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Armorloricus, a new genus of Loricifera (Nanaloricidae) from Trezen ar Skoden (Roscoff, France)

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Abstract: Two new species of Loricifera (Nanaloricidae), *Armorloricus elegans* sp. nov. and *A. davidi* sp. nov. are described as representatives of a new genus from the sediment of Trezen ar Skoden (Roscoff, France) in the vicinity of the type locality of *Nanaloricus mysticus*. Diagnosis and description are based on all life history instars: adults, postlarvae, and Higgins-larvae, all collected from the upper surface layer of shell gravel at 50-55 m depth. The adults of the new genus are characterized by a smooth lorica with large midventral and laterodorsal plates. The dorsal plate of the lorica is longitudinally subdivided into three additional plates. The short mouth cone has an extremely long mouth tube. The clavoscalids and lateroventral trichoscalids display sexual dimorphism in both species. In the males the clavoscalids possess next to the main branch two additional club-shaped branches. The leglike scalids of the second row are smooth, strongly sclerotized, and distally as broad as the clavoscalids. Internally, the prepharyngeal armature of adults is equipped with an additional posterior part called the manubrium, which consists of three fused bracelets. The respective stout Higgins-larvae display an angular lorica and toes winged by two short mucrones ending distally in spared tips. Both the toes and the lorica have a honeycomb sculpture. Additional larval features are short, solid scalids covering the introvert and short locomotory appendages inserting ventrally on the trunk. The distinguishing characters of *Armorloricus* gen. nov. and *Nanaloricus* are discussed in detail. Apart from *Nanaloricus*, this is the first report of an additional taxon of the Nanaloricidae, which results in a revision of the characters at the family level. Investigations of the type material indicate a highly modified status of the Nanaloricidae, which can be shown e.g. in the transformation and arrangement of scalids in the adults and even in the Higgins-larvae. Therefore new scalid distribution schemes of all life instars are included.

Résumé : Armorloricus, *un nouveau genre de Loricifera (Nanaloricidae) de Trezen ar Skoden (Roscoff, France)*. Deux nouvelles espèces de Loricifera Nanaloricidae, *Armorloricus elegans* sp. nov. et *A. davidi* sp.nov sont décrites comme représentatives d'un nouveau genre récolté dans le sédiment de Trezen ar Skoden, au voisinage de la localité type de *Nanaloricus mysticus*. La diagnose et la description sont basées sur tous les stades du cycle de vie des espèces : adultes, postlarves, "larves-Higgins", tous récoltés dans la couche superficielle du sédiment coquillier à 50-55 m de profondeur. Les adultes du nouveau genre sont caractérisés par une lorica lisse avec de larges plaques médio-ventrales et latéro-dorsales. La plaque dorsale de la lorica est subdivisée longitudinalement en trois plaques. Le cône buccal court a un tube buccal extrèmement long. Les clavoscalides et les trichoscalides latéro-ventrales présentent un dimorphisme sexuel chez les deux espèces. Chez les mâles les clavoscalides possèdent près de la branche principale deux branches supplémentaires en forme de massue. Les sca-

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lides en forme de patte de la seconde rangée sont lisses, fortement sclérifiées et distalement aussi larges que les clavoscalides. L'armature pré-pharyngienne interne des adultes est équipée d'une partie postérieure supplémentaire appelée manubrium qui comprend trois bracelets fusionnés. Les robustes "larves-Higgins" ont une lorica angulaire et des orteils dont les extrémités portent deux terminaisons divergentes. Les orteils comme la lorica ont une ornementation en nid d'abeille. Les autres caractères larvaires sont de robustes scalides recouvrant l'introvert et de courts appendices locomoteurs insérés ventralement sur le tronc. Les caractères distinctifs de *Armorloricus* genus nov. et *Nanaloricus* sont discutés en détail. Ceci est la première mention d'un nouveau taxon de Nanaloricidae qui conduit à la révision des caractères apomorphes au niveau de la famille. Des recherches sur le matériel type indiquent un état très modifié des Nanaloricidae par exemple dans la transformation et l'arrangement des scalides chez les adultes et même chez les "larves-Higgins". En conséquence de nouveaux schémas de distribution des scalides à tous les stades sont donnés.

Keywords: Loricifera, Nanaloricidae, *Armorloricus* gen. nov., *A. elegans* sp. nov., *A. davidi* sp. nov. Roscoff, meiofauna, SEM.

Introduction

The first representative of Loricifera, *Nanaloricus mysticus* Kristensen, 1983 was discovered (at Easter-time 1982) in the interstices of a shell gravel (*Dentalium* sand) off the coast of Roscoff, France (Kristensen, 1983). In the vicinity of the type locality, more samples were taken in the following years (1985, 1987, and 1989) which yielded five additional species of Nanaloricidae. These new species were studied by the authors in 2001 during a COBICE project (Copenhagen Biosystematics Centre). Two of these five new species are represented by all instars and resulted in a new taxon of higher rank, which is described in this publication as a new genus of Nanaloricidae. Nanaloricidae are found in shallow to deep coastal waters of many locations, where they inhabit coarse sediments mainly of calcareous origin (Kristensen, 1983; Todaro & Kristensen, 1998; Kristensen, 2003; Gad, 2004).

The exclusively marine Loricifera belong to the smallest known metazoans, in which the size of a single-cell organism is combined with a very complex external morphology and a multicellular anatomy (Kristensen, 1991b). The body of adult Loricifera is bilaterally symmetrical and divided into mouth cone, introvert, neck, thorax and lorica (abdomen). The term Loricifera is derived from the Latin words "*lorica*" meaning "corselet" and "*fera*" meaning "to bear". The anterior body regions are telescopically retractable into the lorica. Apart from the lorica, the main characteristic feature in adults is the spherical introvert armed with eight to nine circles of locomotory and simultaneously sensory scalids (Kristensen, 1991b). The scalids of each circle represent a unique and complicated assemblage. The scalids of the first row are termed clavoscalids referring to their characteristic club shape and have presumably acquired an olfactory function (Kristensen, 1991b, 2002a). Scalids of the remaining seven (eight) circles are named spinoscalids. They are partitioned into segments resembling legs or have a filiform structure. The clavoscalids display sexual dimorphism. In the female of *N. mysticus*, they are spinose and single units. They differ from the male clavoscalids which are divided into branches (Kristensen, 1983). Sexual dimorphism is also present in the lateroventral trichoscalids, which are modified to claspers in males (Kristensen, 1991b). Both sexes possess paired gonads. In female *N. mysticus* a single, large egg is formed in one of the saccate ovaries. The large paired testes of males contain small and rod-headed sperm. Fertilization is unknown and may occur internally; furthermore details of the embryonic development are unknown. All Loricifera have a series of larval instars, which differ clearly from the adults. The larva was named Higgins-larva to honour Robert P. Higgins' first discovery of an adult Loricifera in 1974 (Higgins & Kristensen, 1986). All larvae show similar body compartments, which are largely comparable with the adults. The larval introvert of Nanaloricidae has seven circles of scalids. Many of the scalids are highly modified, mainly in midventral and middorsal positions. The most notable features of Higgins-larvae are the two caudal toes. These caudal appendages articulate jointlike and have lateral leaflike enlargements called mucrones (mucros in Kristensen, 1983). The toes are locomotory organs for crawling and paddling motion (Kristensen, 1991a). Additionally, they may be used for adhesion on sand grains with an adhesive mucus excreted by the internal toe glands. Another unique feature for this type of larva is the presence of two subventral closing plates for the withdrawn introvert and ventrally three pairs of locomotory appendages posterior to the moveable thorax.

The larval instars are separated by moults in the known life history cycle of *N. mysticus*. The metamorphosis to a postlarva occurs inside the exuvium of the last larval instar. The postlarva resembles female specimens in their morphology (Kristensen, 1991a).

Apart from *N. mysticus*, a second species, *N. khaitatus* Todaro & Kristensen, 1998 is included in the genus *Nanaloricus* to this date (see Kristensen, 2003). Nine other species of Loricifera are included in the family Pliciloricidae Higgins & Kristensen, 1986 (Higgins & Kristensen, 1986; Kristensen & Shirayama, 1988). Meanwhile Loricifera were collected from various marine sediments, except from poor mud (Hubbard et al., 1988; Kristensen & Meier, 1986). Their presently known worldwide distribution reaches from the subtidal zone to the deep-sea (Kristensen & Shirayama, 1988; Shirayama & Kristensen, 1988). The discovery of five new species in the same locality, two described here as a new genus, indicates that the Nanaloricidae may have a higher diversity in local habitats of the subtidal zone than hitherto assumed.

Material and methods

The specimens for this study come from five samples taken from the upper surface layer of very clean shell gravel ("Sable à *Polygordius*"). Samples were collected with a Sanders dredge, at Trezen ar Skoden, Roscoff, France (48°45'55''N - 04°06'45''W / 48°45'30''N - 04°06'25''W), at 50-55 m depth. R. M. Kristensen collected all sediment samples with the research vessel "Mysis".

The coarse sediment was soaked in freshwater to osmotically shock the meiofauna and thereby causing the organisms to be released from the sand grains. The meiofauna was extracted by decantation through a 32 µm mesh net. The extracted Loricifera were fixed and preserved in 4% formalin buffered with Borax or in trialdehyde (see Lake, 1973). The type-material was mounted in formalin, which was slowly replaced by glycerol. Then the pure glycerol wholemount preparation was sealed with Glyceel®. The specimens were viewed and photographed with a LEICA differential interference contrast microscope (DIC, type DM RXA, with UCA condenser, DIC prism and motorized zoom up to 2.5x). Drawings were made with the aid of a drawing tubus (Makroeinrichtung FSA25PE).

For electron microscopy trialdehyde fixed material was postfixed with 1% osmium tetroxide and cleaned ultrasonically before being dehydrated through an ethanol series. Thereafter, the specimens were transferred to acetone, critical point dried and coated with gold-paladium. SEM examinations were made with a Cambridge Stereoscan 250 Mk2 and a JEOL JSM-840 scanning electron microscopes. Cross-sections (1 µm thick) of paratype material embedded in epoxy resin (TAAB 812®) for light microscopy (DIC) were stained with toluidine blue-borax. Transmission electron microscopy (TEM) studies were performed on an adult male of the new genus by Neuhaus et al. (1997). The TEM-technique was described in detail in that paper and should be consulted for more details.

The type-material is deposited at the Zoological Museum of Copenhagen, Denmark (ZMUC) under ZMUC-numbers LOR 161-224 and COBICE-numbers GG 013 - 036.

Abbreviations used in figures and text

‘	marks left side position of a structure; symmetrical ones (both sides) unmarked.
ac	anal cone
an	anus
ann	annuli
ap_{1-4}	anal plate number one to four
ba	hairy spinules of spinoscalids
bg	posterior bridge of lorica spikes
bj	ball and socket joint of toe
bp_{1-3}	first to third row of thoracic basal plates
bs	basal plate of spinoscalid
bt	basal plate of toe
bu	buccal tube
c	clavoscalids (1 row position; a, b, c, d positions inside row)
ca	buccal closing apparatus
cl	clasper (modified trichoscalid)
cp	right closing plate of thorax
cr_1	first row of scalids (clavoscalids)
cs	primary element of clavoscalid
csd	distal branch of clavoscalid
csp	proximal branch of clavoscalid
dl	dorsal lorica
dmu	dorsal longitudinal retractor muscle
dp	dorsal plate of lorica
dp_1	middorsal plate of lorica
dp_2	laterodorsal plate of lorica
dv	dorsoventral muscle
ea	lateral locking apparatus of lorica plates
fc	external furca of mouth cone
fl	papillate flosculus
gd	gland duct
gp	pore of subcuticular gland
hi	hinge cuticle of lorica plates
ia	internal prepharyngeal armature
in	introvert
la_1	anterolateral locomotory appendage
la_2	anteromedial locomotory appendage
la_3	anteroventral locomotory appendage
lo	lorica
lp_1	ventrolateral plate of lorica
lp_2	dorsolateral plate of lorica
lr	lorica ridge
ls	spike of lorica
ma	manubrium
mar	margin of lorica
mb	midbrain
mc	mouth cone
mg	midgut

mo mouth opening
mr basal plate row of mouth cone base
mt mouth tube
mu muscle
muc mucrones of larval toe
oe oesophagus
oo oocyte
or oral ridge of larva
or_1 anterior oral ridge of adults
or_2 posterior oral ridge of adults
os oral stylet
p_{1-5} first to fifth row of pharyngeal placoids
pb pharyngeal bulb
pp posterior protrusion
rfl reinforcement of lorica margin
rfs reinforcement of lorica spikes
rt rectum
s spinoscalid (1, 2, 3, 4, 5, 6, 7, row position; a, b, c, d, e, f, g, h, positions inside row)
se_1 posterodorsal seta
se_2 posterolateral sensory seta
se_3 posteroterminal sensory seta
sg_{1-4} first to fourth segments of scalids
sph sphincter
spr row of spinules
sr_{2-8} second to eighth row of spinoscalids
sr_2a type A ss of second row
sr_2b type B ss of second row
sr_3a type A ss of third row
sr_3b type B ss of third row
sr_2-ir irregular pattern of second row ss
sph sphincter
ss spinoscalids
st spine-tip of toe
sv seminal vesicle
sz spermatozoon
tc trichoids of clavoscalids
tg adhesive gland of toe
th unit of thorax
th_1 anterothorax
th_2 interthorax (= neck)
th_3 posterothorax
thr_{1-6} first to six row of thorax plates
to toe
tr_1 upper trichoscalid
tr_2 lower trichoscalid
us ultrasculpture of lorica
va oral valves
vl ventral lorica
vp ventral plate of lorica
ws "window" of lorica spikes

Taxonomy

Phylum LORICIFERA Kristensen, 1983
Family Nanaloricidae Kristensen, 1983
Type genus: *Nanaloricus* Kristensen, 1983
Type species: *Nanaloricus mysticus* Kristensen, 1983
Armorloricus gen. nov.
Type species: *Armorloricus elegans* sp. nov.

Composition: *Armorloricus elegans* sp. nov.; *Armorloricus davidi* sp. nov.

Etymology: the genus name has a dual meaning. *Armor* is the Celtic name for the old kingdom of Brittany, literally meaning "in the sea" and also in the current English equivalent (armor) for Latin *armatura*; *lorica* is Latin for a piece of a warrior's armature, covering the whole trunk and the English equivalent is "corselet" or "leather cuirass"; masculine gender.

Diagnosis of adults
Adults 320 – 430 µm long, length varies in both sexes; with short, well-defined mouth cone bearing eight elevated external furcae of identical length, and distally with extremely long mouth tube. Internal buccal tube with annulations and extremely long, flexible, and telescopically extendable; internal prepharyngeal armature with additional posterior part, called manubrium; large muscular pharyngeal bulb, located in fully extended specimens at level of anterior lorica edge, composed of numerous fibres; internal pharyngeal layer strongly sclerotized with five transversal rows of placoids; all spinose clavoscalids of female basally with field of subdorsal minute spinules; three pairs of male clavoscalids branched and smooth; large spinoscalids of second row broad and strongly sclerotized and segmented in leglike manner with hinge joints; small spinoscalids of second row featherlike, with pronounced club tips in males; scalids of eighth row resemble small beaks; broad formation of secondary flexible anterothoracic region between first and second rows of thoracic basal plates; two circles of trichoscalids. Double trichoscalids separated basally, two trichoscalids modified into short claspers in males. Lorica consisting of 6 large plates, with smooth cuticle (without ultrasculpture), ventral plate broad, dorsal plate narrow and subdivided longitudinally in three additional plates by two longitudinal folds, outer lateral margins of laterodorsal plates folded dorsally cover the dorsal plates partially, elements of laterocaudal articularization of lorica in caudal position (ridges and apposing sockets), anterior edge of lorica with fifteen long spikes, gland ducts of lorica spikes posterior without reservoirs; tiny papillate flosculi on lorica; anal cone dorsal with small anal plates. Internally, dorsal retractor muscles paired and widely separated, dorsoventral muscle bundles inserting on articulate cuticle between ventral and ventrolateral plates. Postlarvae similar to adult females.

