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First time discovery of Loricifera from Australian waters and marine caves

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ORIGINAL ARTICLE

First time discovery of Loricifera from Australian waters and marine caves

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Abstract

Two new species of Loricifera, *Pliciloricus cavernicola* sp. nov. and *Australoricus oculus* gen. nov. et sp. nov., have been found in two submarine caves, Jim's Cave and Fish Rock Cave, off the coast of New South Wales, Australia. This is the first discovery of Loricifera from Australia and additionally from marine caves. This paper is the third paper concerning the meiofauna animals from the two caves. *Pliciloricus cavernicola* sp. nov. is characterized by an adult having a large tripartite mouth cone with six oral stylets; clavoscalids with fine lines; a short, robust double organ; small leg-shaped scalids with three stiff hairs; simple claw-shaped scalids; reduction of trichoscalid basal plates in the first two rows and a midventral plica with three ridges. *Australoricus oculus* gen. nov. et sp. nov. is characterized by a Higgins-larva having a pair of pigmented eyes; the 2nd scalid row missing; six smooth and long filiform scalids in the 6th row; six rectangular plates with two teeth in the 7th row; three pairs of ventral setae; two large lateral lorica plates; three pairs of posterior setae and toes with balloon-shaped mucrones.

Key words: *Australia*, *Australoricus oculus* gen. nov. et sp. nov., *Loricifera*, *marine caves*, *Pliciloricus cavernicola* sp. nov., *zoogeographic implications*

Introduction

The phylum Loricifera was described in 1983 by Kristensen and consists of microscopic metazoans ranging from 100 to 500 μm , and is one of the few phyla with solely microscopic animals, called meiofauna (Mare 1942). Loriciferans are found interstitially in different types of sand, e.g. in shell gravel and fine shell sand on the Faroe Bank (Heiner 2005), or in different types of mud, e.g. 'red clay' from the Izu-Ogasawara trench (Kristensen & Shirayama 1988).

Presently, there are 26 described species in Loricifera included in 8 genera and 3 families. However, several hundreds of species are still waiting to be described. The family Nanaloricidae consists of four genera; *Nanaloricus* with three species (Kristensen 1983; Todaro & Kristensen 1998; Kristensen et al. 2007), *Armorloricus* with three species (Heiner 2004; Kristensen & Gad 2004),

Phoeniciloricus with a single species (Gad 2004), and lastly *Spinoloricus* with a single species (Heiner & Neuhaus 2007). The family Pliciloricidae likewise consists of three genera: *Pliciloricus* with 11 species (Higgins & Kristensen 1986; Gad 2005a,b; Heiner & Kristensen 2005), *Rugiloricus* with 5 species (Higgins & Kristensen 1986; Gad & Arbizu 2005; Heiner 2008) and *Titaniloricus* with 1 species (Gad 2005c). Finally, a new monotypic family Urnaloricidae was described recently (Heiner & Kristensen 2009).

Several theories concerning the origin and dispersal of cave fauna have been presented over the years, especially concerning anchialine caves (see Iliffe 2000). These theories are currently classified into four models: vicariance, deep-sea origin, active migration, and regression (see Iliffe 2000; Kano & Kase 2004). One of the earliest theories was presented by Yager (1981) due to investigations of the crustacean fauna, especially the class Remipedia, in marine caves. The theory, also called the vicariance

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model, proposes that caves are refuges for relict Mesozoic fauna from shallow waters of the Tethys Sea (see Danielopol 1990; Yager & Humphreys 1996; Danielopol et al. 2000). The Tethyan origin and later separation and isolation of the species in marine and anchialine caves is, for example, proposedly found in the tardigrade species *Actinarctus neretinus* Grimaldi De Zio, D'Addabbo Gall, Morone De Lucia, Vaccarella and Grimaldi, 1982, which is found in both an Italian and two Australian caves (Grimaldi De Zio et al. 1982; Boesgaard & Kristensen 2001). The deep-sea origin model proposed by Iliffe et al. (1984) and Hart et al. (1985) suggests that cave species are closely related to deep-sea species, and therefore support dispersal from the deep-sea into the caves via an extensive system of crevices (see Bowman & Iliffe 1985; Bowman et al. 1985). This theory is additionally supported by the same environmental conditions in both habitats, e.g. total darkness, constant temperature, low food source and no influence from waves (Riedl 1966). Two examples supporting this theory are the deep-sea tardigrade family Coronarctidae (see Renaud-Mornant 1987) with the genus *Trogloarctus* (see Villora-Moreno 1996) and the crustacean order Mictacea, which has been found in caves (Bowman et al. 1985) as well as in the deep sea (Sanders et al. 1985; Just & Poore 1988). The active-migration model proposes that the colonization of caves has occurred regardless of geographic or climatic changes (see Iliffe 2000). Hence, the marine species have actively colonized empty niches and therefore they cannot be considered relict species, but are species which at no particular time have colonized the caves. Lastly, the regression model proposes that marine littoral species have been trapped in the caves due to tectonic uplifting and movements, which afterwards has resulted in a regression of the sea and thereby a decrease in salinity to a more freshwater environment (Stock 1980; Holsinger 1988; Iliffe 2000). Examples of this model are several crustacean species found in freshwater or brackish water caves, which have a marine origin (Stock 1980; Holsinger 1988).

The two caves investigated in this study, Jim's Cave and Fish Rock Cave, have a high species diversity with many different genera across phyla, including seven new species of Tardigrada, one new species of Kinorhyncha, several species of Nematoda and Gastrotricha, and additionally two new species of Loricifera (Sørensen et al. 2000; Boesgaard & Kristensen 2001). However, the abundance is very low, with only a few specimens per species, and the only exception being the nematodes, which are found in large numbers. These conclusions agree with other marine caves, e.g. Grotta Cattedrale in

Italy, where four species of Tardigrada have been described (Grimaldi De Zio et al. 1982), and the submarine cave in the French Mediterranean Sea where the deep-sea family Coronarctidae was found (Villora-Moreno 1996).

Until now, no loriciferans have been found in Australian waters except for one single Higgins-larva found by R.M. Kristensen at Chesterfield Islands (belonging to France) while sampling for marine interstitial tardigrades (R.M. Kristensen, personal communication). It is additionally the first report of loriciferans found in marine caves.

Material and methods

Locality description

The two caves, Jim's Cave and Fish Rock Cave, are both located off the coast of New South Wales, Australia (Figure 1). Jim's Cave is a long narrow tunnel of approximately 50 m in length. The cave is a part of a large submarine rock, which is situated 3 km off the coastline, south of the city of Tuncurry (32° 27'S, 152° 32'E). The sediment type in the cave is coarse coralligenous sand with a large amount of detritus. Sediment samples were collected by Tom M. Boesgaard using scuba-diving at four places in the middle of the cave on 13 January 1999 at a depth of about 34 m. For further information on Jim's Cave, see Sørensen et al. (2000) and Boesgaard & Kristensen (2001).

Fish Rock Cave is a 100-m long cave running through the western part of Fish Rock Island. The island is situated 5 km off the coast and south of the city South West Rock (30° 56'S, 153° 06'E). The sediment is coarse coralligenous sand that is rich in detritus. Samples were collected on 11 January 1999 in three different places in the middle of the cave at a depth of 18–20 m. For further information on Fish Rock Cave, see Boesgaard & Kristensen (2001). The GPS positions of the two caves reported here differ from those in Sørensen et al. (2000) and Boesgaard & Kristensen (2001), since a thorough investigation has revealed that the previous described positions were wrong. The sediment samples were taken in the centre of both caves, to be sure that no light or outside currents would disturb or influence the sediment and the meiofauna collected here. Hence, the exchange of planktonic meiofauna animals from the outside environment is considered to be minimal if not zero.

Sampling

The sediment samples were collected from the upper 5–10 cm of sediment in both caves, each sample containing approximately 3 litres of wet sediment. The samples were freshwater shocked and the

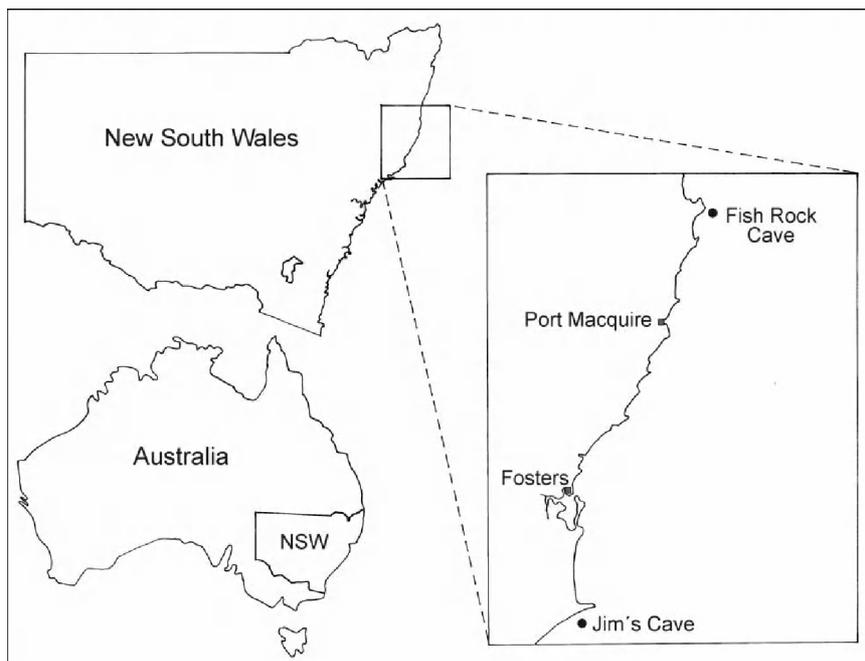


Figure 1. Map of the two locations, Jim's Cave and Fish Rock Cave, New South Wales, Australia.

up-swirled water was decanted through a 'Mermaid bra' with a mesh net of 50 μm . The decanted material was fixed and stored in small containers with 7% formalin buffered with borax. The samples were stained with Rose Bengal and sorted out using a dissecting microscope with a magnification of 40–80 \times .

