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Revision of *Angursa* (Arthrotardigrada: Styraconyxidae) with the description of a new species from Japan

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Abstract. We re-examined the type material of five of the seven described species of the marine tardigrade genus *Angursa* Pollock, 1979, namely, *A. abyssalis* Renaud-Mornant, 1981, *A. bicuspis* Pollock, 1979 (type species), *A. capsula* Bussau, 1992, *A. lanceolata* Renaud-Mornant, 1981, and *A. lingua* Bussau, 1992. In addition, we describe *A. seisuimaruae* sp. nov. from the Sea of Kumano, Japan. Based on new data obtained, we amend the diagnosis of this genus, provide a taxonomic key to species, and discuss their geographical distributions.

Keywords. Beach, biogeography, deep-sea, meiobenthos, Tardigrada.

Fujimoto S. & Hansen J.G. 2019. Revision of *Angursa* (Arthrotardigrada: Styraconyxidae) with the description of a new species from Japan. *European Journal of Taxonomy* 510: 1–19. <https://doi.org/10.5852/ejt.2019.510>

Introduction

The marine tardigrade genus *Angursa* Pollock, 1979 was originally erected for *A. bicuspis* Pollock, 1979, an unarmoured, slender tardigrade possessing claws with two divergent points on its digits (Pollock 1979). The description of this type species was based on a specimen collected from a beach in Massachusetts, USA (type material) and an additional specimen collected from a 400 m deep site off North Carolina, USA (Pollock 1979). Subsequently, Renaud-Mornant (1981) described *A. bicuspis abyssalis* Renaud-Mornant, 1981 and *A. lanceolata* Renaud-Mornant, 1981. *Angursa b. abyssalis* was described based on a specimen from a 2063 m deep site off Angola, Africa (type material), as well as on additional specimens from a 2205 m deep site in the North Atlantic, and from a 460 m deep site in the Mediterranean Sea (Renaud-Mornant 1981). *Angursa lanceolata* was described based on specimens collected from a 2944 m deep site (type material) and a 2800 m deep site off Namibia, Africa (Renaud-Mornant 1981). This second report of the genus by Renaud-Mornant (1981) mentioned the presence

of the median cirrus, leg IV sensory organs, peduncles and proximal pads of the internal digits, which were missing in the description of the type species (Pollock 1979). The finding of another subspecies, *A. bicuspis clavifera* Noda, 1985 from a beach in Japan, further enriched the understanding of the genus by reporting the presence of the secondary and tertiary clavae, seminal receptacles, and leg II and III sensory organs (Noda 1985). The three subspecies of *A. bicuspis* (*A. b. bicuspis*, *A. b. abyssalis*, and *A. b. clavifera*) were elevated to species when two new species, *A. capsula* Bussau, 1992 and *A. lingua* Bussau, 1992, were described from 4140–4170 m deep sites at the manganese nodule area off Peru, South America (Bussau 1992). However, Villora-Moreno (1998) treated *A. abyssalis* as a junior synonym of *A. bicuspis* when he discussed the morphology of *A. antarctica* Villora-Moreno, 1998 which was collected from 352 m (type material) and 416 m deep sites off the South Shetland Islands, Antarctica (for coordinates, see stations L15 and L16 of Sàiz-Salinas *et al.* (1997)). This inconsistency in the taxonomic status of *A. abyssalis* is due to the scanty original description of the type species (Pollock 1979), which was referred to as inadequate for comparison with its congeners by Villora-Moreno (1998). To eliminate the fundamental cause of this problem and to provide a reliable platform for studying this genus, we re-examined the type material and some additional material used in the descriptions of species of *Angursa* except for *A. clavifera* and *A. antarctica*. We also describe a new species from Japan.

Material and methods

The type material examined in this study is deposited in the National Museum of Natural History of the Smithsonian Institution (NMNH; previous acronym: USNM, United States National Museum) (*A. bicuspis*), the Muséum national d'Histoire naturelle, Paris (MNHN) (*A. abyssalis* and *A. lanceolata*), the Senckenberg Natural History Museum, Frankfurt/Main, Germany (SMF) (*A. lingua* and *A. capsula*), and the Zoological Collection of Kyoto University (KUZ) (*A. seisuimaruae* sp. nov.). These specimens were examined using a differential interference contrast microscope Olympus BX51 or BX53.

Angursa seisuimaruae sp. nov. was extracted from a sediment sample dredged in the Sea of Kumano, Japan (33°59.5' N, 136°56.7' E to 33°59.7' N, 136°56.7' E; depth range 768–796 m; distance 370 m) on 10 Nov. 2017 during the T/V *Seisuimaru*'s research cruise No. 1722 (Kimura *et al.* 2018). The sample between mesh sizes 30–450 µm was rinsed with freshwater to give the meiofauna an osmotic shock (Kristensen 1983). The meiofauna was further concentrated by the floatation method using Ludox[®] HS-40 colloidal silica (Sigma-Aldrich Co., St. Louis) (e.g., Giere 2009). Specimens of the new species used in this study were fixed in 4 % buffered formaldehyde. They were observed in distilled water and then mounted in glycerol for permanent slides.

Morphometric values were obtained to the nearest micrometre using Adobe Illustrator CS6. Figures were prepared using Adobe Photoshop CS6, Adobe Illustrator CS6, and GMT version 5.1.1 (Wessel *et al.* 2013).

Abbreviations

an = anus
ap = anal papilla
cE = cirrus E
ec = external cirrus
go = female gonopore
ic = internal cirrus
lc = lateral cirrus
mc = median cirrus
pb = pharyngeal bulb
pc = primary clava

pe = peduncle
pp = proximal pad
sc = secondary clava
se_I = leg I sensory organ
se_{IV} = leg IV sensory organ
sr = seminal receptacle
tc = tertiary clava

Results

Phylum Tardigrada Doyère, 1840
Class Heterotardigrada Marcus, 1927
Order Arthrotardigrada Marcus, 1927

Family Styraconyxidae Kristensen & Renaud-Mornant, 1983 (emended by Fujimoto *et al.* 2017)

Genus *Angursa* Pollock, 1979

Emended diagnosis

Styraconyxidae with slender body; median cirrus present; papillate primary clavae; flat secondary and tertiary clavae; leg I sensory organs present; legs II and III sensory organs occasionally present; leg IV sensory organs papillate; cirri E near caudal margin of body; each digit terminates in claw with two divergent points; peduncles present at base of external digits; seminal receptacles present; terminal positioned anus occasionally with anal papillae.

Angursa bicuspis Pollock, 1979

Fig. 1

Emended diagnosis

Angursa with presence of median cirrus uncertain; primary clavae longer than lateral cirri; pedestals of primary clavae and lateral cirri absent; morphology of secondary and tertiary clavae unknown; simple, tapering cirri E present; leg I sensory organs present; presence of legs II and III sensory organs uncertain; leg IV sensory organs each as papilla with short, apical spine; robust anal papillae present; presence of seminal receptacles uncertain; presence of proximal pads of internal digits uncertain.

Material examined

Holotype

UNITED STATES OF AMERICA • 1 adult; Massachusetts, Buzzard Bay side of Penzance Point, Woods Hole; 41°31'41" N, 70°40'41" W; 9 Jul. 1968; Hummon & Pollock leg.; USNM W 50900.

Remarks

Angursa bicuspis was described based on the holotype and an additional specimen (Pollock 1979). However, their conspecificity has been doubted by Kaczmarek *et al.* (2015) owing to the fact that the two specimens were collected from two different environments of distant localities and that they showed morphological differences (Pollock 1979). As there is no positive evidence to regard the two specimens as conspecific, we support the opinion of Kaczmarek *et al.* (2015) and consider it as sufficient to base our attempt to re-diagnose *A. bicuspis* on only the holotype.

