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ORIGINAL ARTICLE

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Armorloricus kristenseni (Nanaloricidae, Loricifera), a new species from the Faroe Bank (North Atlantic)

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Abstract The year 2003 was the 20th anniversary of the description of the phylum Loricifera and of the type species *Nanaloricus mysticus* Kristensen, 1983, from Roscoff, France. To honour this occasion, a loriciferan of the newly described genus *Armorloricus*, from Roscoff, will be named after the discoverer of the phylum Loricifera, Professor Reinhardt Møbjerg Kristensen. This new species, *Armorloricus kristenseni* sp. nov., was found during two cruises to the Faroe Bank in the North Atlantic, in 1992 and 2001. The specimens were collected at three different stations (one in 1992 and two in 2001) all situated on the plateau itself at a depth of approximately 150 m. The adults are characterized by their elongated shape, the large lateral lorica plates, the very long, feather-like scalids in the third row, the long claspers in the male, and the wheel-like structure of the subcuticle glands inside the lorica plates on the ventral side. The Higgins-larvae are characterized by their long middorsal scalid with a hexagonal base and the small hook-shaped midventral pair of scalids in row 4. Furthermore, the long, paired, serrated scalids in row 6 and the asymmetrical basal plate with numerous teeth in row 7 are also unique characters. For an easier between-family comparison of the different scalids and rows on the introvert, the second row in the adults of Nanaloricidae has been split up into two rows, so that all adult loriciferans posses a total of nine rows on the introvert.

Keywords Loricifera · Nanaloricidae · *Armorloricus* · Faroe Bank · North Atlantic

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Introduction

Loriciferans are bilaterally symmetrical microscopic metazoans, and are mostly from the interstitial spaces of sand, i.e. shell gravel or oolytic sand (Kristensen 1983; Higgins and Kristensen 1986). They are characterized by a body with five sections: a protrusive mouth cone, a head (introvert) with rows of scalids (clavoscalids and spinoscalids), a neck with trichoscalids, a thorax, and an abdomen with a lorica consisting of plates or plicae (folds). The most common larval form of Loricifera, the Higgins-larva, is divided into the same sections as the adults. The Higgins-larvae are characterised by seven rows of scalids, two to three pairs of ventral locomotory setae between the thorax and the abdomen, two to three pairs of posterior sensory setae, and a pair of toes.

At present, Loricifera comprises eleven described species in three genera split between two families. The type species, *Nanaloricus mysticus* Kristensen, 1983 was described from Roscoff, France, and was assigned to the family Nanaloricidae. The description included additional material from the Azores and Fort Pierce, Florida, USA. However, the additional material later turned out not to be conspecific with *N. mysticus*, and the American specimens are currently being described as a new species (R.M. Kristensen, personal communication). A few years later, Todaro and Kristensen (1998) described a new species of the family Nanaloricidae, *N. khaitatus* Todaro and Kristensen, 1998 from Livorno, Italy. This was the first record of *Nanaloricus* from the Mediterranean Sea (Todaro and Kristensen 1998).

Since the description of *N. mysticus*, numerous collections at Roscoff, France have resulted in the finding of several new species of *Nanaloricus* and, additionally, the new genus, *Armorloricus*, from the interstitial spaces of shell gravel in the intertidal zone (50–55 m water depth). Currently, the genus comprises two species, *A. elegans* and *A. davidi*, in which the morphology of the adults and postlarvae are known (Kristensen and Gad 2004). Furthermore, two types of *Armorloricus* larvae (*A.* sp.1 and *A.* sp.2) have been recorded, but it has not yet been

possible to link the larvae with their corresponding adult stages (see Kristensen and Gad 2004).

The adults in the family Nanaloricidae have a short mouth cone with a protruding mouth tube. The mouth tube is extraordinarily long in the genus *Armorloricus* (Kristensen and Gad 2004). The mouth cone consists of numerous complex structures, such as oral stylets, oral furcae and different ridges, which together form a unique structure for sucking out the content of algae or bacteria. In the family Nanaloricidae, sexual dimorphism is displayed in the clavoscalids (first row of scalids on the introvert) where six of the male's eight clavoscalids are branched, and in the modification of the upper proximal appendage of the midventral pair of the double trichoscalid, that is modified into two claspers. These claspers function as a grapping mechanism for holding the female during copulation. Other unique characters of the adult Nanaloricidae are the feather-like scalids and the covering of the abdomen with six large plates. These plates vary in shape, size and ultrasculpture between the different genera.

The Higgins-larvae of Nanaloricidae have unique toes that are laterally flattened, forming leaf-like structures named mucros. These toes are used for crawling and paddling and may vary greatly in shape between the genera (Kristensen 1983, 1991; Kristensen and Gad 2004). The Higgins-larvae have three ventral pairs of locomotory setae and three posterior pairs of sensory setae. The small dorsal setae of the anal plate were overlooked in the original description of Loricifera (Kristensen 1983).

The Nanaloricidae was first thought to be restricted to the intertidal and subtidal zones, but recently this consideration has had to be revised with the finding of a new nanaloricid genus, *Phoeniciloricus*, from a deep-sea trench near Papua New Guinea (Gad 2004). This paper presents another new nanaloricid from non-coastal waters. The species was found at 150 m depth in calcareous sediments on Faroe Bank in the North Atlantic. Based on the presence of the extraordinarily long mouth tube and the lack of honeycomb ultrasculpture in the adults, the species is assigned to the genus *Armorloricus*, and it is named *A. kristenseni* sp. nov. in honour of Professor Reinhardt M. Kristensen.

Methods

The samples were collected during the BIOFAR programme ("Biological Investigations of the Faroe Islands") that started in 1987 with the goal of investigating the marine benthic fauna around the Faroe Islands (Nørrevang et al. 1994). The programme ended in 2003 with a symposium on the Faroe Islands. During the BIOFAR programme, the collection of meiofauna samples was concentrated on the Faroe Bank, which is situated southwest of the Faroe Islands. The Faroe Bank is a large bank that rises from 1000 m deep up to 100 m on the plateau (Nørrevang et al. 1994; Hansen et al. 2001), which corresponds to the definition of a seamount. The material was collected from three stations on the Faroe Bank. The sample from station 786 was collected in 1992 by the Faroese Coastguard vessel "Olavur Halgi". The collections from stations 1991 and 2019 were made in July 2001 with R.V. "Magnus Heinason" of the Faroese Fisheries Laboratory. The samples from station 1991 were taken at a depth of 136 m and from station 2019 at 139 m. An anchor dredge was used on both stations. The sediment on all three stations is composed of fine shell gravel (fShg) or fine shell sand (fShs) (for further information about the stations see Nørrevang et al. 1994). The locations of the stations are shown on Fig. 1. Note that they are all located on the plateau around the 150-m level.

The samples were processed immediately after collection. To release the animals from the sediment, the samples were osmotically shocked with freshwater and the water was then sieved through a fine, 32 μm-mesh net (Gwen's mermaid bra). This was done three times for each sample. The content of the mesh net was fixed in 2–4% formaldehyde buffered with Borax, or in trialdehyde. The animals were sorted out under a dissecting microscope. Prior to sorting, the animals were stained with "Rose Bengal", which binds to their cuticle, making them easier to find. All specimens except one were mounted on microslides, and dehydrated through a graded glycerin series and afterwards sealed with glyceel. The exception, a female (LOR 417 ZMUC), was prepared for SEM. The specimen was fixed with osmium-tetraoxide, and dehydrated through a graded acetone series. Afterwards, the specimen was critical-point dried and sputter-coated with gold-platinum.

The microslide specimens were studied using an Olympus BX51 microscope with differential interference contrast (DIC) and Normarski-technique, connected to an Olympus C-3030 zoom digital camera. The SEM specimen was studied on a JEOL JSM-6335 Field emission scanning electron microscope. All the material is deposited at the Zoological Museum, University of Copenhagen, Denmark (ZMUC).

Results

Phylum Loricifera Kristensen, 1983

Order Nanaloricida Kristensen, 1983

Family Nanaloricidae Kristensen, 1983

Genus *Armorloricus* Kristensen and Gad, 2004

(Type species *Armorloricus elegans* Kristensen and Gad, 2004)

In the diagnosis and description of the adults, the scalid formula for Pliciloridae is adopted (see Higgins and Kristensen 1986), hence the total number of scalid rows is nine, and not eight, such as in the original description of *Armorloricus* (see Kristensen and Gad 2004).

Armorloricus kristenseni, sp. nov.