The sorted specimens were mounted on glass slides in a drop of distilled water for light microscopy. The water was slowly replaced by glycerine through a graded series (5, 10, 25, 50 and 100%). Afterwards the cover slip was sealed with Glyceel[®]. The specimens were studied using an Olympus BX51 light microscope with phase contrast and Nomarski interference. Photomicrographs were taken with an Olympus C-3030 zoom digital camera and illustrations were made using a camera lucida. For more detailed observations, a Zeiss UltraPhot 3 microscope with oil immersion on both the objective and the condenser was used for a magnification of up to 2000 \times .

The type material is deposited at the Zoological Museum, Natural History Museum of Denmark; University of Copenhagen, Denmark under the type numbers LOR 449-452 ZMUC.

An overview of the abbreviations used in the figures with explanations is provided in the Appendix section.

Systematic account

Phylum Loricifera Kristensen, 1983

Order Nanaloricida Kristensen, 1983

Family Pliciloricidae Higgins & Kristensen, 1986

Genus Pliciloricus Higgins & Kristensen, 1986

(type species *Pliciloricus enigmaticus* Higgins & Kristensen, 1986)

Pliciloricus cavernicola sp. nov.

Figures 2–4

Species diagnosis

Adult with a large tripartite mouth cone; a protruding mouth tube with eight oral ridges and six oral stylets; clavoscalids smooth with fine lines and a curved tip; leg-shaped scalids large with three stiff hairs; double organ short and robust with two rows of fine teeth and ending in a tip; small leg-shaped scalids with one anteriorly and two posteriorly oriented stiff hairs; claw-shaped scalids without teeth; rest of the scalids in rows 4–8 simple; 9th row leaf-like scalids long; triangular alternating plates in row 9; three rows of basal plates where there are only 8 plates in the first row, 7 in the second and 15 in the third; 15 trichoscalids, 8 single and serrated and 7 double also serrated; lorica with 22 plicae with a broad midventral plica with 3 transverse ridges; anal cone with six *Nanaloricus*-type flosculi and six warts (*Pliciloricus*-type flosculi).

Type material

The holotype is an adult male (LOR 449 ZMUC, Figures 2–4) sampled on 13 January 1999 from Jim's Cave, New South Wales, Australia. No additional specimens and life history stages of the species were found.

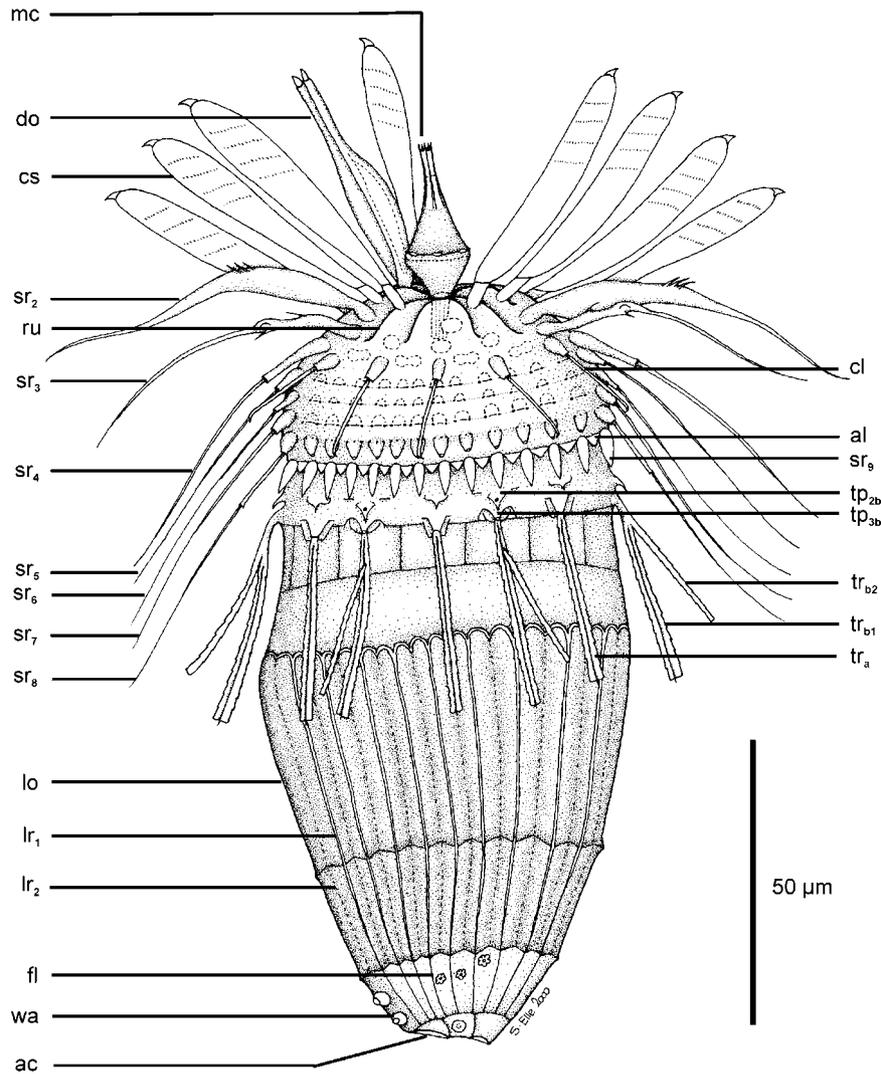


Figure 2. *Pliciloricus cavernicola*, sp. nov. Illustration of the holotypic adult (LOR 449 ZMUC), dorsolateral view.

Etymology

The species name *cavernicola* comes from the Latin word for living in a hole or cave. The name refers to the place, Jim's Cave, where the new species was found.

Description of the adult

The adult holotypic male is 159 μm long including the mouth cone and has a width of 64 μm (Figures 2–3, 4A). The body is divided into five parts: mouth cone, introvert, neck, thorax and abdomen.

The mouth cone (mc) is fully extended (Figure 4B). The mouth cone is 27 μm long and divided into three parts (Figures 2–3). The first part is long and thin with eight primary oral ridges, which terminates into six oral stylets surrounding the mouth opening. The second and third parts are triangular in shape, and between the two parts there are eight cuticular

reinforcements called apodemes (Figure 3). The mouth cone ends in a stalk that connects to the introvert, where a ruff (ru) of cuticular fibres is located.

The introvert has nine rows of scalids. The first row consists of eight clavoscalids (cs) with a length of 49–53 μm . The clavoscalids are divided into three segments, where the first segment is a stalk-like base. The second segment is smooth and longest with four fine lines and the third segment is a curved tip.

The second row consists of seven spinoscalids; five are leg-shaped (sr_2) and two are fused into a double organ (do). The leg-shaped scalids (sr_2) are robust, around 64 μm long and divided into three segments. The first segment is large with three stiff hairs. The last two segments are thin and spinose. The double organ (do) is short (40 μm), very robust and divided into two segments (Figures 2–3, 4D). The first and largest segment has two rows of very fine teeth and the last segment ends in a tip.

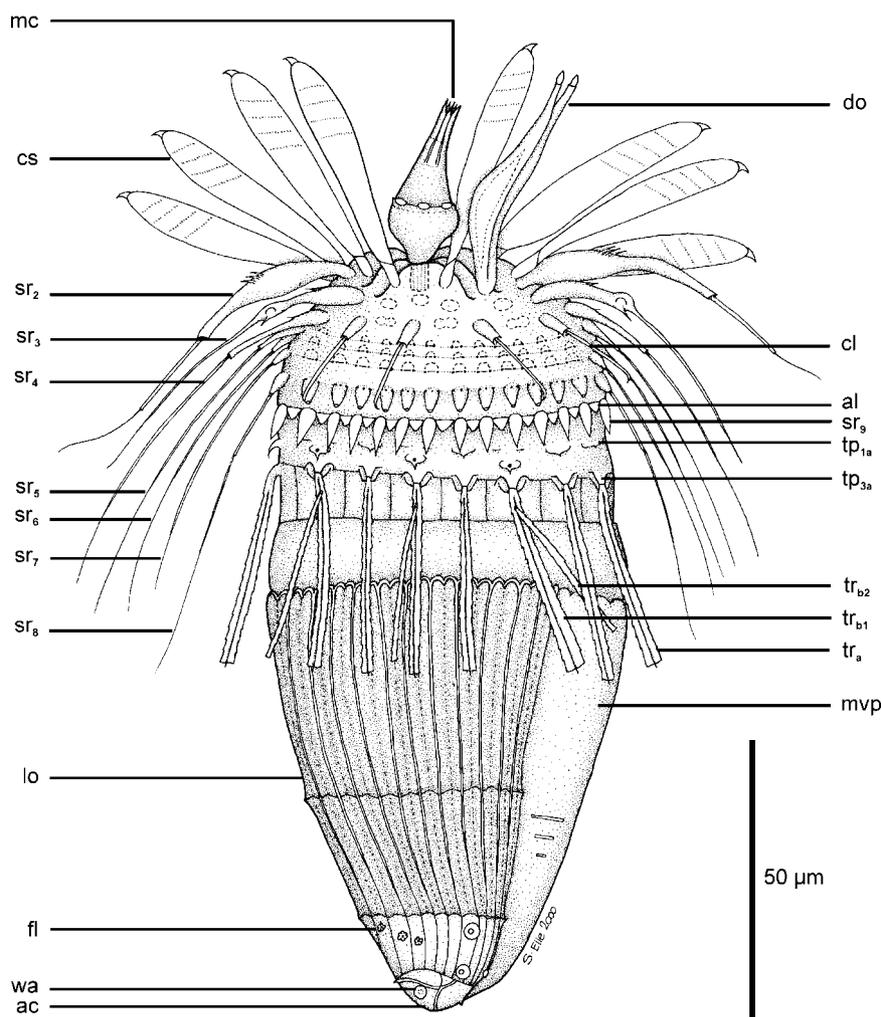


Figure 3. *Pliciloricus cavernicola*, sp. nov. Illustration of the holotypic adult (LOR 449 ZMUC), ventrolateral view.