The holotype is in bad condition. However, our observation confirmed that of Pollock (1979) in the overall body shape (Fig. 1A) and the presence of the internal cirri (Fig. 1B), the external cirri (which is

8 μm , not 5.5 μm as reported by Pollock 1979) (Fig. 1B), the lateral cirri, the primary clavae (Fig. 1B), the leg I sensory organs, the cirri E, the characteristic claws, and the two papillae posterior to the anus (Fig. 1C). Pollock (1979) considered the latter structure as not useful for distinguishing species referring to the variability of the caudal projection of *Batillipes* Richters, 1909 and the fact that it was not observed in the additional specimen. Villora-Moreno (1998) supported this view, but Noda (1985) and Bussau (1992) used this structure to distinguish this species from its congeners (reason not explained). We agree with Noda (1985) and Bussau (1992) for the following two reasons. Firstly, we consider that this character is not homologous to the caudal projection of *Batillipes* as Pollock (1979) suggested, but a developed form of the cuticular fold that closes the anus, homologous to the “two weak protuberances” of *A. antarctica* described by Villora-Moreno (1998). Secondly, as discussed in the previous paragraph, this character’s presence/absence in the two specimens of Pollock (1979) is likely an interspecific variation. Thus, *A. bicuspis* can be easily distinguished from its congeners by the presence of the well-developed anal papillae (Renaud-Mornant 1981; Noda 1985; Bussau 1992; Villora-Moreno 1998), consequently supporting the species status of *A. abyssalis* proposed by Bussau (1992).

In addition to confirming and re-interpreting the original observation (Pollock 1979), we recognize three overlooked characters: a paired globular body fringing the mouth (Fig. 1B), the leg IV sensory organs and the peduncles (3 μm) that do not reach the claws (Fig. 1D). Each leg IV sensory organ consists of a spherical papilla and a short, apical spine (Fig. 1C). An enveloping cuticular sheath of the papilla was not evident, but may have been obscured due to the squeezed state of the specimen. The bad condition of the specimen also hindered our decisions on the presence/absence of the median cirrus, the secondary and tertiary clavae, legs II and III sensory organs, proximal pads of the internal digits and the seminal

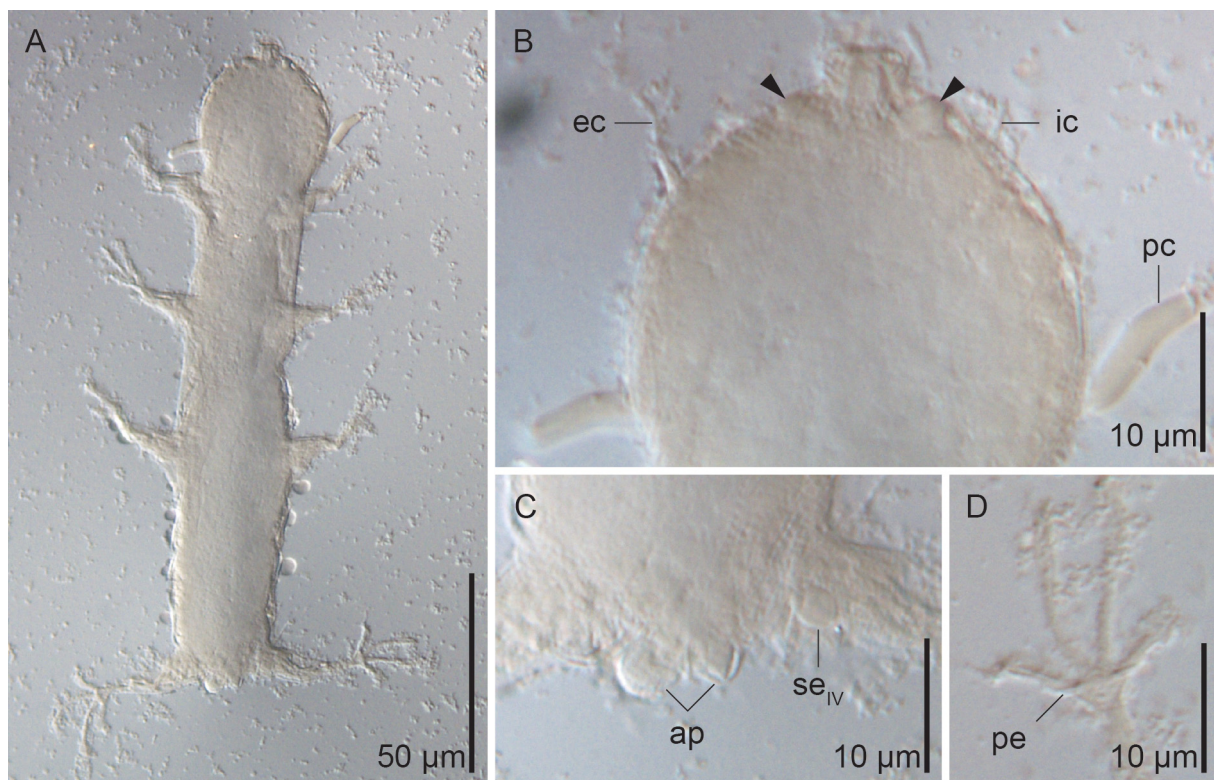


Fig. 1. Micrographs of *Angursa bicuspis* Pollock, 1979 (USNM W 50900). **A.** Habitus. **B.** Cephalic region with paired globular bodies (black arrowheads). **C.** Caudal region. **D.** Leg IV digits.

receptacles. Additional collection of specimens from the type locality is necessary for more detailed discussion on this species morphology.

Angursa abyssalis Renaud-Mornant, 1981

Figs 2–3

Emended diagnosis

Angursa with club-shaped primary clavae longer than lateral cirri; pedestals of primary clavae and lateral cirri absent; flat, distorted-oval secondary clavae; flat, oval tertiary clavae slightly indented near external cirri; tapering cirri E with basal scapi; leg I sensory organs present; legs II and III sensory organs absent; leg IV sensory organs each as papilla enveloped in hemispherical cuticular sheath with short, apical spine; anal papillae absent.

Material examined

Holotype

ATLANTIC OCEAN • adult ♀; Southeast Atlantic, collected from off Angola; 2063 m deep site; 12°03'3 S, 12°20'5 E; Dinét leg.; MNHN AF05/77Ma.

Additional specimens

ATLANTIC OCEAN • 1 adult ♀; North Atlantic; 2205 m deep; Dinét & Vivier leg.; MNHN AP345/560Ma.

MEDITERRANEAN SEA • 1 adult; Cassidaigne Canyon; 460 m deep; Vitiello & Vivier leg.; MNHN AE120/78Ma.

Remarks

There were two primary purposes for the re-examination of this taxon. One purpose was to identify the secondary and tertiary clavae, which were not reported in the original description (Renaud-Mornant 1981). The second purpose was to accurately understand the morphology of the leg IV sensory organs, which was described as hemispherical papillae in the text, but drawn as elongate papillae in the figure of the original description (Renaud-Mornant 1981).

Unfortunately, the secondary and tertiary clavae were not recognised in the holotype, MNHN AF05/77Ma. However, they were evident in the additional specimen, MNHN AP345/560Ma. In this specimen, the paired secondary clavae were positioned in the dorsal area between the median cirrus and

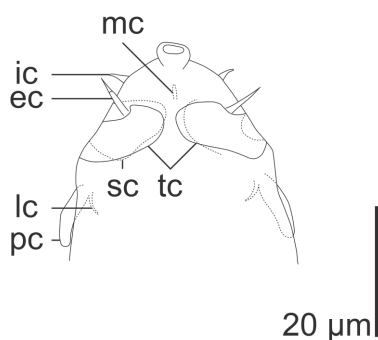


Fig. 2. Drawing of *Angursa abyssalis* Renaud-Mornant, 1981, cephalic region (ventral view) (USNM W 50900).

the primary clavae and each was in the form of a flat, distorted-oval lobe (the complete contour was not recognisable) (Figs 2, 3A). The paired tertiary clavae were position ventrally, immediately posterior to the external cirri and each was in the form of a flat, transversally-elongated lobe with a slight indentation where the external cirrus arises (Figs 2, 3B). In the other additional specimen, MNHN AE120/78Ma, the secondary clavae were not recognised, but a paired structure indicative of clavae (tertiary clavae?) was observed in the latero-ventral position of the cephalic region (Fig. 3C). Further, a paired globular body fringing the mouth was recognised (Fig. 3D).