Diagnosis of adults

Adults 188–340 μm long including mouth tube; mouth tube with six oral stylets and a mouth cone with eight oral furcae; clavoscalids five-segmented with hairs on the second and third segment and with the last segments forming a claw. Six of the eight clavoscalids are branched in the males: row 2 with nine leg-shaped scalids; row 3 with seven feather-like extraordinarily long scalids (53 μm) equipped with numerous fine hairs; row 4 with 16 smaller, leg-shaped scalids; rows 5–7 with 30 uniform scalids; row 8 with 30 trichoscalid-like spinoscalids; row 9 with 30 beak-like scalids situated on plates. Row 1 of the basal plates situated just beneath the introvert; longitudinal and transverse folds present between basal plate rows 1 and 2, basal plates triangular; 15 trichoscalids (eight single and seven double), double trichoscalids separated at their bases. The lorica consists of six large

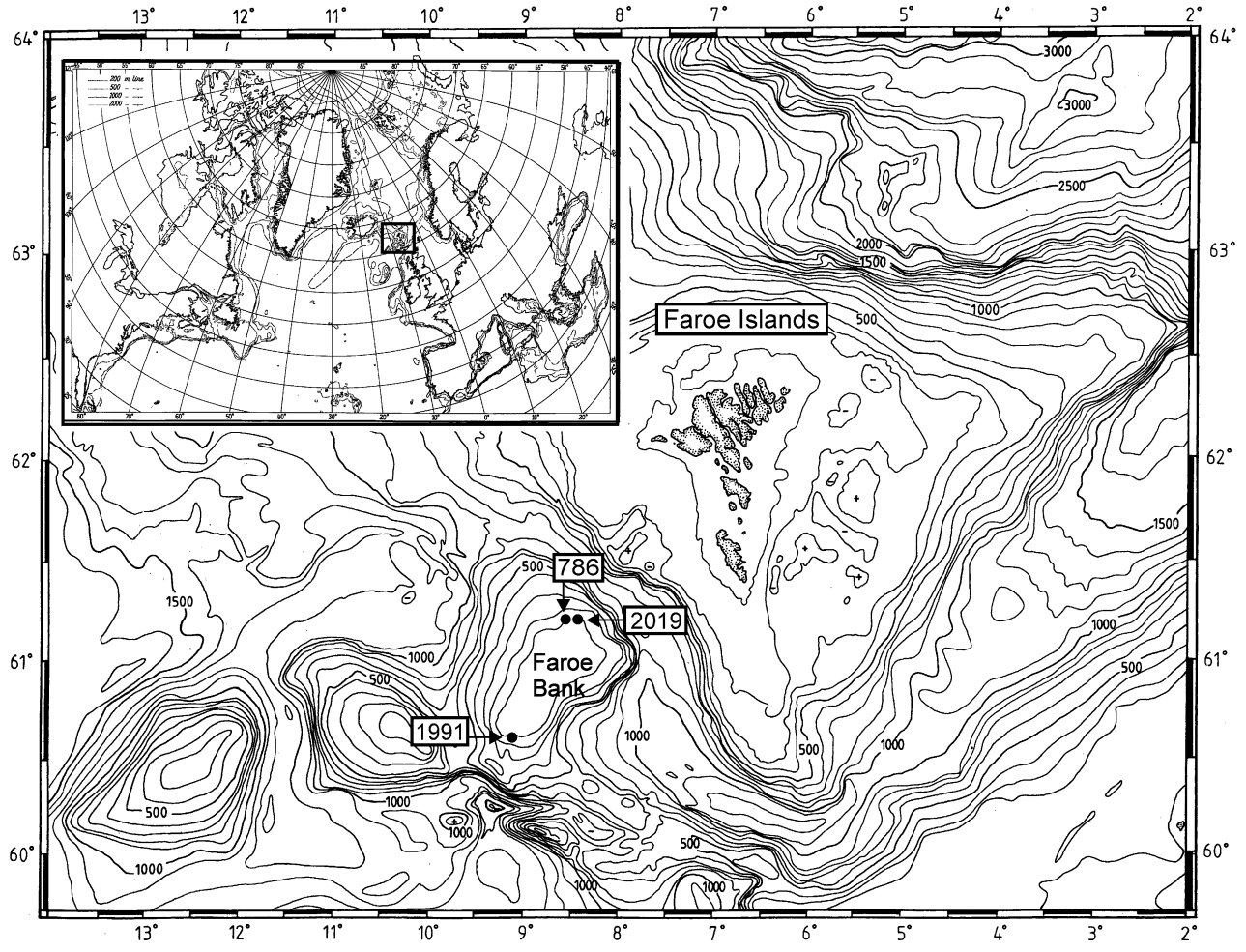

Fig. 1 Map of the Faroe Bank, with the BIOFAR stations 786, 1991 and 2019 located on the plateau

plates without the typical honeycomb ultrasculpture; ventral plate with subcuticle glands forming a "wheel" in the cuticle; two large lateral plates with two spikes on anterior margin; the more ventral spike is twice as long as the other; dorsolateral plates with four micro-flosculi, dorsal plate with one single micro-flosculus located near the anal cone; micro-flosculi without flower-shaped microvilli.

Diagnosis of Higgins-larva

Larvae 160 μm including mouth cone; mouth cone without internal or external armature; eight four-segmented clavoscalids with tips pointing inwards posteriorly, except the ventrolateral pair which is larger and has anteriorly pointed tips; row 2 absent; row 3 with curved spinose scalids; row 4 with a long middorsal scalid (18 μm), a long dorsal pair with broad bases and three spines (25 μm), and a midventral pair of hook-shaped scalids; row 5 with three pairs of large, claw-shaped scalids and a ventrolateral pair of very small scalids; row 6 with two ventral pairs of long scalids (28 μm) with hexagonal bases and a long segment with numerous fine hairs, and a dorsal pair of long scalids with serrated margins; row 7 with middorsal leaf-like scalids, three pairs of plate-like scalids with numerous teeth (two of the pairs are asymmetrical) and three pairs of small spines; three pairs of ventral locomotory setae between the thorax and the abdomen, the innermost seta is claw-like, the other two long (52 μm and 30 μm) with conspicuous knees. Abdomen rectangular with honeycomb ultrasculpture. Toes long (75 μm) with asymmetrical, leaf-like mucros, three pairs of anterior sensory setae (two long, 35 μm and one short, 4 μm) and three 7-lobed flower-shaped *Nanaloricus*-flosculi on the dorsal side of the three separated anal plates.

Type material

The holotype is an adult male (LOR 405 ZMUC) with no internal structures and a pharynx that has been pressed out a bit. The allotype is an adult female (LOR 406 ZMUC) with one egg and some small oocytes in the other ovary. A paratypic Higgins-larva (LOR 407 ZMUC) has also been drawn and described. The additional paratypes in-

