozoanthus* and *Zoanthus* species from photographic records in this study. **A** *Acrozoanthus australiae* at Nusa Penida, Lombok Strait, east Bali, May 26, 1998 **B** *Zoanthus san-sibaricus* at Station BER.26, northeast Buliulin (south of Samama Island), East Kalimantan, Berau Islands, October 15, 2003 **C** *Zoanthus* sp. at west side of Pulau Samalona, Spermonde Archipelago, South Sulawesi, September 16, 1997; and **D** *Zoanthus* sp. west of Gusung (=Pulau Lae–Lae Keke), Spermonde Archipelago, South Sulawesi, October 11 1997.

lau Samalona, Spermonde Archipelago, South Sulawesi (05°07'25"S, 119°20'10"E), September 16, 1997; west of Gusung (=Pulau Lae–Lae Keke), Spermonde Archipelago, South Sulawesi (05°07.5'S, 119°23'E), October 11, 1997.

Description. This group includes all *Zoanthus* spp. specimens that could not be identified to species level (n=10). Almost all of these specimens are 'liberae' or 'intermediae', with polyps rising out from the coenenchyme (see Pax 1910) (Figure 2C). One specimen, RMNH Coel 40560, is more 'immersae' with polyps only slightly protruding from the coenenchyme (average height 2.25 mm, width 2.0 mm, n=10). Overall, polyps for all specimens fit within the range of several described species, with an average for all specimens of a height of 6.7 mm (range 2–17 mm), and width of 3.3 mm (range 1.5–6 mm) (n=10 specimens). Thus, given the high variation within *Zoanthus* species, particularly polyp height based on microenvironment (Ong et al. 2013), and the lack of other diagnostic characteristics, for now these species cannot be identified to species level. Based solely on sizes, two specimens, RMNH Coel 40542 and 40565, have much larger polyps compared to the other specimens (height 10.3 mm, width 4.3 mm; height 10.8 mm, width 4.4 mm), but whether these are a separate species from other specimens or the size difference is due to fixation method in formalin is unknown.

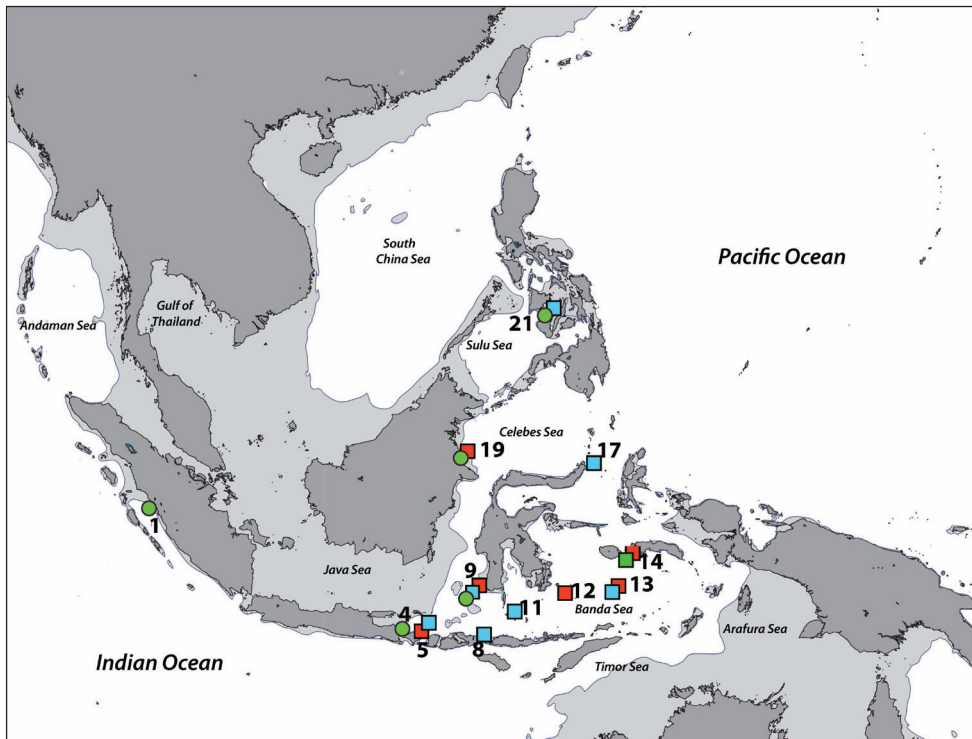


Figure 3. Distribution of *Acrozoanthus* and *Zoanthus* species from specimens and photographic records from this study. *Acrozoanthus australiae* specimens in red, *Z. sansibaricus* in green, and *Zoanthus* sp. in blue. Region numbers correspond to locations given in species' information. Boxes indicate presence of specimens (with or without photographic records), while circles indicate only photographic records. Overlapping symbols indicate the same region.

Distribution. Regions recorded in this study (Figure 3). Eastern Bali (5), Komodo (8), Spermonde Archipelago (9), Taka Bone Rate (11), Maisel Is. (13), Lembah Strait. (17).

Previous records. NA.

Remarks. This designation simply consists of all *Zoanthus* spp. specimens that could not be identified to species-level. It is likely this designation includes more than one species based on depths of specimens sampled. However, as preserved specimens were contracted (polyps closed) and many described *Zoanthus* spp. present no readily diagnostic external characters, identification to species level is not potentially possible without detailed molecular examination. Attempts at molecular identification also failed for these (and most other specimens), perhaps due to initial preservation in 10% seawater formalin for older specimens, or in ethanol with additives for newer specimens.

Genus *Isaurus* Gray, 1828

4. *Isaurus tuberculatus* Gray, 1828

Figures 4A, B, 5

Specimens examined (n=3). RMNH Coel 40472, Rumphius Biohistorical Expedition station 27, Leitimur, south coast, Hutumuri, Ambon Bay, Moluccas (03°41'50"S, 128°17'00"E), intertidal under stones, collected on November 27, 1990 by J.C. den Hartog; RMNH Coel 40473, Rumphius Biohistorical Expedition station 27, Leitimur, south coast, Hutumuri, Ambon Bay, Moluccas (03°41'50"S, 128°17'00"E), intertidal under stones, collected on November 27, 1990 by J.C. den Hartog; RMNH Coel 40567, Fauna Malesiana Marine Sulawesi Expedition station SUL.04, bay south of Pulau Putus, Lembah Strait, North Sulawesi (01°31'N, 125°16'E), depth approx. 1 to 2 m, on October 27, 1994 by J.C. den Hartog.

Photographic records. NA.

Description. Species in this genus are zooxanthellate, not incrusting, with a simple mesogleal sphincter muscle, and have non-erect, recumbent polyps that do not have lacunae or mesogleal canals, unlike *Zoanthus* species. *Isaurus tuberculatus* has tubercles on the exterior surface of polyps (=endodermal invagination) (Figures 4A, B). For detailed discussion of *I. tuberculatus*, refer to Muirhead and Ryland (1985), with phylogenetic analyses in Reimer et al. (2008b).

Specimens examined in this study varied greatly in size from relatively large RMNH Coel 40567 (height 28–31 mm, width = 6–7 mm, n=2 polyps) to relatively small RMNH Coel 40473 (height average 10.6 mm, width average 2.9 mm, n=7 polyps). However, *Isaurus* polyps are known to vary greatly in size both between different colonies and within large colonies (Larson and Larson 1982; Muirhead and Ryland 1985; Reimer et al. 2008b). Furthermore, the two other valid Pacific *Isaurus* spp. besides from *I. tuberculatus* are both very distinct from these specimens, and found in Fiji and southwestern Australia, respectively. Thus, the identity of these specimens as *I. tuberculatus* is largely certain.

Distribution. Regions recorded in this study (Figure 5). Moluccas (14), Lembah Strait (17).

Previous records. Originally described from the West Indies, this species is distributed throughout the subtropical and tropical Atlantic and Indo-Pacific (e.g. Muirhead and Ryland 1985), although populations in each ocean basin likely constitute different species (Reimer et al. 2008a). In the Indo-Pacific, it has previously been reported from the Great Barrier Reef, Fiji, Hawaii (summarized in Muirhead and Ryland 1985), and also from Indonesia (Sinniger et al. 2005), New Caledonia (Laboute and Richer de Forges 2004), and Japan (Reimer et al. 2008b).

Remarks. As seen in previous studies (Reimer et al. 2008b), it appears from the low numbers of specimens here that *Isaurus* is either somewhat rare throughout its range, or cryptic in nature (e.g. well-camouflaged), resulting in few reports of this species.

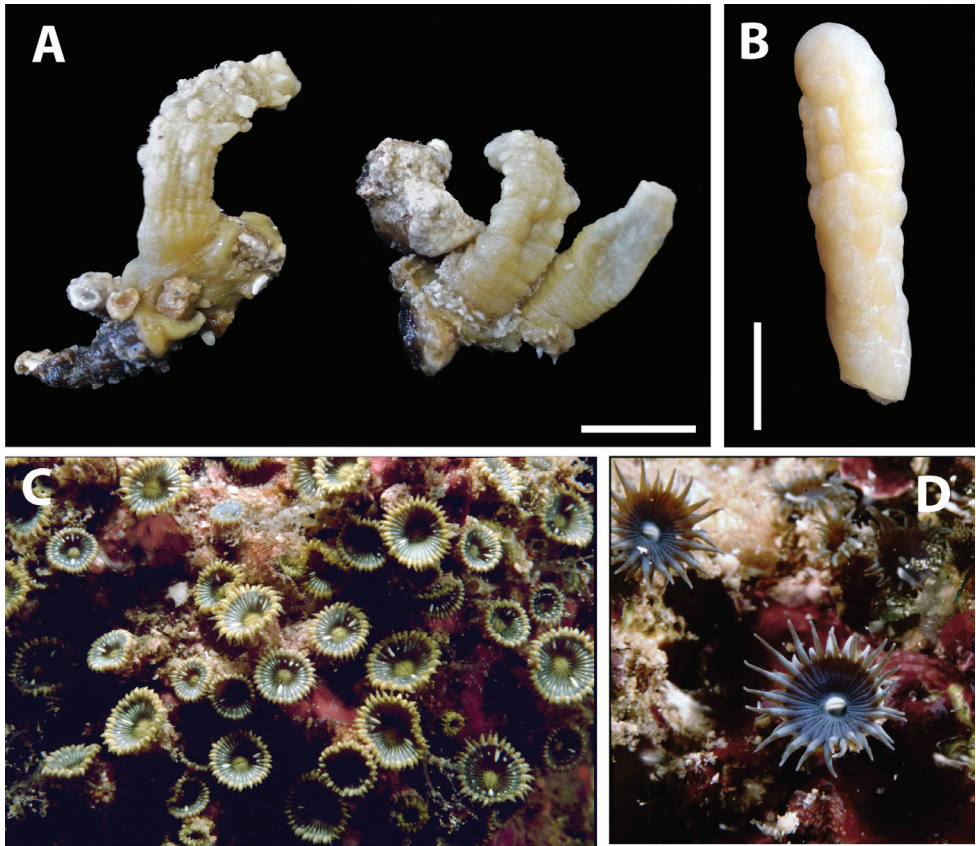


Figure 4. Images of *Isaurus* and *Neozoanthus* species from specimens and photographic records in this study. **A** *Isaurus tuberculatus* specimen RMNH Coel 40567 from Fauna Malesiana Marine Sulawesi Expedition station SUL.04, bay south of Pulau Putus, Lembah Strait, North Sulawesi, depth approx. 1 to 2 m, on October 27, 1994 by J.C. den Hartog **B** *I. tuberculatus* specimen RMNH Coel 40472 from Rumphius Biohistorical Expedition station 27, Leitimur, south coast, Hutumuri, Ambon Bay, Moluccas, intertidal under stones, collected on November 27, 1990 by J.C. den Hartog **C** *Neozoanthus* sp. at station WAK.13, southwest tip of Tolandono Island, REA Wakatobi National Park, Wakatobi, Southeast Sulawesi, on May 9, 2003; and **D** *Neozoanthus* sp. at Lembongan Bay, Nusa Lembongan, Lombok Strait, on May 19, 1998. Scales in **A** and **B** 1 cm.

Family Neozoanthidae Herberts, 1972

Genus *Neozoanthus* Herberts, 1972

5. *Neozoanthus* sp.

Figures 4C, D, 5

Specimen regions. NA.

Specimens examined. NA.

Photographic records (n=8). Gili Selang, eastern Bali (08°23'55"S, 115°42'30"E), on June 3, 1998; Lembongan Bay, Nusa Lembongan, Lombok Strait (08°40'25"S,

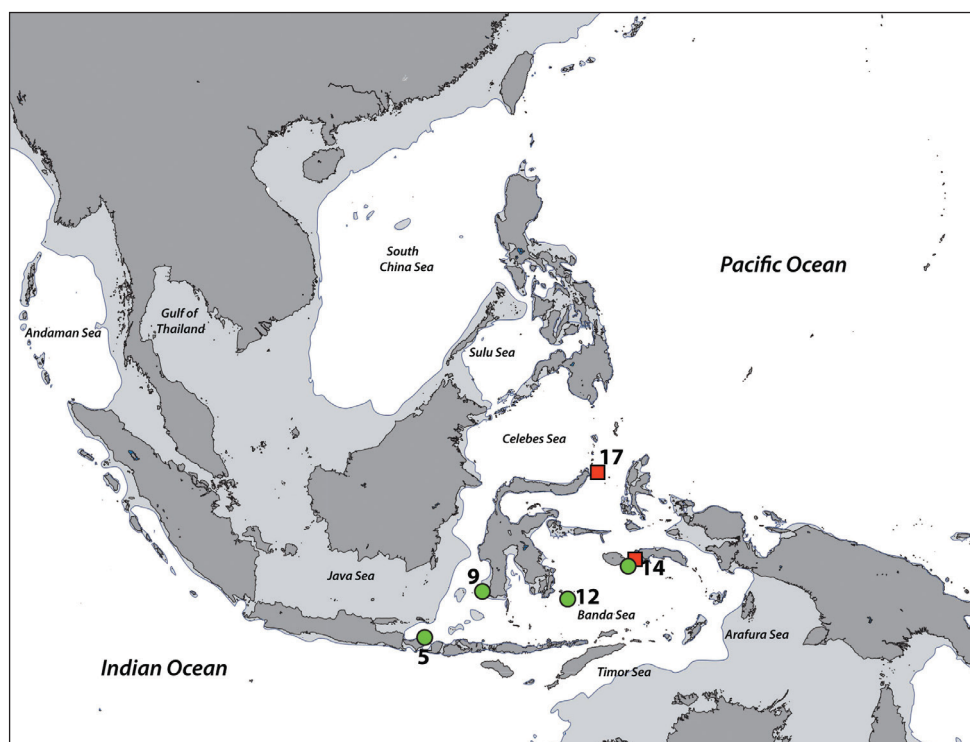


Figure 5. Distribution of *Isaurus* and *Neozoanthus* species from specimens and photographic records from this study. *Isaurus tuberculatus* specimens in red, and *Neozoanthus* sp. in green. Region numbers correspond to locations given in species' information. Boxes indicate presence of specimens (with or without photographic records), while circles indicate only photographic records. Overlapping symbols indicate the same region.

115°26'18"E), on May 19, 26, 27, 29, 1998 (4 records); Tanjung Taal, Nusa Lembongan, Lombok Strait (08°39'33"S, 115°26'37"E), on May 25, 1998; station WAK.22, north channel pass of Karang Koromaha, REA Wakatobi National Park, Wakatobi, Southeast Sulawesi (05°42'54"S, 124°10'53"E), on May 12, 2003; station WAK.13, southwest tip of Tolandono Island, REA Wakatobi National Park, Wakatobi, Southeast Sulawesi (05°46'35"S, 123°53'38"E), on May 9, 2003.

Description. Unique among zoantharians, species in this genus have an endodermal sphincter with brachycnemic mesentery arrangement. Polyps are only partially incrustated, with the oral end of polyps lacking incrustation (Figures 4C, D). Phylogenetically, this genus is closely related to *Isaurus* (within family Zoanthidae). Zooxanthellate. Adapted from Herberts (1972), Reimer et al. (2012a).

Distribution. Regions recorded in this study (Figure 5). Eastern Bali (5), Spermonde Archipelago (9), Tukang Besi Islands (12), Moluccas (14).

Previous records. Species of this genus have been reported from Madagascar (Herberts 1972), southern Japan (Reimer et al. 2011a, 2012a, 2013b), and the southern Great Barrier Reef (Reimer et al. 2011a, 2012a).

Remarks. This genus was originally described from Madagascar with the type species *N. tulearensis* Herberts, 1972. Subsequently, two species have been reported from Australia and Japan (Reimer et al. 2012a). As no specimens exist, it is impossible to determine if the Indonesian photographs constitute one or both of the species reported in Reimer et al. (2012a), or an as of yet undescribed species.

Family Sphenopidae Hertwig, 1882

Genus *Palythoa* Lamouroux, 1816

6. *Palythoa* cf. *mutuki* (Haddon & Shackleton, 1891b)

Figures 6A, B, 7

Specimens examined (n=13): RMNH Coel 40458, harbor pier, Cebu City, Cebu, Philippines, collected in 1976 by M.L. Esmeno; RMNH Coel 40459, harbor pier, Cebu City, Cebu, Philippines, collected in 1976 by M.L. Esmeno; RMNH Coel. 40468, Rumphius Biohistorical Expedition station 29, Hitu, Ambon Bay, Ambon, Moluccas (03°38'05"S, 128°12'36"E), depth = intertidal, collected on November 28, 1990 by M.S.S. Lavaleye; RMNH Coel. 40470, Rumphius Biohistorical Expedition station 4, Leitimur, outer Ambon Bay, Wainitu, Moluccas (03°42'10"S, 128°09'15"E), depth = littoral on old shipwreck, collected on November 7–8, 1990 by H. Strack; RMNH Coel. 40475, Rumphius Biohistorical Expedition station 27, Leitimur, south coast, Hutumuri, Moluccas (03°41'50"S, 128°17'00"E), depth = intertidal, on November 26, 1990 by M.S.S. Lavaleye; RMNH Coel. 40514, Fauna Malesiana Maluku Expedition station MAL.15, Ambon Bay, south coast, cape west of Amahusu, Moluccas (03°44'S, 128°08'E), collected on November 16, 1996; RMNH Coel. 40528, Snellius–II Expedition station 4.096, northeast Komodo, Komodo (08°29'S, 119°34'E), depth = to 30 m, collected on October 26, 1984; RMNH Coel 40532, NNM–LIPI–WWF Bali–Lombok Strait 2001 Expedition station BAL.09, Loloan Batu Agung, Sanur, eastern Bali (08°43'31"S, 115°15'57"E), depth = 10 to 15 m, collected on April 3, 2001 by B.W. Hoeksema; RMNH Coel. 40540, Snellius–II Expedition station 4.010, near Tawiri, Ambon Bay, Moluccas (03°42'S, 128°07'E), depth = 1 to 5 m, collected on September 5, 1984; RMNH Coel. 40559, Snellius–II Expedition sta 4.012, north Pulau Mai, Maisel Islands, Banda Sea (05°28'S, 127°31'E), depth = 0 to 1.5 m, collected on 07.09.1984; RMNH Coel. 40561, Snellius–II Expedition station 4.133, east Pulau Tarupa Kecil, Taka Bone Rate (06°29'S, 121°08'E), depth = 11 m, collected on September 26, 1984; RMNH Coel. 40562, Snellius–II Expedition station 4.096, northeast Komodo, Komodo (08°29'S, 119°34'E), depth = to 30 m, collected on September 20, 1984; RMNH Coel. 40741, Rumphius Biohistorical Expedition station 11, Leitimur, Tanjung Nasaniwe, Moluccas (03°47'10"S, 128°05'20"E), depth = littoral, collected on November 12, 1990;

Photographic records (n=2). Main coast, West Bali (08°06'50"S, 114°30'40"E), May 22, 1998; west Pulau Bone Batang, South Sulawesi, Spermonde Archipelago (05°01'00"S, 119°19'15"E), October 22, 1997.

Description. Originally described from the Torres Strait, Australia, this species was redescribed in detail in Ryland and Lancaster (2003).

Although all specimens in this grouping match with previously reported *P. mutuki* based on sizes (average polyp height 9.6 mm, range 3–31 mm, average width 4.8 mm, range 2–8 mm, n=12 specimens) and overall morphology ('intermediae' or 'liberae' [Pax 1910]; visible capitulary ridges on closed polyps [Ryland and Lancaster 2003]) (Figure 6B), we have identified all specimens in this study as "cf.". Recent work has shown the presence of more than two closely related species groups within *P. mutuki* (Reimer et al. 2006b, 2013a) that are exceedingly difficult to distinguish without molecular data. For this reason, we have preliminarily assigned "cf." to these specimens.

Distribution. Regions recorded in this study (Figure 7). West Bali (4), eastern Bali (5), Komodo Island (8), Spermonde Archipelago (9), Taka Bone Rate (11), Maisel Islands (13), Moluccas (14), Cebu (21).

Previous records. Ryland and Lancaster (2003) in their treatment of *P. mutuki* also mentioned records from Fiji, and synonymized records of other species from Tuvalu (*Gemmaria willeyi* Hill & Whitelegge, 1898), eastern Australia (*G. arenacea* Wilshire, 1909; *P. yongei* Carlgren, 1937; *P. australiensis* Carlgren, 1950) and Singapore (*P. singaporensis* Pax & Müller, 1956) with this species. However, besides from the specimens directly examined by Ryland and Lancaster, there is much confusion over the true identity of these species. For example, Ryland and Lancaster (2003) themselves state that *G. willeyi* is likely a *Zoanthus* species based on the figures in the original description. Ryland and Lancaster state "Probably only the use of genetic methods, so successfully applied by Burnett *et al.* (1997), will settle identities over wide geographic areas".

However, in the Pacific, records of this species with phylogenetic confirmation have previously been reported from the Great Barrier Reef in Australia (Burnett et al. 1997), Singapore (Reimer and Todd 2009), to the south Pacific coast of Japan (e.g. Reimer et al. 2006b, 2007b), New Caledonia (Sinniger 2006), and across to the Galapagos (Reimer and Hickman 2009), and thus it is known that this species has a very wide Indo-Pacific distribution.

Remarks. This species is likely common in Indonesia as in other regions such as Okinawa (Irei et al. 2011) and Taiwan (Reimer et al. 2011c). However, species delineation in *Palythoa* is confused due to the close phylogenetic relationships between *P. mutuki*, *P. tuberculosa*, and some other undescribed species, and a potential reticulate evolutionary history (Reimer et al. 2007b, Shiroma and Reimer 2010, M. Mizuyama and J.D. Reimer unpubl. data). Furthermore, distinguishing *P. mutuki*, from other, more distantly related species such as *P. heliodiscus* based solely on morphology is often difficult (Ryland and Lancaster 2003). For this study, we have included all "*P. mutuki*-like" specimens as one species group for convenience, although it is likely the specimens will encompass more than one species once the taxonomy of this genus is clarified.

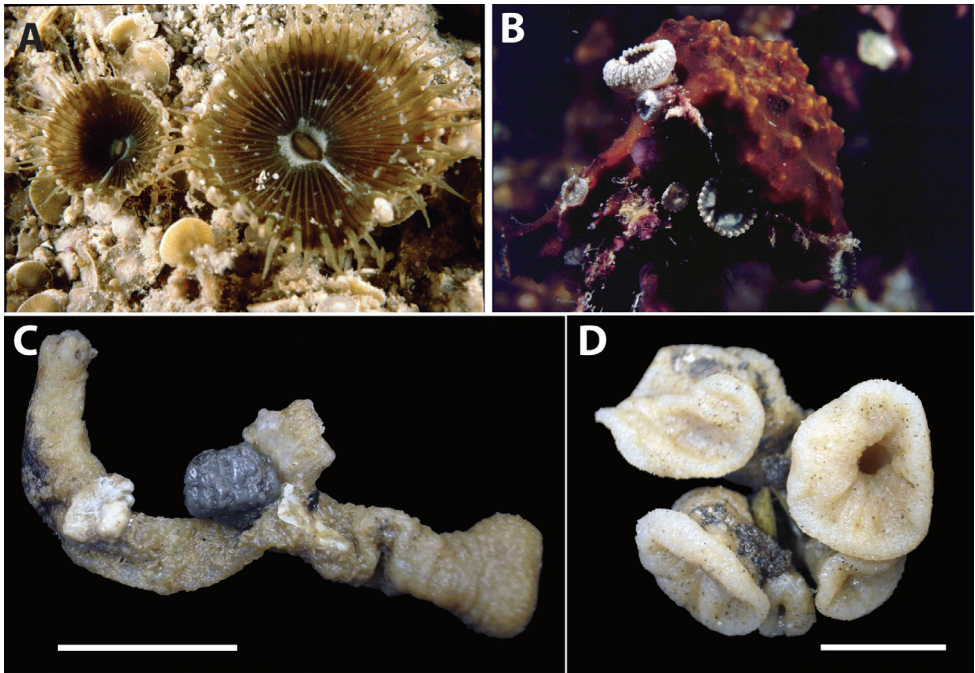


Figure 6. Images of *Palythoa* cf. *mutuki* from specimens and photographic records in this study. **A** *P.* cf. *mutuki* at west Pulau Bone Batang, South Sulawesi, Spermonde Archipelago, October 22, 1997 **B** *P.* cf. *mutuki* at main coast, West Bali, May 22, 1998 **C** *Palythoa* sp. specimen RMNH Coel 40508, Fauna Malesiana Maluku Expedition station MAL.13, west coast near Larike, Ambon, Moluccas, depth = 3 m, collected on November 15, 1996; and **D** *Palythoa* sp. specimen RMNH Coel 40512, Pelabuhan Ratu, Southwest Java, collected on October 13, 1977, by P.H. van Doesburg. Scales in **C** and **D** 1 cm.

7. *Palythoa* sp.

Figures 6C, D, 7

Specimens examined (n=2): RMNH Coel 40508, Fauna Malesiana Maluku Expedition station MAL.13, west coast near Larike, Ambon, Moluccas (03°43'S, 127°56'E), depth = 3 m, collected on November 15, 1996; RMNH Coel 40512, Pelabuhan Ratu, southwest Java (07°01'N, 106°34'E), collected on October 13, 1977, by P.H. van Doesburg.

Photographic records. NA.

Description. This group consists of two specimens that do not clearly fit with previously described *Palythoa* species. Both specimens have dimensions very different from other *Palythoa* specimens reported here; whether this is due to unusual fixation or relaxation methods, or to true phenotypic differences is unknown.

RMNH Coel 40508 (Figure 6C) has very long 'liberae' polyps (average 23.6 mm height, n=4 polyps) that are more robust (average 5 mm, n=4 polyps) than seen in *P. heliodiscus*, but with almost no development of the coenenchyme, unlike as in *P.*

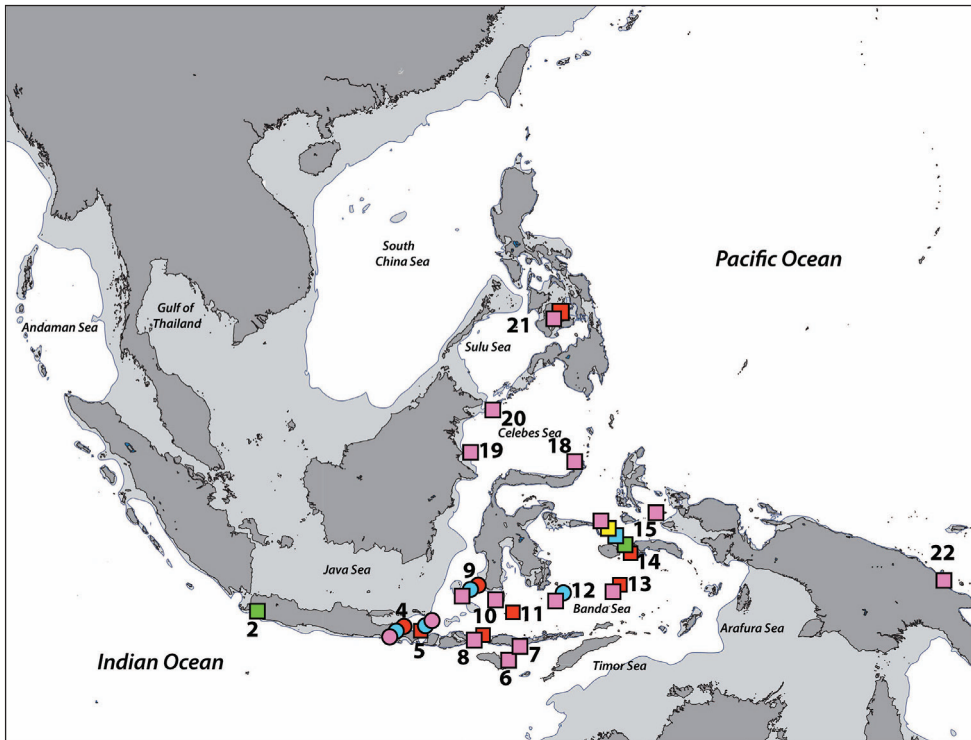


Figure 7. Distribution of *Palythoa* species from specimens and photographic records from this study. *Palythoa* cf. *mutuki* specimens in red, *Palythoa* sp. in green, *P. cf. heliodiscus* in blue, *P. aff. tuberculosa* in yellow, and *P. tuberculosa* in pink. Region numbers correspond to locations given in species' information. Boxes indicate presence of specimens (with or without photographic records), while circles indicate only photographic records. Overlapping symbols indicate the same region.

mutuki or other closely related species. As well, this specimen is from 3 meters depth, a shallower depth than usually seen for *P. heliodiscus*.

RMNH Coel 40512 (Figure 6D) is a small 'intermediae' colony consisting of four polyps that are squat and robust (average width 8.3 mm, $n=3$ polyps, height approximately same as width) with large oral discs (average 12 mm in diameter, $n=3$ polyps) with no tentacles visible and a large oral opening.

Distribution. Regions recorded in this study (Figure 7). Southwest Java (2), Moluccas (14).

Previous records. NA.

Remarks. The morphology of these specimens do not clearly match any described species from the central Indo-Pacific. In particular, specimen RMNH Coel 40512 is different than any other zoantharian previously observed by the first author. However, it is unknown if fixation has resulted in degradation of fine scale structures (e.g. tentacles, which are absent), but the specimen is clearly a zoantharian due to sand encrustation in body wall.

8. *Palythoa* cf. *heliodiscus* (Ryland & Lancaster, 2003)

Figures 7, 8

Specimens examined (n=2). RMNH Coel 40504, Fauna Malesiana Maluku Expedition station MAL.12, north coast near Morela, Ambon, Moluccas (03°33'S, 128°12'E), depth = 35 m, collected on November 13, 1996; RMNH Coel. 40513, Rumphius Biohistorical Expedition station 24, south Seri Bay, Ambon, Moluccas (03°34'50"S, 128°09'45"E), depth = 12 m, November 22, 1990.

Photographic records (n=13). Pulau Ular, off Padang, West Sumatra (01°07'05"S, 100°20'02"E), December 16, 1996; Pemuteran, West Bali (08°11'20"S, 114°50'30"E), May 23, 1998; Tulamben, eastern Bali (08°16'26"S, 115°35'28"E), July 12, 1997; Nusa Lembongan, Lombok Strait (08°40'S, 115°26'E), May 29, 1998; west side Pulau Samalona, Spermonde Archipelago, South Sulawesi (05°07'25"S, 119°20'10"E), November, 1984; northwest side Pulau Samalona, Spermonde Archipelago, South Sulawesi (05°07'25"S, 119°20'10"E), November 23, 1997; northwest Kudingareng Keke, Spermonde Archipelago, South Sulawesi (05°06'15"S, 119°17'10"E), August 6, 1997; west side Pulau Badi, Spermonde Archipelago, South Sulawesi (04°58'06"S, 119°16'57"E), November 1, 1994; REA Wakatobi National Park station WAK.18, southwest Pulau Binongko, Southeast Sulawesi, Wakatobi, Tukang Besi Islands (05°59'48"S, 124°02'55"E), May 10, 2003; REA Wakatobi National Park station WAK.22, north channel pass of Karang Koromaha, Southeast Sulawesi, Wakatobi, Tukang Besi Is. (05°42'54"S, 124°10'53"E), May 12, 2003; Fauna Malesiana Maluku Expedition station MAL.12, north coast near Morela, Ambon (03°33'S, 128°12'E), November 13–14, 1996; East Kalimantan–Berau Expedition station BER.03, south side of Pulau Derawan, East Kalimantan (02°17'03"N, 118°14'49"E), October 16, 2003; Christensen Research Institute, Madang, Papua New Guinea (05°09'30"S, 145°48'10"E), June 1992.

Description. This zooxanthellate species was described in detail recently by Ryland and Lancaster (2003). Superficially similar in appearance to *P. mutuki*, externally the species can be distinguished by its short tentacles (length <20% of oral disk) and subtidal distribution, compared to primarily intertidal *P. mutuki*, which also has longer tentacles (~45% of oral disk) (Ryland and Lancaster 2003).

Sizes of specimens agree well with specimens seen in other localities (average polyp heights 11.3 mm and 17.0 mm for each specimen, range 7–20 mm; average width 3.9 mm and 4.4 mm for each specimen, range 3.5–5.5 mm; n=2 specimens of 8 and 5 polyps, respectively). Depth of collected specimens (12 and 35 m) also fits well with the description of this species as primarily subtidal in the original description, and from data in Okinawa, Japan (e.g. Reimer 2010).

Distribution. Regions recorded in this study (Figure 7). West Bali (4), eastern Bali (5), Spermonde Archipelago (9), Tukang Besi Islands (12), Moluccas (14).

Previous records. *Palythoa heliodiscus* has been reported from Australia (Ryland and Lancaster 2003) and is likely widespread in the Indo-Pacific (Ryland and Lancaster

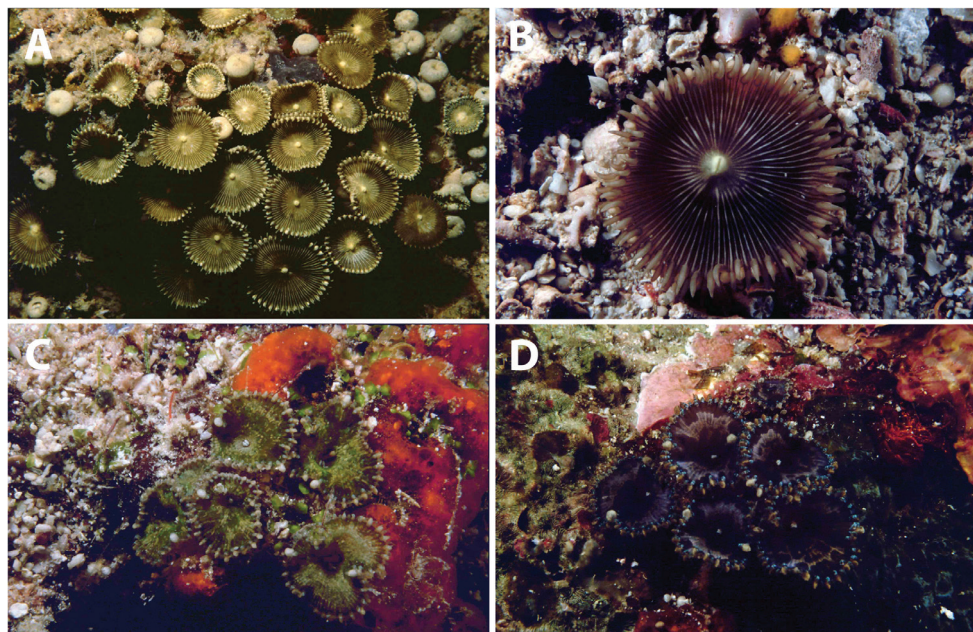


Figure 8. Images of *Palythoa* cf. *heliodiscus* from photographic records in this study. **A** *P.* cf. *heliodiscus* at the northwest side of Pulau Samalona, Spermonde Archipelago, South Sulawesi, November 23, 1997 **B** *P.* cf. *heliodiscus* at the south side of Pulau Derawan, East Kalimantan, October 16, 2003 **C** *P.* cf. *heliodiscus* at REA Wakatobi National Park station WAK.22, north channel pass of Karang Koromaha, Southeast Sulawesi, Wakatobi, Tukang Besi Is., May 12, 2003; and **D** *P.* cf. *heliodiscus* at REA Wakatobi National Park station WAK.18, Southwest Pulau Binongko, Southeast Sulawesi, Wakatobi, Tukang Besi Islands, May 10, 2003.

2003 and references within), as well as Japan (Reimer et al. 2006b), Palau (Reimer et al. 2014a), while *P. toxica* Walsh & Bowers, 1971 has been reported from Hawai'i.

Remarks. We have identified all specimens here as “cf.” as in situ images (Figure 8) there are two different morphotypes. One morphotype matches with *Palythoa heliodiscus*, with a brown oral disk with no patterns (Figures 8A, B), while the other morphotype's polyps have either green or purple oral disks with various semi-irregular patterns, as well as blue/gray or light orange tentacles (Figures 8C, D). Based on data from Okinawa and Australia, both of these morphotypes are almost identical asides from the oral disk coloration and small but consistent differences in ITS-rDNA (T. Nishimura and J.D. Reimer, unpubl. data) that may be either intraspecific or interspecific. Thus, it is still uncertain if the green/purple morphotype is an undescribed species or not (Reimer et al. 2014a).

Furthermore, the overall morphology of the green/purple morphotype closely resembles *P. toxica* from Hawai'i, and whether these Indonesian specimens are *P. toxica* or *P. heliodiscus*, and if these two species are synonyms needs to be ascertained before any formal description occurs. In situ images and further DNA sequences are therefore needed from future specimens.

9. *Palythoa* aff. *tuberculosa* (Esper, 1805)

Figures 7, 9A

Specimens examined (n=1). RMNH Coel 40521, Snellius Expedition, Pulau Haroe-koe, east of Ambon, Ambon, Moluccas, collected on May 03–07, 1930.

Photographic records. NA.

Description. This specimen superficially resembles zooanthellate *Palythoa* sp. yoron sensu Shiroma and Reimer (2010) with its very well developed coenenchyme and ‘intermediae–immersae’ morphology (Figure 9B). However, there are some differences between this specimen and *P. sp. yoron* from Okinawa. The current specimen consists of two large portions of colonies consisting of >50 polyps, while *P. sp. yoron* usually is found in very small colonies of <10 polyps. As well, *P. sp. yoron* consists of a very well developed coenenchyme from which all individual polyps partially emerge, while the current specimen appears to consist more of large robust polyps that have merged together at many locations, but not at others, giving the specimen the appearance of *P. tuberculosa* from the top, and often of *P. mutuki* from side angles. On the other hand, *P. sp. yoron* has an appearance, although intermediate between *P. tuberculosa* and *P. mutuki*, unique to and of itself. Polyps’ height (when not merged) is approximately 7.0 mm, and average width is 7.3 mm (n=10 polyps). Thus, for now, this specimen is identified as *P. aff. tuberculosa*. For details on *P. tuberculosa*, refer to the relevant species section below.

Distribution. Regions recorded in this study (Figure 7): Moluccas (14).

Previous records: NA.

Remarks. This specimen is unlike any other previous specimen observed in the field or museums by the first author. Unfortunately, as it was collected in 1930, attempts to acquire utilizable DNA sequences able to distinguish this specimen’s affinity were unsuccessful, and identification was made on gross morphology alone.

10. *Palythoa tuberculosa* Esper, 1805

Figures 7, 9B

Specimens examined (n=31). RMNH Coel 40465, Rumphius Biohistorical Expedition station 11, Leitimur, Tanjung Nasaniwe, Ambon, Moluccas (03°47'10"S, 128°05'20"E), depth = 2–5 m, collected on November 12, 1990; RMNH Coel 40466, Rumphius Biohistorical Expedition station 30, Hitu, Baguala Bay, Suli, Ambon, Moluccas (03°37'40"S, 128°17'50"E), collected on November 29, 1990; RMNH Coel 40467, Rumphius Biohistorical Expedition station 15, Hitu, Baguala Bay, 0.5 km west of Tial, Ambon, Moluccas (03°38'20"S, 128°19'40"E), depth = 2 m, collected on November 13–14, 1990; RMNH Coel 40471, Rumphius Biohistorical Expedition station 4, Leitimur, Ambon Bay, outer bay, Wainitu (near Ambon City), Ambon, Moluccas (03°42'10"S, 128°09'15"E), littoral on old shipwreck, collected on November 7–8, 1990 by H. Strack; RMNH Coel 40474, Rumphius Biohistorical Expedi-

tion station 27, Leitimur, south coast, Hutumuri, Ambon, Moluccas (03°41'50"S, 128°17'00"E), depth = 1 to 3 m, collected on November 27, 1990 by J.C. den Hartog; RMNH Coel 40505, south side of Barang Lompo, Spermonde Archipelago, South Sulawesi (05°03'23"S, 119°19'45"E), depth = 18 m, collected on October 18, 1980, by H. Moll; RMNH Coel 40511, west side of Pulau Samalona, Spermonde Archipelago, South Sulawesi (05°07'25"S, 119°20'10"E), depth = 2.5 m, collected on September 4, 1980 by H. Moll; RMNH Coel. 40517, west side of Pulau Samalona, Spermonde Archipelago, South Sulawesi (05°07'25"S, 119°20'10"E), depth = 2.5 m, collected on September 4, 1980 by H. Moll; RMNH Coel 40519, Snellius Expedition, Rumah Fija, Bo Islands, Halmahera Sea, collected on October 7, 1930; RMNH Coel 40522, Snellius Expedition, Sulu Islands, Philippines, collected on September 11–17, 1930; RMNH Coel 40523, Snellius Expedition, probably Indonesia, no locality data; RMNH Coel 40524, Snellius–II Expedition station 4.011, reef edge west of Mai, Maisel Islands, Banda Sea (05°28'S, 127°31'E), depth = 1–30 m, collected on September 7, 1984; RMNH Coel 40526, Snellius–II Expedition station 4.030, west coast of Pulau Binongko, Southeast Sulawesi, Tukang Besi Islands, Wakatobi (05°55'S, 123°59'E), depth approx. 2 m, September 10, 1984; RMNH Coel 40527, Snellius–II Expedition station 4.030, west coast of Pulau Binongko, Southeast Sulawesi, Tukang Besi Islands, Wakatobi (05°55'S, 123°59'E), depth approx. 0.5 m, September 10, 1984; RMNH Coel 40529, Snellius–II Expedition station 4.030, west coast of Pulau Binongko, Southeast Sulawesi, Tukang Besi Islands, Wakatobi (05°55'S, 123°59'E), depth approx. 8 m, September 10, 1984; RMNH Coel 40530, Snellius–II Expedition station 4.071, Slawi Bay, east Komodo, Komodo (08°34'30"S, 119°31'18"E), depth sublittoral, collected on September 17, 1984; RMNH Coel 40531, Snellius–II Expedition station 4.030, west coast of Pulau Binongko, Southeast Sulawesi, Tukang Besi Islands, Wakatobi (05°55'S, 123°59'E), depth approx. 3 to 4 m, September 10, 1984; RMNH Coel 40534, Snellius–II Expedition station 4.169, reef north of Pulau Bahuluang, Southwest Salayer, Salayer Island, South Sulawesi (06°27'S, 120°26'E), collected on September 30, 1984; RMNH Coel 40535, Snellius–II Expedition station 4.059, off Melolo, northeast Sumba (09°52'30"S, 120°40'18"E), collected on September 14, 1984; RMNH Coel 40541, Snellius–II Expedition station 4.006, Ambon Bay near Eri, Ambon, Moluccas (03°45'S, 128°08'E), depth approx. 3 m, collected on August 29, 1984; RMNH Coel 40543, Snellius–II Expedition station 4.006, Ambon Bay near Eri, Ambon, Moluccas (03°45'S, 128°08'E), depth = 0 to 10 m, collected on August 29, 1984; RMNH Coel 40548, Snellius–II Expedition station 4.052, east of Melolo, northeast Sumba (09°55'S, 120°45'E), depth approx. 3 m, collected on September 13, 1984; RMNH Coel 40552, Snellius–II Expedition station 4.048, east of Melolo, northeast Sumba (09°54'00"S, 120°43'30"E), depth = 12 m, collected on September 14, 1984; RMNH Coel 40553, Snellius–II Expedition station 4.096, northeast cape, Komodo (08°29'S, 119°34'E), depth to 30 m, collected on September 20, 1984; RMNH Coel 40555, Snellius–II Expedition station 4.096, northeast cape, Komodo (08°29'S, 119°34'E), depth to 30 m, collected on September 20, 1984; RMNH Coel 40557, Snellius–II Expedition station 4.096, northeast cape, Komo-

do (08°29'S, 119°34'E), depth = “shallow water”, collected on September 20, 1984; RMNH Coel 40568, northwest of Pulau Kapoposang, Spermonde Archipelago, South Sulawesi (04°41'40"S, 118°54'55"E), collected on May 2, 1998 by B.W. Hoeksema; RMNH Coel 40769, Snellius Expedition, Eude, South Flores, collected on March 6–8, 1930; RMNH Coel 40770, Snellius Expedition, Maratua, Berau Islands, East Kalimantan, collected on October 14–17, 1930; RMNH Coel 40771, Snellius Expedition, Maratua, Berau Islands, East Kalimantan, collected on October 14–17, 1930; RMNH Coel 40772, Snellius–II Expedition station 4.006, Ambon Bay near Eri, Ambon, Moluccas (03°45'S, 128°08'E), depth = 0 to 10 m, collected on August 29, 1984.

Photographic records (n=12). Pemuteran, West Bali (08°08'S, 114°41'E), May 20, 1998; Pemuteran, West Bali (08°08'S, 114°41'E), May 23, 1998; Napoleon Reef, West Bali (08°08'S, 114°41'E), May 20, 1998; Nusa Lembongan, Lombok Strait, East Bali, July 13, 1997; Nusa Lembongan, Lombok Strait, east Bali, July 19, 1997; Nusa Lembongan, Lombok Strait, east Bali, May 26, 1998; south of Pulau Samalona, Spermonde Archipelago, South Sulawesi (05°07'45"S, 119°20'25"E), October 27, 1997; northwest Pulau Samalona, Spermonde Archipelago, South Sulawesi (05°07'25"S, 119°20'10"E), November 25, 1997; Fauna Malesiana Maluku Expedition station MAL.12, north coast near Morela, Ambon, Moluccas November 13, 1996; North Sulawesi, Bunaken, (01°36'N, 124°47'E), April 9, 1996; Cebu, Philippines, November 21, 1998; Madang, Papua New Guinea, June 1992.

Description. This zooxanthellate species was originally described from India (Esper 1805), and subsequently redescribed utilizing specimens from the Red Sea (Klunzinger 1877). Recent work by Hibino et al. (2013) indicates the species may include some junior synonyms, and has a wide distribution across the subtropical and tropical Indo-Pacific. Polyps are embedded within a well-developed coenenchyme ('immersae', Pax 1910), and colonies vary in color from fluorescent green-yellow to dark brown or even ochre (Figure 9A).

Specimens in this study averaged 4.7 mm in polyp diameter (n=29 specimens), ranging from 2 to 8 mm. One specimen, RMNH Coel 40553, was notable for its very small polyps (average diameter 2.4 mm, n=10 polyps). Other colonies ranged from 3.1 to 6.5 mm in average diameter, similar to previous reported sizes. All specimens were 'immersae'. Generally, morphology fit well within the accepted range of *P. tuberculosa* (see Table 1 in Hibino et al. 2013), although some specimens' polyps were somewhat smaller than previously observed. These smaller sizes may also be partly due to preservation methods.

Distribution. Regions recorded in this study (Figure 7). West Bali (4), east Bali (5), northeast Sumba (6), south Flores (7), Komodo (8), Spermonde Archipelago (9), Salayer Island (10), Tukang Besi Islands (12), Maisel Islands (13), Moluccas (14), Bo Islands (15), Bunaken (18), Berau Islands (19), Sulu Islands (20), Cebu (21), Madang (22).

Previous records. This species has been phylogenetically confirmed as distributed over the entire subtropical and tropical Indo-Pacific, from at least the Red Sea to Singapore (Reimer and Todd 2009), Taiwan (Reimer et al. 2011c), Japan (e.g. Reimer et al. 2006a), New Caledonia (Sinniger 2006), and the Galapagos Islands (Reimer and Hickman 2009).

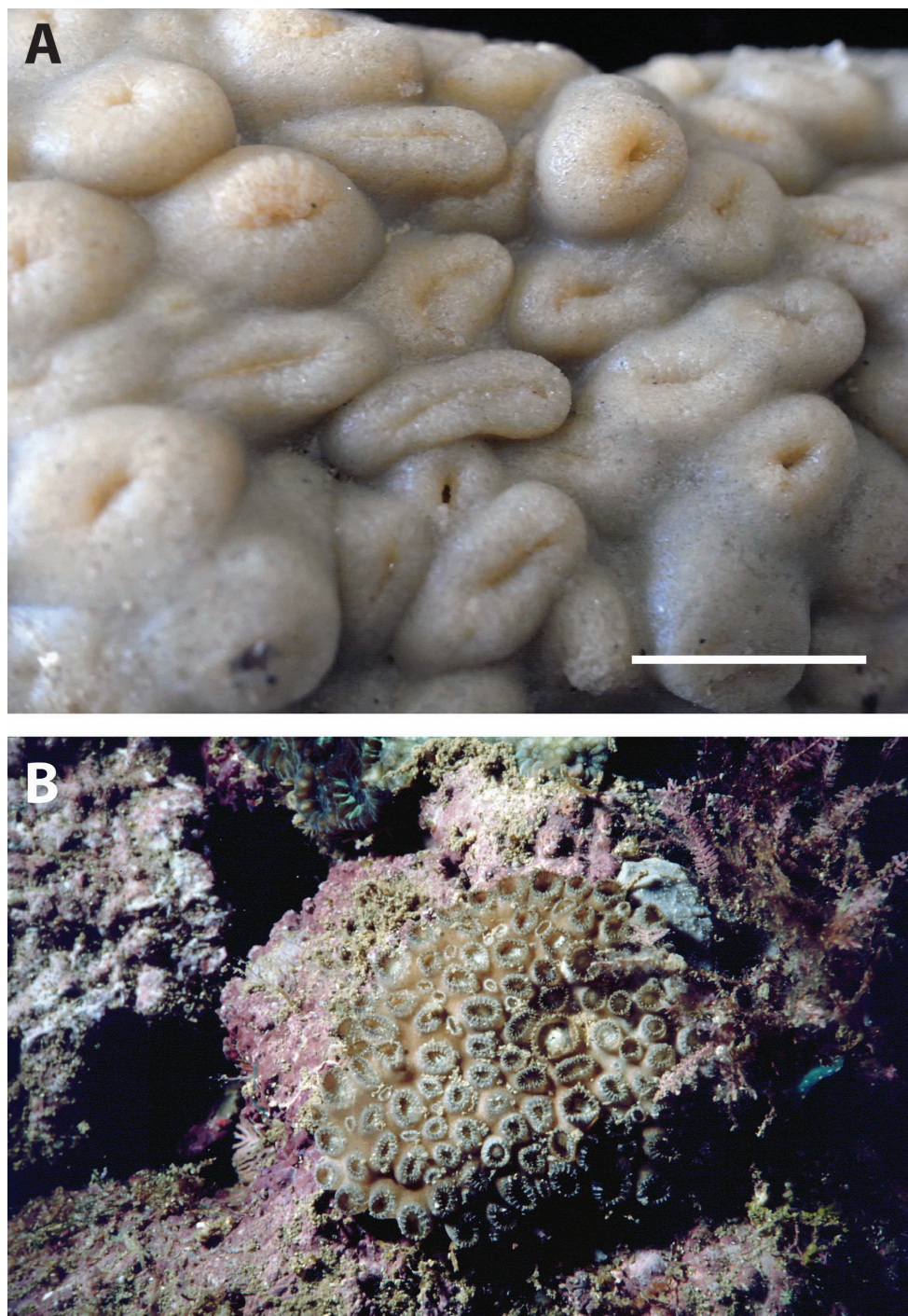


Figure 9. Images of *Palythoa tuberculosa* and *P. aff. tuberculosa* from specimens and photographic records in this study. **A** *P. aff. tuberculosa* specimen RMNH Coel 40521, Snellius Expedition, Sulu Islands, Philippines, collected on September 11–17, 1930; and **B** *P. tuberculosa* at Madang, Papua New Guinea, June 1992. Scale in **A** 1 cm.