The leg IV sensory organs were recognised in all three specimens. The holotype and MNHN AP345/560Ma had leg IV sensory organs consisting of papillae enveloped in hemispherical cuticular sheaths with short, apical spines (Fig. 3E) similar to that described in the text of the original description (Renaud-Mornant 1981). On the other hand, the leg IV sensory organs of MNHN AE120/78Ma lacked the enveloping cuticular sheaths and the papillae appeared slightly elongate and also constricted at the base (Fig. 3F) as in fig. 1A of Renaud-Mornant (1981). Further, it is clear that fig. 1C of Renaud-Mornant (1981) is based on MNHN AE120/78Ma (Fig. 3F).

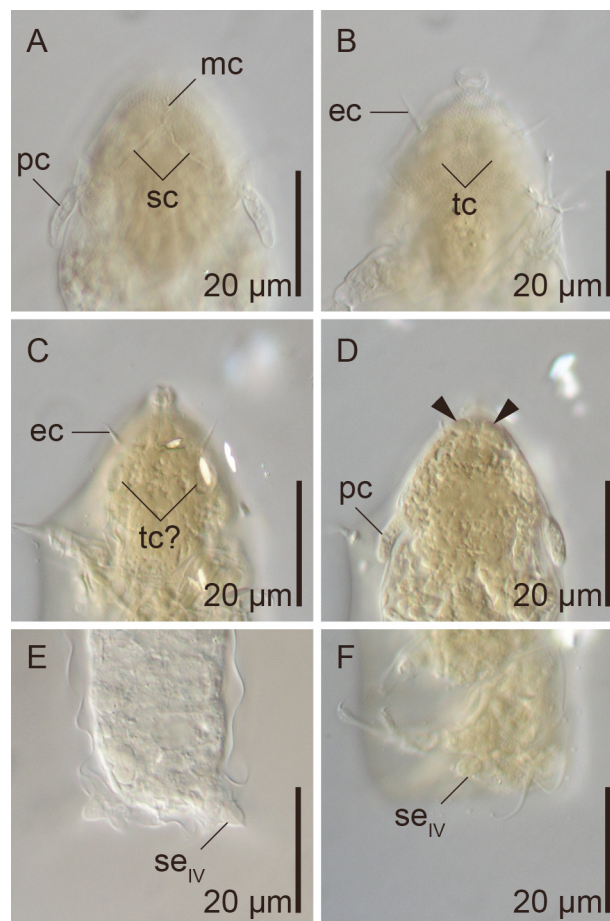


Fig. 3. Micrographs of specimens observed by Renaud-Mornant (1981) to describe *Angursa abyssalis* Renaud-Mornant, 1981 (A–B, E) and of *Angursa* sp. (C–D, F) by the present authors. **A.** Cephalic region (dorsal view) (MNHN AP345/560Ma). **B.** Cephalic region (ventral view) (MNHN AP345/560Ma). **C.** Cephalic region (ventral view) (MNHN AE120/78Ma). **D.** Cephalic region with paired globular bodies (black arrowhead) (MNHN AE120/78Ma). **E.** Leg IV sensory organs (MNHN AF05/77Ma). **F.** Leg IV sensory organ (MNHN AE120/78Ma).

Other morphological characters of the three specimens confirm the original description (Renaud-Mornant 1981) except that a scapus was observed in one of the external cirri of the MNHN AP345/560Ma (Fig. 2). Here we provide measurements of the holotype missing in the original description: internal cirrus, 3 μm ; external cirrus, 6 μm ; primary clava, 10 μm ; leg IV sensory organ, 5 μm long and 3 μm in diameter.

Our re-examination reveals that the term “balloon-shaped” used by Bussau (1992) and Villora-Moreno (1998) (probably based on the figure in the original description of Renaud-Mornant 1981) to describe the sensory organs of leg IV of *A. abyssalis* is inadequate since those of the holotype and MNHN AP345/560Ma had a hemispherical appearance. Further, we consider MNHN AE120/78Ma with “balloon-shaped” leg IV sensory organs (in the sense of Bussau 1992 and Villora-Moreno 1998) as an undescribed species. The difference in the morphology of the tertiary clavae also supports this view. However, MNHN AE120/78Ma is not in an acceptable condition for species description.

Based on the observation of the holotype and MNHN AP345/560Ma, *Angursa abyssalis* resembles *A. clavifera* and *A. capsula* by the club-shaped primary clavae longer than the lateral cirri, the leg IV sensory organs in hemispherical shape, and the lack of the anal papillae (Noda 1985; Bussau 1992). However, it differs from *A. clavifera* by the larger secondary clavae, the tertiary clavae slightly indented around the external cirri, and the absence of sensory organs on legs II and III (Noda 1985). It differs from *A. capsula* by the larger and closer situated pair of secondary clavae (3 μm apart in MNHN AP345/560Ma and 9 μm apart in *A. capsula* measured from the drawing of a paratype female in the original description see Bussau 1992), the tertiary clavae slightly indented around the external cirri (Bussau 1992) and a much shorter cirrus E (10 μm (body length, 141 μm) in *A. abyssalis* versus 19 μm (170 μm) in *A. capsula*).

Angursa lanceolata Renaud-Mornant, 1981

Fig. 4

Emended diagnosis

Angursa with bulbous primary clavae terminating in apices shorter than lateral cirri; pedestals of primary clavae and lateral cirri present; flat secondary clavae present; morphology of tertiary clavae unknown; lance-like cirri E; Leg I sensory organs present; legs II and III sensory organs absent; leg IV sensory organs each as elongate papilla with short apical spine; anal papillae absent.

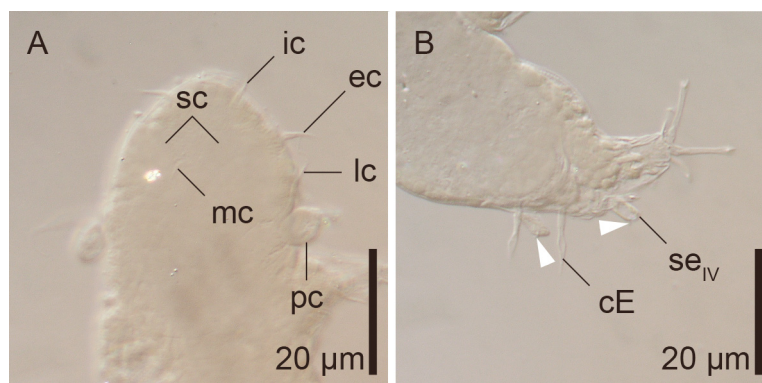


Fig. 4. Micrographs of *Angursa lanceolata* Renaud-Mornant, 1981 paratype. **A.** Cephalic region. **B.** Caudal region with leg IV sensory organ terminating in short, apical spine (white arrowheads).

Material examined

Paratype

ATLANTIC OCEAN • 1 adult; mounted with the dried out holotype; Dinet leg.; AE128.