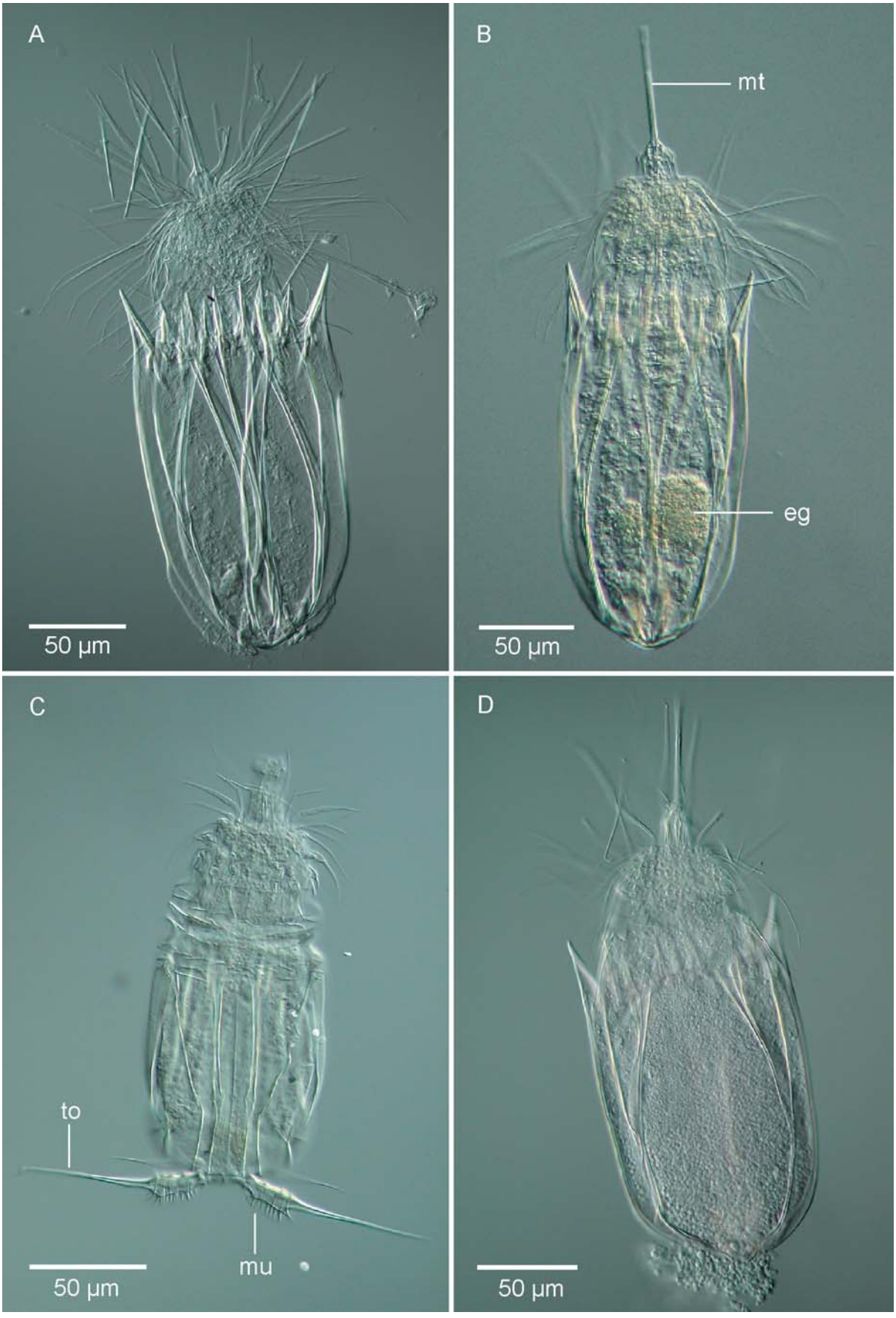

Fig. 2A–D Nomarski DIC micrographs of *Armorloricus kristenseni* sp. nov. **A** Holotypic male (LOR 405 ZMUC), **B** allotypic female (LOR 406 ZMUC), **C** Higgins-larva (LOR 414 ZMUC) and **D** postlarva (LOR 411 ZMUC). *eg* egg, *mt* mouth tube, *mu* mucros, *to* toe

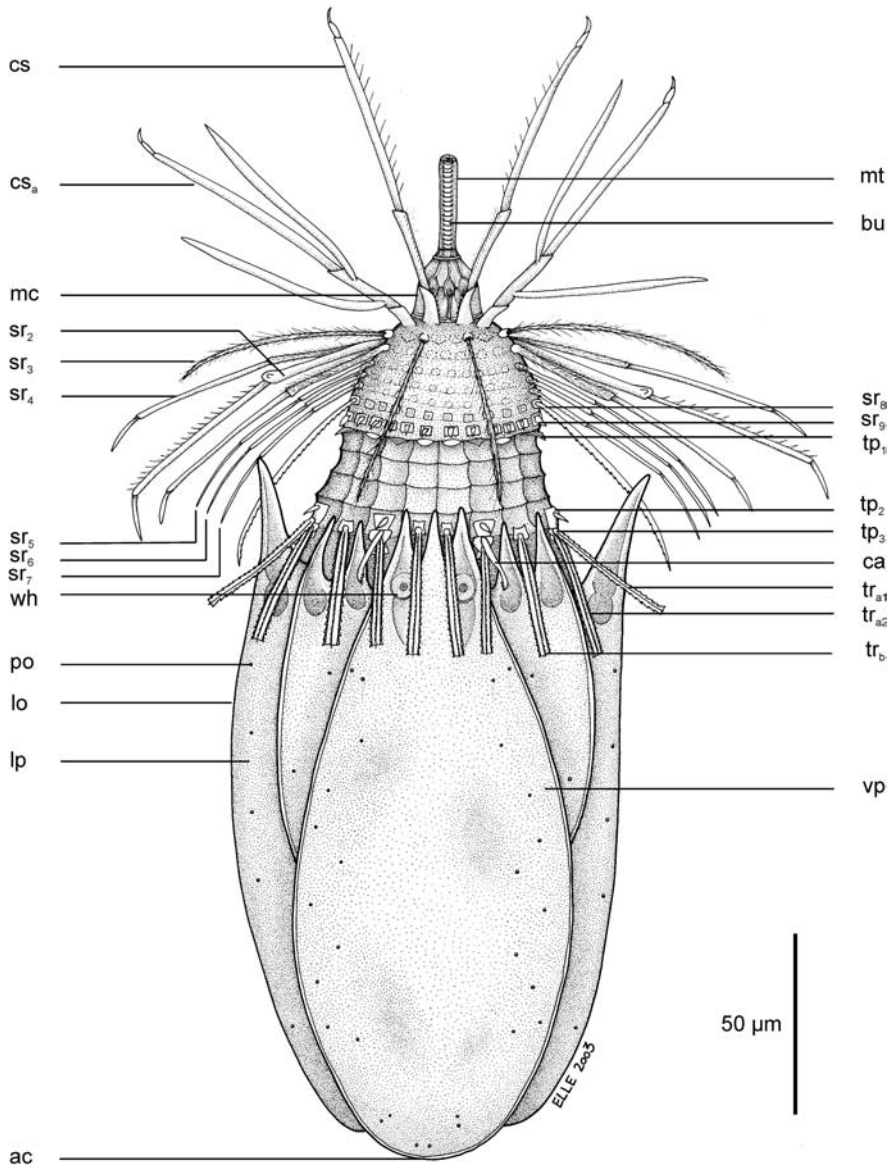

Fig. 3 Illustration of *A. kristenseni* sp. nov., holotypic male (LOR 405 ZMUC), ventral view. Note: only the four ventral clavoscalids, two branched and two unbranched, are shown. *ac* anal cone, *bu* buccal tube, *ca* claspers, *cs* unbranched clavoscalid in first row, cs_a branched clavoscalid in first row of males, *lo* lorica, *lp* lateral lorica plates, *mc* mouth cone, *mt* mouth tube, *po* pore on the lorica plates, $sr_{2–9}$ scalid rows 2–9, $tp_{1–3}$ trichoscalid plates 1–3, tr_{a1} primary appendage of double trichoscalid, tr_{a2} secondary appendage of double trichoscalid, tr_b single trichoscalid, *vp* ventral lorica plate, *wh* wheel-like structure of the subcuticular glands

clude four females (LOR 408–411 ZMUC), two postlarvae (LOR 412–413 ZMUC), one exuvium of a lorica (LOR 414 ZMUC), two Higgins-larvae (LOR 415–416 ZMUC) on microslides and one adult female (LOR 417 ZMUC) on a stub for SEM. All the specimens except one were collected in 2001 from stations 1991 and 2019. The exception is one of the Higgins-larvae (LOR 415 ZMUC) that were collected in 1992 from station 786.

Etymology

The species name *kristenseni* is in honour of Professor Reinhardt Møbjerg Kristensen, who described the phylum Loricifera in 1983. It is a tribute for the 20th anniversary of the description of Loricifera and for his help and participation in collecting the specimens during the collection trip in 2001 to the Faroe Bank with the ship R.V. "Magnus Heinason" from the Faroese Fisheries Laboratory.