Remarks. It is highly likely this species is the senior synonym of *P. caesia* Dana, 1846 (Hibino et al. 2013), described from Fiji and commonly reported from Australia (Burnett et al. 1997). This species is also part of the *P. tuberculosa*–*P. mutuki* species complex (Reimer et al. 2007b, M. Mizuyama and J.D. Reimer unpubl. data).

Genus *Sphenopus* Steenstrup, 1856

11. *Sphenopus marsupialis* (Gmelin, 1791)

Figures 10A, B, 11

Specimens examined (n=2). RMNH Coel 40506, East Kalimantan–Berau Expedition station BER.14, lighthouse northeast side of Pulau Panjang, Berau Islands, East Kalimantan (02°23'14"N, 118°12'34"E), depth = 12 m, collected on October 09, 2003 by B.W. Hoeksema; RMNH Coel 40509, East Kalimantan–Berau Expedition station BER.01, east side of Pulau Derawan, Berau Islands, East Kalimantan (02°17'32"N, 118°15'43"E), depth = 14 m, collected on October 11, 2003 by B.W. Hoeksema.

Photographic records (n=7). west Pulau Barang Caddi, Spermonde Archipelago, South Sulawesi (05°05'08"S, 119°18'55"E), October 06, 1997; east Bone Lola shoal, Spermonde Archipelago, South Sulawesi (05°03'15"S, 119°21'30"E), October 27, 1997; east Pulau Kudingareng Keke, Spermonde Archipelago, South Sulawesi (05°06'15"S, 119°17'35"E), September 17, 1997; north Pulau Kudingareng Keke, Spermonde Archipelago, South Sulawesi (05°06'07"S, 119°17'15"E), October 1, 1997; station BER.01, east Pulau Derawan, East Kalimantan, Berau Islands (02°17'32"N, 118°15'43"E), October 11, 2003; station BER.14, lighthouse northeast Pulau Panjang Island, East Kalimantan, Berau Islands (02°23'14"N, 118°12'34"E), October 9, 2003; station BER.24, southeast Pulau Samama, East Kalimantan, Berau Islands (02°07'51"N, 118°20'23"E), October 15, 2003.

Description. The type species of the azooxanthellate genus *Sphenopus*, this species has an Indo-West Pacific distribution (Reimer et al. 2012b). Uniquely for the order, species in this genus are unitary (not colonial), and usually free-living, as they are not attached to substrate, and instead embedded in sand or loose gravel/substrate (Figures 10A, B). Individuals can often grow to large sizes (for zoantharians); up to several cm in both length and polyp diameter. Taxonomic examination of this genus is quite limited, with only two recent studies (Soong et al. 1999, Reimer et al. 2012b), both of which clearly state that further research is needed to more clearly understand this group.

Specimen RMNH Coel 40506 consists of seven polyps, with an average height of 24.4 mm (range 18.5 to 30 mm), and an average width of 8.4 mm (range 6 to 11 mm). The non-peduncle portions of the polyps are 15–20 mm in height, with the remainder made up of peduncle.

Specimen RMNH Coel 40506 has some polyps (five of seven) somewhat different in morphology from RMNH Coel 40509 and other Naturalis *S. marsupialis* specimens from the Indian Ocean. These polyps have regularly spaced small round “tubercles”

(approx. 1 mm in diameter) on the upper half of their scapus arranged in vertical lines ($n=8-14$ vertical tubercle lines on each polyp, with 6–10 tubercles per line), making this portion of the polyp appear furrowed. As well, polyps have a small, stubby “peduncle” (2 to 5 mm in width) that is not attached to any hard substrate, intermediate between *S. marsupialis* with its completely rounded bottom end and *S. pedunculatus* with its long, attached peduncle. For now, we identify these specimens as *S. marsupialis* as their peduncles were not attached to the substrate, but it is clear more examination of these specimens is needed.

Specimen RMNH Coel 40509 consists of two polyps of different sizes, with the smaller one being 16 by 5 mm, and the larger one 24 by 15 mm. Both polyps have no peduncle and are tapered. Both polyps are somewhat rugged on their outer surface, with no discernable tubercles, and have intermittent (=not one clear stripe) small darker vertical patterns in between the capitulary ridges only on the top 3–5 mm of the oral end of polyps.

Distribution. Regions recorded in this study (Figure 11). Spermonde Archipelago (9), Berau Islands (19).

Previous records. This species has been reported from many locations in the Indo-West Pacific, including Taiwan (Soong et al. 1999) and Brunei Darussalam (Reimer et al. 2012b).

Remarks. Specimen RMNH Coel 40506 may be similar to a putative undescribed *Sphenopus* species mentioned in Soong et al. (1999) from Taiwan based on its smaller size.

12. *Sphenopus pedunculatus* Hertwig, 1888

Figures 10C, D, 11

Specimens examined ($n=2$). RMNH Coel 40507, Kepulauan Seribu Expedition station SER.29, north side of Pulau Tikus, Thousand Islands off Jakarta, northwest Java ($05^{\circ}51'13''S$, $106^{\circ}34'43''E$), depth = 30 m, collected on September 18, 2005 by B.W. Hoeksema; RMNH Coel 40510, East Kalimantan–Berau Expedition station BER.03, south side of Pulau Derawan, East Kalimantan ($02^{\circ}17'03''N$, $118^{\circ}14'49''E$), depth = 15 m, collected on October 21, 2003 by B.W. Hoeksema.

Photographic records ($n=2$). Images of RMNH Coel. 40507 and RMNH Coel 40510 as above.

Description. This azooxanthellate species was originally described from the Philippines, and has not been reported in the literature for over 80 years, excepting two brief mentions in Reimer et al. (2012b). Easily discernable from other *Sphenopus* species by the presence of a ‘foot’ (=peduncle) that is attached to substrate (e.g. small rocks).

The two specimens here varied in length from 33 to 62 mm in polyp length, and had a width between 9 to 11 mm (polyp head). The “swollen”, non-peduncle part of the polyp was between 15 to 20 mm in height, with the remainder of the length made up of the peduncle, which was between 0.5 to 3 mm in width. RMNH Coel 40507 polyps were generally smooth in appearance, while the upper portions of polyps of

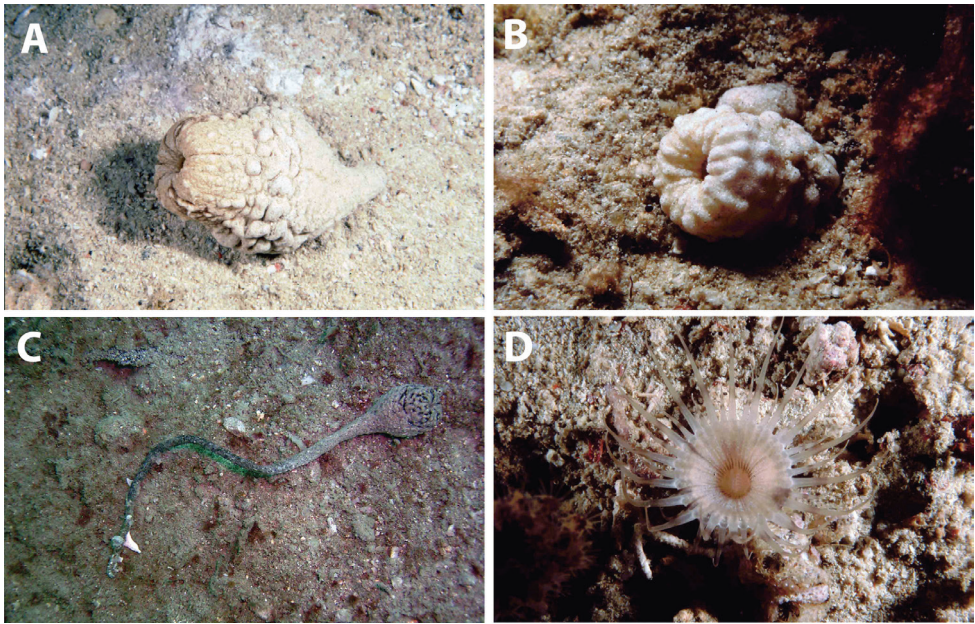


Figure 10. Images of *Sphenopus* species from photographic records in this study. **A** *S. marsupialis* at east Bone Lola shoal, Spermonde Archipelago, South Sulawesi, October 27, 1997 **B** *S. marsupialis* at station BER.14, lighthouse northeast Pulau Panjang Island, East Kalimantan, Berau Islands, October 9, 2003 **C** *S. pedunculatus* specimen RMNH Coel 40507, Kepulauan Seribu Expedition station SER.29, north side of Pulau Tikus, Thousand Islands off Jakarta, northwest Java, depth = 30 m, collected on September 18, 2005 by B.W. Hoeksema; and **D** *S. pedunculatus* specimen RMNH Coel 40510, East Kalimantan–Berau Expedition station BER.03, south side of Pulau Derawan, East Kalimantan, depth = 15 m, collected on October 21, 2003 by B.W. Hoeksema.

RMNH Coel 40510 were somewhat rugged, with small round tubercles 0.5 mm in diameter roughly arranged in vertical lines. The spaces between these small tubercles were colored a much darker color than the remainder of the polyps' outer surfaces. The peduncle of specimens and images (Figure 10C) are much thinner and longer than the sketch in Hertwig (1888). However, so few data are available for this (and other *Sphenopus* species) that currently nothing is known about intraspecific variation, and for now, we group these two specimens within this species.

Distribution. Regions recorded in this study (Figure 11). Northwest Java (3), Berau Islands (19).

Previous records. This species was originally described from the Philippines, but has not been mentioned in recent literature (except for Reimer et al. 2012b), and hence very little is known on its distribution or ecology.

Remarks. It is unknown as to whether the peduncle is a morphological characteristic that forms only when there is a hard substrate available, and this needs to be investigated to confirm this is truly a different species from *S. marsupialis*.

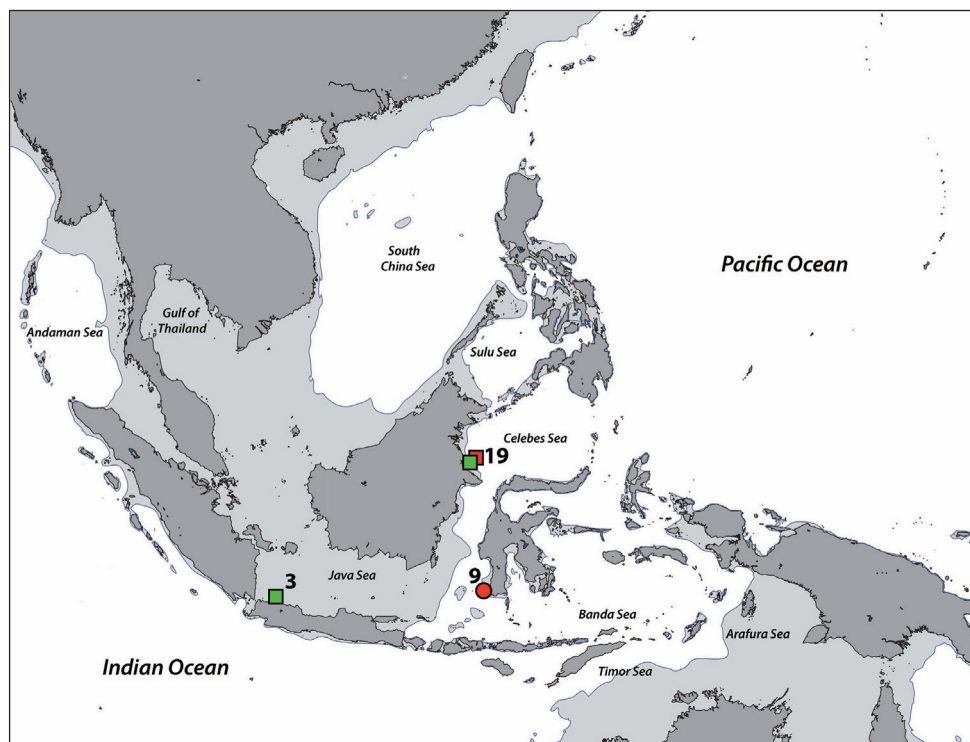


Figure 11. Distribution of *Sphenopus* species from specimens and photographic records from this study. *Sphenopus marsupialis* specimens in red, and *S. pedunculatus* in green. Region numbers correspond to locations given in species' information. Boxes indicate presence of specimens (with or without photographic records), while circles indicate only photographic records. Overlapping symbols indicate the same region.

Suborder Macrocnemina Haddon & Shackleton, 1891a

Family Hydrozoanthidae Sinniger, Reimer & Pawlowski, 2010

Genus *Hydrozoanthus* Sinniger, Reimer & Pawlowski, 2010

13. *Hydrozoanthus gracilis* (Lwowsky, 1913) sensu Di Camillo et al. (2010)

Figures 12A, B, 13

Specimens examined (n=3). RMNH Coel 40692, Snellius–II Expedition station 4.098, East Komodo, Komodo (08°29'54"S, 119°38'06"E), depth = 75 m, collected on September 19, 1984 by rectangular dredge; RMNH Coel. 40518, Snellius–II Expedition station 4.022, north Pulau Mai, Maisel Islands, Banda Sea (05°29'S, 127°32'E), depth = 0 to 1.5 m, collected on September 7, 1984; RMNH Coel 3816, Snellius Expedition, Sipangkat Island, near Siburu Island, Sulu Islands, Philippines, collected on September 10–14, 1929.

Photographic records (n=5). Southwest Nusa Penida, eastern Bali (08°49'S, 115°34"E), May 25, 1998; Desa Ped, Nusa Penida, Lombok Strait, east Bali

(08°40'28"S, 115°30'50"E), May 25, 1998; east Tanjung Taal, Nusa Lembongan, Lombok Strait, east Bali (08°39'33"S, 115°26'37"E), May 24, 1998; Fauna Maleisiana Maluku Expedition station MAL.21, west of Lilibooi, north coast Ambon Bay, Ambon, Moluccas (03°44'S, 128°02'E), November 20, 1996; East Kalimantan Program station BER.16, northeast Pulau Maratua, East Kalimantan, Berau Islands (02°17'29"N, 118°35'29"E), October 10, 2003.

Description. As originally and previously described (Di Camillo et al. 2010), this azooxanthellate, colonial species is found as an epibiont on hydrozoans, particularly *Plumularia habereri* Stechow, 1909. In this study, this species consists of only one morphotype, with a gray to brown scapus, and reddish-brown oral disk and tentacles (Figure 12B). The appearance matches well with the morphotype of the species observed by Di Camillo et al. (2010).

In this study, measurements are only available for two specimens, with polyps averaging 2.4 mm in height and 2.1 mm in width. These data also fit well with Di Camillo et al. (2010), who mention polyp heights of 2–5 mm, widths of 1.6 to 3 mm, with 32 tentacles and mesenteries.

Distribution. Regions recorded in this study (Figure 13). East Bali (5), Komodo Island (8), Maisel Islands (13), Moluccas (14), Berau Islands (19), Sulu Islands (20).

Previous records. Originally reported from Sagami Bay, Japan (Lwowsky 1913), and subsequently reported from Taiwan (Reimer et al. 2011c), New Caledonia (Sinniger 2006), and Indonesia (Sinniger et al. 2005, Di Camillo et al. 2010). It appears this species has an Indo-West Pacific distribution.

Remarks. This morphotype differs from the other known morphotype of the species (*sensu* Carlgren 1934) associated with this binomen, which is yellow in coloration. The original description of the species from Sagami Bay, Japan by Lwowsky (1913) was of a “gray, sandy” morphotype, but this was preserved in formalin, and thus could be either morphotype discussed here, or even a different one altogether. Phylogenetic analyses have shown subtle differences of sequences of specimens within this species (Sinniger et al. 2008), indicating that taxonomic revision may be needed in the future for this species group.

14. *Hydrozoanthus* sp. 1

Figures 12C, 13

Specimens examined. NA.

Photographic records (n=1). Balicasag Island, Cebu Strait, Philippines (09°31'01"N 123°41'04"E), November 21, 1999.

Description. Similar to *H. gracilis* above, this azooxanthellate, colonial species is found as an epibiont on *Plumularia habereri*. As described in Di Camillo et al. (2010; as *Parazoanthus* sp.), this species has much smaller polyps than *H. gracilis*, forming colonies only on the main branch(es) of *Pl. habereri* colonies. Polyps are much less in-

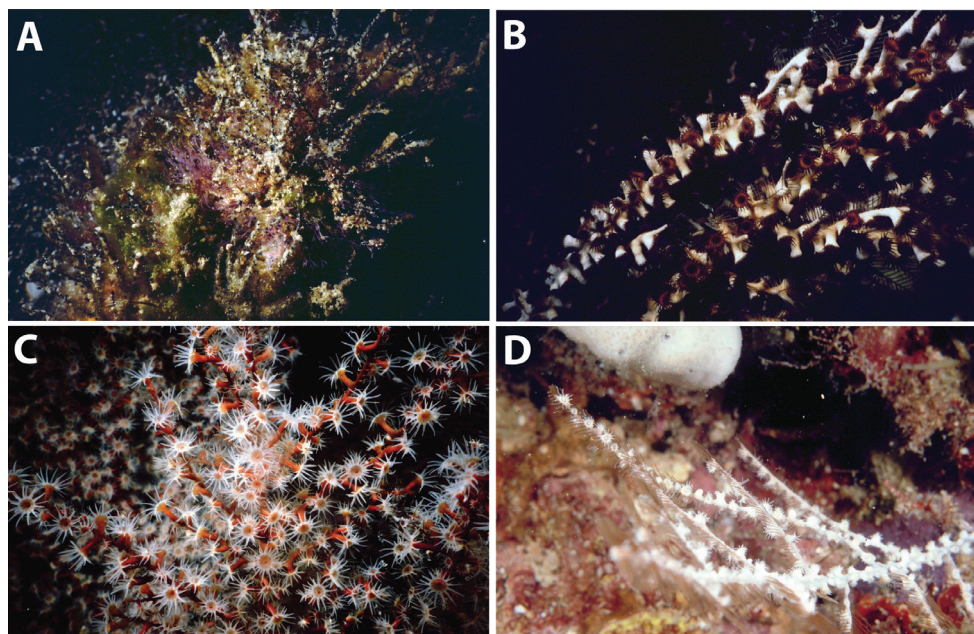


Figure 12. Images of *Hydrozoanthus* species from photographic records in this study. **A** *H. gracilis* from Fauna Malesiana Maluku Expedition, station MAL.21, west of Lilibooi, north coast Ambon Bay, Ambon, Moluccas, November 20, 1996 **B** *H. gracilis* at Southwest Nusa Penida, east Bali, May 25, 1998 **C** *Hydrozoanthus* sp. 1 at Balicasag Island, Cebu Strait, Philippines, November 21, 1999; and **D** *Hydrozoanthus* sp. 2 at East Kalimantan Program station BER.20, Tanjung Pandan shoal, Southwest of Pulau Panjang, East Kalimantan, Berau Islands, October 22, 2003.

crusted than *H. gracilis*. The *Pl. habereri* colonies hosting this species are much bigger than those with *H. gracilis*, as shown by (Di Camillo et al. 2010). Red scapus with yellow tentacles, 22 to 24 tentacles slightly longer than oral disk diameter (Figure 12C).

Distribution. Regions recorded in this study (Figure 13). Cebu (21).

Previous records. Reported from Bunaken, North Sulawesi, in Di Camillo et al. (2010).

Remarks. This undescribed species was informally and well described by Di Camillo et al. (2010) as “*Parazoanthus* sp.”. Specimens and DNA sequences are needed to properly describe this species.

15. *Hydrozoanthus* sp. 2

Figures 12D, 13

Specimens examined. NA.

Photographic records (n=1). East Kalimantan Program station BER.20, Tanjung Pandan shoal, southwest of Pulau Panjang, East Kalimantan, Berau Islands (02°19'15"N, 118°06'33"E), October 22, 2003.

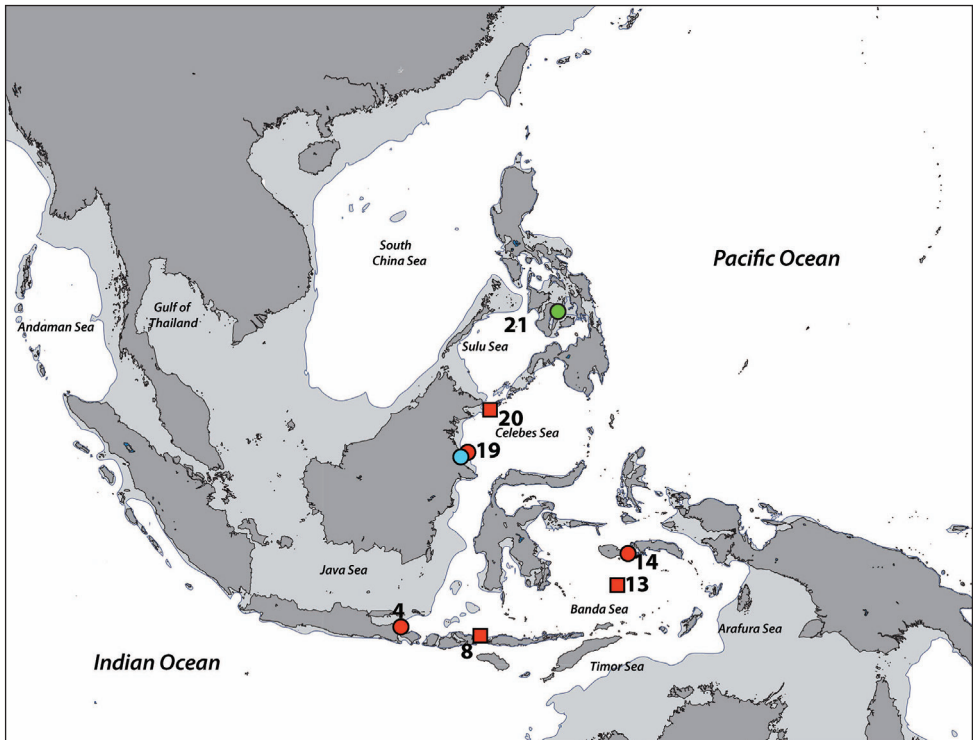


Figure 13. Distribution of *Hydrozoanthus* species from specimens and photographic records from this study. *Hydrozoanthus gracilis* specimens in red, *Hydrozoanthus* sp. 1 in green, and *Hydrozoanthus* sp. 2 in blue. Region numbers correspond to locations given in species' information. Boxes indicate presence of specimens (with or without photographic records), while circles indicate only photographic records. Overlapping symbols indicate the same region.

Description. Similar to *H. gracilis* and *Hydrozoanthus* sp. 1 above, this azooxanthellate, colonial species is found as an epibiont on *Plumularia habereri*. Similar to *Hydrozoanthus* sp. 1, this completely white species has much smaller polyps than *H. gracilis*, forming colonies only on the main branch(es) of *Pl. habereri* colonies (Figure 12D). Polyps are much less incrustated than *H. gracilis*.

Regions recorded in this study (Figure 13). Berau Islands (19).

Previous records. NA.

Remarks. This undescribed species may be a different colored morphotype of *Hydrozoanthus* sp. 1 (above) informally described by Di Camillo et al. (2010) as "*Parazoanthus* sp.". Specimens and DNA sequences are needed to properly describe this species.

Genus *Terrazoanthus* Reimer & Fujii, 2010**16. *Terrazoanthus* sp. 1**

Figures 14A, B, 15

Specimens examined (n=1). RMNH Coel 40469, Fauna Malesiana Maluku Expedition station MAL.05, Leitimur, outer Ambon Bay, Tanjung Bentang, Ambon, Moluccas (03°35'S, 128°05'E), depth = NA, collected on November 7, 1996 by J.C. den Hartog.

Photographic records (n=1). West Pulau Badi, Spermonde Archipelago, South Sulawesi (04°58'06"S, 119°16'57"E), September 29, 1997.

Description. Azooxanthellate. Polyps well free and clear of coenenchyme. Outer surface of polyps covered with dense incrustation of irregularly sized sand particles, reminiscent of *Microzoanthus* sp. Oral disk semi-translucent with dark, almost black coloration, except for oral opening, which is much lighter in color. 40 to 50 tentacles, at least as long as oral disk diameter, with same blackish coloration as oral disk, with terminal 1/4 whitish in coloration. Colonies attached to non-living substrate. Specimen RMNH Coel 40469 is apparently a fragment of a whole colony, while the photographic record shows a colony of approximately 50 polyps arising from a common coenenchyme (Figure 14A). The single specimen had polyps averaging 6.8 mm in length (n=3) and 3.1 mm in width (n=6).

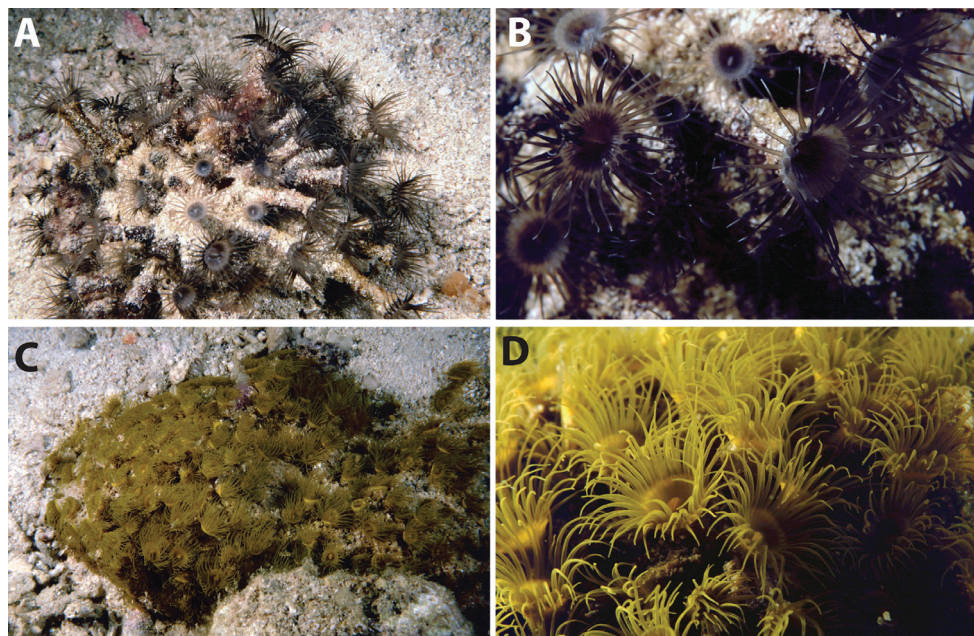


Figure 14. Images of *Terrazoanthus* species from photographic records in this study. **A** and **B** *Terrazoanthus* sp. 1 at the west side of Pulau Badi, Spermonde Archipelago, South Sulawesi, September 29, 1997; and **C** and **D** *Terrazoanthus* sp. 2 at the west side of Bone Lola shoal, Spermonde Archipelago, South Sulawesi, April 22, 1998.

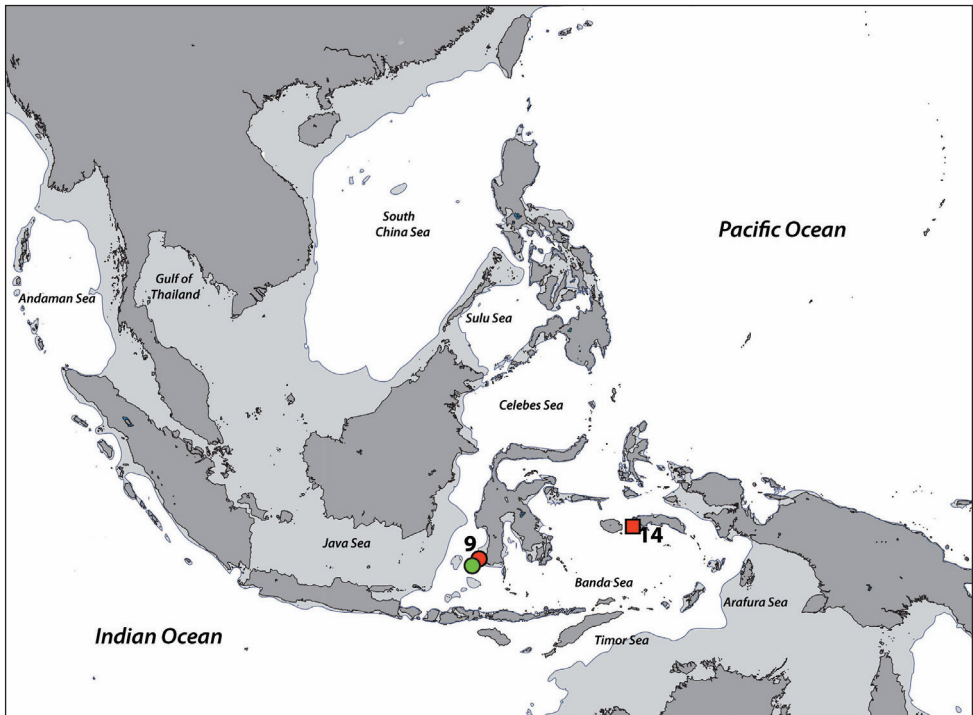


Figure 15. Distribution of *Terrazoanthus* species from specimens and photographic records from this study. *Terrazoanthus* sp. 1 specimens in red, and *Terrazoanthus* sp. 2 in green. Region numbers correspond to locations given in species' information. Boxes indicate presence of specimens (with or without photographic records), while circles indicate only photographic records. Overlapping symbols indicate the same region.

Distribution. Regions recorded in this study (Figure 15). Spermonde Archipelago (9), Moluccas (14).

Previous records. None, although similar undescribed specimens have been photographed in the Philippines (P. Poppe, pers. comm.), and collected from Okinawa, Japan (Reimer, unpubl. data), indicating a potential West Pacific distribution.

Remarks. This species is similar in appearance but different in coloration to *T. onoi* from the Galapagos and west coast of Central and South America.

17. *Terrazoanthus* sp. 2

Figures 14C, D, 15

Specimens examined. NA.

Photographic records (n=1). West Bone Lola shoal, Spermonde Archipelago, South Sulawesi (05°03'15"S, 119°21'15"E), April 22, 1998.

Description. With only a single photographic record available, even an informal description of this undescribed species is limited. Besides from yellow coloration, this

species is outwardly similar to *Terrazoanthus* sp. 1 above. Polyps appear to be more crowded than in *Terrazoanthus* sp. 1, with 40 to 54 yellow tentacles longer than oral disk diameter (Figure 14D).

Regions recorded in this study (Figure 15). Spermonde Archipelago (9).

Overall distribution. Unknown, although similar specimens have been photographed in the Philippines (P. Poppe, pers. comm.).

Remarks. This species has been traded in the aquarium trade as “yellow polyps”, and is thought to be distributed primarily in Indonesia, yet no museum specimens exist, preventing this species from being formally described. Colonies often appear to be intermixed with *Zoanthus* spp. colonies in shallow water (J.D. Reimer, pers. obs.). Although undescribed, this putative species has been placed with the genus *Terrazoanthus* based on DNA sequences acquired from aquarium trade polyps (Sinniger et al. 2005, Reimer and Fujii 2010).

Family Parazoanthidae Delage & Hérourard, 1901

18. Parazoanthidae sp. 1

Figures 16A, B, 17

Specimens examined (n=2). RMNH Coel 40766, Fauna Malesiana Maluku Expedition station MAL.09, southwest coast, Ambon, Latuhalat, Moluccas (03°46'S, 128°06'E), depth = to 24 m, collected on November 11, 1996; RMNH Coel 40768, Snellius Expedition, Pulau Bo Islands, Halmahera Sea, collected on October 5, 1930.

Photographic records (n=1). Station BER.30, north of Lighthouse 1 Reef, south of Pulau Derawan, East Kalimantan, Berau Islands (02°16'02"N, 118°14'23"E), October 22, 2003.

Description. Azooxanthellate, epibiotic on *Keroeides* sp., polyps approximately the same height as width (approximately 1–3 mm), connected by coenenchyme visible on the outer surface of the octocoral colony. Polyps numerous, placed between smaller octocoral polyps, pale yellow in coloration, with outer surface of polyps slightly reddish in color similar to host octocoral. Tentacles relatively short, approximately half of the oral disk diameter, also pale yellow, and approximately 20 in number (Figure 16A).

Specimen RMNH Coel 40766 is larger than RMNH Coel 40768 (polyp average width 2.6 mm vs 1.6 mm, respectively). However, the latter specimen is quite old (from the original Snellius Expedition) and this difference may be due to fixation methods.

Distribution. Regions recorded in this study (Figure 17). Moluccas (14), Bo Islands (15), Berau Islands (19).

Previous records. NA.

Remarks. Only two specimens and one photographic record of this undescribed species exist. However, these records are each from different expeditions, and it is reasonable to expect that this species is at least distributed in the Banda and Celebes Seas.

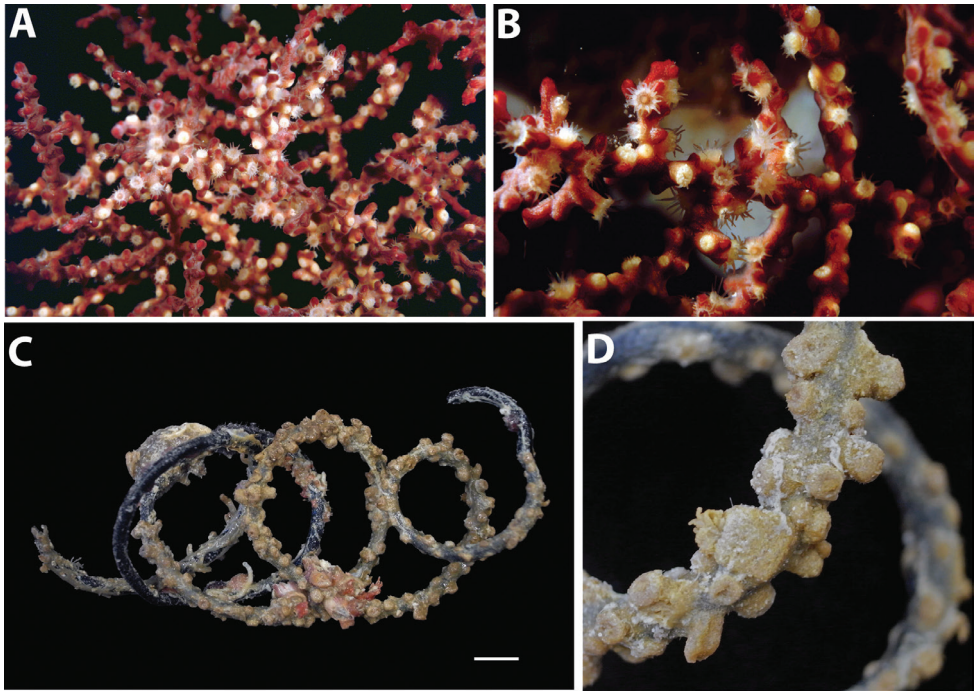


Figure 16. Images of Parazoanthidae sp. 1 and Parazoanthidae sp. 2 from specimens and photographic records in this study. **A** and **B** Parazoanthidae sp. 1 at station BER.30, north of Lighthouse 1 Reef, south of Pulau Derawan, East Kalimantan, Berau Islands, October 22, 2003. Note octocoral polyps on antipatharian on left side of image **C** and **D** Parazoanthidae sp. 2 specimen RMNH Coel 40762, Snellius–II Expedition, Station 4.227, west Pulau Tinanja, Taka Bone Rate, depth = 60 m, collected on October 15, 1984 by rectangular dredge. Scale in **C** 1 cm.

Recently, many different genera in the family Parazoanthidae have been described based on a combination of epizoitic relationships and phylogenetic analyses (e.g. Sinniger et al. 2010, 2013). However, no parazoanthids have been reported in association with *Keroeides*, and therefore currently it is impossible to place these specimens and records into a genus without both further examination of specimens combined with DNA sequence data.

19. Parazoanthidae sp. 2

Figures 16C, D, 17

Specimens examined (n=1). RMNH Coel 40762, Snellius–II Expedition, Station 4.227, west Pulau Tinanja, Taka Bone Rate (06°32'48"S, 121°09'36"E), depth = 60 m, collected on October 15, 1984 by rectangular dredge.

Photographic records. NA.

Description. Epibiotic on *Cirripathes* sp. (specimen RMNH Coel 24832). Polyps of this azooxanthellate zoantharian specimen are relatively small (average

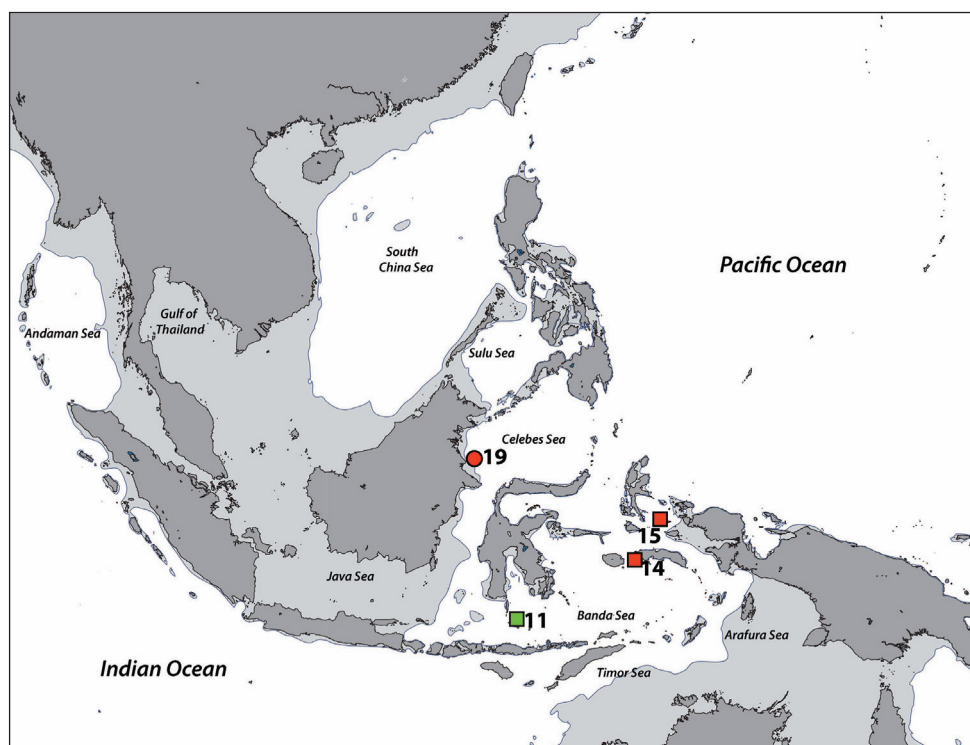


Figure 17. Distribution of Parazoanthidae sp. 1 and Parazoanthidae sp. 2 from specimens and photographic records from this study. Parazoanthidae sp. 1 specimens in red, and Parazoanthidae sp. 2 in green. Region numbers correspond to locations given in species' information. Boxes indicate presence of specimens (with or without photographic records), while circles indicate only photographic records.

width 2.1 mm, $n=8$ polyps) and do not protrude much from the coenenchyme, with polyp height approximately same as width. Polyps and coenenchyme are heavily encrusted, and golden yellow-brown in color. Coenenchyme forms a thin sheath over the antipatharian surface. Capitulary ridges not clearly discernable. Polyps form semi-regular vertical rows over short distances of the antipatharian (e.g. approx. 5 cm), but with no observable pattern for the entire colony (Figure 16C). Colony encrusts the top approximately 1/2 of the *Cirripathes* specimen; starting approximately 15 cm from the bottom holdfast. The *Cirripathes* colony's proximal tip appears to be broken off and missing.

Distribution. Regions recorded in this study (Figure 17). Taka Bone Rate (11). **Past records.** NA.

Remarks. This species may belong to genus *Antipathozoanthus*, which was described recently by Sinniger et al. (2010) and includes species from both the Atlantic and Indo-Pacific, with reports of specimens also from the Red Sea (Reimer et al. 2014b). It is likely several undescribed *Antipathozoanthus* species are present in the Indo-Pacific, as only one *Antipathozoanthus* species from the Galapagos has been formally described. In situ images and DNA sequences are needed to formally describe this species.

Genus *Parazoanthus* Haddon & Shackleton, 1891a**20. *Parazoanthus* sp. 1**

Figures 18A, 19

Specimens examined. NA.

Photographic records (n=3). West side of Pulau Kudengareng Keke, Spermonde Archipelago, South Sulawesi (05°06'20"S, 119°17'03"E), June 4, 1997; Cabilao Island, Cebu Strait, Philippines (09°52'35"N, 123°46'33"E), November 16, 1999; station WAK.24, Ndaa Atoll northwest outer slope, REA Wakatobi National Park, Tukang Besi Islands, Wakatobi, Southeast Sulawesi, (05°38'46"S, 124°02'42"E), May 12, 2003.

Description. Very small (polyp diameter likely approximately 1 mm) azooxanthellate polyps regularly spaced and embedded within encrusting sponge tissue (Figure 18A). Polyps differentially colored from sponges; dark red (Cebu), yellow (Pulau Kudengareng Keke), white (Wakatobi). Tentacles up to 24 in number (in images here), as long as diameter of oral disk.

Distribution. Regions recorded in this study (Figure 19). Spermonde Archipelago (9), Tukang Besi Islands (12), Cebu (21).

Past records. Previously, similar specimens have been reported from Japan (Sinniger et al. 2008) and the Red Sea (Reimer et al. 2014b).

Remarks. Based on phylogenetic data (J. Montenegro, F. Sinniger and J.D. Reimer, unpubl. data) it appears that this group includes several undescribed species. The species has been found on cave ceilings (Figure 18A), which may explain why it is azooxanthellate as in some other hexacorals with white polyps (Hoeksema 2012b, Reimer et al. 2014, Irei et al. subm).

21. *Parazoanthus* sp. 2

Figures 18B, 19

Specimens examined (n=4). RMNH Coel 40544, Snellius–II Expedition Station 4.061, east of Melolo, northeast Sumba (09°54'12"S, 120°43'30"E), depth = 50 m, collected on September 15, 1984 by rectangular dredge; RMNH Coel. 40570, station 9, reef slope of southwest Pulau Nain, Bunaken, North Sulawesi (01°46'N, 124°45'E), collected on May 8, 1998 by B.W. Hoeksema; RMNH Coel 40572, Ternate Expedition Station TER.27, Tanjung Ratemu (south of river), west Halmahera Sea, North Moluccas (00°54'45"N, 127°29'10"E), depth = 20 m, collected on November 8, 2009 by B.W. Hoeksema; RMNH Coel 40757, Indonesia 2012 Expedition, Station LEM.34, west Pulau Sarena Kecil Lembeh, North Sulawesi (01°27'26"N, 125°13'31"E), depth = 22 m, collected on February 17, 2012 by B.W. Hoeksema.

Photographic records (n=3). West Pulau Kudengareng Keke, Spermonde Archipelago, South Sulawesi (05°06'20"S, 119°17'03"E), June 4, 1997; southeast Likuan,

Bunaken, North Sulawesi (01°36'N, 124°47'E), May 10, 1998; Main coast, West Bali (08°06'50"S, 114°30'40"E), May 22, 1998.

Description. Azooxanthellate, epibiotic on encrusting sponges, with 3 to 6 polyps arising in groups from a common coenenchyme, or occasionally arising in rows from stolons (Figure 18B). Polyps (oral disk, tentacles, scapus) pale yellow/cream in color. 36 to 40 tentacles, longer in length than oral disk diameter. Specimens' preserved polyps (n=2 specimens, 10 polyps per specimen) averaged 5.8 mm in height (range 4 to 8 mm) and 3.3 mm in width (range 2.5 to 5 mm).

Distribution. Regions recorded in this study (Figure 19). West Bali (4), north-east Sumba (6), Spermonde Archipelago (9), west Halmahera Sea (16), Lembah Strait (17), Bunaken (18).

Past records. NA.

Remarks. The only sponge-associated *Parazoanthus* species formally described from the Indo-Pacific are *P. elongatus* McMurrich, 1904 from the west coast of South America and New Zealand (Sinniger and Haussermann 2009) and *P. darwini* Reimer & Fujii, 2010 from the Galapagos. Thus, no similar species have been reported from past or recent zoantharian work in surrounding CIP regions, and therefore it is likely that these specimens constitute an undescribed species. Although *Parazoanthus* has recently been taxonomically redescribed (Sinniger et al. 2010), and the species now only encompasses sponge-associated species, the genus is still paraphyletic and taxonomic revision is needed. DNA sequences from undescribed species are needed to correctly place specimens such as these into the correct clade.

22. *Parazoanthus* sp. 3

Figures 18C, D, 19

Specimens examined (n=2). RMNH Coel 40525, Snellius–II Expedition station 4.100, east of Komodo Island (08°28.6'S, 119°37.3'E), depth 91 m, collected on September 19, 1984 by rectangular dredge; RMNH Coel 40545, Snellius–II Expedition station 4.051, east of Melolo, northeast Sumba (09°53.5'S, 120°42.7'E), depth 75–90 m, collected on September 13, 1984 by rectangular dredge.

Photographic records. NA.

Description. This putative azooxanthellate species is similar in size to *Parazoanthus* sp. 2 above, with polyps of average 6.1 mm in height (range 2.5 to 10 mm; n=2 colonies) and average width of 3.2 mm (range 2 to 4 mm). Some small dark incrustations visible on lower half (=aboral) of polyps' scapus. Approximately 20 capitulary ridges, indicating tentacle counts of approximately 40. Polyps range from cream (RMNH Coel 40525) to tan (RMNH Coel 50545) in color when preserved. Polyps arise from a well-developed stoloniferous coenenchyme in rows, with most found along the upper and outer edges of flat, paddle-shaped sponges (Figures 18C, D). No polyps found on the lower 'foot' or 'stalk' of sponges.

Distribution. Regions recorded in this study (Figure 19). Northeast Sumba (6), Komodo Island (8).

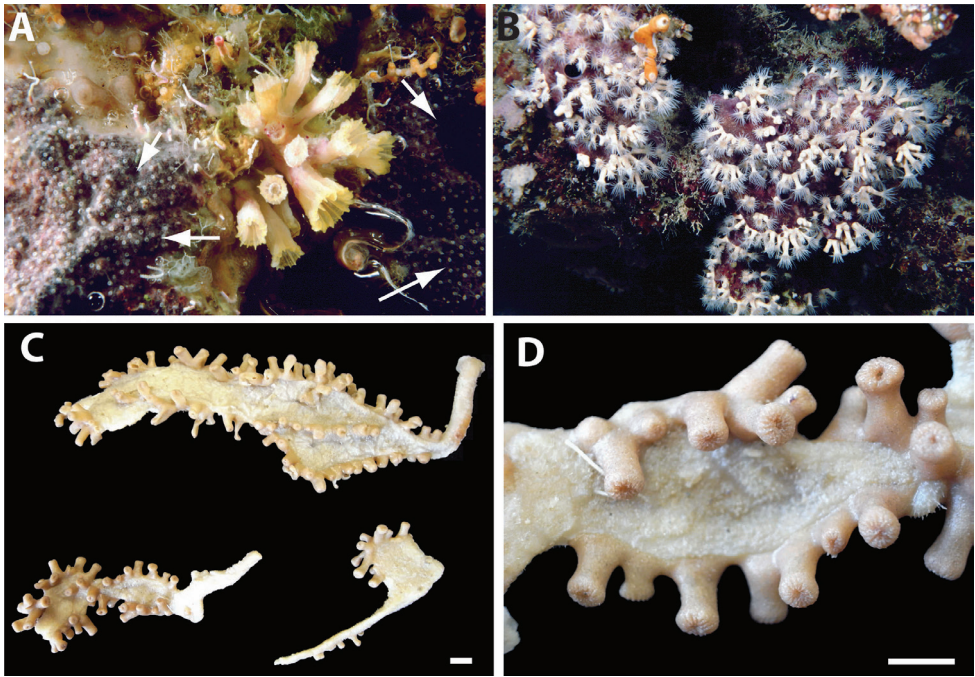


Figure 18. Images of *Parazoanthus* species from specimens and photographic records in this study. **A** *Parazoanthus* sp. 1 on cave ceiling at station WAK.24, Ndaa Atoll northwest outer slope, REA Wakatobi National Park, Southeast Sulawesi, Tukang Besi Islands, Wakatobi, May 12, 2003 **B** *Parazoanthus* sp. 2 at Southeast Likuan, Bunaken, North Sulawesi, May 10, 1998; and **C** and **D** *Parazoanthus* sp. 3 specimen RMNH Coel 40545, Snellius–II Expedition station 4.051, east of Melolo, northeast Sumba, depth = 75 to 90 m, collected on September 13, 1984 by rectangular dredge. Scales in **C** and **D** 1 cm.

Past records. NA.

Remarks. Similar in size to *Parazoanthus* sp. 2 above, we have included these two specimens as a separate putative species in this study. This is partly due to specimens being in association with a different sponge species (compare Figures 18B, C), as host specificity may differ between species (e.g. Crocker and Reiswig 1981; Swain and Wulff 2007). As well, *Parazoanthus* sp. 3 specimens are from deeper depths (75 to 91 m as opposed to 20 to 50 m) than *Parazoanthus* sp. 2.