Remarks

The primary clavae were described as leaf-shaped by Renaud-Mornant (1981), but the primary clavae of the paratype we observed were bulbous papillae (8 μm long, 6 μm in diameter) with blunt apices (the apex were only recognised in one of the clavae) (Fig. 4A). Their neighbouring sensory organs, the lateral cirri (17 μm) (Fig. 4A), were apparently longer than reported in the original description (11 μm) (Renaud-Mornant 1981). As it was drawn in the original description, the pedestals that support the primary clavae and the lateral cirri were apparent (Fig. 4A). We recognised the flat secondary clavae (Fig. 4A) which had already been mentioned as slightly hollow formations by Renaud-Mornant (1981), but their contours were difficult to observe. The presence and morphology of the tertiary clavae could not be revealed in this study. The characteristic cirri E (Fig. 4B) were confirmed, but their proportion seem slightly different that the drawing provided by Renaud-Mornant (1981). We recognised the short, apical spines of the leg IV sensory organs (Fig. 4B) which were overlooked in the original description (Renaud-Mornant 1981). Other measurements of the paratype are as follows: body length, 136 μm ; median cirrus, 3 μm ; internal cirrus, 6 μm ; external cirrus, 6 μm ; cirrus E, 11 μm ; leg I sensory organ, 6 μm ; leg IV sensory organ, 5 μm .

Angursa lanceolata closely resembles *A. lingua* by the bulbous primary clavae shorter than the lateral cirri, the apparent pedestals that support these two sensory organs, and the elongate leg IV sensory organs with apical spines (Renaud-Mornant 1981; Bussau 1992). However, these two species are easily distinguished from each other by the longer cephalic cirri and cirri E in *A. lingua* (median cirrus, 10 μm ; internal cirrus, 9 μm ; external cirrus 13 μm ; lateral cirrus 28 μm ; cirrus E, 20 μm (body length, 145 μm)) and by the lance-shaped cirri E in *A. lanceolata* versus tongue-shaped cirri E in *A. lingua* (Renaud-Mornant 1981; Bussau 1992).

Angursa capsula Bussau, 1992

Fig. 5

Material examined

All three specimens were collected from a manganese nodule area off Peru, but it is not clear whether the paratypes observed in this study were collected with the holotype or at a nearby site on a different day since the museum catalogue numbers were not mentioned in the original description (Bussau 1992).

Holotype

PACIFIC OCEAN • adult ♀; tropical SE Pacific, Peru Basin, collected from a manganese nodule area off Peru, 4140–4170 m deep; 07°03'84" S, 88°28'15" W; 17 Feb. 1989; SMF 28.

Paratypes

PACIFIC OCEAN • 2 specimens collected from a manganese nodule area off Peru; SMF 29, SMF 30.

Remarks

The re-examination of the type material revealed the presence of the paired globular body fringing the mouth in the holotype (Fig. 5A), the shallow bases of the primary clavae and the lateral cirri which we do not regard as pedestals, and the morphology of the leg IV sensory organs (Fig. 5B) to be not significantly different from those of *A. abyssalis* and *A. clavifera* (Renaud-Mornant 1981; Noda 1985). The third point is especially important as its “capsule-shaped” leg IV sensory organ has been the primary

diagnostic character for this species (Bussau 1992). The secondary and tertiary clavae were now very difficult to observe in the holotype. They were observed in SMF 29, but their complete contours were difficult to recognize.

Angursa lingua Bussau, 1992

Material examined

Out of the 19 specimens designated as type material (Bussau 1992), paratypes SMF 34, SMF 38, SMF 39, SMF 42, and SMF 43 were observed. However, the mounting media were dried out in SMF 34, SMF 38, SMF 39 and SMF 42. Due to the same problem discussed for *A. capsula*, the collection locality of each specimen is not clear.

Remarks

No new information was obtained from the detailed observation of SMF 43.

Angursa antarctica Villora-Moreno, 1998

Emended diagnosis

Angursa with bulbous primary clavae shorter than lateral cirri; pedestals of primary clavae and lateral cirri absent; morphology of secondary clavae unknown; flat tertiary clavae around external cirri; tapering cirri E with annulated scapi situated on short cirrophores; leg I sensory organs present; legs II and III sensory organs absent; leg IV sensory organs each as papilla enveloped in hemispherical cuticular sheath with short, apical spine; weak anal papillae present.

Remarks

We amend the diagnosis of *A. antarctica* to include the information on the anal papillae noted in the original description (Villora-Moreno 1998) as well as the common pedestals of the primary clavae and

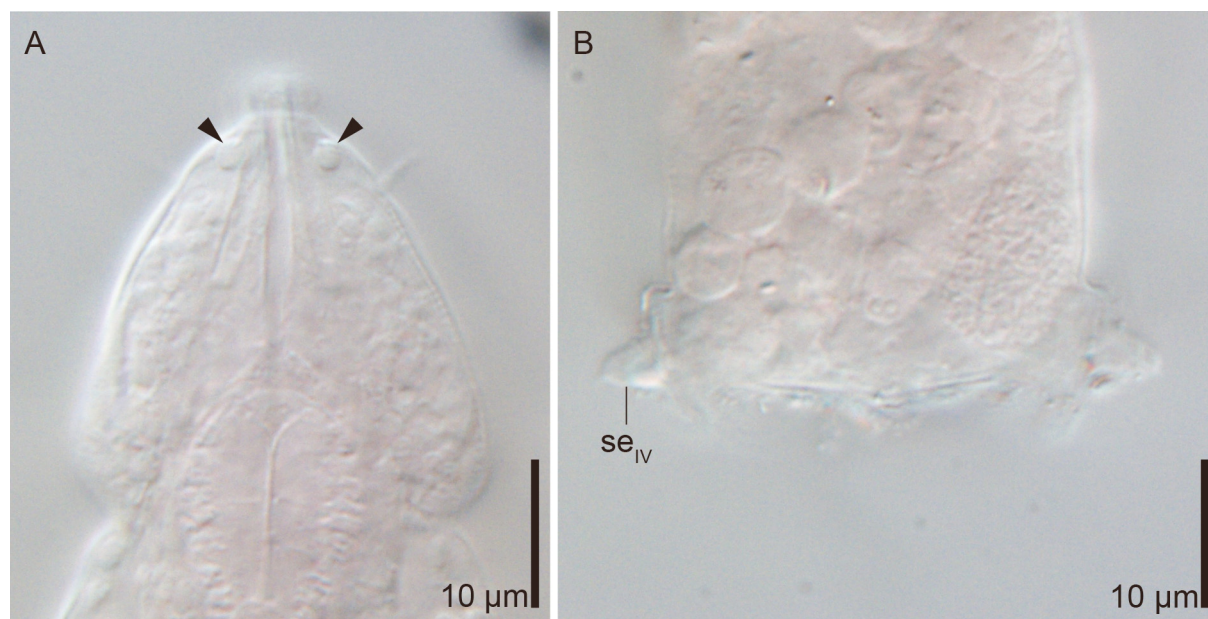


Fig. 5. Micrographs of *Angursa capsula* Bussau, 1992 (SMF 28). **A.** Cephalic region with paired globular bodies (black arrowheads). **B.** Caudal region.

the lateral cirri that Villora-Moreno (1998) considered as a distinguishing character but did not include in the diagnosis of *A. antarctica*. Furthermore, Villora-Moreno (1998) reported the presence of the secondary clavae around the external cirri. As the external cirri are positioned ventrally, we believe that the clavae Villora-Moreno (1998) observed should be referred to as tertiary clavae which are always positioned ventrally in the genus.

Angursa seisuimaruae sp. nov.

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Figs 6–7

Angursa sp. – Kimura *et al.* 2018: table 23.

Diagnosis

Angursa with club-shaped primary clavae longer than lateral cirri; pedestals of primary clavae and lateral cirri absent; D-shaped secondary clavae; three-lobed tertiary clavae; leg I sensory organs as subdivided spines; legs II and III sensory organs absent; leg IV sensory organs each as papilla enveloped in hemispherical cuticular sheath with short, apical spine; anal papillae absent; seminal receptacles open latero-ventrally with short, sinuous ducts.

Etymology

The specific epithet refers to the T/V *Seisuimaru* of Mie University.