Description of the adults

The holotypic male (Figs. 2A, 3) is 278 µm long, including the mouth tube, and the allotypic female is 332 µm long, also including the mouth tube (Figs. 2B, 4). The body of the allotypic female is quite slim, with a diameter of 97 µm at the broadest point of the abdomen. In contrast, the diameter of the abdomen of the holotypic male is 105 µm. The mouth tube (mt) of the holotypic male is not fully extended and therefore the body appears somewhat shorter than the female's. Because of the contraction of the mouth tube, the six oral stylets are not visible outside the mouth tube. Contrary to this, the mouth tube (mt) of the allotypic female is fully extended (82 µm) and the six oral stylets (os) are visible at the end of the mouth tube. The buccal tube (bu) is spiral-shaped and can be telescoped inside the mouth tube. Further down on the mouth cone (mc) there are eight oral furcae with posterior and anterior oral ridges (or_1 and or_2) (Fig. 5D, E). Each

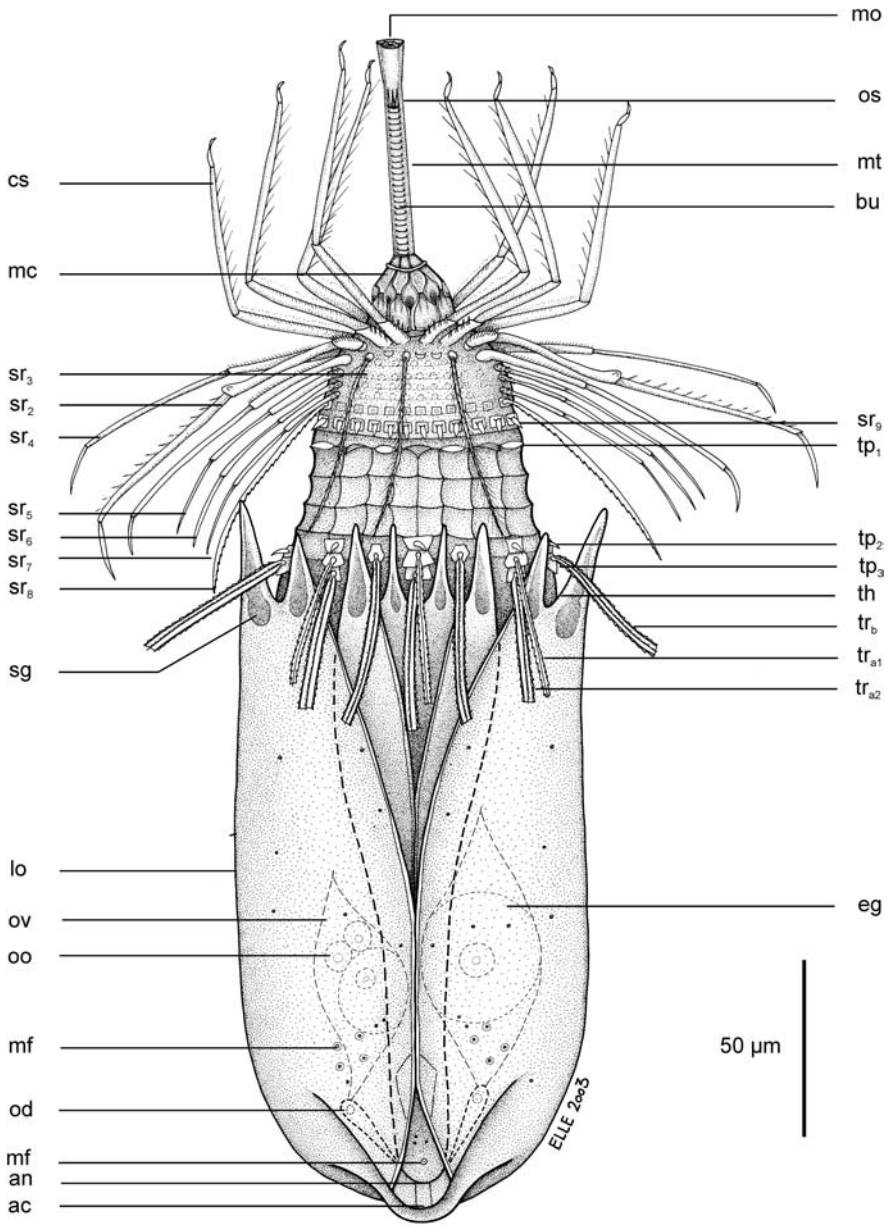

Fig. 4 Illustration of *A. kristenseni* sp. nov., allotypic female (LOR 406 ZMUC), dorsal view. Note: all eight clavoscalids are shown. *ac* anal cone, *an* anus, *bu* buccal tube, *cs* unbranched clavoscalid in first row, *eg* egg, *lo* lorica, *mc* mouth cone, *mf* micro-flosculus, *mo* mouth opening, *mt* mouth tube, *od* ovary duct, *oo* oocyte, *os* oral stylet, *ov* ovary, *sg* subcuticular epidermal gland, $sr_{2–9}$ scalid rows 2–9, *th* thorax, $tp_{1–3}$ trichoscalid plates 1–3, tr_{a1} primary appendage of double trichoscalid, tr_{a2} secondary appendage of double trichoscalid, tr_b single trichoscalid

furcae alternates with a supportive ridge for reinforcement. Eight transverse cuticularized rectangular plates are located between the mouth cone and the introvert.

The introvert has nine rows of scalids (Fig. 9A). Row 1 consists of eight clavoscalids in both sexes. In the males, six of the eight clavoscalids are modified into branched clavoscalids (cs_a) consisting of one main branch and two secondary branches. In contrast, all eight clavoscalids in the females and the midventral clavoscalid pair in the male (cs) are unbranched and divided into five segments. The first basal segment is short. The second is of medium length and has numerous fine hairs. The third segment is long, approximately half the length of the whole scalid, and with a few thick hairs. The two most distal segments are very short and the terminal one is hook-shaped. The main branch of the branched clavoscalids (cs_a) has five segments that correspond to the unbranched clavoscalids. The two secondary branches are one-segmented and club-shaped and are located on the second segment. There are no hairs on the branched scalids.

The scalids in rows 2–9 are called spinoscalids ($sr_{2–9}$) (Fig. 5F). Row 2 consists of nine leg-shaped scalids (sr_2). The leg-shaped spinoscalids have five segments. The first segment has a small bulbous base and the second one is short with several minute hairs (Fig. 6A, B). The third segment is long with a posteriorly located knee. The fourth segment is about half the length of the total scalid and has spines scattered on the whole segment. The last segment is a strong, claw-shaped spine. Row 3 consists of seven feather-like scalids (sr_3). The feather-like scalids are long (64 μm) with numerous long, thin hairs (Fig. 6C). The alternation between the second and third row is not regular, since in the midventral and middorsal position