Family Epizoanthidae Delage & Hérourard, 1901

Genus *Epizoanthus* Gray, 1867

23. *Epizoanthus illoricatus* Tischbiersek, 1930

Figures 20A, 21

Specimens examined (n=4). RMNH Coel 40533, Snellius–II Expedition Station 4.222, south of Pulau Tarupa Kecil, Taka Bone Rate (06°31'30"S, 121°08'00"E),

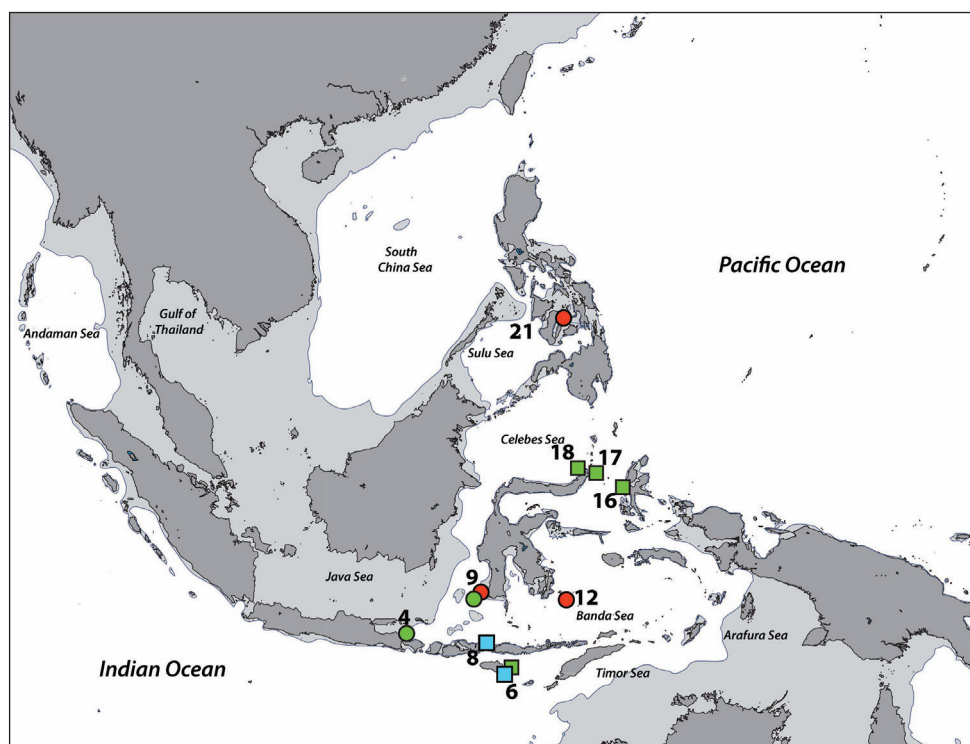


Figure 19. Distribution of *Parazoanthus* species from specimens and photographic records from this study. *Parazoanthus* sp. 1 specimens in red, *Parazoanthus* sp. 2 in green, and *Parazoanthus* sp. 3 in blue. Region numbers correspond to locations given in species' information. Boxes indicate presence of specimens (with or without photographic records), while circles indicate only photographic records. Overlapping symbols indicate the same region.

depth 58 m, collected on October 15, 1984 by rectangular dredge; RMNH Coel 40546, Snellius–II Expedition Station 4.051, east of Melolo, northeast Sumba (09°53'30"S, 120°42'42"E), depth = 75 to 90 m, collected on September 13, 1984 by rectangular dredge; RMNH Coel 40571, Ternate Expedition Station TER.27, Tanjung Ratemu, south of river, west Halmahera Sea (00°54'44"N, 127°29'10"E), depth = 20 m, collected on November 08, 2007 by B.W. Hoeksema; RMNH Coel 40758, station LEM.32, north Sarena Kecil, Lembah Strait, North Sulawesi (01°27'26"N, 125°13'38"E), depth = 30 m, collected on February 16, 2012 by B.W. Hoeksema.

Photographic records (n=6). West Menjangan, West Bali (08°05'33"S, 114°29'47"E) May 22, 1998 (3 different specimens); Maluku Expedition station MAL.21, north coast Ambon Bay, Tanjung Hatupero, east of Lilibooi, Ambon (03°44'S, 128°02'E), November 20, 1996; southeast Likuan, Bunaken, North Sulawesi (01°36'N, 124°47'E), May 10, 1998; station BER.04, south Pulau Derawan, East Kalimantan (02°17'03"N, 118°14'49"E), October 18, 2003.

Description. Originally described from the Philippines. Azooxanthellate. Polyps of this species often grow at the outer bends of the zig-zag shaped tubes, and combined

with polyps' smaller size and thin coenenchyme (Figure 20A), colonies appear to be much less crowded than as seen in *E. aff. illoricatus* (Figure 20B).

Polyps of specimens in the RMNH collection are generally less than 1 mm in diameter, and never more than 2 mm, and of approximately equal height. Coenenchyme generally light gray in color, oral disk and tentacles semi-translucent brown. Tentacles in images 20–22 in number, much thinner than as seen in *Epizoanthus aff. illoricatus* below, with orange or white colored proximal tips, longer in length than oral disk diameter. The two deeper specimens (RMNH Coel 40533 and 40546) have highly developed thin coenenchymes covering the entire worm tubes' surface, and are both dark black in color. On the other hand, the shallower specimens had some unitary polyps, and colonial polyps were often in clusters of two or three with poorly developed coenenchyme.

The morphological characters and dimensions observed in the specimens in this study agree well with the original description by Tischbierek (1930).

Distribution. Regions recorded in this study (Figure 21). West Bali (4), north-east Sumba (6), Take Bone Rate (11), Moluccas (14), west Halmahera Sea (16), Lembeh Strait (17), Bunaken (18), Berau Islands (19).

Past records. Originally described from Manila, and subsequently reported from Taiwan (Reimer et al. 2013a), New Caledonia (Sinniger 2006), Palau (Reimer et al. 2014a), and Osprey Reef, Australia in the Coral Sea (Lindsay et al. 2012), indicating a western Indo-Pacific distribution. Found from specimens in this study as shallow as 20 m, and as deep as 90 m, similar to depths reported at Osprey Reef (=82.5 m) (Lindsay et al. 2012).

Remarks. Until this report, any *Epizoanthus* spp. on a zig-zag shaped eunicid worm was recorded as *E. illoricatus*. However, from the preliminary analyses here, it appears that there may be two or more species within this group. Thus, previous records must be treated with caution.

24. *Epizoanthus aff. illoricatus* Tischbierek, 1930

Figures 20B, 21

Specimens (n=2). RMNH Coel 40536, Snellius–II Station 4.058, east of Melolo, northeast Sumba (09°51'S, 120°45'E), depth = 180 m, collected on September 14, 1984 by rectangular dredge; RMNH Coel 40547, Snellius–II Station 4.051, east of Melolo, northeast Sumba (09°53'30"S, 120°42'42"E), depth = 75 to 90 m, collected on September 13, 1984 by rectangular dredge.

Photographic records (n=12). Desa Ped, north Nusa Penida, east Bali (08°40'28"S, 115°30'50"E), May 28, 1998; 4 specimens from Tulamben, east Bali (08°16'26"S, 115°35'28"E), July 9–10, 1997; Nusa Penida, east Bali, (08°40'23"S, 115°29'13"E), May 27, 1998; Kapoposang, Spermonde Archipelago, South Sulawesi (04°41'40"S, 118°54'55"E), June 24, 1997, August 8, 1997; west Pulau Samalona, Spermonde Archipelago, South Sulawesi (05°07'30"S, 119°20'15"E), September 16,

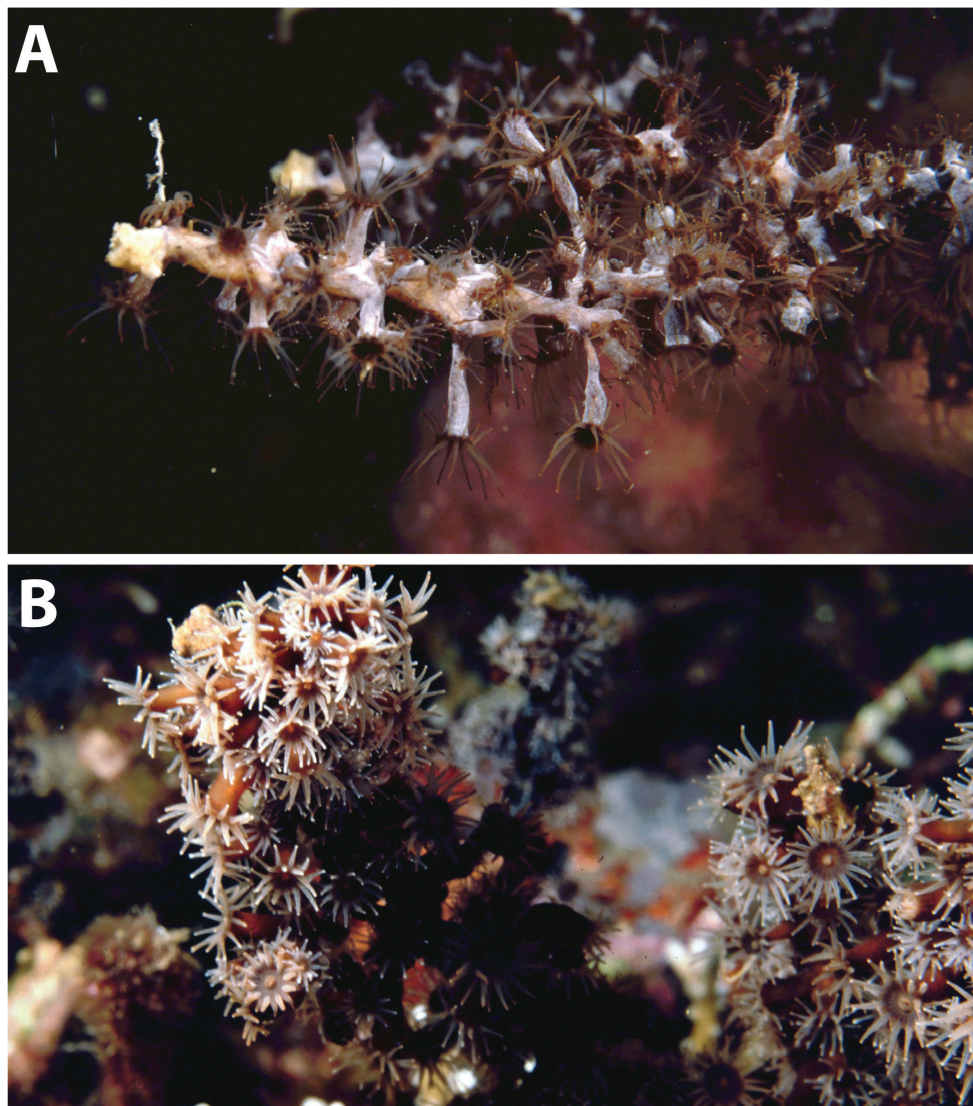


Figure 20. Images of *Epizoanthus* species from specimens and photographic records in this study. **A** *Epizoanthus illorricatus* at west Pulau Menjangan, West Bali, May 22, 1998; and **B** *Epizoanthus* aff. *illorricatus* at Tulamben, east coast of Bali, July 10, 1997.

1997; Fauna Malesiana Maluku Expedition station MAL.10, south coast of Ambon Bay, east of Eri, Ambon (03°45'S, 128°08'E), November 12, 1996; Maluku Expedition station MAL.12, north coast near Morela, Ambon (03°33'S, 128°12'E), November 13–14, 1996; Maluku Expedition station MAL.19, Tanjung Batu Dua, east of Hatu, north coast Ambon Bay, Ambon (03°43'S, 128°03'E), November 19, 1996; Fauna Malesiana Marine Sulawesi Expedition station SUL.16, bay east of Tanjung Labuhankompeni, Pulau Lembah, Lembah Strait, North Sulawesi (01°26'N,

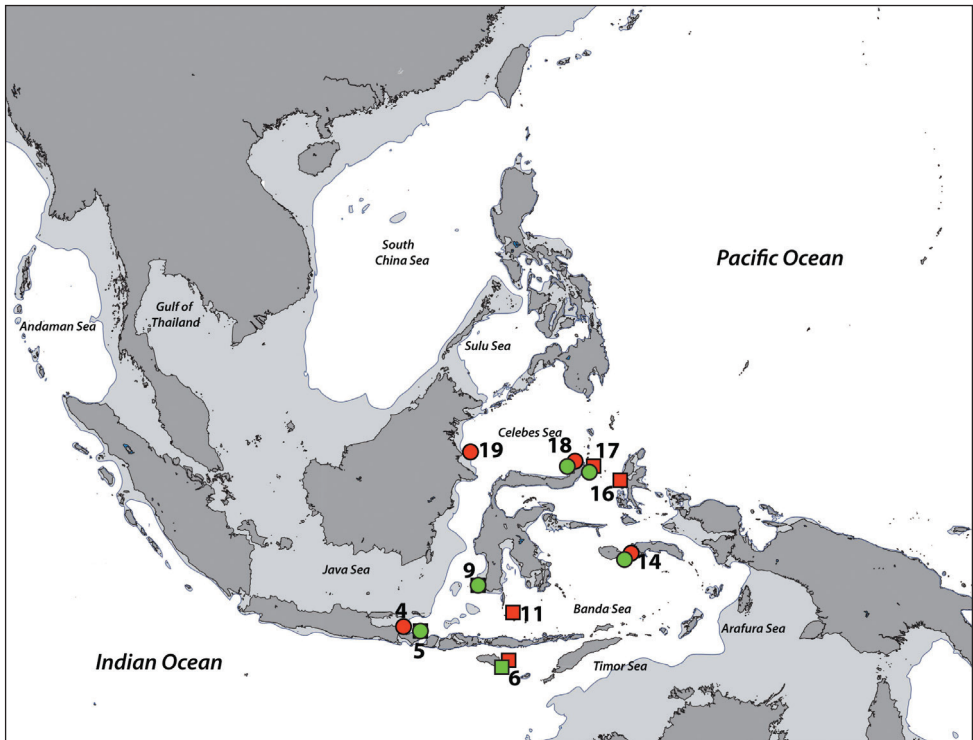


Figure 21. Distribution of *Epizoanthus* species from specimens and photographic records from this study. *Epizoanthus illorricatus* specimens in red, and *Epizoanthus* aff. *illorricatus* in green. Region numbers correspond to locations given in species' information. Boxes indicate presence of specimens (with or without photographic records), while circles indicate only photographic records.

125°11'E), October 23, 1994; west Pulau Siladen, Bunaken, North Sulawesi (01°38'N, 124°46'E), May 2, 1998.

Description. Azooxanthellate. As *E. illorricatus* above, obligate epibiont on eunicid worms. Polyps of this putative species are at least twice as big in diameter as *E. illorricatus* (average 2.1 mm, compared with a maximum of 2 mm for *E. illorricatus*), and many times bigger in terms of volume. Additionally, both specimens have brown coenenchyme and scapus, different from the light gray coenenchyme and brownish oral disk reported for *E. illorricatus* (Figure 20B). In situ images show colonies with cream, brown, red-brown, orange-brown or tan coenenchyme and scapus, often with white tentacles that are comparatively shorter and thicker than in *E. illorricatus*. The coenenchyme of this putative species is much more developed than *E. illorricatus*, with polyps arising from not only bends of the zig-zag shaped eunicid tube, but also from other locations. The result is a colony that has a higher density of polyps than *E. illorricatus*. In *E. illorricatus*, often the zig-zag shape of the eunicid tube is visible between polyps, but this is rarely the case in *E. aff. illorricatus* (Figure 20B).

Distribution. Regions recorded in this study (Figure 21): East Bali (5), northeast Sumba (6), Spermonde Archipelago (9), Moluccas (14), Lembeh Strait (17), Bunaken (18).

Past records. NA.

Remarks. Although the two specimens here were found at deeper depths (75 to 190 m), numerous photographic records show that this species and *E. illorricatus* have an overlapping depth range. Examination of DNA sequences combined with detailed morphological analyses should help clear up the relationship between this putative species and *E. illorricatus*, although preliminary molecular analyses show differences between the two groups (H. Kise and J.D. Reimer, unpubl. data). It is likely records and museum specimens identified as *E. illorricatus* from the central Indo-Pacific include both types mentioned in this study.

Discussion

Examination of the Naturalis zoantharian collection resulted in 24 species being identified, 12 from suborder Brachycnemina and 12 from Macrocnemina. While by no means an extensive collection, with most specimens from Indonesia, these results indicate that the Central Indo-Pacific waters are at least as diverse in numbers of species, genera, and families as surrounding regions of Australia, Singapore, and Japan. In Australia, an examination of the brachycnemic shallow water zoantharians of the Great Barrier Reef indicated the presence of eight species (Burnett et al. 1997), while in Okinawa, 12 brachycnemic species have been previously reported (Reimer 2010), and in Taiwan 10 species (Reimer et al. 2013a). These previous reports did not include macrocnemic species, but from the brachycnemic results alone, Indonesia does appear to have zoantharian species diversity at least as high as Okinawa, one of the most well examined regions. Finally, as many macrocnemic species live in deeper areas or in caves and other less-examined ecosystems (Sinniger et al. 2013), we expect the number of zoantharian species in the shallow waters of Indonesia to be higher than the initial estimate in this study, and further investigations should confirm this idea.

The discussion of total numbers of shallow water zoantharian species is clearly still in the preliminary stages given the lack of focused sampling throughout most regions of the world, as well as the continuous discovery of new species and genera (Reimer et al. 2007a, Sinniger et al. 2010, Fujii and Reimer 2011, 2013). Still, the initial species numbers from this study should provide a basis upon which future zoantharian studies can build on. Furthermore, it should not be forgotten that the previous reports listed above from other Indo-Pacific regions were all conducted by zoantharian specialists collecting specimens in the field, while the Indonesian specimens in the Naturalis collection constitute only part of a broad sampling effort of benthic invertebrates without the participation of any zoantharian specialists. Thus, our prediction that the total number of shallow water zoantharian species in Indonesia will be considerably higher than reported in this study is almost certainly accurate, particularly given the recent

discovery of widespread yet cryptic zoantharian species from coral reef environments (Fujii and Reimer 2011, 2013) not yet reported from Indonesia.

Further supporting the possibility of Indonesia harboring a diverse zoantharian fauna is the fact that the specimens examined in the Naturalis collection are primarily from eastern Indonesia (e.g. Sulawesi and Banda Sea, Fig. 1), with few or no specimens from other regions such as the islands of Java and New Guinea, and only one locality in the Philippines and Papua New Guinea. Future collection efforts must be focused on these unexamined regions if we are to obtain a clear understanding of zoantharian diversity in the CIP. Additionally, the deep sea (>200 m depth) has been recently speculated to harbor much undiscovered zoantharian diversity (Sinniger et al. 2013) and yet in this study only three of the zoantharian species were found in waters >50 m in depth. Exploring the deeper waters in the Indonesian region will undoubtedly result in further discoveries.

Of the 24 total species listed in this study, at least nine (and perhaps up to 12 if *Palythoa* spp. are included) are likely undescribed species. Some, such as *Terrazoanthus* sp. 2, have been known for years in the global aquarium trade, yet still no museum specimens exist, and thus we cannot formally describe them within this manuscript. Without formal descriptions and a clear understanding of species, future conservation work cannot proceed effectively, and immediate taxonomic efforts should focus on the obtaining of specimens and a formal description of this species. Similarly, many photographic records exist for *Neozoanthus* sp., yet no specimens are in the Naturalis collection.

Three other species that are almost certainly undescribed species are *Parazoanthus* sp. 1, *Parazoanthus* sp. 2 and *Parazoanthus* sp. 3. Until now, only two sponge-associated *Parazoanthus* species has been formally described from the Pacific, and none from sub-tropical or tropical waters. Five other species, *Hydrozoanthus* sp. 1, *Hydrozoanthus* sp. 2, *Parazoanthidae* sp. 1, *Parazoanthidae* sp. 2, and *Terrazoanthus* sp. 1, are also very likely to be undescribed species, but with only photographic records, or one or two specimens existing for these species, additional specimens and molecular data are needed to properly describe them.

Conclusions

In conclusion, this study provides a starting point for zoantharian research in the Coral Triangle. We were able to discern 24 different morphological species based on specimen examination combined with photographic records. However, based on recent previous research, phylogenetic analyses of specimens would likely result in somewhat different results due to both high levels of intraspecific morphological variation in some species (Burnett et al. 1997, Reimer et al. 2004) and also morphological convergence between other phylogenetically distinct species (Sinniger and Haussermann 2009). These previous studies demonstrate how difficult it often is to properly identify zoantharian species without molecular data.

Furthermore, this study demonstrates that the central Indo-Pacific likely harbors very high levels of zoantharian diversity, as the numbers of putative species from this

study (24) include a large number of undescribed species, and total numbers are as high or higher than previously reported for any other region.

Finally, it is hoped that this study can serve as a template for the study of other understudied coral reef benthos in the Coral Triangle. In this study, past photographic records proved to be invaluable in aiding species identification, and understanding species distributions. Thus, while museum collections should remain the key tool in taxonomic and biogeographic research (Rainbow 2009, Hoeksema et al. 2011, Rocha et al. 2014), archived in situ images can provide additional information.

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References

- Appeltans W, Ah Yong ST, Anderson G, Angel MV, Artois T, Bailly N, Bamber RN, Barber A, Bartsch I, Berta A, Błażewicz-Paszkowycz M, Bock P, Boxshall GA, Boyko CB, Brandão SN, Bray RA, Bruce NL, Cairns SD, Chan TY, Chan L, Collins AG, Cribb T, Curini-Galletti M, Dahdouh-Guebas F, Davie PJF, Dawson MN, De Clerck O, De Cock W, De Grave S, De Voogd NJ, Domning DP, Emig C, Erséus C, Eschmeyer

- W, Fauchald K, Fautin DG, Feist SW, Franssen CHJM, Furuya H, Garcia–Alvarez O, Gerken S, Gibson D, Gittenberger A, Gofas S, Gómez–Daglio L, Gordon DP, Guiry MD, Hernandez F, Hoeksema BW, Hopcroft R, Jaume D, Kirk P, Koedam N, Koenemann S, Kolb JB, Kristensen RM, Kroh A, Lambert G, Lazarus DB, Lemaitre R, Longshaw M, Lowry JK, Macpherson E, Madin LP, Mah C, Mapstone G, McLaughlin PA, Mees J, Meland K, Messing C, Mills C, Molodtsova T, Mooi R, Neuhaus B, Ng PKL, Nielsen C, Norenburg J, Opresko DM, Osawa M, Paulay G, Perrin W, Pilger J, Poore GCB, Pugh P, Read GB, Reimer JD, Rius M, Rocha R, Saiz–Salinas J, Scarabino V, Schierwater B, Schmidt–Rhaesa A, Schnabel K, Schotte M, Schuchert P, Schwabe E, Segers H, Self–Sullivan C, Schenkar N, Siegel V, Sterrer W, Stöhr S, Swalla B, Tasker M, Thuesen EV, Timm T, Todaro A, Turon X, Tyler S, Uetz P, Van der Land J, Vanhoorne B, Van Ofwegen LP, Van Soest RWM, Vanaverbeke J, Walker–Smith GK, Walter TC, Warren A, Williams GC, Wilson S, Costello M (2012) The magnitude of global marine species diversity. *Current Biology* 22: 2189–2202. doi: 10.1016/j.cub.2012.09.036
- Best MB, Hoeksema BW, Moka W, Moll H, Suharsono, Sutarna IN (1989) Recent scleractinian coral species collected during the Snellius–II Expedition. *Netherlands Journal of Sea Research* 23: 107–115. doi: 10.1016/0077-7579(89)90005-7
- Boschma H (1936) The Snellius–Expedition in the eastern part of the Netherlands East–Indies 1929–1930. Vol. VI. Biological data. Brill, Leiden, 1–29.
- Burnett WJ, Benzie JAH, Beardmore JA, Ryland JS (1994) High genetic variability and patchiness in a common Great Barrier Reef zoanthid (*Palythoa caesia*). *Marine Biology* 121: 153–160. doi: 10.1007/BF00349484
- Burnett WJ, Benzie JAH, Beardmore JA, Ryland JS (1995) Patterns of genetic subdivision in populations of a clonal cnidarian, *Zoanthus coppingeri*, from the Great Barrier Reef. *Marine Biology* 122: 665–673. doi: 10.1007/BF00350688
- Burnett WJ, Benzie JAH, Beardmore JA, Ryland JS (1997) Zoanthids (Anthozoa, Hexacoralia) from the Great Barrier Reef and Torres Strait, Australia: systematics, evolution and a key to species. *Coral Reefs* 16: 55–68. doi: 10.1007/s003380050060
- Carlgren O (1900) Ostafrikanische Actinien. *Jahrbuch der Hamburgischen wissenschaftlichen Anstalten* 17: 21–144.
- Carlgren O (1934) Über einige ostasiatische Zoantharien. *Arkiv för Zoologi* 28: 1–11.
- Carlgren O (1937) Ceriantharia and Zoantharia. *Scientific Reports of the Great Barrier Reef Expedition* 5: 177–207.
- Carlgren O (1950) Corallimorpharia, Actiniaria and Zoantharia from New South Wales and South Queensland. *Arkiv för Zoologi* 1: 131–146.
- Colin PL, Arneson C (1995) *Tropical Pacific Invertebrates*. Coral Reef Press, Beverley Hills, 296 pp.
- Crocker LA, Reiswig HM (1981) Host specificity in sponge encrusting Zoanthidea (Anthozoa, Zoantharia) of Barbados, West–Indies. *Marine Biology* 65: 231–236. doi: 10.1007/BF00397116
- Dana JD (1846) Zoophytes. Volume 7 of the United States Exploring Expedition during the years 1838, 1939, 1840, 1841, 1842 under the command of Charles Wilkes, U.S.N. Lea and Blanchard, Philadelphia.

- Delage Y, Hérourard E (1901) Zoanthidés. – Zoanthidae. In: Reinwald C (Ed.) *Traité de Zoologie concrète*. Tome II – 2e Partie. Les Coelentérés, Paris, 654–667.
- Den Hartog JC (1997) The sea anemone fauna of Indonesian coral reefs. In: Tomascik T, Mah AJ, Nontji A, Moosa MK (Eds) *The ecology of the Indonesian seas 1*. Periplus Editions, Singapore, 351–370.
- Di Camillo CG, Bo M, Puce S, Bavestrello G (2010) Association between *Dentitheca habereri* (Cnidaria: Hydrozoa) and two zoanthids. *Italian Journal of Zoology* 77: 81–91. doi: 10.1080/11250000902740962
- Erhardt H, Knop D (2005) *Corals. Indo-Pacific Field Guide*. Ikan, Frankfurt, 305 pp.
- Esper EJC (1805) *Die Pflanzenthiere in Abbildungen nach der Natur mit Farben erleuchtet nebst Beschreibungen*. Raspe, Nürnberg. Theilen 1–3, Lieferungen 13. [in German and Latin]
- Fosså SV, Nilsen AJ (1998) *The modern coral reef aquarium*. Volume 2. Birgit Schmettkamp Verlag, Bornheim.
- Fujii T, Reimer JD (2011) Phylogeny of the highly divergent family Microzoanthidae (Anthozoa, Hexacorallia) from the Pacific. *Zoologica Scripta* 40: 418–431. doi: 10.1111/j.1463-6409.2011.00479.x
- Fujii T, Reimer JD (2013) A new family of diminutive zooxanthellate zoanthids (Hexacorallia: Zoantharia). *Zoological Journal of the Linnean Society* 169: 509–522. doi: 10.1111/zoj.12075
- Gittenberger A, Draisma S, Arbi U, Langenberg V, Erftemeijer P, Tuti Y, Hoeksema BW (2014) Coral reef organisms as bioregion indicators off Halmahera, Moluccas, Indonesia. *Aquatic Conservation: Marine and Freshwater Ecosystems*. doi: 10.1002/aqc.2495
- Gmelin JF (1791) *Caroli a Linne Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Editio decima tertia, aucta, reformata. Georg Emanuel Beer, Lipsiae.
- Gosliner TM, Behrens DW, Williams GC (1996) *Coral Reef Animals of the Indo-Pacific*. Sea Challengers, Monterey, 314 pp.
- Gray JE (1828) Radiata. In: *Spicilegium Zoologica; or original figures and short systematic descriptions of new and unfigured animals*. Treüttel, Würtz and Co., London, 1: 12 pp.
- Gray JE (1832) The animal flowers, or Zoantharia, and the stellated corals. pp 94–106. In: *Synopsis of the Contents of the British Museum*. Twenty-Sixth Edition. G Woodfall and Son, London, [iv] + 236 pp.
- Gray JE (1867) Notes on Zoanthinae, with descriptions of some new genera. *Proceedings of the Zoological Society of London* 1867(1): 233–240, figs 1–5.
- Haddon AC (1895) Branched worm-tubes and *Acrozoanthus*. *Scientific Proceedings of the Royal Dublin Society VIII*: 344–346.
- Haddon AC, Shackleton AM (1891a) The Zoantheae. A revision of the British Actiniae. Part II. Reports on the zoological collections made in the Torres Straits by AC Haddon, 1888–1889. *Scientific Transactions of the Royal Dublin Society*, ser. 2, 4(12): 609–672, pls. 58–60.
- Haddon AC, Shackleton AM (1891b) Reports on the zoological collections made in Torres Straits by Professor A.C. Haddon, 1888–1889. Actiniae: I. Zoantheae. *Scientific Transactions of the Royal Dublin Society* 4: 673–701.
- Herberts C (1972) Étude systématique de quelques zoanthaires tempérés et tropicaux. *Tethys Supplement* 3: 69–156.

- Hertwig R (1882) Report on the Actiniaria dredged by HMS Challenger during the years 1873–1876. Report on the scientific results of the exploring voyage of HMS Challenger 1873–1876. Zoology 6: 1–122.
- Hertwig R (1888) Report on the Actiniaria dredged by HMS Challenger during the years 1873–1876. Supplement. Report on the scientific results of the exploring voyage of HMS Challenger 1873–1876. Zoology 26: 4–56.
- Hibino Y, Todd P, Yang SY, Benayahu Y, Reimer JD (2013) Molecular and morphological evidence for conspecificity of two common Indo-Pacific species of *Palythoa* (Cnidaria: Anthozoa). Hydrobiologia 733(1): 31–43. doi: 10.1007/s10750-013-1587-5
- Hill JP, Whitelegge T (1898) Sub-Class Zoantharia. In: Whitelegge T (Ed.) The Hydrozoa, Scyphozoa, Actinozoa, and Vermes of Funafuti, 385–391. Memoirs of the Australian Museum 3: 371–394.
- Hoeksema BW (1993) Mushroom corals (Scleractinia: Fungiidae) of Madang Lagoon, northern Papua New Guinea: an annotated checklist with the description of *Cantharellus jebbi* spec. nov. Zoologische Mededelingen, Leiden 67: 1–19.
- Hoeksema BW (2004) Marine biodiversity of the coastal area of the Berau region, East Kalimantan, Indonesia. Progress report East Kalimantan Program – Pilot phase (October 2003), Naturalis, Leiden, 1–82.
- Hoeksema BW (2007) Delineation of the Indo-Malayan Centre of maximum marine biodiversity: the Coral Triangle. In: Renema W (Ed.) Biogeography, Time and Place: Distributions, Barriers and Islands. Springer, Dordrecht, 117–178. doi: 10.1007/978-1-4020-6374-9_5
- Hoeksema BW (2012a) Distribution patterns of mushroom corals (Scleractinia: Fungiidae) across the Spermonde Shelf, South Sulawesi. Raffles Bulletin of Zoology 60: 183–212.
- Hoeksema BW (2012b) Forever in the dark: the cave-dwelling azooxanthellate reef coral *Leptoseris troglodyta* sp. n. (Scleractinia, Agariciidae). ZooKeys 228: 21–37. doi: 10.3897/zookeys.228.3798
- Hoeksema BW, Putra KS (2000) The reef coral fauna of Bali in the centre of marine diversity. Proceedings 9th International Coral Reef Symposium 1: 173–178.
- Hoeksema BW, Tuti Y (2001) Marine biodiversity of Lombok Strait, Bali: Preliminary research report. NNM Naturalis, Leiden, 1–16.
- Hoeksema BW, Van der Meij SET (2010) Crossing marine lines at Ternate: Capacity building of junior scientist in Indonesia for marine biodiversity assessments. Naturalis, Leiden, 1–85.
- Hoeksema BW, Crowther AL (2011) Masquerade, mimicry and crypsis of the polymorphic sea anemone *Phyllodiscus semoni* and its aggregations in South Sulawesi. Contributions to Zoology 80: 251–268.
- Hoeksema BW, Van der Land J, Van der Meij SET, Van Ofwegen LP, Reijnen BT, Van Soest RWM, De Voogd NJ (2011) Unforeseen importance of historical collections as baselines to determine biotic change of coral reefs: the Saba Bank case. Marine Ecology 32: 135–141. doi: 10.1111/j.1439-0485.2011.00434.x
- Irei Y, Nozawa Y, Reimer JD (2011) Distribution patterns of five zoanthid species in Okinawa Island, Japan. Zoological Studies 50: 426–433.

- Jonker L, Johan O (1999) Checklist of the scleractinian coral species from the waters of Padang (West Sumatra, Indonesia) held in the coral collection of Bung Hatta University. Beagle: Records of the Museums and Art Galleries of the Northern Territory 15: 47–54.
- Kamezaki M, Higa M, Hirose M, Suda S, Reimer JD (2013) Different zooxanthellae types in populations of the zoanthid *Zoanthus sansibaricus* along depth gradients in Okinawa, Japan. Marine Biodiversity 43: 61–70. doi: 10.1007/s12526-012-0119-2
- Klunzinger KB (1877) Die Korallthiere des Rothen Meeres. 1: Die Alcyonarien und Malacodermen. Verlag der Gutmann'schen Buchhandlung (Otto Enslin), Berlin. [in German and Latin]
- Laboute P, Richer de Forges B (2004) Lagons et récifs de Nouvelle-Calédonie. Éditions Catherine Ledru, Nouméa, 520 pp.
- Lamarck JBP (1801) Zoanthe. *Zoantha*. pp. 363. In: Système des animaux vertèbres, ou Tableau général des classes, des ordres et des genres de ces animaux; Présentant leurs caractères essentiels et leur distribution, d'après la considération de leurs rapports naturels et leur organisation, et suivant l'arrangement établis dans les galeries du Muséum d'Hist. Naturelle, parmi leur dépouilles conservées; Précédé du discours d'ouverture du Cours de Zoologie, donné dans le Muséum National d'Histoire Naturelle l'an 8 de la République. Déterville, Paris, vol. 1, [viii] + 432 pp.
- Lamouroux JVF (1816) Histoire des Polypiers Coralligènes Flexibles, Vulgairement Nommés Zoophytes. F Poisson, Caen.
- Larson KS, Larson RJ (1982) On the ecology of *Isaurus duchassaingii* (Andres) (Cnidaria: Zoanthidea) from South Water Cay, Belize. In: Rutzler K, MacIntyre IG (Eds) The Atlantic barrier ecosystem at Carrie Bow Cay, Belize, I: structure and communities Smithsonian Contributions to the Marine Science 12, Washington, D.C., 475–488.
- Lindsay DJ, Yoshida H, Uemura K, Yamamoto H, Ishibashi H, Nishikawa J, Reimer JD, Fitzpatrick R (2012) The unthered remotely-operated vehicle PICASSO-1 and its deployment from chartered dive vessels for deep-sea surveys off Okinawa, Japan, and Osprey Reef, Coral Sea, Australia. Marine Technology Society Journal 46: 20–32. doi: 10.4031/MTSJ.46.4.3
- Lwowsky FF (1913) Revision der Gattung *Sidisia* Gray (*Epizoanthus* auct.). Ein Beitrag zur Kenntnis der Zoanthiden. Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere 34(5–6): 557–614, 15 figs, pl. 19.
- McMurrich JP (1904) The Actiniae of the Plate Collection. Zoologische Jahrbücher, Abteilung für Systematik Supplement 6, 215–306.
- Moll H (1983) Zonation and diversity of Scleractinia on reefs off S.W. Sulawesi. PhD Thesis, Leiden University, 1–107.
- Muirhead A, Ryland JS (1985) A review of the genus *Isaurus* Gray 1828 (Zoanthidea), including new records from Fiji. Journal of Natural History 19: 323–335. doi: 10.1080/00222938500770241
- Ong CWD, Reimer JD, Todd PA (2013) Morphologically plastic responses to shading in the zoanthids *Zoanthus sansibaricus* and *Palythoa tuberculosa*. Marine Biology 160: 1053–1064. doi: 10.1007/s00227-012-2158-4
- Pax F (1910) Studien an westindischen Actinien. In: Spengel JW (Ed.) Ergebnisse einer Zoologischen Forschungsreise nach westindien von Prof. W. Kukenthal and Dr. Hartmeyer R im Jahre, 1907. Fischer G, Jena, Zoologische Jahrbücher Supplement 11: 157–330.

- Pax F, Müller I (1956) La collection de Zoanthaires du Musée océanographique de Monaco. Bulletin de l'Institut océanographique 53(1076): 1–27.
- Pet-Soede L, Erdmann M (2004) Rapid Ecological Assessment Wakatobi National Park. Directorate General of Forest Protection and Nature Conservation, Ministry of Forestry, Jakarta; Marine Program, WWF Indonesia, Bali; The Nature Conservancy, Southeast Asia Center for Marine Protected Areas, Bali.
- Rafinesque CS (1815) Analyse de la nature ou tableau de l'univers et des corps organisés. Privately published, Palerme, 224 pp.
- Rainbow PS (2009) Marine biological collections in the 21st century. Zoologica Scripta 38 (Supplement 1): 33–40. doi: 10.1111/j.1463-6409.2007.00313.x
- Reimer JD (2010) Key to field identification of shallow water brachycnemic zoanthids (Order Zoantharia: Suborder Brachycnemina) present in Okinawa. Galaxea 12: 23–29. doi: 10.3755/galaxea.12.23
- Reimer JD, Hickman C (2009) Preliminary survey of zooxanthellate zoanthids (Cnidaria: Hexacorallia) of the Galápagos and associated symbiotic dinoflagellates (*Symbiodinium* spp.). Galápagos Research 66: 14–19.
- Reimer JD, Todd PA (2009) Preliminary molecular examination of zooxanthellate zoanthid (Hexacorallia, Zoantharia) and associated zooxanthellae (*Symbiodinium* spp.) diversity in Singapore. Raffles Bulletin of Zoology. Supplement 22: 103–120.
- Reimer JD, Fujii T (2010) Four new species and one new genus of zoanthids (Cnidaria: Hexacorallia) from the Galápagos. ZooKeys 42: 1–36. doi: 10.3897/zookeys.42.378
- Reimer JD, Ono S, Takishita K, Fujiwara Y, Tsukahara J (2004) Reconsidering *Zoanthus* spp. diversity: molecular evidence of conspecificity within four previously presumed species. Zoological Science 21(5): 517–525. doi: 10.2108/zsj.21.517
- Reimer JD, Ono S, Iwama A, Tsukahara J, Takishita K, Maruyama T (2006a) Morphological and molecular revision of *Zoanthus* (Anthozoa: Hexacorallia) from southwestern Japan with description of two new species. Zoological Science 23 (3): 261–275. doi: 10.2108/zsj.23.261
- Reimer JD, Ono S, Takishita K, Tsukahara J, Maruyama T (2006b) Molecular evidence suggesting species in the zoanthid genera *Palythoa* and *Protopalythoa* (Anthozoa: Hexacorallia) are congeneric. Zoological Science 23(1): 87–94. doi: 10.2108/zsj.23.87
- Reimer JD, Hirano S, Fujiwara Y, Sinniger F, Maruyama T (2007a) Morphological and molecular characterization of *Abyssozoanthus nankaiensis*, a new family, new genus and new species of deep-sea zoanthid (Anthozoa: Hexacorallia: Zoantharia) from a northwest Pacific methane cold seep. Invertebrate Systematics 21(3): 255–262. doi: 10.1071/IS06008
- Reimer JD, Takishita K, Ono S, Maruyama T (2007b) Diversity and evolution in the zoanthid genus *Palythoa* (Cnidaria: Hexacorallia) utilizing nuclear ITS–rDNA. Coral Reefs 26: 399–410. doi: 10.1007/s00338-007-0210-5
- Reimer JD, Ono S, Sinniger F, Tsukahara J (2008a) Distribution of zooxanthellate zoanthid species (Zoantharia: Anthozoa: Hexacorallia) in southern Japan limited by cold temperatures. Galaxea 10: 57–67. doi: 10.3755/galaxea.10.57
- Reimer JD, Ono S, Tsukahara J, Iwase F (2008b) Molecular characterization of the zoanthid genus *Isaurus* (Anthozoa: Hexacorallia) and its zooxanthellae (*Symbiodinium* spp.). Marine Biology 153: 351–363. doi: 10.1007/s00227-007-0811-0

- Reimer JD, Nakachi S, Hirose M, Hirose E, Hashiguchi S (2010) Using hydrofluoric acid for morphological investigations of zoanthids (Cnidaria: Anthozoa): a critical assessment of methodology and necessity. *Marine Biotechnology* 12: 605–617. doi: 10.1007/s10126-009-9249-3
- Reimer JD, Hirose M, Irei Y, Obuchi M, Sinniger F (2011a) The sands of time: Rediscovery of the genus *Neozoanthus* (Cnidaria: Hexacorallia) and evolutionary aspects of sand encrustation in brachycnemic zoanthids. *Marine Biology* 158: 983–993. doi: 10.1007/s00227-011-1624-8
- Reimer JD, Ishikawa SA, Hirose M (2011b) New records and molecular characterization of *Acrozoanthus* (Cnidaria: Anthozoa: Zoanthidae) from Taiwan. *Marine Biodiversity* 41: 313–323. doi: 10.1007/s12526-010-0069-5
- Reimer JD, Obuchi M, Irei Y, Fujii T, Nozawa Y (2011c) Shallow water brachycnemic zoanthids (Cnidaria: Hexacorallia) from Taiwan: a preliminary survey. *Zoological Studies* 50: 363–371.
- Reimer JD, Irei Y, Fujii T (2012a) Two new species of *Neozoanthus* (Cnidaria, Hexacorallia, Zoantharia) from the Pacific. *ZooKeys* 246: 69–87. doi: 10.3897/zookeys.246.3886
- Reimer JD, Lin M, Fujii T, Lane DJW, Hoeksema BW (2012b) The phylogenetic position of the solitary zoanthid genus *Sphenopus* (Cnidaria: Hexacorallia). *Contributions to Zoology* 81: 43–54.
- Reimer JD, Albinsky D, Yang SY, Lorion J (2014a) Zoanthid (Cnidaria: Anthozoa: Hexacorallia: Zoantharia) species of coral reefs in Palau. *Marine Biodiversity* 44: 37–44. doi: 10.1007/s12526-013-0180-5
- Reimer JD, Irei Y, Fujii T, Yang SY (2013a) Phylogenetic analyses of shallow water zoanthids (Cnidaria: Hexacorallia) and their *Symbiodinium* spp. from Taiwan. *Zoological Studies* 52: 38; 1–16.
- Reimer JD, Irei Y, Naruse T (2013b) A record of *Neozoanthus* cf. *uchina* Reimer, Irei & Fujii, 2012 from the Yaeyama Islands, southern Ryukyu Islands, Japan. *Fauna Ryukyana* 7: 1–7.
- Reimer JD, Uyeno D, Berumen ML (2014b) First records of Parazoanthidae and Microzoanthidae (Anthozoa: Hexacorallia: Zoantharia) from the Red Sea. *Marine Biodiversity Records* 7: e7, 1–3. doi: 10.1017/S1755267214000025
- Roberts CM, McClean CJ, Veron JEN, Hawkins JP, Allen GR, McAllister DE, Mittermeier CG, Schueler FW, Spalding M, Wells F, Vynne C, Werner TB (2002) Marine conservation hotspots and conservation priorities for tropical reefs. *Science* 295:1280–1284. doi: 10.1126/science.1067728
- Rocha LA, Aleixo A, Allen G, Almeda F, Baldwin CC, Barclay MV, Bates JM, Bauer AM, Benzoni F, Berns CM, Berumen ML, Blackburn DC, Blum S, Bolanos F, Bowie RC, Britz R, Brown RM, Cadena CD, Carpenter K, Ceriaco LM, Chakrabarty P, Chaves G, Choat JH, Clements KD, Collette BB, Collins A, Coyne J, Cracraft J, Daniel T, de Carvalho MR, de Queiroz K, Di Dario F, Drewes R, Dumbacher JP, Engilis A Jr, Erdmann MV, Eschmeyer W, Feldman CR, Fisher BL, Fjeldsa J, Fritsch PW, Fuchs J, Getahun A, Gill A, Gomon M, Gosliner T, Graves GR, Griswold CE, Guralnick R, Hartel K, Helgen KM, Ho H, Iskandar DT, Iwamoto T, Jaafar Z, James HF, Johnson D, Kavanaugh D, Knowlton N, Lacey E, Larson HK, Last P, Leis JM, Lessios H, Liebherr J, Lowman M, Mahler DL, Mamonekene V, Matsuura K, Mayer GC, Mays H Jr, McCosker J, McDiarmid RW, McGuire J, Miller

- MJ, Mooi R, Mooi RD, Moritz C, Myers P, Nachman MW, Nussbaum RA, Foighil DO, Parenti LR, Parham JF, Paul E, Paulay G, Perez-Eman J, Perez-Matus A, Poe S, Pogonoski J, Rabosky DL, Randall JE, Reimer JD, Robertson DR, Rodel MO, Rodrigues MT, Roopnarine P, Ruber L, Ryan MJ, Sheldon F, Shinohara G, Short A, Simison WB, Smith-Vaniz WF, Springer VG, Stiassny M, Tello JG, Thompson CW, Trnski T, Tucker P, Valqui T, Vecchione M, Verheyen E, Wainwright PC, Wheeler TA, White WT, Will K, Williams JT, Williams G, Wilson EO, Winker K, Winterbottom R, Witt CC (2014) Specimen collection: An essential tool. *Science* 344: 815–816. doi: 10.1126/science.344.6186.814
- Ryland JS (1997) Budding in *Acrozoanthus* Saville–Kent, 1893 (Anthozoa: Zoanthidea). In: den Hartog JC (Ed.) Proceedings of the 6th International Conference of Coelenterate Biology. Nationaal Natuurhistorisch Museum, Leiden, 423–428.
- Ryland JS, Lancaster JE (2003) Revision for methods separating species of *Protopalythoa* (Hexacorallia: Zoanthidea) in the tropical west Pacific. *Invertebrate Systematics* 17: 407–428. doi: 10.1071/IS02008
- Ryland JS, Lancaster JE (2004) A review of zoanthid nematocyst types and their population structure. *Hydrobiologia* 530/531: 407–428. doi: 10.1007/s10750-004-2685-1
- Saville–Kent W (1893) The Great Barrier Reef of Australia; its products and potentialities. WH Allen and Company, London. doi: 10.5962/bhl.title.58247
- Shiroma E, Reimer JD (2010) Investigations into the reproductive patterns, ecology and morphology in the zoanthid genus *Palythoa* (Cnidaria: Anthozoa: Hexacorallia) in Okinawa, Japan. *Zoological Studies* 49: 182–194.
- Sinniger F (2006) Zoanthids of New Caledonia. In: Payri C, Richier de Forges B (Eds) Compendium of marine species from New Caledonia. IRD Editions, Noumea, 127–128.
- Sinniger F, Haussermann V (2009) Zoanthids (Cnidaria: Hexacorallia: Zoantharia) from shallow waters of the southern Chilean fjord region, with descriptions of a new genus and two new species. *Organisms, Diversity & Evolution* 9: 23–36. doi: 10.1016/j.ode.2008.10.003
- Sinniger F, Montoya–Burgos JI, Chevaldonné P, Pawlowski J (2005) Phylogeny of the order Zoantharia (Anthozoa, Hexacorallia) based on the mitochondrial ribosomal genes. *Marine Biology* 147: 1121–1128. doi: 10.1007/s00227-005-0016-3
- Sinniger F, Reimer JD, Pawlowski J (2008) Potential of DNA sequences to identify zoanthids (Cnidaria: Zoantharia). *Zoological Science* 25: 1253–1260. doi: 10.2108/zsj.25.1253
- Sinniger F, Reimer JD, Pawlowski J (2010) The Parazoanthidae DNA taxonomy: description of two new genera. *Marine Biodiversity* 40: 57–70. doi: 10.1007/s12526-009-0034-3
- Sinniger F, Ocana OV, Baco AR (2013) Diversity of zoanthids (Anthozoa: Hexacorallia) on Hawaiian seamounts: description of the Hawaiian gold coral and additional zoanthids. *PLoS ONE* 8: e52607. doi: 10.1371/journal.pone.0052607
- Soong K, Shiau YS, Chen CP (1999) Morphological and life history divergence of the zoanthid, *Sphenopus marsupialis* off the Taiwanese coast. *Zoological Studies* 38: 333–343.
- Stechow E (1909) Hydroidpolypen der japanischen Ostküste. I. Teil: Athecata und Plumularidae, Abhandlungen der mathematisch-physikalischen Klasse der Königlich. Bayerischen Akademie der Wissenschaften 1: 1–111, suppl., 6: 1–111.
- Steenstrup JJS (1856) *Sphenopus marsupialis* (Gmelin). Saerskilt Aftryk. Af det Kongelige danske Videnskabernes Selkabs Forhandling.

- Strack HL (1993) Results of the Rumphius Biohistorical Expedition to Ambon (1990). Part 1. General account and list of stations. *Zoologische Verhandelingen* 289: 1–72.
- Swain TD (2010) Evolutionary transitions in symbioses: dramatic reductions in bathymetric and geographic ranges of Zoanthidea coincide with loss of symbioses with invertebrates. *Molecular Ecology* 19: 2587–2598. doi: 10.1111/j.1365-294X.2010.04672.x
- Swain TD, Wulff JL (2007) Diversity and specificity of Caribbean sponge–zoanthid symbioses: a foundation for understanding the adaptive significance of symbioses and generating hypotheses about higher–order systematics. *Biological Journal of the Linnean Society* 92(4): 695–711. doi: 10.1111/j.1095-8312.2007.00861.x
- Tischbierek H (1930) Zoanthiden auf Wurmrohren. *Zoologischer Anzeiger* 91: 91–95.
- Tuti Y, Soemodihardjo S (2006) Coral reef ecosystem in the Seribu Islands. LIPI Press, Jakarta, 179 pp.
- Van der Land J (1994) Fieldreport Sulawesi Expedition 1994. National Museum of Natural History, Leiden, 1–9.
- Van der Land J (1996) Progress report Fauna Malesiana Marine Maluku Expedition 1996. National Museum of Natural History, Leiden, 1–31.
- Van der Land J, Sukarno (1986) The Snellius–II Expedition progress report. Theme IV Coral Reefs. Part one. RV Tyro and KM Samudera, September – November 1984. Royal Netherlands Academy of Arts and Sciences, Amsterdam, and Indonesian Institute of Sciences, Jakarta, 1–76. Enclosure 2: 1–22, Enclosure 3: 1–22.
- Veron JEN, DeVantier LM, Turak E, Green AL, Kininmonth S, Stafford–Smith M, Peterson N (2009) Delineating the Coral Triangle. *Galaxea Journal of Coral Reef Studies* 11: 91–100. doi: 10.3755/galaxea.11.91
- Veron JEN, DeVantier LM, Turak E, Green AL, Kininmonth S, Stafford–Smith M, Peterson N (2011) The Coral Triangle. In: Dubinsky Z, Stambler N (Eds) *Coral Reefs: an Ecosystem in Transition*. Springer, Dordrecht, 47–55. doi: 10.1007/978-94-007-0114-4_5
- Walsh GE, Bowers RL (1971) A review of Hawaiian zoanthids with descriptions of three new species. *Zoological Journal of the Linnean Society* 50: 161–180. doi: 10.1111/j.1096-3642.1971.tb00757.x
- Wilsmore LJ (1909) On some Zoantheae from Queensland and the New Hebrides. *Journal of the Linnean Society (Zoology)* 30: 315–328.