Type material

Holotype

PACIFIC OCEAN • adult ♀; Northwestern Pacific, Japan, Sea of Kumano; between 33°59.5' N, 136°56.7' E and 33°59.7' N, 136°56.7' E; 768–796 m below sea level; 10 Nov. 2017; mounted in glycerol; Fujimoto leg.; KUZ Z2066.

Paratype

PACIFIC OCEAN • 1 adult ♀; same data as for holotype; KUZ Z2067.

Type locality

Sea of Kumano, Northwestern Pacific (between 33°59.5' N, 136°56.7' E and 33°59.7' N, 136°56.7' E; depth range, 768–796 m) (Kimura *et al.* 2018).

Description of holotype

Adult female with unarmoured, slender body (143 µm long; 35 µm wide between legs II and III) (Figs 6, 7A). Epicuticular pillars visible.

Cephalic region with unpaired median cirrus, paired internal cirri, paired external cirri, paired lateral cirri, paired primary clavae, paired secondary clavae, paired tertiary clavae, and mouth opening. Median cirrus (1 µm) positioned dorsally. Internal cirri (5 µm) inserted on anterior margin of body each consisting of scapus (2 µm) and distal flagellar part with blunt tip (2 µm). External cirri (9 µm) inserted ventrally each consisting of scapus (5 µm) and distal flagellar part with blunt tip (5 µm). Lateral cirri (4 µm) positioned dorso-laterally. Primary clavae (10 µm) positioned immediately ventral to lateral cirri and both organs inserted directly on body with no apparent pedestal (only very slight rise). Primary clavae club-shaped and distal half slightly bent posteriorly. Secondary clavae (Figs 6, 7B) present posterior to median cirrus as flat, D-shaped structures without epicuticular pillars. Tertiary clavae (Figs 6, 7C) indented around external cirri, giving impression of three-lobed structures (one lobe directed anteriorly,

interior to external cirri; second lobe developed interior to first lobe; third lobe developed posterior to external cirri) without epicuticular pillars. Anteriorly directed mouth at antero-most position of body. Buccal apparatus dissolved and only pharyngeal bulb recognised (length 14 μm , width 11 μm).

Paired cirri E (18 μm) (Figs 6, 7D) as simple, tapering spines without recognisable annulation, inserted dorsally slightly anterior to leg IV.

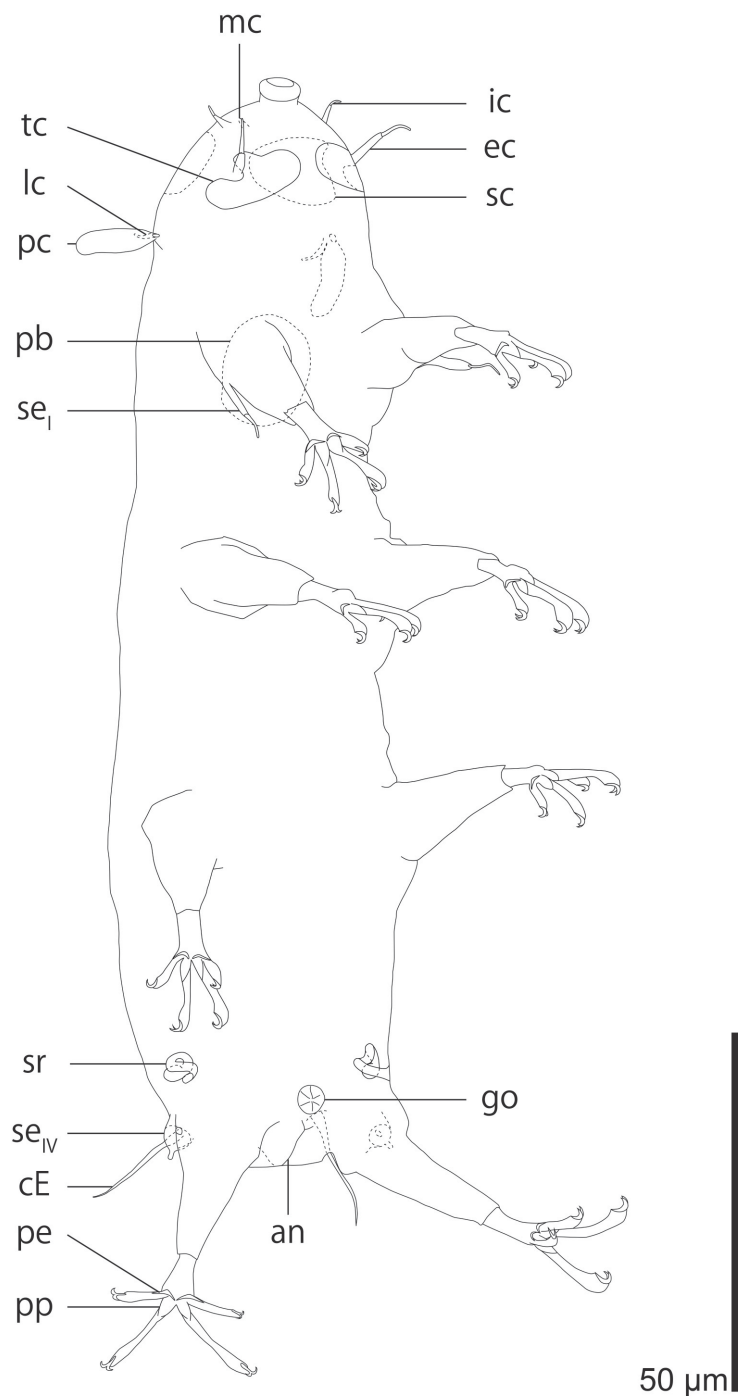


Fig. 6. Drawing of *Angursa seisuimaruae* sp. nov. (KUZ Z2066).

Each leg consists of indistinct coxa, femur, indistinct tibia, and tarsus bearing four digits terminating in claws with two divergent points. Leg I sensory organ (10 μm) (Figs 6, 7E) present on femur as spine consisting of proximal portion and distal portion with blunt tip. Legs II and III lack sensory organs. Leg IV sensory organs (4 μm) (Figs 6, 7D) present at base of leg IV each as papilla enveloped in hemispherical cuticular sheath with short, apical spine. Internal digits have proximal pads and lack peduncles (Figs 6, 7E). External digits have arched peduncles at their base which never reach claws (Figs 6, 7E). Internal digits always longer than external digits and leg IV has longer digits than those of legs I–III (leg I, internal digits 9 μm /external digits 6 μm ; leg II, 9/6; leg III, 10/6; leg IV, 13/7).

Rosette-like gonopore (4 μm in diameter) (Figs 6, 7F) situated 2 μm anterior to anus. Longitudinal cuticular fold of anus reach dorsal side (Figs 6, 7D). Paired seminal receptacles (Figs 6, 7F) positioned near latero-ventral margin of body, at level slightly anterior to gonopore. Each seminal receptacle duct runs interiorly, antero-dorsally, and then postero-ventrally terminating in round vesicle.