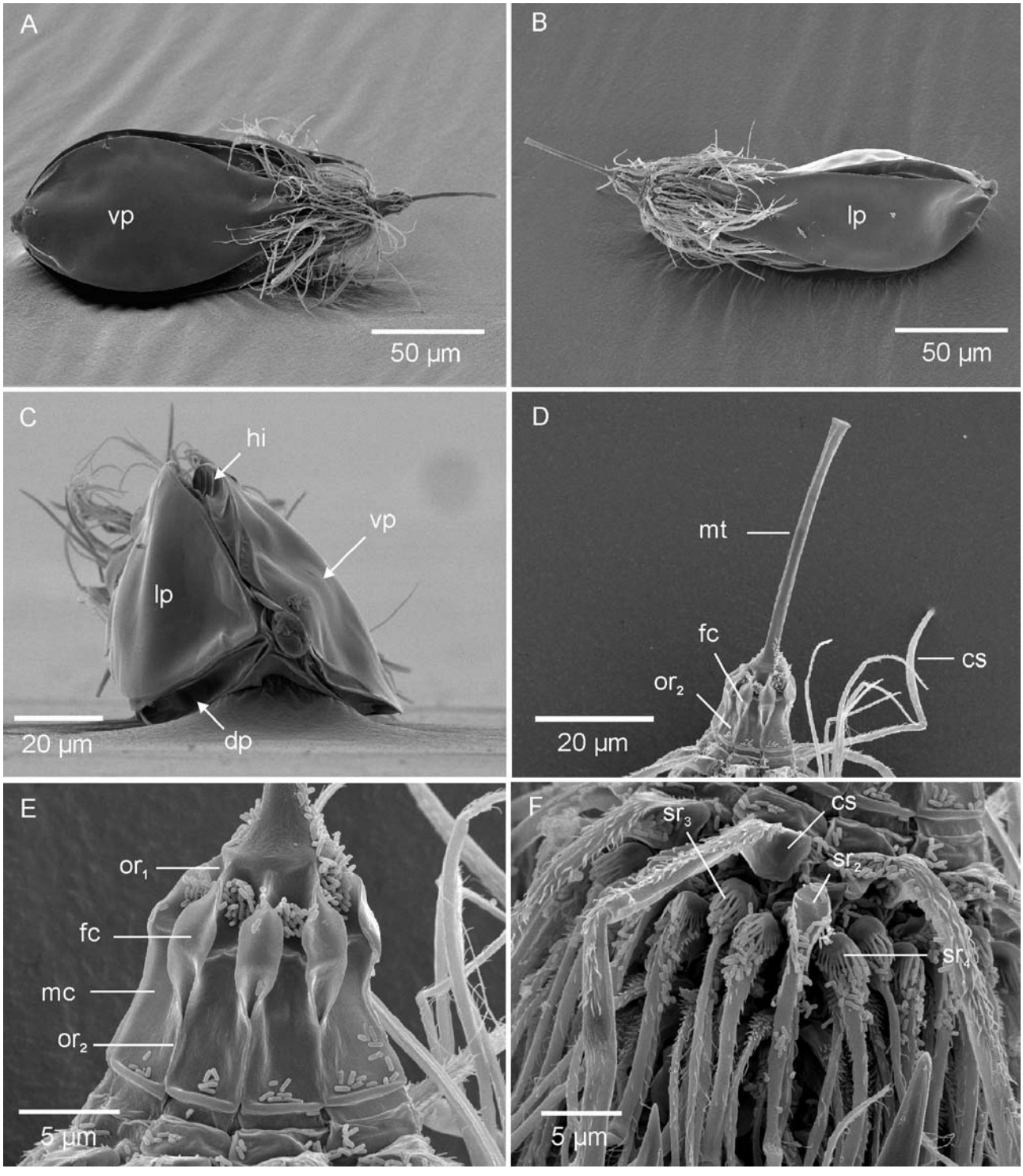

Fig. 5A–F SEM micrographs of *A. kristenseni* sp. nov., adult female (LOR 416 ZMUC). **A** ventral view, **B** lateral view, **C** posterior view, **D** mouth cone and mouth tube, **E** close-up of mouth cone and **F** introvert with the different rows of scalids. *cs* unbranched clavoscalid in first row, *dp* dorsal lorica plate, *fc* oral furcal, *hi* hinge, *lp* lateral lorica plates, *mc* mouth cone, *mt* mouth tube, or_1 anterior oral ridge, or_2 posterior oral ridge, $sr_{2–4}$ scalid rows 2–4, *vp* ventral lorica plate

there are no feather-like scalids under the two leg-shaped scalids.

Row 4 consists of 16 scalids of only one type (sr_4), a smaller leg-shaped scalid with three segments. The first segment has a bulbous base with many fine hairs (Fig. 6B). The second segment is long and smooth. The third segment is a spine formed like a claw.

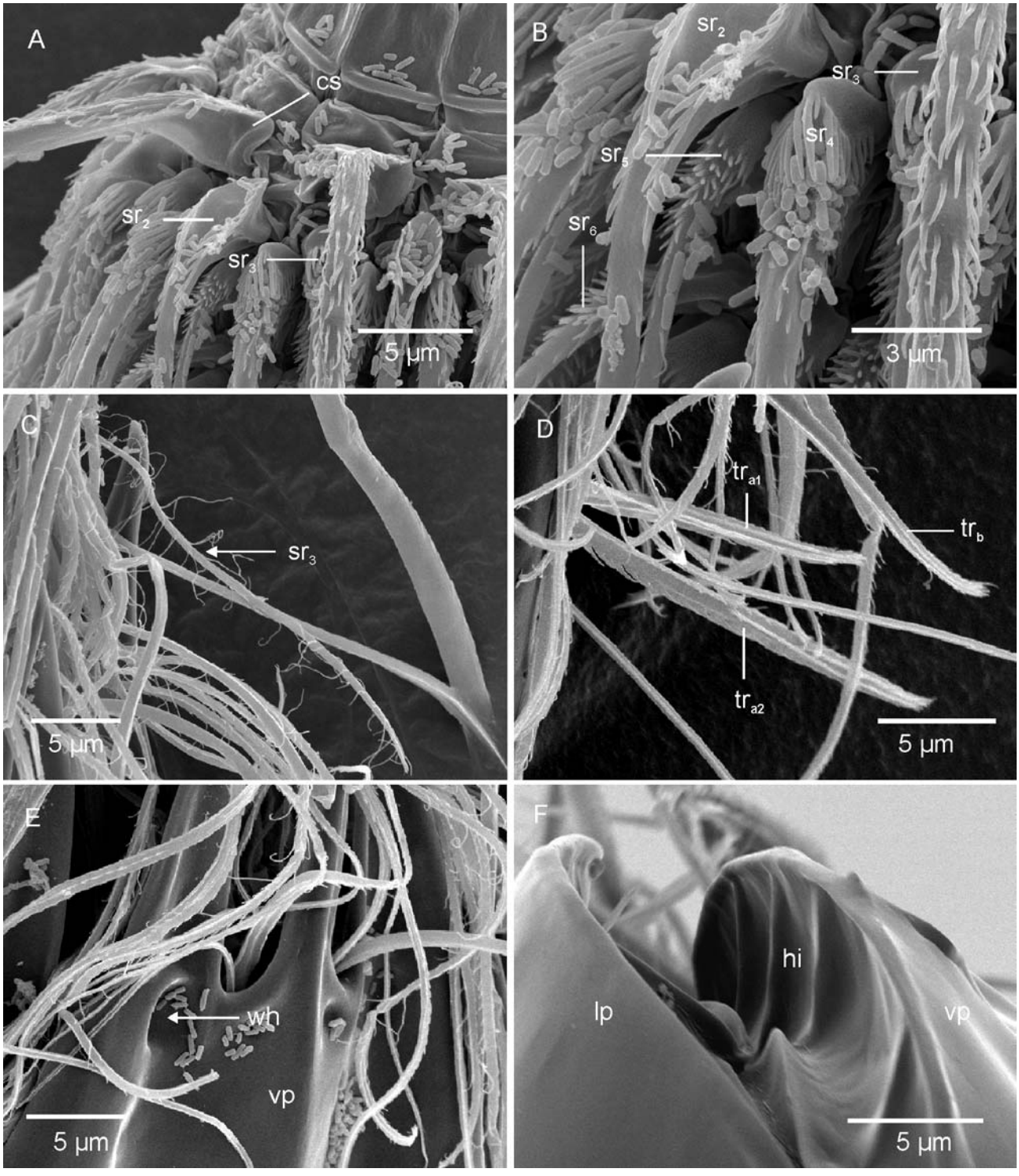

Fig. 6A–F SEM micrographs of *A. kristenseni* sp. nov., adult female (LOR 416 ZMUC). **A** close-up of the 1st to 3rd rows, **B** close-up of the 2nd to 6th rows, **C** feather-like scalids, **D** double and single trichoscalids, **E** wheel-like structure on the ventral plate and **F** hinge between the ventral and one of the lateral plates. *cs* unbranched clavoscalid in first row, *hi* hinge, *lp* lateral lorica plates, $sr_{2–6}$ scalid rows 2–6, tr_{a1} primary appendage of double trichoscalid, tr_{a2} secondary appendage of double trichoscalid, tr_b single trichoscalid, *vp* ventral lorica plate, *wh* wheel-like structure of the subcuticular gland

Rows 5–7 have 30 uniform spinoscalids in each row. These scalids (sr_5-sr_7) consist of three segments in which tubercles are located on the bases of the first segments. Row 8 consists of 30 trichoscalid-like scalids (sr_8). The scalids have a basal plate and serrated margins. Row 9 consists of 30 beak-like scalids (sr_9) with a large rectangular basal plate.

In the neck region, there are three rows of basal plates with 15 plates in each row and a row of trichoscalids (Fig. 6D). Row 1 of the basal plates (tp_1) is situated just below row 9 of the spinoscalids. In row 1, there are two types of alternating plates, round and triangular. After basal plate row 1 there is a region with longitudinal and transverse folds. There are eight single (tr_b) and seven double (tr_a) trichoscalids in the trichoscalid row. The single trichoscalids have two basal plates (tp_{2-3}) that are more or less fused. The single trichoscalids (tr_b) are about 30 μm long, and the longest pair is situated ventrally. The trichoscalids have serrated medial margins. The primary appendage of the double trichoscalid (tr_{a1}) is connected to the second basal plate (tp_2), which is split into two plates. The upper part of the secondary basal plate (tp_2) has a spine and the primary appendage is connected to the lower part of the second plate (tp_2). The secondary appendage (tr_{a2}) is connected to the third basal plate (tp_3). All the basal plates in the 2nd and 3rd rows are triangular. The primary appendage and the secondary appendage are both 38 μm long and have serrated margins, even though the primary appendage lacks serration on the ridge. On the ventral side, two of the primary appendages of the double trichoscalids (tr_{a1}) are modified into claspers (ca) in the male (Fig. 3). These claspers are long (16 μm) and have three terminal teeth. The claspers are used for holding the female during copulation, but no live observations have been made on *A. kristenseni* sp. nov.

The thorax region (th) has no appendages and is difficult to examine because the spikes from the lorica hide the thorax.