Two species of Naididae (Annelida, Clitellata) from southern Tibet, China

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Abstract

One new species of Naidinae (Oligochaeta, Naididae), *Nais badia* sp. n. and one new record species from China, *Tubifex montanus* Kowalewski, 1919 (Tubificinae) are found in southern Tibet. The new species is distinguished from congeners by its large area of reddish brown pigment in the anterior segments I–VIII, serrate hairs, pectinate needles with 1–2 intermediate teeth, ventral chaetae partly with 1–2 fine intermediate teeth and wave-like movements. The new material of the species *Tubifex montanus* differs slightly from the previous descriptions by its vas deferens entering atrium subapically, wide ental end of penial sheath and smooth hair chaetae.

Keywords

Nais badia, *Tubifex montanus*, Naididae, new species, new record species, taxonomy, southern Tibet

Introduction

The Tibetan Plateau is one of the biodiversity hotspots around the globe for its unique natural environment (Li and Fang 1999), which accounts for the rich occurrence of endemic species of various taxa in this region, such as *Triplophysa cakaensis* (Cobitidae) (Cao and Zhu 1988), *Schizothorax waltoni* (Cyprinidae) (Chen and Chen 2010), and *Alona aliensis* (Chydoridae) (Chiang et al. 1983). What about oligochaetes? In the 20th century, there were only seven species of oligochaetes recorded in Tibet (Stephenson 1909; Černosvitov 1942; Liang 1963, 1979; Liang et al. 1998). Recently, He recorded 26 species in Tibet (He 2011; He et al. 2012), though focusing mainly on large rivers

(Yarlung Zangbo River) and brackish lakes (Lake Nam Co and Lake Yamzho Yumco). Some freshwater wetlands among mountains in Tibet had been neglected, which we thought may be the ideal habitats for aquatic oligochaetes. In this paper, we describe one new species, *Nais badia* sp. n., and one new record of *Tubifex montanus* Kowalewski, 1919 found in a freshwater wetland of Cuomujiri Mountain, southern Tibet.

Materials and methods

The sampling site was in a wetland of Cuomujiri Mountain, southern Tibet of China. (29°47'46"N, 94°24'53"E), ca 3,990 m above sea level. The substrate type was silt, and hydrophytes were abundant. Water depth was 10–20 cm, water temperature 11.5 °C, pH 6.23, dissolved oxygen 9.14 mg/L, and conductivity 19.3 µs/cm.

The samples were collected with a D-frame dip net, and cleaned through a 250 µm sieve. Large worms were sorted in a white porcelain dish manually and small individuals were sorted with a dissecting microscope. Specimens were all preserved in 10% formalin. Some specimens were investigated with a Scanning Election Microscopy (SEM) to reveal more details of the chaetae. Some were stained with borax carmine, dehydrated in a series of alcohol, cleared in xylene and mounted whole in Canada balsam for careful observation. Parameters of external morphology were established under glycerine mounts. Other parameters were studied on permanent mounts. Drawings were made with a camera lucida. All microscopic observations, including live observations, were documented photographically. The types and other specimens were all deposited in the Institute of Hydrobiology (IHB), Chinese Academy of Sciences (CAS), Wuhan, China.

Abbreviations in the figures

Roman numbers = segment number, SEM = Scanning Electron Microscopy, at = atrium, mp = male pore, pe = penis, pr = prostate gland, ps = penial sheath, sf = sperm funnel, sp = spermatheca, spp = spermathecal pore, vd = vas deferens.

Taxonomy

Family Naididae

Subfamily Naidinae

Nais badia sp. n.

<http://zoobank.org/B20893C6-27F2-4BF1-8A63-FE6EDA75BCF6>

Figs 1, 2, 3; Table 1

Holotype. IHB XZ20130630a, whole-mounted specimen, immature.

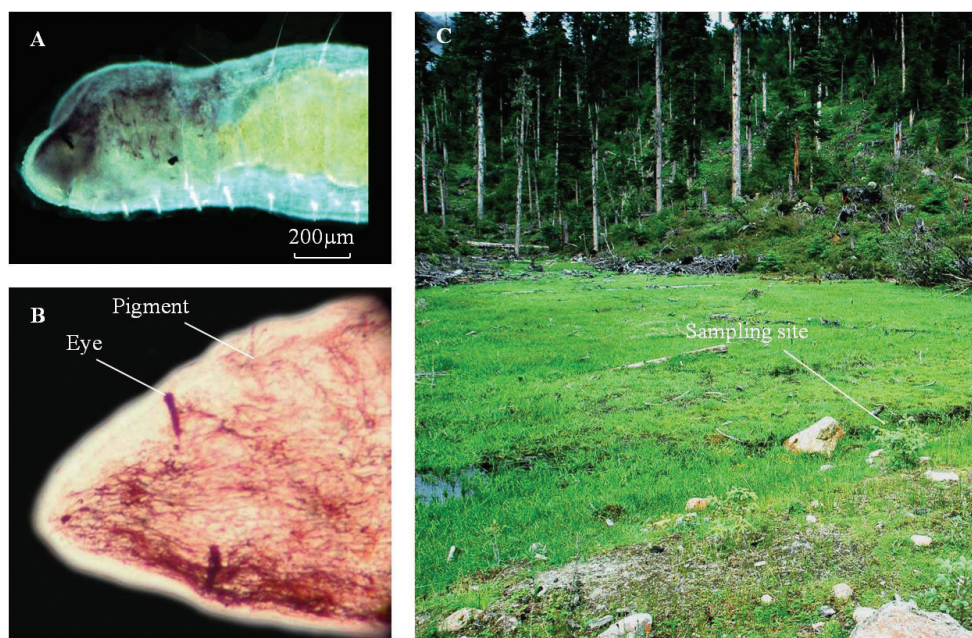


Figure 1. *Nais badia* sp. n. **A** anterior reddish brown pigment in segments I–VIII **B** dorsal view of the head, live worm **C** habitat.

Type locality. Wetland in Cuomujiri Mountain (29°47'46"N, 94°24'53"E), southern Tibet of China. 30 June 2013, collected by H.Z. Wang, Y.D. Cui, Y.J. He and Y. Peng.

Paratypes. IHB XZ20130630b–f, 2 whole-mounted specimens (mature), 2 whole-mounted specimens (immature), 1 specimen is used for scanning electron microscopy. 30 June 2013, collected from the type locality.

Other material. 40 specimens are preserved in 10% formalin. 30 June 2013, collected from the type locality.

Etymology. The specific name “*badia*” is Latin for “badius”, and refers to this worm’s large area of reddish brown pigment in anterior segments I–VIII.

Description. Length 4.2–9.1 mm (Holotype 7.2 mm), width at V 0.3–0.6 mm (Holotype 0.6 mm). Segments 24–54 (Holotype 52). Prostomium conical, eyes present, large area of reddish brown pigment in segments I–VIII (Fig. 1A–B). Clitellum inconspicuous. Coelomocytes present. Stomach dilatation sudden in VII–VIII. Wave-like movements.

Dorsal chaetae beginning in VI onwards (Fig. 2A). Hairs (0)1–3 per bundle, 137–325 μm long, all serrate (Fig. 2B–C). Needles (0)2–3 per bundle, 80–90 μm long, distal tooth slightly longer than the proximal one (VII 3.8 μm/3.2 μm), completely pectinate with 1–2 intermediate teeth (Fig. 2D), nodulus often inconspicuous, 1/3 from the distal end (Fig. 3C). Ventral chaetae in II–V 7–8 per bundle, the rest 2–6(7) per bundle, 105–128 μm long, distal tooth longer and thinner than the proximal one (7.5 μm/5 μm), about 50% of ventral chaetae with 1–2 fine inter-

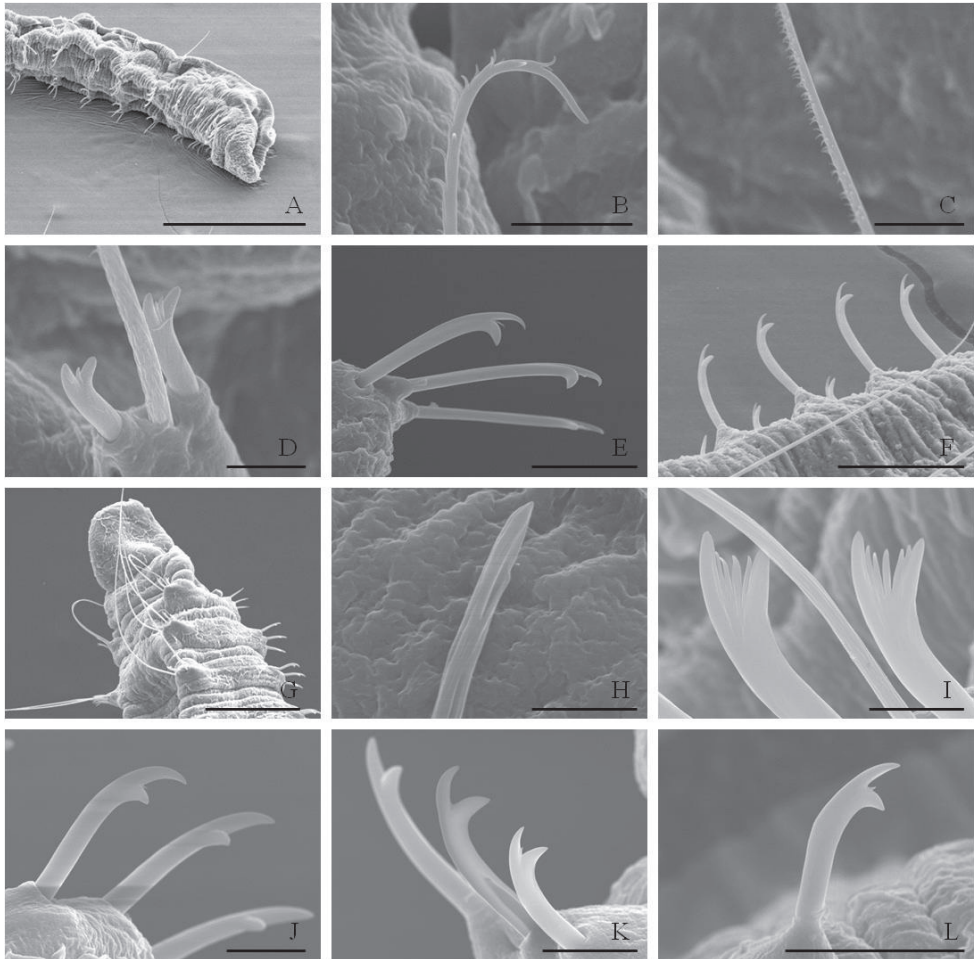


Figure 2. SEM micrographs **A–F** *Nais badia* sp. n. **A** lateral view of anterior body **B–C** hairs in VIII and VI **D** needles in VI **E–F** ventral chaetae in XIII and posterior. **G–L** *Tubifex montanus* **G** lateral view of the head **H** hairs in XI **I** needles in II **J–L** ventral chaetae in IV, XIII and posterior. Scale bar: **A** 300 μm , **B**, **D** and **I** 5 μm , **C**, **J** and **K** 10 μm , **E** and **L** 20 μm , **F** 40 μm , **G** 100 μm , **H** 2 μm .

mediate teeth (Fig. 2E–F), nodulus median or slightly distal (Fig. 3A–B). Penial chaetae 4 on each side in VI, with a simple hook, 115–155 μm long, 4.2–6.3 μm thick (Fig. 3D).

Pharyngeal glands in II–III. Clitellum in V–VI. Male genitalia paired in V–VI (Fig. 3E). Vasa deferentia 260–273 μm long, with prostate gland cells covering only on their posterior part, join atria subapically (Fig. 3E, vd and pr). Atrial ampullae large and ovoid, 150–160 μm long, 70–90 μm wide, ducts short and narrow (Fig. 3E, at). Spermathecal ampullae globular, length 80–100 μm , width 75–90 μm , spermathecal ducts long and narrow, length 60–70 μm , width 15–16 μm (Fig. 3E, sp).

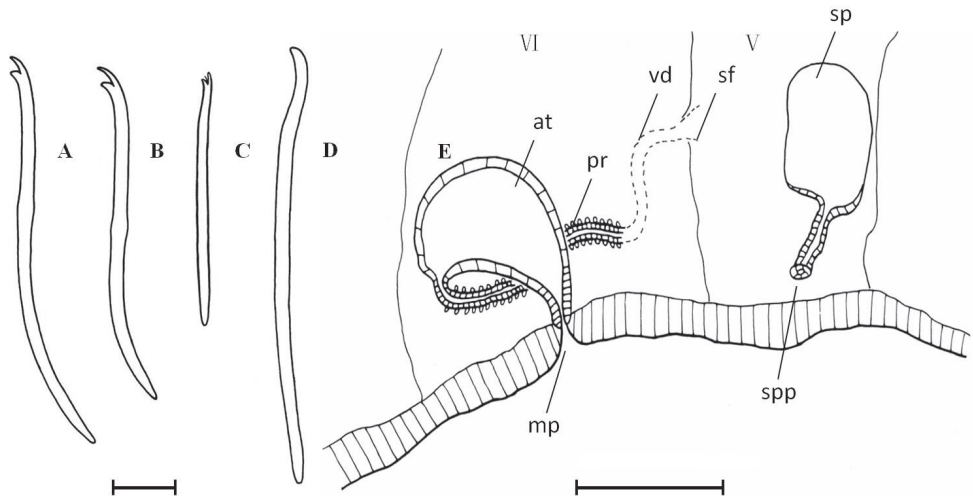


Figure 3. *Nais badia* sp. n. **A–B** ventral chaetae in V and X **C** dorsal bifid in X **D** penial chaeta in VI **E** lateral view of male duct and spermatheca in segments V–VI. Scale bar: **A–D** 20 μ m, **E** 120 μ m.








Distribution. Known only from Cuomujiri Mountain, southern Tibet of China. High mountain, wetland, hydrophytes abundant (Fig. 1C).

Remarks. The presence of eyes, dorsal chaetae beginning in VI consisting of hairs and double-pronged needles, pharynx in II–III, stomach beginning in VII, coelomocytes present, spermathecae with distinct ducts, male ducts paired in V–VI, vas deferens with prostate glands joining atrium subapically, atrium without prostate, penial chaetae present with a simple hook, indicate that this new species fits the definition of *Nais* Müller, 1773 (Sperber 1948; Brinkhurst and Jamieson 1971).

Nais badia sp. n. is distinguished from congeners for having a large area of reddish brown pigment in anterior segments I–VIII, hairs all serrate, needles pectinate with 1–2 intermediate teeth, ventral chaetae with (0)1–2 fine intermediate teeth (Only visible under SEM) and wave-like movements (Table 1). We are hence of the opinion that it can be described as new to science.

This new species is similar to *Nais africana* Brinkhurst, 1966 for having pectinate needles, but differs from it by its ventral chaetae in II–V differing from the rest, although the position of *Nais africana* in the genus is regarded as uncertain due to a lack of detailed examination of live worms and sectioned materials (Brinkhurst 1966). *Nais elinguis* resembles the new species on the needles and simple pointed penial chaetae, but its long and wide atrial duct, slow stomach dilatations and the vas deferens which is completely surrounded by abundant prostate gland cells are significantly different from the new species. With regard to the vas deferens completely surrounded by prostate gland cells on their posterior part, this new species is similar to *Nais communis*, *Nais variabilis* and *Nais pardalis*. However, some characteristic features of these species distinguish them from the new species. *Nais communis* eyes are generally absent, stomach dilatations are slow and the atrium is as long as the duct. *Nais variabilis*, *Nais pardalis*

Table 1. Comparison of *Nais badia* sp. n. with allied species.

Species	<i>Nais badia</i> sp. n.	<i>Nais africana</i>	<i>Nais elinguis</i>	<i>Nais communis</i>	<i>Nais variabilis</i>	<i>Nais pardalis</i>	<i>Nais bretscheri</i>
Pigment	Reddish brown in I-VIII	-	Anterior end reddish brown	Brown in I-V	Pigment in I-V or absent	Brown anteriorly	Anterior end heavily pigmented
Stomach	Dilatation sudden	-	Dilatation gradual	Dilatation gradual	Dilatation sudden	Dilatation sudden, with elongated cells	Dilatation gradual
Swimming	Wave-like movements	-	Lateral movements	No swimming	Spiral movements	Spiral movements	Spiral movements
Penial chaetae	4	Present	4–5	2–3	2–3	3	2
Ventral chaetae	3–8	3–4	2–5	2–6	2–7	1–5	1–7
II-V & rest	Similar	Different	Similar	Similar	Different	Different	Different
Hairs	1–3, serrate	1–2	1–3	1–2	1–2	1–2	1–2
Number	2–3, pectinate	1–2, pectinate	1–3	1–2	1–2	1–2	1–2
Shape							
Needles							
Spermathecae	Roundish, duct long and narrow	-	Large and elongated, duct long and narrow	Large, duct narrow	Ovoid, duct strong and dilated	Ovoid, duct well defined with a distal dwelling	Duct not dilated
Vasa deferentia	Surrounded by abundant gland cells only on their posterior part	-	Completely surrounded by abundant gland cells	Thick with prostate on their posterior part	Surrounded by strong gland cells on their posterior part	Surrounded by prostate gland cells in front of the atria	With prostate glands
Atria	Pear-shaped, duct short and narrow	-	Globular, duct long and wide, well defined	Roundish, as long as duct	Pear-shaped, duct short and narrow or swollen	Pear-shaped, duct poorly defined and narrow	Globular
Distribution	Southern Tibet, China	Skoonspruit, Transvaal	Cosmopolitan	Cosmopolitan	Cosmopolitan	Cosmopolitan	Cosmopolitan
References	Present research	Brinkhurst 1966	Sperber 1948; Brinkhurst and Jamieson 1971; Semernoy 2004				

and *Nais bretscheri* all have the ventral chaetae in II–V that differ from the remaining segments. *Nais pardalis* the stomach has obvious elongated cells. *Nais bretscheri* the ventral chaetae have typical giant chaetae.

Subfamily Tubificinae

Tubifex montanus Kowalewski, 1919

Figs 2, 4; Table 2

Tubifex montanus Kowalewski: Hrabě 1939, 1981; Brinkhurst and Jamieson 1971.

Examined material. IHB XZ20130630g-i, 2 whole-mounted mature specimens although only 1 specimen has male ducts that can be observed and measured, 1 specimen is used for scanning electron microscopy. Wetland in Cuomujiri Mountain (29°47'46"N, 94°24'53"E) of southern Tibet, China. 30 June 2013, collected by H.Z. Wang, Y.D. Cui, Y.J. He and Y. Peng.

Description. Length 10–12 mm, width at XI 0.4–0.7 mm. Segments 41–56. Prostomium obtuse. Clitellum inconspicuous. No coelomocytes.

Dorsal chaetae (0)1–3 hairs and 1–3 needles per bundle. Hairs smooth (Fig. 2H–I), 180–463 µm long. Needles almost palmate (3–11 teeth or more, Fig. 2I and Fig. 4D), 40–100 µm long, two short outer teeth nearly equal (7.5 µm/7.5 µm). Ventral chaetae 60–100 µm long with (0)1–2 fine intermediate teeth partly (Fig. 2J–L and Fig. 4A–C), anteriorly 3–4 per bundle with upper tooth slightly thinner than and nearly 2–3 times as long as the lower (7.5 µm/3 µm), in midbody 1–2 per bundle with two nearly equal teeth (5 µm/5 µm), posteriorly 1–2 per bundle with upper tooth nearly 2 to 3 times as long as the lower (5 µm/2 µm). Ventral chaetae in XI present but unmodified.

Pharyngeal glands in II–V. Chloragogen cells beginning in VI onwards. Male ducts paired in X–XI (Fig. 4F). Vas deferens 722 µm long or more, nearly 2.2 times longer than the atrium, uniform and forming numerous loops in XI, ciliated throughout and entering narrow atrium subapically (Fig. 4F, vd). Atrium pear-shaped, with quite long ejaculatory duct, and gradually becomes narrower toward the ectal end, 343 µm long (Fig. 4F, at). Large compact prostate gland empties into the atrial ampulla near the sperm duct outlet, 137 µm long, 83 µm wide (Fig. 4F, pr). Penis cylindrical, 132 µm long, surrounded by a cuticularized, funnel-like penial sheath (Fig. 4E), 172 µm long and 71 µm wide at the ental end. Spermatheca absent. Testes paired in X. Ovaries paired in XI.

Distribution. Cuomujiri Mountain, southern Tibet of China. A wetland with abundant hydrophytes. Tatra Mountains, Europe (Hrabě 1939; Brinkhurst and Jamieson 1971).

Remarks. According to the characteristics of a long vas deferens entering pear-shaped atrium subapically, large compact prostate gland with stalk-like attachments

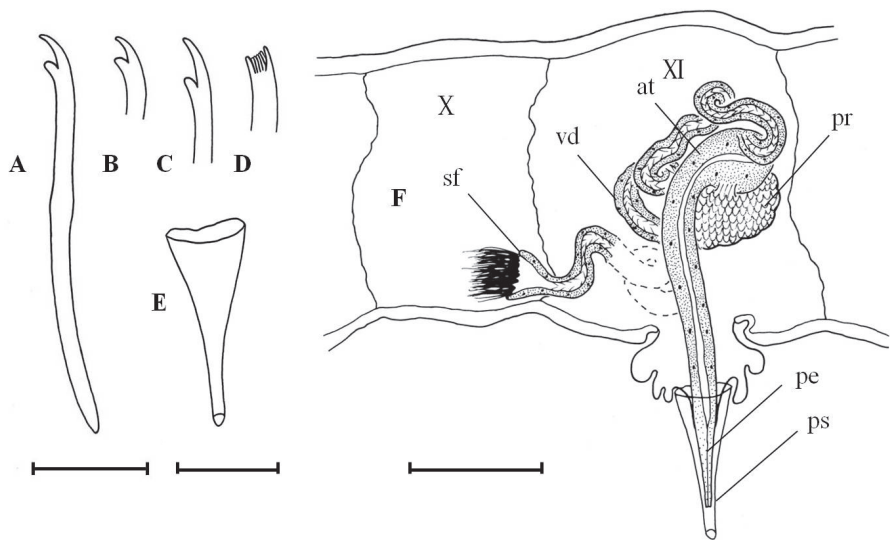
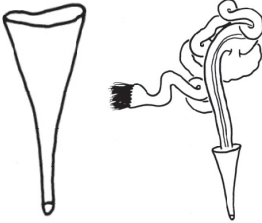
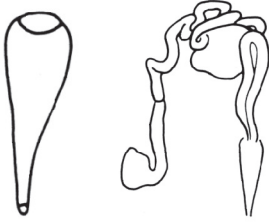


Figure 4. *Tubifex montanus* **A–C** ventral chaetae in II, XVIII and XXIX **D** dorsal chaetae in VI **E** penial sheath **F** lateral view of male duct in segments X–XI. Scale bar: **A–D** 20 μm, **E** 80 μm, **F** 160 μm.

Table 2. Comparison of *Tubifex montanus* from Tibet and Europe.

Regions		Tibet	Europe
Body length (mm)		10–12	8 to 12
Body width (mm)		0.4–0.7	0.7
Segment number		41–56	40 to 50
Chaetae		Hairs smooth (1–3), needles palmate (1–3), ventral chaetae serrate partly (1–4)	Hairs hispid (2–3), needles palmate (2–3), ventral chaetae serrate (3–5)
Male ducts	Vasa deferentia	Ciliated along entire length, all one width, entering narrow atrium subapically, nearly 2.2 times longer than the atrium.	Ciliated along entire length, all one width, entering narrow atrium apically, nearly 1.5 times longer than the atrium.
	Atria	Pear-shaped	Asymmetrical, pear-shaped
	Prostate glands	Large compact prostate with stalk-like attachments to atrial ampulla near sperm duct outlet	Large compact prostate empties into the atrial ampulla near sperm duct outlet
	Penial sheaths	Funnel-like, cuticular tube	Conical, somewhat bent cuticular tube
Drawing			
Spermathecae		Absent	Absent
Distribution		Cuomujiri Mountain, southern Tibet, China	Tatra Mountains, Europe
References		Present research	Hrabě 1939, 1981; Brinkhurst and Jamieson 1971

to atrium and penis with funnel-like penial sheath, the species fits the definition of *Tubifex* Lamarck, 1816 (Brinkhurst and Jamieson 1971).

The new material resembles *Tubifex montanus* Kowalewski, 1919 in absence of spermathecae, vas deferens nearly of a similar length with cilia throughout, pear-shaped atrium with quite long ejaculatory duct gradually becoming narrower toward the ectal end, large compact prostate gland emptying into the atrial ampullae near the sperm duct outlet, cylindrical penis, surrounded by cuticularized and funnel-like penial sheath, and nearly the same type of dorsal ventral chaetae (Table 2).

However, the new material differs slightly from the description by Hrabě (1939, 1981) by having the vas deferens entering the atrium subapically, straight penis sheath with ental end wider and smooth hair chaetae.

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References

- Brinkhurst RO (1966) A contribution towards a revision of the aquatic Oligochaeta of Africa. *Zoologica Africana* 2: 131–166.
- Brinkhurst RO, Jamieson BGM (1971) *Aquatic Oligochaeta of the World*. Oliver and Boyd, Edinburgh, 860 pp.
- Cao WX, Zhu SQ (1988) Two new species of genus *Triplophysa* from Qinghai-Tibet Plateau, China. *Acta Zoologica Sinica* 13: 201–204. [in Chinese with English abstract]
- Černosvitov L (1942) Oligochaeta from Tibet. *Proceedings of Zoological Society of London* 111: 281–287.
- Chen F, Chen YF (2010) Investigation and protection strategies of fishes of Lhasa River. *Acta Hydrobiologica Sinica* 34(2): 278–285. doi: 10.3724/SP.J.1035.2009.00278 [in Chinese with English abstract]
- Chiang SZ, Shen YF, Gong XJ (1983) *Aquatic invertebrates of the Tibetan Plateau. The Series of the Scientific Expedition to Qinghai-Xizang Plateau*. Academia Sinica, Beijing, 492 pp. [in Chinese]
- He XB (2011) *Studies on Fauna of Aquatic Oligochaeta (Annelida) in Tibet and Four Large Rivers of China*. PhD Thesis, Institute of Hydrobiology, Chinese Academy of Sciences, 210 pp. [in Chinese with English abstract]
- He XB, Cui YD, Wang HZ (2012) Two new species of Tubificinae (Annelida, Clitellata, Naididae) from Tibet, China. *Zootaxa* 3458: 159–165.

- Hrabě S (1939) Oligochètes aquatiques des Hautes Tatras. Věstník. Československé Zoologické Společnosti 6/7: 209–236.
- Hrabě S (1981) Vodní máloštětinatci (Oligochaeta) Československa. Acta Universitatis Carolinae Biologica 1979: 1–167.
- Li JJ, Fang XM (1999) Uplift of the Tibetan Plateau and environmental changes. Chinese Science Bulletin 44(23): 2117–2124. doi: 10.1007/BF03182692
- Liang YL (1963) Studies on the aquatic Oligochaeta of China I. Descriptions of new naids and branchiobdellids. Acta Zoologica Sinica 15: 560–570. [in Chinese with English abstract]
- Liang YL, Fang ZC, Zhang TN (1979) A new genus and species of Enchytraeidae from Tibet. Acta Zootaxonomica Sinica 4: 312–315. [in Chinese with English abstract]
- Liang YL, Wang HZ, Xie ZC (1998) Studies on the aquatic Oligochaeta of China IV. Diagnoses of new records and rare species of Naididae and Tubificidae. Acta Hydrobiologica Sinica 22: 54–61. [in Chinese with English abstract]
- Semernoy VP (2004) Oligochaeta of Lake Baikal. Nauka, Novosibirsk, 528 pp. [in Russian]
- Sperber C (1948) A taxonomical study of the Naididae. Zoologiska Bidrag Uppsala 28: 1–296.
- Stephenson J (1909) Report on a collection of smaller Oligochaeta made by Captain FH, Stewart IMS, in Tibet. Records of the Indian Museum 3(2): 105–114.

Morphological and karyotypic differences within and among populations of *Radopholus similis*

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Abstract

Twenty populations of *Radopholus similis* from three countries and different hosts (19 populations from ornamental plants and one population from ginger) were compared using morphological characters, morphometrics and karyotype between progeny from both single females and 30 females of each population. Morphological diversity existed in and among the populations, even within the progeny nematodes from single nematodes compared to that of 30 females. The labial disc shape, the number of head annuli, the terminated position of lateral lips, the number of genital papillae before cloacal apertures and female and male tail terminal shape showed variation. In addition, genital papillae arranged in a double row before cloacal apertures was first found in two ornamental populations. The karyotype of all the 20 populations was $n = 5$. Combining our results and previous studies, we support that *R. citrophilus* is a synonym of *R. similis*, and that it is not possible to distinguish physiological races or pathotypes of *R. similis* according to morphological characters or karyotype.

Keywords

Burrowing nematode, optical and SEM microscopy, morphological comparison, karyotype

Introduction

The burrowing nematode, *Radopholus similis* (Cobb, 1893) Thorne, 1949, is an important parasitic plant nematode has made great damages on many economic crops, and is on the list of quarantined pests in many countries (Anonymous 2004; Haegeman et al 2010). *Radopholus similis* is widely distributed in tropical and subtropical regions with extensive host ranges, up to 250 species (Holdeman 1986), including not only *Musa* spp., *Citrus* spp., *Piper nigrum*, *Saccharum sinensis*, *Camellia sinensis* and other economic crops, but also ornamental plants belonging to the Araceae, Marantaceae, Bromeliaceae, Musaceae and Palmae (Williams and Siddiqi 1973, Bridge 1993, Duncan and Cohn 1990; Loof 1991, Anonymous 2004).

In the mid-1960s, Ducharme and Birchfield (1956) proposed that there were two physiological races (pathotypes) of *R. similis*; the morphologically similar banana race and the citrus race. The banana race infected only banana but not citrus and vice versa (Ducharme and Birchfield 1956, Hahn et al. 1996b, Valette et al. 1998). Van Weerdt (1958) measured the morphological characters of these two races, and did not find any differences between the two. Huettel and Yaegashi (1988) reported that there were some differences in the morphology of the female labial disc, the lateral lip position, the number of annuli terminated at the vulva and the number of genital papillae anterior to the cloacal aperture in the male between the two races when viewed by scanning electron microscope (SEM). These morphological differences were thought to be used to differentiate between the different races; therefore, Huettel et al. (1984) proposed to treat the citrus race as an independent species, *Radopholus citrophilus* Huettel, Dickson, David & Kaplan, 1984. However, Valette et al. (1998) did not agree, studying two banana races of *R. similis* from Africa by SEM, and finding that there were morphological overlaps within the four proposed distinguishing characters, and thereby treated *R. citrophilus* as a synonym of *R. similis*. These findings were later confirmed by other studies (Koshy et al. 1991, Elbadri et al. 1998, Elbadri et al. 1999a, 1999b).

Cytogenetics is an important tool to reveal the phylogenetic relationships within nematode species (Triantaphyllou 1970), and the differences in karyotype is of phylogenetic significance in the study of indistinguishable races within species (Triantaphyllou and Hirschmann 1966). Karyotype and cell development have been reported in the study of many parasitic plant nematodes, i.e. root-knot nematodes, *Meloidogyne* spp., pine wood nematodes, *Bursaphelenchus* spp., and the burrowing nematodes *Radopholus* spp. Some nematologists thought chromosome number, egg cells and gonad cells were helpful in distinguishing different populations (Huettel and Dickson 1981a, Huettel et al. 1984a, 1984b, Aoyagi and Ishibashi 1983, Bolla and Boschert 1993, van der Beek et al. 1998, Kaplan and Opperman 2000, Hasegawa et al. 2004, Liu and Williamson 2006). Huettel and Dickson (1981a, b) even reported that the haploid chromosome number of karyotype of two physiological races of *R. similis* was $n = 4$ (banana race) and $n = 5$ (citrus race). Huettel et al. (1984b) confirmed the result by studying 17 populations of *R. similis*, proposing that using haploid chromosome number of karyotype was more reliable to distinguish citrus races from banana races. However,

Rivas and Roman (1985) and Hahn et al. (1996a) found that the haploid chromosome number of some banana races was also 5. While Goo and Sipes (1999) studied the haploid chromosome of six isolates of *R. similis* collected from Anthurium, banana and Calathea in Hawaii, and found the chromosome number ranged within isolates from $n = 4-7$. Kaplan and Opperman (2000) studied the karyotype of 56 populations of *R. similis*, and demonstrated that citrus races and banana races could mate and produce offspring showing a similar morphology of *R. similis*, and all the chromosome numbers of these offspring was 5; therefore, it was inappropriate to determine different races only according to different karyotypes.

In this study, morphometry, ultrastructural morphology and haploid karyotype of the progeny of single females and 30 females from the same population of 20 populations of *R. similis*, collected from greenhouses and plants intercepted from abroad, were studied and analyzed.

Materials and methods

Nematode populations

Twenty populations of *R. similis* were established on carrot disc cultures (Moody et al. 1973). The populations were originally isolated from ornamental plants and ginger (Table 1). Sterile water was added into the carrot disc dishes to get nematodes suspension in the benchtop, and a single young female was picked and inoculate to a new carrot disc callus with a tiny sterile water drop on it. At the same time, 30 females from the same population weretransferred to another new callus in the benchtop. Progeny from 30 females and single females of each *R. similis* population were collected for further study after 60 days on carrot discs.

Morphological study. Specimens were heat-killed and fixed by adding 4% hot formaldehyde, and transferred to anhydrous glycerin according to Seinhorst's method (Seinhorst 1959). Females and males were separated and mounted on permanent slides (Seinhorst 1959), and 20 females and 20 males were measured for progeny of single female and 30 females of each population, respectively. All measurements and photomicrographs were made using a Nikon 90i microscope with camera. For ultrastructure morphological observations, the method described by Xu et al. (2009) was utilized, and the parameters were measured according to de Man's formula (de Man 1890). All the progeny of single females were coded by adding "s" behind the population code number, e.g. RsA represented the progeny of 30 females of *Calathea zebrina* population inoculated on carrot discs, and RsAs represented the progeny of single female inoculated on carrot discs of the same population.

Karyotypic study. In order to observe chromosomes in eggs or adult nematodes of *R. similis*, fluorescence staining method was used as described by Kaplan and Opperman (2000) only with minor modifications. In brief, nematodes and eggs were collected from the carrot disc dishes and washed twice with sterile distilled water. After the

Table 1. Origin of *Radopholus similis* populations used in this study.

Code	Original collection locations	Host plant
RsA	Netherlands (intercepted)	<i>Calathea zebrina</i>
RsB	China	<i>Ravenia rivularis</i>
RsC	Netherlands (intercepted)	<i>Calathea</i> sp.
RsD	China	<i>Chamaedorea cataractarum</i>
RsE	China	<i>Philodendron</i> sp.
RsG	China	<i>Chamaedorea cataractarum</i>
RsH	China	<i>Philodendron</i> sp.
RsI	China	<i>Anthurium andraeanum</i>
RsJ	China	<i>Anthurium andraeanum</i>
RsK	China	<i>Calathea zebrina</i>
RsL	China	<i>Epipremnum aureum</i>
RsM	Malaysia (intercepted)	<i>Sranvaesia</i> sp.
RsN	China	<i>Chrysalidocarpus lutescens</i>
RsP	China	<i>Calathea zebrina</i>
RsT	China	<i>Calathea</i> sp.
RsS	China	<i>Calathea makoyana</i>
RsV	China (Hong Kong)	<i>Anthurium andraeanum</i>
RsW	China	<i>Anthurium andraeanum</i>
RsY	China	<i>Anthurium andraeanum</i>
RsXj	Singapore (intercepted)	<i>Zingiber officinale</i> Roscoe

supernatant was removed, 200 µl of Carnoy’s solution was added to fix the pellet for 5 minutes. After removal of the fixative, the pellet was incubated in 100% methanol for 20 minutes. The pellet was rinsed twice with phosphate buffered saline (PBS) for 5 minutes, then incubated in a washing buffer for 10 minutes and washed again with PBS and sterile water. The nematodes and eggs were stained with DAPI (4’, 6-diamidino-2-phenylindole) (Sigma-Aldrich Inc.) (1 µg/ml) for 5 minutes, washed once with PBS, and incubated overnight in fluorescence quenching agent. The specimens were made in half permanent slides, and viewed with a Nikon fluorescent microscope (90i).

Results

Morphological characteristics

All 20 populations of *R. similis* exhibited all of reported morphological characters (Tables 2, 3). The female body was almost straight to slightly ventrally curved after heat killed (Figure 1A). The head was low and a little rounded, continuous or slightly offset with body contour (Figure 1E, Figure 5A–C). Lateral field had four incisures and obviously areolated (Figure 4G–H). The middle band was equal or a little wider than the two lateral bands. The stylet was well-developed, shape and size of dorsal basal knobs and two subventral knobs almost identical in shape and size; dorsal gland orifice was

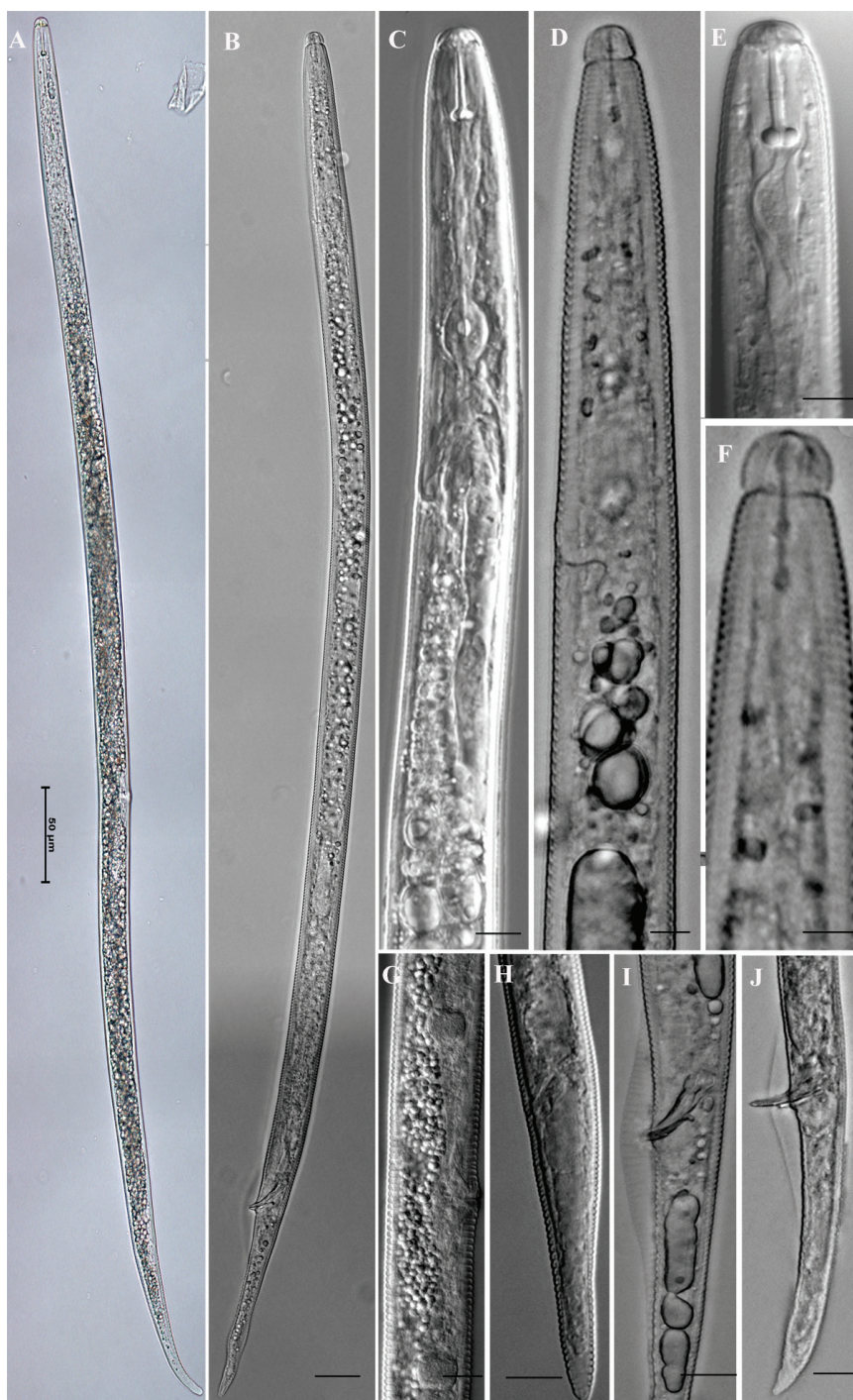


Figure 1. Morphology of *Radopholus similis* Female: **A** whole body **C** anterior part of body **E** lip region and stylet **G** vulva region **H** tail. Male: **B** whole body **D** anterior part of body **F** lip region and stylet **I** cloacal region **J** tail Scale bar: **A** = 50 µm; **B**, **H** = 20 µm; **C**, **E**, **G**, **I**, **J** = 10 µm; **D**, **F** = 5 µm.

Table 2. Morphometrics of *Radopholus similis* females from offspring of mixed females and single female from 20 populations (n = 20), respectively (measurements: μm).

Code ^a	<i>L</i>	<i>a</i>	<i>b</i>	<i>b'</i>	<i>c</i>	<i>c'</i>	<i>V</i>	<i>V'</i>	<i>G_L</i>
RsA	781.6±31.48 (700–842.5)	27.9±1.61 (24.4–30.6)	6±0.35 (5.3–6.6)	4.9±0.29 (4.3–5.3)	9.1±0.52 (8.4–10.5)	4.4±0.28 (3.9–4.9)	55.1±1.2 (52.4–56.7)	62.2±1.25 (59.4–64.3)	28.7±3.21 (20.6–33.4)
RsAs	743.4±26.54 (705–798.8)	35.1±2.2 (31.6–39)	6±0.34 (5.5–6.9)	4.8±0.19 (4.4–5.1)	8.7±0.37 (8.1–9.7)	5.6±0.38 (4.8–6.4)	55.5±0.83 (53.2–57.7)	62.8±0.9 (60.2–64.8)	20.3±2.22 (18.1–26.7)
RsK	706.8±52.57 (513.8–776.3)	26.2±2.2 (17.9–28.7)	6.1±0.54 (4.8–7)	4.7±0.37 (3.3–5)	8.4±0.68 (5.7–8.9)	4.3±0.3 (3.7–4.9)	57.9±6.13 (52.4–83)	64.1±1.78 (60–68.6)	35.0±5.25 (25.3–47.2)
RsKs	682.4±41.81 (617.5–755)	31.5±2.58 (26.3–36.1)	5.6±0.47 (5–6.9)	4.5±0.3 (3.7–5.1)	8.2±0.39 (7.5–9)	5.2±0.59 (4.2–6.4)	56±0.92 (53.1–58.7)	63.7±1.17 (60–66)	23.1±3.3 (19.5–32.5)
RsP	674.8±33.08 (597.5–748)	31.4±1.81 (28.1–34.2)	5.5±0.3 (4.9–6)	4.3±0.18 (4–4.6)	9.2±0.51 (7.7–9.9)	4.3±0.36 (3.6–4.9)	56.9±1.82 (55.3–64.2)	63.4±0.69 (62.1–64.1)	23.5±2.79 (19–30.2)
RsPs	667.7±21.87 (613–713.8)	33.1±1.46 (30.1–36.4)	5.4±0.4 (4.5–6.1)	4.1±0.19 (3.8–4.5)	9.1±0.39 (8.3–9.7)	4.5±0.32 (4–5.1)	56.8±1.55 (53.2–62.4)	63.9±1.81 (59.8–70.2)	22.9±2.36 (19.9–29.9)
RsC	795.9±27.64 (730–843.8)	27.1±2.3 (22.1–29.4)	5.8±0.58 (4.9–6.7)	4.8±0.18 (4.5–5.1)	8.8±0.42 (7.9–9.6)	4.6±0.32 (4.1–5.3)	55.2±0.91 (53.2–57.1)	62.3±1.06 (60.2–65.1)	33.6±2.49 (30.1–37.7)
RsCs	722.3±34.64 (647.5–767.5)	33.6±2.79 (28.5–37.9)	5.8±0.42 (4.8–6.6)	4.6±0.23 (4.1–5.2)	8.8±0.31 (8.2–9.4)	5.2±0.47 (4.5–6.4)	55.1±1.82 (49.1–57.9)	62.4±1.77 (55.6–65.5)	23.6±3.56 (18.4–30.9)
RsS	743.8±23.6 (702.5–778.8)	28±1.47 (25.5–30.6)	6.3±0.7 (5.3–7.9)	4.9±0.16 (4.5–5.1)	8.5±0.34 (8–9.3)	4.8±0.32 (4.1–5.7)	55.3±1.55 (51.9–60.2)	62.7±1.8 (58.3–68.4)	27.7±2.53 (23.2–31.5)
RsSs	719.9±29.35 (670–778)	30.8±3.04 (26.2–36.6)	5.9±1.59 (5–14.2)	4.5±0.22 (4.1–4.9)	8.6±0.44 (7.9–9.7)	5±0.52 (3.9–6.1)	56.4±1.89 (54.1–61.6)	63.8±2.12 (61.2–70.3)	23±3.24 (18.6–29.9)
RsT	736.9±22.67 (701.3–775)	29.6±1.96 (26.9–33.7)	5.3±0.32 (4.7–6.1)	4.4±0.19 (4.1–4.8)	9.3±0.52 (8.4–10.6)	4±0.33 (3.4–4.5)	56.2±0.92 (54.3–57.9)	63.1±0.97 (61.2–65.1)	22.9±1.59 (20–26.6)
RsTs	664.8±26.97 (610–718.8)	33.4±2.69 (28.2–39.1)	5.4±0.29 (4.7–5.9)	4.1±0.22 (3.7–4.5)	9.3±0.41 (8.3–10)	4.6±0.31 (3.9–5.1)	57.3±1.44 (51.2–59.4)	64.2±1.46 (58–66.4)	20.9±2.49 (18.2–28.5)
RsB	678.5±29.83 (625–742.5)	27.9±1.34 (25.5–30.5)	5.1±0.35 (4.5–5.6)	4.3±0.18 (4–4.6)	8.8±0.48 (8.2–9.8)	4±0.24 (3.6–4.6)	56.4±0.81 (54.7–57.7)	63.7±0.99 (61.7–65.3)	23.7±2.87 (19.5–31.4)
RsBs	677.9±34.8 (608.8–743.8)	31.1±1.73 (27.8–34.9)	5.4±0.33 (4.8–6.2)	4.2±0.2 (3.8–4.6)	9.1±0.36 (8.5–9.8)	4.4±0.36 (3.9–5.5)	56.8±1.24 (54.2–61)	63.6±1.37 (61–68.6)	22.3±2.56 (19.1–27.4)
RsD	735.4±30.88 (687.5–785)	28±1.66 (25.2–31.1)	5.9±0.41 (5.4–6.9)	4.8±0.24 (4.3–5.1)	9.6±0.44 (8.9–10.3)	3.7±0.25 (3.4–4.4)	57.1±0.71 (55.4–58.3)	63.8±0.91 (62.2–65.7)	27.8±2.62 (23.8–31.4)
RsDs	651.6±16.06 (617.5–692.5)	32.9±2.41 (28.7–37.6)	5.5±0.24 (5–6)	4.4±0.19 (3.9–4.7)	9.5±0.43 (8.6–10.4)	4.3±0.31 (3.8–5.1)	57.4±1.29 (54.3–62)	64.2±1.41 (60.9–69.4)	20.7±1.55 (18.1–25.5)
RsG	741.1±30.95 (681.3–810)	28.9±1.75 (25.8–32.4)	5.6±0.27 (5.2–6)	4.5±0.24 (4.1–5)	9.1±0.37 (8.4–9.8)	4.1±0.19 (3.6–4.4)	56.2±0.81 (54.7–57.5)	63.2±0.97 (61.6–64.9)	26.6±3.72 (21.7–35.6)
RsGs	661.6±24.14 (606.3–713.8)	34.6±2.18 (28.6–38.8)	5.6±0.37 (4.9–6.5)	4.1±0.18 (3.8–4.5)	9.2±0.32 (8.5–9.9)	4.6±0.32 (4–5.3)	56.5±0.84 (55.2–59)	63.5±0.92 (62.2–66.7)	20.9±1.95 (16.8–25.6)
RsE	676.9±29.04 (612.5–727.5)	28.9±1.91 (25.7–32.3)	5.2±0.25 (4.7–5.6)	4.4±0.16 (4–4.6)	8.9±0.48 (8.2–9.8)	4.1±0.31 (3.5–4.7)	56.7±0.81 (54.5–58.3)	63.9±0.95 (61.1–65.5)	23.7±2.91 (19.4–31.5)
RsEs	661.9±50.81 (545–747.5)	33.1±2.76 (27.4–37.3)	5.4±0.39 (4.6–6.2)	4.2±0.28 (3.5–4.7)	9.2±0.44 (8.5–10.3)	4.6±0.45 (3.9–5.6)	57±1.06 (54.9–59.7)	64±1.22 (61.3–67.3)	22.2±2.96 (16.8–29.2)
RsH	764.1±27.22 (705–803.8)	30±2.9 (25.6–35.7)	6±0.53 (5.4–7.1)	4.9±0.21 (4.4–5.4)	8.8±0.34 (8.2–9.4)	4.7±0.33 (4.2–5.1)	55.9±1.08 (53.5–58.2)	63.4±1.48 (60.6–67.9)	28±2.73 (22.8–33.3)
RsHs	682.9±32.03 (622.5–743.8)	32.7±1.97 (28.6–37)	5.7±0.33 (4.9–6.4)	4.4±0.32 (3.8–4.9)	8.4±0.27 (7.9–9.1)	5.6±0.34 (5–6.6)	56.1±2.04 (53.9–61.6)	63.6±2.32 (60.9–70)	19.3±1.6 (16.4–22.7)
RsI	680.8±21.62 (643.8–730)	29.9±1.88 (26.7–34.6)	5.7±0.49 (5–6.8)	4.5±0.19 (4.1–4.9)	9.6±0.58 (8.7–11.2)	4±0.32 (3.4–4.5)	56.7±1.08 (54.6–58.7)	63.3±1.06 (61.1–65.1)	23.6±3.61 (18.7–31.6)
RsIs	666.6±25.04 (611.3–725)	32.7±2.16 (27.7–35.2)	5.5±0.28 (5–6.1)	4.4±0.19 (3.9–4.8)	9.5±0.55 (8.6–11.1)	4.5±0.42 (3.1–5)	57.4±1.68 (56–64.2)	64.1±1.32 (62.4–68.3)	21.8±3.4 (18–30.2)
RsJ	718.2±18.03 (682.5–742.5)	26.5±1.22 (24.8–29.6)	5.8±0.4 (5.1–6.9)	4.9±0.15 (4.6–5.1)	8.6±0.46 (8–9.5)	4.2±0.18 (3.9–4.5)	57.3±1.81 (55–63.8)	64.9±2.05 (62.4–72.2)	31.5±2.47 (27.4–35.8)

Code ^a	<i>L</i>	<i>a</i>	<i>b</i>	<i>b'</i>	<i>c</i>	<i>c'</i>	<i>V</i>	<i>V'</i>	<i>G_L</i>
RsJs	661.2±25.38 (617–718.8)	32.1±2.77 (24.7–37.1)	5.6±0.32 (5.1–6.4)	4.5±0.23 (4–4.9)	8.1±0.33 (7.5–8.8)	5.2±0.39 (4.1–5.8)	56.5±1.19 (54.6–60.4)	64.3±1.17 (62.1–67.4)	21.5±2.24 (18.8–28.4)
RsV	730.5±29.23 (675–775)	30.3±1.7 (27–33.9)	5.3±0.26 (4.9–6)	4.4±0.19 (4–4.8)	9.3±0.56 (8.5–10.2)	4.1±0.33 (3.6–4.7)	56.4±0.81 (54.9–57.5)	63.3±0.83 (61.7–64.5)	27.7±2.96 (22.4–32.8)
RsVs	693.8±41.54 (632.8–797.5)	32.1±1.69 (29.3–35.1)	5.5±0.4 (4.9–6.8)	4.3±0.24 (3.9–5)	9.2±0.44 (8.4–10.5)	4.5±0.4 (3.7–5.2)	57.3±1.3 (54.8–60.8)	64.4±1.4 (61.9–67.7)	22.3±3.62 (17.7–31.5)
RsW	742.7±20.94 (717.5–790)	26.7±0.95 (24–28)	6.1±0.28 (5.8–6.8)	5.1±0.26 (4.3–5.5)	8.6±0.38 (7.8–9.3)	4.3±0.33 (3.4–4.8)	56.4±1.18 (54.7–59.7)	64±1.27 (61.7–67.8)	31.5±4.39 (24.4–40.3)
RsWs	659.3±26.3 (617.5–731.3)	29.3±2.6 (24.9–33.9)	5.6±0.45 (5–6.6)	4.5±0.35 (3.9–5.2)	8.2±0.37 (7.7–9.2)	5±0.48 (4.3–5.8)	56±0.91 (54.4–58.2)	63.7±1.21 (60.3–65.5)	23.7±3.06 (19.3–28.9)
RsY	731.7±19.73 (690–756.8)	26.5±1.3 (24.3–28.2)	6.2±0.35 (5.8–6.8)	4.7±0.2 (4.5–5.1)	9.5±0.43 (8.9–10.1)	3.7±0.12 (3.6–4)	57.1±0.79 (56–58.5)	63.8±0.89 (62.1–65.4)	29±4.79 (19.1–34.5)
RsYs	689.7±24.91 (628.8–732.5)	32.9±1.82 (29.6–38)	5.5±0.32 (4.9–6.2)	4.3±0.14 (4–4.6)	9.2±0.34 (8.8–10)	4.6±0.29 (4.1–5)	57.1±0.96 (55.5–59.1)	64.1±1.09 (62.2–66.4)	20.9±1.88 (18.3–26.1)
RsL	665.8±45.12 (615.5–812.5)	31.7±1.89 (28.8–36.1)	5.4±0.44 (5–6.8)	4.1±0.26 (3.7–4.7)	9.1±0.34 (8.6–9.9)	4.5±0.31 (3.9–4.8)	57.4±0.95 (55.5–58.8)	64.4±0.9 (62.5–66)	21.7±1.6 (20–25.1)
RsLs	661.8±33.1 (597.5–742)	31±1.86 (27.1–34.7)	5.5±0.26 (5–6)	4.3±0.19 (3.8–4.6)	9.2±0.5 (8.4–10.4)	4.2±0.26 (3.7–4.6)	56.4±1.27 (54.1–60.6)	63.3±1.52 (61.1–67.9)	22.1±2.23 (19.5–30.1)
RsM	656.7±21.99 (595–688.8)	30.8±1.29 (28.8–33.7)	5.1±0.31 (4.6–5.9)	4.3±0.23 (3.9–4.7)	9.2±0.42 (8.1–10.2)	4.3±0.28 (3.7–5)	56.4±1.16 (52.9–58.2)	63.2±1.52 (59.1–65.8)	20.1±1.2 (17.8–22.8)
RsMs	666.9±32.64 (613.8–788.8)	33.8±1.78 (28.8–37.2)	5.5±0.33 (4.9–6.2)	4.3±0.2 (3.9–4.7)	9.3±0.46 (8.2–10)	4.5±0.39 (3.8–5.4)	57±0.75 (55.7–59.3)	63.9±0.89 (62.1–66.5)	20.7±1.49 (17.1–24.4)
RsN	689.3±30.12 (630–735)	30.8±1.77 (25.9–33.5)	5.3±0.26 (4.8–5.9)	4.4±0.17 (4.2–4.7)	9±0.47 (8.2–10.2)	4.5±0.38 (3.6–5.3)	56.3±1.03 (54.5–58.7)	63.4±1.34 (60.5–66.1)	24.2±2.14 (19.7–28.7)
RsNs	666.3±19.02 (632.5–705)	33.3±2.36 (29–37.6)	5.4±0.22 (4.9–5.8)	4.2±0.17 (3.9–4.5)	9.1±0.36 (8.4–9.9)	4.6±0.29 (3.7–5)	57.2±0.86 (55.8–58.7)	64.4±0.95 (62.4–66)	20.4±2.36 (17.6–27.8)
RsXJ	708.3±21.11 (671.3–756.3)	26.5±1.38 (24.4–28.9)	5.3±0.2 (4.9–5.7)	4.8±0.13 (4.5–5)	8.4±0.33 (7.5–8.9)	4.2±0.22 (3.8–4.5)	56.7±1.45 (54.2–61.1)	64.4±1.59 (61.6–69.3)	30.4±3.66 (26.3–40.3)
RsXJs	659.9±16.65 (631.3–691.3)	29.9±1.08 (27.6–32.6)	5.7±0.3 (5.2–6.4)	4.6±0.2 (4.2–5.1)	8.5±0.37 (7.9–9.5)	4.9±0.27 (4.3–5.3)	56.8±1.31 (55.1–61)	64.2±1.76 (58.5–69.2)	21.1±1.31 (17.5–23.3)

Table 2. Continued.