Diagnosis of Higgins-larva
Larvae obviously smaller than adults, 130-155 µm; cylindrically, simple mouth cone without internal or external armature; clavoscalids segmented and spinose; spinoscalids even spinose or hooklike, seventh row of scalids consists of single spiny basal plates; thorax divided by 5-6 transverse rows of thoracic plates, plates folded transversally in singular manner; collar region reduced and marked by two big ventral plates enlarged to form closing apparatus for retractable introvert; three short pairs of locomotory setae between thorax and lorica; lorica with rectangular outline, slightly sclerotized and defined by longitudinal ridges; cuticle with strongly developed honeycomb ultrasculpture; caudal toes modified into locomotory organs with lateral broad, but short, leaf-like mucrones, the latter terminating in distal tip pointing outwards; anus situated dorsocaudally on anal cone; anal plates dorsally with three well-developed papillate flosculi and tiny pair of anteroterminal setae; additionally two long pairs of sensory setae present in caudal region.

Armorloricus elegans sp. nov.
Figs 1-3, 7A, 8A-E, 19A, 19C, 19E and 19G.
Measurements in Table 1.

Type material: holotypic male (mounted on slide LOR 161 ZMUC / GG COBICE 013), allotypic female (mounted on slide LOR 162/ GG COBICE 014), and paratypes: 10 females (mounted on slides LOR 163 - 170 + LOR 178-179 ZMUC), 7 males (mounted on slides LOR 171-177 ZMUC), 7 postlarvae (mounted on slides LOR 180-186 ZMUC). Additional material: SEM-stubs LOR 257-260 ZMUC; one male serially cross-sectioned on glass-slides (LOR 225-249 ZMUC) and one is serially longitudinal-sectioned on glass-slides (LOR 250-256 ZMUC).

Type locality: Trezen ar Skoden, Roscoff, France, Station: RMK 071285, 50 m depth, (48°45'55''N - 04°06'45''W), July 12, 1985; and Station: RMK 071489, 50 m depth (48°45'55''N - 04°06'45''W) July 14, 1989.

Etymology: from the latin *elegans* (elegant); masculine gender.

Description of male (holotype)
Holotypic male (Figs 1-2) fully extended, 340 µm in total length, from tip of mouth tube to caudal end. Maximum diameter of trunk in middle of lorica, 118 µm wide. Specimen represents species of medium size with rounded, cup-shaped lorica. Body divided into mouth cone, introvert, thorax, and loricate abdomen. Abdomen slightly compressed dorsoventrally.
External morphology
First body part non-extendable, rigid mouth cone extruded and separated from introvert by transversal row of eight cuticular plates. Mouth cone divided into two parts: mouth cone itself, as short, broad basal section (mc) and long mouth tube (mt) as slim terminal section. Mouth cone basally surrounded by eight identical oral furcae (fc) as heavily sclerotized and pronounced supporting structures. Eight oral ridges present, reduced in length and separate in anterior (or_1) and posterior parts (or_2), which frame each furca on both sides. Mouth tube extremely narrow, funnel-like and twice as long as proximal mouth cone. Terminal part of mouth tube can be protruded telescopically. Mouth opening (mo) terminally on tip of mouth tube. Ring of six oral stylets (os) inside mouth. Stylets can be seen extended from mouth opening.

Spherical introvert (in) densely covered by eight rows or circles of scalids. First row (cr_1) with eight strongly sclerotized and slightly anteriorly oriented clavoscalids. Six of the eight clavoscalids with specific male structure. Dorsal, dorsolateral, and ventrolateral pairs of clavoscalids divided into primary element (cs) and two secondary branches, a distal (csd) and a proximal one (csp). Primary elements comparable to unmodified clavoscalids of the female, divided into four segments. First segment smooth and with swollen base of medium length and oval in section. Second segment long, laterally flattened and connected via hinge joint with first segment. Last two segments small. Terminal segment with tip oriented upwards. Two club-shaped secondary branches originate from primary element. Proximal branch inserting lateroventrally, distal branch laterodorsally. Distal branch of same length as second segment of primary element, but slightly narrower. Proximal branch of nearly same length as primary element, but twice as wide as distal branch. Ventral pair of clavoscalids unmodified and of same basic structure as in the female, but with smooth bases.

Next seven rows consisting of spinoscalids (sr_{2-7}) oriented posteriorly. Spinoscalids of second to sixth rows with bulbous bases. All bulbous bases more or less densely covered with minute spinules. Spinoscalids of fourth to seventh rows arising from small rectangular basal plates (bs).

Second row (sr_2) consisting of 16 spinoscalids of two different types. Nine being type A scalids (sr_2a), of same length as clavoscalids. They are the most strongly sclerotized scalids, and consist of three segments. First segment basally with small lateral spinules. Fourth segment laterally flattened and as broad as clavoscalids. Terminal segment being a strong clawlike spine. These nine strong type A spinoscalids alternating with seven smaller type B spinoscalids (sr_2b) consisting of only two segments. First segment small and bulbous with fewer but longer spines as found in type A spinoscalids. Second segment long, rigid, filiform and with numerous fine hairy spinules scattered over entire length, giving spinoscalids featherlike appearance. Tips of second segment slightly pronounced.

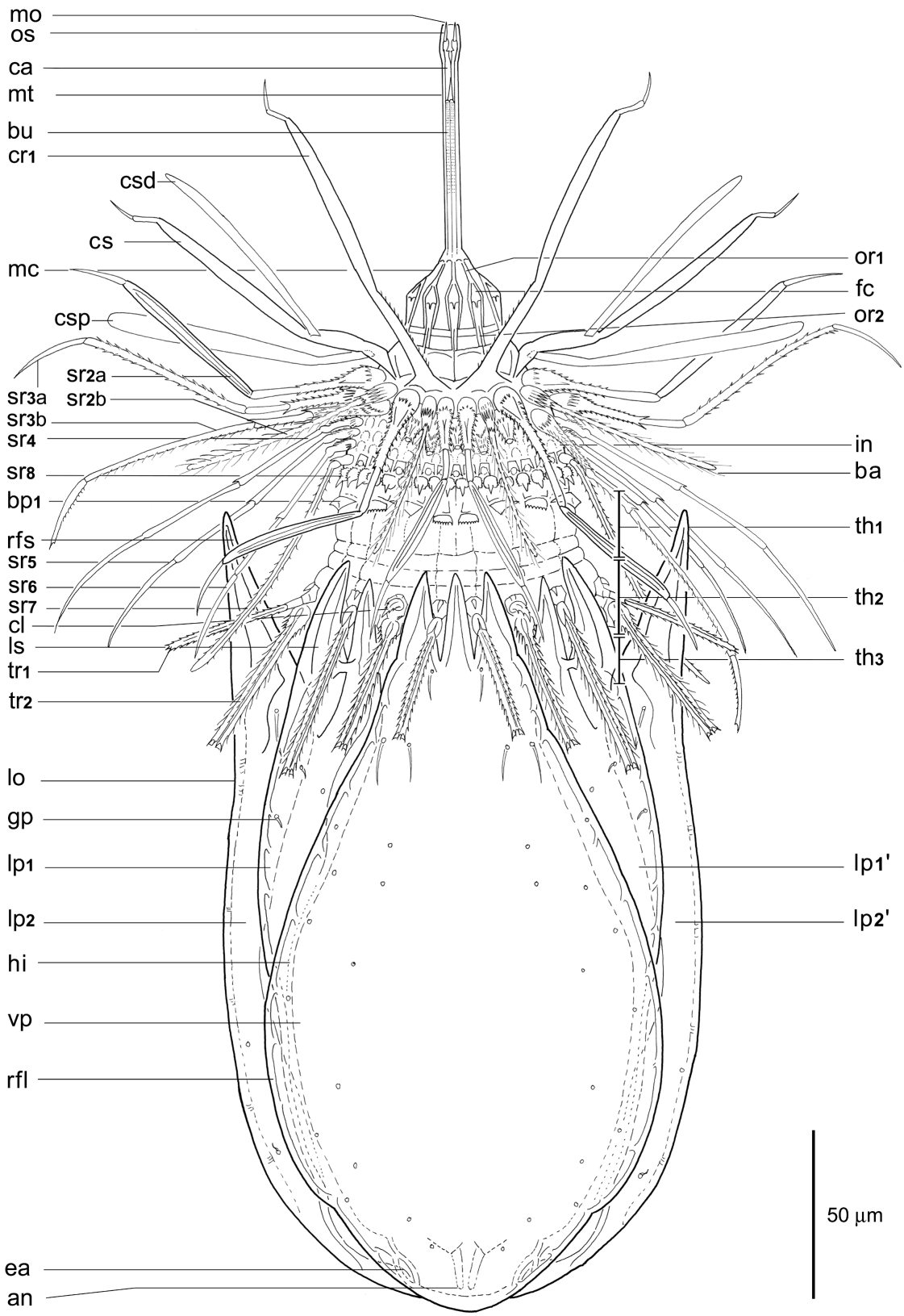


Figure 1. *Armorloricus elegans* sp. nov., holotypic male, ventral view.
Figure 1. *Armorloricus elegans* sp. nov., holotype mâle, vue ventrale.

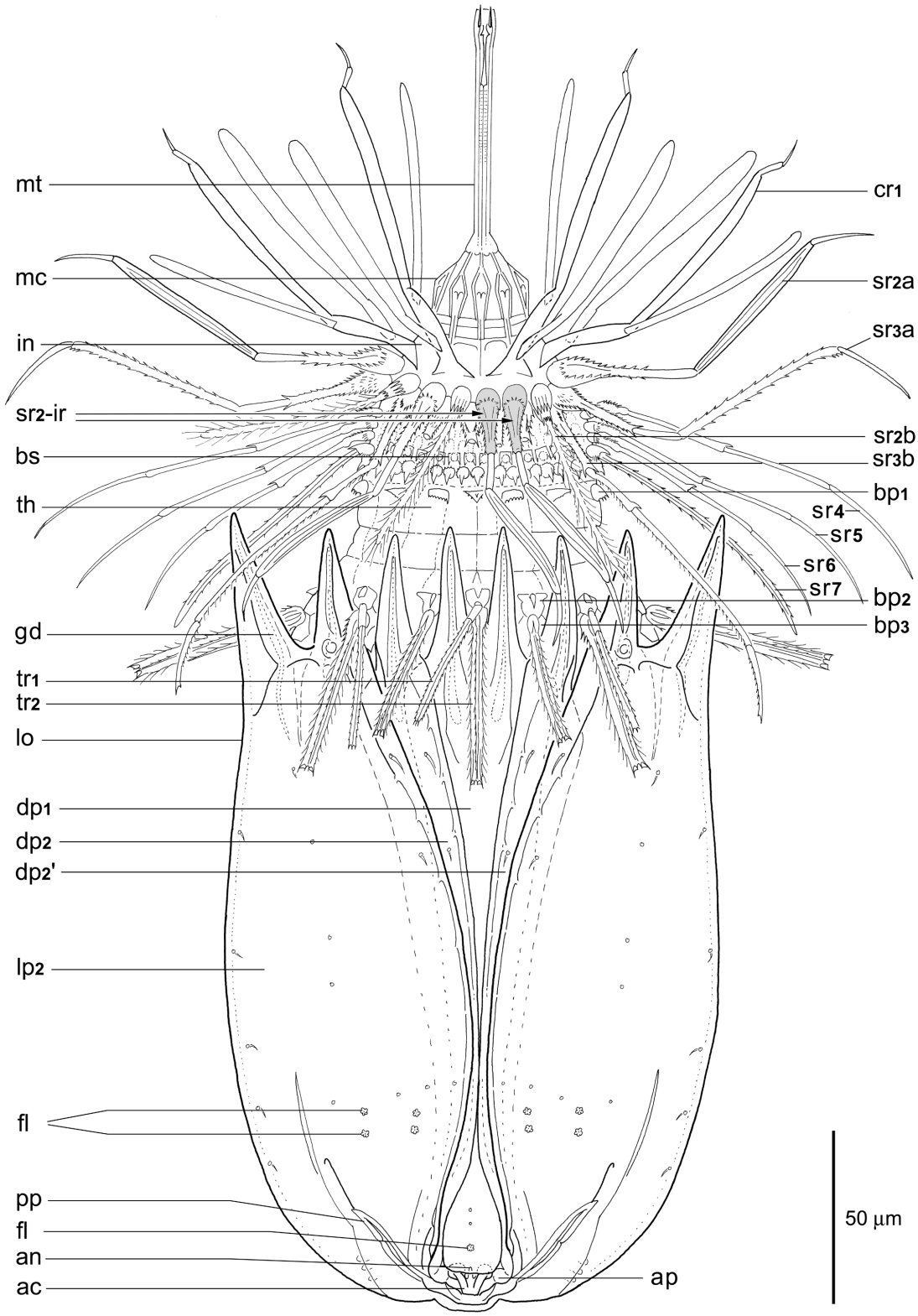


Figure 2. *Armorloricus elegans* sp. nov., holotypic male, dorsal view.
Figure 2. *Armorloricus elegans* sp. nov., holotype mâle, vue dorsale.

Alternating arrangement of sr_2-spinoscalids irregular ventrally at midline and dorsally beside midline where two type A spinoscalids stand close together, and where one type B spinoscalid is lacking (Fig. 2, sr_2-ir).

Third row (sr_3) of scalids also with 16 spinoscalids of two different types, but without irregularities in alternating arrangement. Both spinoscalid types leglike and divided into three segments. First segments spiny, and with well-developed hinge joints between second and third segments which bear two lateral spines each. Eight type A spinoscalids (sr_3a) bigger than others and distally smooth, but with laterally serrated margins in proximal quarter. Terminal segments pointed, spinose. Remaining eight type B spinoscalids (sr_3b) slightly smaller and equipped with tiny spinules over their full lengths. Their terminal segments ending in double claw-tips. These scalids being homologous with claw-shaped type B spinoscalids of other loriciferans (e.g. *Pliciloricus*-species).

Fourth (sr_4) through sixth (sr_6) rows each with circle of 30 uniform spinoscalids. All of them filiform and more flexible than any scalid described before and consisting of four segments. Basal segments short and with hinge joints, terminal segments elongated. Seventh row (sr_7) also with 30 spinoscalids, but being more flattened, trichoid, and not divided into segments than previous scalids. All with finely serrated lateral margins and inserting on small rectangular basal plates (bs). Eighth (last) row of scalids with 30 small posteriorly oriented hooklike teeth arising from small, rounded, and spiny basal plates.

Thorax as next body region subdivided into three subregions: antero-, inter-, and posterothorax. Anterothorax (th_1) with one row of 15 basal plates called first row of thoracic basal plates and consisting of a zone of flexible cuticle between this row of plates and the next. This first row (bp_1) of thoracic basal plates immediately behind eighth row of scalids belonging to the introvert. Both separated by a small constriction only. Seven of the basal plates of the first thoracic row rectangular with posterior fringes of small denticles and alternating with eight triangular formations. All plates resemble more protruded protoscalids than the flat basal plates of next two rows. These two rows, the second and third thoracic rows of basal plates constitute the second subdivision of thorax, called interthorax (th_2) or neck which also carries 22 trichoscalids (8 single and 7 "double").