The lorica consists of six smooth lorica plates with a total of 15 spikes. The anterior margins of the lorica plates cover the posterior part of the thorax. The spikes are very strong, with internal ducts of epidermal subcuticle glands (sg). The midventral plate (vp) has three spikes and the subcuticle glands form two wheel-like structures (wh) in the cuticle (Fig. 6E). The lateral plates are large (lp), covering most of the dorsal plate (dp) (Fig. 5B), and join the ventral plate through hinges (hi) at their posterior ends (Fig. 6F). Hence, the body appears triangular in cross-section (Fig. 5C). The more ventral spike on the lateral plate is almost twice as long as the other spikes. The ventrolateral plates are small and almost covered by the large ventral plate. The middorsal plate has four spikes and, at the anterior end of the lorica, it is divided into three parts. Around the edges, several pores (po) are located in a more or less symmetrical pattern. Four micro-flosculi (mf) are located posteriorly on each of the dorsolateral plates, and one single micro-flosculus (mf) is located on the posterior part of the dorsal plate. The micro-flosculus lacks the flower-shaped microvilli but has a central, long cilium extending from the opening of the cuticle. Beneath the dorsal plate, there are three anal plates that form the anal cone (ac). The reproductive system could not be observed in the holotypic male. In the allotypic female there are two ovary ducts (od) that are situated between the dorsal plate and the anal cone and form the opening of the two ovaries (ov). Inside one of the ovaries there are three small oocytes (oo), and inside the other one large egg (eg). Seminal receptacles were not observed.

Description of postlarva (paratype)

The postlarvae (Fig. 2D) are morphologically identical to the females except for the absence of the seventh row of spinoscalids on the introvert. Mature gonads are absent, and instead glandular cells and coelomocytes fill the body. Generally, the postlarvae are smaller than the adults (80–90% of adult size) and their abdomens appear more rectangular (Fig. 2D). The two paratypic postlarvae measure 269 μm (LOR 413 ZMUC) and 275 μm (LOR 412 ZMUC) long.

Description of Higgins-larva (paratype)

The paratypic Higgins-larva is 160 μm long including the mouth cone (Figs. 2C, 7, 8). The widest diameter of the trunk is 59 μm. The mouth cone (mc) lacks internal and external armature. Six oral valves close the mouth opening (mo) anteriorly.

The introvert has only six rows of scalids, since the second row (sr_2) is missing (Fig. 9B). The scalids are more or less arranged in functional units rather than rows. Hence the different rows are difficult to observe (Fig. 9B). The bilateral symmetry is very clear on the introvert. In row 1 there are eight clavoscalids (cs). These clavoscalids are long (33 μm), spinose and divided into four segments. The first segment is a small bulbous base. The second and third are of equal length and the fourth is a claw-shaped inward-pointing spine. The ventrolateral pair differs from the others. The scalids are thicker and the claw-shaped spine is pointing posteriorly. Row 2 (sr_2) is missing. Row 3 (sr_3) consists of 15 two-segmented spinoscalids, eight on the ventral side and seven on the dorsal. The first segment consists of a swollen base with a long shaft ending in a well-developed hinge joint connecting to the second segment. The four midventral scalids are shorter and straighter than the others. The ventrolateral pair, located next to the four midventral pairs, has a conspicuous hinge joint and the two segments articulate in a 90-degree angle. The middorsal scalid is also shorter than the others and points anteriorly (Fig. 8). The last pairs in this row (two ventral and two lateral) are bent, with the second spinose segment curved upwards. Row 4 consists of 15 spinoscalids (sr_4) of various appearances and lengths. The midventral pair of spinoscalids (sr_{4a}, Fig. 9B) is small and hook-shaped, with a large bulbous base (Fig. 7). The

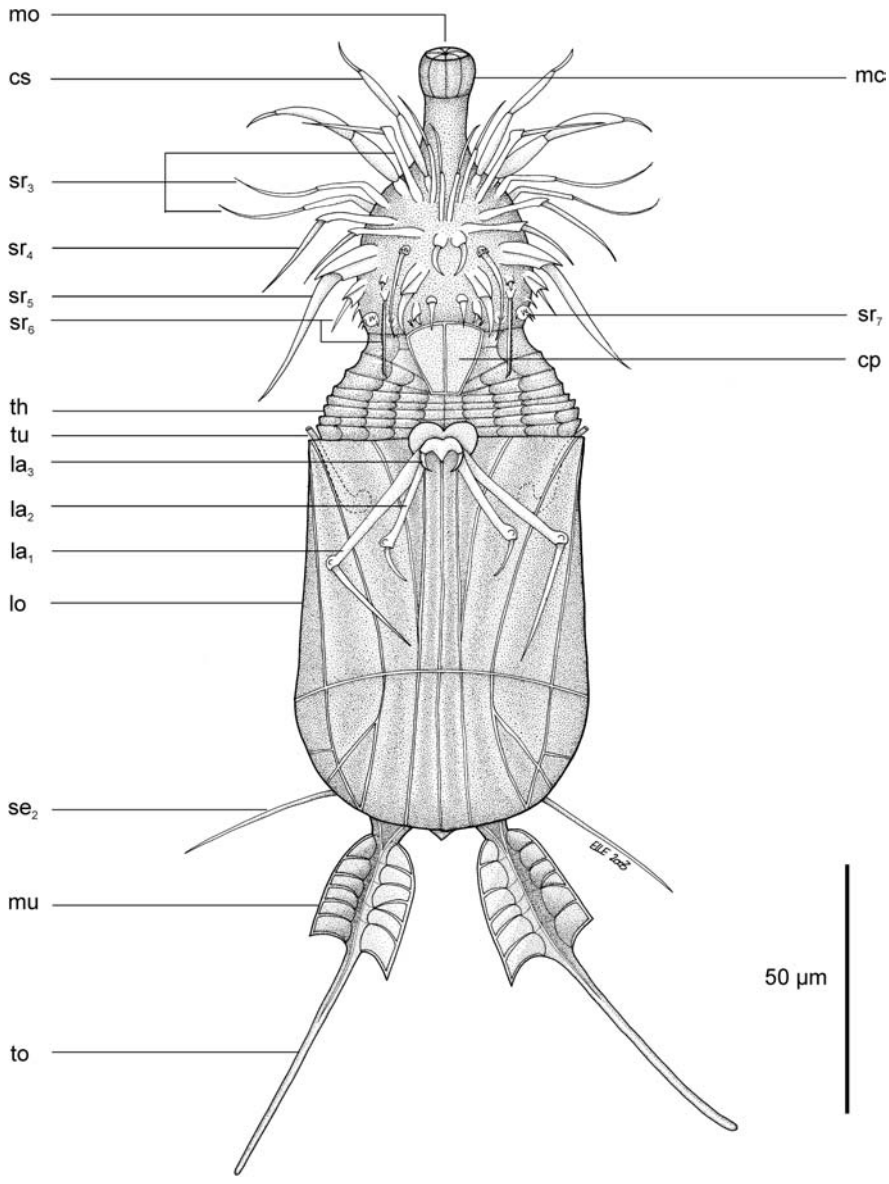

Fig. 7 Illustration of *A. kristenseni* sp. nov., Higgins-larva (LOR 407 ZMUC), ventral view. *cp* closing plate of thorax, *cs* unbranched clavoscalid in first row, la_1 anterolateral seta, la_2 anteromedial seta, la_3 anteroventral seta, *lo* lorica, *mc* mouth cone, *mo* mouth opening, *mu* mucros, se_2 posterolateral setae, sr_{3-7} scalid rows 3–7, *th* thorax, *to* toe, *tu* tubes

middorsal scalid (sr_{4h}) has a large hexagonal plate with a long (18 μm), thin appendage, which is attached under the plate. The two pairs located on the ventral side (sr_{4b+g}) consist of a large base with three spines and a long second segment. The dorsal pair is longer (25 μm) than the ventral pair (20 μm). Two lateroventral pairs (sr_{4c+d}) and one laterodorsal pair (sr_{4f}) are leg-shaped, equally sized and shaped as the curve-shaped scalids in row 3, except that the lateroventral pairs do not curve as much as the others. The last pair of spinoscalids (sr_{4e}) are lateral, uniformly long (35 μm) and lack segmentation. Row 5 consists of 15 spinoscalids (sr_5). There are three pairs of large, claw-shaped scalids that are divided into two segments (sr_{5b+d+f}). The first segment is an enlarged base with a diagonal ridge and a distal spine. The second segment is long and spinose. The spinoscalids of the midventral pair (sr_{5a}) are small (8 μm) with rounded bases and located just above the closing plate (cp). A pair of small, tooth-like spinoscalids is located in between the large claw-shaped scalids on the ventral side (sr_{5c}). The middorsal spinoscalid of the 5th row is a triangular plate with a small spine (sr_{5h}). Next to the middorsal scalid there is a pair of scalids with rounded bases and a diagonal ridge that ends in a large spine (sr_{5g}). Located laterally is an additional pair (sr_{5e}) that lacks the diagonal ridge. Row 6 consists of 13 spinoscalids (sr_6). The middorsal scalid is small and ends into a little tip (sr_{6g}). The pair next to the middorsal scalid and the lateral pair (sr_{6d+f}) are long scalids (~28 μm) with a hexagonal plate and a long secondary segment with fine hairs on both margins. Between the two pairs is a pair with rounded bases that end in a spine (sr_{6e}). The latter is the same type as in row 5. Ventrally, there are only six scalids. The small midventral pair is tooth-like (sr_{6a}). The next pair (sr_{6b}) is long (18 μm) with a rectangular base, and the second segment is long and serrated on the lateral mar-