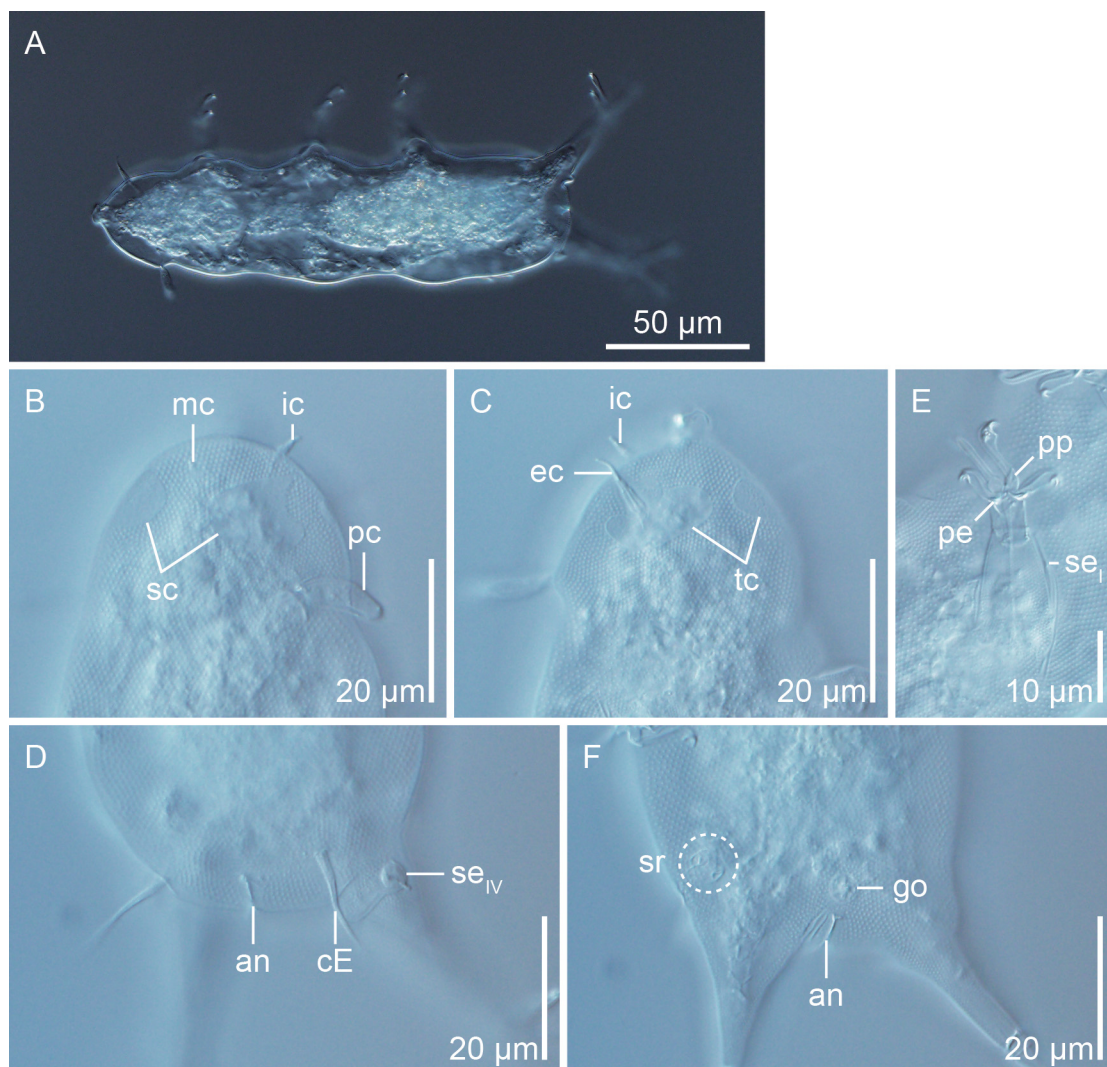


Fig. 7. Micrographs of *Angursa seisuimaruae* sp. nov. (KUZ Z2066). **A.** Habitus. **B.** Cephalic region (dorsal). **C.** Cephalic region (ventral). **D.** Caudal region (dorsal). **E.** Leg I. **F.** Caudal region (ventral).

Description of paratype

Cephalic region accidentally destroyed during cleaning of specimen before observation and mouth opening, buccal apparatus, median cirrus, secondary clavae, and tertiary clavae not recognized. Primary clava (11 µm) and scapi of internal, external, and lateral cirri recognized on torn cuticle. Presence of scapi suggests subdivision of lateral cirri as in the internal and external cirri. Gonopore and anus recognised before permanent preparation in lateral positioned body. Other characters confirm that of holotype (cirrus E, 17 µm; leg I sensory organ, 10 µm; leg IV sensory organ, 4 µm).

Remarks

Angursa seisuimaruae sp. nov. resembles *A. abyssalis*, *A. clavifera*, and *A. capsula* by the club-shaped primary clavae longer than the lateral cirri, the leg IV sensory organs in hemispherical shape, and the lack of the anal papillae (Renaud-Mornant 1981; Noda 1985; Bussau 1992). However, the new species is distinguished from all three species by its D-shaped secondary clavae and its three-lobed tertiary clavae (Noda 1985; Bussau 1992). Further, the new species's seminal receptacle ducts are shorter than *A. clavifera*'s spiral ones (Noda 1985).

Identification key to *Angursa* species

1. Club-shaped primary clavae longer than lateral cirri 2 (*A. bicuspis* group)
 - Bulbous primary clavae shorter than lateral cirri 6 (*A. lanceolata* group)
2. Well developed anal papillae *A. bicuspis* Pollock, 1979
 - Anal papillae absent 3
3. Legs II and III sensory organs present; spiral seminal receptacle ducts *A. clavifera* Noda, 1985
 - Leg II and III sensory organs absent 4
4. Three-lobed tertiary clavae; D-shaped secondary clavae; seminal receptacles present
 - *A. seisuimaruae* sp. nov.
 - Tertiary clavae with no indentation or only slightly indented around external cirri 5
5. Secondary clavae situated close together (ca 3 µm); short (10 µm) cirrus E
 - *A. abyssalis* Renaud-Mornant, 1981
 - Secondary clavae situated apart (ca 9 µm); long (19 µm) cirrus E *A. capsula* Bussau, 1992
6. Leg IV sensory organs as papillae enveloped in hemispherical sheaths; cirri E with annulated scapi *A. antarctica* Villora-Moreno, 1998
 - Leg IV sensory organs as elongate papillae 7
7. Cirri E lance-shaped *A. lanceolata* Renaud-Mornant, 1981
 - Cirri E tongue-shaped *A. lingua* Bussau, 1992

Discussion

Morphology

Based on our re-examination of material used in the previous descriptions of species of *Angursa*, we warranted the species status of *Angursa bicuspis* and *A. abyssalis*, rejecting the proposal by Villora-Moreno (1998) to consider the former species as a senior synonym of the latter. Therefore, the genus *Angursa* has eight described species including the new species: *A. abyssalis*, *A. antarctica*, *A. bicuspis* (type species), *A. capsula*, *A. clavifera*, *A. lanceolata*, *A. lingua*, and *A. seisuimaruae* sp. nov. (see

original description in Pollock 1979; Renaud-Mornant 1981; Noda 1985; Bussau 1992; Villora-Moreno 1998).

We confirm the emended diagnosis of *Angursa* by Bussau (1992) and recognize that all eight species have smooth, slender bodies with legs terminating in two internal digits with proximal pads and two external digits with peduncles, all four bearing claws with two divergent points (Renaud-Mornant 1981; Noda 1985; Bussau 1992; Villora-Moreno 1998) except for *A. bicuspis* with the proximal pads not reported in the original description (Pollock 1979) and not recognised in this study most probably due to the bad condition of the specimen (Fig. 1D). In addition to confirming the generic characters proposed by Bussau (1992), our new information on the secondary and tertiary clavae, seminal receptacles, and anal papillae discussed below were implemented in our amended generic diagnosis.

Previously, neither secondary nor tertiary clavae were reported in *A. abyssalis*, *A. bicuspis*, and *A. lanceolata* (Pollock 1979; Renaud-Mornant 1981) and the secondary clavae were not reported in *A. antarctica* (Villora-Moreno 1998; see also amended diagnosis provided in this study), but in this study, we recognised both clavae types in *A. abyssalis* (Figs 2, 3A–B) and the secondary clavae in *A. lanceolata* (Fig. 4A). Therefore *A. abyssalis*, *A. capsula*, *A. clavifera*, *A. lingua* and *A. seisuimaruae* sp. nov. (Noda 1985; Bussau 1992) have both clavae types, *A. antarctica* (tertiary clavae present) and *A. lanceolata* (secondary clavae present) have at least one of the types, whereas *A. bicuspis* is the only species with no report of the two clava types (Pollock 1979). Regarding this character distribution in the genus and our experience of the difficulty in observing these clavae after permanent preparation in *A. seisuimaruae* sp. nov. and the difficulty in re-observing them in *A. capsula*, we deem it likely that all *Angursa* species have both the secondary and tertiary clavae but overlooked in some species due to the condition of the specimen. Despite the difficulty in observation, the morphologies of these two clavae are useful to distinguish species and we recommend the description of their detailed morphologies (especially before permanent preparation in glycerol) when documenting species of *Angursa*.