Basal plates of second thoracic row (bp_2) trapeziform and with a small erect tooth on each. Basal plates of third thoracic row (bp_3) similar in structure and slightly larger. Second and third row of basal plates carrying a circle of trichoscalids each. Circle of second row with seven short, rigid, and inflexible trichoscalids (tr_1) with finely serrated lateral margins. Trichoscalids emerging with smooth shafts from small depressions. One pair of these trichoscalids on both sides of ventral lorica plate transformed into two spinose claspers (cl) of reduced length (7 µm). Circle of third row of basal plates with fifteen trichoscalids (tr_2) being longer, more rigid and broader than those of second row. Triangular bases of these trichoscalids rounded, enlarged, and with lateral fringes of small stiff spinules. Lateral margins strongly serrated; serration fine and having hairy appearance. Trichoscalids in cross-section flat and with a central canal. Third margin protruding perpendicularly from longitudinal axis with same serration as lateral margins. Trichoscalids of both circles with blunt ends looking like cut off, but with four fine points at tip. Seven trichoscalids each of the second and third rows forming "paired trichoscalids" with separate and not fused bases like the "double trichoscalids" of species of *Pliciloricus*. Transition zone between interthorax and loricate abdomen formed by narrow and less flexible posterothorax (th_3) consisting of a small stretch of thin cuticle and without appendages.

Abdomen covered by massively sclerotized lorica plates (lo). Surface of cup-shaped lorica entirely smooth and shiny, with no ultrasculpture whatsoever. Lorica divided into three broad and three narrow longitudinal plates connected by hinge cuticles (hi). To prevent sliding movements, midventral and both ventrolateral plates laterocaudally united by locking apparatus (ea) of ridges and opposing sockets. Anterior edge of lorica armed with 15 strong lorica spikes (ls). All spikes with lateral reinforcements of thicker cuticle (rfs) and internally along their entire length with long ducts of subcuticular epidermal glands (gd). Lorica plates penetrated by several small pores (gp) concentrated closely to the slightly reinforced lateral margins (rfs). All pores connected with unicellular subcuticular epidermal glands. Ventral side covered by broad shieldlike midventral plate (vp), anteriorly equipped with three small spikes. Ventrolateral plates (lp_1) slim and covered partly by midventral plates. Dorsally with two wide dorsolateral plates (lp_2) partly covered by narrow dorsal plate (dp) (Figs 2, 8B). Dorsal plate with four long anterior lorica spikes and entirely subdivided by indented longitudinal folds into three additional plates: right laterodorsal plate (dp_2), middorsal plate (dp_1), and left laterodorsal plate (dp_2'). Indented longitudinal folds originating in the gaps between ventral and lateral spikes. Outer lateral margins of laterodorsal plates folded up and extending over remaining portion of plates. Cluster of four micro-flosculi (fl) located posteriorly on each dorsolateral plate. Middorsal plate with blunt caudal end as well as with single micro-flosculus, and overlapping small anal cone (ac). Anal cone subdivided dorsally into three anal plates (ap), covering anus (an) shield-like (Figs 2, 8D). Two slim and long cuticular structures, resembling lanceolated protrusions (pp), originate and diverge from each flank of anal area (Figs 2, 8B).

Description of female (Allotype)

Allotypic female (Figs 3, 7A) apart from tip of mouth tube completely extended, 300 µm in total length. Maximum width of trunk in middle of lorica, 120 µm wide.

External morphology

Mouth cone (mc) as in male. Mouth tube (mt) only half extended. In this position oral stylets and oral closing apparatus located at level of basal sections of mouth tube indicating that terminal section of mouth tube can be protruded and vary in length. Introvert (in) of female also covered by eight rows of scalids. Main sexual dimorphism expressed in structure of clavoscalids. Eight clavoscalids uniform in structure: not branched as in male, more spinose, longer, and appearing more sclerotized. All of them connected with triangular bases by hinge joints. Bases also triangular in section. Each clavoscalid divided into four segments. First two segments long and connected by an additional hinge joint. First segment (sg_1) forms unit with base and dorsally possesses dense pat of trichoids (tc) as extremely small, hairy cuticular structures (Fig. 3). Second segment (sg_2) laterally flattened and with subdorsal row of minute spinules. Third segment (sg_3) narrow and small. Distal segment (sg_4) ending in upwards oriented tip.

Type B spinoscalids (sr_2b) of second row less pronounced than in male, fine hairy spinules less visible. Nine large segmented type A (sr_2a) spinoscalids of same structure as in male. Irregularities in alternating arrangement of sr_2-spinoscalids also present in female; two type A spinoscalids located close together. Remaining rows of spinoscalids as in male. Trichoscalids (tr_1) of second row of basal plates located on both sides of ventral plate not transformed into short claspers as in male.

Lorica and all associated structures as in holotypic male. Arrangement of subcuticular glands (gd) in lorica spikes easiest visible on ventral side of allotypic female (Fig. 3). In most cases, a large, single main duct and an additional small duct are to be seen in each spike, the ducts reaching down to where posterothorax connects with lorica plates. Subcuticular glands lack large lacunae proximally (as found in the genus *Nanaloricus*).

Description of postlarva (Paratype)

Postlarva completely extended, morphologically identical with female, except smaller size (80%) and lack of gonads and of the sixth row of spinoscalids. Additionally, mouth cone smaller, in relation to total body length. Body length 300 µm only (with totally extruded mouth tube) and maximum lorica diameter, 116 µm.

Internal anatomy of adults

For detailed description of mouth cone and associated internal structures see Fig. 18. Long mouth tube (mt) widening posteriorly at level of oral stylets and oral closing apparatus (ca). All six oral stylets (or) articulating with internal cuticular layer of mouth. Stylets not part of buccal tube, can be protruded from mouth opening as shown in paratypes of *A. elegans* sp. nov. Oral stylets followed by oral closing apparatus of mouth tube which closes it. Buccal tube (115 µm) 25% longer than mouth cone (90 µm) and well sclerotized. Posterior part of buccal tube (bu) can be telescopically protruded from mouth opening. Characteristic fine annulation (ann) present on inner cuticular layer of buccal tube. Buccal tube lies inside mouth cone and extends through the brain into large pharynx bulb (pb). Posterior third of buccal tube triradiate in section and provided with three well-sclerotized longitudinal edges. Posteriorly, buccal tube united with complex triradiate prepharyngeal armature (ia) evolved from a hexagonal one. Prepharyngeal armature having an outer anterior and an inner posterior part. Posterior part composed of three primary supporting elements which along their entire lengths are fused longitudinally with the buccal tube. Three secondarily reduced accessory elements alternate with primary elements which are not connected with buccal tube. All primary and secondary elements fused transversally into three plates forming an outer pyramidal unit covering posterior and inner parts of armature at half-length. Posterior part of armature being a complex unit mainly composed of three strong cuticular bracelets, called manubrium (ma). Bracelets fused transversally and anchoring armature in pharyngeal bulb.

Separation of the mouth cone and the large pharyngeal bulb is a unique feature of Nanaloricidae and consequently also found in *Armorloricus* gen. nov. In extended specimens muscular pharyngeal bulb located deeply inside trunk behind brain at level of anterior lorica edge. Three corners of triradiate myoepithelial pharyngeal lumen paved with five rods of cuticular placoids (p_1-p_5) (Figs 18, 7E). Myoephithelial cells forming placoids to which muscles attach directly. Placoids connected chainlike longitudinally. These connections persist, even when tissue of bulb disintegrate in exuvium (Fig. 7F).

Oesophagus (oe) short, glandular and lined with cuticle connected with pharyngeal bulb by six short thickenings of basal laminae surrounding pharyngeal bulb. Saccate midgut with thick walls composed of large absorptive cells. In postlarva, midgut walls swollen and occupying whole body cavity. Midgut walls entirely filled with large granular vesicles and round yellowish cells. Short hindgut lined with cuticle. Anus opening dorsocaudally and covered with three anal plates.

Saccate testis of holotypic male filled with late spermatids. Two large seminal vesicles contain only spermatozoa. Mature spermatozoa have long flagellum, slim head and well developed acrosome (Fig. 8D, sz). Female reproductive system with paired dorsal ovaries and laterodorsal oviducts opening caudally. Only one large oocyte mature each time in one ovary. In some females a single egg clearly visible, other ovary filled with small

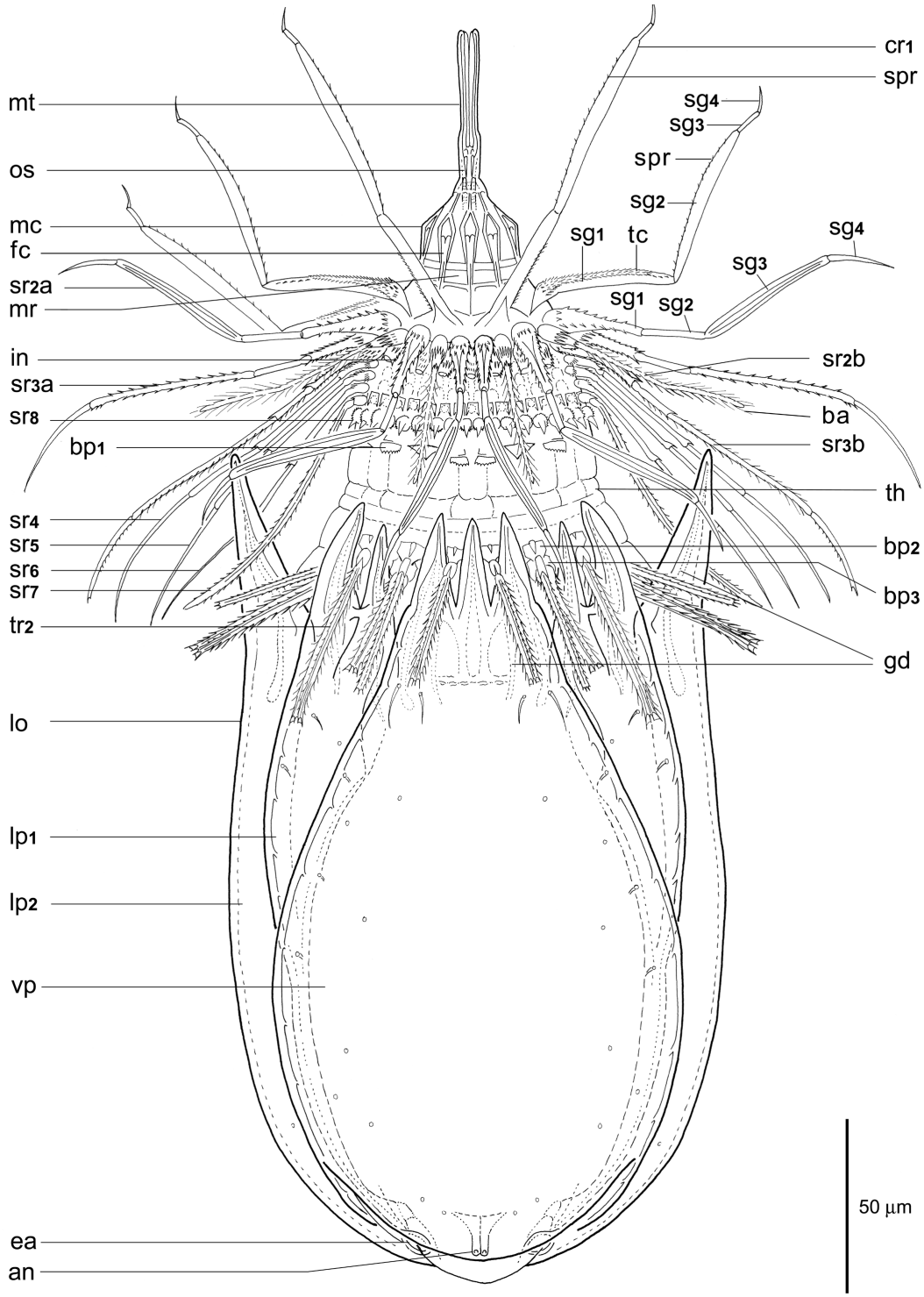


Figure 3. *Armorloricus elegans* sp. nov., allotypic female, ventral view.
Figure 3. *Armorloricus elegans* sp. nov., allotype femelle, vue ventrale.

oocytes. Fertilization may be internal. One female seen with spermatozoa surrounding gonopore (Fig. 8D). Postlarva without gonads.

Trunk muscles of specimens of *Armorloricus* gen. nov. consist of longitudinal, diagonal, and dorsoventral bundles of cross-striated muscle fibres. Outer diagonal muscles of

Table 1. Morphometric data of the type material of *Armorloricus elegans* sp. nov. and *Armorloricus davidi* sp. nov. (measurements in µm).

Tableau 1. Données morphométriques du matériel type de *Armorloricus elegans* sp. nov. et *A. davidi* sp.nov. (mesures en µm).

	Armorloricus elegans sp. nov.				*Armorloricus davidi* sp. nov.		
	Male (holotype)	Female (allotype)	Female (paratype)	Postlarva (paratype)	Male (holotype)	Female (allotype)	Female (paratype)
Length of:							
Body (total)	340	300	350	300	380	425	425
mouth cone	90	(60)[1]	85	77	120	125	115
buccal tube	115	105	105	100	130	135	134
oral stylets	4	4	4	3,6	8	8	8
internal armature	10	10	10	10	20	18	18
manubrium	10	10	10	9,8	25	20	20
external furca	14	14	14	13,5	16	16	16
introvert	36	32	33	30	30	35	36
thorax	65	52	65	50	43	48	47
ventral lo plate[c]	186	176	195	170	220	240	225
dorsal lo plate[2]	198	180	200	176	224	246	230
ventral spikes	22	20	20	18	26	28	28
dorsal spikes	32	30	30	25	40	42	42
lateral spikes	46	36	36	30	49	52	50
cr_1	95	88	100	86	100	110	110
primary element	90	-	-	-	95	-	-
distal branch	60	-	-	-	72	-	-
proximal branch	83	-	-	-	88	-	-
sr_2a / sr_2b	108 / 50	100 / 50	110 / 52	90 / 45	135 / 50	150 / 60	150 / 58
sr_3a / sr_3b	95 / 86	90 / 78	100 / 90	86 / 75	105 /98	120 / 108	115 / 100
sr_4	75	72	85	70	85	115	110
sr_5	65	63	78	59	78	108	103
sr_6	55	53	56	50	70	98	95
sr_7	60	58	70	55	80	102	100
sr_8	6	6	6	4	12	13	13
trd_2	48	46	46	40	58	60	60
trm_1	32	30	30	27	35	45	45
maximum width of:							
lorica	118	120	120	116	150	162	160
ventral lo plate	85	96	90	90	105	130	125
dorsal lo plate	48	46	48	50	55	62	60
pharynx bulb	28	27	28	25	34	35	35

[1]These parts of the body are not fully extended. [2]Length of lorica (lo) plates include anterior spikes. Measurements of scalids take into consideration the average length of most scalids per row.

lorica reduced to separate strong bundles. Bundles attached to two neighbouring lorica plates crossing angle formed by plates and thus connecting them (Fig. 19C). In the middle of lorica two big bundles of dorsoventral muscles (dv) hold dorsolateral and midventral plates together. Trunk is flattened when dorsoventral muscles contract. Strong dorsal retractor muscles of introvert (dmu) extend through whole body. Retractor attached caudally and forming two large, lateral and widely separated bundles and one additional smaller median bundle (Fig. 19G).

Armorloricus davidi sp. nov.
Figs 4-6, 7B-F, 8F.

Measurements in Table 1.

Type material: holotype male (mounted on slide LOR 264 ZMUC/GG COBICE 015), allotype female (mounted on slide LOR 265 ZMUC/GG COBICE 016), and paratypes: 4 females (mounted on slides LOR 266-269 ZMUC), 1 male (mounted on slide LOR 270 ZMUC). Additional 3 specimens are mounted on SEM-stubs (LOR 277-279 ZMUC). One specimen is semi-thin sectioned on glass slides (LOR 197-224 ZMUC) and ultrasectioned on grids for TEM.

Type locality: Trezen ar Skoden, Roscoff, France, Station: RMK 071285, 50 m depth, (48°45'55''N - 04°06'45''W), July 12, 1985; and Station RMK: 071489, 50 m depth (48°45'55''N - 04°06'45''W) July 14, 1989.