The third row consists of 15 smaller leg-shaped spinoscalids (sr_3) (length = 53 μm). Each scalid has one large stiff hair pointing anteriorly and two smaller stiff hairs pointing posteriorly. The different segments are difficult to determine in these scalids.

The fourth row consists of 15 claw-shaped scalids (cl) and 15 simple spinoscalids (sr_4). The claw-shaped scalids (cl) are without any teeth, 19 μm long and two-segmented. Distally the last segment curves inwards. The simple spinoscalids (sr_4) are two-segmented and 55 μm long.

The fifth through the seventh rows (sr_{5-7}) consist of 30 simple two-segmented spinoscalids in each row. The spinoscalids are 51–52 μm long. The eighth row consists of 30 simple three-segmented spinoscalids (sr_8). The scalids are 52–54 μm long and not serrated.

The ninth row consists of 30 leaf-like scalids (sr_9) alternating with 30 'alternating' plates (al). The leaf-like scalids are 6 μm long and uniform. The 'alternating' plates are triangular.

The neck has three rows of trichoscalids basal plates (tp_{1-3}), eight single trichoscalids (tr_a) and seven double trichoscalids (tr_b) (Figures 2–4B). The first row of basal plates consists of eight triangular plates with a spine (tp_{1a} , Figure 3). This row has only eight basal plates, since the usual seven alternating type B plates in this row have been reduced. Instead of the type B basal plate, there are two tiny lines. The second basal plate row consists of only seven triangular basal plates with a pore (tp_{2b} , Figure 2). The third row of basal plates consists of eight rectangular type A basal plates (tp_{3a} , Figure 3) alternating with seven rectangular type B basal plates (tp_{3b} , Figure 2). The eight single trichoscalids (tr_a) are inserted on the eight type A basal plates (tp_{3a}). The single trichoscalids (tr_a) are 35 μm long with serration down the lateral margins and on the ridge in the middle (Figure 4E). The seven double trichoscalids (tr_b) consist of two appendages and are inserted on the seven type B basal plates (tp_{3b}). The primary appendage (tr_{b1}) is 34 μm long with serration down

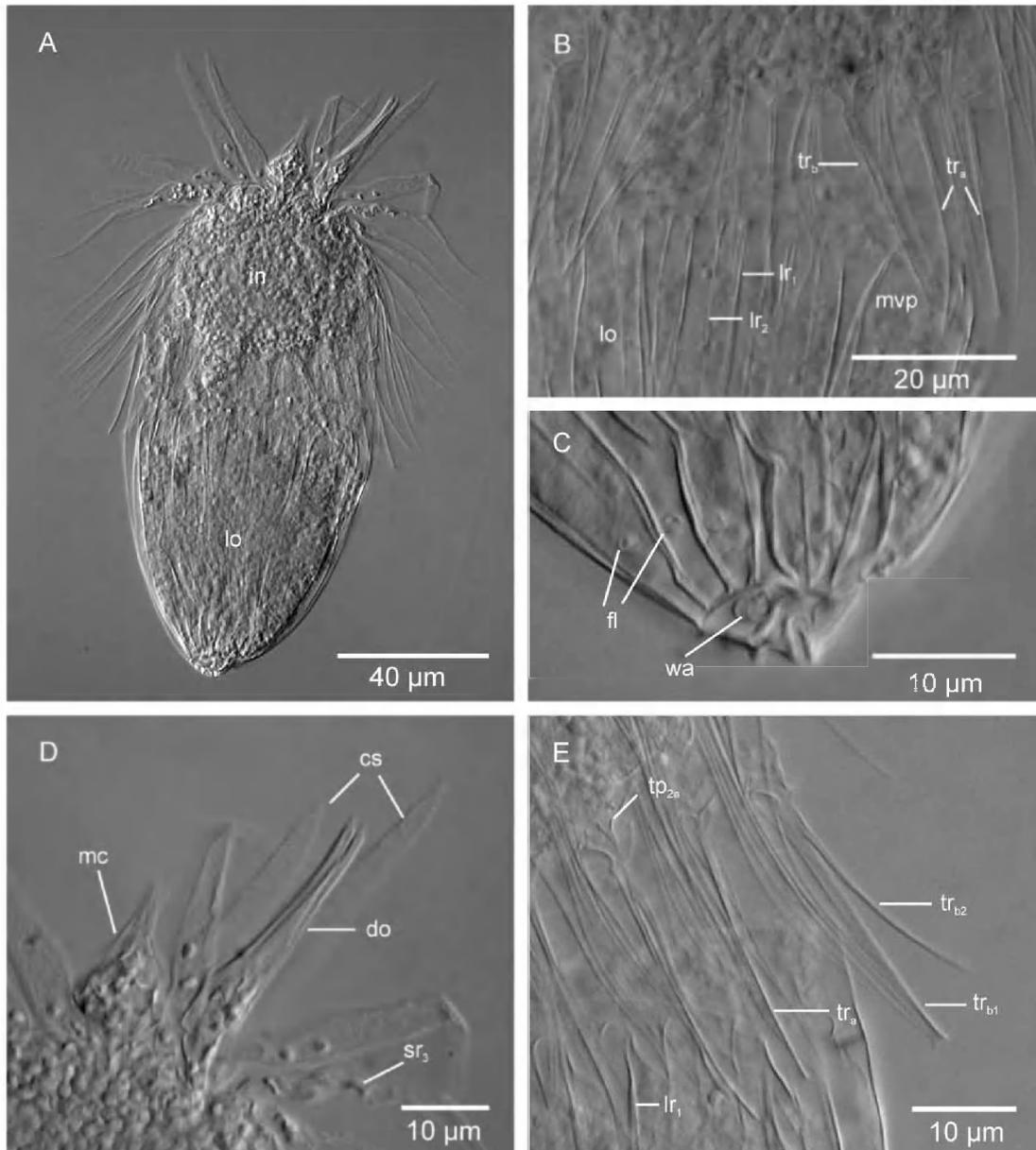


Figure 4. Photos of *Piciloricus cavernicola*, sp. nov. (A) Overview. (B) Thorax with trichoscalids. (C) Anal cone with *N*-flosculi and warts. (D) Mouth cone, double organ and clavoscalids. (E) Single and double trichoscalids. Male holotype (LOR 449 ZMUC).

the lateral margins and on the middle ridge (Figure 4E). The secondary appendage (tr_{b2}) is 27 μm long and serrated only on the margins and does not have a middle ridge (Figure 4E). The thorax lacks appendages and has two folds. The anterior fold is in additional longitudinally subdivided into 15 parts.

The abdomen or lorica (lo) consists of 22 plicae including the large midventral plica (mvp, Figures 3, 4B). The plicae are separated from each other by a primary double ridge (lr_1) and a weaker single secondary ridge (lr_2) that runs through every plica (Figure 4B). The plicae are finely sculptured in a

dotted pattern and have two transverse ridges. The dotted pattern is not so distinct in the more posterior part. The midventral plica (mvp) is broad, consisting of three fused plicae, and has three short transverse ridges located close together (Figure 3). Posteriorly on both lateral sides there are three *Nanaloricus*-type flosculi (fl), which results in a total of six small flosculi in all (Figures 3, 4C). Additionally there are two pairs of warts (wa) on the posterior plicae close to the midventral plica and one pair on the anal cone (ac) (Figures 3, 4C). The anal cone (ac) is divided into six plates.

Taxonomic comments

Pliciloricus cavernicola sp. nov. is a new species belonging to the genus *Pliciloricus*, since the adult possesses several genus-specific characters such as a double organ in the second row, eight single and seven double trichoscalids on the neck, and an abdomen consisting of 22 plicae. So far 11 species of the genus *Pliciloricus* have been described, which makes this genus the most species-rich. Generally, the *Pliciloricus* species differ from each other in the shape of the clavoscalids, the double organ, the claw-shaped scalids, the 9th row scalids, the shape and length of the trichoscalids and their basal plates, the shape of the midventral plica and the position and type of flosculi and/or warts (see Table I). Some of these unique characters are discussed in detail below.

The clavoscalids of *P. cavernicola* sp. nov. are smooth with fine transverse lines. This type of clavoscalid is also found in three other pliciloricid species: *P. gracilis* Higgins & Kristensen, 1986, *P. hadalis* Kristensen & Shirayama, 1988 and *P. senicirrus* Gad, 2005 (Table I). In contrast to this, *P. leocaudatus* Heiner & Kristensen, 2005, *P. pedicularis* and *P. corvus* Gad, 2005 do not resemble *P. cavernicola* sp. nov., since their clavoscalids have many thick transverse cross-walls (Gad 2005a,b; Heiner & Kristensen 2005). Likewise, *P. dubius* Higgins & Kristensen, 1986, *P. profundus* Higgins & Kristensen, 1986 and *P. shukeri* Heiner & Kristensen, 2005 have simple clavoscalids with reinforced dorsal margins.

A short, robust double organ with fine teeth along the edges and with a distal tip is presently only found in *P. cavernicola* sp. nov. and *P. leocaudatus* from the Faroe Bank, whereas the other *Pliciloricus* species possess other types (Heiner & Kristensen 2005). Nearly all described species in *Pliciloricus* including *P. cavernicola* sp. nov. have simple claw-shaped scalids in the 4th row without teeth; the only exceptions are *P. shukeri*, *P. pedicularis* and *P. senicirrus*, which possess robust claw-shaped scalids with teeth or denticles (Gad 2005a,b; Heiner & Kristensen 2005). Additionally, all *Pliciloricus* species except for *P. corvus* have smooth leaf or beak-like scalids in the 9th row (Gad 2005b). The species *P. cavernicola* sp. nov., *P. dubius* and *P. senicirrus* have in addition to warts (*Pliciloricus*-type flosculi) also *Nanaloricus*-type flosculi, which is a unique character for these three species (Table I) (Higgins & Kristensen 1986; Gad 2005b).