Code	G_2	Stylet	Tail	h	Ran	MB	Distance from stylet knob to dorsal gland origin	Pharynx length
RsA	25.5±2.93 (20.6–30)	18.5±0.71 (17.3–19.4)	85.9±5.28 (77.5–95)	11.9±1.84 (8.7–15.3)	47.1±4.23 (40–54)	63.7±2.35 (59.2–67.8)	4.6±0.52 (4.1–5.1)	144.2±9.8 (131.6–170.3)
RsAs	18.7±1.65 (16.3–22.7)	19.1±0.44 (18.4–19.4)	85.3±4.05 (77.5–95)	10.5±2.6 (7.1–18.9)	50.3±4.09 (44–57)	63.8±2.59 (59.2–69.4)	4.6±0.48 (4.1–5.1)	138±7.46 (123.4–154)
RsK	31.7±5.79 (22.6–47.7)	17.8±0.62 (17.3–19.4)	84.4±2.97 (78.8–90)	9.6±2.06 (6.1–14.3)	43.4±4.29 (38–55)	62.9±2.69 (57.1–69.4)	4.5±0.5 (4.1–5.1)	134.1±4.79 (123.4–139.7)
RsKs	21.1±1.96 (18.2–25.6)	18.5±0.47 (17.3–19.4)	83.3±4.12 (76.3–90.5)	9.5±1.75 (6.1–13.5)	44.1±3.13 (38–52)	60.2±2 (56.1–64.3)	4.3±0.41 (3.1–5.1)	132.2±8.15 (114.2–153)
RsP	22.7±2.26 (20–28.6)	19.1±0.45 (18.4–19.4)	73.4±4.52 (66.3–82.5)	11.2±1.01 (9.2–13.3)	50.9±6.96 (32–61)	60.6±2.08 (55.1–64.3)	4.4±0.53 (3.1–5.1)	140±6.36 (130.6–151)
RsPs	21.3±1.56 (17.9–24.7)	19.1±0.43 (18.4–19.4)	73.8±4.22 (67–83.8)	11.6±1.17 (9.2–14.1)	51.8±5.37 (38–60)	62.1±1.91 (58.1–66.3)	4.1±0.26 (4.1–5.1)	143.9±7.94 (126.5–159.1)
RsC	28.9±2.21 (24.9–32.4)	18.7±0.67 (17.3–19.4)	90.9±4.18 (85–102.5)	12.3±2.13 (9.2–17.3)	45.4±3.79 (39–52)	65.8±1.67 (63.2–69.9)	5±0.4 (4.1–5.6)	144.6±6.72 (133.6–160.1)
RsCs	20.5±3.01 (16.3–28.3)	19±0.51 (17.9–19.4)	82.4±4.81 (72.5–92.5)	9.7±1.49 (7.1–13.8)	44.4±4.84 (36–57)	64.6±2.35 (60.2–70.4)	4.3±0.42 (4.1–5.1)	139.2±7.36 (125–154)
RsS	25.9±2.79 (20.4–30)	18.5±0.6 (17.3–19.4)	87.5±3.79 (80–93.8)	11±2.37 (8.2–15.3)	46.1±3.54 (40–51)	63.9±1.63 (61.2–66.3)	4.3±0.41 (3.6–5.1)	133.6±7.59 (124.4–158.1)
RsSs	20.7±2.28 (17.1–26.6)	19.1±0.42 (18.4–19.9)	83.9±5.79 (72.5–93.8)	9.4±2.38 (2.6–13.3)	48.8±5.37 (39–59)	64.8±2.68 (60.2–70.4)	4.2±0.33 (4.1–5.1)	141.7±8 (124.4–154)
RsT	21.7±3.19 (18.4–30.7)	18.8±0.51 (18.4–19.4)	79.3±3.88 (72.5–86.3)	12.8±1.28 (10.7–15.8)	47.7±4.88 (37–58)	63±1.67 (60.2–66.3)	4.2±0.31 (4.1–5.1)	147.7±7.26 (134.1–163.2)
RsTs	19.6±1.72 (17.4–24.9)	19±0.49 (18.4–19.9)	71.8±3.57 (63–78.8)	13±1.04 (11.2–14.8)	45.8±3.46 (39–53)	63.4±2.67 (57.1–67.3)	4.2±0.39 (3.1–5.1)	143.7±6.91 (131.6–164.2)
RsB	22.2±1.6 (19.5–24.)	18.1±0.47 (17.3–18.4)	77.6±4.57 (67.5–85)	13.9±1.63 (10.2–16.3)	46.7±5.67 (34–58)	61.5±2.2 (56.1–64.8)	3.9±0.43 (3.1–5.1)	140±6.5 (125–155)
RsBs	20.5±2.15 (17.4–25.9)	19.4±0.25 (18.4–19.9)	74.2±3.42 (65–80)	12.7±1.66 (8.2–15.3)	46.5±4.36 (37–58)	63.3±2.56 (59.2–67.3)	4.3±0.53 (3.1–5.1)	145.2±9.18 (125.5–165.2)
RsG	23.8±2.4 (19.1–27.5)	18.3±0.52 (17.3–19.4)	81.3±4.39 (72.5–90)	14.2±1.45 (11.2–16.3)	47.1±3.46 (40–53)	63.2±1.91 (60.2–67.3)	4.3±0.58 (3.1–5.1)	145.9±5.04 (135.7–157.1)
RsGs	19.7±1.74 (16.5–26.2)	19.1±0.42 (18.4–19.4)	72.3±3.64 (63.8–78.8)	13.1±1.06 (10.7–15.3)	46.4±3.19 (41–53)	62.7±2.32 (58.1–67.3)	4.4±0.53 (3.1–5.1)	140±5.83 (129.5–151)
RsD	24.6±2.49 (21.2–30.4)	19.1±0.6 (18.4–20.4)	76.5±4.01 (67.5–81.3)	12.7±1.03 (11.2–15.3)	46.4±4.43 (39–58)	63.2±1.86 (61.2–67.3)	4.3±0.45 (4.1–5.1)	133.9±5.44 (125–143.8)
RsDs	19.8±1.08 (17.8–22.6)	19.3±0.42 (18.4–20.4)	68.8±3.39 (59.5–76.3)	11.8±1.16 (8.7–14.3)	45.5±3.43 (35–51)	61.1±2.57 (54.1–66.3)	4.6±0.5 (4.1–5.1)	130.2±6.89 (121.4–152)
RsE	21.3±2.04 (16.8–23.6)	18.6±0.45 (18.4–19.4)	75.9±3.93 (70–85)	13.3±1.22 (11.2–16.3)	47.3±4.36 (40–60)	60.8±1.94 (58.1–64.3)	3.7±0.5 (3.1–4.1)	137±6.35 (126.5–149.9)
RsEs	20.5±2.49 (16.9–26.4)	18.9±0.51 (18.4–19.9)	71.9±5.26 (61.3–80)	12.9±1.49 (10.2–16.8)	45.5±4.16 (35–52)	62.7±2.49 (57.1–67.3)	4.3±0.41 (4.1–5.1)	142.2±7.27 (126.5–156.1)
RsH	24.7±2.75 (19.5–28.9)	19±0.5 (18.4–19.4)	86.9±4.4 (80–95)	10.3±1.62 (6.6–13.3)	46.1±4.17 (38–53)	64±2.52 (57.1–68.3)	4.3±0.42 (4.1–5.1)	137.4±6.97 (126.5–152)
RsHs	18.4±1.49 (15.7–23.1)	19.1±0.5 (17.3–19.4)	81.6±4.17 (73.8–88.8)	8.9±1.61 (5.6–12)	48.1±3.61 (41–54)	62.7±2.41 (59.2–70.4)	4.6±0.49 (4.1–5.1)	139±8.68 (124.4–159.1)
RsI	20.9±2.23 (17.7–25.6)	18.5±0.6 (17.3–19.4)	71.2±3.81 (62.5–77.5)	13.8±1.41 (11.2–17.3)	43.5±3.56 (38–49)	57.6±1.78 (54.1–60.2)	4.1±0.62 (3.1–5.1)	132.5±5.92 (119.3–145.9)
RsIs	20.2±2.06 (17.5–25.2)	18.9±0.55 (17.3–19.4)	70.7±4.5 (55–76.3)	12.3±1.6 (8.2–14.8)	44.2±4.62 (33–54)	61±2.25 (53–64.3)	4.3±0.39 (4.1–5.1)	135.2±6.78 (119.3–148.9)
RsJ	27.5±2.92 (22.6–32.7)	18.1±0.69 (17.3–19.4)	83.5±4.23 (72.5–90)	12.6±1.75 (8.7–15.3)	41.8±2.59 (37–45)	62±1.79 (59.2–65.3)	4.5±0.55 (3.6–5.1)	130±4.37 (122.4–138.2)

Code	G_2	Stylet	Tail	b	Ran	MB	Distance from stylet knob to dorsal gland origin	Pharynx length
RsJs	19.8±1.81 (17.5–24.6)	18.5±0.42 (17.3–19.4)	81.6±3.84 (75–88.8)	10±1.94 (6.1–14.3)	44.7±4.17 (39–55)	59.2±1.87 (56.1–62.2)	4.3±0.51 (3.1–5.1)	127.6±6.6 (118.3–143.8)
RsV	25.2±2.82 (21.8–31.7)	18.8±0.75 (17.3–19.4)	79.1±4.93 (67.5–87.5)	11.6±1.13 (9.2–13.3)	48.5±4.62 (38–57)	62.3±1.32 (59.2–65.3)	4.3±0.34 (4.1–5.1)	147±8.66 (132.6–164.2)
RsVs	20.8±1.92 (18–26)	19.2±0.35 (18.4–19.4)	75.9±5.56 (67.5–86.3)	11.4±1.66 (8.2–14.3)	46.3±4.78 (38–56)	62.8±1.89 (58.1–67.3)	4.4±0.42 (4.1–5.1)	141.3±5.86 (129.5–153)
RsW	29.4±3.24 (25–36.2)	18.4±0.47 (17.3–19.4)	86.9±4.62 (77.5–95)	11±1.73 (8.2–15.3)	41.4±4.45 (36–53)	61.7±2.05 (55.1–64.3)	4.4±0.48 (4.1–5.1)	128.1±7.37 (114.2–151)
RsWs	22.5±3.49 (17.9–30.4)	18.3±0.41 (17.3–19.4)	80.2±4.57 (71.3–86.3)	10.1±1.96 (6.6–14.3)	42.8±3.92 (36–52)	59.2±1.92 (55.1–62.2)	4.1±0.43 (3.1–5.1)	127.8±9.39 (113.2–146.9)
RsY	27.8±3.68 (21.9–34.5)	19.6±0.43 (19.4–20.4)	77±4.22 (72.5–85)	12.7±1.31 (10.7–14.8)	46.4±2.59 (42–51)	64.2±1.76 (61.2–68.3)	4.6±0.51 (4.1–5.1)	136.1±6.67 (128.5–146.9)
RsYs	19.9±1.21 (17.7–23.5)	19.4±0.46 (18.4–20.4)	74.9±3.27 (69.5–81.3)	12.4±1.32 (10.2–15.8)	47.9±2.98 (41–53)	63.7±1.96 (59.2–67.3)	4.6±0.7 (3.1–6.1)	140.3±5.44 (125.5–153)
RsL	20.3±1.47 (18–23.2)	19.3±0.48 (18.4–20.4)	72.9±5.59 (65.5–90)	12.3±0.91 (10.7–13.8)	49±4.9 (38–58)	63.8±2.58 (58.1–67.3)	4.5±0.51 (4.1–5.1)	147±9.47 (120.4–161.2)
RsLs	20.6±2.22 (18.3–30)	19.2±0.6 (18.4–20.4)	72.1±4.4 (64.8–83.8)	12±1.22 (9.2–14.3)	48.6±5.13 (38–57)	59.5±2.02 (56.1–64.3)	4±0.31 (3.1–5.1)	133.8±10.06 (106.1–156.1)
RsM	18.4±1.1 (15.7–20.4)	18.6±0.53 (17.3–19.4)	71.6±3.18 (66.3–77.5)	12.1±1.25 (9.2–14.3)	45.3±3.39 (39–52)	59.1±2.14 (55.1–63.2)	3.9±0.63 (3.1–5.1)	133.3±7.06 (123.4–144.8)
RsMs	19.9±1.15 (17.7–22.6)	19.3±0.6 (18.4–21.4)	71.7±4.43 (65–83.8)	12.3±1.22 (10.2–14.8)	46.2±3.53 (40–55)	62.1±3.42 (56.1–70.4)	4.6±0.47 (4.1–5.1)	137.4±8.07 (122.4–155)
RsN	21.3±1.99 (19–27.6)	18.9±0.62 (18.4–20.4)	76.9±3.96 (70–82.5)	13.5±1.49 (10.2–16.3)	44.4±3.15 (39–51)	60.8±2.33 (56.1–64.3)	4.1±0.23 (4.1–5.1)	139.2±6.68 (128.5–149.4)
RsNs	19.5±1.86 (16–24.3)	19.2±0.39 (18.4–19.4)	73.5±3.1 (68.8–81.3)	13.2±1.17 (10.7–15.3)	47.8±4.97 (37–56)	63±2.81 (58.1–72.4)	4.3±0.45 (3.1–5.1)	142.8±7.96 (128.5–168.3)
RsXJ	28.1±3.03 (22.8–34)	17.7±0.51 (17.3–18.4)	84.8±2.8 (80–90)	8±2.96 (5.6–19.4)	37.5±1.61 (35–40)	59.9±3.07 (53–65.3)	3.7±0.5 (3.1–4.1)	130.8±3.65 (122.4–136.7)
RsXjs	20.1±1.42 (16.9–23.6)	18.4±0.38 (17.3–19.4)	77.5±3.9 (67.5–86.3)	7.5±1.44 (3.6–10.2)	37.9±3.61 (24–46)	61±2.08 (58.1–65.3)	4.1±0.4 (3.1–5.1)	127.1±6.67 (116.3–144.8)

^aCode of progeny from 30 females (Codes as RsA et al) and a single young female nematode (Coded as RsAs et al) of different population of *Radopholus similis*, RsA/RsAs: intercepted from *Calathea zebrine* in Netherlands; RsB/RsBs: collected from *Ravenia rivularis* in China; RsC/RsCs: intercepted from *Calathea* sp. in Netherlands; RsD/RsDs, RsG/RsGs: collected from *Chamaedorea cataractarum* in China; RsE/RsEs, RsH/RsHs: collected from *Philodendron* sp. in China; RsI/RsIs, RsJ/RsJs, RsV/RsVs, RsW/RsWs, RsY/RsYs: collected from *Anthurium andraeanum* in China; RsK/RsKs, RsP/RsPs: collected from *Calathea zebrine* in China; RsL/RsLs: collected from *Epipremnum aureum* in China; RsM/RsMs: intercepted from *Stranvaesia* sp. in Malaysia; RsN/RsNs: collected from *Chrysalidocarpus lutescens* in China; RsT/RsTs: collected from *Calathea* sp. in China; RsS/RsSs: collected from *Calathea makoyana* in China; RsXj/RsXjs: intercepted from *Zingiber officinale* Roscoe in Singapore.

Table 3. Morphometrics of *Radopholus similis* males from offspring of mixed females and single female from 20 populations (n = 20), respectively (measurements: μm).

Code ^b	<i>L</i>	<i>a</i>	<i>c</i>	<i>c'</i>	<i>stylet</i>	<i>MB</i>	genital length	testis length
RsA	660.2±20.45 (601.2–692.5)	37.2±2.67 (32.1–41)	7.5±0.36 (6.8–8.3)	6.8±0.49 (6–7.7)	13.7±0.9 (11.2–15.3)	52.9±2.27 (49–57.1)	186.6±16.11 (162.5–222.5)	54.2±10.23 (33.7–79.6)
RsAs	708.5±21.67 (660–763.8)	43±3.11 (37.1–47.6)	7.4±0.93 (4.1–8.1)	7.5±1.47 (6.3–13.1)	13.3±0.83 (11.2–14.3)	58.9±2.44 (53–64.3)	179.1±16.41 (146.9–217.5)	51.2±10.18 (30.6–78.5)
RsK	644.1±40.47 (577.5–770)	38.1±2.49 (31.8–44)	7.3±0.32 (6.3–7.7)	6.9±0.49 (6.2–7.8)	12±0.73 (11.2–13.3)	53.9±2.03 (52–60.2)	206.3±18.45 (180–245)	59.5±17.08 (27.5–89.8)
RsKs	618.8±33.06 (542.5–732.5)	38±2.85 (32.5–43.1)	7.4±0.45 (6.4–8.7)	6.5±0.51 (5.7–7.7)	11.9±0.94 (10.2–13.3)	54.8±2.29 (50–59.2)	191.5±23.06 (127.5–232.6)	46.3±18.76 (24.5–108.1)
RsP	647.9±22.15 (612.5–702.5)	37.3±1.8 (32.9–40.8)	8.4±0.35 (7.9–9.4)	5.7±0.29 (5–6.1)	11.6±0.57 (11.2–13.3)	56±1.79 (52–58.1)	206.4±23.65 (155–240)	77.1±14.19 (54.1–98.9)
RsPs	632.6±24.35 (567.5–676.3)	38.6±2.41 (32.9–43.2)	8.5±0.37 (7.8–9.3)	5.7±0.35 (5.2–6.3)	11.9±1.24 (10.2–14.3)	59.4±2.50 (54.1–63.2)	196.4±23.71 (157.5–247.5)	57.4±12.82 (27.5–90.8)
RsC	666.4±26.44 (605–707.5)	41.4±2.8 (38.4–47.5)	7.7±0.23 (7.4–8.2)	6.8±0.34 (6.4–7.5)	13.2±0.34 (12.2–13.8)	55.9±3.35 (51–65.3)	218.8±27.7 (163.2–250.9)	63.6±12.7 (41.8–84.7)
RsCs	662.8±30.59 (613.8–730)	40.9±2.41 (36.2–45.8)	7.7±0.3 (7.2–8.5)	6.8±0.42 (6–7.7)	13.5±0.48 (12.8–14.8)	57.6±3.07 (52–62.2)	174.2±26.64 (122.4–232.5)	38.2±8.39 (22.4–56.1)
RsS	656.3±16.05 (621.3–677.5)	38.1±1.61 (35.5–41)	7.6±0.26 (7.28–3)	6.6±0.41 (5.8–7.4)	13.6±0.74 (12.2–14.8)	55.6±2.61 (53–63.2)	215.2±14.67 (192.8–247.9)	57.3±6.66 (45.9–69.4)
RsSs	670.3±26.22 (622.5–717.5)	38.5±3.27 (33.1–43.8)	7.6±0.43 (6.6–8.7)	6.8±0.65 (5.2–8.1)	13.2±1.36 (10.2–14.8)	58.4±3.28 (50–62.2)	208.4±19.83 (170–257.5)	49.6±17.73 (27.5–111.7)
RsT	615.3±29.52 (548.8–680)	37.4±2.38 (33.4–42)	8.2±0.27 (7.7–8.6)	5.8±0.26 (5.3–6.2)	12.6±1.32 (11.2–15.3)	55.5±2.32 (50–60.2)	180.8±23.16 (142.5–225)	49.6±17.65 (23.5–96.9)
RsTs	615.2±29.1 (545–695)	37.3±2.84 (31.1–43)	8.4±0.4 (7.8–9.3)	5.8±0.28 (5.4–6.3)	11.9±2.19 (9.2–16.3)	60.7±2.77 (55.1–65.3)	190.5±19.95 (142.8–230)	52.3±19.84 (12.2–107.1)
RsB	607.1±15.75 (571.3–637.5)	32.5±1.93 (29.1–36.8)	8±0.33 (7.4–8.6)	5.9±0.42 (5.2–6.8)	12.6±1.46 (10.2–16.3)	54.7±2.08 (51–59.2)	174.1±21.71 (132.5–217.5)	39.1±19.73 (16.3–78.5)
RsBs	613.7±20.8 (555–662.5)	36.4±2.8 (31.1–42.1)	8.2±0.31 (7.7–8.9)	5.8±0.39 (5–6.6)	14.1±0.7 (12.2–15.3)	57.7±2.49 (53–62.2)	201.7±18.7 (167.5–230)	75±25.33 (31.6–123.4)
RsG	621.5±21.13 (572.5–657.5)	35.1±2.2 (30.8–38.6)	8.2±0.33 (7.7–8.8)	5.8±0.43 (5.2–6.6)	14.1±0.53 (13.3–15.3)	56.3±2.72 (51–62.2)	197.5±13.45 (180–222.5)	57.1±13.56 (35.7–84.7)
RsGs	605.9±20.04 (550–643.8)	37±2.59 (33.7–42.9)	8.4±0.31 (7.8–9.2)	5.7±0.38 (4.1–6.2)	11.9±1.56 (10.2–14.3)	56.8±2.81 (51–62.2)	170.2±17.31 (133.6–215)	42±14.63 (21.4–95.9)
RsD	620.3±26.7 (575–670)	34.4±2.7 (31.3–42.3)	8.4±0.34 (7.6–8.9)	5.5±0.37 (5.1–6.2)	12.6±0.94 (11.2–14.3)	55.7±1.8 (52–59.2)	190.8±16.55 (170–220)	68.7±10.39 (34.7–82.6)
RsDs	594.8±23.14 (547.5–632.5)	38±1.84 (33.1–42)	8.6±0.49 (8–9.9)	5.5±0.37 (4.8–6.2)	12.4±1.68 (10.2–16.3)	58.1±2.53 (53–62.2)	179.7±22.53 (137.5–224.4)	50.3±16.14 (27.5–105.1)
RsE	611.4±21.39 (556.3–641.3)	34.1±1.4 (30.5–36.5)	8±0.24 (7.7–8.7)	5.8±0.37 (5.3–6.4)	12.5±0.71 (11.2–13.3)	54.1±2.21 (9–58.1)	190.1±12.02 (160–205)	59.5±12.47 (27.5–83.6)
RsEs	616.8±33.67 (540.5–723.8)	38.4±2.5 (32.6–44.5)	8.4±0.47 (7.6–10.3)	5.8±0.3 (5.1–6.3)	13.5±1.54 (10.2–15.3)	58.3±2.18 (53–63.2)	175.5±22.26 (125–217.5)	46±14.18 (23.5–84.7)
RsH	676.9±26.49 (631.3–717.5)	35.4±2.1 (31.9–38.7)	7.4±0.24 (6.7–7.7)	6.9±0.51 (6.2–8.1)	13±0.87 (11.2–14.3)	55.1±1.4 (52.5–57.1)	195.4±16 (167.5–227.5)	49.7±9.07 (35.7–71.4)
RsHs	651.6±41.32 (527.5–710)	39±3.08 (33.3–47.3)	7.6±0.27 (6.9–8.3)	7±0.5 (6.2–8)	12±1.22 (9.2–14.3)	58.3±2.7 (50–65.3)	188.3±16.89 (155–232.6)	45.3±20.32 (23.5–95.9)
RsI	612±20.85 (572.5–641.3)	38.6±1.5 (35.4–42.3)	8.3±0.29 (7.7–8.8)	6.1±0.34 (5.4–6.7)	12.9±0.67 (11.2–13.8)	53±1.87 (50–56.1)	175.3±21.38 (140–215)	51.9±12.75 (30.6–77.5)
RsIs	609±22.36 (551.3–641.3)	37.5±2.19 (33.9–41.8)	8.4±0.29 (7.8–9.2)	5.8±0.3 (5.2–6.4)	12.4±1.22 (10.2–14.3)	56.5±3.04 (49–61.2)	173.3±18.33 (122.5–207.1)	44.3±12.74 (20.4–84.7)
RsJ	615.5±33.84 (536.3–672.5)	35.9±2.1 (30.6–40.7)	7.4±0.26 (6.9–7.9)	6.5±0.47 (5.6–7.3)	12.2±0.89 (11.2–14.3)	52.5±2.2 (46.9–58.1)	202.5±21.52 (162.5–260)	61.8±10.88 (27.5–78.5)

Code ^b	<i>L</i>	<i>a</i>	<i>c</i>	<i>c'</i>	<i>stylet</i>	<i>MB</i>	genital length	testis length
RsJs	605.9±29.72 (554.5–650)	36.9±2.78 (31.7–42.8)	7.5±0.27 (6.8–8)	6.2±0.42 (5.4–7.1)	12.4±0.94 (11.2–15.3)	55.1±2.16 (52–60.2)	193.7±19.45 (160–233.6)	41.6±13.32 (27.5–82.6)
RsV	614.8±22.17 (570–650)	36.1±2.3 (31.9–41.6)	8.3±0.26 (7.8–8.8)	5.7±0.47 (5.1–7.4)	14.8±0.69 (13.3–15.3)	56.6±2.74 (52–62.2)	196.7±16.22 (161.2–222.4)	74.4±16.95 (37.7–98.9)
RsVs	620.8±28.16 (568–713.8)	38±1.83 (35.4–41)	8.3±0.34 (7.5–9)	5.8±0.47 (5.1–7.1)	11.6±1.9 (9.2–14.3)	58.5±1.63 (55.1–63.2)	188±15.62 (150–217.5)	52.7±14.08 (16.3–82.6)
RsW	602.2±20.24 (567.5–627.5)	37.1±3.7 (31.4–41.7)	7.3±7.28 (6.5–7.8)	6.5±6.57 (5.5–7.4)	11.1±0.71 (10.2–12.2)	53.1±53.24 (51–57.1)	196.1±18.2 (157.5–232.5)	47.5±8.7 (32.6–62.2)
RsWs	600.2±30.42 (555–675)	35.1±2.33 (30.1–39.1)	7.5±0.3 (6.9–8.1)	6.3±0.39 (5.3–7.3)	13.4±0.85 (12.2–15.3)	54.7±2.17 (50–58.1)	194.2±13.23 (176.5–227.5)	45.8±21.71 (22.4–119.3)
RsY	619.5±18.67 (578.8–648.8)	35.5±2.0 (31.5–40.4)	8.4±0.28 (8–9)	5.5±0.5 (4.5–6.6)	14.8±0.68 (13.8–16.3)	55.5±1.96 (52–58.1)	194.7±15.86 (155–222.4)	65.8±17.7 (34.7–87.7)
RsYs	632±26.48 (586.3–687.5)	37.7±2.58 (29.3–41.7)	8.5±0.3 (8.1–9.2)	5.8±0.7 (4.9–9.1)	12±1.78 (10.2–15.3)	60.3±2.04 (57.1–64.3)	202.4±21.84 (147.5–253)	59.9±16.67 (30.6–104)
RsL	618.3±22.94 (581.3–658.8)	38.8±2.7 (34.6–43.6)	8.3±0.36 (7.7–9)	5.6±0.31 (5.1–6.2)	15.1±0.83 (13.3–16.3)	61.3±1.8 (58.1–64.3)	182.8±16.68 (143.8–227.5)	38.1±9.71 (24.5–56.1)
RsLs	611.9±30.33 (560–658.8)	36.8±1.98 (33.5–39.4)	8.2±0.34 (7.7–8.7)	5.6±0.33 (5.3–6.3)	11.3±1.41 (9.7–14.3)	57.2±2.85 (47.9–61.2)	201.6±28 (152.5–247.5)	66.7±20.69 (31.6–106.1)
RsM	638.5±16.48 (610–662.5)	36.2±2.1 (32.2–40.7)	8.5±0.27 (7.9–9)	5.7±0.34 (5.3–6.5)	13.1±1.03 (11.7–15.3)	55.1±2.17 (52–60.7)	195.2±21.54 (157.5–237.5)	64.5±17.27 (41.8–104)
RsMs	622±27.21 (577.5–687.5)	37.6±1.97 (33.7–40.3)	8.4±0.34 (7.7–9.2)	5.7±0.35 (4.9–6.5)	13.9±1.08 (11.2–15.3)	59.1±2.63 (54.1–65.3)	188.8±21.89 (147.5–227.5)	59.5±18.89 (17.3–93.8)
RsN	619.4±22.21 (572.5–655)	37.6±2.1 (33.1–41.2)	8.1±0.37 (7.5–9)	6±0.32 (5.6–6.8)	13.3±0.92 (11.2–14.3)	55.4±2.18 (51–60.2)	189.4±22.92 (147.5–235)	57.4±14.3 (28.6–80.6)
RsNs	605.4±18.97 (567.5–637.5)	38.6±2.62 (32.5–43.8)	8.2±0.31 (7.5–9.2)	5.9±0.43 (5.1–7.3)	13±2.18 (9.2–15.3)	58.8±3.37 (53–66.3)	185.9±28.28 (150–244.8)	60.1±28.12 (28.6–124.4)
RsXJ	617.2±29.31 (570–712.5)	32.8±3.3 (30.3–37.8)	7.7±7.8 (7.2–8.6)	6±6.09 (5.5–6.7)	11.6±0.49 (11.2–12.2)	52.7±53.22 (51–61.2)	187±14.09 (160–205)	51.2±11.37 (35.7–70.4)
RsXjs	624.3±15.12 (583.8–645)	36.1±1.81 (31.3–39.8)	7.7±0.22 (7.2–8.2)	6±0.39 (4.9–6.8)	12.2±1.88 (10.2–15.3)	56.3±2.18 (51–60.2)	203.2±9.63 (177.5–222.5)	57.7±10.23 (41.8–75.5)

Table 3. Continued.

Code	<i>Tail</i>	<i>b</i>	gubernaculum length	spicule length	distance from anterior to excretory core	lip height	body diameter	number of genital papilla
RsA	88.8±5.84 (77.5–98.8)	7.2±1.07 (5.1–9.2)	10.7±0.68 (9.2–11.7)	18.7±1.09 (16.3–20.4)	89.3±2.86 (84.7–94.9)	6.3±0.24 (6.1–6.6)	17.8±1.32 (16.3–20)	0–6
RsAs	97.6±18.2 (85–163.8)	7.5±1.43 (5.6–12.2)	11.1±0.9 (8.2–12.4)	19.8±1.7 (14.3–21.4)	96.1±3.33 (87.7–104)	6.2±0.25 (5.6–6.6)	16.5±1.22 (15–18.8)	0–6
RsK	88.8±5.35 (77.5–101.3)	6.2±1.09 (4.6–8.7)	10.7±0.6 (9.7–12)	18.4±1.77 (16.3–23.5)	92.2±4.03 (86.2–102)	6±0.37 (5.6–7.1)	16.9±1.08 (15–18.8)	0
RsKs	83.3±5.62 (72.5–96.3)	6.5±1.38 (4.6–9.7)	10.1±0.66 (8.2–11.2)	18.1±1.23 (16.3–21.4)	88.8±3.21 (81.6–94.9)	5.9±0.3 (5.3–6.6)	16.4±1.43 (14.5–20)	0–1
RsP	77±3.48 (72.5–87.5)	7±1.02 (5.1–8.7)	11.1±0.48 (10.2–12.2)	19.7±1.45 (15.3–21.4)	92.4±3.73 (83.6–97.9)	6.1±0.11 (5.6–6.1)	17.4±1.09 (15–20)	2–9
RsPs	74.8±3.84 (66.3–82.5)	6.5±1.25 (4.1–9.2)	11.2±0.52 (9.7–12.8)	20±0.93 (18.4–21.4)	91.1±3.58 (85.7–99.5)	6.1±0.25 (5.1–6.6)	16.4±1.27 (15–19.8)	8
RsC	86.8±4.55 (77.5–95)	8.5±2.47 (4.6–12.8)	10.8±0.56 (9.7–11.7)	18.9±0.9 (17.3–20.4)	91±4.07 (84.2–97.9)	5.9±0.34 (5.1–6.2)	16.2±1.43 (13.8–17.8)	0–3
RsCs	86±4.64 (78.8–96.3)	7.2±1.59 (5.1–13.3)	10.8±0.68 (9.7–11.7)	18.9±1.2 (16.3–22.4)	91.7±4.28 (84.7–101)	6±0.25 (5.6–6.6)	16.2±1.01 (14.8–18.8)	0–3
RsS	86±3.79 (80–92.5)	7.7±1.6 (5.1–10.7)	10.8±0.62 (9.7–11.7)	18.5±0.6 (17.9–19.4)	93.1±3.95 (86.2–100)	6±0.21 (5.6–6.1)	17.3±0.47 (16.3–17.8)	0
RsSs	83.9±5.79 (72.5–93.8)	6.6±1.61 (3.6–9.7)	11.2±0.9 (9.2–12.2)	19.3±1.14 (16.3–21.9)	94.7±3.39 (86.7–100)	6.1±0.19 (5.6–6.6)	17.5±1.27 (15–20)	0
RsT	75.4±3.12 (70–83.8)	7±1.05 (5.1–9.2)	10.8±1.06 (8.2–12.2)	20.1±1.43 (17.3–23)	95.9±5.39 (87.7–109.1)	5.9±0.33 (5.3–6.6)	16.5±1.18 (15–18)	0–5
RsTs	73.1±3.22 (67.5–78.8)	7.6±1.06 (5.6–9.7)	10.6±0.72 (8.7–11.7)	20.1±1.28 (16.3–22.4)	94.7±3.8 (87.7–102.5)	5.9±0.25 (5.6–6.1)	16.6±1.38 (15–20)	4–5
RsB	76.3±3.33 (67.5–81.3)	7.8±1.24 (5.6–10.2)	10.8±1.05 (9.2–12)	20.5±1.55 (17.3–23.5)	90.4±3.11 (83.6–96.4)	5.9±0.26 (5.6–6.1)	18.8±1.2 (16.3–20.5)	4–6
RsBs	74.8±3.73 (66.3–82.5)	7.6±1.38 (5.1–10.7)	11±0.63 (8.7–12)	20.2±1.02 (18.4–22.4)	95.1±3.25 (89.8–102)	5.8±0.31 (5.1–6.1)	17±1.54 (15–20)	4–5
RsG	76.1±3.73 (67.5–82.5)	7.9±0.82 (6.6–9.2)	11.1±0.63 (10.2–12.2)	20.5±1.5 (18.4–23.5)	94.2±2.58 (89.8–98.9)	6±0.24 (5.6–6.1)	17.7±0.98 (16.3–20)	8
RsGs	72.1±3.02 (67.5–78.8)	7.4±0.92 (5.1–9.2)	10.8±0.72 (8.7–11.7)	20.1±1.42 (17.3–25.5)	91.2±4.53 (78.5–97.9)	5.7±0.29 (5.1–6.1)	16.4±1.1 (14.8–18)	8
RsD	74.2±3.9 (66.3–83.8)	7.9±1.05 (4.6–9.2)	11.4±0.58 (10.2–12.2)	21±1.41 (18.4–24.5)	92.7±4.26 (85.2–100)	6.1±0.3 (5.2–6.5)	18.1±1.56 (15–20)	0–6
RsDs	69.4±4.28 (60–76.3)	7±0.83 (5.6–8.7)	10.9±0.6 (9.4–12.2)	19.8±0.97 (17.3–21.4)	90.9±3.33 (84.7–96.4)	5.9±0.3 (5.1–6.1)	15.7±0.82 (14.5–18)	2–7
RsE	76.4±3.11 (71.3–82.5)	7.7±0.6 (6.1–8.7)	11±0.48 (10.2–11.7)	19.8±1.09 (18.4–22.4)	91.3±4 (84.2–98.4)	5.9±0.25 (5.6–6.1)	17.9±0.85 (16.3–20)	4–5
RsEs	73.9±3.83 (65–81.3)	7.3±0.94 (5.1–9.2)	10.7±0.7 (9.2–11.7)	19.8±1.07 (17.3–21.4)	94.6±4.13 (85.7–103)	5.9±0.29 (5.1–6.1)	16.1±1.27 (13.8–19.5)	0–6
RsH	91.1±4.07 (82.5–98.8)	6.8±1.92 (4.1–10.7)	11.2±1.03 (9.2–12.2)	19.2±1.26 (17.3–22.4)	94.5±5.05 (83.1–106.1)	6±0.21 (5.6–6.1)	19.2±0.92 (17.5–21.3)	5
RsHs	86.3±5.99 (71.3–96.3)	5.1±1.03 (3.1–7.7)	10.4±0.81 (8.7–11.7)	18.7±1.49 (16.3–23.5)	91.7±5.11 (78–102)	5.7±0.29 (5.1–6.1)	16.8±1.36 (15–18.8)	0–4
RsI	74.2±2.91 (67.5–78.8)	7.6±0.95 (6.1–9.2)	10.9±0.65 (9.7–11.7)	19.7±0.99 (18.4–21.4)	91.1±3.62 (84.7–98.9)	5.6±0.35 (5.1–6.1)	15.9±0.68 (15–17)	5
RsIs	72.7±4.01 (62.5–79.8)	7.8±1.42 (6.1–12.8)	11.1±0.5 (9.4–12.2)	20.4±0.92 (18.4–22.4)	89.5±3.9 (82.1–97.9)	5.9±0.25 (5.6–6.1)	16.3±0.91 (15–17.5)	3–5
RsJ	82.9±3.42 (77.5–91.3)	7.5±1.85 (4.6–12.2)	10.1±0.66 (9.2–11.2)	17.2±0.78 (16.3–19.4)	87.9±4.06 (83.6–96.9)	6.1±0.35 (5.1–7.1)	17.2±1.08 (15–18.8)	0

Code	Tail	<i>b</i>	gubernaculum length	spicule length	distance from anterior to excretory core	lip height	body diameter	number of genital papilla
RsJs	80.5±4.63 (73.8–87.5)	6.9±1.39 (4.6–10.2)	10.1±0.58 (9.2–11.2)	18.4±0.93 (17.3–20.4)	88.6±4.06 (80.6–95.9)	6.1±0.17 (5.6–6.2)	16.5±1.27 (13.8–18.8)	0
RsV	74±2.62 (68.8–80)	6.4±1.03 (4.6–8.2)	11±0.47 (10.2–11.7)	20.1±0.87 (18.4–21.9)	93.3±3.47 (85.7–98.9)	5.9±0.26 (5.6–6.1)	17.1±1.28 (15–20)	4–7
RsVs	74.6±5.12 (66.3–88.8)	6.6±1.31 (3.6–9.7)	11±0.58 (9.2–11.7)	20.3±1.05 (17.3–21.4)	93.2±3.79 (85.7–103)	5.8±0.33 (5.1–6.6)	16.4±1.04 (15–17.5)	4
RsW	83.1±4.54 (75–92.5)	7±1.1 (5.1–9.2)	10.2±0.88 (8.2–11.2)	17.4±1.37 (15.3–20.4)	87.6±2.52 (82.6–93.3)	6±0.19 (5.6–6.1)	16.3±1.11 (15–18.8)	0
RsWs	80.3±4.56 (71.3–92.5)	6.5±1.76 (3.6–10.1)	10±0.68 (8.7–11.2)	18.1±1.08 (16.3–20.4)	86.3±4.92 (74.5–95.9)	6±0.31 (5.1–6.6)	17.1±1.02 (15–18.8)	1
RsY	73.7±3.16 (67.5–78.8)	6.8±1.28 (4.6–9.7)	11.5±0.4 (10.7–12.1)	20.8±1.1 (18.4–22.4)	96.9±3.96 (88.2–104.6)	6.1±0.05 (6.1–6.3)	17.5±1.08 (15.3–20)	0
RsYs	74.6±3.96 (66.3–81.3)	7.5±1.12 (5.6–10.2)	11±0.69 (8.7–11.7)	20.5±1.03 (16.3–22.4)	95.4±2.47 (89.8–100)	6±0.3 (5.1–6.6)	16.9±1.24 (15–20)	0
RsL	74.8±4.24 (67.5–83.8)	6.8±1.25 (4.6–10.2)	10.9±0.51 (10.2–12)	20±0.71 (18.9–21.9)	94.1±2.94 (87.7–97.9)	5.9±0.27 (5.3–6.1)	16±1.16 (15–18)	2–6
RsLs	73.5±4.22 (67–81.3)	6.9±1.4 (4.6–11.7)	11.2±0.53 (9.7–12)	20.5±1.01 (18.4–22.4)	89.9±3.27 (82.6–94.9)	6±0.24 (5.6–6.1)	17.4±1.42 (14.8–20)	6
RsM	75.3±2.94 (67.5–81.3)	7.1±1.03 (5.6–9.2)	11.4±0.53 (10.2–12.2)	20.2±1.12 (18.4–22.4)	95.8±3.53 (90.8–104)	6±0.23 (5.6–6.1)	17.7±1.25 (15–20.5)	7–8
RsMs	74.5±4.89 (67.5–86.3)	6.6±1.22 (4.6–9.2)	10.4±1.1 (7.7–12)	20.2±2.01 (15.3–24.5)	94.1±3.84 (87.7–102)	6±0.27 (5.6–6.6)	16.6±1.06 (15–18.8)	6–8
RsN	76.7±4.27 (70–86.3)	6.9±1.25 (4.6–9.2)	10.9±0.61 (9.7–12.2)	20±1.15 (18–24)	92.4±4.03 (85.7–100)	5.9±0.26 (5.6–6.1)	16.5±0.75 (15–18)	4–6
RsNs	73.5±3.43 (66.3–83.8)	7.2±0.8 (6.1–9.2)	10.7±0.76 (8.2–11.7)	20±1.1 (17.3–21.4)	94.1±3.94 (88.7–102)	5.8±0.31 (5.1–6.1)	15.7±1.18 (13.8–18.8)	3–6
RsXJ	79.8±3.55 (72.5–86.3)	6±1.26 (4.6–9.7)	10.6±0.44 (9.7–11.2)	19.4±1.4 (17.3–19.8)	90.3±3.23 (84.7–95.9)	6±0.29 (5.1–6.1)	18.8±1.09 (16.3–20)	0
RsXjs	80.8±2.87 (73.8–85.5)	6±1.06 (4.6–8.2)	10.4±0.73 (8.2–11.7)	19.3±1.11 (15.3–20.9)	92.9±2.6 (88.7–97.4)	5.8±0.3 (5.3–6.1)	17.3±0.89 (15–20)	0

^bCode of progeny from 30 females (Codes as RsA et al) and a single young female nematode (Coded as RsAs et al) of different population of *Radopholus similis*, RsA/RsAs: intercepted from *Calathea zebrine* in Netherlands; RsB/RsBs: collected from *Ravenia rivularis* in China; RsC/RsCs: intercepted from *Calathea* sp. in Netherlands; RsD/RsDs, RsG/RsGs: collected from *Chamaedorea cataractarum* in China; RsE/RsEs, RsH/RsHs: collected from *Philodendron* sp. in China; RsI/RsIs, RsJ/RsJs, RsV/RsVs, RsW/RsWs, RsY/RsYs: collected from *Anthurium andraeanum* in China; RsK/RsKs, RsP/RsPs: collected from *Calathea zebrine* in China; RsL/RsLs: collected from *Epipremnum aureum* in China; RsM/RsMs: intercepted from *Stranvaesia* sp. in Malaysia; RsN/RsNs: collected from *Chrysalidocarpus lutescens* in China; RsT/RsTs: collected from *Calathea* sp. in China; RsS/RsSs: collected from *Calathea makoyana* in China; RsXj/RsXjs: intercepted from *Zingiber officinale* Roscoe in Singapore.