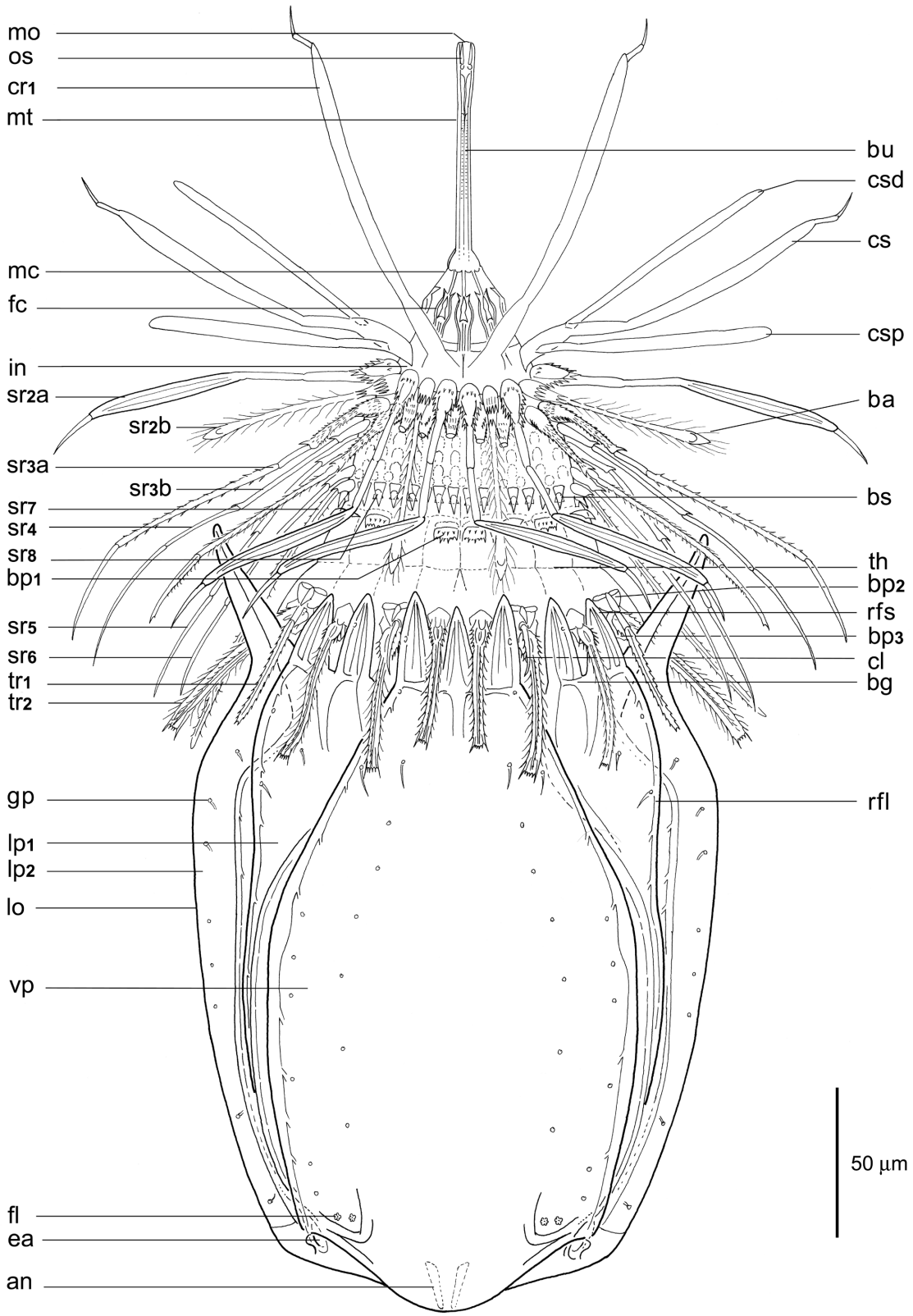


Figure 4. *Armorloricus davidi* sp. nov., holotypic male, ventral view.
Figure 4. *Armorloricus davidi* sp. nov., holotype mâle, vue ventrale.

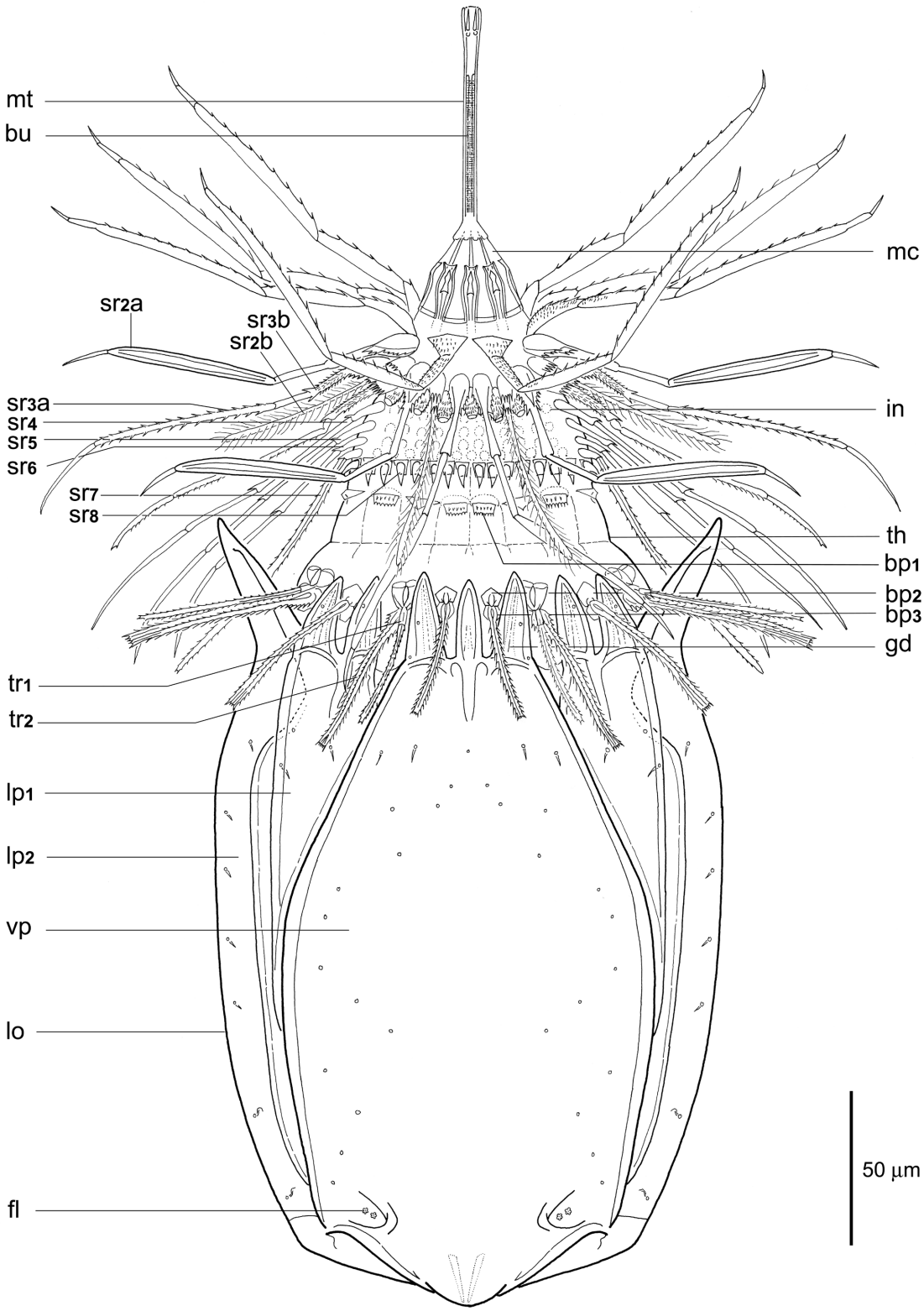


Figure 5. *Armorloricus davidi* sp. nov., allotypic female, ventral view.
Figure 5. *Armorloricus davidi* sp. nov., allotype female, vue ventrale.

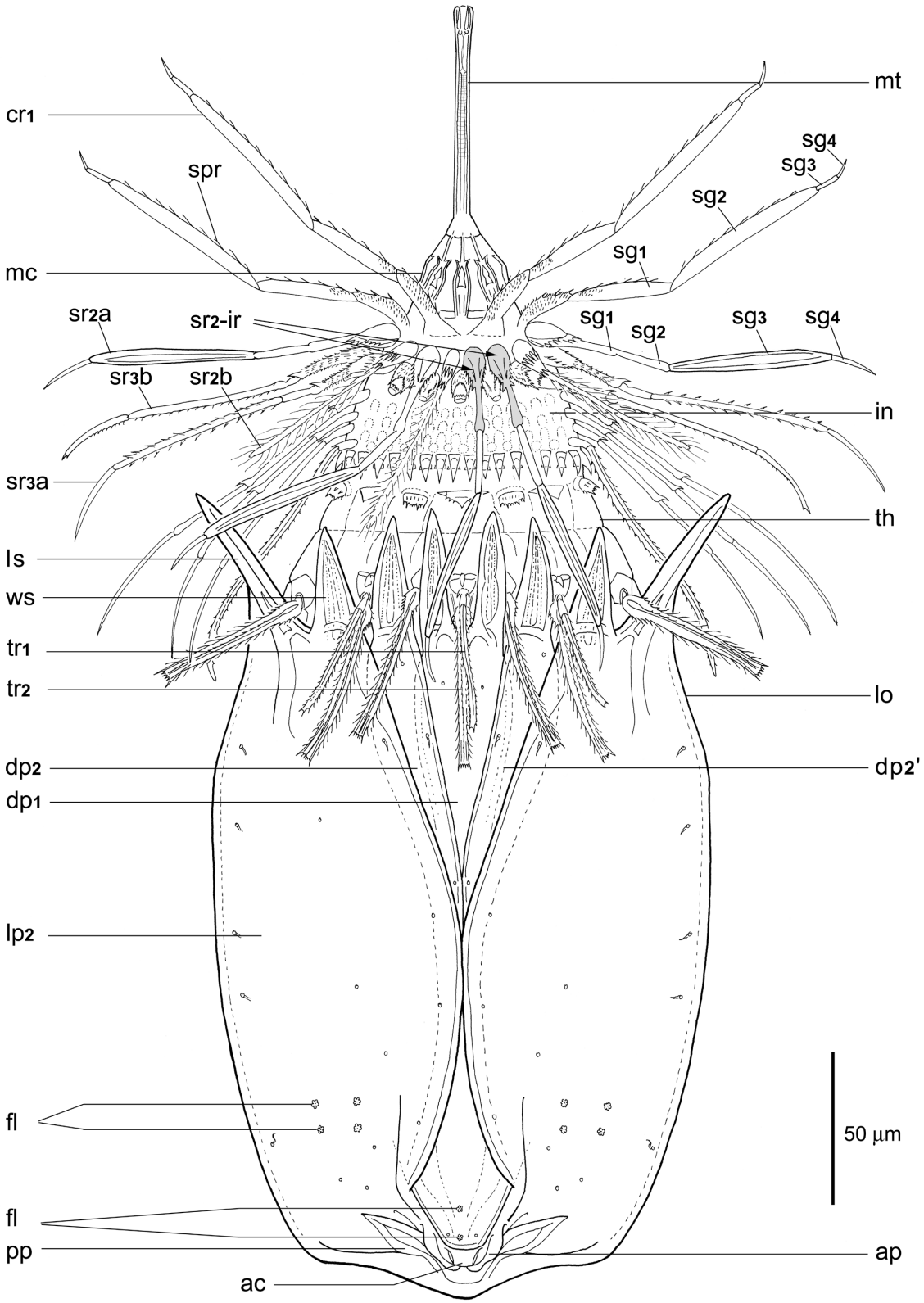


Figure 6. *Armorloricus davidi* sp. nov., allotypic female, dorsal view.
Figure 6. *Armorloricus davidi* sp. nov., allotype femelle, vue dorsale.

Etymology: The species name is in honour to David Møbjerg Kristensen, who participated in all collection trips (1982, 85, 87 and 89) to Roscoff.

Description of male (holotype)

Species large and robust with conspicuous angular lorica. Holotypic male (Figs 4, 7B) 380 µm long, measured from tip of mouth cone to caudal end. Maximum wide of trunk 150 µm at level of anterior lorica. Body divided into same regions as *A. elegans*. Lorica flattened ventrally and more rounded caudally. Mounted specimen with all body regions fully extended.

External morphology

Mouth cone (mc) extruded from introvert. Mouth cone basally separated from introvert by eight narrow plates. Basal part of mouth cone short, broad and surrounded by eight oral furcae (fc) of identical structure. Oral furcae originated from sclerotized and elevated oral ridges, which frame furcae posteriorly and anteriorly. Furcae serve as attachment for eight internal oral muscles (mouth cone retractors). Anteriorly, each furca ends in two lateral peaks. Mouth tube (mt) funnel-like, elongate, and two times longer than mouth cone section. Mouth opening (mo) located at terminal end of mouth tube. Mouth opening internally lined by a ring of six minute extended oral stylets.

Spherical introvert (in) covered by eight narrowly spaced rows of scalids. First row with eight anteriorly oriented clavoscalids. Six of these modified. Dorsal, dorsolateral, and ventrolateral pairs branched: two secondary branches originate from primary element (cs). Primary elements divided into four segments. They resemble a pair of unmodified, ventral clavoscalids (cr_1) of the female. In the male they are smooth and not clearly divided into five segments. First segment smooth, with swollen base of medium length. Bases have round diameter in section. Second segment long, laterally flattened and connected with first segment via hinge joint. Third segment narrow and small. Terminal segment spinose and oriented upwards. Two secondary branches originate closely together from basal segment, proximal branch (csp) inserting lateroventrally and distal branch (csd) laterodorsally. Secondary branches not reaching end of second segment of primary element. Distal branch slim and half as broad as second segment of primary element. Proximal branch as broad as second segment. Both secondary branches with club-shaped end.

Spinoscalids of following seven rows oriented posteriorly. Spinoscalids of second to sixth row with pronounced and spiny bulbous bases. Spinoscalids of fourth to seventh row arising from small rectangular basal plates. Second row (sr_2) consisting of 16 spinoscalids of two different alternating types. Nine of them being long, leglike, and strongly sclerotized. They are called type A (sr_2a) spinoscalids and alternate regularly with seven shorter type B (sr_2b) spinoscalids which resemble feathers. Type A spinoscalids have the same length as clavoscalids. Each of them divided into three segments. Third segment laterally flattened, more sclerotized than the others, and of same width as the clavoscalids. Terminal segment with strong clawlike spine. Type B spinoscalids with only two segments. Second segment long, filiform, rigid, and undivided and having numerous fine hairy spinules scattered along its entire length (featherlike spinoscalids). Tips of type B spinoscalids of holotypic male (and paratypic male) well pronounced and clublike. Alternating arrangement of sr_2-spinoscalids irregular in ventral position and beside dorsal midline. In these positions, two type A spinoscalids stand close together and like in female (Fig. 6) there are no type B spinoscalids.

Third row (sr_3) also with 16 spinoscalids which are segmented leglike and of two different types in a regular alternating arrangement. Bases and first segment of both types of spinoscalid covered with minute spinules. Both types of spinoscalids also agree in well-developed hinge joints flanked by a pair of lateral spines between second and third segments. Eight type A spinoscalids (sr_3a) larger and distally smoother, but with bands of small spinules along lateral margins in proximal quarter. Terminal sections pointed and spinose. Remaining eight type B spinoscalids (sr_3b) shorter, without serrated lateral margins, but covered with tiny spinules along their entire lengths. Spinose segment terminally with double claw-tips.

