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A new species of the deep-sea copepod genus *Scutogerulus* (Calanoida: Arietellidae) from the hyperbenthic waters of Okinawa, Japan

Abstract A new species of the rare arietellid genus *Scutogerulus* is described from deep hyperbenthic waters off Okinawa, southwestern Japan. This is the second species of the genus. Phylogenetically significant characteristics known only on the basis of the type species are confirmed by the discovery of the new congener, in particular: (1) the genital system of the female exhibits the most plesiomorphic condition of any arietellid genus; (2) the well developed setae on the endopodal segments of the maxillae and maxillipeds are modified into 'shield-like setae' similar to the 'button setae' in another arietelloidean family, the Augaptilidae; (3) the outer distal spine on the first exopodal segment of leg 1 is absent.

Key words Hyperbenthic, Crustacea, Copepoda, Calanoida, marine plankton

Introduction

The oceans cover 71% of the Earth's surface to an average depth of 3.7 km and the fauna of this vast pelagic biome, the largest on the planet, is dominated by the copepod crustaceans. At its base, between the pelagic and the surface of the sea bed is a transition zone, the hyperbenthic. It is relatively difficult to sample, especially in deep waters, and the inhabitants of the hyperbenthic zone are poorly known. During a faunistic survey of the hyperbenthic copepods around Okinawa, southwestern Japan, a new species of the rare arietellid genus Scutogerulus was discovered from Japanese waters. Arietellids are a basal family within the Calanoida and this is only the second species of the genus. The type species S. pelophilus Bradford, 1969 was collected from the hyperbenthic waters of the New Zealand slope (Bradford, 1969). The male of S. pelophilus described by Bradford (1969) was assigned to a different monotypic genus, Campaneria Ohtsuka, Boxshall & Roe, 1994 (Ohtsuka et al., 1994), as already suggested in Bradford's original description. The female genital system of Scutogerulus was interpreted as the most plesiomorphic condition found in all the arietellid genera (Ohtsuka et al., 1994). In contrast the genus also bears specialised structures on setae of the maxillae and maxillipeds, which were referred to as 'shield-shaped appendages' by Bradford (1969).

The hyperbenthic calanoid copepods of the subtropical waters of Japan seem to be highly diversified. A new species of the enigmatic clausocalanoidean genus *Neoscolecithrix* has

recently been recorded from off Okinawa, in addition to common hyperbenthic members of the families Pseudocyclopidae, Ridgewayiidae, Arietellidae, Pseudodiaptomidae, Phaennidae, Scolecitrichidae, Tharybidae and Aetideidae (Barthélémy *et al.*, 1998; Ohtsuka *et al.*, 1991, 1994, 1996, 2002, 2003; Walter *et al.*, 2002; Ohtsuka, unpublished data). The present paper describes the new species of *Scutogerulus* using both light and scanning electron microscopy.

Materials and methods

The copepods were collected from hyperbenthic waters off Kuroshima Island, Okinawa, southwestern Japan (26° 19.18'N, 127° 25.56'E) at a depth of 596–606 m, on 24 May 2003, using a NORPAC plankton net (mesh size: 0.33 mm) attached to the mouth of a beam trawl. These were fixed in 10% neutralized formalin/sea-water immediately after capture, and transferred into 70% ethanol. Dissected appendages were mounted on glass slides in CMC-10 mounting media (Masters Company, Inc.). All drawings were made with the aid of a camera lucida attached to a differential interference microscope (Nikon Optiphoto). One female of the new species was observed with a scanning electron microscope (Jeol T-20).

Terminology follows Huys & Boxshall (1991). Type specimens are deposited at the Natural History Museum, London (BMNH), and at the Kitakyushu Museum of Natural History and Human History, Kokura (KMNH).



Figure 1 Scutogerulus boettgerschnackae n. sp., female, holotype. A. Habitus, dorsal view; B. Habitus, lateral view; C. Posterior margin of prosome and genital double-somite, lateral view; D. Rostrum; E. Urosome and posterior margin of prosome, dorsal view; F. Genital double-somite, ventral view, gonopore (indicated by large arrowhead) and copulatory pore (by small arrowhead); G. Genital system, gonopore (indicated by large arrowhead) and copulatory pore (by small arrowhead); G. Genital system, posterior row of setules missing; I. Antennule 17th (XIX) to 23rd (XXVI–XXVIII) segments; J. Posterior row of setules on first three segments; K. Last two antennulary segments (XXIV–XXV and XXVI–XXVIII).