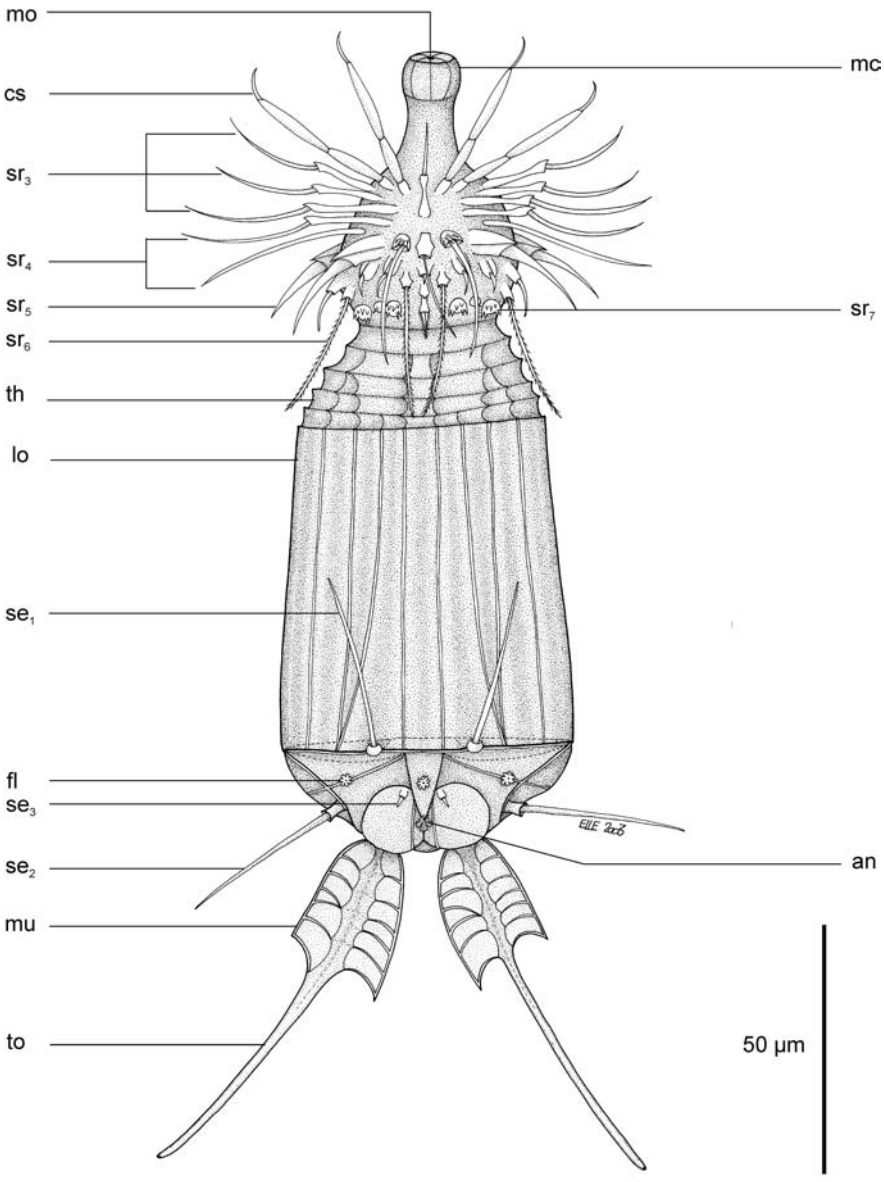

Fig. 8 Illustration of *A. kristenseni* sp. nov., Higgins-larva (LOR 407 ZMUC), dorsal view. *an* anus, *cs* unbranched clavoscalid in first row, fl flosculus (*Nanaloricus*-type) on larva, *lo* lorica, *mc* mouth cone, *mo* mouth opening, *mu* mucros, se_1 posterodorsal setae, se_2 posterolateral setae, se_2 posteroterminal setae, sr_{3-7} scalid rows 3–7, *th* thorax, *to* toe

gins. The last row of scalids consists of a lateral pair of claw-shaped scalids, the same type as seen in row 5 (sr_{6c}). Row 7 consists of 15 spinoscalids (sr_7), a middorsal leaf-like scalid (sr_{7h}), and three pairs of teeth-like scalids with basal plates with numerous teeth (sr_{7c+e+g}) alternating with four pairs of protoscalids ($sr_{7a+b+d+f}$). The leaf-like structure (sr_{7h}) has two segments, the last is secondarily divided and with many fine hairs. The dorsal pair of the teeth-like scalids has two teeth on each side of the plate and two to three teeth on the plate itself (sr_{7g}). The other two pairs (sr_{7c+e}) also have the same number of teeth, although the teeth on the sides of the plates are not symmetrical; the teeth of the ventrolateral pair (sr_{7c}) are longer laterally and the teeth of dorsolateral pair (sr_{7e}) are longer dorsally.

The scalids in each row are more or less reduced, especially on the ventral side where the midventral scalids of the fifth and sixth rows, together with the two closing plates (cp), form a closing apparatus, for when the introvert is drawn into the body cavity.

The thorax (th) has several transversal folds (six ventral and five dorsal) that can slide into each other like an accordion. This is seen clearly on the ventral side (Fig. 7). On the ventral side, two large closing plates (cp) are situated in between the first transverse fold that is secondarily divided into three folds. Two to three longitudinal folds are seen additionally across the transverse folds.

Three pairs of locomotory appendages (setae) are present ventrally between the thorax and the abdomen. The lateral pair (la_1) is very long (52 μm), with a conspicuous knee and a pointed end. The medial pair (la_2) is 30 μm long, also with a conspicuous knee, but with a stump end. The innermost pair (la_3) are formed as claws, 8 μm in length. The three pairs of setae are basally fused with a heart-shaped plate that covers part of the last thorax row.