Fourth (sr_4) through sixth (sr_6) rows with circle of 30 uniform and filiform spinoscalids each. All of them of four segments and flexible in structure. Their short bases with hinge joints. Terminal segments elongated. Seventh row (sr_7) with 30 more flattened and unsegmented spinoscalids, their margins having widely separated and fin serrations, thus resembling trichoscalids on thoracic region. Spinoscalids inserted on introvert via small basal plates. Eighth row (sr_8) with of 30 strong hooks resembling beaks, which insert on trapezoidal basal plates (bs).

Thorax as next body region subdivided into three subregions: antero-, inter-, and posterothorax. Anterothorax (th_1) with one row of 15 basal plates called first row of thoracic basal plates and consisting of a zone of flexible cuticle between this row of plates and the next. This first row (bp_1) of thoracic basal plates immediately behind eighth row of scalids belonging to the introvert. Both separated by a small constriction only. Seven of the basal plates of the first thoracic row rectangular with posterior fringes of small denticles and alternating with eight triangular formations. All plates more like protruded protoscalids than like flat basal plates of next two rows. These two rows, the second and third thoracic rows of basal plates constitute the second subdivision of thorax, called interthorax (th_2) or neck which also carries 22 trichoscalids (8 single and 7 paired).

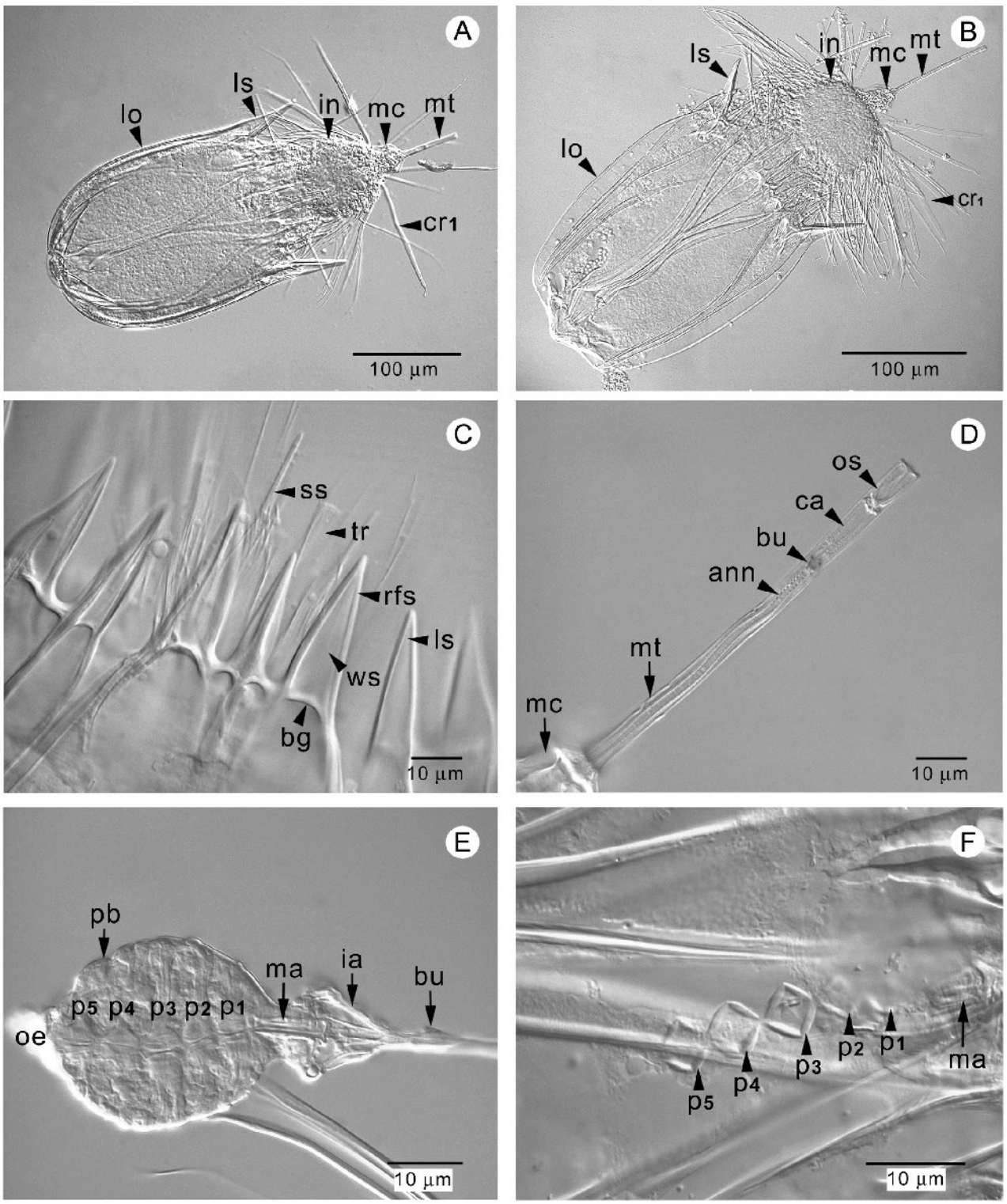


Figure 7. Features of adults; interference-contrast photographs. **A.** Female allotype of *A. elegans* sp. nov., habitus, dorsal view; **B.** male holotype of *A. davidi* sp. nov, habitus, dorsal view; **C-F.** details of *A. davidi* sp. nov. **C.** anterior edge of ventral plate; **D.** mouth cone and mouth tube; **E.** pharyngeal bulb with manubrium and prepharyngeal armature; **F.** placoids of pharyngeal bulb.

Figure 7. Caractères des adultes ; photographies en contraste interférentiel. **A.** Allotype femelle de *A. elegans* sp. nov., habitus, vue dorsale. **B.** Holotype mâle de *A. davidi* sp. nov., habitus, vue dorsale. **C-F.** détails de *A. davidi* sp. nov. **C.** bord antérieur de la plaque ventrale ; **D.** cône et tube buccaux ; **E.** bulbe pharyngien avec manubrium et armature pré-pharyngienne ; **F.** placoïdes du bulbe pharyngien.

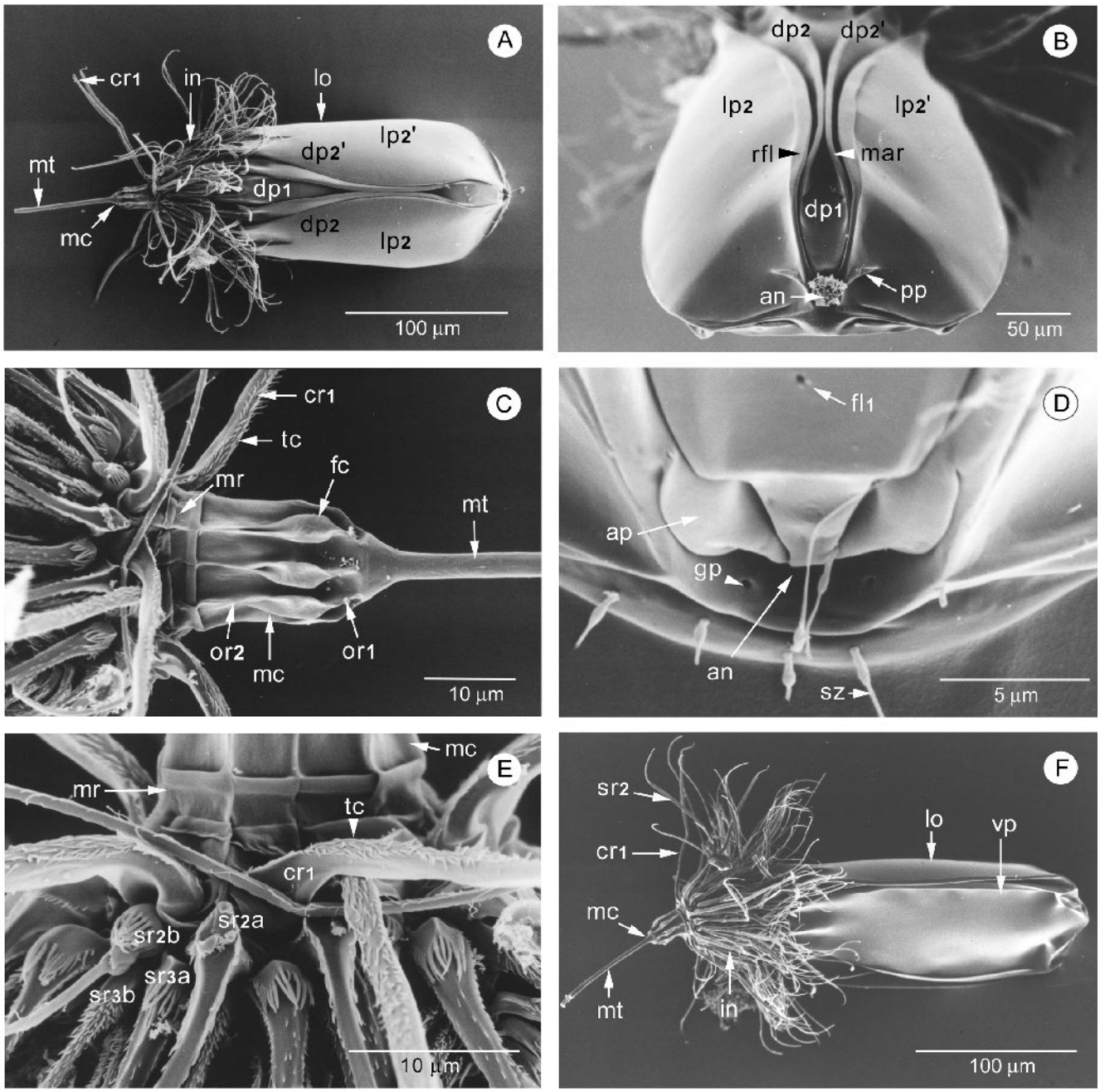


Figure 8. Features of adults; SEM micrographs. **A-D** Female of *A. elegans* sp. nov.; **A.** habitus, dorsal view; **B.** posterior end of lorica, dorsal view; (*mar*) upfolded margins of dorsal plate; (*rfl*) reinforcement of plate margin; **C.** female of *A. elegans* sp. nov.; introvert, ventral view; **D.** anal cone, dorsal view, note the attached spermatozoa (*sz*); **E.** bases of scalids, ventral view. **F.** female of *A. davidi* sp. nov., habitus.

Figure 8. Caractères des adultes ; micrographies MEB. **A-D.** Femelle de *A. elegans* sp. nov. ; **A.** habitus, vue dorsale. **B.** Partie postérieure de la lorica, vue dorsale ; (*mar*) bords dépliés de la plaque dorsale ; (*rfl*) renforcement des bords de la plaque ; **C.** Femelle de *A. elegans* sp. nov., introvert, vue ventrale ; **D.** cône anal, vue dorsale, notez les spermatozoïdes attachés (*sz*) ; **E.** base des scalides, vue ventrale ; **F.** Femelle de *A. davidi* sp. nov., habitus.

Eight basal plates of second thoracic row (bp_2) large and heart shaped, each equipped with prominent erect tooth alternating with seven small pentagonal basal plates. All basal plates of third thoracic row (bp_3) also pentagonal and smaller than basal plates of second row.

Second and third row of basal plates carrying a circle of trichoscalids each. Circle of second row with seven short and slim trichoscalids (tr_1) with finely serrated lateral

margins. Trichoscalids with smooth shafts and double pointed tips. One ventral pair of these trichoscalids on both sides of midventral lorica plate transformed into two short (10 µm) spinose claspers (Fig. 4, cl). Circle of third row of basal plates with fifteen trichoscalids (tr_2) being longer, more rigid and broader than those of second row. Triangular bases of these trichoscalids rounded, enlarged, and with lateral fringes of small stiff spinules. Lateral margins strongly serrated; serration consisting of small spinules. Trichoscalids of third row of basal plates insert posteriorly on plates and being flat in cross-section and with a central canal. Third margin protruding perpendicularly from longitudinal axis with same serration as lateral margins. Ends of trichoscalids look like cut off, but extend into six fine points. Seven trichoscalids each of the second and third rows forming "double trichoscalids", both clearly separated basally. Transition zone between interthorax and abdomen formed by narrow posterothorax consisting of a small stretch of thin cuticle and without appendages.

Abdomen covered by massive, sclerotized, lorica (lo) resulting in a pronounced rectangular habitus. Surface of lorica smooth and shiny, without any kind of ultrasculpture. Lorica divided into three broad and three narrow longitudinal plates. Plates connect laterally by thin hinge cuticles. Single midventral and both lateral plates laterocaudally united by ridges and opposing sockets. Anteriorly, lorica armed with 15 strong spikes. Lateral margins of spikes reinforced by thick cuticular walls. Additional transverse reinforcements called bridges of lorica spikes (bg) separate spikes posteriorly (Fig. 7C). Cuticle between reinforced margins depressed and thin. This area being called "window" (ws). All "windows" internally with long ducts of subcuticular glands (gd) running trough each spike. Lorica plates penetrated by several small pores (gp) concentrated closely along reinforced lateral margins. Ventral side covered by large shieldlike, plain main plate (vp) with anteriorly three broad spikes. This plate has posteriorly two additional, conspicuous, arched and elevated reinforcements on the same level as locking apparatus of lorica plates (ea). These reinforcements environs depressions, surrounding a pair of ventral micro-flosculi (fl) each. Ventrolateral plates (lp_1) slim, equipped anteriorly with two broad spikes, and partly covered by midventral plate. Two broad dorsolateral plates (lp_2), partly cover narrow dorsal plate (see female, Fig. 6, dp). Dorsolateral plates posteriorly each with transverse ridges. Dorsal plate subdivided by deep longitudinal folds originating in the gaps between ventral and lateral spikes into three plates (see female, Fig.6, dp_2, dp_1, dp_2'). Rim of these plates together with four long anterior spikes. Outer lateral margins of laterodorsal plates folded up, turned backwards, and thus partly covering remaining parts of the same plate. Each dorsolateral plate with cluster of four micro-flosculi posteriorly on. Caudal end of middorsal plate rounded and overlaping anal cone. Two micro-flosculi near end of middorsal plate (fl). Anal cone (Fig. 4, ac) subdivided dorsally into three anal plates (ap), which cover anus (an) shieldlike. Lorica on both sides of anal area with two broad, short cuticular formations, resembling wing-shaped posterior protrusions (pp).

Description of female (Allotype)

Allotypic female (Figs 5-6) entirely extended, 425 µm long. Maximum wide of trunk in middle of lorica, 162 µm.

External morphology

Mouth tube (mt) fully extended and of same structure as in male. Introvert (in) also covered by eight rows of scalids. Clavoscalids strongly sexually dimorphic. In female, all eight clavoscalids uniform and not divided into branches, also longer and more sclerotized than in male. They are spinose and divided into five segments. First segment dorsally covered by trichoids, and connected with introvert via triangular bases that form well developed hinge joints. Distal part of first segment slightly enlarged and narrowly set off from scalid base. Second and third segments long, laterally flattened, and subdorsal margin with row of small spinules (Fig. 6, spr). First, second and third segments connected by hinge joints. Last two segments small and narrow.

Featherlike unsegmented type B spinoscalids of second row (sr_2) less pronounced than in male. Fine hairy spinules less visible and tips of scalids not enlarged. Nine large leglike segmented type A spinoscalids of structure as in holotypic male. Irregularity in alternating arrangement of ventral sr_2-spinoscalids and those beside at dorsal midline also present in female (Fig. 6, sr_2-ir). Trichoscalids of second row of basal plates on both sides of ventral plate, not modified into claspers as in holotypic male.

Lorica in all details identical with that of holotypic male, accept for pores pattern on large ventral plate. Pores present in same number but arranged in more irregular pattern.

Description of postlarva

Postlarva unknown.