Systematics

Family Arietellidae Sars, 1902 Genus *Scutogerulus* Bradford, 1969

Scutogerulus boettgerschnackae n. sp. (Figs 1-4)

Material examined. 6Q, near bottom off Kuroshima Island, Okinawa, southwestern Japan (26°19.18′N, 127°25.56′E; 596– 606 m depth), 24 May 2003. Collector: S. Ohtsuka.

Types. Holotype: 1^Q, partly dissected and appendages mounted on glass slides, body in vial, BMNH 2003.964. Paratypes: 1 \circ , partly dissected and appendages mounted on glass slides, body in vial, BMNH 2003.965; 2 \circ \circ , whole specimens, BMNH 2003.966-967; 2 \circ \circ , whole specimens, KMNH IvR 500,101 and 500,102.

Body length. Holotype 3.01 mm; paratypes 2.79, 2.84, 2.90, 2.90, 2.93 mm.

Description

Female

Body (Fig. 1A, B) compact, with postero-lateral angles of prosome ends produced into round processes reaching beyond



Figure 2 SEM micrographs of *Scutogerulus boettgerschnackae* n. sp., female. A. Genital double-somite, ventral view, gonopores and copulatory pore indicated large and small arrows, respectively, left side damaged; B. Right gonopore (indicated by large arrow) and copulatory pore (by small arrow); C. Left leg 5, anterior surface, vestigial exopod (?) indicated by arrow; D–G. 'Shield setae' on maxillary endopod. Scales: 0.1 mm (A); 0.01 mm (B, D); 0.02 mm (C); 0.002 mm (E–G).

middle of genital double-somite (Fig. 1C); prosome 2.5 times longer than urosome; cephalosome incompletely fused to first pediger; rostrum (Fig. 1D) relatively wide, with paired filaments at tip; second and third pedigers each produced posteroventrolaterally into round projection; fourth and fifth pedigers completely coalescent. Urosome (Fig. 1A, E) 4-segmented; genital double-somite swollen laterally at midlength; genital system paired and symmetrically arranged (Fig. 1F, G); gonopore and copulatory pore sharing common slit (see Fig. 2A, B), located anteriorly and posteriorly, respectively; seminal receptacle compact (Fig. 1F, G); second urosomite nearly as long as third; caudal rami symmetrical, inner margins ornamented with fine setules; minute seta I located anterolaterally; seta V longest; seta VII originating dorsally from inner distal corner.

Antennule (Fig. 1H-K) indistinctly 23-segmented, extending to distal margin of third urosomite (Fig. 1B); first

to 12th (XIV) segments each with long setules along posterior margin (Fig. 1J; all missing in Fig. 1H). Fusion pattern and armature elements as follows (compiled from both antennules): I-III = 7 + 2 ae, IV = 2, V = 2 + ae, VI = 2, VII = 2 + aeae, VIII = 2, IX = 2 + ae, X = 2(1 spiniform) + ae, XI - XII = 4 + ae2 ae (ae on XII rudimentary), XIII = 2 + ae, XIV-XV = 4 +2 ae, XVI = 2 + ae, XVII = 2 + ae, XVIII = 2 + ae, XIX = 2 + ae, XIXae, XX = 2 + ae, XXI = 2 + ae, XXII = 1, XXIII = 1, XXIV - aeXXV = 2 + 2 + ae, XXVI - XXVII = 8 + ae. Antenna (Fig. 3A, B) with 2-segmented endopod and indistinctly 9segmented exopod; setal formula of exopod 0, 0, 1, 1, 1, 1, 1, 0, 3; proximal endopodal segment unarmed, distal segment with 2 unequal setae subterminally (representing armature of second endopodal segment) and 5 setae terminally. Mandibular cutting edge (Fig. 3C) with 1 mono-, 1 bi- and 1 tri-cuspidate teeth and 2 patches of short spinules. Mandibular



Figure 3 Scutogerulus boettgerschnackae n. sp., female, holotype. A. Antenna; B. Antennary exopod; C. Mandibular cutting edge; D. Mandibular palp; E. Maxillule; F. Maxillulary basis and endopod (vestigial seta on basis arrowed); G. Maxilla; H. Basal spine of maxilla; I. Maxilliped (with setae a and b labelled); J. Seta of maxillipedal endopod with modified 'shield-shaped' setules; K. Two apostome phoronts (?) on maxillipedal setae.