Generally, *P. cavernicola* sp. nov. resembles mostly the two species from Faroe Bank; *P. leocaudatus* with regards to the double organ, the claw-shaped scalids and the leaf-shaped scalids of the 9th row, and *P. shukeri* regarding the shape of the mouth cone

Table I. Some of the adult characters differing between species of *Pliciloricus*.

	Shape of cl	Shape of do	Shape of cl	Shape of st ₉	Shape of tr _a	Shape of tr _{b1}	Shape of tr _{b2}	N-flosculi
<i>P. cavernicola</i>	With fine lines/striae	Short and robust ending in a tip	Simple without teeth	Smooth beak or leaf-like	Long and highly serrated	Long and highly serrated	Long and highly serrated	Present
<i>P. dubius</i>	Simple with reinforced dorsal margin	Short with two crescent-shaped rami	Simple without teeth	Smooth beak or leaf-like	Long and slightly serrated	Long and slightly serrated	Long and slightly serrated	Present
<i>P. gracilis</i>	With fine lines/striae	Simple without serrated	Simple without teeth	Smooth beak or leaf-like	Long and highly serrated	Long and highly serrated	Long and highly serrated	Absent
<i>P. profundus</i>	Simple with reinforced dorsal margin	Simple without serrated	Simple without teeth	Smooth beak or leaf-like	Long and highly serrated	Long and highly serrated	Long and highly serrated	Absent
<i>P. hadalis</i>	With fine lines/striae	Simple without serrated	Simple without teeth	Smooth beak or leaf-like	Long and slightly serrated	Long and slightly serrated	Long and slightly serrated	Absent
<i>P. leocaudatus</i>	Transverse cross-walls	Short and robust ending in a tip	Simple without teeth	Smooth beak or leaf-like	Long and highly serrated	Long and highly serrated	Long and highly serrated	Absent
<i>P. shukeri</i>	Simple with reinforced dorsal margin	Very long with teeth along the entire segment	Robust with teeth	Smooth beak or leaf-like	Long and slightly serrated	Short and hairy	Long and slightly serrated	Absent
<i>P. pedicularis</i>	Transverse cross-walls	Very long with teeth along the entire segment	Robust with teeth	Smooth beak or leaf-like	Long and highly serrated	Long and highly serrated	Long and highly serrated	Present
<i>P. corvus</i>	Transverse cross-walls	Short with two crescent-shaped rami	Simple without teeth	Tricuspid beak-like	Long and highly serrated	Long and highly serrated	Long and highly serrated	Absent
<i>P. senicirrus</i>	With fine lines/striae	Short with two crescent-shaped rami	Robust with teeth	Smooth beak or leaf-like	Long and highly serrated	Long and highly serrated	Long and highly serrated	Present

and the smooth simple spinoscalids of rows 5–8 (Heiner & Kristensen 2005). The differences between *P. cavernicola* sp. nov. and *P. leocaudatus* are: the mouth cone, the clavoscalids, the total number of scalids in the 2nd row, the scalids in the 8th row and the position of alternating plates. The mouth cone in *P. leocaudatus* is small and round, whereas it is larger and tripartite in *P. cavernicola* sp. nov. The clavoscalids in *P. cavernicola* sp. nov. are all identical with fine lines, which is not the case in *P. leocaudatus*, since here the scalids possess spines along the edges and some of them are modified. There are seven spinoscalids in the 2nd row in *P. cavernicola* sp. nov. and 11 spinoscalids in *P. leocaudatus*. Lastly, the spinoscalids of rows 5–8 in *P. leocaudatus* are serrated, whereas they are smooth and simpler in *P. cavernicola* sp. nov., and the alternating plates are positioned in the 8th row in *P. leocaudatus* but in the 9th in *P. cavernicola* sp. nov. (see Heiner & Kristensen 2005). The difference between *P. cavernicola* sp. nov. and *P. shukeri* is that there are six oral stylets in the mouth opening in the former and only three in the latter. Additionally, *P. shukeri* has nearly twice as long a double organ than in *P. cavernicola* sp. nov. and possesses a secondary double organ, which is not found in *P. cavernicola* sp. nov. (see Heiner & Kristensen 2005).

Phylum Loricifera Kristensen, 1983

Order Nanaloricida Kristensen, 1983

Family Nanaloricidae Kristensen, 1983

***Australoricus* gen. nov.**

Genus diagnosis

Higgins-larva possessing a mouth cone with a mouth opening surrounded by a six-petal structure; external and internal armature absent; 2nd row missing; 3rd to 5th row with typical two-segmented spinoscalids; 6th row with six long and smooth filiform scalids (the dorsal pair is shorter than the other two) alternating with seven spine-like scalids; 7th row with six rectangular plates with two teeth alternating with six spine-like scalids and one long serrated midventral scalid; three pairs of ventral setae, two of them with a conspicuous knee; laterally two tubes between the thorax and lorica; lorica with honeycomb ultrasculpture; two large lateral lorica plates with a distinct 130° angle; distinct transverse ventral fold; a pair of toes with balloon-shaped mucrones, three pairs of posterior setae; three flosculi.

Etymology

The first part, *Austra*, of the genus name *Australoricus* refers to the country Australia where the new genus was found, and the second part, *loricus*, is the Latin word for corselet or girdle, masculine gender.

***Australoricus oculatus* gen. nov. et sp. nov.**

Figures 5–7

Species diagnosis

Same as genus.

Type material

The holotype is a Higgins-larva (LOR 450 ZMUC, Figure 5) from Jim's Cave, New South Wales, Australia. Additionally there are two paratypes: one Higgins-larva (LOR 451 ZMUC, Figure 6) from Fish Rock Cave and one Higgins-larva (LOR 452 ZMUC) from Jim's Cave. No other life stages were found.

Etymology

The species name *oculatus* is from the Latin word for eyes, which refers to the eyes situated on the introvert of the Higgins-larva. This is the first time eyes have ever been found on any species of Loricifera.

Description of Higgins-larva

The holotypic Higgins-larva is 153 µm long including the mouth cone and 59 µm wide (Figure 5). The paratypic Higgins-larva is 166 µm long and with a diameter of 66 µm (Figure 6). The mouth cone (mc) lacks both internal and external armature. Anteriorly, the mouth opening is surrounded by a six-petal structure.

The introvert bears six rows of scalids, since the second row is missing (Figures 5, 6, 8A, Table II). The first row (cs) consists of eight clavoscalids. The clavoscalids are 29–32 µm long and divided into three segments. The first and second segment is of equal lengths and the third is a spine pointing centrally. Situated between the clavoscalids there is a pair of pigmented spots, eyes (ey). The second row of scalids is missing.

The third row (sr₃) consists of 15 spinoscalids. Dorsally there are seven scalids, where the three middorsal ones are simple two-segmented scalids with a robust first segment and a slightly curved second segment (Figure 5). The four laterodorsal scalids are straight and two-segmented. The last segment ends in a curved tip with a few fine hairs in

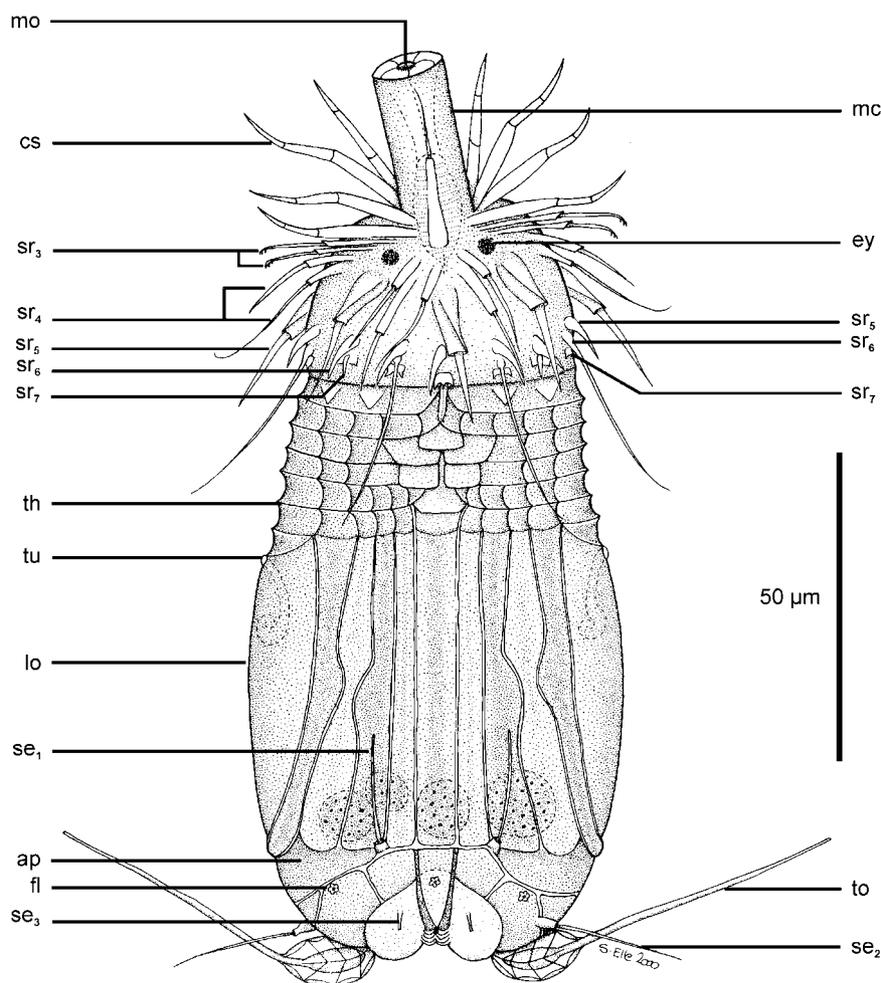


Figure 5. *Australoricus oculatus*, gen. nov. et sp. nov. Illustration of the holotypic Higgins-larva (LOR 450 ZMUC), dorsal view.

the end. This type of scalid is also found midventrally, where there are four scalids with fine hairs in the end (Figure 6). The last four scalids on the ventral side are simple two-segmented scalids.