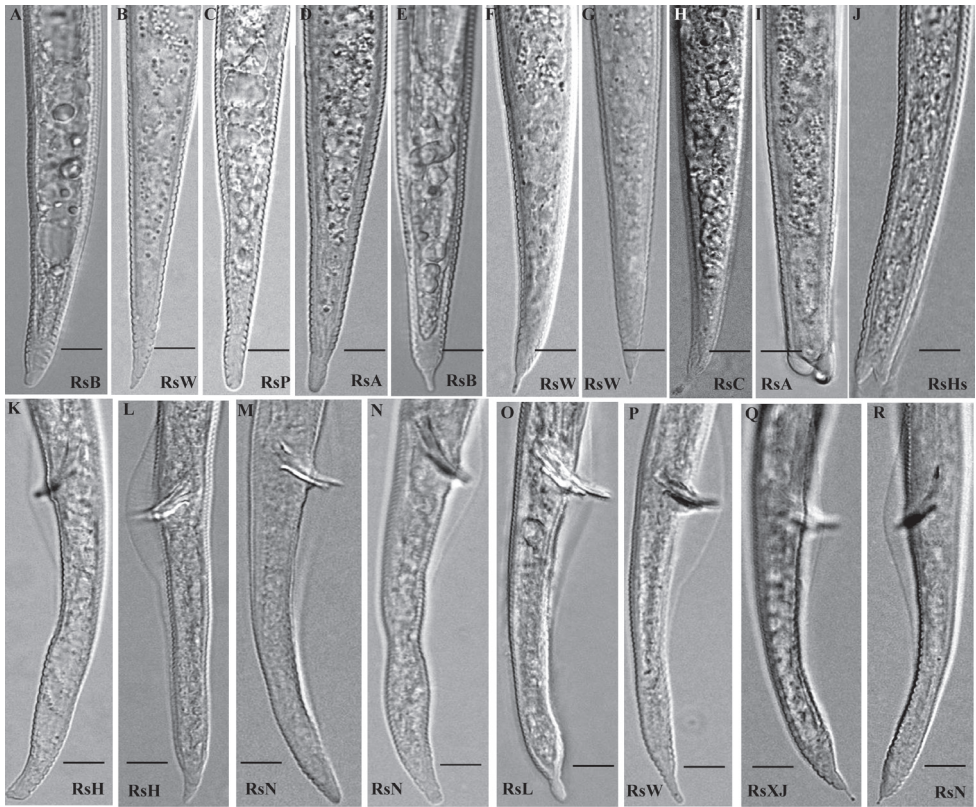


Figure 2. Tail morphology of *Radopholus similis* Female: **A–B** Type I tail **C–D** Type II tail **E–H** Type III tail **I–J** Type IV tail. Male: **L–M** Type I tail **K, N** Type II tail **O–R** Type III tail. **A, E:** RsB; **B, F, G, P:** RsW; **C:** RsP; **D, I:** RsA; **H:** RsC; **J:** RsHs; **K–L:** RsH; **M–N:** R:RsN; **O:** RsL; **Q:** RsXJ. Scale bar: **A–R** = 10 μ m.

near the stylet base (Figure 1E). The excretory pore opened ventrally 0–2 annuli behind the hemizonid, approx. 2–3 annuli long in diam. The oesophageal gland overlapped the intestine dorsally (Figure 1C). The vulva situated in the postmedian part of the body. The vulva was flat or slightly projecting (Figure 1G). The reproductive system was didelphic, extended, with oocytes in a single row. The spermatheca was round or oval, with rod-shaped sperm (Figure 1G). The gonad inflexion exists in some populations and the anterior gonad was longer than the posterior one. The tail was mostly subconoid (Figure 1H, Figure 2A–I), longer than 70 μ m, with average hyaline part of tail longer than 5.6 μ m. Male: The lip region was high and round, hemispherical, clearly offset with body contour, bearing 3–5 annuli (Figure 1F, Figure 5D–F). The stylet was weak, without base knob or only with slightly expanded base. The median bulb and gland of the esophagus degenerate (Figure 1D). The excretory pore opened ventrally at 0–1 annulus behind hemizonid. Single testis extended forward. The gubernaculum extended over cloacal pore, approx. half length of spicule. The bursa was obvious, extending more than 47%–90% length of tail (Figure 1I–J, Figure 5R–V).

Morphological observations of progeny of 30 females

Females. The shortest individual female (513.8 μm) was found in the RsK population from *C. zebrina*, and the shortest females with average length of 656.7 μm were from the RsM population from *Stranvaesia* sp.. The longest individual female (843.8 μm) and the longest females with average length of 795.9 μm were found in the RsC population from *Calathea* sp.. Head diameter and height were almost identical in all the populations and ranged from 9.8×4.3 μm to 9.1×4 μm . The number of head annuli varied in and among populations, with 2 annuli in the RsS and RxXj populations, 3–4 annuli in the RsL, RsT, RsV and RsY populations, and 3 annuli in the remaining populations. The stylet length varied from 17.3 μm to 19.6 μm . Tail length and shape varied in and among populations. The longest tails with average length of 90.9 μm was found in the RsC population. The shortest tails with average length of 71.2 μm was found in the RsI population. The most and least tail annulations (61 and 32, respectively) were all found in the RsP population. The average length of the hyaline part of the tail of all populations was longer than 5.6 μm , 97.5% of these individuals was longer than 7 μm , and only 0.5% was 5.6 μm . In addition, the shortest and longest hyaline part of tail were all from the RsH population (3.1 μm and 10.7 μm , respectively). Tail shape showed four different types (I–IV). The type I tail is conoid, slightly or abruptly slender to tail terminus, tail terminus sharp or blunt round, which showed in the RsB, RsI, RsL and RsW populations (Figure 2A, B; Figure 5K, L, N, Q). The type II tail is conoid, then sub-cylindrical, tail terminus round which showed in the RsP and RsA population (Figure 2C, D; Figure 5J). The type III tail is conoid with a fingerlike terminus which showed in the RsB, RsW and RsC populations (Figure 2E–H). The type IV tail is conoid with forked ends showed in the RsA population (Figure 2I). Among these, type I and II tail shapes were more frequent than the other two. In addition, tail shapes were not identical within the same population. The RsA population showed types II and IV, and the RsW population showed types I and II. The RsB, RsN and RsV populations showed types I, II and III, whereas the other populations showed most tail shapes as types I and II.

Males. The shortest individual male (572.5 μm) was found in the population from *A. andraeanum* coded as RsJ, and the shortest males with average length of 602.2 μm were from the same host population but RsW. The longest male (770 μm) was found in the RsK population from *C. zebrina*, and the longest males with average length of 676.9 μm were found in the RsH population from *Philodendron* sp. The longest spicule (20.8 μm) was found in the RsY population, and the shortest (17.2 μm) in the RsJ population. Tail shape varied in and among populations: RsA, RsJ and RsW populations had type I and type III tails (Figure 2P). The RsB, RsI, RsL and RsT populations had type II and type III tails (Figure 2O). The RsXj population had type I, II and III tails (Figure 2Q). The RsK, RsG, RsP and RsV had type I, II and III tails. The RsN population had type I (Figure 2M), II (Figure 2N) and III tails (Figure 2R). The remaining populations had type I and type II tails.

Morphological observations of progeny of single females. Females. The shortest female was found in the RsEs population (545 μm), and the shortest females with average length of 651.6 μm were found in the RsDs population. The longest individual female and longest females were found in the RsAs population (body length = 798.8 μm , the average body length = 743.4 μm , respectively). The head diameter and height varied from $9 \times 4 \mu\text{m}$ – $9.6 \times 4.1 \mu\text{m}$, and the stylet length varied from 18.3 μm to 19.4 μm . The head annuli varied in and among the populations. Two head annuli were found in the RsXJs population, 3 in the RsAs, RsEs, RsHs, RsIs, RsKs, RsLs, RsTs, RsKs and RsYs populations, 4 in the RsBs, RsDs, RsGs, RsJs, RsNs and RsPs populations, and 3–4 in the RsCs, RsMs and RsVs populations. The longest tails of female with average length of 85.3 μm were from the RsAs population, and shortest tails (68.8 μm) were from the RsDs population. The highest number of tail annuli (60) was from the RsPs population, and the least (24) was from the RsXJs population. Tail shape varied also. The tail type I predominated in the RsBs, RsCs, RsEs, RsLs, RsMs, RsPs, RsSs and RsYs populations (Figure 5I). Tail type I and II were found in the RsGs and RsTs population. Tail type I and III were found in the RsJs population (Figure 5O). Tail type I and III were found in the RsWs population (Figure 5G). Tail types II and III were found in the RsGs and RsTs population. Tail types I, II and III were each found in the RsAs, RsIs, RsNs and RsVs populations. Tail types II, III and IV were found in the RsHs populations (Figure 2J). And tail types I, II and III were found in the RsKs population.

Males. The shortest male was found in the RsHs population (527.5 μm), and the shortest males with average length of 594.8 μm were found in the RsDs populations. The longest male and longest males were both from the RsAs population (body length = 763.8 μm , the average length = 708.5 μm , respectively). The longest spicule was found in the RsLs and RsYs populations (20.5 μm), and the shortest spicule was found in the RsKs and RsWs population (18.1 μm). The tail shape varied also. In the RsJs and RsXJs population, the tail type was I. In the RsAs and RsSs population, the tail type was I and II; in the RsKs population, the tail types were I and III. In the RsMs and RsPs populations, the tail types were II and III. In the remaining populations, tail tail types were I, II and III.

Scanning electron microscopy observation. Nematodes progeny of 30 females.

Females. The main differences in morphological characters of females observed by SEM were shape of labial disc, terminal position of lateral lip and annuli terminated at vulva. The shape of the labial disc of all the 20 populations was divided into three types: hexagonal (RsC) (Figure 3B), with the two dorsal lip and ventral lip obviously not fused; round-elongate, due to the fusion of the two dorsal lips and the ventral lips, respectively (RsD, RsG, RsH and RsL populations) (Figure 3D); and sub-hexagonal, because of the two dorsal lips and two ventral lips partially fused, with a depression formed between the two dorsal lips and two ventral lips (all the other populations) (Figure 3A, E). The lateral lips terminated differently depending on the population. In the RsS and RsXJ populations, the lateral lips appeared to terminate at the end of second head annulus (Figure 3I, P). In the RsA, RsG, RsV and RsW populations, the lateral lips terminated before the third annulus (Figure 3M). In the RsB, RsC, RsD, RsH, RsJ, RsM and RsN populations, the lateral lips extended to the end of the third head annulus (Figure 3C, G). In the RsI, RsK, RsP and RsY populations, the lateral

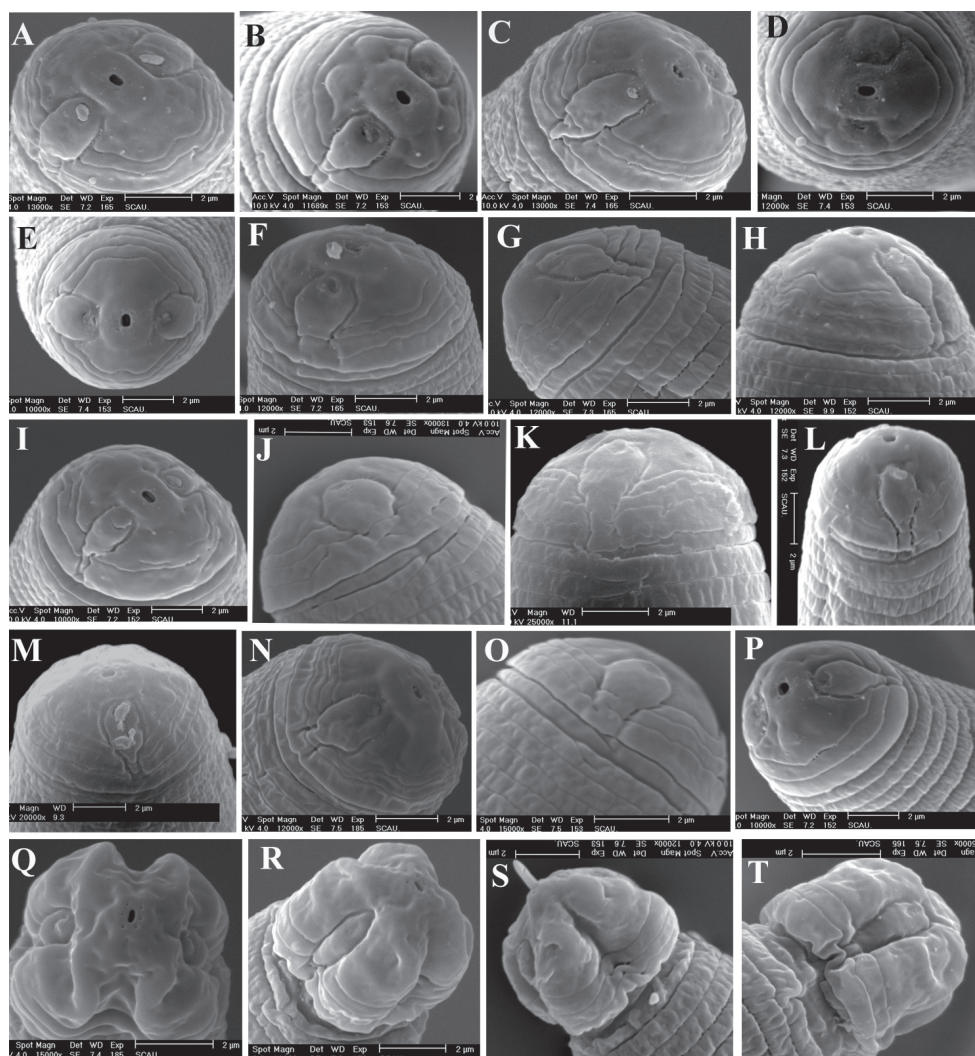


Figure 3. Lip region morphology of female and male of *Radopholus similis* Female: **A** Face view of RsA **B** Face view of RsC **C** Face view of RsD **D** Face view of RsT **E** Face view of RsE **F** Lateral view of RsE **G** Lateral view of RsE **H** Lateral view of RsK **I** Lateral view of RsXJ **J** Lateral view of RsT **K** Lateral view of RsP **L** Lateral view of RsL **M** Lateral view of RsY **N** Lateral view of RsEs **O** Lateral view of RsT **P** Lateral view of RsXJ. Male: **Q** Face view of RsTs **R** Lateral view of RsY **S** Lateral view of RsV **T** Lateral view of RsN.

lips terminated at the end of the fourth head annulus (Figure 3H, K). In the RsL population, the lateral lips terminated over the end of the last annulus (Figure 3L). In the RsE population, one side of the lateral lips terminated at the end of the third annulus, and the other side of lateral lips terminated in middle of the second head annulus (Figure 3F). In the RsT population, one side of the lateral lips terminated before the third annulus, and the other side of lateral lips terminated at the end of third annulus (Figure 3J, O). The annuli terminated differently in the vulval area also varied in and among the populations. Among them, one annulus terminated at the vulva were found in the

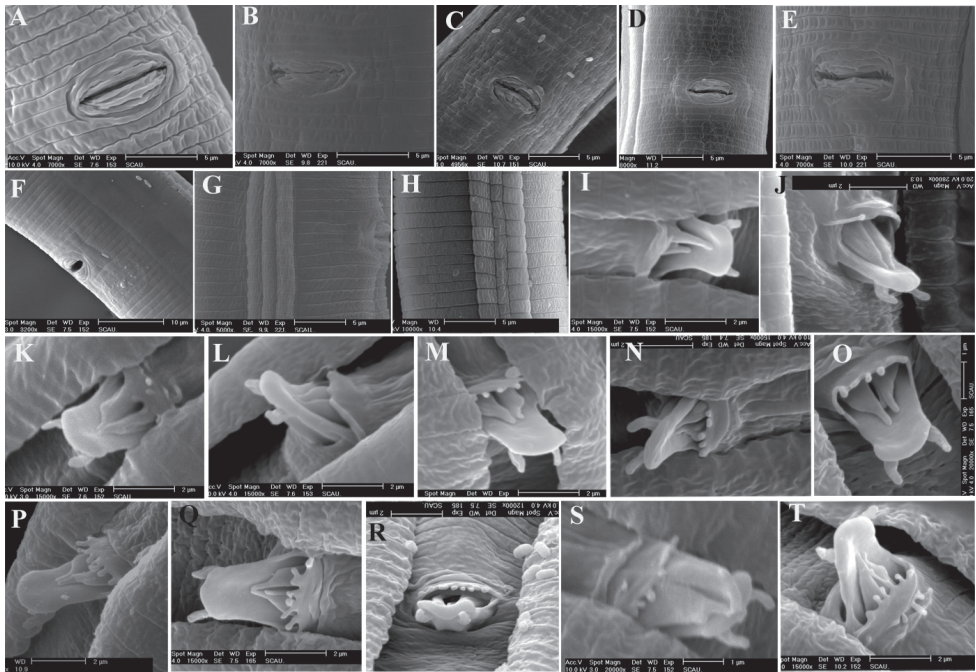


Figure 4. Annuli terminated at vulvar, incisures and genital papillae in cloacal region of *Radopholus similis*. Annuli terminated at vulvar region of females: **A** One annulus in RsC **B** One and two annuli on each side in RsN **C** One and three annuli on each side in RxXJs **D** Three annuli in RsP **E** Two annuli in RsK **F** Four annuli in RsW. Incisures in lateral region of females: **G** RsH **H** RsJs. Number of genital papillae in cloacal region of males: **I** 0 genital papillae of RsEs **J** 1 genital papillae of RsKs. 2 genital papillae of RsP **L** 3 genital papillae of RsC **M** 4 genital papillae of RsB **N** 5 genital papillae of RsTs **O** 5 genital papillae of RsI **P** 6 genital papillae of RsB **Q** 7 genital papillae of RsM **R** 8 genital papillae of RsG **S** 8 genital papillae in double row of RsD **T** 9 genital papillae in double row of RsP.

RSC and RsM populations (Figure 4A), two annuli in the RsA, RsB, RsD, RsG, RsE, RsH, RsI, RsJ, RsK, RsL, RsT, and RsV populations (Figure 4E), and three annuli in the RsP and RsS populations (Figure 4D). In addition, two or four annuli terminated at the vulva were found in the RsW population (Figure 4F). Whereas one on one side and two on the other side were found in the RsN, RsY and RsXj populations (Figure 4B).

Males. The main differences in morphological characters of males observed by SEM were in head shape and number of genital papillae on the anterior cloacal apertures. The head region was four-lobed, formed by a longitudinal constriction, and the first annuli were wider than the remaining head annuli (Figure 3Q–T). Three annuli were found in the RsA, RsI, RsJ, RsK and RsN populations (Figure 3T), and four annuli in the remaining populations (Figure 3R). The number of genital papillae on the anterior cloacal apertures varied in and among populations, usually 0–9 in a single row (Figure 4I–R), but in the RsD and RsP populations, the genital papillae were arranged in a double row (Figure 4S–T).

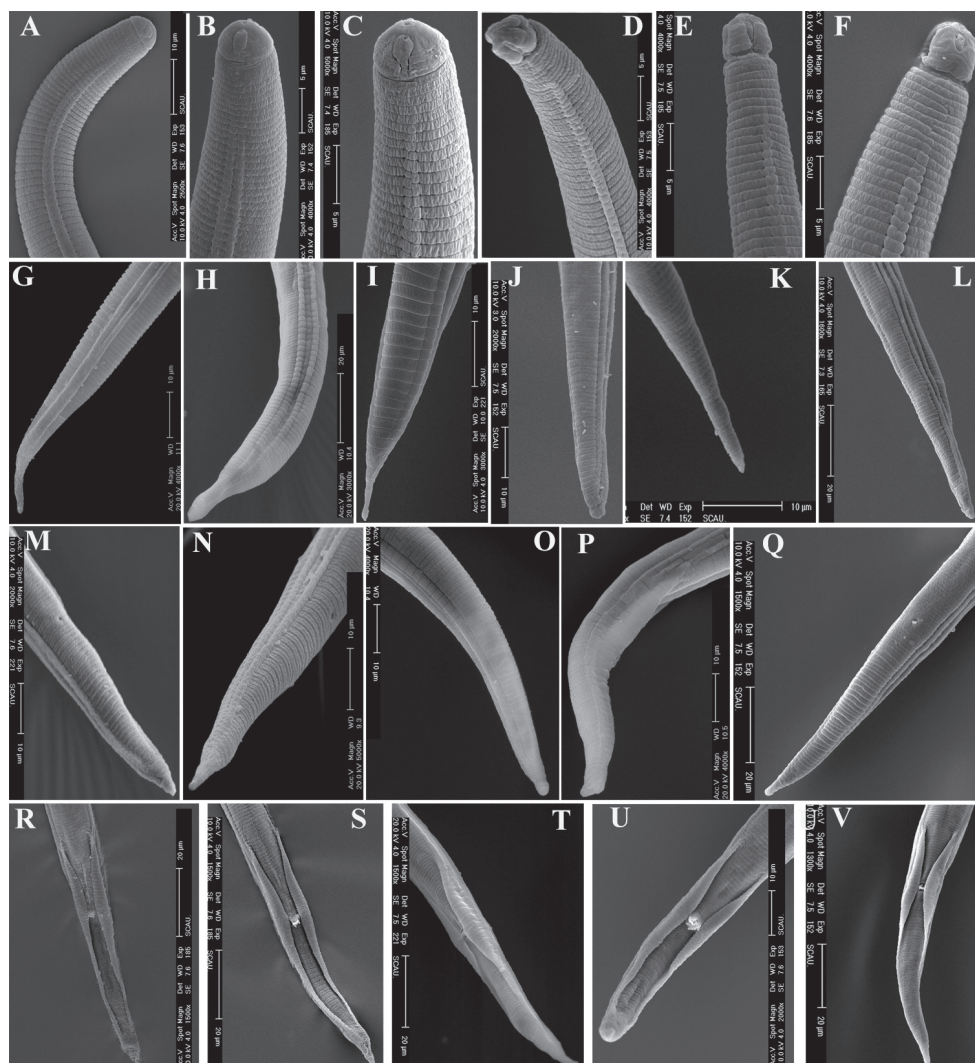


Figure 5. Anterior region and tail of *Radopholus similis* Anterior region. **A** Female RsTs **B** Female RsL **C** Female RsLs **D** Male RsV **E** Male RsXJ **F** Male RsAs Female tails **G** Female type I of RsWs **H** RsXJs **I** RsCs **J** RsP **K** RsW **L** RsI **M** RsXJs **N** RsW **O** RsJs **P** RsXJs **Q** RsL. Male tails: **R** RsG **S** RsLs **T** RsHs **U** RsVs **V** RsS.

Nematode progeny of the single females. Observation of the progeny of the single female by SEM showed no obvious differences between the progeny of the 30 females and the single female inoculated on carrot discs, but some variations were found within the same population. Regarding the terminal position of lateral lips, only the RsBs, RsDs, RsMs and RsSs populations showed the same position with their counterpart of progeny of the 30 females, but the remaining populations did not. In the RsHs and RsXjs populations, the lateral lips terminated at the end of the second head annulus. In the RsCs population, the lateral lips terminated before the third head annulus. In the

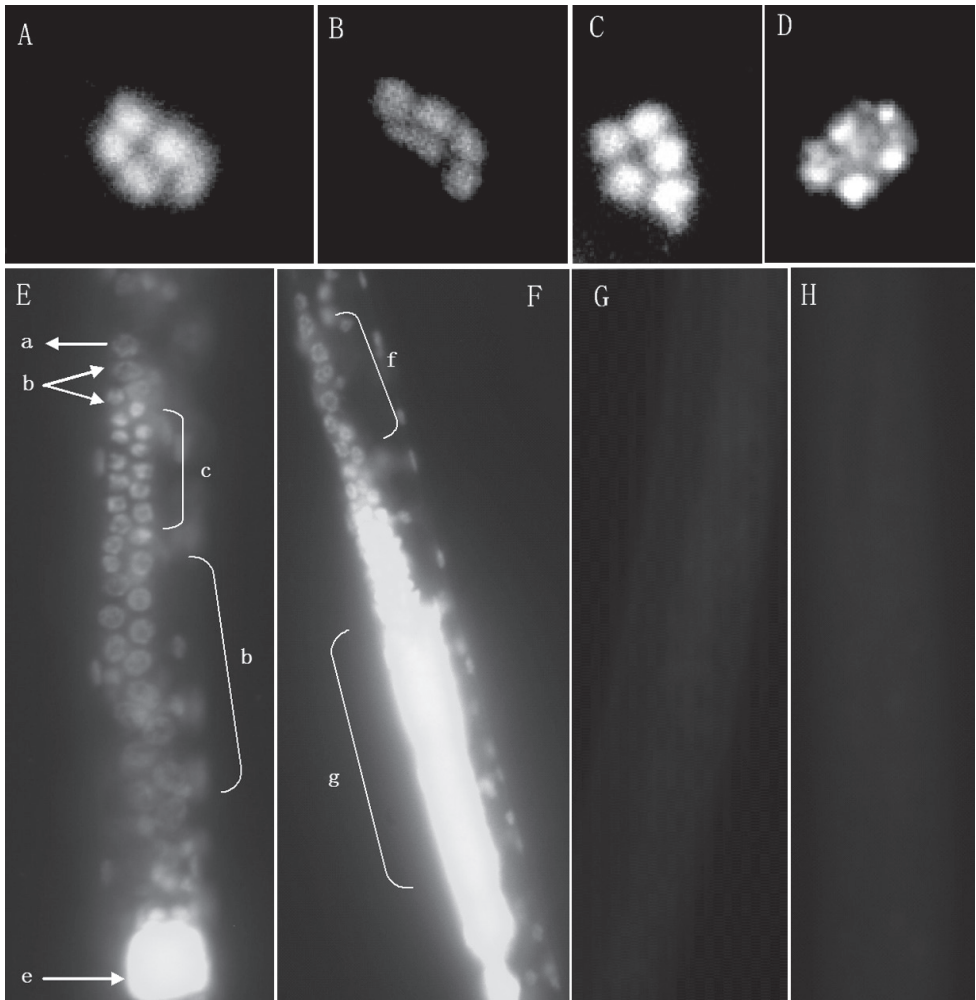


Figure 6. Haploid chromosomes and genital cells of *Radopholus similis* stained with DAPI Haploid chromosomes. **A** RsB population **B** RsL population **C** RsN population **D** RsY population; Genital cells **E** Female stained with DAPI **F** Male stained with DAPI **G** Female Non-stained with DAPI **H** Male non-stained with DAPI Arrows Arrow a: Cap cell; Arrow b: Somatic cells; Arrow c: Germinal zone; Arrow d: growth zone; Arrow e: spermatheca; Arrow f: testis; Arrow g: seminal vesicle.

RsAs, RsEs, RsKs, RsTs and RsVs populations, the lateral lips terminated in the middle of the third head annulus. In the RsGs, RsIs, RsLs, RsWs and RsYs populations, the lateral lips terminated at the end of the third head annulus. In the RsJs, RsNs and RsPs populations, the lateral lips terminated at the end of the fourth head annulus. Populations RsAs, RsBs, RsCs, RsDs, RsFs, RsGs, RsIs, RsJs, RsLs, RsMs, RsTs, RsVs and RsYs had the same annuli termination at the vulva as their counterpart of progeny of the 30 females, whereas the remaining populations did not. They were one annulus in the RsHs, RsSs and RsWs populations, two in the RsNs RsPs and RsYs populations, one on

one side and two on the other side in the RsEs and RsKs populations, and one on one side and three annuli on the other side in the RsXjs population. Regarding the number of genital papillae on the anterior cloacal apertures of males, the same variations were observed within and among the populations with the progeny of the 30 nematodes.

Morphological comparison between single female progeny and 30 females progeny. There were no obvious morphological differences between single female progeny and corresponding 30 female progeny. Some variations within some measurements were noted but overlap of morphological measurements existed. Among them, in all populations except the RsM population, the average female body length of progeny of single female was shorter than that of 30 females from the same population. However, the average male body lengths were similar. Tail type varied within and among the same populations from progeny of single female and 30 females, and only the female tail type of the RsTs, RsNs and RsVs populations and the male tail type of the RsVs populations were identical with the corresponding 30 females from the same population. All other populations showed divergence but with morphological character overlap.

Karyotype analysis. Staining burrowing nematode eggs at the single cell stage with DAPI enabled counting of chromosomes in polar bodies, and the result showed that all the twenty populations of *R. similis* have the same haploid karyotype $n = 5$ (Figure 6A–D).

Specimens that had not been stained with DAPI were also examined to ensure that we were not observing auto-fluorescence. After staining adult nematodes of *R. similis*, strong fluorescence in the spermatheca and testis was detected in females and males. Highly condensed chromosomes in meiosis were detected in genital ovaries (Figure 6D–H). We also observed the female reproductive system to be didelphic and the ovotestes to have extended glands, which were made up with ovary, oviduct, spermatozoa and uterus. A cap cell and three somatic cells were found at the tip of each ovary, and germina zone showed strong fluorescence because of highly condensed nucleic acids. The next growth zone showed the cytoplasm of single cells because of less condensed nucleic acid (Figure 6E).

Discussion

Morphological variations within different populations

All the morphological characters of *R. similis* populations in this study were similar to those described by Huettel et al. (1986), Koshy et al. (1991) and Elbadri et al. (1999a, 1999b), even though there were some variations of morphological characters and measurements in and among populations. Our results showed that the lateral field structure and all morphometric values were almost stable. The main morphological diversity was manifested in number of female head annuli, shapes of female labial disc, terminal position of female lateral lips, number of annuli terminating at the vulval area, number of genital papillae before the male cloacal aperture, and tail shapes of females and males.

Elbadri et al. (1999a) analyzed the morphological characters in and among ten banana populations of *R. similis* from Africa. The number of head annuli varied between 2–5. The labial disc was round or flat round. The lateral lip was terminated before the second or third head annulus, or at the end of the fourth or fifth head annulus. In addition, the lateral lips of the Ugandan and South African populations terminated at the different positions on both sides of the body. The annuli terminated at the vulva varied between 2–3 and the number of genital papillae on the anterior cloacal apertures varied between 0–8. Elbadri et al. (1999b) also compared the morphological characters in and among eight populations of *R. similis* extracted from different hosts (banana, pepper, citrus and ornamental plants) from different continents (Asia, the Americas, Europe and Oceania), and found that in the banana and pepper populations, the number of head annuli varied between 2–4 and the shape of labial disc varied from hexagonal, subhexagonal and flat round. In the ornamental populations, the number of head annuli was 3, and the shape of labial disc was hexagonal. The lateral lips terminated at the end of the third annulus, or in the middle of the second or third annuli in all these populations. The number of annuli terminated at the vulva area varied from 1–3 on both sides, and in some nematodes. the number of annuli terminated at the vulva was different on both sides of the vulva. In addition, the number of genital papillae varied between 0–7 in and among populations.

Our study showed that the shape of female labial discs was hexagonal, sub-hexagonal and round-elongate. The number of female head annuli varied from 2–4. The terminated position of female lateral lips showed different situations which varied in and among populations. The number of genital papillae before male cloacal aperture varied from 0–9 in and among populations. What is interesting is that the genital papillae were arranged in double rows in two of the ornamental populations, RsP population from *C. zebrina* and RsD from *C. cataractarum*, and this number was 9 and 8 respectively. The tail shape varied the most, was usually conoid, widely cylindrical or bearing a pointed end, and only one intercepted RsA population from *C. zebrina* showed forked ends. All 20 populations showed much more variations in tail shape than as described by Huettel et al. (1986) and Elbadri et al. (1999a, 1999b). Although the differences of morphological characters in and among various populations existed, these differences exist not only among the populations but also exist between the individuals within the same populations, so based on these morphological characters, we cannot separate different geographic or host populations of *R. similis*.

Huettel and Yaegashi (1988) treated two physiological races of *R. similis sensu lato* as two independent species, *R. similis sensu stricto* (not attacking citrus) and *R. citrophilus* (attacking citrus) according to the four different ultrastructures observed by SEM. They separated *R. similis sensu stricto* from *R. citrophilus* by the former having a hexagonal labial disc, the lateral lips terminated at the end of the third annulus, the annuli terminated at the vulva being 2, the number of genital papillae of male cloacal aperture varying between 0–2, and the latter having a round labial disc, the lateral lips terminated at the end of the third annulus, the annuli terminated at the vulva numbering 3, and the number of genital papillae of male cloacal aperture varied between 3–7. However, Koshy et al. (1991), Elbadri et al. (1998), Valette et al. (1998) and Elbadri et

al. (1999a, 1999b) studied more populations of *R. similis sensu lato*, and demonstrated that the four specific morphological characters between *R. similis sensu stricto* and *R. citrophilus* described by Huettel and Yaegashi (1988) showed considerable overlap, and they also treated *R. citrophilus* as a synonym of *R. similis*. Our results also show that the four morphological characters of the 20 populations showed considerable overlap in and among populations, even between the progeny of single females and that of 30 females from the same population. In addition, all 20 populations showed other morphological divergences, whether in morphometric values or in morphological characters. Even most of morphometric values and characters showed some variation in the progeny of the single females. The ultrastructure of nematodes from the progeny of single females also showed some variations compared to their corresponding progeny of 30 females. Therefore, according to the our and reported morphological characters, we cannot separate *R. citrophilus* as a separate species, and we cannot even separate different populations of *R. similis*.

Karyotype variations analysis of *Radopholus similis*. Huettel and Dickson (1981a) and Huettel et al. (1984a) reported the chromosome numbers of banana and citrus races of *R. similis* as $n = 4$ and $n = 5$, respectively. Huettel et al. (1984a) reported the karyotype of three ornamental plant populations, and the karyotype from *Philodendron* sp. and *Calathea* sp. populations as $n = 4$, while that of *Anthurium* was $n = 5$; therefore, they proposed that citrus race can be distinguished from banana race based on the haploid number of chromosomes. Hahn et al. (1996a) and Kaplan and Opperman (2000) reported that the chromosome number of banana races of *R. similis* was 5. In this study, among the 20 populations, including two *Philodendron*, six *Calathea* sp. and five *Anthurium* populations, the results showed that the haploid chromosome number of all the populations was 5. Therefore, our results confirm previous studies, and we can conclude that it is impossible to separate different races of *R. similis* according to karyotype.

Conclusion

According to the morphological characters and karyotype of the 20 populations of *R. similis*, a diversity of morphological characters of *R. similis* exists in and among the populations. According to our and previously reported results, we also suggest the banana race and citrus race of *R. similis* cannot be separated, and *R. citrophilus* cannot be accepted as a sibling species by optical or SEM morphological values and characters or by karyotype.

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References

- Anonymous (2004) *Radopholus citrophilus* and *Radopholus similis*. <http://www.eppo.org>
- Aoyagi M, Ishibashi N (1983) Gametogenesis of the pine wood nematode, *Bursaphelenchus xylophilus*. Japanese Journal of Nematology 13: 20–25.
- Bolla RI, Boschert M (1993) Pinewood nematode species complex: interbreeding potential and chromosome number. Journal of Nematology 25(2): 227–238.
- Bridge J (1993) Worldwide distribution of the major nematode parasites of bananas and plantains. In: Gold CS, Cemmil B (Eds) Biological and integrated control of highland banana and plantain pests and diseases. IITA, Nigeria, 185–198.
- Ducharme EP, Birchfield W (1956) Physiologic races of the burrowing nematode. Phytopathology 46: 615–616.
- Duncan LW, Cohn E (1990) Nematode parasites of citrus. In: Luc M, Sikora RA, Bridge J, Albans S (Eds) Plant parasitic nematodes in subtropical and tropical agriculture. CAB International, UK, 321–346.
- Elbadri GAA, Geraert E, Moens M (1998) Morphological differences among *Radopholus* (Thorne, 1949) populations from ornamentals in Europe (Pratylenchidae: Nematoda). Mededelingen-Faculteit Landbouwkundige en Toegepaste Biologische Wetenschappen, Universiteit Gent 63(2): 599–608.
- Elbadri GAA, Geraert E, Moens M (1999a) Morphological differences among *Radopholus* populations from banana from Africa (Nematoda: Tylenchida). Journal of Nematode Morphology and Systematics 2: 1–16.
- Elbadri GAA, Geraert E, Moens M (1999b) Morphological differences among *Radopholus similis* (Cobb, 1893) Thorne, 1949 populations. Russian Journal of Nematology 7(2): 139–153.
- Goo MYC, Sipes BS (1999) Chromosome number and reproductive isolates of *Radopholus similis* from Hawaii. International Journal of Nematology 9: 43–46.
- Haegeman A, Elsen A, de Waele D, Gheysen G (2010) Emerging molecular knowledge on *Radopholus similis*, an important nematode pest of banana. Molecular Plant Pathology 11(3): 315–323. doi: 10.1111/j.1364-3703.2010.00614.x
- Hahn ML, Burrows PR, Gnanapragasam NC, Bridge J, Vines NJ, Wright DJ (1994) Molecular diversity amongst *Radopholus similis* populations from Sri Lanka detected by RAPD analysis. Fundamental and Applied Nematology 17(3): 275–281.
- Hahn ML, Burrows PR, Wright DJ (1996a) Genomic diversity between *Radopholus similis* population from around the world detected by RAPD-PCR analysis. Nematropica 42(5): 537–545.
- Hahn ML, Sarah JL, Boisseau M, Vines NJ, Wright PR (1996b) Reproductive fitness and pathogenic potential of selected *Radopholus* populations on two banana cultivars. Plant Pathology 45: 223–231. doi: 10.1046/j.1365-3059.1996.d01-128.x
- Hasegawa K, Miwa S, Futaim K, Miwa J (2004) Early embryogenesis of the pinewood nematode *Bursaphelenchus xylophilus*. Development, Growth and Differentiation 46: 153–161. doi: 10.1111/j.1440-169X.2003.00734.x
- Holdeman QL (1986) The burrowing nematode *Radopholus similis*, *sensu lato*. Nematology Publication, California Department of Food and Agriculture, Division of Plant Industry, USA, CA.

- Huettel RN, Dickson DW (1981a) Karyology and oogenesis of *Radopholus similis* (Cobb) Thorne. *Journal of Nematology* 13(1): 16–20.
- Huettel RN, Dickson DW (1981b) Parthenogenesis in the Two Races of *Radopholus similis* from Florida. *Journal of Nematology* 13(1): 13–15.
- Huettel RN, Dickson DW, Kaplan DT (1984a) Chromosome number of populations of *Radopholus similis* from North, Central and South America, Hawaii and Indonesia. *Revue de Nematologie* 17: 113–116.
- Huettel RN, Dickson DW, Kaplan DT (1984b) *Radopholus citrophilus* sp.n. (Nematoda), a sibling species of *Radopholus similis*. *Proceedings of the Helminthological Society, Washington* 51: 32–35.
- Huettel RN, Kaplan DT, Dickson DW (1986) Characterisation of a new burrowing nematode population, *Radopholus citrophilus*, from Hawaii. *Journal of Nematology* 18(1): 50–54.
- Huettel RN, Yaegashi T (1988) Morphological differences between *Radopholus citrophilus* and *R. similis*. *Journal of Nematology* 20(1): 150–157.
- Kaplan DT, Opperman CH (2000) Reproductive strategies and karyotype of the burrowing nematode, *Radopholus similis*. *Journal of Nematology* 32(2): 126–133.
- Koshy PK, Jasy T, Mathew J, Nampoothiri CK (1991) Morphometric variability in *Radopholus similis*. *Indian Journal of Nematology* 21(1): 24–38.
- Liu QL, Williamson VM (2006) Host-specific pathogenicity and genome differences between inbred strains of *Meloidogyne hapla*. *Journal of Nematology* 38(1): 158–164.
- Loof PAA (1991). The Family Pratylenchidae Thorne, 1949. In: Nickle WR (Ed.) *Munaf of Agriculture Nematology*. Marcel Dekker Inc., New York, 363–422.
- Rivas X, Roman J (1985) Oogenesis y reproduccion de una poblacion de *Radopholus similis* de Puerto Rico. *Nematropica* 15: 19–25.
- Seinhorst JW (1959) A rapid method for the transfer of nematodes from fixative to anhydrous glycerin. *Nematologica* 4: 67–69. doi: 10.1163/187529259X00381
- Triantaphyllou AC (1970) Cytogenetic aspects of evolution of the family Heteroderidae. *Journal of Nematology* 2: 26–32.
- Triantaphyllou AC, Hirschmann H (1966) Gametogenesis and reproduction in the wheat nematode, *Anguina tritici*. *Nematologica* 12: 437–442. doi: 10.1163/187529266X00932
- Valette C, Mounport D, Nicole M, Sarah J, Baujard P (1998) Scanning electron microscope study of two African population of *Radopholus similis* (Nematoda: Pratylenchidae) and proposal of *R. citrophilus* as a junior synonym of *R. similis*. *Fundamental and Applied Nematology* 21: 139–146.
- van der Beek JG, Los JA, Pijnacker LP (1998) Cytology of parthenogenesis of five *Meloidogyne* species. *Fundamental and Applied Nematology* 21(4): 393–399.
- Van Weerd LG (1958) Studies on the biology of *Radopholus similis* (Cobb, 1893) Thorne, 1949. Part 2. Morphological variations within and between progenies of single females. *Nematologica* 3: 184–196. doi: 10.1163/187529258X00418
- Williams KJO, Siddiqi MR (1973) *Radopholus similis*. *CIH Description of Plant-parasitic Nematodes* 2(27): 1–4.
- Xu C, Xie H, Wang J, Wu Y, Zhang C, Jin X (2009) Morphological and molecular identification of the nematodes parasitizing the roots and stems of *Astragalus membranaceus* and *Dioscorea opposita* from China. *Nematologia mediterranea* 37: 39–44.

First report of the presence of *Acartia bispinosa* Carl, 1907 (Copepoda, Calanoida) in a semi-enclosed Bay (Sharm El-Maya), northern Red Sea with some notes on its seasonal variation in abundance and body size

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Abstract

The calanoid copepod, *Acartia bispinosa* Carl, 1907, is reported for the first time in the Red Sea, where it is found to be an important copepod in the mesozooplankton community structure of the Sharm El-Maya Bay. Female and male are fully redescribed and illustrated of as the mouthparts of this species have never previously been described and figured. *Acartia bispinosa* was collected in the plankton samples throughout the year and showed two peaks of abundance, a pronounced one in April (4234 individuals m⁻³), and second smaller peak during November (1784 individuals m⁻³). The average total length of females varied between 1.32 and 1.53 mm at the end of June and January respectively. For males, the average total length fluctuated between 1.07 and 1.16 mm at end of June and March respectively. Temperature showed an inverse relationship with the body length ($P > 0.001$) and seemed to be one of the prime factors affecting the body length of both sexes.

Keywords

Copepods, *Acartia bispinosa*, morphology, seasonal abundance, body size, Red Sea

Introduction

Acartiidae Sars, 1903 is a speciose family of copepods, that inhabits estuarine and neritic environments all over the world from boreal to tropical regions (Bradford 1976, Mauchline 1998, Belmonte and Potenza 2001). They are thought to be mainly adapted to high food concentrations, which are encountered in estuaries and upwelling regions. They are key organisms to link between the primary producers and secondary consumers in many neritic and inlet waters (Putland and Iverson 2007), since they are the major consumers for phytoplankton and microzooplankton and serve as a prey for fish larvae (Seki and Shimizu 1997). A number of *Acartia* species produce diapause eggs, which allow them to lie dormant in the sediment and to appear in the plankton when the conditions are favorable (e.g. Engel 2005).

So far, nine species of *Acartia* have been recorded from the Red Sea (Halim 1969, Razouls et al. 2014), namely, *Acartia* (*Acanthacartia*) *fossae* Gurney, 1927, *Acartia* (*Acartia*) *danae* Giesbrecht, 1889, *Acartia* (*Acartia*) *negligens* Dana, 1849, *Acartia* (*Acartiura*) *clausi* Giesbrecht, 1889, *Acartia* (*Acartiura*) *longiremis* (Lilljeborg, 1853), *Acartia* (*Odontacartia*) *centrura* Giesbrecht, 1889, *Acartia* (*Odontacartia*) *erythraea* Giesbrecht, 1889, *Acartia* *eremeevi* Pavlova & Shmeleva, 2010 and *Acartia* *mollicula* Pavlova & Shmeleva, 2010. During a year round study of the planktonic copepods in the coastal waters of a semi-enclosed bay near Sharm El-Sheikh, northern Red Sea, four species of *Acartia* (*A. centrura*, *A. fossae*, *A. danae* and *A. negligens*) were collected, in addition to a newly recorded species to the Red Sea (*Acartia* (*Odontacartia*) *bispinosa* Carl, 1907), which was found to be a dominant species in our samples. In this paper, *Acartia bispinosa* is redescribed and illustrated, since the original description is limited as well as the mouthparts of this species have never previously been described. Also, the seasonal variations in their abundance and body size in relation to the different environmental parameters were discussed.

Materials and methods

Acartia bispinosa specimens were collected at monthly intervals from Sharm El-Ma-ya Bay (with an average depth of 3 m), in the northern Red Sea (27°51'36"N and 34°17'39"E) using a conical 0.1 mm mesh plankton net (mouth diameter of 0.4 m and total length of 160 cm) fitted with a Hydro-Bios flowmeter, from January to December 2009. The net was towed horizontally for ten minutes 0.5 m beneath the sea surface and filtered volume was estimated from the flowmeter reading and the net diameter. Immediately after collection, samples were fixed in a final concentration of 4% formaldehyde-seawater until analyses after several months. According to Durbin and Durbin (1978), the period of preservation has no significant effect on the length of *Acartia*. From each sample, 50 specimens of both adult females and males of *A. bispinosa* were measured for the total length and the prosome length using a Nikon stereomicroscope (205A) equipped with the software LAS (Leica Application Suite).

Microscopic examinations and dissections were made in lactophenol using bright-field and differential interference microscopes (Nikon E600). For detailed observation, specimens were stained with a 0.1% chlorazol-black E solution. Drawings were made with a camera lucida. Terminology follows Huys and Boxshall (1991). For scanning electronic microscopy (SEM), whole copepods or the dissected parts were mounted on stubs, dehydrated with liquid nitrogen, coated with white gold, and examined in a JEOL, JSM-5600LV scanning electron microscope. Temperature, pH, salinity and dissolved oxygen from the surface water were measured using a multiparameter water quality meter (Horiba U-50). For chlorophyll *a*, five liters of surface water were collected and filtered through 35 mm diameter Sartorius membrane filters (pore size 0.45 μm), extracted in 90% acetone and analyzed spectrophotometrically following Parsons et al. (1984). The Pearson correlation coefficient at a confidence limit of 95% was applied to study the relationship between the abundance of *Acartia* and the other environmental factors. Also, ANOVA was used in order to test if differences between months regarding body size were significant or not. All these statistical analyses were performed with the help of SPSS software (Version 16).

Results

Description

Order Calanoida G. O. Sars, 1902

Superfamily: Diaptomoidea Baird, 1850

Family: Acartiidae Sars, 1903

Genus: *Acartia* Dana, 1846

***Acartia (Odontacartia) bispinosa* Carl, 1907**

Acartia amboinensis (F): Sewell 1914 a (p. 242, figs 1–7 Only female).

A. tokiokai Mori 1942 (p. 556, pl. 11, figs 1–18)

A. hamata C.B. Wilson 1950 (p. 152, figs 1–5)

Description. Female: Body (Fig. 1A, B) slender; prosome 5-segmented; rostrum (Fig. 1C) with two long rostral filaments and paired frontal sensilla (Figs 1C, 2A). Nauplius eye present. Cephalosome and first pediger completely separate; fourth and fifth pediger fused; fifth pediger with lateral strong projection, posterodorsal spine and fine setule on each side (Fig. 1A, F–G). Urosome 3-segmented; genital compound somite (Fig. 1D–G) slightly longer than wide, carrying two spines postero-dorsally reaching nearly one-third of second urosomite, posteroventral margin furnished with very fine hairs (Figs 1E, 2B); second and third segments naked. Caudal rami symmetrical; with 5 transverse rows of fine setules dorsally and 1 row anteroventrally (Fig. 1D–E), each ramus bearing six setae.

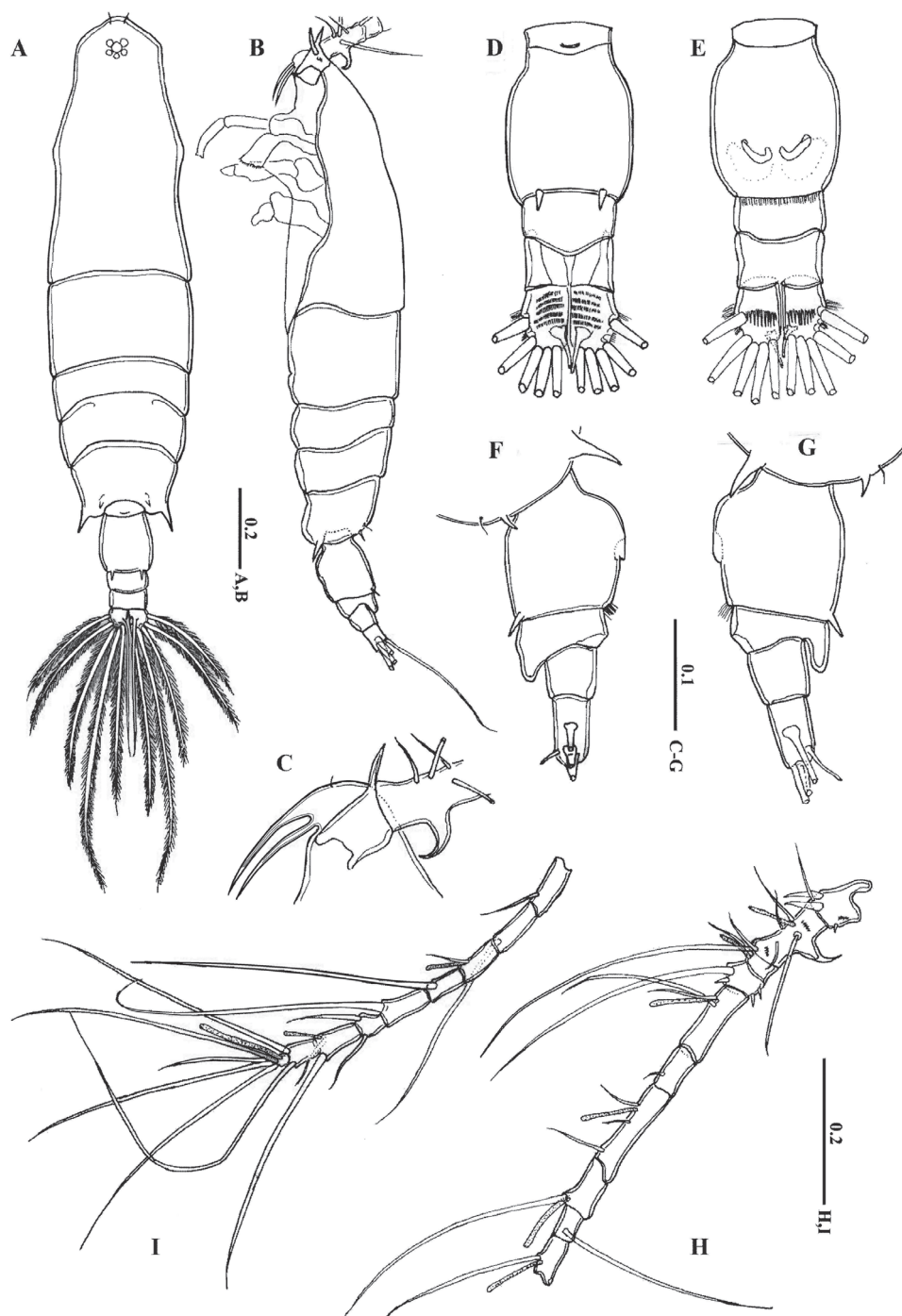


Figure 1. *Acartia bispinosa* female from the northern Red Sea. **A** habitus, dorsal view **B** habitus, lateral view **C** rostrum and proximal part of the antennule, lateral view **D** urosome, dorsal view **E** urosome, ventral view **F** urosome, later view right **G** urosome, lateral view left **H–I** antennule. All scale bars in mm.