palp (Fig. 3D) with basis bearing row of setules; endopod rudimentary, 1-segmented, with 2 unequal setae terminally; exopod 5-segmented, setal formula 1, 1, 1, 1, 2. Maxillule (Fig. 3E, F) with praecoxal arthrite bearing 1 short process, 4 spinulose spines and row of fine setules; coxal epipodite with 6 setae; coxal endite with 1 long spinulose seta; basis bearing 1 vestigial element (see Fig. 3F, arrowed) and 2 rows of fine setules; endopod bulbous, with 1 short, spinulose seta terminally; exopod lamellar, with 3 long, plumose setae at tip. Maxilla (Fig. 3G) relatively delicate in comparison to those of other arietellids; first praecoxal endite with 1 spinulose seta and rudimentary element; second praecoxal endite with single seta; first and second coxal endites each with 2 spinulose setae; basis bearing stout, spinulose spine (Fig. 3H); endopod 4-segmented, setal formula 1, 3, 2, 2; all endopodal setae ornamented with row of modified 'shield-like' setules (see Fig. 2D–G). Maxilliped (Fig. 3I) with syncoxa bearing 3 spinulose setae subterminally; basis with 2 spinulose setae and dense patch of short spinules; first endopodal segment incompletely incorporated into basis, with 1 spinulose seta; second to sixth endopodal segments with setation 4, 4, 3, 3, 4, including 1, 1, 2, 2, 2 shield-like setae (Fig. 3J), respectively; setae 'a' and'b' (see Ohtsuka *et al.*, 1994) rudimentary.



Figure 4 *Scutogerulus boettgerschnackae* n. sp., female, holotype. A. Leg 1, anterior; B. Leg 2, anterior; C. Leg 3, anterior; D. Leg 4, posterior; E. Right leg 5 and intercoxal sclerite, anterior (arrowhead showing putative vestigial exopod); F. Left leg 5, posterior.

Seta and spine formula of legs 1 to 4 (Fig. 4A–D) as follows:

	Coxa	Basis	Exopod	Endopod
			1 2 3	
Leg 1	0-1	0-1	0-1; I-1; I, I, 4	0-1; 0-2; 2, 2, 1
Leg 2	0-1	0-0	I-1; I-1; III, I, 5	0-1; 0-2; 2, 2, 4
Leg 3	0-1	0-0	I-1; I-1; III, I, 5	0-1; 0-2; 2, 2, 4
Leg 4	0-0	1-0	I-1; I-1; III, I, 5	0-1; 0-2; 2, 2, 3

Leg 1 (Fig. 4A) lacking outer element on first exopodal segment; tuft of fine setules present midway along margin of third exopodal segment. Legs 2 (Fig. 4B) and 3 (Fig. 4C) each with outer distal corner of second endopodal segment produced into minute prominence. Legs 5 (Figs 2C, 4E) nearly symmetrical, each leg consisting of lamellar plate incompletely fused to intercoxal sclerite; lamellar plate with long plumose seta subterminally and shorter one on posterior surface; small, subterminal or terminal knob on each plate possibly representing exopod (see Fig. 2C).

Male

Unknown.

Remarks

The new species is easily distinguished from the type species *Scutogerulus pelophilus* (characters in parentheses) by: (1) female leg 5 more reduced, comprising only lamellar plates incompletely fused to intercoxal sclerite (2-segmented exopod and 1-segmented endopod); (2) proximal process on maxillulary praecoxal arthrite shorter; (3) inner basal element of maxillule reduced (a distinct short seta); (4) leg 1 without outer basal seta.

The type species *S. pelophilus* was redescribed on the basis of one paratypic female by Ohtsuka *et al.* (1994), but the fusion pattern and armature elements of the antennule of the type species were incorrectly described in part: (XIV = 2 + ae, XV-XVI = 4 + 2 ae) should be replaced by (XIV-XV = 4 + 2 ae, XVI = 2 + ae). The row of long setules along the posterior margin of the antennule extends from the first (I–III) to the 12th (XIV) segments in the new species, but only from the first to the 11th (XIII) in *S. pelophilus*. However, since scars of missing setules are easily overlooked, the setular row may well have extended to the 12th (XIV) segment in the latter species.