The fourth row (sr_4) consists of 15 spinoscalids of different types. The three middorsal scalids are simple two-segmented scalids, similar to those in the previous row. Laterodorsally, there is additionally a pair of simple two-segmented scalids and a pair of whip-like two-segmented scalids. The whip-like scalids have a long second segment that ends in a very curvy tip resembling a whip. Lateroventrally, there is also a pair of whip-like scalids, although the scalids here are one-segmented. Additionally, on the dorsal side there are two pairs of simple two-segmented scalids and a pair of scalids with fine hairs in the end. The most lateral pair of the simple scalids has a more bulbous first segment with a large knee. The midventral hairy pair of scalids is shorter and the first segment is bulbous compared to the other hairy scalids (Figure 6).

The fifth row (sr_5) consists of 15 spinoscalids of two different types. There are seven large claw-shaped scalids. These scalids are divided into two segments, where the first is very large and bulbous with a diagonal ridge. The second segment is spinose and long. The seven claw-shaped scalids alternate with eight spine-like scalids. These eight spine-like scalids are one-segmented and robust. The spines are located just above the very long scalids of the sixth row.

The sixth row (sr_6) consists of 13 spinoscalids. There are six long filiform scalids alternating with seven spine-like scalids. The long filiform scalids are 26–30 μm long and two-segmented. The first segment is short and nearly covered by the scalids of the previous row. The second segment is long and whip-like. The dorsal pair is shorter, around 15 μm long, than the other two pairs. The lateral pair of the long scalids together with the spine-like scalids of the previous rows is shown in both figures (Figures 5–6).

The seventh row consists of 13 spinoscalids (sr_7). Positioned below the long scalids of the previous row

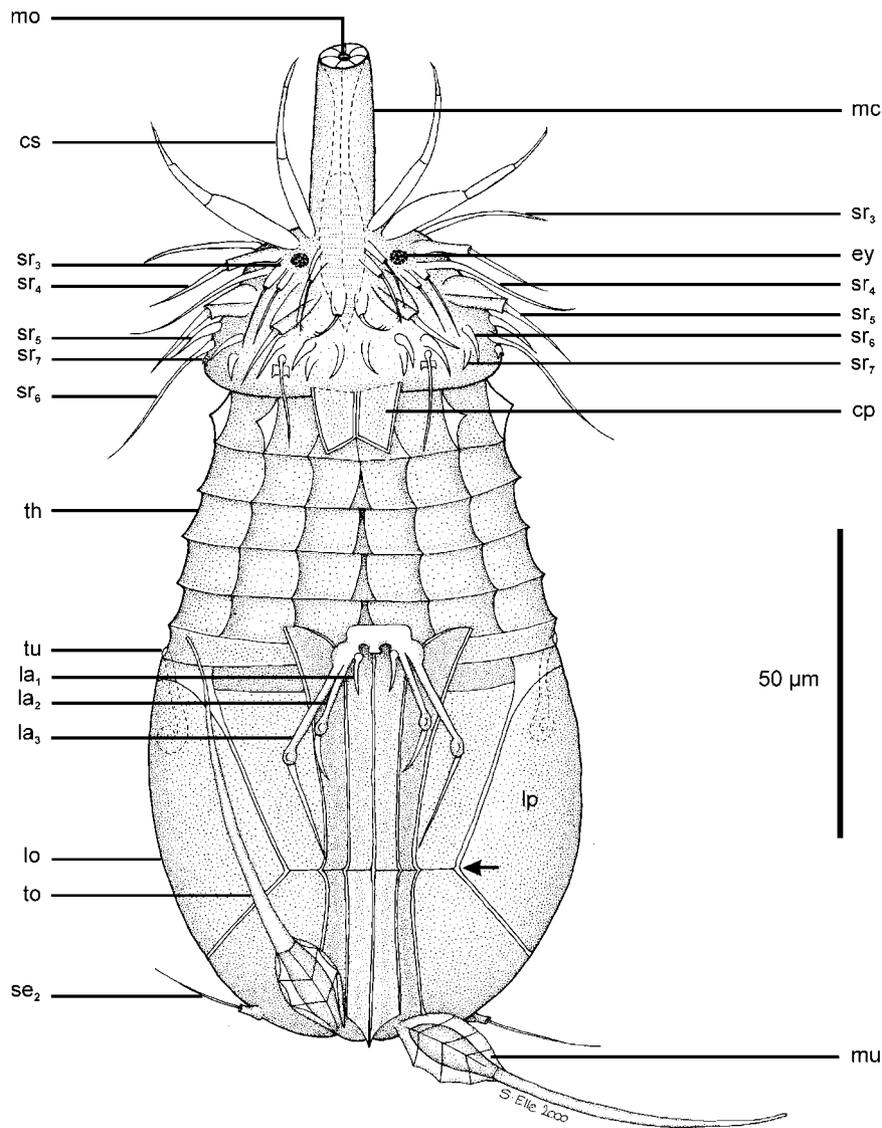


Figure 6. *Australoricus oculatus*, gen. nov. et sp. nov. Illustration of the paratype Higgins-larva (LOR 451 ZMUC), ventral view.

there are six plate-like scalids (Figures 5–6). The scalids resemble a large rectangular plate with two teeth at the edges. The six plate-like scalids alternate with six spine-like scalids and one middorsal scalid. The middorsal scalid consists of a rectangular plate with three small spines together with a long serrated segment.

The thorax shows six transversal folds and several longitudinal folds. These folds function like an accordion to facilitate the retraction of the introvert. Two closing plates (cp) are located midventrally on the thorax just below the introvert (Figure 6). The two plates form a closing apparatus when the introvert is retracted into the body. Between the thorax and the abdomen there are ventrally three pairs of locomotory setae. The three pairs are inserted on a rectangular plate (Figures 6, 7D). The

most lateral pair of setae (la_1) is 39 μm long with a large conspicuous knee ending in a pointy tip. The median pair of setae (la_2) is 22 μm long with a conspicuous knee and a pointy tip, which curves slightly inwards ventrally. The most ventral pair of setae (la_3) is 7 μm long with a pointy end.

The abdomen or lorica is oval with a distinct honeycomb ultrasculpture (not shown on Figures 5 and 6, but shown in Figure 7B,D,E). The lorica has 17 longitudinal folds. There are two large lateral plates (lp), both with a distinct 130° angle ventrally where they meet the transverse ventral fold (see arrows, Figures 6, 7D). Laterally between the thorax and the abdomen, there are two tubes (tu) that connect to multicellular glands inside the abdomen (Figure 7E). The abdomen ends in a large anal field consisting of several anal plates (ap). Two toes are

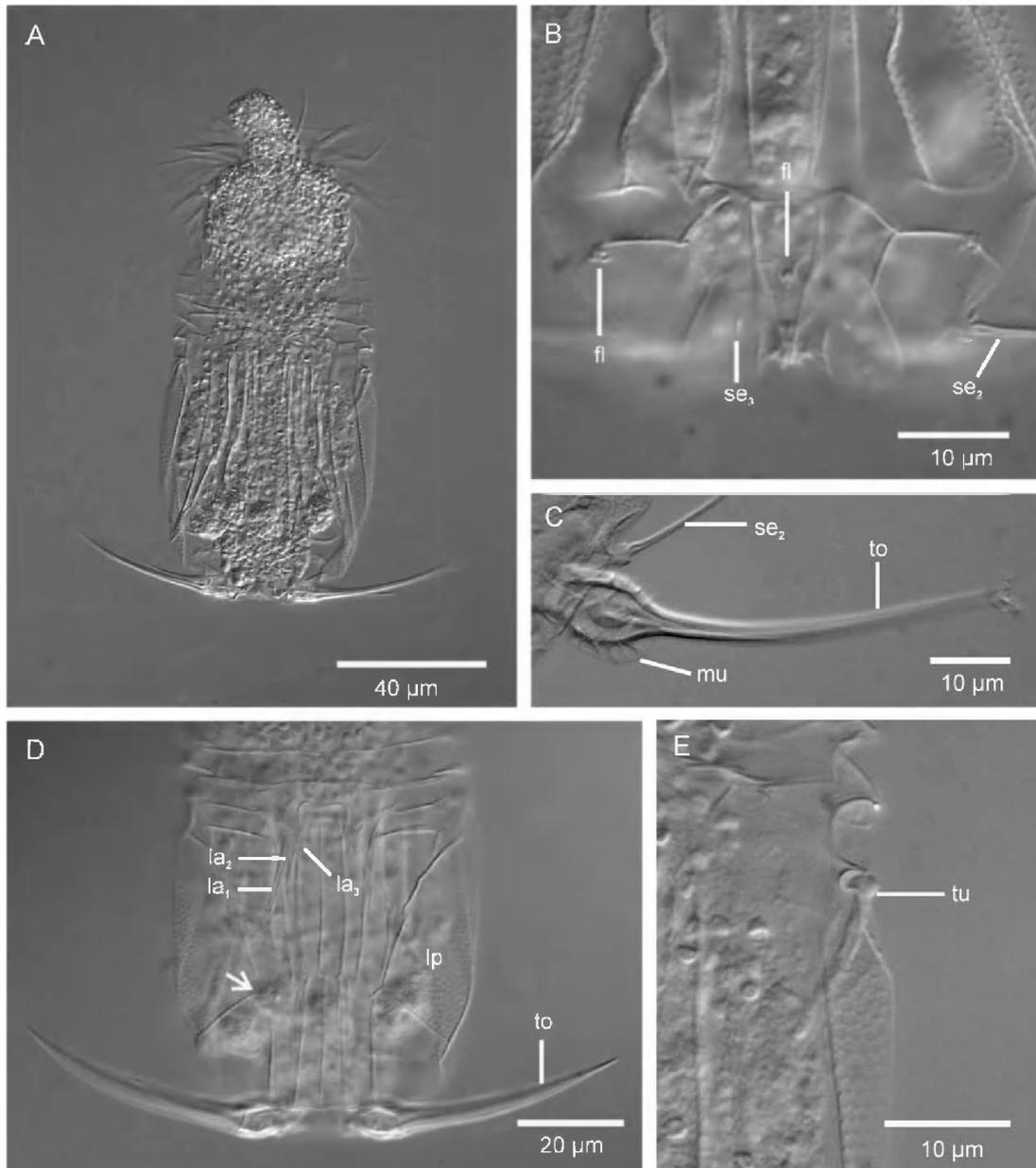


Figure 7. Photos of *Australoricus oculatus*, gen. nov. et sp. nov. (A) Overview. (B) Dorsal view of anal field. (C) Toe with balloon-shaped mucro. (D) Ventral view of lorica and anal field. (E) The lateral tube. A,B and D,E: holotypic Higgins-larva (LOR 450 ZMUC), and C: paratypic Higgins-larva (LOR 451 ZMUC).

connected to the anal field. The toes are 62 μm long in the holotype (Figure 5) and 68 μm in the paratype (Figure 6). The mucrones (mu) positioned basally on the toes, have a large round balloon-shaped three-dimensional structure (Figure 7C). It is therefore not flat as seen in other nanaloricids. There are additionally three pairs of posterior setae located on the anal field (Figure 7B). The dorsal pair of sensory setae (se_1) is 17 μm long and has a rounded base. The lateral pair of setae (se_2) is 26 μm long with a rectangular base. The last pair of setae (se_3) is positioned on the two basal plates of the anal field and they are 3 μm long. There are two flower-shaped

Nanaloricus-flosculi located dorsally and one flosculus middorsally on the central triangular anal plate (Figure 7B). The anus is located below the single flosculus and between the posteroterminal setae.