The seminal receptacles of *A. clavifera* and *A. seisuimaruae* sp. nov. (Figs 6, 7F) exhibit interspecific variation (Noda 1985). Although this character is not always easy to observe, we assume its presence in the other congeners (so far unknown) and have included the seminal receptacles in the generic diagnosis. In the future, we expect this character to play an important role in identification of *Angursa* species.

We recognize the two papillae reported by Pollock (1979) for *A. bicuspis* as a taxonomic valid character and called them the anal papillae (Fig. 1C). Other than *A. bicuspis*, *A. antarctica* has a weakly developed pair (Villora-Moreno 1998; see also amended diagnosis for this species). We consider this character and the terminally positioned anus known in all species (Pollock 1979; Renaud-Mornant 1981; Noda 1985; Bussau 1992; Villora-Moreno 1998) characteristics of *Angursa* and have incorporated them in the generic diagnosis.

In addition to new information on morphological characters we deem as characteristic of *Angursa* and significant for distinguishing species, we observed a pair of globular bodies fringing the mouth in *A. bicuspis* (Fig. 1B), *Angursa* sp. (Fig. 3D), *A. capsula* (Fig. 5A). Despite its easily-spotted state in these three species, it was not recognised in the well-preserved holotype of *A. seisuimaruae* sp. nov. We consider this structure as a potential character that may be useful for species identification but more observation of specimens are necessary to understand its nature, e.g., intra- and inter-specific variations and function (might be similar to the small sensory organ surrounding the mouth cone in *Renaudarctus* Kristensen & Higgins, 1984; see Kristensen & Higgins 1984; Hansen *et al.* 2012), and to utilise in taxonomy. Interspecific variation was stated for the size of the peduncles by Villora-Moreno (1998), but we did not recognize any significance in this character based on literature (Renaud-Mornant 1981; Noda 1985; Bussau 1992; Villora-Moreno 1998) and our observation.

Our morphological comparison of species of *Angursa* also led us to recognize two morpho-groups in *Angursa*: the *A. bicuspis* group and the *A. lanceolata* group which might indicate two evolutionary lineages in the genus (implemented in the identification key). However, since these groups are detected solely on morphological data, molecular phylogenetic analyses are needed to test this hypothesis. The *A. bicuspis* group is comprised of *A. abyssalis*, *A. bicuspis*, *A. capsula*, *A. clavifera*, and *A. seisuimaruae* sp. nov. and shares the following character states: club-shaped primary clavae longer than lateral cirri with common pedestals weakly developed (Pollock 1979; Renaud-Mornant 1981; Noda 1985; Bussau 1992). The species of this group also have in common the simple, tapering cirri E and the leg IV sensory organs enveloped in hemispherical cuticular sheaths (the cuticular sheaths are not evident in *A. bicuspis*) (Pollock 1979; Renaud-Mornant 1981; Noda 1985; Bussau 1992). The *A. lanceolata* group is comprised of *A. lanceolata*, *A. lingua*, and *A. antarctica* and shares the following character states: bulbous primary clavae shorter than lateral cirri with apparent common pedestals (Renaud-Mornant 1981; Bussau 1992; Villora-Moreno 1998). *Angursa lanceolata* and *A. lingua* also have in common the cirri E with modified tips and the leg IV sensory organs as elongate papillae, in contrast to those of *A. antarctica* that resemble the *A. bicuspis* group (Renaud-Mornant 1981; Bussau 1992; Villora-Moreno 1998).

Biogeography

As a consequence of our re-examination including the reinstatement of *A. abyssalis*, the distribution records of both *A. bicuspis* and *A. abyssalis* need to be updated.

As revealed in the present study, the original diagnosis of *A. bicuspis* constitutes a combination of two different species. Therefore, only the holotype should be regarded as a valid record of *A. bicuspis* and the additional specimen from a 400 m deep site off the coast of North Carolina, USA as an unidentified species. All subsequent records of *A. bicuspis* (D'Addabbo Gallo *et al.* 1987; Grimaldi de Zio & D'Addabbo Gallo 1987; Accogli *et al.* 2011) are presumed records of *A. b. abyssalis* inferred from subsequent studies (De Zio Grimaldi & Gallo D'Addabbo 2001; Gallo D'Addabbo *et al.* 2001; De Zio Grimaldi *et al.* 2003) and from context (Accogli *et al.* 2011) and they will be discussed in the next paragraph.

Regarding *A. abyssalis* (reported as *A. b. abyssalis*), our re-examination of the three specimens from Renaud-Mornant (1981) revealed that only the holotype from a 2063 m deep site off Angola (MNHN AF05/77Ma) and the specimen from a 2205 m deep site in the North Atlantic (MNHN AP345/560Ma) are acceptable as *A. abyssalis* and that specimen from a 460 m deep site in the Mediterranean (MNHN AE120/78Ma) is an undescribed species. This was based on the change in the diagnostic morphology of the leg IV sensory organs. Confirmation of this morphology for all records is crucial for confidently identifying the re-diagnosed *A. abyssalis*. Unfortunately, no record after Renaud-Mornant (1981) mentioned the morphological detail of their "*A. b. abyssalis*" or "*A. bicuspis*" specimens (D'Addabbo Gallo *et al.* 1987; Grimaldi de Zio & D'Addabbo Gallo 1987; Sandulli *et al.* 1999; De Zio Grimaldi & Gallo D'Addabbo 2001; Gallo D'Addabbo *et al.* 2001; De Zio Grimaldi *et al.* 2003; Accogli *et al.* 2011; Romano *et al.* 2011) and we suggest these records as reports of unidentified species. Further, these reports are from two distant geographical regions, the Mediterranean (D'Addabbo Gallo *et al.* 1987; Grimaldi de Zio & D'Addabbo Gallo 1987; Sandulli *et al.* 1999; De Zio Grimaldi & Gallo D'Addabbo 2001; Gallo D'Addabbo *et al.* 2001; De Zio Grimaldi *et al.* 2003; Accogli *et al.* 2011) and the Gulf of Mexico (Romano *et al.* 2011), and we should consider the possibility of these records to include more than one species. It is also noteworthy that De Zio Grimaldi *et al.* (2003) notes "*A. b. abyssalis*" from Amendolara Shoal (D'Addabbo Gallo *et al.* 1987; Grimaldi de Zio & D'Addabbo Gallo 1987) is like *A. bicuspis* which might suggest multiple species from the Mediterranean including MNHN AE120/78Ma of Renaud-Mornant (1981).

A summary of the records with our new interpretation of *A. abyssalis* and *A. bicuspis* is provided as Fig. 8.