Cysts, probably phoronts of apostome ciliates (cf. Sewell, 1951; Grimes & Bradbury, 1992), were observed attached to

setae on the maxillipeds (Fig. 3K). Each cyst was about 7- $10 \,\mu\text{m}$ in long axis with a short stalk of ca. $2 \,\mu\text{m}$. Apostome phoronts have been found on the body surfaces of both shallowand deep-water planktonic copepods (Sewell, 1951; Grimes & Bradbury, 1992; Ohtsuka et al., 2003, unpublished data). According to Sewell (1951), the frequency of occurrence of these cysts on copepods increased with depth (~1500 m) by comparison with the surface waters. However, attached stages are very common in the shallow waters of the USA and Japan (Grimes & Bradbury, 1992; Ohtsuka et al., unpublished data). A unique life cycle of the apostome Vampyrophyra pelagica (Chatton & Lwoff, 1930) carried on coastal planktonic copepods was proposed by Grimes & Bradbury (1992). We have found a clear seasonal pattern in the occurrence and host specificity of this apostome in the Seto Inland Sea, western Japan (Ohtsuka et al., unpublished data).

Etymology. The new specific name is named in honor of Dr Ruth Böttger-Schnack of the Institut für Meereskunde an der Universität Kiel.

Discussion

In their phylogenetic study of the Arietellidae, Ohtsuka et al. (1994) recognised the monotypic genus Scutogerulus as distinct. The following phylogenetically important, generic characteristics are rigorously reconfirmed by the discovery of the new species: (1) the primitive female genital system (plesiomorphy); (2) the presence of modified 'shield-shaped setules (Bradford, 1969)' on the setae on the maxillary and maxillipedal endopods (autapomorphy); (3) the loss of the outer distal spine from the first exopodal segment of leg 1 (autapomorphy). The first of these is significant with reference to the phylogeny of calanoids. The type of female genital system in which a gonopore and a copulatory pore share a common slit is retained in the most primitive calanoid family Pseudocyclopidae (Huys & Boxshall, 1991; Haridas et al., 1994; Cuoc et al., 1997; Ohtsuka et al., 1999) and probably in the Boholinidae. In the Arietellidae only Scutogerulus retains such a system (see Ohtsuka et al., 1994). This symplesiomorphy has previously been regarded as evidence of a close relationship between the Arietellidae and the Pseudocyclopidae by Andronov (1974), Park (1986) and Bradford-Grieve (2002).

The modified 'shield-shaped' setules are not found in other calanoids. The fine structure of the 'button setae' on the maxillae and maxillipeds of the carnivorous arietelloidean family Augaptilidae, in particular the genus *Euaugaptilus*, has been examined by Boxshall (1985) and Matsuura & Nishida (2000). They concluded from a functional morphological point of view that these unique structures may function as shock absorbers during prey capture. The 'shield' shape of the maxillae and maxillipeds of *Scutogerulus* is superficially similar to the 'disc' shape on the setae of *Euaugaptilus*. However, these structures differ remarkably in: (1) the 'shield' is crescent-shaped in *Scutogerulus* (see Fig. 2D–G), while the 'disc' is semicircular or circular in *Euaugaptilus* (see Matsuura & Nishida, 2000: their Fig. 2); (2) the 'shields' are arranged in a single row in *Scutogerulus*, whereas two rows of 'discs' arranged either side-by-side or alternately are present in *Euaugaptilus*; (3) each 'shield' is furnished with two supplementary plates beneath it (see Fig. 2F), which are absent in *Euaugaptilus*; (4) the 'stalk' connecting the 'shield' to a seta is lamellar in *Scutogerulus*, but columnar in *Euaugaptilus* (see Matsuura & Nishida, 2000: their Figs 3, 4); (5) the 'shield' is positioned obliquely to the seta, while the 'disc' is parallel to it; (6) the outer surface of 'shield' is wrinkled (this may have been an artefact caused during SEM processing) in *Scutogerulus* but smooth in *Euaugaptilus*. Since the internal structure of the 'shield' has not yet been examined, its function cannot be addressed in detail.

The genus Scutogerulus appears to be carnivorous based on gut contents containing copepod fragments (present study) as in other arietellid genera (Ohtsuka & Mitsuzumi, 1990; Ohtsuka et al., 1991, 1994). Shallow-water arietellid genera such as Paramisophria Scott, 1897 and Metacalanus Cleve, 1901 bear relatively simple spinulose setae on the maxillae and maxillipeds, while deep-sea forms such as Arietellus Giesbrecht, 1892 and Scutogerulus carry specialized setae on these feeding appendages (Ohtsuka et al., 1994; present study). This seems to be an adaptive strategy of calanoids in the oligotrophic deep-sea environment: efficient capture on prey and/or some kind of specialised feeding. This hypothesis is supported by a fact that only oceanic carnivorous calanoid families such as Augaptilidae (Boxshall, 1985; Matsuura & Nishida, 2000) and Candaciidae (Ohtsuka & Onbé, 1989) bear exclusively specialised structures on setae on the maxillae and/or maxillipeds.

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