Internally four large clusters of cells are found in the posterior end of the lorica (Figure 5). These cells might be glandular cells or early embryonic germ cells.

Taxonomic comments

Australoricus oculatus gen. nov. et sp. nov. is both a new species and a new genus in the family

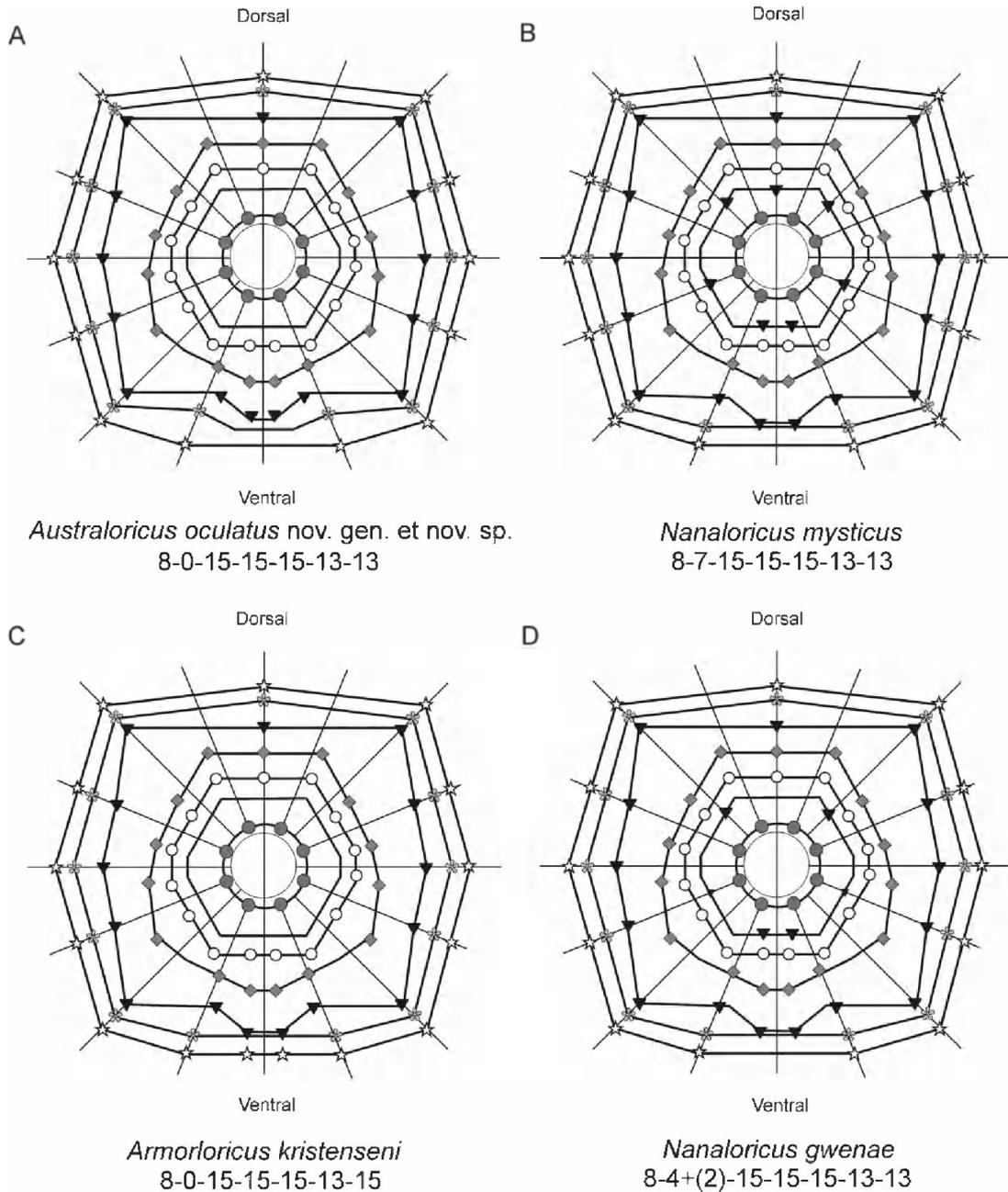


Figure 8. Scalid diagrams of larval introvert of Nanaloricidae. (A) *Australoricus oculatus* gen. nov. et sp. nov. (B) *Nanaloricus mysticus* (see Kristensen 1983). (C) *Armorloricus kristenseni* (see Heiner 2004). (D) *Nanaloricus gwenae* (see Kristensen et al. 2007).

Nanaloricidae with these family larval characters: Higgins-larva without external and internal armature; introvert with six or seven rows of scalids, lorica with honeycomb or indistinct honeycomb ultrasculpture; three pairs of ventrolateral setae; three pairs of posterior setae; toes with different types of leaf-like structures (mucrones).

The new genus *Australoricus* has these species and genus-specific characters: the 2nd row of scalids is missing; six long filiform and smooth scalids in the 6th row, where the dorsal pair is shorter than the

others; six rectangular plates with two large teeth in the 7th row; two large lorical lateral plates with a 130° angle; long toes with large balloon-shaped mucrones.

All described nanaloricid species show a high variation in the shape and number of scalids (see Table II). Especially the 2nd and the 3rd rows are problematic, since they are positioned close together and have the same type of scalids. Loss of scalids in the 2nd row is found in two other species, *Armorloricus elegans* Kristensen & Gad, 2004 (described as

Table II. The number of scalids in the different rows of the Higgins-larvae of the family Nanaloricidae.

	1st row	2nd row	3rd row	4th row	5th row	6th row	7th row	References
<i>Nanadoricus mysticus</i>	8	7	15	15 (7+8)	15 (7+8)	13 (5+8)	13 (6+7)	Kristensen (1991a)
<i>Nanadoricus khaitatus</i>	8	?	?	?	?	?	?	Todaro & Kristensen (1998)
<i>Nanadoricus gwenae</i>	8	4+(2)	15	15	15	13	13	Kristensen et al. (2007)
<i>Armorloricus elegans</i>	8	0	15	15	15	15	15	Kristensen & Gad (2004)
<i>Armorloricus davidi</i>	8	4	15	15 (7+8)	15 (7+8)	15 (7+8)	15 (7+8)	Kristensen & Gad (2004)
<i>Armorloricus kristenseni</i>	8	0	15	15	15	13	15	Heiner (2004)
<i>Phoeniciloricus simplidigitatus</i>	8	10	15	15	15 (7+8)	13 (6+7)	15 (7+8)	Gad (2004)
<i>Spinoloricus turbatio</i>	8	6	15	15	15	13	13	Heiner & Neuhaus (2007)
<i>Australoricus oculatus</i> gen. nov. et sp. nov.	8	0	15	15	15 (7+8)	13	13	

Armorloricus sp. I: see Kristensen & Gad 2004), and *Armorloricus kristenseni* Heiner, 2004 (Figure 8C). It seems that this character varies a lot, since the last and third species of *Armorloricus*, *A. davidi* Kristensen & Gad, 2004 (described as *Armorloricus* sp. II: see Kristensen & Gad 2004) do possess spinoscalids in the 2nd row, even though there are only four scalids in the row. In *Nanadoricus mysticus* Kristensen, 1983 there are seven scalids in the 2nd row (Figure 8B) and in *Nanadoricus gwenae* Kristensen, Heiner & Higgins, 2007 there are either four or six (Figure 8D), and in *Spinoloricus turbatio* Heiner & Neuhaus, 2007 there are six. The shape and size of the six long filiform scalids of the 6th row varies between all described nanaloricid species. In *A. oculatus* gen. nov. et sp. nov. all six are smooth and the dorsal pair is the shortest. This is also found in *S. turbatio*; however, here the ventral pair is shorter than the other two (Heiner & Neuhaus 2007). In *A. kristenseni* there are dorsally four serrated and ventrally two smooth whip-like scalids (Heiner 2004) and in *N. gwenae* all six are serrated (Kristensen et al. 2007). Contrary to this, in *Nanadoricus khaitatus* Todaro & Kristensen, 1998, *N. mysticus*, *A. elegans* and *A. davidi* there are totally only four filiform scalids, since the ventral pair has been reduced to small spike-like scalids instead (see Kristensen 1983; Todaro & Kristensen 1998; Kristensen & Gad 2004). In *A. oculatus* gen. nov. et sp. nov. the plates on the 7th row are rectangular in shape with two teeth on the sides. This type of plates are also found in *S. turbatio* (Heiner & Neuhaus 2007) and *Phoeniciloricus simplidigitatus* Gad, 2004, whereas the plates are large round or rectangular with many teeth in *Armorloricus* (see Kristensen & Gad 2004) and the plates in *Nanadoricus* are subdivided into two small plates with numerous small teeth (Kristensen 1983; Kristensen et al. 2007). The mucrones on the toes in *A. oculatus* gen. nov. et sp. nov. are very different from those of other nanaloricid genera. The mucrones are three-dimensional, large and balloon-shaped, and not flat as recorded in the other genera (see e.g. Kristensen & Gad 2004, figure 14D).