Other species of *Angursa*, *A. antarctica*, *A. capsula*, *A. lanceolata*, and *A. seisuimaruae* sp. nov. are known only near their type localities and their distributions do not cross any known dispersal barrier (Renaud-Mornant 1981; Bussau 1992; Villora-Moreno 1998). However, *A. clavifera* and *A. lingua* are also known from localities distant from their type localities (Noda 1985, 1994; Bussau 1992; Da Rocha *et al.* 2013; Okanishi *et al.* 2016). *Angursa clavifera* is known from a beach in the Ryukyu Islands (Noda 1994) far apart from other beaches in the Japanese Islands (type locality) (Noda 1985). Although the Japanese and Ryukyu Islands are both under the influence of a warm current, Kuroshio, they are known to harbour different species in some marine invertebrate genera (e.g., tideland snails: Kojima *et al.* 2003; limpets: Nakayama *et al.* 2017) and we consider this as a potential dispersal barrier for marine tardigrades, especially for those that favor the intertidal zone. Therefore, we think that the record of this species from the Ryukyu Islands (Noda 1994) is dubious. Considering the possibility of cryptic speciation, we would need molecular data in combination with detailed morphological examination

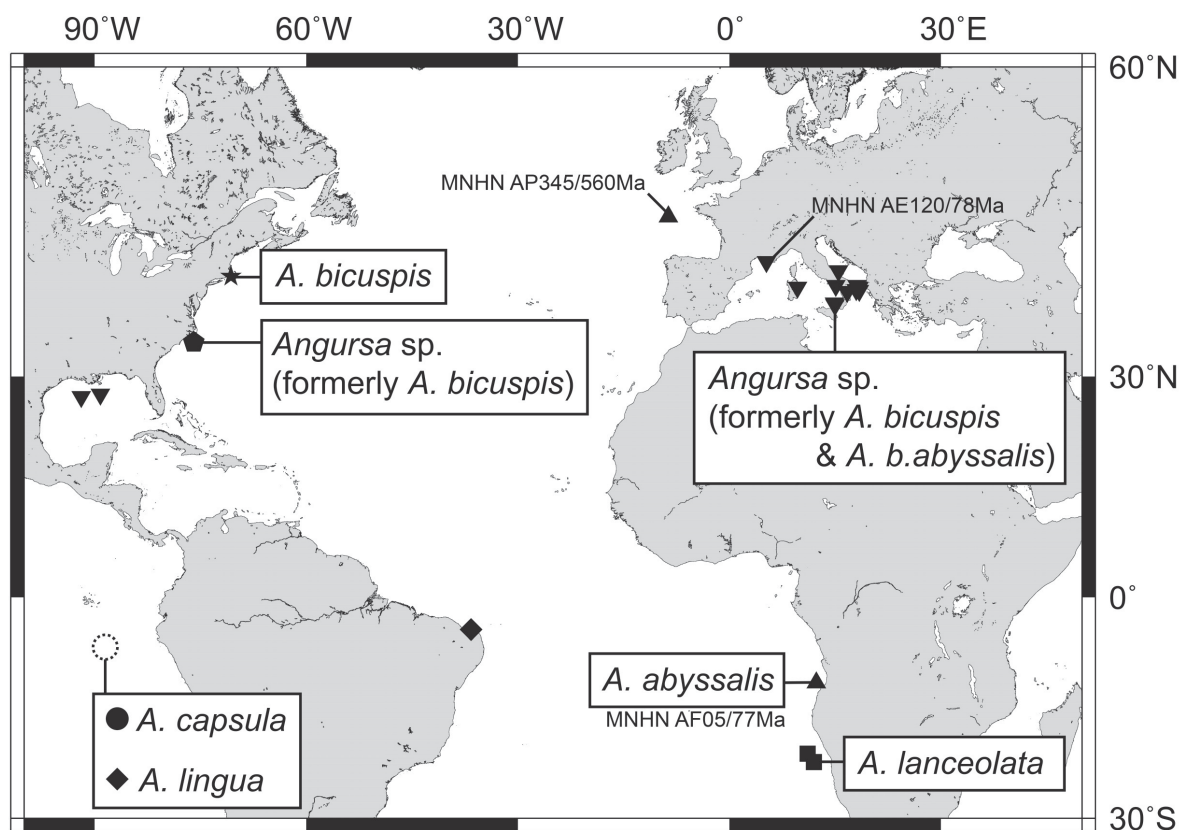


Fig. 8. Records of *Angursa abyssalis* Renaud-Mornant, 1981, *A. bicuspis* Pollock, 1979, and some other species. Three specimens originally identified as *A. b. abyssalis* (Renaud-Mornant 1981) are labelled with their museum catalogue number. Localities are based on the following literature summarized in Kaczmarek *et al.* (2015): Pollock (1979); Renaud-Mornant (1981); D’Addabbo Gallo *et al.* (1987); Grimaldi de Zio & D’Addabbo Gallo (1987); Bussau (1992); Sandulli *et al.* (1999); De Zio Grimaldi & Gallo D’Addabbo (2001); Gallo D’Addabbo *et al.* (2001); De Zio Grimaldi *et al.* (2003); Accogli *et al.* (2011), and Romano *et al.* (2011). The map was originally generated with GMT ver. 5.1.1 (Wessel *et al.* 2013).

to verify this hypothesis. Another record of this species is from a 175–177 m deep site off the coast of the type locality (Okanishi *et al.* 2016). According to the morphology reported (Okanishi *et al.* 2016), the specimen definitely belongs to the *A. bicuspis* group, but there is no positive evidence to support its species identity as *A. clavifera* and we regard this report as a record of an unidentified species. The reports of *A. lingua* from the Brazilian continental shelf (20 m and 100 m deep) (Da Rocha *et al.* 2013) has been suspected by Kaczmarek *et al.* (2015) since the species was originally described from Peruvian abyssal depths (4140–4170 m) (Bussau 1992). In addition to this ecological perspective, we would like to note that the two localities (Bussau 1992; Da Rocha *et al.* 2013) are intervened by the Panama Isthmus. This geological barrier is already known to restrict the gene flow of meiofauna (nemertean genus *Ototyphlonemertes* Diesing, 1863; Leasi *et al.* 2016) and we reckon the two populations have undergone cryptic speciation.

To improve our scanty knowledge of the biogeographical pattern of *Angursa*, we first need to accumulate reports with high standard identification, documenting as many characters as possible, especially the secondary and tertiary clavae and seminal receptacles which have received limited attention despite being crucial to the validity of species identification. At the same time, the use of molecular markers (at least the mitochondrial cytochrome oxidase subunit I) is inevitable to detect cryptic speciation and to understand the phylogenetic history of these animals in the geographic context.

Acknowledgements

The National Museum of Natural History of the Smithsonian Institute is thanked for the loan of the type material of *A. bicuspis*. The Senckenberg Natural History Museum, Frankfurt/Main, Germany is thanked for the loan of the type material of *A. lingua* and *A. capsula*. The authors also greatly appreciated the generous support from Tarek Meziane and Cédric Hubas, the Museum national d'Histoire naturelle, Paris, France who provided the type material of *A. abyssalis* and *A. lanceolata*. The captain and crew of the T/V *Seisuiamaru* of Mie University, Taeko Kimura of Mie University, and the scientists of the research cruise No. 1722 are warmly thanked for their assistance in collecting *A. seisuiamaruae* sp. nov. This work was funded by the Carlsberg Foundation (grant no. 2012 01 0127 and CF15-0189) and the European Commission's (FP6) Integrated Infrastructure Initiative Programme, SYNTHESYS to FR-TAF 2836 to JGH.

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Manuscript received: 13 November 2018

Manuscript accepted: 21 January 2019

Published on: 28 March 2019

Topic editor: Rudy Jocqué

Desk editor: Marianne Salaiün

Printed versions of all papers are also deposited in the libraries of the institutes that are members of the *EJT* consortium: Muséum national d’Histoire naturelle, Paris, France; Botanic Garden Meise, Belgium; Royal Museum for Central Africa, Tervuren, Belgium; Royal Belgian Institute of Natural Sciences, Brussels, Belgium; Natural History Museum of Denmark, Copenhagen, Denmark; Naturalis Biodiversity Center, Leiden, the Netherlands; Museo Nacional de Ciencias Naturales-CSIC, Madrid, Spain; Real Jardín Botánico de Madrid CSIC, Spain; Zoological Research Museum Alexander Koenig, Bonn, Germany.

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Band/Volume: [0510](#)

Autor(en)/Author(s): Fujimoto Shinta

Artikel/Article: [Revision of Angursa \(Arthrotardigrada: Styraconyxidae\) with the description of a new species from Japan 1-19](#)