Internal anatomy of adults

Similar to the anatomy described in *A. elegans* sp. nov. For details of bucco-pharyngeal apparatus see Fig. 7D-F.

Differential diagnosis

Adult *A. elegans* sp. nov. and *A. davidi* sp. nov. differ in the following features: (1) *A. davidi* sp. nov. larger than *A. elegans* sp. nov., (2) lorica more angular in *A. davidi* sp. nov., more cup-shaped in *A. elegans* sp. nov., (3) external oral furcae of *A. davidi* sp. nov. distally with pairs of minute pointed tips lacking in *A. elegans* sp. nov., (4) secondary branches of clavoscalids slightly shorter than primary element in *A. davidi* sp. nov. but of same length in *A. elegans* sp. nov. and ventral unmodified pair of

clavoscalids with smooth bases in males of *A. davidi* sp. nov., with minute trichoids on bases of males of *A. elegans* sp. nov., (5) clavoscalids five-segmented and with subdorsal line of pronounced spinules in females of *A. davidi* sp. nov., clavoscalids four-segmented and with subdorsal line of minute spinules in females of *A. elegans* sp. nov., (6) featherlike unsegmented type B spinoscalids of second row with enlarged club-shaped tips in males of *A. davidi* sp. nov., tips indistinct *A. elegans* sp. nov., (7) toothlike scalids of eighth row larger in *A. davidi* sp. nov. and with more conspicuous basal plates than in *A. elegans* sp. nov., (8) rectangular basal plates of first row more spiny in *A. davidi* sp. nov. than in *A. elegans* sp. nov., (9) small protrusions of second row of basal plates more pronounced in *A. davidi* sp. nov. than in *A. elegans* sp. nov., (10) anterior spikes of lorica with additional proximal reinforcement (bridge) and windows in *A. davidi* sp. nov., these lacking in *A. elegans* sp. nov., (11) pattern of cuticular lorica pores of *A. davidi* sp. nov. different from that of *A. elegans* sp. nov., (12) ventral plate caudally with arched reinforcements and additional pairs of micro-flosculi in *A. davidi* sp. nov., these absent in *A. elegans* sp. nov., (13) dorsolateral plates with transverse posterior ridges in *A. davidi* sp. nov., lacking in *A. elegans* sp. nov., (14) caudal end of middorsal plate with two micro-flosculi in *A. davidi* sp. nov., and one micro-flosculum in *A. elegans* sp. nov., (15) triangular protrusions of lorica in caudal position broad and shorter in *A. davidi* sp. nov. than in *A. elegans* sp. nov.

General remarks

There is only indirect evidence to conclude that the Higgins-larvae described below belong to the adults of *Armorloricus* gen. nov. since no moulting stage from larva to postlarva was found. The postlarvae however, can be assigned because they generally already show features of adult females as was first shown for *N. mysticus* (see Kristensen, 1991a). In the collected material there is only the postlarvae of *Armorloricus elegans* sp. nov. They demonstrate that the postlarvae differ morphologically from the female in lacking the sixth row of spinoscalids. This may be a general characteristic of all postlarvae of Nanaloricidae. The Higgins-larvae described below are assumed to belong to *Armorloricus* gen. nov., because they were found in the same samples at the same localities. Other records of this type of Higgins-larva together with the respective adults are known from the Faroe Bank and were collected during the BIOFAR programme in 1992 and 2001.

There are two new species of *Armorloricus* gen. nov. but it is unclear which of the larvae belongs to which species. The problem is temporarily solved here by describing the larvae as unidentified species (*Armorloricus* sp. I and sp. II) leaving this problem to be clarified in the future.

Description of Higgins-larva Armorloricus *sp. I*

Figs 9-10, 13-14.

Measurements in table 2.

Examined material: 10 Higgins-larvae (mounted on slides LOR 187-196 ZMUC). Three additional specimens (LOR 261-263 ZMUC) are mounted on stubs for SEM.

Sampling locality: Trezen ar Skoden, Roscoff, France, Station: RMK 071285, 50 m depth, (48°45’55’’N - 04°06’45’’W), July 12, 1985; and Station: RMK 071489, 50 m depth (48°45’55’’N - 04°06’45’’W) July 14, 1989.

Higgins-larva of *Armorloricus* sp. I (LOR 187 ZMUC; Figs 9-10, 13A-E) with stubby body, angular lorica, and short mucrones. Body 158 µm long; widest diameter of trunk in middle of lorica, 58 µm. Body divided into regions similar to those found in adults: mouth cone, introvert, thorax and lorica. All body regions fully extended in mounted specimen. Higgins-larvae of this type generally more clearly bilaterally symmetrical than adults.

External morphology

Flexible mouth cone (mc) entirely extended from introvert and consisting in one long conical section. External and internal armature lacking. Just a few delicate longitudinal oral ridges (or) visible in anterior region of mouth cone. Terminal mouth opening can be closed by six weakly developed oral valves (va).

Spherical introvert (in) densely covered with only six rows of scalids. Each row with at most 15 scalids. Scalids on ventral and dorsal side differ in length and structure. Bilateral symmetry of larval body most apparent at level of introvert. Spinoscalids without strict circular arrangement as described for adults. Groups of scalids can be combined to functional units longitudinally or transversally. Scalids on introvert arranged in rows posteriorly, but anteriorly arrangement difficult to detect because scalids deviate from normal order and are highly transformed.

First row with eight spinose clavoscalids (cr_1), four ventral ones divided into two segments, four dorsal ones into three. Ventral pair of clavoscalids shortest; dorsal pair longest. Next two rows with elongate spinoscalids (sr), which stand so close together that separate rows are difficult to make out. Second row of spinoscalids seems to be lacking (in contrast to Higgins-larva of *Armorloricus* sp. II). Third row (sr_3), however, with full set of 15 spinoscalids which are composed of two segments. Basal segment with slightly enlarged base and long narrow stalk. This stalk connected by well-developed hinge joint with long spinose second segment generally ending in single tips. Four ventral scalids short. Remaining eleven lateral and dorsal scalids longer and with intermediate third segment.

Next rows all with 15 spinoscalids. Starting at ventral midline, each pair of fourth row (sr_4) of scalids transformed and displaced either up or down. For a better overview and

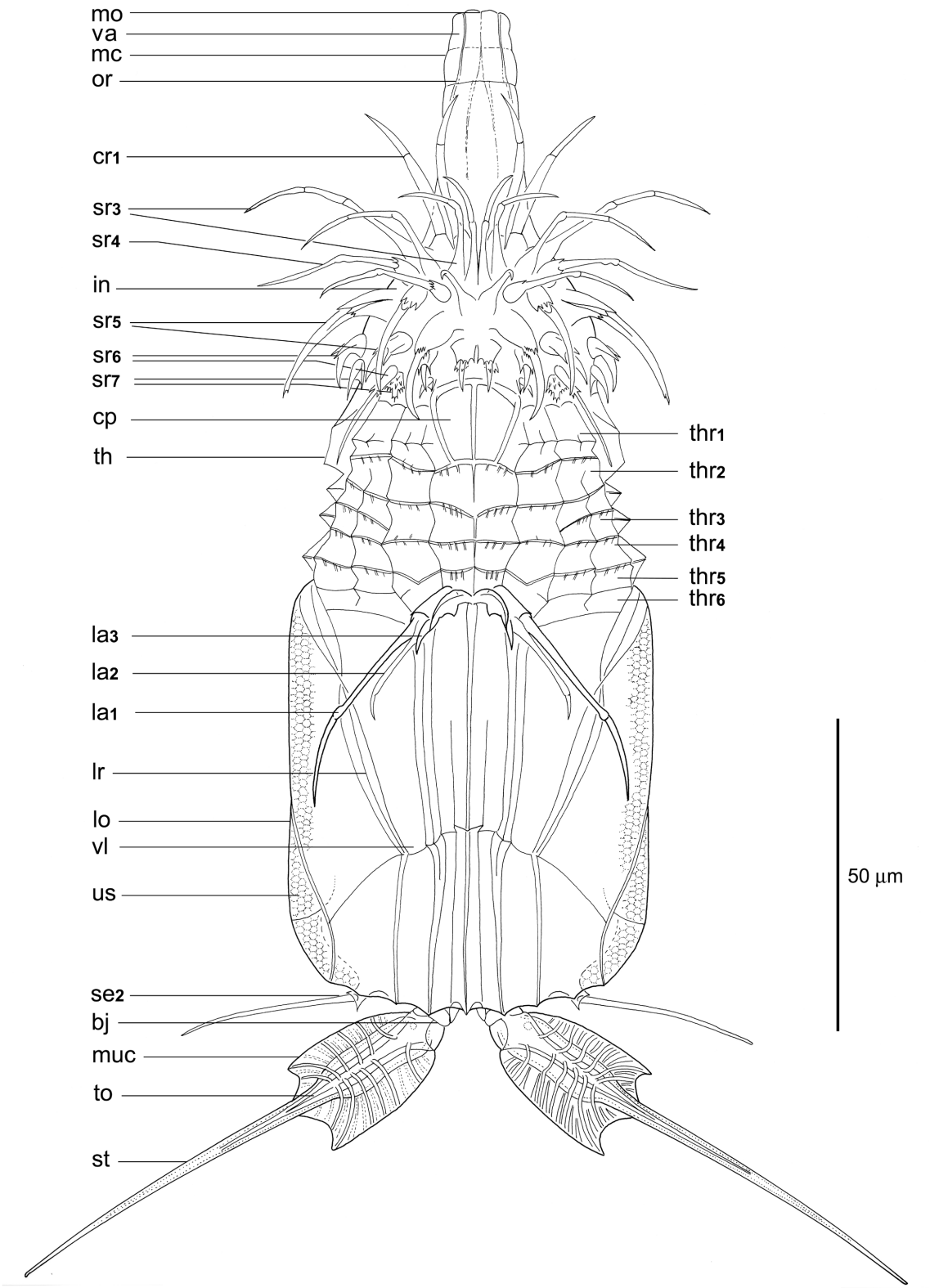


Figure 9. *Armorloricus* sp. I, Higgins-larva, ventral view.
Figure 9. *Armorloricus* sp. I, "Larve-Higgins" vue ventrale.

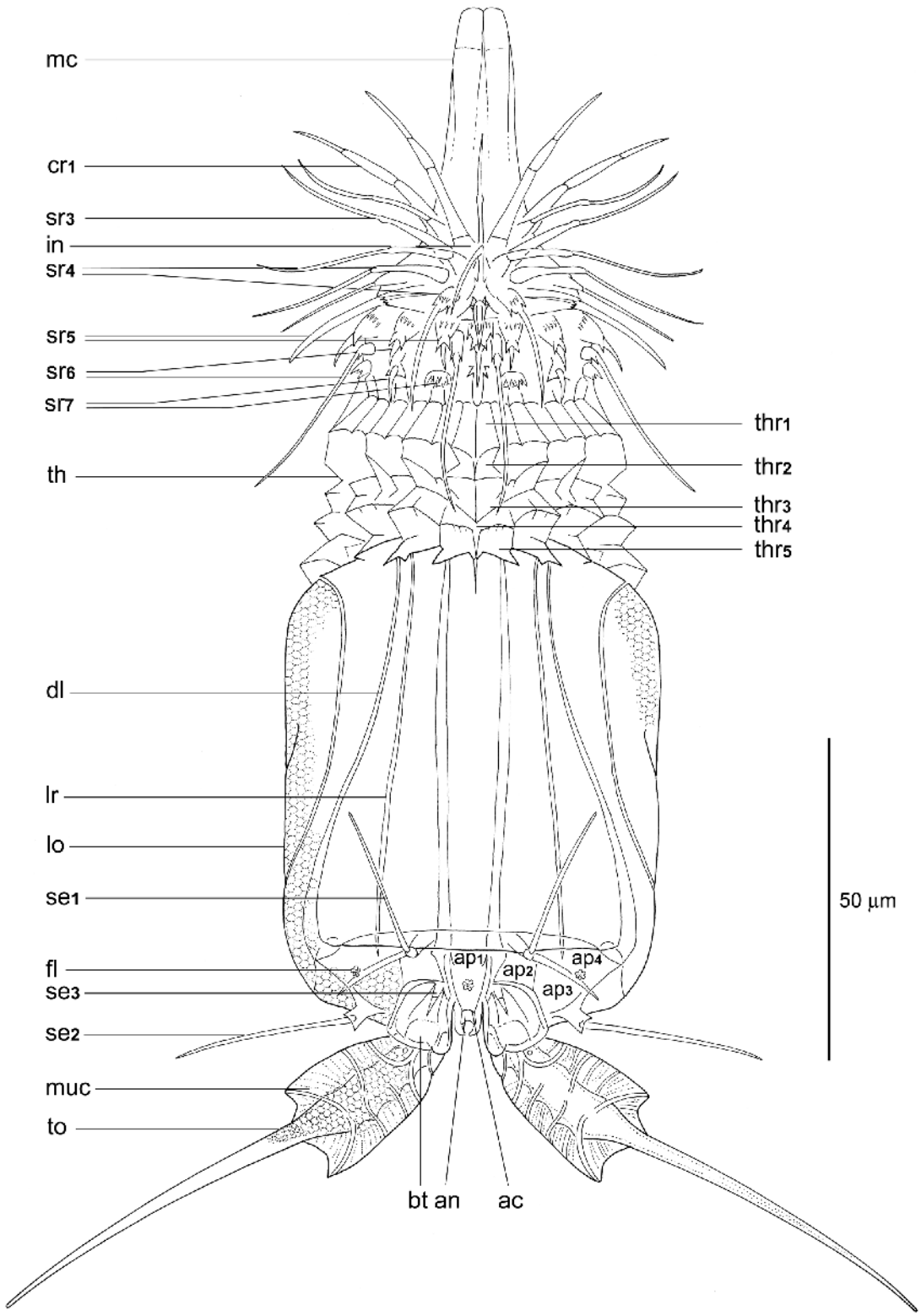


Figure 10. *Armorloricus* sp. I., Higgins-larva, dorsal view.
Figure 10. *Armorloricus* sp. I, « Larve-Higgins » vue dorsale.

comparison of different species scalids have been given serial numbers (Fig. 15): a and a' stand for ventral pair of scalids, h for single dorsal scalid, a' to g' for scalids of right side as seen from ventral view. To give on example of complex scalid transformations the fourth row will be described here in detail: ventral pair (s4a, a') of spinoscalids hooklike. Next pair (s4b, b') antennalike, with slightly separated bases. Following pair (s4c, s4c') strong, spinose, arched, and with clearly separated spiny bases. Lateral pair (s4d, s4d') more like scalids of previous row. Two dorsolateral pairs (s4e, e', s4f, f') long, filiform, and most clearly antennalike, with bent bases and long spinose upwards curving last segment, dorsal pair (s4g, s4g') similar to arched ventral scalids (s4c, s4c'). Single middorsal spinoscalid (s_4h) slightly reduced in size.

Fifth row (sr_5) with seven upper large clawlike spinoscalids (s5b, b', d, d', f, f', h) alternating with eight smaller lower spinoscalids (s5a, a', c, c', e, e', g, g'). Upper spinoscalids divided into two segments. First segment conical, basally enlarged and distally armed with three subdorsal spinules. Second segment spinose ending in double tip. Lower spinoscalids with conical basal segments, each flanked by pair of subdorsal thorns, and with clawlike distal segments.

Upper seven spinoscalids (s6b, b', d, d', f, f', h) of sixth row (sr_6) with same structure as those of previous row, alternating not with eight but with six long, filiform, and flexible lower spinoscalids (s6b, c', e, e', g, g') which are twice as long ventrally. This indicates that two spinoscalids are lacking in both ventral positions. Last and seventh row (sr_7) of scalids with eight triangular spiny projections alternating with seven erect teeth on basal plates. Single spine in middorsal position leaf-like (s7h).