Discussion

Pigmented eyes

The Higgins-larva of *A. oculatus* gen. nov. et sp. nov. possesses two large, pigmented spots (eyes); however, the eyes disappeared after mounting the animal in glycerine. The presence of eyes has never before been recorded in any other species of Loricifera. This is probably due to the fast disappearance of the eyes in various media. Sediment

samples with loriciferans are usually fixed in 5% formalin, and this might be the reason why eyes have not been observed before. An argument for the presence of eyes in other loriciferans is that head sensory organs have been found in several other meiofauna phyla such as Gastrotricha, Kinorhyncha, Rotifera and Nematoda (see e.g. Liesenjohn et al. 2006 for Gastrotricha; Zelinka 1928, Kristensen & Higgins 1991, and Neuhaus 1997 for Kinorhyncha; Clément & Wurdak 1991 for Rotifera; and Wright 1991 for marine nematodes). Ultrastructural studies of these groups have shown a great variation in the morphology of the head sensory organs. This is also the case for Kinorhyncha, for example, where nine red pigmented eye spots have been observed in live specimens of several species of *Echinoderes* by Zelinka (1928). Kristensen & Higgins (1991) and Neuhaus (1997) studied the cephalic sensory organ in several species of the order Homalorhagida ultrastructurally. In these species, the head sensory organ constitutes a single pair, which is not pigmented. Finally, it is a curious fact that the first loriciferan found with eyes is found in a marine cave, since cave living animals or troglobites typically have reduction or loss of eyes

as a result of living in total darkness (Humphreys 2000; Iliffe 2000).

Distribution of Loricifera

Loriciferan research is, after more than 20 years, still in its preliminary stage with regards to number of described species, as shown presently by only 28 described species worldwide including the two described here (Figures 9–10, Tables III and IV). The species distribution is restricted to only 12 locations worldwide. The majority of species have been collected on few collection trips such as BIOFAR to the Faroe Bank (see Heiner 2004, 2005, 2008; Heiner & Kristensen 2005, 2009), DIVA-1 to the Angola Basin (Gad 2005a,b), expedition no. 42 of R/V *Meteor* to the Great Meteor Seamount (Gad 2005c) and in two well-studied areas, Roscoff, France (Kristensen 1983; Kristensen & Gad 2004) and North Carolina, USA (Higgins & Kristensen 1986) (see Tables III and IV). The remaining species correlate to patchy findings of loriciferans during various collections of other meiofauna. Hence, only a few observations can be made concerning the geographic distribution of the loriciferan species.

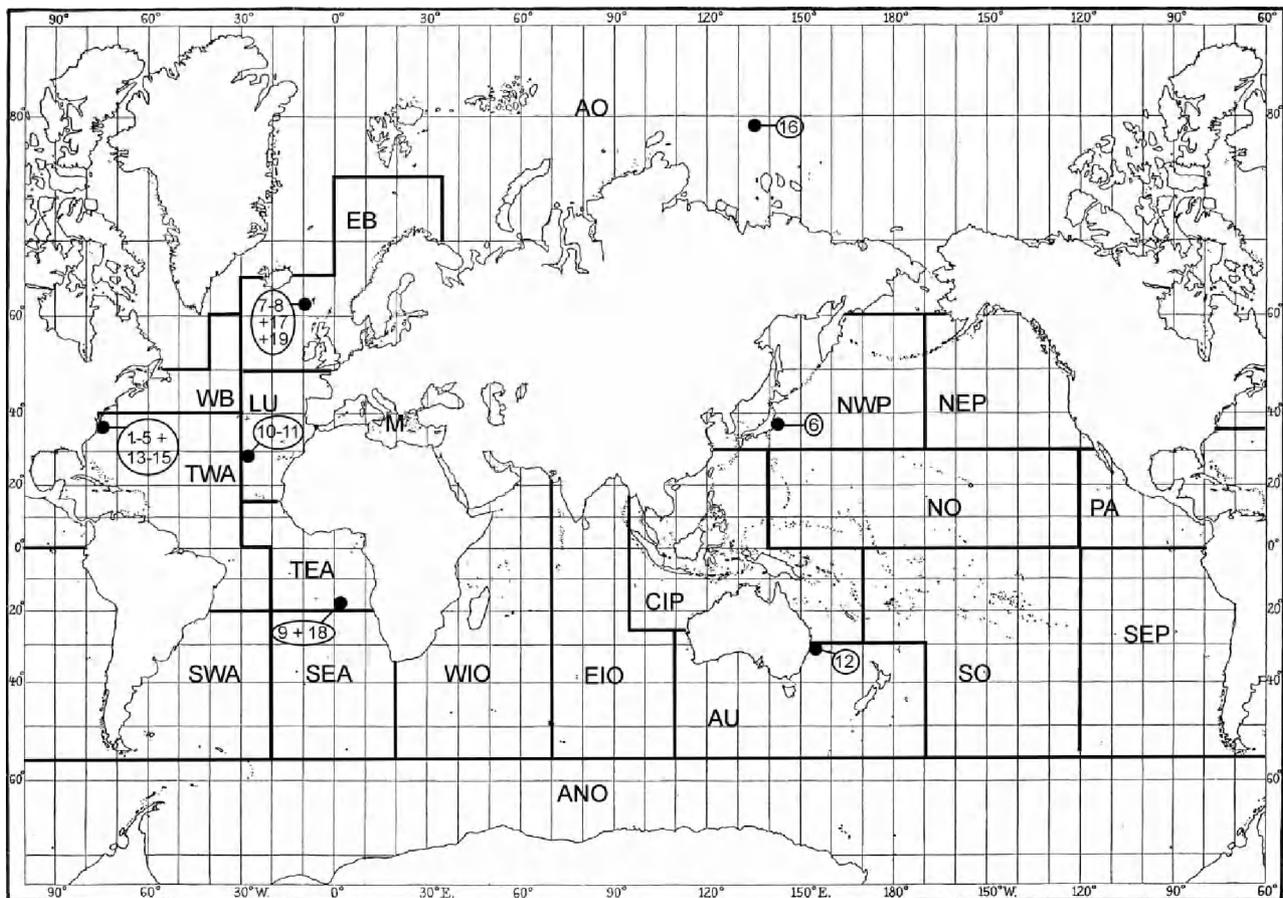


Figure 9. Distribution of the families Pliciloricidae and Urnaloricidae (see Table III).

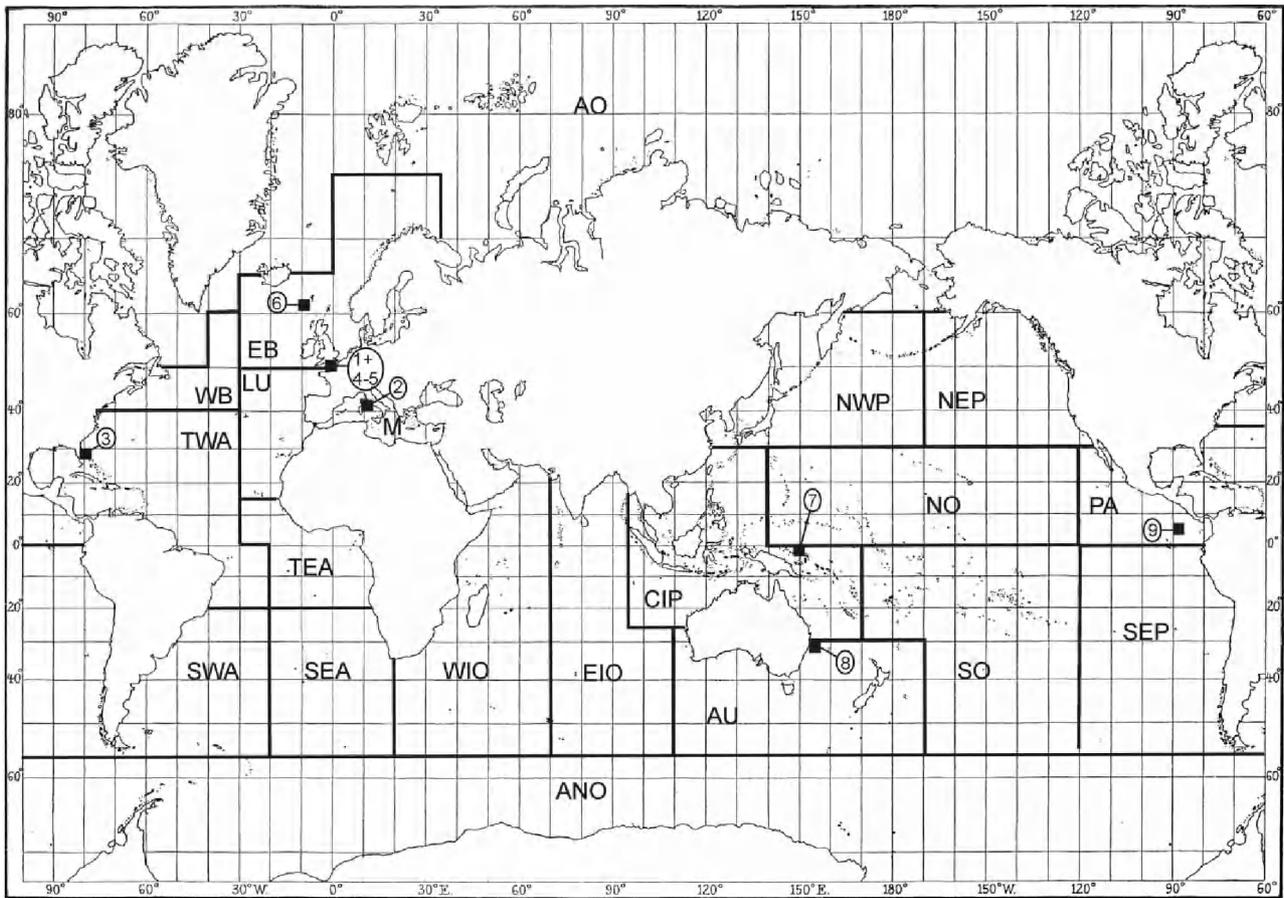


Figure 10. Distribution of the family Nanaloricidae (see Table IV).