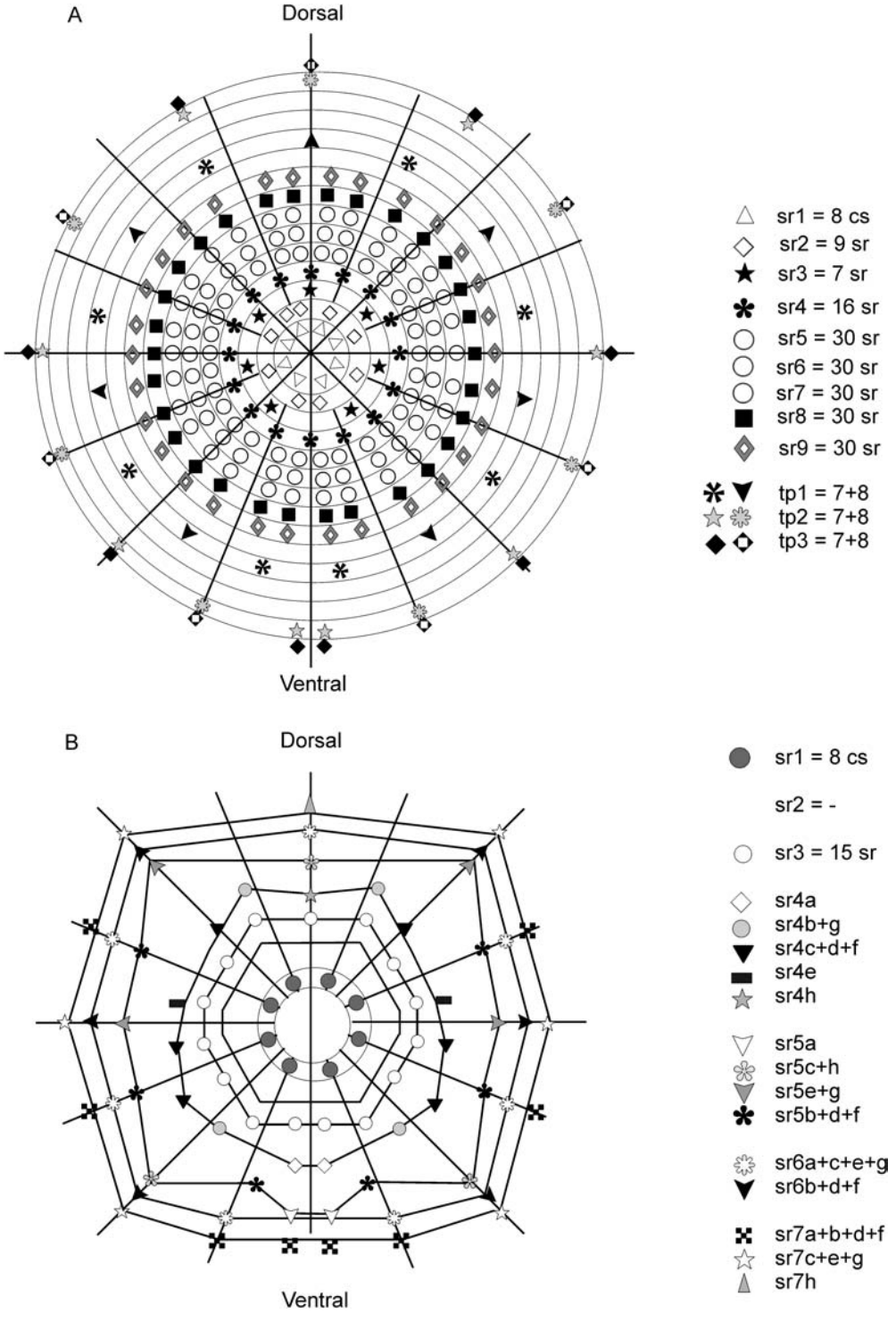

Fig. 9A, B Diagram of the scalid rows of the introvert of *A. kristenseni* sp. nov. **A** adult and **B** Higgins-larva. sr_{1-9} Scalid rows 1–9, tp_{1-3} trichoscalid plates 1–3

The abdomen is rectangular and the lorica has a very distinct honeycomb ultrasculpture (not shown on Figs. 7, 8). The lorica has 22 longitudinal folds. Two multicellular glands, that are extended into two tubes (tu), are located on the anterior end on the lateroventral side of the lorica.

The two toes (to) measure 75 μm and are basally enlarged in a leaf-like structure named the mucros (mu). The mucros terminate into pronounced tips and have five transverse ridges on each side of the leaf. The mucros are asymmetrical, since the tips on the interior margins are longer than those on the exterior. The toes are connected to the abdomen by ball and socket joints. A pore is situated terminally on both toes. Dorsally, there are three pairs of posterior appendages (setae). The dorsal pair of sensory setae (se_1) is very long (35 μm) and has a rounded base. The lateral pair (se_2) is the same length as the dorsal pair, but with a more rectangular base. The dorsoterminal pair of setae (se_3) is reduced (4 μm) and has a rectangular

base. The central anal plate is triangular and has a single, 7-lobed, flower-shaped *Nanaloricus*-flosculus (fl). On the two lateral anal plates, there are two pairs of very distinct ridges, and two 7-lobed, flower-shaped *Nanaloricus*-flosculi (fl) are located on one of them. The anus (an) is located beneath the central anal plate, surrounded by a three-lobed area and the two large basal plates of the toes.

Discussion

Diagnostic features

The presence of an extraordinarily long mouth tube and six smooth lorica plates without honeycomb ultrasculpture clearly designates the new species to the genus *Armorloricus*. With the description of *A. kristenseni* sp. nov., *Armorloricus* now contains three distinct species. *A. kristenseni* is easily recognized by the presence the longer, feather-like scalids (Fig. 6C), the wheel-like structure of the subcuticular glands (Figs. 3, 6E) and the long claspers with teeth in the male (Fig. 3).

The adults of *Armorloricus kristenseni* sp. nov. look superficially more like *A. elegans* in the shape of the lorica (Figs. 3, 4, 5A–C) and the location of the microflosculi (Fig. 4), than *A. davidi*. In *A. elegans* and *A. davidi*, there are two types of arthropod-like scalids in the third row, which is equivalent to the fourth row in *A. kristenseni* sp. nov., where there is only one type of scalid (Kristensen and Gad 2004). The spinoscalids and the trichoscalids are more robust in *A. elegans* and *A. davidi* compared to *A. kristenseni* sp. nov. (Kristensen and Gad 2004).

The Higgins-larva of *A. kristenseni* sp. nov. resembles the Higgins-larva of *Armorloricus* sp.1 (Kristensen and Gad 2004). Comparison of the larvae of *A. kristenseni* and *Armorloricus* sp.1 reveals numerous similarities, such as the shape of the whole larva, the shape of the lorica, the shape of the toes and the scalids on the introvert. They both have a rectangular lorica, and the mucros on the toes are both asymmetrical. The spinoscalids on the introvert are very similar, except that the long scalids of the sixth row on the dorsal side are longer in *A. kristenseni* sp. nov. and the scalids in the seventh row in *A. kristenseni* sp. nov. are not symmetrical, contrary to *Armorloricus* sp.1 and *Armorloricus* sp.2 (Kristensen and Gad 2004). The ventral setae resemble the ones in *Armorloricus* sp.2, except for the anteroventral setae (la_3) which are shorter and more claw-like in *A. kristenseni* sp. nov. The knee-like hinge in the other two setae (la_1 and la_2) is larger in *A. kristenseni* sp. nov., than in the other species (Kristensen and Gad 2004).

Number of scalid rows

Since the beginning of loriciferan research, the interpretation of the scalid rows in the adults has been highly debated. In the family Pliciloricidae, there are nine rows of scalids on the introvert (Higgins and Kristensen 1986). In the original description of *N. mysticus* Kristensen, 1983 the adults were described as having nine rows of scalids. The ninth row described by Kristensen (1983) consists of only 15 plates, which differ considerably from the spinoscalids in the previous rows. The 15 plates resemble the other thoracic basal plates found further down. Therefore Kristensen and Gad (2004) described this row as the first row of basal plates (tp_1) that had moved closer to the introvert. With the reinterpretation of the ninth row Kristensen and Gad (2004) concluded that there were only eight rows on the introvert in the family Nanaloricidae. However, the last four posterior rows (rows 5–9 in Pliciloricidae and rows 4–8 in Nanaloricidae) are very similar in both families and should be considered homologous. Hence, they should be the starting point in numbering the rows (see Kristensen 1983; Higgins and Kristensen 1986; Kristensen and Gad 2004). A consistency in the number of rows between the families is crucial when comparing the different scalids across genera. Therefore, a splitting of row 2 in Nanaloricidae into a second and third row would provide more consistency (Fig. 9A). Currently, there is an alternation in row 2 between nine leg-shaped scalids and seven feather-like scalids (Kristensen 1983; Kristensen and Gad 2004). This alternation is uneven, since there are two leg-shaped scalids located next to each other on both the ventral and the dorsal side. This unevenness on both sides, and not just on the ventral as usually seen, indicates that there must be two rows instead of one. The splitting of row 2 is done so that the large, leg-shaped scalids (sr_2) are in row 2, as in Pliciloricidae, and the feather-like scalids (sr_3) are in row 3, where these scalids correspond to the smaller leg-shaped scalids in Pliciloricidae (Fig. 9A). When introducing a new row, the third row with the claw-shaped and the two-segmented scalids (two different types of arthropod-like scalids) in the genera *Armorloricus* and *Nanaloricus* becomes the fourth row (Kristensen and Gad 2004). This also corresponds with row 4 in Pliciloricidae (Higgins and Kristensen 1986). Another argument is the statement by Kristensen and Gad (2004) in the original description of *Armorloricus*, that the scalids sr_{3b} in *A. elegans* and *A. davidi* are identical to the claw-shaped scalids in row 4 of the family Pliciloricidae. Therefore, the third row in Nanaloricidae is identical to the fourth in Pliciloricidae.

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