Ventral spinoscalids of fifth to seventh rows short hooks assumed to function as grasping or clinging devices. Enlargement of plates (cp, cp') forming closing apparatus for withdrawn introvert, causing the ventral scalids to be shifted upwards and concentrated in a smaller sector.

Thorax (th) flexible and resembling accordion-bellows. Its thin cuticle divided into six ventral and five dorsal transverse rows of thoracic plates (thr_{1-5}). Ventral plates larger than dorsal ones. All plates transversally folded once. First row of plates distinctly subdivided, showing more folds in the vicinity of last row of scalids. This area together with pair of large ventral closing plates, represents undeveloped collar region.

Ventrally, there are three pairs of segmented appendages situated in transition zone between thorax and lorica. Two outer ones (la_1, la_2) resemble spinoscalids of introvert. First segment long and connected with spinose second segment by well-developed hinge joint. Third inner pair of appendages (Figs. 13E, 14B, la_3) short and hooklike. All three appendages basally fused, forming single plates connected via joints with trunk.

Rectangular abdomen of larva covered with slightly thicker cuticle, which forms lorica (lo). Lorica divided by 13 primary, deep longitudinal folds (lr), dividing it into fields of different size. Surface of lorica with well-developed honeycomb ultrasculpture (us), less distinct in other parts of body (Fig.14).

Toes (to) extending from lateroventral region of caudal end of lorica and articulating with ball and socket joints (bj). Distally, toes drawn out into solid and hollow spines (st), making up 70% of their total length. Toes enlarged basally and laterally with leaflike mucrones (muc). Mucrones short, ending in two diverging pointed tips (Figs 9, 10, 14D), and crossed by six elevated ridges of primary reinforcements. Many additional, fine striae not raised above surface of cuticle. Rims of mucrones closed and smooth. Proximal part of toes perforate by tiny pores, all concentrated in lateral lines. Lorica also with three pairs of posterior sensory setae. Two lateral ones with separate hinge-joint bases. Pair of reduced posteroterminal setae (Figs 10, 14F, se_3) located on anal cone, pair of posterodorsal setae (se_1) on posterior end of lorica, and pair of posterolateral sensory setae (se_2) located laterocaudally. Pairs of posterodorsal and posterolateral setae thin and identical in length (Table 2). Anal cone (ac) situated dorsally, and surrounded by nine anal plates (ap). Central anal plate (ap_1) with upwards arching margins and single central flosculus (fl), posteriorly flanked by two massive, shieldlike, sclerotized basal plates of toes (bt) which overlap toe joints with their posterior margins. Anus (an) located posterior to central anal plate. Two lateralmost anal plates (ap_4, ap_4') with pair of papillate flosculi (Figs 10, 14F, fl).

Internal anatomy

Conical mouth cone with large ovoid pharynx. Pharynx walls lined with strong cuticle layer, but without any kind of internal armature. All larvae investigated with internal organs embedded in tissue of storage cells containing large granules. Granular cells cover most of other anatomical details. Detectable pair of round and transparent formations in the anterior region of introvert and four large round sacklike cellular clusters at caudal end. These clusters could be large and paired adhesive toe-glands (Fig. 13C, tg) because of the ducts extending into enlarged basal part of toes.

Description of Higgins-larva Armorloricus *sp. II*

Figs 11-12.

Measurements in table 2.

Examined material: 4 Higgins-larvae (mounted on slides LOR 273-276 ZMUC).

Sampling locality: Trezen ar Skoden, Roscoff, France, Station: RMK 071285, 50 m depth, (48°45'55''N - 04°06'45''W), July 12, 1985; and Station: RMK 071489, 50 m depth (48°45'55''N - 04°06'45''W) July 14, 1989.

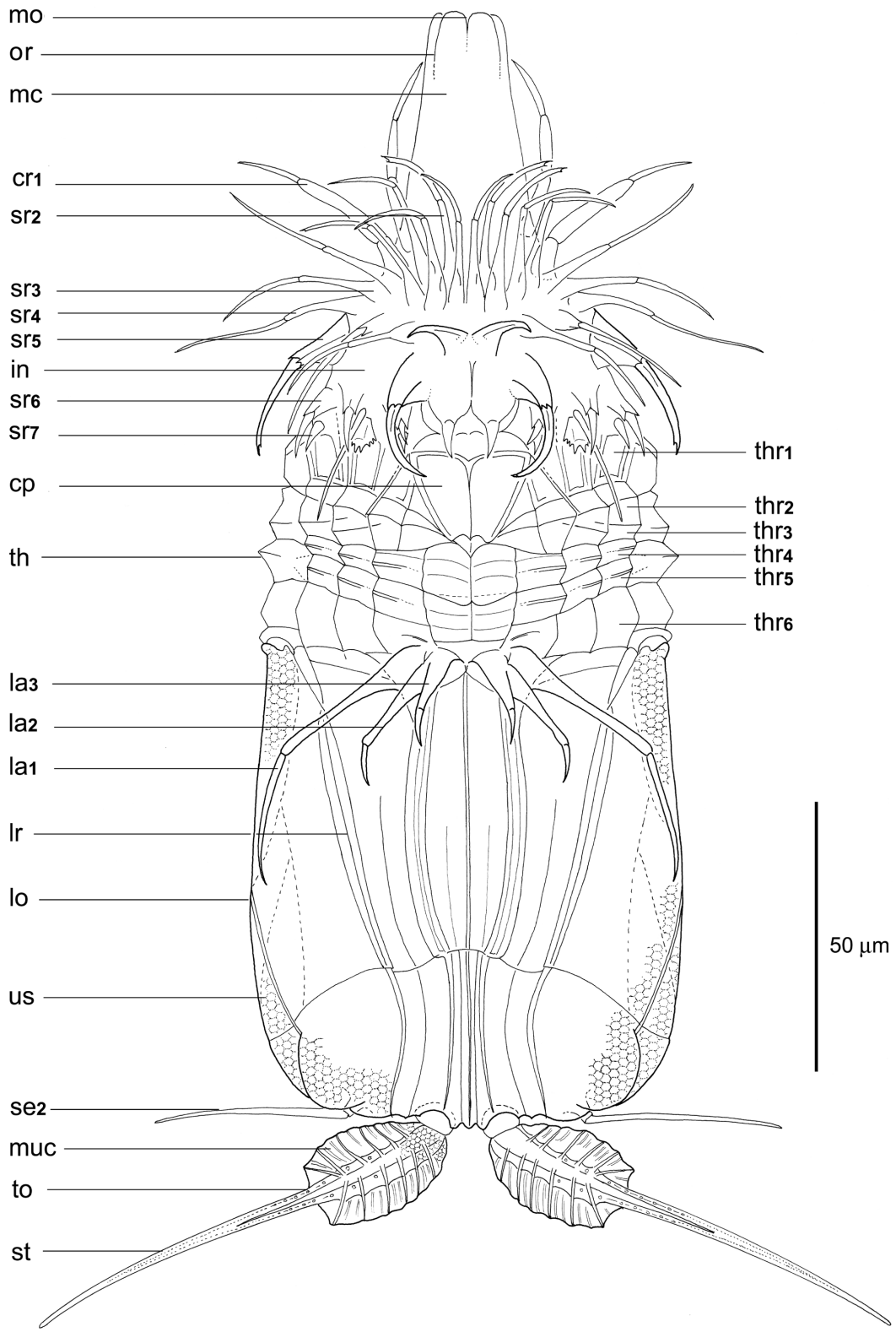


Figure 11. *Armorloricus* sp. II., Higgins-larva, ventral view.
Figure 11. *Armorloricus* sp. II, "Larve-Higgins" vue ventrale."

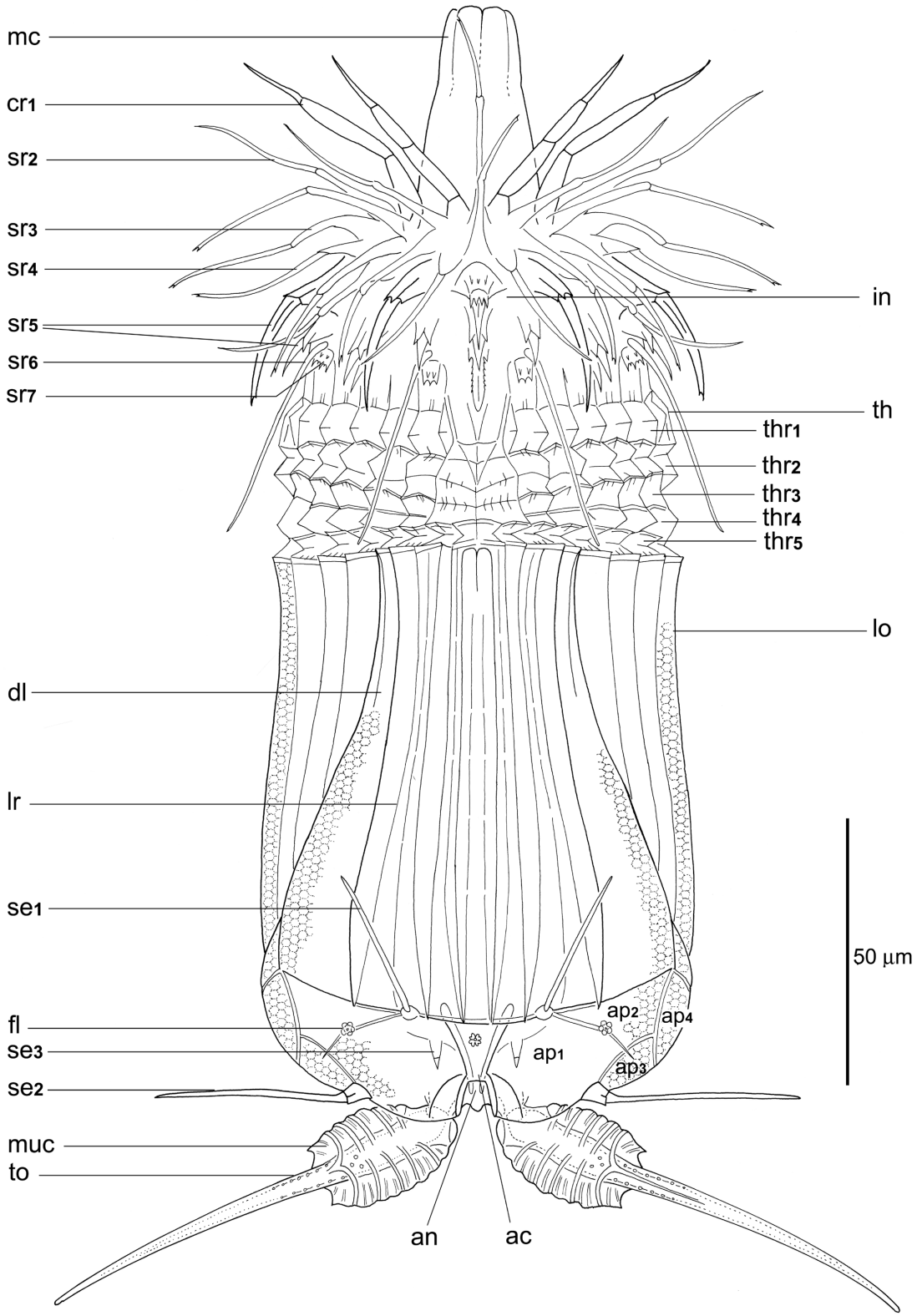


Figure 12. *Armorloricus* sp. II., Higgins-larva, dorsal view.
Figure 12. *Armorloricus* sp. II, "Larve-Higgins" vue dorsale.

Table 2. Morphometric data of Higgins-larvae of *Armorloricus* sp. I and sp. II (measurements in µm).

Tableau 2. Données morphométriques des "larves-Higgins" de *Armorloricus* sp. I et sp. II (mesures en µm).

	Armorloricus sp. I unknown stage	*Armorloricus* sp. II Unknown stage
Length of:		
Body	158	206
Mouth cone	37	(45)*
Pharynx	35	50
Introvert	23	(33)*
Thorax	34	(37)*
Lorica	67	104
la_1	37	52
la_2	24	22
la_3	7	10
toes	82	98
mucrones	23	30
se_1	24	38
se_2	30	40
se_3	4	6
Wide of:		
Lorica	58	90
mucrones	15	17

* Parts of the larval body, which are not fully extended.

Higgins-larva of *Armorloricus* sp. II (LOR 273 ZMUC/ GG 034; Figs 11-12) represented by robust specimen, with rectangular lorica and short mucrones surrounding bases of toes. Body 206 µm long; widest diameter of trunk in middle of lorica, 90 µm. Body not fully extended, mouth cone partly withdrawn and thorax half contracted.

External morphology

Flexible mouth cone (mc) consists of one long, conical section and basally inserted on introvert. Neither external nor internal armature of mouth cone present. Six delicate longitudinal ridges (or) sculpture only the anterior region around mouth opening. Mouth opening situated terminally; slightly retracted and closed by oral valves.

Introvert (in) spherical and densely covered by seven rows of tightly arranged scalids. Each row contains at most of 15 scalids. Up to fifth row, ordered rows of scalids present in posterior region of introvert. In anterior region of introvert spinoscalids irregularly arranged and deviate from otherwise strict order. Some of spinoscalids strongly transformed, especially in ventral sector of introvert. This sector of scalids posteriorly corresponds with pair of large ventral closing plates (cp) in thoracic region.

First row of scalids with eight spinose clavoscalids (cr_1) divided into three segments. Ventral clavoscalids of first row slightly shorter than dorsal ones. Next two rows of scalids with elongate and tightly arranged spinoscalids. Second row of scalids incomplete with only four spinoscalids. Third row (sr_3) with full set of 15 spinoscalids. Spinoscalids of second and third row divided into two segments. Basal segment with slightly enlarged base and long narrow stalk. This stalk connected by well-developed hinge joint with long spinose second segment generally ending in double tips. All following rows with maximum number of 15 spinoscalids, which differ in structure. Each pair at ventral midline of fourth row (sr_3) modified and displaced to an upper or lower position. Modifications of scalids of these rows almost identical with those described for Higgins-larva of *Armorloricus* sp. I. Only ventral pair of spinoscalids (s4a, s4a') very much stronger and of more pronounced hooklike appearance and single spinoscalid (s4g) in middorsal position not reduced (please compare the scalid arrangement with *Armorloricus* sp. I, Fig. 15.)

Fifth row (sr_5) with two kinds of spinoscalids. Seven large upper spinoscalids alternating with eight smaller lower spinoscalids. Both types divided into two segments. First segment of large upper spinoscalids basally enlarged, conical, and distally with dorsal spinules. Spinose second segment ending in double tips. Eight smaller lower spinoscalids also with conical base, but distally flanked with conspicuous pair of thorns. Distal segments of these scalids clawlike.

Seven upper scalids of sixth row (sr_6) have same structure as lower ones of the fifth row. Six lower, longer, and more flexible spinoscalids complete the sixth row in alternating order. Dorsal lower spinoscalids twice as long as ventral ones. Ventral pair of spinoscalids missing.

Seventh row (sr_7) with eight rectangular, projecting plates with dentate posterior margins alternating with seven erect teeth. Single spine in middorsal position flatt, smooth, and leaflike (s7h). Both ventral rectangular projecting plates smaller and totally concealed by two spinoscalids of fifth row above.

Thorax (th) flexible and with six ventral and five dorsal transverse rows of thoracic plates (thr). Ventral plates larger than dorsal ones. All thoracic plates transversally folded once. First row of thoracic plates subdivided by additional folds or with additional plates below with last row of scalids. Together with large pair of ventral plates (cp), this area represents collarlike body region as closing apparatus for withdrawn introvert.