Loriciferans are found in exclusively marine habitats ranging from 7 to 8260 m depth, in sediments ranging from fine sand, to shell gravel to deep-sea

mud, and have been found in the Atlantic, Pacific and Arctic Oceans (Kristensen & Shirayama 1988; Todaro & Kristensen 1998; Kristensen & Gad 2004;

Table III. Distribution of the families Pliciloricidae and Urnaloricidae (numbers refer to locations ● in Figure 9).

No.	Species	Locality	Region	Authority
1	<i>Pliciloricus gracilis</i>	North and South Carolina	TWA	Higgins & Kristensen, 1986
2	<i>Pliciloricus enigmaticus</i>	North and South Carolina	TWA	Higgins & Kristensen, 1986
3	<i>Pliciloricus dubius</i>	North and South Carolina	TWA	Higgins & Kristensen, 1986
4	<i>Pliciloricus profundus</i>	North and South Carolina	TWA	Higgins & Kristensen, 1986
5	<i>Pliciloricus orphanus</i>	North and South Carolina	TWA	Higgins & Kristensen, 1986
6	<i>Pliciloricus hadalis</i>	Izu-Ogasawara Trench	NWP	Kristensen & Shirayama, 1988
7	<i>Pliciloricus leocaudatus</i>	Faroe Bank, Faroe Islands	EB	Heiner & Kristensen, 2005
8	<i>Pliciloricus shukeri</i>	Faroe Bank, Faroe Islands	EB	Heiner & Kristensen, 2005
9	<i>Pliciloricus pedicularis</i>	Angola Basin, Namibia	TEA	Gad, 2005
10	<i>Pliciloricus corvus</i>	Great Meteor Seamount, Atlantic	LU	Gad, 2005
11	<i>Pliciloricus senicirrus</i>	Great Meteor Seamount, Atlantic	LU	Gad, 2005
12	<i>Pliciloricus cavernicola</i> sp. nov.	New South Wales, Australia	AU	Heiner, Boesgaard & Kristensen, herein
13	<i>Rugiloricus carolinensis</i>	North and South Carolina	TWA	Higgins & Kristensen, 1986
14	<i>Rugiloricus cauliculus</i>	North and South Carolina	TWA	Higgins & Kristensen, 1986
15	<i>Rugiloricus ornatus</i>	North and South Carolina	TWA	Higgins & Kristensen, 1986
16	<i>Rugiloricus polaris</i>	Laptev Sea	AO	Gad & Arbizu, 2005
17	<i>Rugiloricus bacatus</i>	Faroe Bank, Faroe Islands	EB	Heiner, 2008
18	<i>Titamiloricus inexpectatovus</i>	Angola Basin, Namibia	TEA	Gad, 2005
19	<i>Urnaloricus gadi</i>	Faroe Bank, Faroe Islands	EB	Heiner & Kristensen, 2009

Table IV. Distribution of the family Nanaloricidae (numbers refers to locations ■ in Figure 10).

No:	Species	Locality	Region	Authority
1	<i>Nanaloricus mysticus</i>	Roscoff, France	LU	Kristensen, 1983
2	<i>Nanaloricus khaitatus</i>	Livorno, Italy	M	Todaro & Kristensen, 1998
3	<i>Nanaloricus gwenae</i>	Fort Pierce, USA	TWA	Kristensen, Heiner & Higgins, 2007
4	<i>Armorloricus elegans</i>	Roscoff, France	LU	Kristensen & Gad, 2004
5	<i>Armorloricus davidi</i>	Roscoff, France	LU	Kristensen & Gad, 2004
6	<i>Armorloricus kristenseni</i>	Faroe Bank, Faroe Islands	EB	Heiner, 2004
7	<i>Phoeniciloricus simplidigitatus</i>	Kilinailau Tranch, PNG	SO	Gad, 2004
8	<i>Australoricus oculatus</i> gen. nov. et sp. nov.	New South Wales, Australia	AU	Heiner, Boesgaard & Kristensen, herein
9	<i>Spinoloricus turbatio</i>	Galapagos Spreading Center	PA	Heiner & Neuhaus, 2007

Gad & Arbizu 2005). Previously, it was suspected that the family Nanaloricidae only constituted shallow water species; however, this was contradicted by the discovery of *Phoeniciloricus simplidigitatus* and later again by *Spinoloricus turbatio* (see Gad 2004; Heiner & Neuhaus 2007). It is now apparent that the species distribution is more correlated with sediment type and amount of detritus than with depth, e.g. *P. simplidigitatus* is a deep-sea species from 1813 m though the sediment is fine volcanic sand not clay (Gad 2004). Typically, the species of Pliciloricidae are found in more muddy or fine-grained sediments with some organic detritus compared to the more clean shell gravel in which species of Nanaloricidae live. This is most evident at the Faroe Bank, where typically the pliciloricids are found on the slopes whereas the nanaloricids are found on the plateau (see Heiner 2005). However, there are of course exceptions to this rule, e.g. *Pliciloricus cavernicola* nov. sp. is found in coarse sand in Jim's Cave; however, in this case there is a lot of detritus.

In the Pacific region only three species have been described: *Pliciloricus hadalis*, *Phoeniciloricus simplidigitatus* and *Spinoloricus turbatio* are all deep-sea species (see Kristensen & Shirayama 1988; Gad 2004; Heiner & Neuhaus 2007). However, an additional nine undescribed species have been found near the Galapagos Spreading Center (see Heiner & Neuhaus 2007), and three undescribed species have been found in the deep sea near North Island and Chatham Rise, New Zealand (Heiner, personal observation).

Zoogeographic implications

Investigations on the animals living inside caves have commonly concentrated on larger animals, e.g. fish and crustaceans, whereas research on meiofauna in caves is very scarce. Additionally, the research has typically concentrated on limestone, volcanic anchialine caves across the tropical region, and only little focus has been on submarine caves (Ilfie 2000). Almost all research on meiofauna in sub-

marine caves comes exclusively from Mediterranean caves such as *Grotto Piccola del Ciolo*, Lecce, Italy (Todaro & Shirley 2003; Todaro et al. 2006), *Trois Pépés*, East of Marseille, France (Villora-Moreno 1996), *Grotta Cattedrale*, Italy (Grimaldi De Zio et al. 1982) and two caves on the Island of San Domino (Sandulli et al. 1999; D'Addabbo Gallo et al. 2001).

Density inventories of all major meiofauna groups have been performed in *Grotto Piccola del Ciolo* and in the caves of San Domino. These yield fairly high meiofauna densities and species diversities (see Sandulli et al. 1999; Todaro et al. 2006). In comparison, the species diversity of the major meiofauna groups is also quite high in the two Australian caves, where several species of gastrotrichs, nematodes, harpacticoid crustaceans and polychaetes and a single kinorhynch species have been found, although the density is quite low, with only a few specimens per species (see Sørensen et al. 2000; Boesgaard & Kristensen 2001). In *Grotto Piccola del Ciolo*, the species diversity is high for Gastrotricha with 16 species of which four are new to science (Todaro et al. 2006). Likewise for the two San Domino caves, 21 species of Tardigrada were found including two new species (Sandulli et al. 1999). This correlates well with the studied tardigrade fauna from the two Australian caves where the species diversity is also high, with 19 species where 7 are new to science (R.M. Kristensen, personal communication).

Another similarity between the three cave areas is that all the species found in the caves are species, which are typically not found outside the caves. Hence, these species are probably true cave animals and might be of either deep-sea origin as, for example, the tardigrade genus *Trogloarctus* (see Villora-Moreno 1996) or a Thethyan origin as, for example, the tardigrade *Arctinarctus neretimus*, which for the latter has been found in caves in both Italy and Australia (Boesgaard & Kristensen 2001). Regarding the loriciferans from Jim's Cave and

Fish Rock Cave, nothing concerning their possible origin can be said. No loriciferans, except for one single larva from Chesterfield Islands, have been found close to Australian waters and related islands, even though the tardigrade fauna has intensively been investigated along the Australian beaches (R.M. Kristensen, personal communication). The cave loriciferans mostly resemble species found in shell gravel and coarse sand on the Faroe Bank or in Roscoff, France (Kristensen & Gad 2004; Heiner & Kristensen 2005). Therefore, an explanation to the missing loriciferans might be that the coarse coralligenous sediment inside the caves differs greatly from the finer sediment found along the Australian beaches. Hence, again, it is presumably more the sediment composition than anything else that affects the species composition. This is probably also the case for the tardigrade fauna (see Boesgaard & Kristensen 2001).

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Appendix

The abbreviations used herein follow Heiner & Neuhaus (2007).

ac, anal cone; al, alternating plate of 9th row; ap, anal plate; cl, claw-shaped scalids of 4th row; cp, closing plate of thorax; cs, clavoscalid of 1st row; do, double organ; ey, eyes; fl, flosculus; in, introvert; la1, anterolateral seta; la2, anteromedian seta; la3, anteroventral seta; lo, lorica; lp, lateral plate; lr1, primary double ridge of lorica; lr2, secondary ridge of lorica; mc, mouth cone; mo, mouth opening; mu, mucro; mvp, midventral plica; ru, ruff; se1, posterodorsal setae; se2, posterolateral setae; se3, posteroterminal setae; sr₂₋₉, scalid of rows 2–9; th, thorax; to, toe; tp₁₋₃, trichoscalid plates 1–3; tr_a, single trichoscalid; tr_{b1}, primary appendage of double trichoscalid; tr_{b2}, secondary appendage of double trichoscalid; tu, tubes; wa, warts.

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