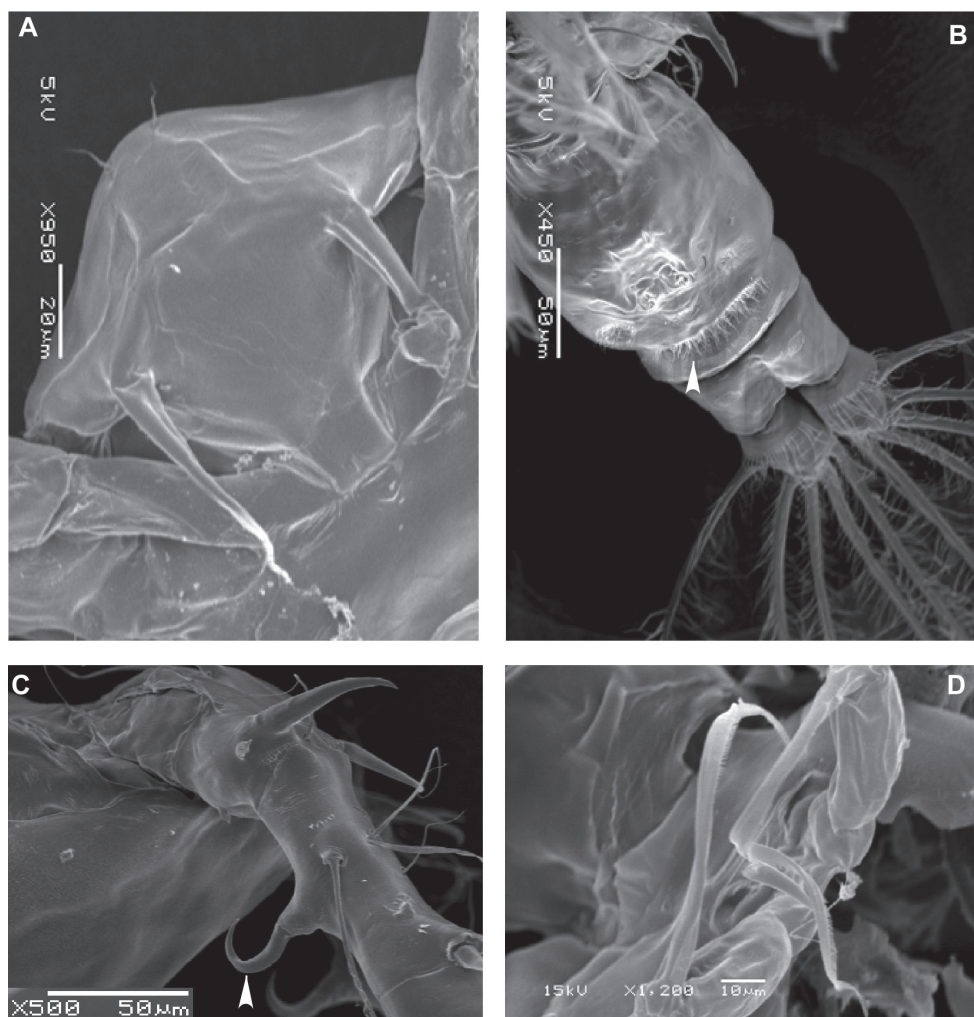


Figure 2. SEM micrographs of *Acartia bispinosa* female from the northern Red Sea. **A** rostrum, ventral view **B** urosome, fine hairs on the posterior margin of genital compound somite indicated by arrow, ventral view **C** proximal part of antennule, claw-like curved spine indicated by arrow, lateral view **D** Female leg 5.

Antennule (Fig. 1H, I) incompletely 19-segmented; second to third and fourth to sixth segments partly fused on dorsal surface; segmentation and setation patterns as follows (SS specialized spine): (1) I=1+2SS, (2) II–VI=6+SS+1 aesthetasc (ae), (3) VII–VIII=2, (4) IX–X=2 (1 spiniform), (5) XI–XII=2+ae, (6) XIII=1, (7) XIV–XV=3+ae, (8) XVI=1+ae, (9) XVII=1, (10) XVIII=1+ae, (11) XIX=1, (12) XX=1, (13) XXI=1+ae, (14) XXII=1, (15) XXIII=1, (16) XXIV=1+1, (17) XXV=1+1+ae, (18) XXVI=1+1, (19) XXVII–XXVIII=4+ae. First segment with short spine at distal half and 2–3 spinules on dorsal surface; second segment with strong claw-like spine curved proximally from mid-posterior margin (Figs 1C, 2C), transverse row of 2–3 spinules on proximal

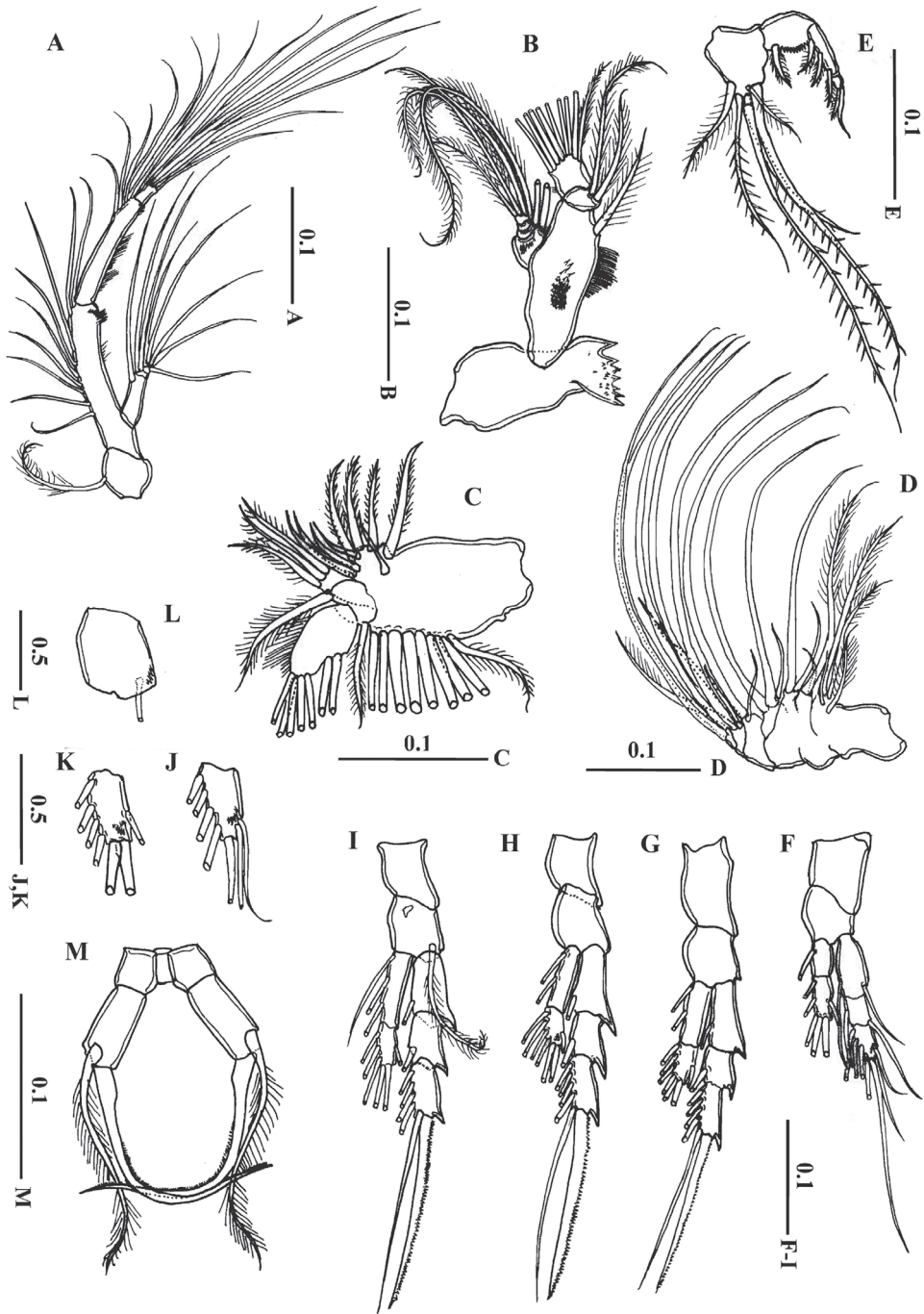


Figure 3. *Acartia bispinosa* female from the northern Red Sea. **A** antenna **B** mandible **C** maxillule **D** maxilla **E** maxilliped **F** Leg 1 **G** leg 2, posterior surface **H** Leg 3, posterior surface **I** leg 4, posterior surface **J** third exopodal segment of leg 1, anterior surface **K** second endopodal segment of leg 3, anterior surface **L** basis of leg 4, anterior surface **M** leg 5 anterior surface. All scale bars in mm.

half of dorsal surface and transverse row of 4 spinules on distal half of dorsal surface; fourth segment with 2 spines dorsally.

Antenna (Fig. 3A): long; coxa with one seta; basis and first endopodal segment completely fused forming elongate allobasis carrying 9 setae along medial margin and oblique row of tiny spinules on distal part of anterior surface; exopod short, 4-segmented with setal formula of 1, 2, 2, 3. Second (first free) endopodal segment elongated bearing 7 setae and furnished with hairs along lateral margin; third (second free) endopodal segment short bearing 7 setae.

Mandible (Fig. 3B): coxa with well-developed gnathobase; basis with 1 medial seta and group of fine spinules posteriorly; exopod 5-segmented, with setal formula of 1, 1, 1, 1, 2; endopod 2-segmented, with 2 and 9 setae on first and second segment respectively.

Maxillule (Fig. 3C): praecoxa and coxa incompletely fused; praecoxal arthrite (endite) with 9 setae; coxal endite with 3 setae, coxal exite bearing 9 setae; basis with thick medial seta and short lateral seta; exopod 1-segmented and bearing 2 setae laterally and 5 setae terminally; endopod absent.

Maxilla (Fig. 3D): precoxa and coxa incompletely fused; with 4 endites, each carrying short seta on each and 3, 1, 1, 2 long setae, respectively; basis with 1 long seta and 1 short seta; endopod 4-segmented, with 5 long setae, 2 medium setae and 1 short seta.

Maxilliped (Fig. 3E) comprising robust syncoxa, basis, and 2-segmented endopod; syncoxal endite with 6 setae (2 short, 2 medium and 2 long); basis bearing 1 short spiniform seta; endopod 2-segmented, first segment with 3 medial spine-like setae, second segment tapered at end carrying 2 setae (later one spiniform and elongated at tip).

Swimming legs 1 to 4 (Fig. 3F–I) biramous, with 3-segmented exopod and 2-segmented endopod; third exopodal segment of leg 1 with 4–5 spinules proximally on the ventral surface (Fig. 3J); second endopodal segment of leg 3 with group of tiny spinules proximally on the ventral surface (Fig. 3K); basis of leg 4 with 4 spinules ventrally (Fig. 3L). Seta and spine formula as follows:

	Coxa	Basis	Exopod segments			Endopod segments	
			1	2	3	1	2
Leg 1	0–0	0–0	1–1;	1–1;	2,I,4	0–1;	1, 3, 2
Leg 2	0–0	0–0	0–1;	0–1;	0,I,5	0–2;	1, 2, 4
Leg 3	0–0	0–0	0–1;	0–1;	0,I,5	0–2;	1, 2, 4
Leg 4	0–0	0–1	0–1;	0–1;	0,I,5	0–3;	1, 2, 3

Leg 5 (Fig. 3M): coxae completely fused to intercoxal sclerite; basis about 1.5 times longer than wide; lateral seta nearly as long as claw-like exopod; exopod reduced and swollen at the base posteriorly and distal two-third furnished medially with very fine spinules (Fig. 2D).

Male: Body (Fig. 4A) slender; rostral filaments long and thin (Fig. 4B). Fifth pediger with 2 subequal pointed posterior processes, smaller than in female, 2 dorsolateral spines and fine setules on each side (Fig. 4C, D). First urosomite with rows of soft

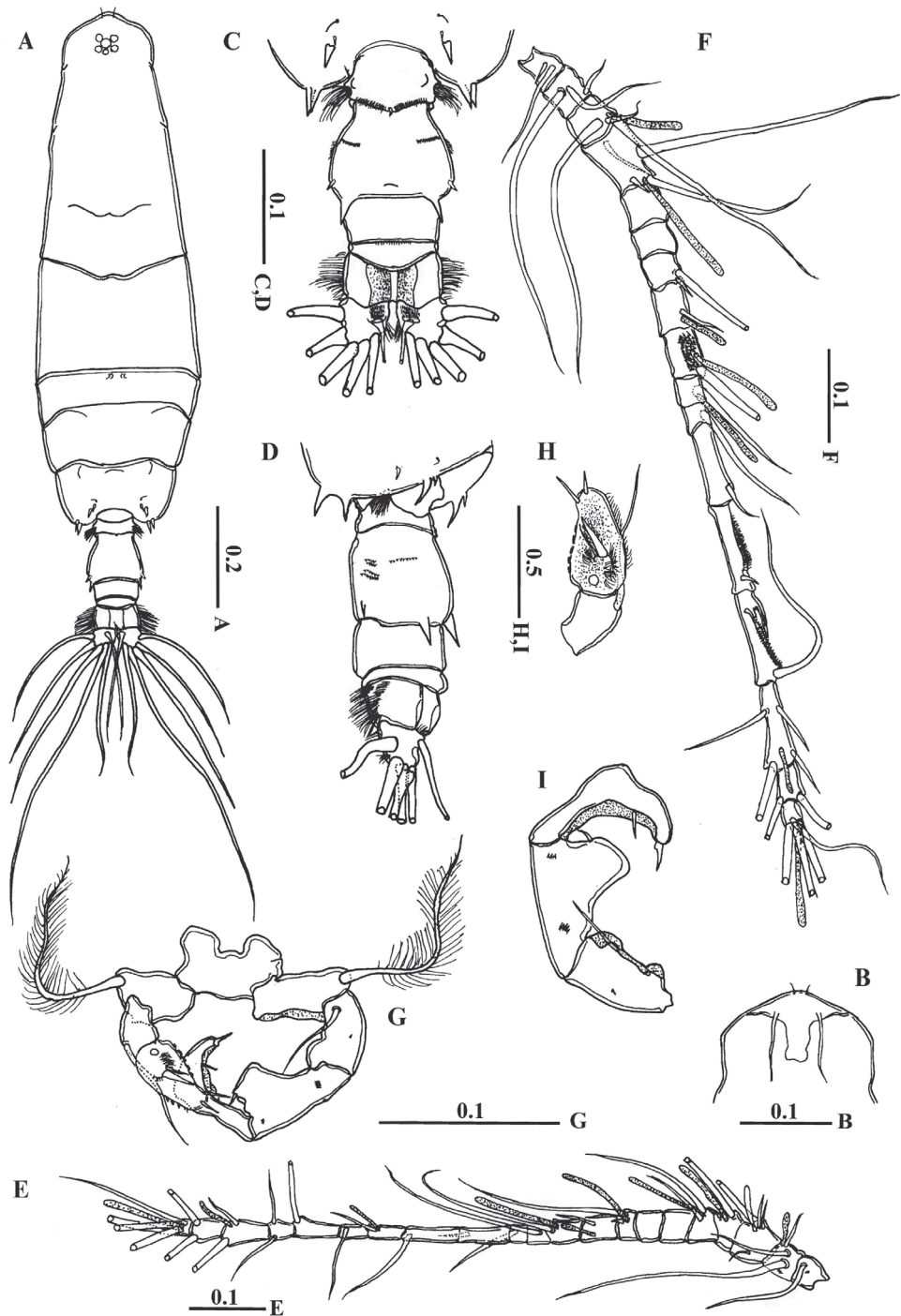


Figure 4. *Acartia bispinosa* male from the northern Red Sea. **A** habitus, dorsal view **B** rostrum, ventral view **C** urosome, dorsal view **D** urosome, latero-ventral view **E** left antennule **F** right antennule **G** leg 5 **H** terminal segment of left exopod of leg 5 **I** terminal segment of right exopod of leg 5. All scale bars in mm.

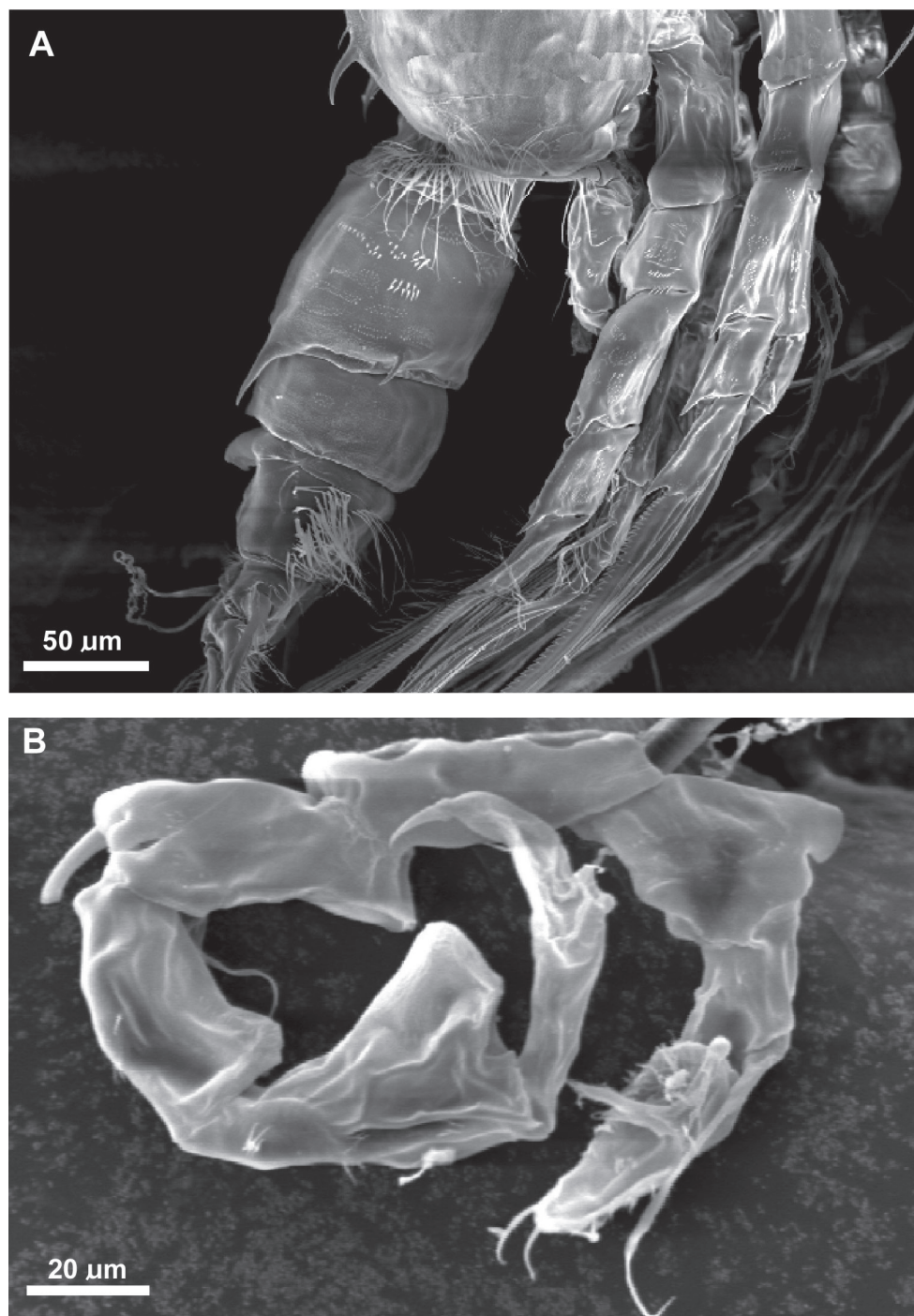


Figure 5. SEM micrographs of *Acartia bispinosa* male from the northern Red Sea. **A** abdomen, lateral view **B** leg 5, posterior surface.

hairs on lateral and posterior margin (Fig. 4C, D). Second urosomite with 2 strong dorsolateral spines on posterior margin reaching slightly more than two-thirds of the following somite, 2 ventrolateral small spines, 2 dorsolateral groups of fine spinules ventrolaterally on both sides and dorsolateral row of fine setules along posterior margin (Figs 4C, D, 5A). Third and fourth urosomites with very fine setules along posterior margins. Anal somite bearing short hairs on lateral surface. Caudal ramus with transverse rows of fine setules at the base of medial dorsal seta and with hairs along lateral margin and along distal half of medial margin.

Left antennule (Fig. 4E) 21-segmented; segmentation and setation patterns as follows: (1) I=1, (2) II–IV=3, (3) V–IX=4+ae, (4) X=2+ae, (5) XI=2+ae, (6) XII=unarmed, (7) XIII=unarmed, (8) XIV=2 (1 spiniform)+ae, (9) XV=1+ae, (10) XVI=1+ae, (11) XVII=1, (12) XVIII=1, (13) XIX=1, (14) XX=1, (15) XXI=1+ae, (16) XXII=1, (17) XXIII=1, (18) XXIV=1+1, (19) XXV=1+1+ae, (20) XXVI=1+1, (21) XXVII–XXVIII=4+ae.

Right antennule (Fig. 4F) 17-segmented, with geniculation between thirteenth and fourteen segments; second to fourth segments partly fused on dorsal surface; segmentation and setation patterns as follows: (1) I=2, (2) II–VI=3, (3) VII–VIII=3+ae, (4) IX–XI=4 (1 spiniform)+ae, (5) XII=unarmed, (6) XIII=unarmed, (7) XIV=2 (1 spiniform)+ae, (8) XV=1+ae, (9) XVI=1+ae, (10) XVII=1, (11) XVIII=1+ae, (12) XIX=1, (13) XX=1, (14) XXI–XXIII=2+process, (15) XXIV–XXV=2+2+ae, (16) XXVI=1+1, (17) XXVII–XXVIII=4+ae. Ninth segment covered with tiny spinules on the dorsal surface.

Other mouthparts and leg 1 to leg 4 as in female. Male leg 5 (Figs 4G, 5B) asymmetrical; intercoxal sclerite completely fused to both coxae. Left leg 5 basis nearly two times longer than wide and armed with long later seta; exopod 2-segmented; proximal exopodal segment shorter than distal exopodal segment carrying one seta distally; distal exopodal segment carrying 2 terminal spines, a stout spine at mid-anterior surface with fine setae near its base, 5 groups of very tiny spinules along medial margin, and several spinules along lateral margin (Fig. 4H). Right leg 5 comprising basis armed with lateral seta and 3-segmented exopod; first exopodal segment with 1 long seta; second exopodal segment with distal projection carrying 1 small spine medially and 2 groups of fine spinules on the posterior surface; third exopodal segment armed with terminal stout spine and 1 spine medially near distal end (Fig. 4I).

Variations

Acartia bispinosa showed some variations in both sexes. In female left projection of prosome can be bifurcated (Fig. 6A), genital compound somite sometimes bearing 2 posterodorsal spines on right side (Fig. 6B), genital compound somite with row of fine spinules anterodorsally on both sides (Fig. 6C), and the degree of leg 5 exopod curvature also varied (Fig. 6D). In male, the lateral projections are with three spines on the posterior corner of fifth pediger (Fig. 6E, F). Also, the number and position of posterodorsally spines of the last pediger varied within species (Fig. 6F–H). Second urosomite sometimes with 2 spines on the right locus (Fig. 6I).

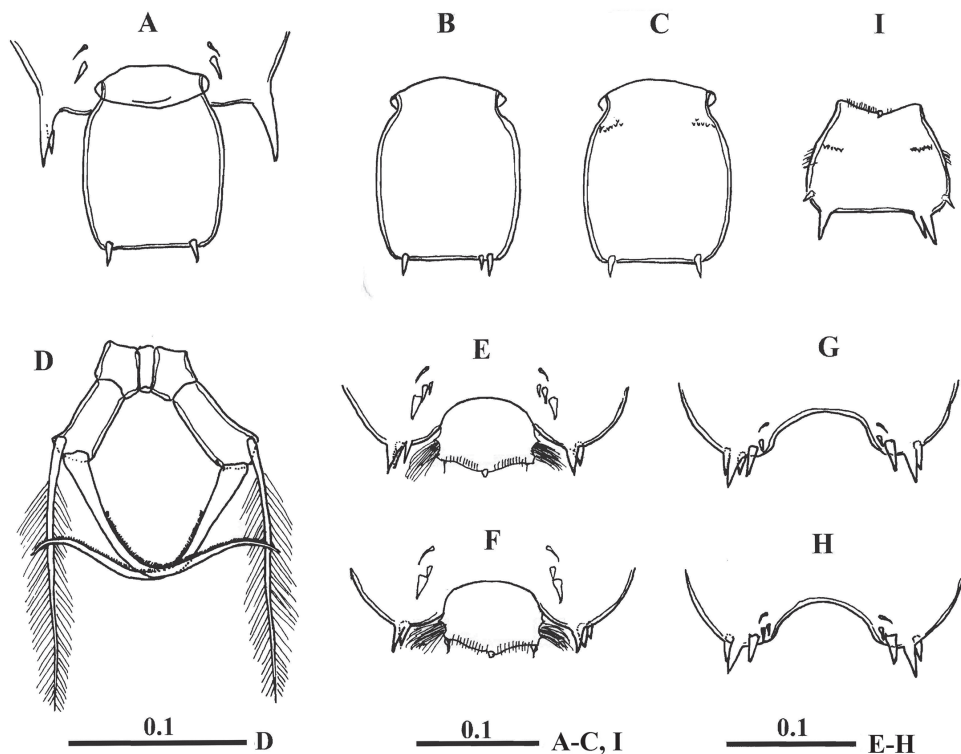


Figure 6. Variations in *Acartia bispinosa* from the northern Red Sea. **A–C** female genital compound somite **D** female leg 5 **E–H** male last pediger **I** male second urosomite. All scale bars in mm.

Seasonal patterns of environmental factors, abundance and body size

Temperature, salinity and chlorophyll *a* measurements over the 12 months investigation are presented in Figure 7. Temperature shows a cyclical annual pattern with the highest value recorded in the end of July (31.2 °C), and the minimum at the end of December (20.1 °C). Salinity was fairly stable (Fig. 7A), showing slight variation between 40 psu in the colder period and 40.3 psu in July–August (annual average: 40.1 psu). Hydrogen ion and dissolved oxygen concentrations showed nearly the same pattern varying between minima of 7.73 and 6.4 mg/l in July and maxima of 8.16 and 7.3 mg/l in January respectively (Fig. 7B). Chlorophyll *a* showed an annual average of 0.54 $\mu\text{g l}^{-1}$ with the maximum recorded in July (1.35 $\mu\text{g l}^{-1}$) with a small increase of 0.82 $\mu\text{g l}^{-1}$ in April (Fig. 7C).

Adults of *A. bispinosa* were present in the plankton samples throughout the year in our study area with an annual average of 716 individuals m^{-3} , forming 12.7% of total zooplankton community. Their abundance pattern showed two peaks (Fig. 7C), a more pronounced one occurred at the end of April (4234 individuals m^{-3} , constituting 84% of total zooplankton community) and the second peak was in November (1784 individuals m^{-3}). During December–March, very low numbers were found in

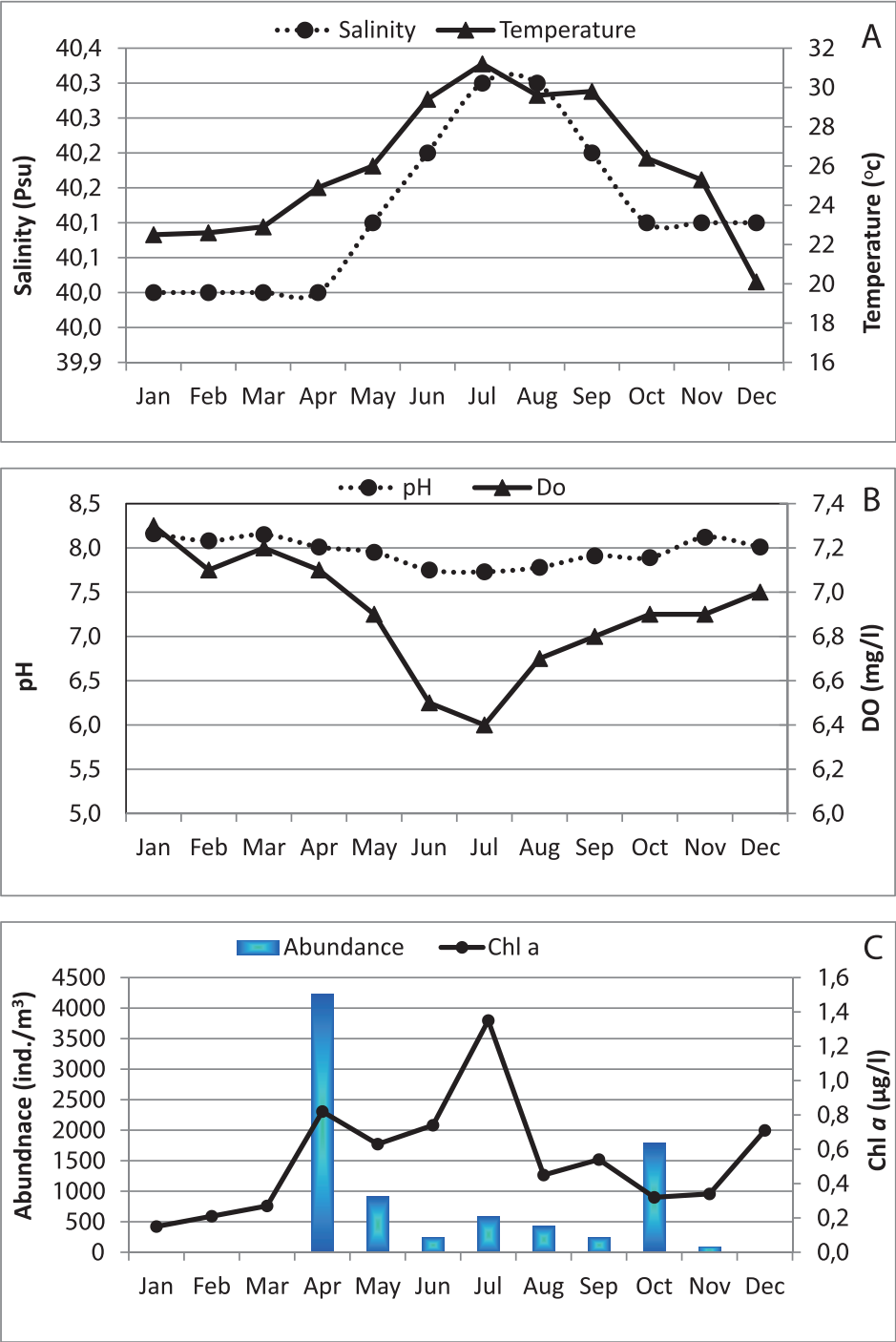


Figure 7. Seasonal patterns at Sharm El-Maya Bay, the northern Red Sea. **A** Temperature and Salinity **B** pH and dissolved oxygen concentrations (DO), and **C** Chlorophyll *a* concentration (chl *a*) and abundance of *Acartia bispinosa*.

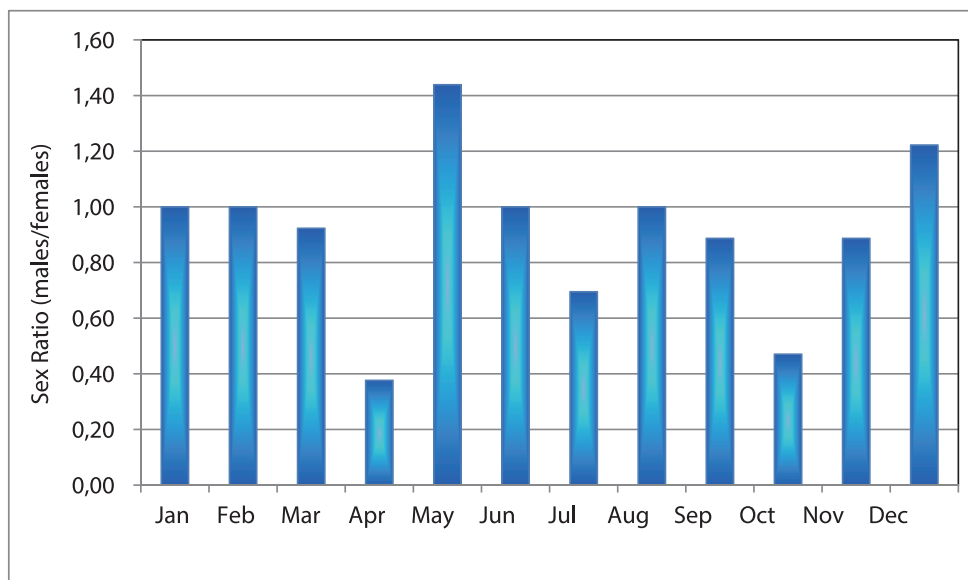


Figure 8. Seasonal variation in males/females sex ratio in the copepod *Acartia bispinosa* in the study area.

the samples (not more than 12 individuals m^{-3}). Statistically, no significant correlation was observed between the abundance and temperature as well as between the former and chlorophyll *a* concentration ($P > 0.05$, $r = 0.065$ and 0.288 respectively). In this study, the sex ratio (males/females) of *A. bispinosa* showed a clear variation pattern with higher proportion of females observed during the end of April (Spring) and end of October (Autumn) as compared to early summer (end of May and June). The males ratio increased only at the end of May and December forming 60 and 55% of the adult density (Fig. 8).

The minimum, maximum, mean, standard error and standard deviation of total length as well as the prosome length of *A. bispinosa* are given in Table 1. In females the highest body size in terms of total length (1.57 mm) and prosome length (1.34 mm) appeared in January and the lowest of 1.20 and 1.02 mm were observed at the end of June. The highest total and prosome length of the male (1.19 and 0.99 mm) were observed in March respectively (Table 1). On the other hand, their lowest value appeared in June.

In Figure 9, box and whisker plots for total and prosome length of both sexes are shown depicting the median value within a box defined by the interquartile range, and the whiskers representing the range. The total body and prosome length of female decreased from a maximum in January to a minimum at the end of June with a slight increase in late summer and early winter (Fig. 9A). In males, the pattern of variation in total and prosome length showed the maximum in late winter-early spring and minimum in June (Fig. 9B). Also mean values total and prosome length of *A. bispinosa* showed nearly the same pattern with minima in June for both sexes and maxima in January for female and in March for male.

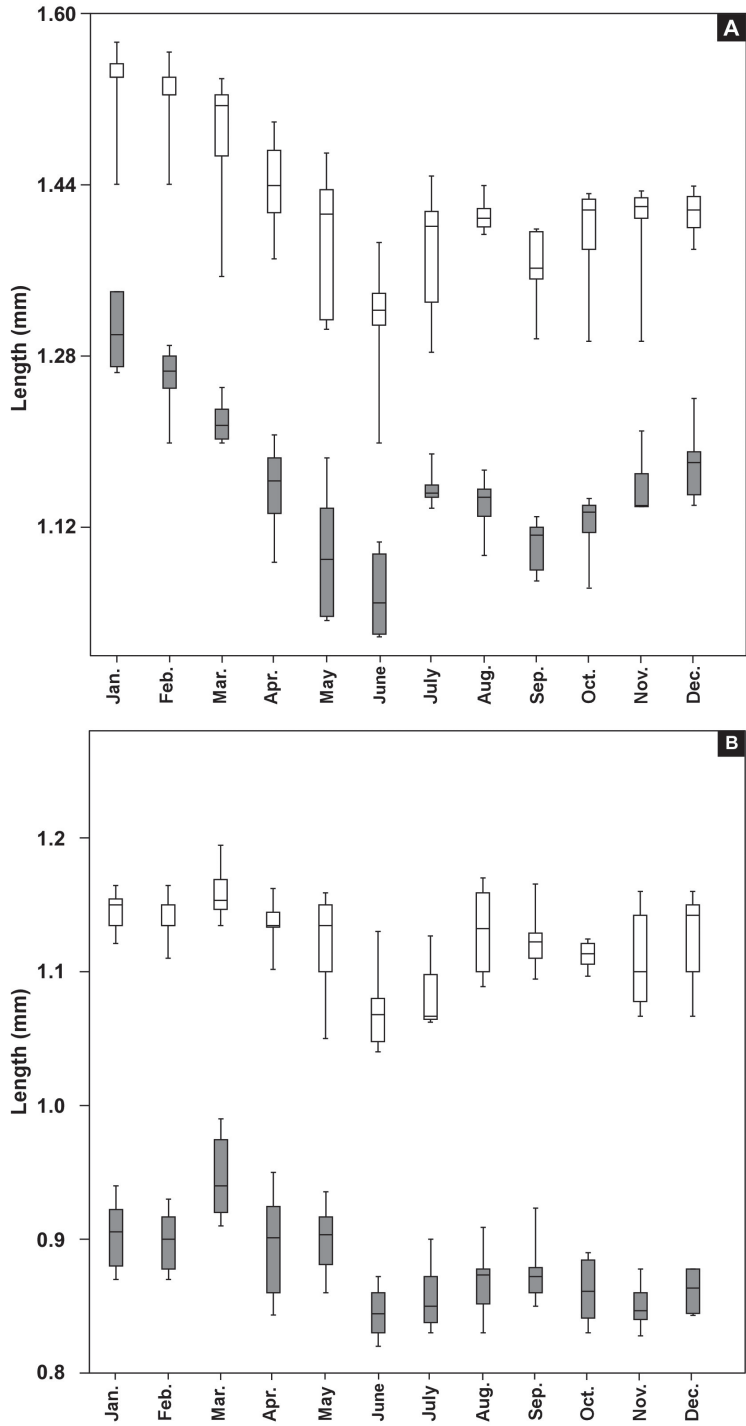


Figure 9. Box and whisker plot of seasonal variations of total and prosome length of female **A** and male **B** of *Acartia bispinosa* (total length: open symbol, prosome length: filled symbol).

Table 1. Minimum, maximum, mean, standard error (SE) and standard deviation (SD) in total and prosome length of *Acartia bispinosa* sampled in the study area.

Sex	Length (mm)	Minimum (mm)	Maximum (mm)	Mean (mm)	SE (mm)	SD (mm)
Female	Total	1.20 (June)	1.57 (Jan.)	1.42	0.017	0.059
	Prosome	1.02 (June)	1.34 (Jan.)	1.16	0.020	0.071
Male	Total	1.04 (June)	1.19 (Jan.)	1.12	0.007	0.026
	Prosome	0.83 (June)	0.99 (Mar.)	0.88	0.008	0.028

Table 2. Pearson's correlation coefficient between length measurements of *Acartia bispinosa* and environmental factors in the northern Red Sea.

Sex	Length	Temp.	pH	Salinity	DO	Chl. <i>a</i>
Female	Total	-0.631	0.621	0.658	0.771	-0.523
		0.028	0.031	0.020	0.003	0.081
	Prosome	-0.647	0.610	0.590	0.704	-0.461
		-0.023	0.035	0.043	0.011	0.132
Male	Total	-0.609	0.708	-0.597	0.851	-0.677
		0.036	0.010	0.041	0.000	0.016
	Prosome	-0.333	0.394	-0.571	0.544	-0.350
		0.290	0.205	0.052	0.067	0.269

Table 3. Regression analysis of mean total and prosome length (mm) of *Acartia bispinosa* against surface water temperature in the northern Red Sea. (TL: Total length, PL: Prosome length and T: Water temperature).

Sex	Temperature regression equation	r ²	Sign.
Female	TL= -0.012 T+1.721	0.398	0.028
	PL= -0.013 T+1.499	0.419	0.023
Male	TL= -0.005 T+1.241	0.371	0.036
	PL= -0.002T+0.950	0.111	0.290

Results of analysis of variance (ANOVA) showed significant differences between months for both female and male total length ($F= 36.97$, $P < 0.000$ for female and $F= 15.29$, $P < 0.000$ for male). Statistically, total and prosome length of females are inversely correlated with temperature ($r= -0.639$ and -0.664 respectively, $P < 0.05$) and positively with pH, salinity and dissolved oxygen (Tables 2,3). It did not show any significant correlation with chlorophyll *a* concentration ($r= -0.512$ and -0.441 respectively, $P > 0.05$). Concerning the male, total length showed negative correlations with temperature, salinity as well as chlorophyll *a*, and positive with other parameters (Tables 2, 3), while prosome length did not show any relationship with the measured environmental variables.

Discussion

The original descriptions of *A. bispinosa* were brief and the drawings incomplete. Some morphological features were probably overlooked or undescribed by the previous au-

thors (Carl 1907, Steuer 1923, Nishida 1985, Mulyadi 2004). Examination of the *A. bispinosa* from the Red Sea revealed some shortcoming in earlier descriptions. Newly confirmed features include: (1) the posteroventral margin of female genital compound somite furnished with fine hairs, (2) the female caudal rami carrying a row of setules anteroventrally, (3) the distal two-third of female leg 5 exopod furnished medially with fine spinules, (4) the last metasomal segment of the male has 2 unequal dorsolateral spines on each side. (5) the second urosomite of the male with 2 dorsolateral groups of fine spinules ventrolaterally on both sides and dorsolateral row of fine setules along posterior margin, (6) the third and fourth urosomites with very fine setules along posterior margins, and (7) the second exopodal segment of the male right leg 5 carrying 2 groups of fine spinules on the posterior surface. This species was more precisely illustrated from the Japanese waters by Nishida (1985) than in the original description. In his paper the above stated feature (4) was already mentioned. The antennules, mouth parts and legs 1–4 of this species are first illustrated and describe herein, according to the conventions of Huys and Boxshall (1991).

In genus *Acartia*, there are currently 62 valid species (Razouls et al. 2014) provisionally divided into seven subgenera: *Acartia* Dana, 1846, *Acartiura* Steuer, 1915, *Euacartia* Steuer, 1915, *Hypoacartia* Steuer, 1915, *Acanthacartia* Steuer, 1915, *Odontacartia* Steuer, 1915, and *Planktacartia* Steuer, 1915. The *Acartia* subgenus *Odontacartia* includes twelve species (*A. amboinensis* Carl, 1907, *A. australis* Farran, 1936, *A. bispinosa*, *A. bowmani* Abraham, 1976, *A. centrura*, *A. erythraea*, *A. japonica* Mori, 1940, *A. lilljeborgii* Giesbrecht, 1889, *A. mertoni* Steuer, 1917, *A. ohtsukai* Ueda & Bucklin, 2006, *A. pacifica* Steuer, 1915, and *A. spinicauda* Giesbrecht, 1889) which is categorized into 3 species group as proposed by Steuer (1923) and Ueda and Bucklin (2006), i.e. *erythraea* group (*A. erythraea*, *A. amboinensis*, *A. australis*, *A. bispinosa*, *A. japonica*), the *centrura* group (*A. centrura*, *A. spinicauda*) and the *pacifica* group (*A. pacifica*, *A. mertoni* and *A. ohtsukai*) and two intermediate species, *A. bowmani* and *A. lilljeborgii*.

Acartia bispinosa closely resembles *A. amboinensis* and *A. erythraea*, but it differs from the latter two species in the following characteristics in the female: (1) the second segment of antennule with strong claw-like spine curved proximally from midposterior margin, (2) the exopod of the female leg 5 reduced and swollen at the base posteriorly and distal two-thirds furnished medially with very fine spinules; in the male: (1) left leg 5 distal segment with 2 terminal spines, a stout spine on the mid-anterior surface with fine setae near its base and tuft of hairs proximally, row of spinules along medial margin, and several spinules along lateral margin.

We report this particular species from the Red Sea for the first time. There are three possible explanations of this discovery: 1) most of the plankton studies in the Red Sea were focused mainly in oceanic regions resulting in ruling out of this species which were dominant mainly in the neritic waters, 2) it may have been present but overlooked or misidentified in the previous studies and 3) it may be a representative of an invasive species transported in the Red Sea by human activities (possibly in ballast water). In a way we can conclude that the presence of this species in the Red Sea is

obviously due to the overlooking by previous authors (e.g. Khalil and Abd El-Rahman 1997, Aamer et al. 2007), due to the resemblance of this species with *A. amboinensis*, *A. centrura* and *A. erythraea*. Also, it can be considered as a normal extension or distribution of the species since most of the Red Sea fauna is Indo-West Pacific in origin.

Acartia bispinosa is distributed mainly in the Indo-West Pacific region. It has been recorded from Ambon Bay, Malaysian coastal waters (Carl 1907, Mulyadi 2004), Persian Gulf (Pesta 1912), coastal water of Sri-Lanka (Sewell 1914), neritic waters of Seychelles, south western Indian Ocean (Steuer 1923, Conway et al. 2003), Tudor Creek, Kenya (Revis 1988), Butaritari lagoon, Gilbert Island and the Fiji Island (Wilson 1950 as *A. hamata*), Great Barrier Reef of Palau (Hamner and Carleton 1979, Saitoh et al. 2011), Dee Why Lagoon, Sydney, Australia (Rissik et al. 2009), New Caledonia, South Pacific Ocean (Binet 1984, 1985), Katae Bay (Simane Peninsula) and Kabira Bay (Ishigaki Island, Japan) (Mori 1942 as *A. tokiokai*, Nishida 1985 respectively), coastal waters of western Bay of Bengal, northern Indian Ocean (Madhupratap and Haridas 1986). From the distribution pattern, it is evident that this particular species is recorded mainly from tropical and subtropical neritic waters and lagoons which are inhabited with coral reefs and mangrove forests with an average temperature more than 20 °C which is quite similar to the coral reef distribution patterns in these areas (Fig. 10).

The seasonal distribution patterns of *A. bispinosa* clearly showed a pronounced peak at the end of April (temperature: 24.9 °C) and a smaller one at the end of October (temperature: 26.4 °C). This pattern is similar to those found in a tidal mangrove-fringing reef lagoon in Kenya, western Indian Ocean (Revis 1988). In his study, Revis (1988) reported the presence of *A. bispinosa* in the plankton samples from December to July with prominent peaks during March-April and also in December with a somewhat similar temperature of the present investigation. Also, Tafe and Griffiths (1983) during their studies in Port Hacking, New South Wales, Australia pointed out the disappearance of *A. bispinosa* from the plankton samples during June-August and its further re-emergence in higher numbers during March-April (4736 ind. m⁻³) when the temperature was in a range between 20.5–22.6 °C. This may suggest that 20–28 °C is the optimal temperature for maximum production of *A. bispinosa*.

Monthly variations in the abundance of *A. bispinosa* did not show correlation with any of the measured environmental parameters (temperature, pH, salinity, dissolved oxygen and chlorophyll *a* concentration). This implies that water temperature alone could not explain the variation in the abundance of *A. bispinosa*, although water temperature as well as food quantity and quality has been suggested as key parameters influencing the abundance of many *Acartia* species (Dam et al. 1994, Pagano and Saint-Jean 1994, Jonasdottir 1994, Jonasdottir and Kiorboe 1996, Gubanova 2000). In the present study, despite the high chlorophyll *a* concentration in summer due to outbreak of the diatom, *Hemiaulus hauckii* Grunow ex Van Heurck, 1882 and the cyanobacteria, *Trichodesmium* spp., no subsequent significant changes in the abundance or body sizes were noticed. This may be due to the particular food preference of *A. bispinosa* and further non usage of the available food matter effectively. Also, the current species is

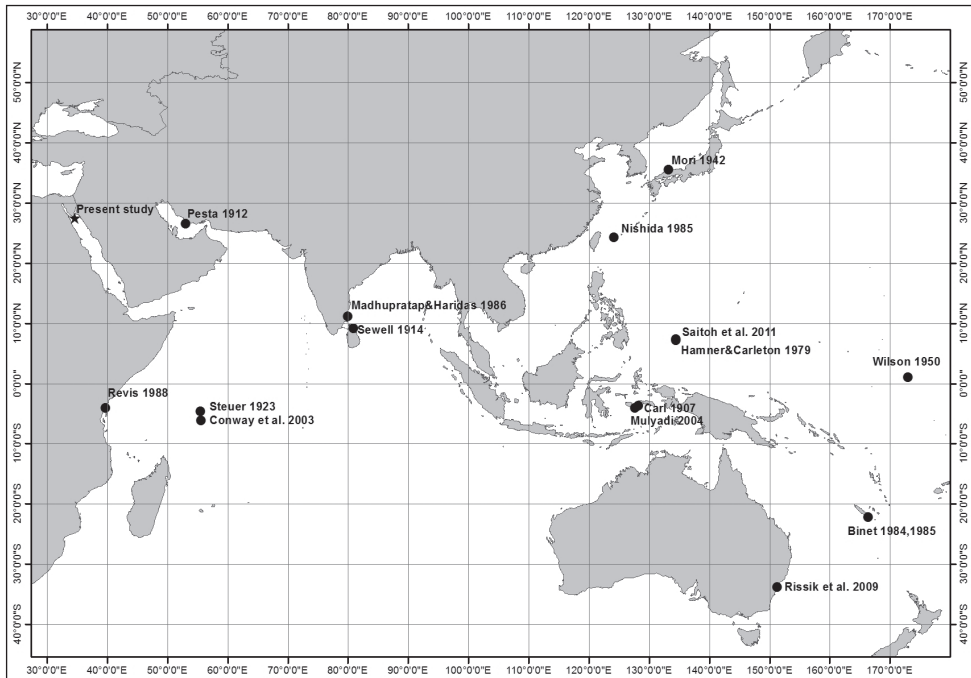


Figure 10. Distribution of *Acartia bispinosa* based on previous records and on the present study (Note that its distribution is restricted between 35°N and 32°S).

well known for its omnivorous behavior (Tafe and Griffiths 1983), which revealed the importance of other non-algal food items (bacteria, ciliates and detritus). Moreover, the quality of the food may be more important rather than its high concentration to assure optimal growth (Klein Breteler et al. 1990, Hart and Santer 1994).

The character of changes in the population dynamics of *A. bispinosa* as well as the very low densities of this species in the plankton from December to March allow us to conclude that the dominance of adult females in April and October, during the condition of gradual warming and cooling of coastal water, is linked to resting eggs, that are capable to give a new generation. Correspondingly, resting eggs of *Acartia* were found in bottom sediment of the different bays all over the world (Lee and McAlice 1979, Liang and Uye 1996). Some authors (Uye and Kasahara 1979, Uye 1980, Onoue et al. 2004) emphasize the importance of such eggs of neritic copepods for maintaining their population potential in the bays and bights through unfavorable seasons.

Seasonal variations in the body sizes have often been observed in marine invertebrates including copepods. In our study, the total length of *A. bispinosa* varies less than 51.9% and 41.2% around the annual means for both the females and the males respectively. The observed seasonal variability of the body size, seems to be inversely related to temperature, as confirmed by the Pearson correlation. Similar seasonal variability in size with a winter maximum are commonly observed in copepods (Deevey 1960, Uye et al. 1982, Liang and Uye 1996, Belmonte and Cavallo 1997, Mauchline 1998, Ric-

cardi and Mariotto 2000, Ara 2002, Gaudy and Verriopoulos 2004, Tellioglu 2006, Bozkurt and Can 2014). Among the other factors affecting copepod body size, food availability seems to be of great importance, at least in some ecosystems (Deevey 1960, Durbin et al. 1983, Viitasalo et al. 1995). According to Deevey (1960) the seasonal temperature range determines its relative importance along with food in affecting the copepod body size: when the annual mean range was 14 °C or more. In the present study, the temperature range was 10.1 °C and this may explain the weak correlations between *Acartia* abundance with that of temperature and chlorophyll *a* concentration.

Variations in prosomal ends, genital somite and leg 5 of both sexes are common within other species of *Acartia* as reported in many previous works (e.g. Ueda 1986, Garmew et al. 1994, Hirst and Castro-Longoria 1998, Soh and Suh 2000, Ueda and Bucklin 2006).

In the present study, *A. bispinosa* has been observed as a monospecific aggregation in the study area during daytime at the end of April. In tropical reef environments many acartiid copepod species exhibit swarming. For example, *Acartia* (*Acanthacartia*) *spinata* Esterly, 1911 and *A. tonsa* Dana, 1849 were reported by Emery (1968) on Caribbean reef and *A. australis* and *A. bispinosa*, were observed in aggregations on Great Barrier Reef (Hamner and Carleton 1979). Similarly, swarms of *A. hamata* were found in the fringing coral reefs of Sesoko island, southern Japan (Ueda et al. 1983) as well as *Acartia* swarms in Conch Reef off Florida (Heidelberg et al. 2010). Most of the swarms of this species appeared as monospecific aggregations, which is a common phenomenon in copepods (Ueda et al. 1983, Ambler et al. 1991). According to many authors (Hamner and Carleton 1979, Ueda et al. 1983, Ambler et al. 1991, Buskey 1998), the advantages of swarming behavior in copepods are: (1) protection against predation, (2) reduction of dispersion by currents, (3) facilitating and enhancing mating opportunity, and (4) keeping in good position to feed on coral mucus.

Conclusion

In this study we have reported the presence of *A. bispinosa* in the Red Sea for the first time with full redescription. There are three possible explanations of this discovery: 1) most of the plankton studies in the Red Sea were focused mainly in oceanic regions resulting in ruling out of this species which were dominant mainly in the neritic waters, 2) it may have been present but overlooked or misidentified in the previous studies and 3) it may be a representative of an invasive species transported in the Red Sea anthropogenically (possibly in ballast water). The seasonal distribution patterns of *A. bispinosa* clearly showed a pronounced peak at the end of April and a smaller one at the end of October during the condition of gradual warming and cooling of coastal water, that may be linked to resting eggs, that are capable to give a new generation. Females showed their highest total and prosome length in January and the lowest were observed at the end of June. The highest total and prosome length of the male were detected in March and the lowest value appeared in June. This variability of the body size, seems to be inversely related to temperature, indicating the influence of other environmental parameters.

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References

- Aamer MA, El-Sherbiny MM, Gab-Alla AA, Kotb MM (2007) Ecological studies on zooplankton standing crop of Sharm El-Maiya Bay, Sharm El-Sheikh, northern Red Sea. *Catrina* 1(1): 73–80.
- Ambler JWD, Ferrari FD, Fomshel JA (1991) Population structure and swarm formation of the cyclopoid Copepod *Dioithona oculata* near mangrove bays. *Journal of Plankton Research* 13: 1257–1272. doi: 10.1093/plankt/13.6.1257
- Ara K (2002) Temporal variability and production of *Temora turbinata* (Copepoda: Calanoida) in the Cananeia lagoon estuarine system, Sao Paulo, Brazil. *Scientia Marina* 66(4): 399–406. doi: 10.3989/scimar.2002.66n4399
- Belmonte G, Cavallo A (1997) Body size and its variability in the copepod *Acartia margalefi* (Calanoida) from Lake Acquatina (SE Italy). *Italian Journal Zoology* 64: 377–382. doi: 10.1080/11250009709356225
- Belmonte G, Potenza D (2001) Biogeography of the family Acartiidae (Calanoida) in the Ponto-Mediterranean Province. *Hydrobiologia* 453/454: 171–176. doi: 10.1023/A:1013192623131
- Binet D (1984) Copépodes planctoniques du lagon de Nouvelle-Calédonie: facteurs écologiques et associations d'espèces. *Marine Biology* 82(2): 143–156. doi: 10.1007/BF00394098
- Binet D (1985) Essai d'utilisation de la diversité spécifique dans l'analyse des communautés de copépodes planctoniques du lagon de Nouvelle-Calédonie. *Marine Biology* 88(1): 85–100. doi: 10.1007/BF00393047
- Bozkurt A, Can MF (2014) Seasonal variations in body length and fecundity of 2 copepod species: *Thermocyclops crassus* (Fischer, 1853) and *Eudiaptomus drieschi* (Poppe and Mrázek, 1895). *Turkish Journal of Zoology* 38: 222–228. doi: 10.3906/zoo-1007-7
- Bradford JM (1976) Partial revision of the *Acartia* subgenus *Acartiura* (Copepoda: Calanoida: Acartiidae). *New Zealand Journal of Marine and Freshwater Research* 10: 159–202. doi: 10.1080/00288330.1976.9515606
- Buskey EJ (1998) Components of mating behavior in planktonic copepods. *Journal of Marine Systems* 15: 13–21. doi: 10.1016/S0924-7963(97)00045-6
- Carl J (1907) Copépodes d'Amboine. *Revue suisse Zoologie* 15: 7–18.
- Conway DVP, White RG, Hugues-Dit-Ciles J, Gallienne C, Robins DV (2003) Guide to the coastal and surface zooplankton of the South-Western Indian Ocean. Marine Biological Association of the United Kingdom. Occasional Publication No 15. Subclass Copepoda, 76–263.

- Dam HG, Peterson WT, Bellantoni DC (1994) Seasonal feeding and fecundity of the calanoid copepod *Acartia* in Long Island sound: is omnivory important to egg production? *Hydrobiologia* 293: 191–199. doi: 10.1007/BF00229941
- Deevey GB (1960) Relative effects of temperature and food on seasonal variation in length of marine copepods in some eastern American and western European waters. *Bulletin of the Bingham Oceanographic Collection* 17: 54–85.
- Durbin EG, Durbin AG (1978) Length and weight relationship of *Acartia clausi* from Narragansett Bay, Rhode Island. *Limnology and Oceanography* 23:958–969. doi: 10.4319/lo.1978.23.5.0958
- Durbin EG, Smayda J, Veritym PG (1983) Food limitation of production by adult *Acartia tonsa* in Narragansett Bay, Rhode Island. *Limnology and Oceanography* 28: 1199–1213. doi: 10.4319/lo.1983.28.6.1199
- Emery AR (1968) Preliminary observations on coral reef plankton. *Limnology and Oceanography* 13: 293–303. doi: 10.4319/lo.1968.13.2.0293
- Engel M (2005) Calanoid copepod resting eggs-a safeguard against adverse environmental conditions in the German Bight and the Kara Sea? *Ber Polarforsch Meeresforsch* 508: 1–108.
- Garmew TG, Hammond S, Mercantini A, Morgan J, Neunert C, Fornshell JA (1994) Morphological variability of geographically distinct populations of the estuarine copepod *Acartia tonsa*. *Hydrobiologia* 292/293: 149–156. doi: 10.1007/BF00229935
- Gaudy R, Verriopoulos G (2004) Spatial and seasonal variations in size, body volume and body proportion (prosoma : urosome ratio) of the copepod *Acartia tonsa* in semi-closed ecosystem (Berre Lagoon, western Mediterranean). *Hydrobiologia* 51: 219–231. doi: 10.1023/B:hydr.0000018190.34856.d2
- Gubanova A (2000) Occurrence of *Acartia tonsa* Dana in the Black Sea. Was it introduced from the Mediterranean? *Mediterranean Marine Science* 1(1): 105–109. doi: 10.12681/mms.281
- Halim Y (1969) Plankton of the Red Sea. *Oceanography and Marine Biology: an Annual Review* 7: 231–275.
- Hamner WM, Carleton JH (1979) Copepod swarms : attributes and role in coral reef ecosystems. *Limnology and Oceanography* 24: 1–14. doi: 10.4319/lo.1979.24.1.0001
- Hart RC, Santer B (1994) Nutritional suitability of some uni-algal diets for freshwater calanoids: unexpected inadequacies of commonly used greens and others. *Freshwater Biology* 31: 109–116. doi: 10.1111/j.1365-2427.1994.tb00843.x
- Heidelberg K, O'neil K, Bythell JC, Kenneth P, Seben KP (2010) Vertical distribution and diel patterns of zooplankton abundance and biomass at Conch Reef, Florida Keys (USA). *Journal of Plankton Research* 32 (1): 75–91. doi: 10.1093/plankt/fbp101
- Hirst AG, Castro-Longoria E (1998) *Acartia biflosa* (Copepoda: Calanoida): a clarification of the species and its varieties *inermis* and *intermedia*. *Journal of Plankton Research* 20: 1119–1130. doi: 10.1093/plankt/20.6.1119
- Huys R, Boxshall GA (1991) *Copepod Evolution*. Ray Society, London, 159, 468 pp.
- Jonasdottir SH (1994) Effects of food quality on the reproduction success of *Acartia tonsa* and *Acartia hudsonica*: laboratory observations. *Marine Biology* 121: 67–81. doi: 10.1007/BF00349475
- Jonasdottir SH, Kiorboe T (1996) Copepod recruitment and food composition: do diatoms affect hatching success? *Marine Biology* 125: 743–750. doi: 10.1007/BF00349257

- Khalil MT, Abd El-Rahman NS (1997) Abundance and diversity of surface zooplankton in the Gulf of Aqaba, Red Sea, Egypt. *Journal of Plankton Research* 19: 927–936. doi: 10.1093/plankt/19.7.927
- Klein Breteler WCM, Schogt N, Gonzales SR (1990) On the role of food quality in grazing and development of life stages, and genetic change of body size during cultivation of pelagic copepods. *Journal of Experimental Marine Biology and Ecology* 135: 177–189. doi: 10.1016/0022-0981(90)90117-U
- Lee WY, McAlice BJ (1979) Seasonal succession and breeding cycle of three species of *Acartia* (Copepoda, Calanoida) in a Maine Estuary. *Estuaries* 2(4): 228–235. doi: 10.2307/1351569
- Liang D, Uye S (1996) Population dynamics and production of the planktonic copepods in a eutrophic inlet of the inland sea of Japan. II. *Acartia omorii*. *Marine Biology* 125: 109–117. doi: 10.1007/BF00350765
- Madhupratap M, Haridas P (1986) Epipelagic calanoid copepods of the northern Indian Ocean. *Oceanologica Acta* 9(2): 105–117.
- Mauchline J (1998) The biology of calanoid copepods. *Advances in Marine Biology*, 33, Academic press, London, 710 pp.
- Mori T (1942) Systematic studies of the plankton organisms occurring in Iwayama Bay, Palao. IV. Copepoda from the bay and adjacent waters. *The Palao Tropical Biological Station Studies* 2(3): 549–580.
- Mulyadi (2004) The pelagic calanoid copepods of the families Acartiidae, Aetideidae, Augaptilidae, Calanidae, Calocalanidae, Candaciidae, Centropagidae, Clausocalanidae, Eucalanidae, Euchaetidae, Heterorhabdidae, Metrinidae, Paracalanidae, Phaennidae, Pseudodiaptomidae. *Research Center for Biology, Indonesia Institute of Sciences, Bogor, Indonesia*, 195 pp.
- Nishida S (1985) Pelagic copepods from Kabira Bay, Ishigaki Island, southwestern Japan, with the description of a new species of the genus *Pseudodiaptomus*. *Publications of the Seto Marine Biological Laboratory* 30(1-3): 125–144.
- Onoue Y, Toda T, Ban S (2004) Morphological features and hatching patterns of eggs in *Acartia steueri* (Crustacea, Copepoda) from Sagami Bay, Japan. *Hydrobiologia* 511: 17–24. doi: 10.1023/B:HYDR.0000014013.37891.46
- Pagano M, Saint-Jean L (1994) In situ metabolic budget for the calanoid copepod *Acartia clausi* in a tropical brackish water lagoon (Ebrie Lagoon, Ivory Coast). *Hydrobiologia* 272: 147–161. doi: 10.1007/BF00006518
- Parsons TR, Maita Y, Lalli CM (1984) A manual of chemical and biological methods for seawater and analysis. Pergamon Press, New York, 173 pp.
- Pesta O (1912) Crustaceen. 1. Teil: Copepoden aus dem Golf von Persien. *Wissenschaftliche Ergebnisse der Expedition nach Mesopotamien. Annalen des K.K. Naturhistorischen Hofmuseums, Wien* 26: 39–62.
- Putland JN, Iverson RL (2007) Ecology of *Acartia tonsa* in Apalachicola Bay, Florida, and implications of river water diversion. *Marine Ecology Progress Series* 340: 173–187. doi: 10.3354/meps340173
- Razouls C, de Bovée F, Kouwenberg J, Desreumaux N (2014) Diversity and Geographic Distribution of Marine Planktonic Copepods. <http://copepodes.obs-banyuls.fr/en> [accessed January 1, 2014]

- Revis N (1988) Preliminary observations on copepods of Tudor Creek, Mombasa, Kenya. *Hydrobiologia* 167/168: 343–350. doi: 10.1007/BF00026323
- Riccardi N, Mariotto L (2000) Seasonal variations in copepod body length: a comparison between different species in the Lagoon of Venice. *Aquatic Ecology* 34: 243–252. doi: 10.1023/A:1009971507797
- Rissik D, Shon EH, Newell B, Baird ME, Suthers IM (2009) Plankton dynamics due to rainfall, eutrophication, dilution, grazing and assimilation in an urbanized coastal lagoon. *Estuarine, Coastal and Shelf Science* 84: 99–107. doi: 10.1016/j.ecss.2009.06.009
- Saitoh S-I, Suzuki H, Hanzawa N, Tamate HB (2011) Species diversity and community structure of pelagic copepods in the marine lakes of Palau. *Hydrobiologia* 666(1): 85–97. doi: 10.1007/s10750-010-0095-0
- Seki J, Shimizu I (1997) Distribution of zooplankton communities during spring to early summer in the Pacific coastal waters near Hiroo, Hokkaido. *Bulletin of the Plankton Society of Japan* 44: 21–30. [in Japanese with English abstract]
- Sewell RBS (1914) Notes on the surface Copepoda of the Gulf of Mannar. *Spolia Zeylan* 9: 191–262.
- Soh HY, Suh HL (2000) A new species of *Acartia* (Copepoda, Calanoida) from the Yellow Sea. *Journal of Plankton Research* 22(2): 321–337. doi: 10.1093/plankt/22.2.321
- Steuer A (1923) Bausteine zu einer monographie der copepodengattung *Acartia*. *Arbeiten aus dem Zoologischen Institute der Universität Innsbruck* 1(5): 91–144.
- Tafe DJ, Griffiths FB (1983) Seasonal abundance, geographical distribution and feeding types of the copepod species dominant in Port Hacking, New South Wales. In: Cuff WR, Tomczak MJr (Eds) *Synthesis and Modeling of Intermittent Estuaries*. Springer-Verlag, Berlin, Heidelberg, New York, 109–133. doi: 10.1029/LN003p0109
- Tellioglu A (2006) Seasonal variations in copepod body length: a comparison between different species in Keban Dam Lake, Turkey. *Crustaceana* 79(1): 11–22. doi: 10.1163/156854006776759761
- Ueda H (1986) Taxonomic reexamination and geographic distribution of copepods known as *Acartia clausi* in Japanese coastal and inlet waters. *Journal of the Oceanographical Society of Japan* 42: 134–138. doi: 10.1007/BF02109100
- Ueda H, Bucklin A (2006) *Acartia* (*Odontacartia*) *ohsukai*, a new brackish–water calanoid copepod from Ariake Bay, Japan, with a redescription of the closely related *A. pacifica* from the Seto Inland Sea. *Hydrobiologia* 560: 77–91. doi: 10.1007/s10750-005-9513-0
- Ueda H, Kuwahara A, Tanaka M, Azeta M (1983) Underwater observations on copepod swarms in temperate and subtropical waters. *Marine Ecology Progress Series* 11(2): 165–171. doi: 10.3354/meps011165
- Uye S, Iwai Y, Kasahara S (1982) Reproductive biology of *Pseudodiaptomus marinus* in the central part of the Inland Sea of Japan. *Bulletin of the Plankton Society of Japan* 29: 25–35.
- Uye S (1980) Development of neritic copepods *Acartia clausi* and *A. steueri*. I. Some environmental factors affecting egg development and the nature of resting eggs. *Bulletin of the Plankton Society of Japan* 27(1): 1–9.
- Uye S, Kasahara S (1979) Life history of marine planktonic copepods in neritic region with special reference to the role of resting eggs. *Bulletin of the Plankton Society of Japan* 25: 109–122.

- Viitasalo M, Koski M, Pellikka K, Johansson S (1995) Seasonal and long-term variations in the body size of planktonic copepods in the Baltic Sea. *Marine Biology* 123(2): 241–250. doi: 10.1007/BF00353615
- Wilson CB (1950) Copepods gathered by the United States Fisheries Steamer “Albatross” from 1887 to 1909, chiefly in the Pacific Ocean. *Bulletin of the United States National Museum* 100, 14, (4) I-IX: 141–441.

Kakuna taibaiensis sp. n. and a newly recorded species of *Dicranotropis* (Hemiptera, Fulgoroidea, Delphacidae) from China

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Abstract

One new species of the delphacid genus *Kakuna* Matsumura, *K. taibaiensis* Ren & Qin, **sp. n.** is described from Mt. Taibai in Shaanxi Province, China. *Dicranotropis montana* (Horvath, 1897) is reported for the first time from China. Habitus photos and illustrations of male genitalia of the two species are given.

Keywords

Auchenorrhyncha, planthoppers, Fulgoromorpha, taxonomy, distribution

Introduction

The genus *Kakuna* was established by Matsumura (1935) for the type species *K. kuwayamai* Matsumura, 1935 from Japan (Hokkaido, Sapporo). Ding (2006) regarded *Parametopina* Yang as a junior synonym of *Kakuna* Matsumura and transferred *Parametopina yushaniae* Yang to *Kakuna*. Recently, Chen and Yang (2010) redefined the generic

characteristics and added three more species, *K. lii*, *K. nonspina* and *K. zhongtuana* to the genus from southwestern China (Guizhou). To date, five *Kakuna* species are known all distributed in China and Japan. In this paper, we add a new species, *K. taibaiensis* from Mt. Taibai (China: Shaanxi) and provide a key to all species in this genus.

Another delphacid species, *Dicranotropis montana*, was described by Horvath (1897), which was originally arranged as a member of the genus *Stiroma* Fieber. Ashe (1982) studied the type material of this species and transferred it into *Dicranotropis* Fieber. This species is currently distributed in the Palearctic Region. After checking the specimens collected in 2010 (now deposited in the Entomological Museum in NWAUFU), we found this species in Hebei (northern China) and record it for the first time in the Chinese fauna.

Material and methods

All specimens examined in this study are deposited in the Entomological Museum, Northwest A & F University, Yangling, Shaanxi, China (NWAUFU). The genital segments of the examined specimens were macerated in 10% KOH and drawn from preparations in glycerin jelly with the aid of a light microscope. Illustrations of the specimens were made using a Leica MZ 12.5 stereomicroscope. Habitus photos were taken using a Scientific Digital micrography system equipped with an Auto-montage imaging system and a highly sensitive QIMAGING Retiga 4000R digital camera (CCD). Multiple photographs were compiled into final images. The terminology in this paper follows that of Ding (2006). Measurements of the body length were from the apex of the vertex to the posterior tip of the abdomen (macropterous) or to the tip of abdomen (brachypterous). All measurements are in millimeters (mm).

Taxonomy

Kakuna Matsumura, 1935

Kakuna Matsumura 1935: 76; Ding 2006: 404; Chen and Yang 2010: 30. Type species: *Kakuna kuwayamai* Matsumura, 1935, by original designation.

Parametopina Yang, 1989: 308. Type species: *Parametopina yushaniae* Yang 1989: 308, synonymized by Ding 2006: 404.

Diagnosis. Relatively large, brown delphacids. Head including eyes narrower than pronotum. Submedian carinae uniting at apex of vertex. Fastigium in lateral view rounded. Dorsum of body with a milky longitudinal stripe from middle of vertex to middle of posterior margin of forewing. Median carina of frons forked at extreme base. Antennae cylindrical. Forewing with large, longitudinal, brown marking. Metabasitarsus longer than tarsomere 2 + 3 combined, calcar thin, tectiform, with many black-tipped teeth on lateral margin. Male pygofer in lateral view with laterodorsal angle

produced, medioventral process absent. Diaphragm of pygofer narrow, dorsal margin produced dorsad. Suspensorium ventrally ring-like. Aedeagus tubular, long. Parameres fairly developed, apically convergent. Anal segment deeply sunk into dorsal emargination of pygofer, ring-like, caudoventral processes present or absent.

Distribution. China (Guizhou, Taiwan, Zhejiang, Fujian, Shaanxi), Japan.

Key to species in the genus *Kakuna* (males)

- 1 Male anal segment produced caudoventrally.....2
- Male anal segment not produced caudoventrally.....3
- 2 Male anal segment with two spine-like processes along caudoventral margin; mediodorsal processes of diaphragm separated at bases; aedeagus not bearing spinous processes at apex. China (Guizhou).....*K. nonspinata* Chen & Yang
- Male anal segment with an elongate process at caudoventral margin; mediodorsal processes of diaphragm fused at their bases; aedeagus bearing spinous processes at apex. China (Taiwan)*K. yushaniae* (Yang)
- 3 Aedeagus in profile distinctly expanded at apex, dorsal margin with spinous processes4
- Aedeagus in profile not expanded at apex, dorsal margin without spinous processes5
- 4 Mediodorsal processes of diaphragm curved laterad apically; aedeagus without spinous processes ventrally near apex. China (Guizhou)*K. lii* Chen & Yang
- Mediodorsal processes of diaphragm straight apically; aedeagus with spinous processes ventrally near apex. China (Zhejiang, Fujian, Guizhou), Japan (Hokkaido, Honshu, Kyushu)*K. kuwayamai* Matsumura
- 5 Mediodorsal processes of diaphragm long, reaching to the level of anal segment; aedeagus in profile curved ventrad medially; inner margins of parameres with denticles medially. China (Shaanxi)*K. taibaiensis* Ren & Qin, sp. n.
- Mediodorsal processes of diaphragm short, not reaching to the level of anal segment; aedeagus in profile curved dorsad medially; inner margins of parameres without denticles but with a nipple-like process medially. China (Guizhou)*K. zhongtuana* Chen & Yang

Kakuna taibaiensis Ren & Qin, sp. n.

<http://zoobank.org/0DE83AE8-F62C-4649-8C6E-459D960AA940>

Figs 1–16

Description. Macropterous male: Body length: male 5.82–5.91 mm; forewing length: male 5.06–5.13 mm (n=2).

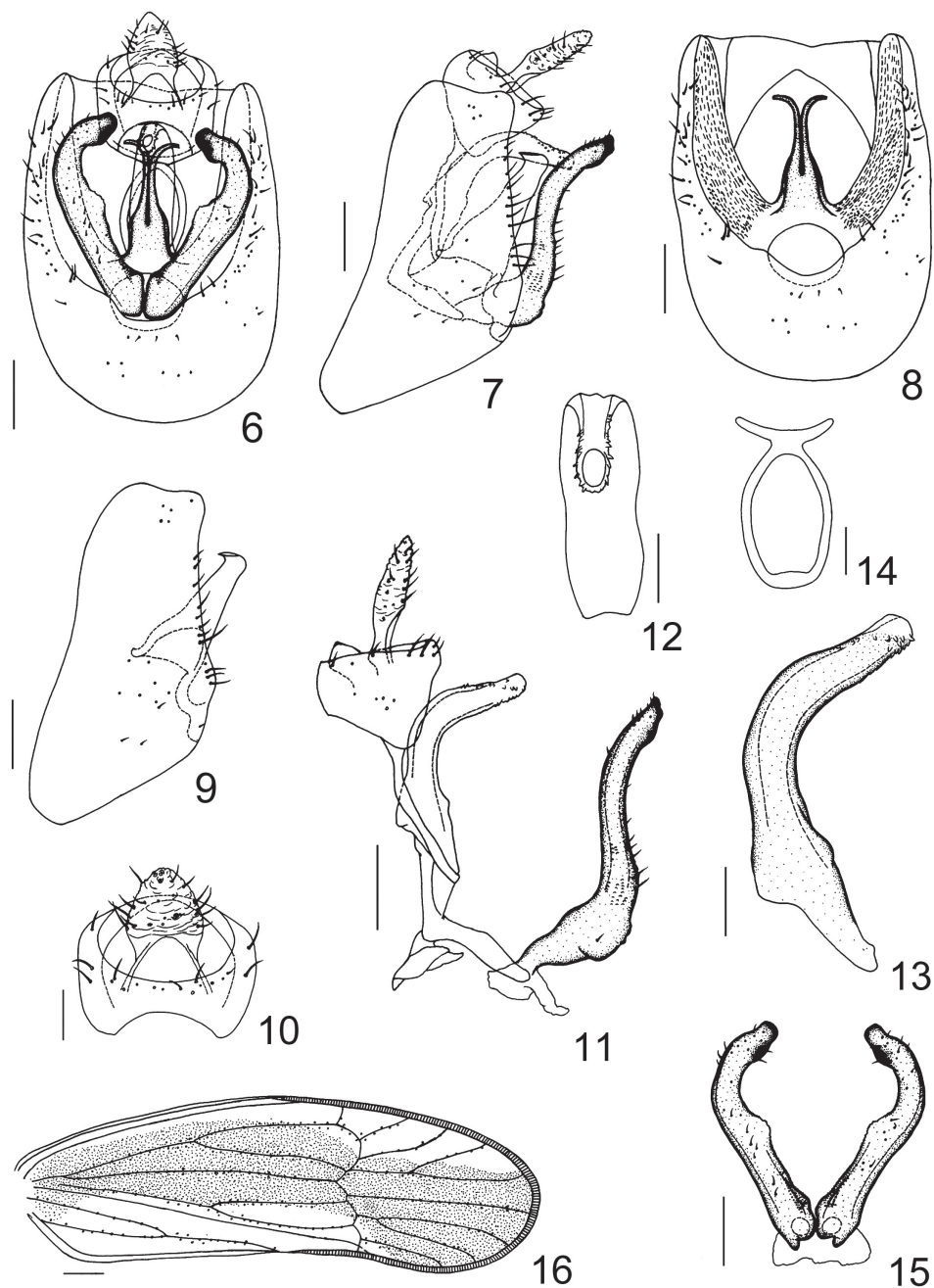


Figures 1–5. *Kakuna taibaiensis* Ren & Qin, sp. n. **1** male adult, dorsal view **2** male adult, left lateral view **3** head and thorax, dorsal view **4** frons and clypeus **5** metatarsus and post-tibial spur. Scale bars = 1.0 mm (Figs **1**, **2**); 0.5 mm (Figs **3–5**).

Color. General color brown. Ocelli reddish brown, eyes black. Dorsum of body with a milky longitudinal stripe from the junction of Y-shaped carina to the middle of posterior margin of forewing. Forewing yellowish brown, membrane has a large, longitudinal, fuscous marking from base of costal area to apex, veins fuscous, longitudinal veins ornamented with blackish brown granules. Abdomen fuscous. Fore and middle legs brown, hind legs yellowish brown, apices of spines on tibiae and tarsi black.

Structure. Head including eyes narrower than pronotum (about 0.81:1) (Figs 1, 3). Vertex shorter in midline than wide at base (about 0.82:1), narrower at apex than at base (about 0.78:1), lateral margins slightly concave in dorsal view, submedian carinae convex, originating from near 1/3 base of lateral carinae and uniting at apex of vertex (Figs 1, 3). Y-shaped carina distinct, basal compartment shallowly concave (Fig. 3). Fastigium rounded (Fig. 2). Frons longer in midline than maximum width about 2.05:1, widest above the level of ocelli, median carina conspicuous, forked at extreme base (Fig. 4). Postclypeus wider at base than frons at apex, post- and anteclypeus together approximately $0.86 \times$ of the length of frons (Fig. 4). Rostrum almost reaching mesotrochanters. Antennae terete, nearly attaining middle level of postclypeus, scape longer than wide at apex (about 1.83:1), shorter than pedicel (about 0.52:1) (Fig. 4).

Pronotum in midline slightly shorter than length of vertex (about 0.79:1), lateral carinae developed, slightly curved, not reaching posterior margin (Fig. 3). Mesonotum medially ca. 1.64 times longer than vertex and pronotum together, lateral carina almost straight, reaching posterior margin, median carina obscure apically (Fig. 3). Forewings long and narrow, longer than widest part about 3.35:1, widest in middle (Figs 1, 2, 16). Spination of apex of hind leg 5 (3+2) (tibia), 8 (6+2) (basitarsus) and 4 (2nd



Figures 6–16. *Kakuna taibaiensis* Ren & Qin, sp. n. **6** male genitalia, posterior view **7** male genitalia, left lateral view **8** male pygofer, posterior view **9** male pygofer, left lateral view **10** anal segment, posterior view **11** anal segment, aedeagal complex, connective and parameres, left lateral view **12** aedeagus, dorsocaudal view **13** aedeagus, left lateral view **14** suspensorium, posterior view **15** parameres, posterior view **16** forewing. Scale bars = 0.2 mm (Figs 6–9, 11, 15); 0.1 mm (Figs 10, 12–14); 0.5 mm (Fig. 16).

tarsomere) (Fig. 5). Metabasisarsus distinctly longer than tarsomere 2+3 combined (about 1.79:1), calcar shorter than metabasisarsus (about 0.77:1), thin, bearing 29 black-tipped teeth on lateral margin (Fig. 5).

Male genitalia. Male pygofer slightly wider ventrally than dorsally, laterodorsal angles roundly produced caudad; in posterior view with opening longer than wide, ventral margin shallowly excavated, medioventral process absent (Figs 6–9). Susensorium ventrally ring-like, dorsally with a process at each side leading to the anal segment ventrolaterally (Fig. 14). Diaphragm narrow, mediodorsal processes fairly developed, pillar-like, basally with a broad common stalk, thence contiguous apicad, apical part separated and curved laterad, tips truncated (Figs 6, 8). Parameres fairly long, reaching to the level of anal segment, in posterior view contiguous basally, apical 2/5 convergent mesad, apices rounded, inner margins expanded and ornamented with denticles medially (Figs 6, 11, 15). Aedeagus tubular, arch-shaped in profile, moderately dilated near the base, near apex on the dorsal side to the ventral apex provided with small teeth, gonopore apical on the slightly membranous dorsal side (Figs 12, 13). Male anal segment deeply sunk into dorsal emargination of pygofer, ring-like, caudoventral processes absent (Figs 6, 7, 10, 11).

Type materials. Holotype. ♂ (macropterous, NWAFU), China, Shaanxi Province, Mt. Taibai, 13-VIII-2010, by light trap, coll. A. P. Dong. **Paratype.** 1♂ (macropterous, NWAFU), same data as holotype.

Female. Unknown.

Host plant. Unknown.

Etymology. The species epithet is named after the type locality, Mt. Taibai in Shaanxi, China.

Distribution. Known currently from the type locality in northwest China (Shaanxi Province).

Remarks. *Kakuna taibaiensis* is similar to *K. zhongtuana* Chen & Yang (2010) in the male anal segment not produced caudoventrally, aedeagus not bearing spinous processes and mediodorsal processes of diaphragm having a common stalk basally. However, the new species differs from the latter in the mediodorsal processes fairly long, reaching to the level of anal segment (mediodorsal processes short, not reaching to the level of anal segment in *zhongtuana*), aedeagus curved ventrad medially in profile (aedeagus curved dorsad medially in profile in *zhongtuana*), parameres rounded at apex in posterior view, inner margins ornamented with denticles medially (parameres acute at apex and adorned with a nipple-like process medially along each inner margin in *zhongtuana*).

Discussion. The Himalaya-Qinling-Huai River line is the most distinctive barrier and may serve as the division of the Palaearctic and Oriental Regions since the Pleistocene. However, the north-south transitional affects have been much more pronounced in species and a broad transitional zone has resulted (Zhang 2002). The new finding in this paper based on the specimens from Mt. Taibai (the main peak of Mts. Qinling in Shaanxi, China) confirms the suggestion of Chen and Yang (2010) that

the members of the genus *Kakuna* have extended into the southern area of the Palearctic Region. During our investigations of Delphacidae on Mt. Taibai, we found many species in this family have extended into the border of the two Regions which were traditionally thought to be confined in the Palearctic or Oriental Region only, including some new species described in recent years (Qin 2007, Qin et al. 2012). We suspect that the delphacid fauna in this border area will be more extensive if more investigations are conducted.

***Dicranotropis montana* (Horvath, 1897)**

new record to China

Figs 17–34

Stiroma montana Horvath 1897: 625.

Dicranotropis tenellula Dlabola 1965: 84; Emeljanov 1977: 109, synonymized by Asche 1982: 30.

Dicranotropis gratiosa Dlabola 1997: 315, synonymized by Holzinger 1999: 259.

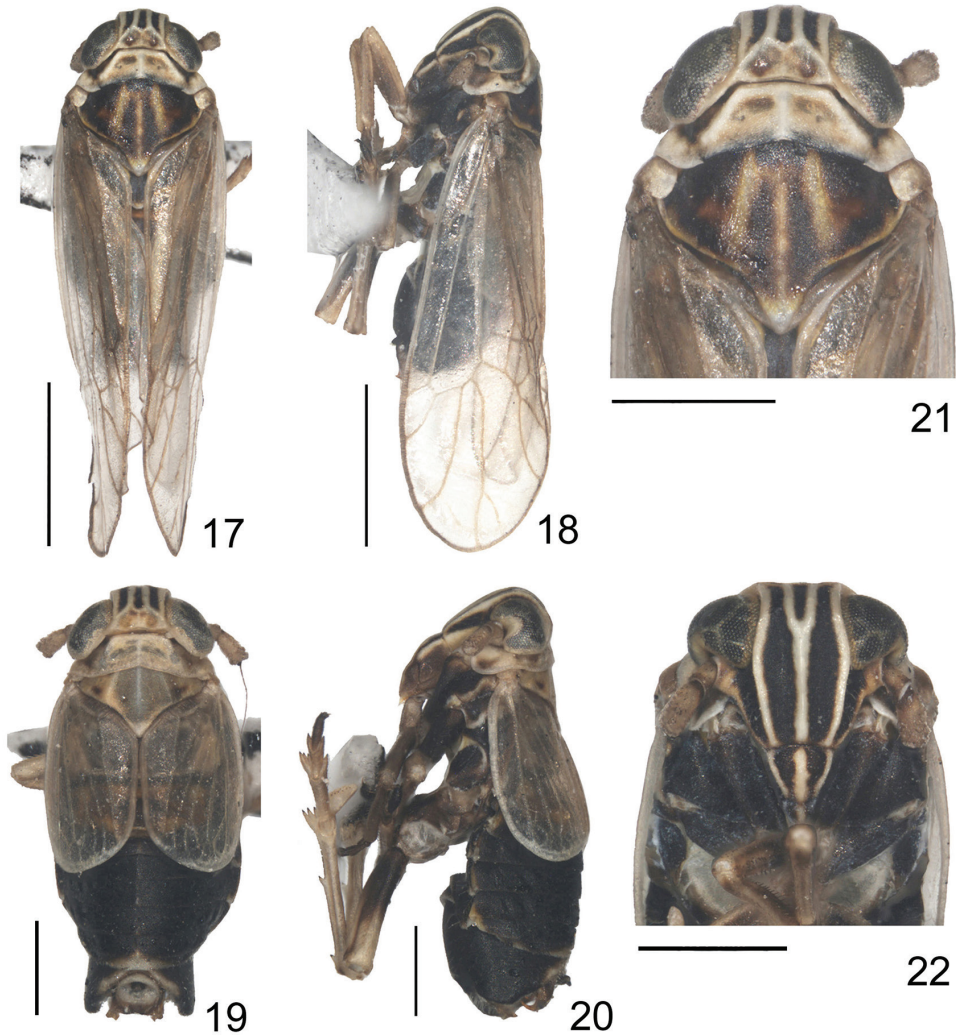
Dicranotropis montanus Vilbaste 1965: 15, synonymized by Asche 1982: 30.

Dicranotropis montana (Horvath), Asche 1982: 30; Holzinger 1999: 259; Holzinger et al. 2003: 267; Nickel 2003: 55; Trivellone 2010: 100.

Description. Macropterous male: Body length (from apex of vertex to the tip of forewing): male 3.40–3.64 mm, female 3.44–3.90 mm; forewing length: male 2.72–2.96 mm, female 3.04–3.24 mm. Brachypterous male: Body length (from apex of vertex to the tip of abdomen): male 2.24–2.56 mm, female 2.64–2.96 mm; forewing length: male 0.99–1.08 mm, female 1.04–1.24 mm.

Color. General color of male (macropterous) blackish brown. Ocelli reddish black, eyes grayish black. Vertex anteriorly, frons, clypeus, lateral area of pronotum behind eyes black. Antennae yellowish brown except apex of scape and base of pedicle fuscous. Pronotum between lateral carinae and laterobasal angles sordid whitish. All carinae and margins of vertex, frons and clypeus whitish. Rostrum fuscous at apex. Mesonotum mostly dark brown, scutellum whitish apically. Abdomen dark. Legs brown to yellowish brown. Tegmina subhyaline, veins yellowish brown. Female with ovipositor brown. Male (brachypterous) with the same color as macropterous except pronotum, mesonotum and tegmina yellowish brown, abdomen of female mostly yellowish white, abdomen with small brown spots dorsally and ventrally on each segment.

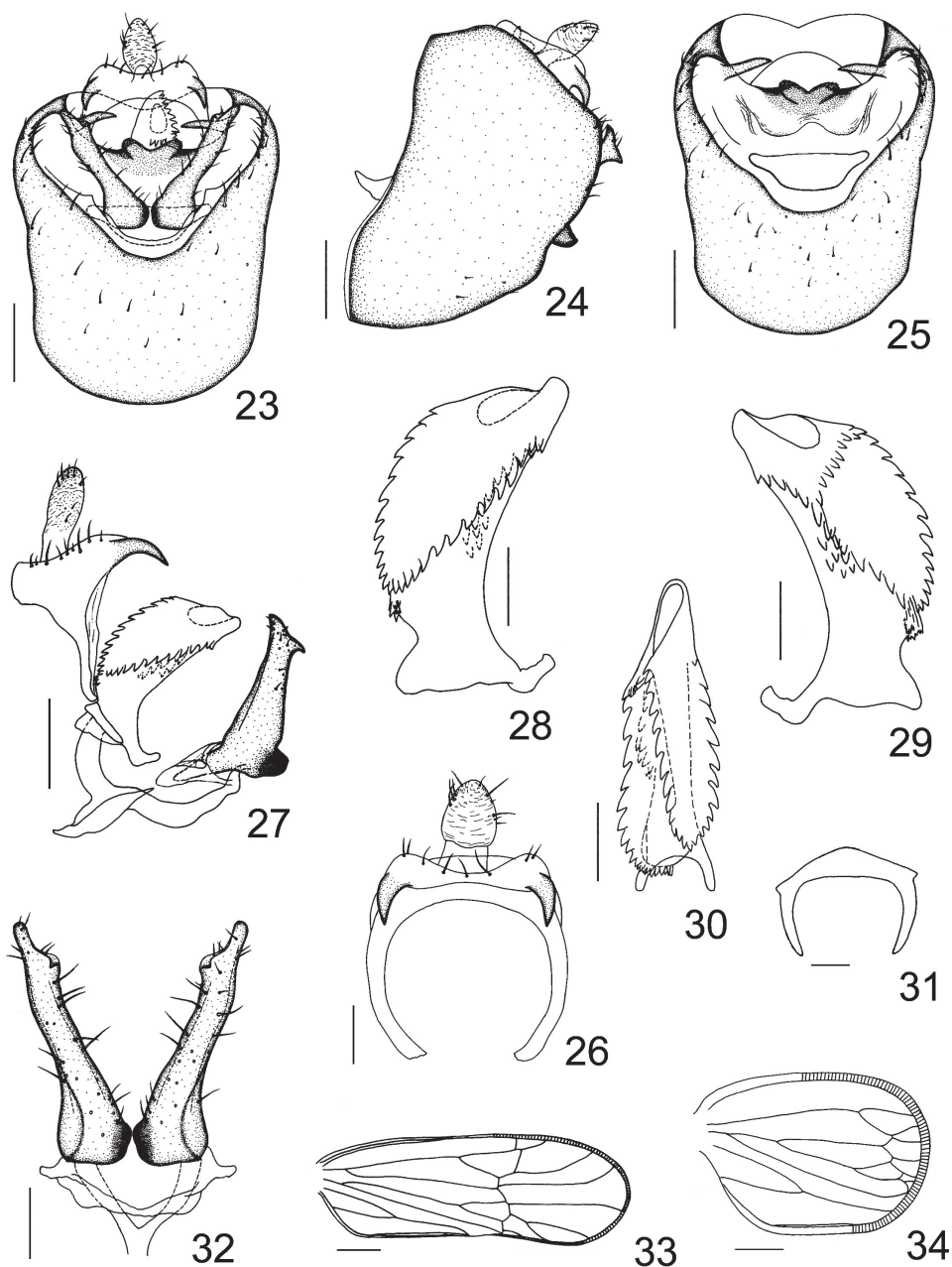
Structure. Head including eyes slightly narrower than pronotum (about 0.92:1). Vertex shorter in midline than wide at base (about 0.62:1), narrower at apex than at base (about 0.89:1). Submedian carinae originating from near 1/4 base of lateral carinae, not uniting at apex of vertex. Y-shaped carina distinct (Figs 17, 19, 21). Frons longer in midline than maximum width about 1.64:1, widest above the level of ocelli, carinae conspicuous, median carina forked at basal fourth (Fig. 22). Postclypeus broader



Figures 17–22. *Dicranotropis montana* (Horvath, 1897) **17** macropterous male, dorsal view **18** macropterous male, left lateral view **19** brachypterous male, dorsal view **20** brachypterous male, left lateral view **21** head and thorax (macropterous male), dorsal view **22** frons and clypeus (brachypterous male). Scale bars = 1.0 mm (Figs **17**, **18**); 0.5 mm (Figs **19–22**).

at base than frons at apex, postclypeus and anteclypeus together approximately $0.80 \times$ the length of the frons (Fig. 22). Rostrum almost reaching mesotrochanters. Antennae terete, reaching frontoclypeal suture, scape longer than apical width (about 1.59:1), shorter than pedicel (about 0.64:1) (Figs 18, 20, 22).

Pronotum shorter than vertex in midline (about 0.91:1), lateral carinae straight, not reaching to posterior margin (Figs 17, 19, 21). Mesonotum medially ca. 1.34



Figures 23–34. *Dicranotropis montana* (Horvath, 1897). **23** male genitalia, posterior view **24** male genitalia, left lateral view **25** male pygofer, posterior view **26** anal segment, posterior view **27** anal segment, aedeagal complex, connective and parameres, left lateral view **28** aedeagus, left lateral view **29** aedeagus, right lateral view **30** aedeagus, dorsal view **31** suspensorium, posterior view **32** parameres, posterior view **33** macropterous forewing **34** brachypterous forewing. Scale bars = 0.2 mm (Figs 23–25, 27); 0.1 mm (Figs 26, 28–30, 32); 0.04 mm (Fig. 31); 0.5 mm (Fig. 33); 0.25 mm (Fig. 34).

times longer than vertex and pronotum together, lateral carina reaching posterior margin, median carina obscure apically (Figs 17, 21). Macropterous forewings surpassing tip of abdomen approximately 2/5 of its total length (Figs 17, 18), longer than widest part (about 2.86:1). Spinal formula of hind leg 5–7–4, post-tibial spur shorter than metabasitarsus, sparsely with about 8 tiny teeth along hind margin.

Male genitalia. Male pygofer in profile wider ventrally than dorsally, anterior margin distinctly convex submedially (Fig. 24); in posterior view opening of pygofer obcordate, medioventral process absent (Figs 23, 25), below laterodorsal angle interiorly with a spine-like process on each side, transverse-directed (Figs 23, 25). Suspensorium n-shaped, dorsally arched medially with two small triangular processes on both ends (Fig. 31). Diaphragm broad, mediodorsal processes strongly sclerotized and laterally beset with many granulations, incised medially (Figs 23, 25). Opening for parameres large, dorsal margin nearly straight, lateral margins slightly sinuate (Fig. 25). Parameres long, contiguous at bases, narrowed and divergent apically, inner margins expanded subapically, in profile apical margin emarginated in two triangular processes (Fig. 27). Aedeagus tubular, short and broad, with five rows of teeth on surface, including four longitudinal rows and one transverse row basad of gonopore (Figs 28, 29, 30). Male anal segment ring-like, laterodistal angles produced into a short, stout spinose process on each side (Figs 23, 24, 26, 27).

Species examined. 23 ♂♂ 22 ♀♀ (macropterous) and 35 ♂♂ 46 ♀♀ (brachypterous), China: Hebei Province, Mt. Xiaowutai, 24-VI-2009, coll. D. Z. Qin.

Distribution. China (Hebei), Russia, Austria, Switzerland, Germany, France, Italy, Hungary, Romania, Mongolia.

Host plant. Unknown.

Discussion. Dlabola (1965) established *D. tenellula* Dlabola based on the specimens from Mongolia; Vilbaste (1965) described *D. montana* Vilbaste from Russia but it was regarded as a junior synonymy of *D. tenellula* Dlabola by Emeljanov (1977). Asche (1982) treated both *D. tenellula* Dlabola and *D. montana* Vilbaste as junior synonyms of *D. montana* (Horvath, 1897). However, the treatment of *D. tenellula* Dlabola was not accepted by Anufriev and Emeljanov (1988). Holzinger et al. (2003) studied the *Dicranotropis* species in central Europe, in *D. montana* (Horvath) part, they redrew the male genitalia of this species and noted: “according to Emeljanov and Gnezdilov (pers. common.), the central Asian *Dicranotropis tenellula* Dlabola, 1965 is not conspecific with *D. montana* (Horvath, 1897)”. After checking the specimens deposited in NWAFU, and also these illustrations of male genitalia provided by Dlabola (1965, 1997), Vilbaste (1965), Anufriev and Emeljanov (1988), Holzinger (1999) and Holzinger et al. (2003), we found *D. tenellula* Dlabola to be very similar to *D. montana* (Horvath) and very difficult to distinguish. We hope the status of *D. tenellula* can be reconsidered and firmly established using more advanced methods in the future. Here we consider *D. tenellula* Dlabola as a junior synonym of *D. montana* (Horvath).

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References

- Anufriev GA, Emeljanov AF (1988) Suborder Cicadinea (Auchenorrhyncha)-Cicadas. In: Ler PA (Ed.) Keys to the identification of insects of the Soviet Far East. Vol. 2: Homoptera and Heteroptera. Nauka, Leningrad, 12–495.
- Asche M (1982) Zur Kenntnis einiger von Geza Horvath beschriebener Delphaciden (Homoptera Cicadina Fulgoromorpha). Marburger Entomologische Publikationen 1(7): 25–36.
- Chen XS, Yang L (2010) Oriental bamboo delphacid planthoppers: three new species of genus *Kakuna* Matsumura (Hemiptera: Fulgoromorpha: Delphacidae) from Guizhou Province, China. Zootaxa 2344: 29–38.
- Ding JH (2006) Fauna Sinica. Insecta Vol. 45. Homoptera Delphacidae. Editorial Committee of Fauna Sinica, Chinese Academy of Science. Science Press, Beijing, China, 776 pp.
- Dlabola J (1965) Ergebnisse der zoologischen Forschungen von Dr. Z. Kaszab in der Mongolei. 54; Homoptera, Auchenorrhyncha. Acta Faunistica Entomologica Musei Nationalis Pragae 11(100): 79–136.
- Dlabola J (1997) *Mycterodus* verwandte Taxone und sieben neue Zikadenarten (Homoptera, Auchenorrhyncha). Acta Entomologica Musei Nationalis Pragae 44 (1995): 301–319.
- Emeljanov AF (1977) Leaf-hoppers (Homoptera, Auchenorrhyncha) from the Mongolian People's Republic based mainly on materials of the Soviet-Mongolian zoological expeditions (1967–1969). Nasekomye Mongolii 5: 96–195.
- Holzinger WE (1999) Taxonomie und Verbreitung ausgewählter Zikadenarten Österreichs (Insecta: Hemiptera: Auchenorrhyncha). Faunistische Abhandlungen Staatliches Museum für Tierkunde Dresden 21(17): 259–264.
- Holzinger WE, Kammerlander I, Nickel H (2003) The Auchenorrhyncha of Central Europe—Die Zikaden Mitteleuropas Fulgoromorpha, Cicadomorpha excl. Cicadellidae. Brill Publishers, Leiden, the Netherlands, 673 pp.
- Horvath G (1897) Homoptera nova ex Hungaria. Termeszetráji Füzetek, Budapest 20: 620–643.
- Matsumura S (1935) Supplementary note to the revision of *Stenocranus* and its allied species in Japan-Empire. Insecta Matsumurana 10: 71–78.
- Nickel H (2003) The Leafhoppers and Planthoppers of Germany (Hemiptera, Auchenorrhyncha): patterns and strategies in a highly diverse group of phytophagous insects. Pensoft Series Faunistica No. 28, Sofia-Moscow, Keltern, 1–460.
- Qin DZ (2007) Two new species of the Chinese endemic delphacid genus *Neuterthron* Ding (Hemiptera: Fulgoromorpha) from Yunnan and Shaanxi Provinces. Zootaxa 1547: 59–64.

- Qin DZ, Liu TT, Lin YF (2012) A new species in the *Bambusiphaga fascia* group (Hemiptera, Fulgoroidea, Delphacidae) from China, with a key to all species in the group. *Acta Zootaxonomica Sinica* 37(4): 777–780.
- Trivellone V (2010) Contribution to the knowledge of the Auchenorrhyncha fauna of bogs and fens of Ticino and Grisons, with some new records for Switzerland (Hemiptera: Fulgoro-morpha et Cicadomorpha). *Cicadina* 11: 97–106.
- Vilbaste J (1965) Über die Zikadenfauna des Altais (in Russian). *Akademia Nauk. Tartu* 1–144.
- Yang CT (1989) Delphacidae of Taiwan (II) (Homoptera: Fulgoroidea). *National Science Council Special Publication* 6: 334 pp.
- Zhang RZ (2002) Geological events and mammalian distribution in China. *Acta Zoologica Sinica* 48(2): 141–153.