Three pairs of segmented locomotory appendages ventrally on posterior margin of thorax. Appendages resembling ventral spinoscalids of introvert. First segment long and with enlarged bases, which continue as narrow stalks. Stalks connected with spinose second segment by hinge joints. Most lateral pair (la_1) longest; subventral pair (la_3) shortest and hook-like. All three pairs of appendages united basally and forming single plate with anterior joint. Lorica rectangular (lo) and divided into fields of different

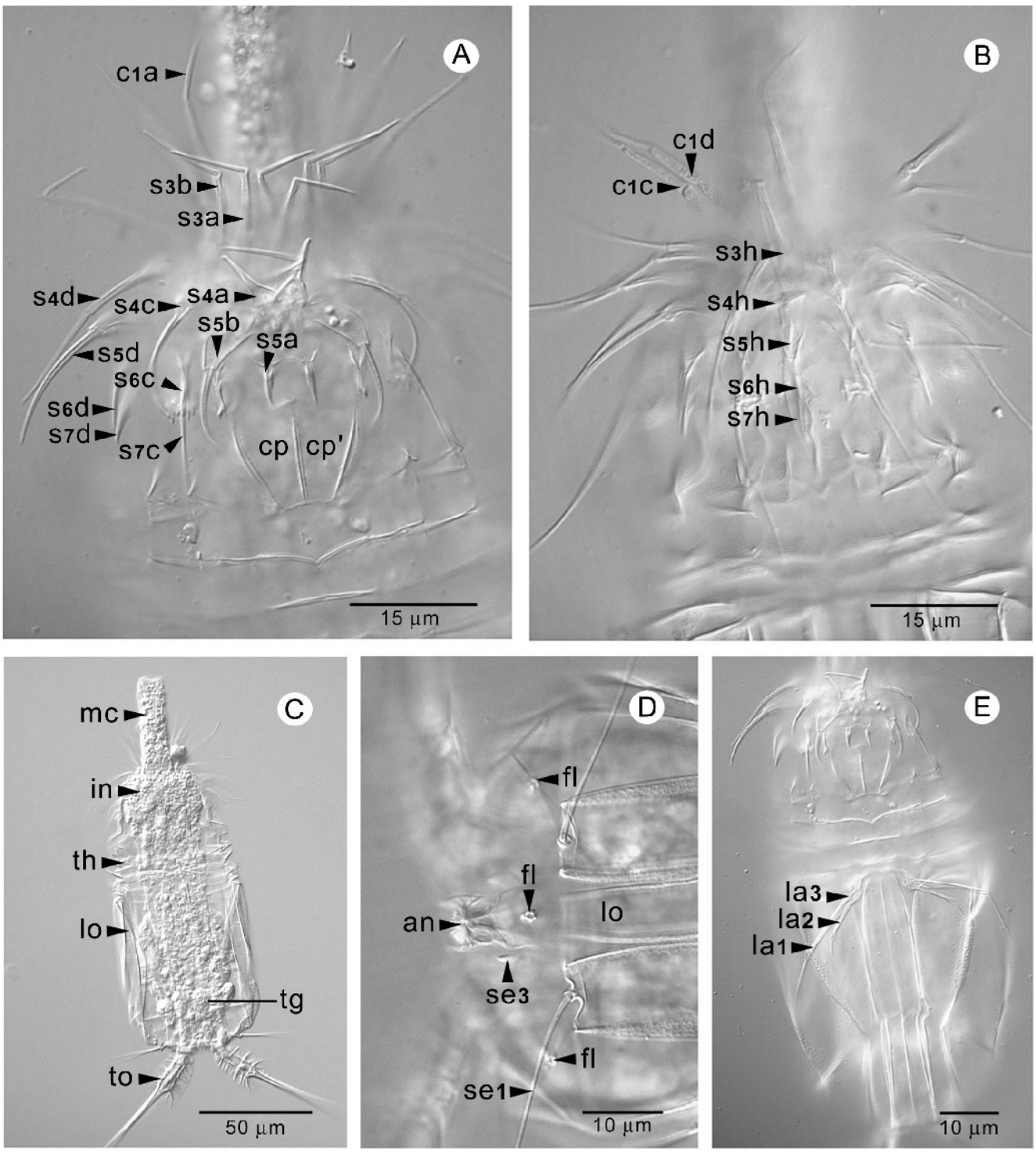


Figure 13. Feature of Higgins-larva sp. I; interference-contrast photographs. **A.** introvert, ventral view; **B.** introvert, dorsal view; **C.** habitus of Higgins-larva, ventral view; **D.** anal cone, dorsal view; **E.** ventral side with locomotory appendages.

Figure 13. Caractères de la "Larve-Higgins" de *Armorloricus* sp. I ; photographies en contraste interférentiel. **A.** introvert, vue ventrale ; **B.** introvert, vue dorsale ; **C.** habitus, vue ventrale ; **D.** cône anal vue dorsale ; **E.** côté ventral avec les appendices locomoteurs.

size by 24 primary, deep, longitudinal folds (lr). Body cuticle with well-developed honeycomb ultrasculpture, most conspicuous on lorica.

Toes (to) articulate with ball and socket joints lateroventrally at caudal end of lorica. Terminal spine reaching about 60 % of total toe length. Toe bases enlarged,

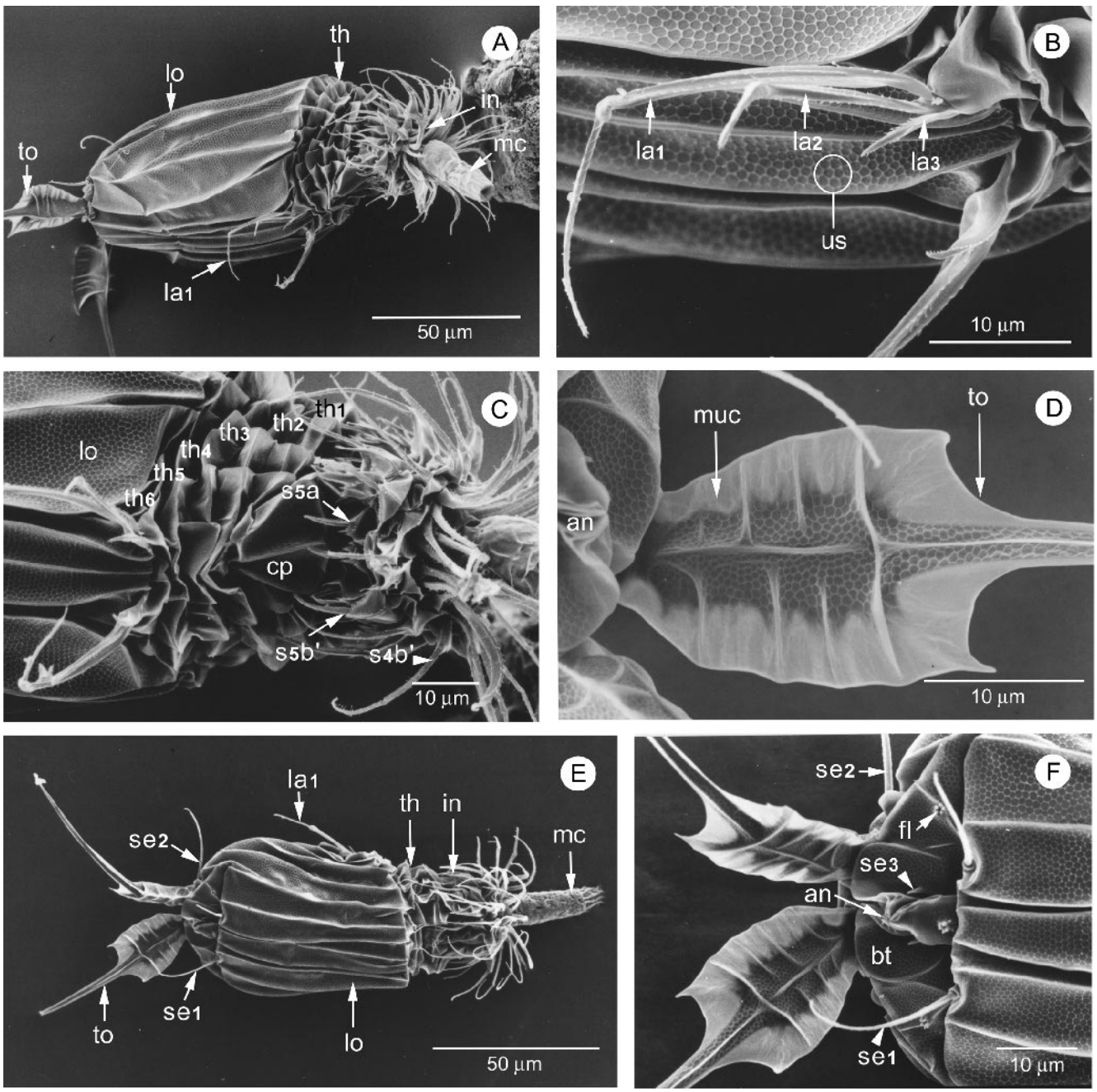


Figure 14. Feature of Higgins-larva of *Armorloricus* sp. I.; SEM micrographs. **A.** habitus, latero-ventral view; **B.** focus of ventral pairs of locomotory appendages; **C.** introvert, ventral view; **D.** toe with mucrones, dorsal view; **E.** habitus, dorsal view; **F.** anal cone, dorsal view.

Figure 14. Caractères de la "Larve-Higgins" de *Armorloricus* sp. ; micrographies MEB. **A.** habitus, vue latero-ventrale ; **B.** détail de la paire d'appendices locomoteurs ventraux ; **C.** introvert, vue ventrale ; **D.** orteil, vue dorsale ; **E.** habitus, vue dorsale ; **F.** cône anal, vue dorsale.

flat and with leaflike mucrones (Figs 11-12, muc) on each side. Mucrones ending in less defined tips. Six conspicuous primary ridges and many fine striae cross mucrones transversally. Rims of mucrones irregular and undulated. Many microscopic pores perforate bases of toes on both sides. Three pairs of posterior sensory setae on anal plates. Lateral and dorsal pairs of posterior setae with separate base. Reduced posteroterminal setae (se_3) centrally on right

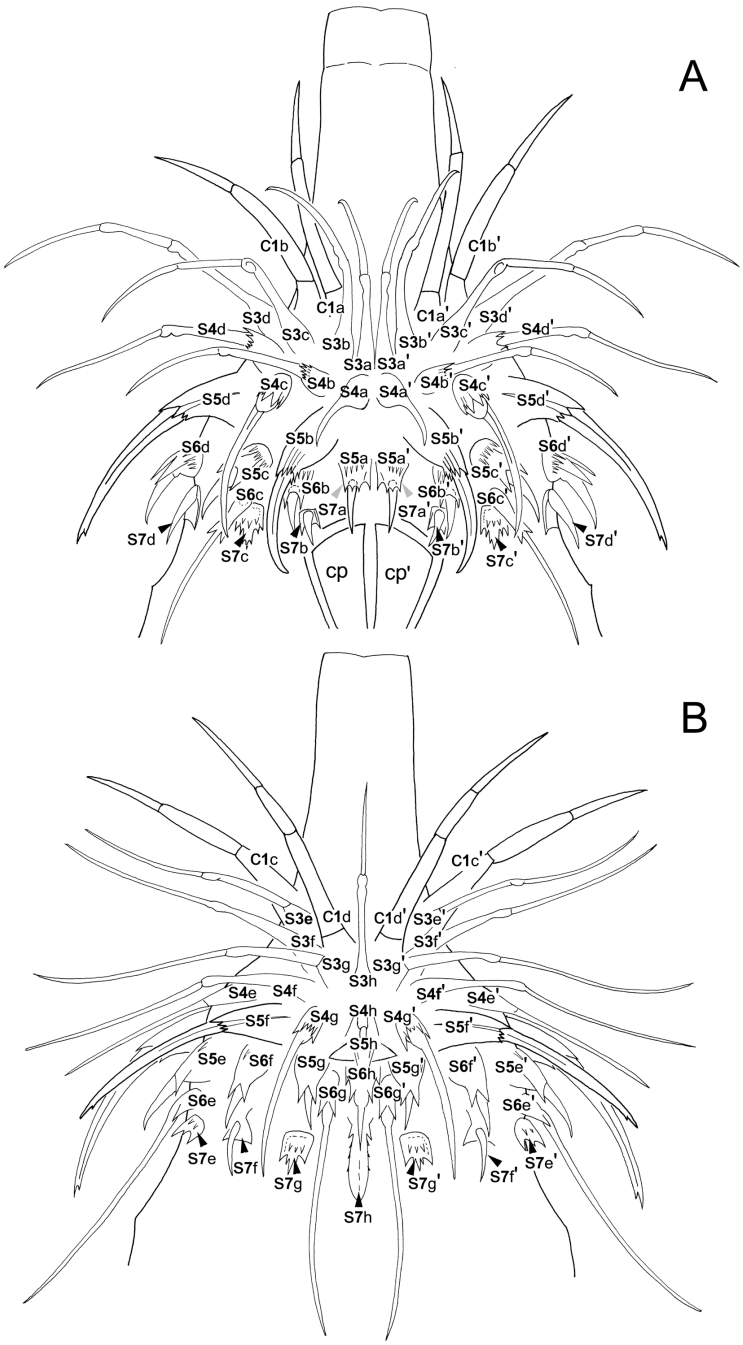


Figure 15. Scalid arrangement on the introvert of the Higgins-larva of *Armorloricus* sp. I, optic section: the second row of scalids is missing. **A.** numbering of scalids in ventral view; **B.** numbering of scalids in dorsal view.

Figure 15. Disposition des scalides sur l'introvert de la "Larve-Higgins" de *Armorloricus* sp. I, section optique : la deuxième rangée de scalides manque. **A.** dénombrement des scalides en vue ventrale ; **B.** dénombrement des scalides en vue dorsale.

and left anal plate. Pair of stiff and long posterodorsal setae (se_1) on posterior end of lorica. Pair of posterolateral setae (se_2) longest and inserting laterocaudally. Anal cone (ac) dorsoterminally and surrounded by seven anal plates. Opening of anus terminally beneath central anal plate. Three papillate flosculi (fl) dorsally on anal plates. One single flosculus more centrally than other pairs of flosculi, have a more lateral position. Two large anal plates ap_1 overlap the ventral toe joints from behind.

Differential diagnosis

Morphometric data in Table 2.

The Higgins-larvae of *Armorloricus* sp. I and *Armorloricus* sp. II are mainly distinguished by (1) structure of toes, toes longer in larva of sp. I., with tips of mucrones diverging more widely than in larva of sp. II. Furthermore, rims of mucrones undulated in sp. II larva, but are smooth and coherent in sp. I larva. Further features are (2) locomotory appendages shorter in sp. I larva than in sp. II larva, (3) second row of scalids totally absent in sp. I larva, only four remaining spinoscalids forming second row of sp. II larva, (4) slight differences present in structure of scalids, sp. I larva with longer and more filiform scalids, lateral scalids of the third row with additional third segment, sp. II larva with more solid and shorter scalids, scalids of second and third row always with two segments; plate-like elements of seventh row more square-shaped and dentate in sp. II larva instead of triangular as in sp. I larva.

Cross-sections of corresponding regions of Armorloricus elegans *sp. nov. and* Nanaloricus mysticus

1 µm epoxy resin cross-sections were performed on paratype material of both *Armorloricus elegans* sp. nov. (male, Fig. 19A, C, E and G) and *Nanaloricus mysticus* (female, Fig. 19B, D, F and H) for light microscopy (Fig. 19). The body cavity of both species is strongly reduced or absent. The transition zone between the thorax and the lorica is shown in Fig. 19A and B. This part of the thorax is called the posterothorax, which lacks appendages and is always retracted inside the lorica. The cuticle of *A. elegans* sp. nov. is thinner in this region than in *N. mysticus*. The 15 lorical spikes (ls) are clearly observed in both sections. The spikes are hollow with a duct of a multicellular gland. Furthermore, the two types (tr1 and tr2) of trichoscalids are visible in cross-sections. The trichoscalids are

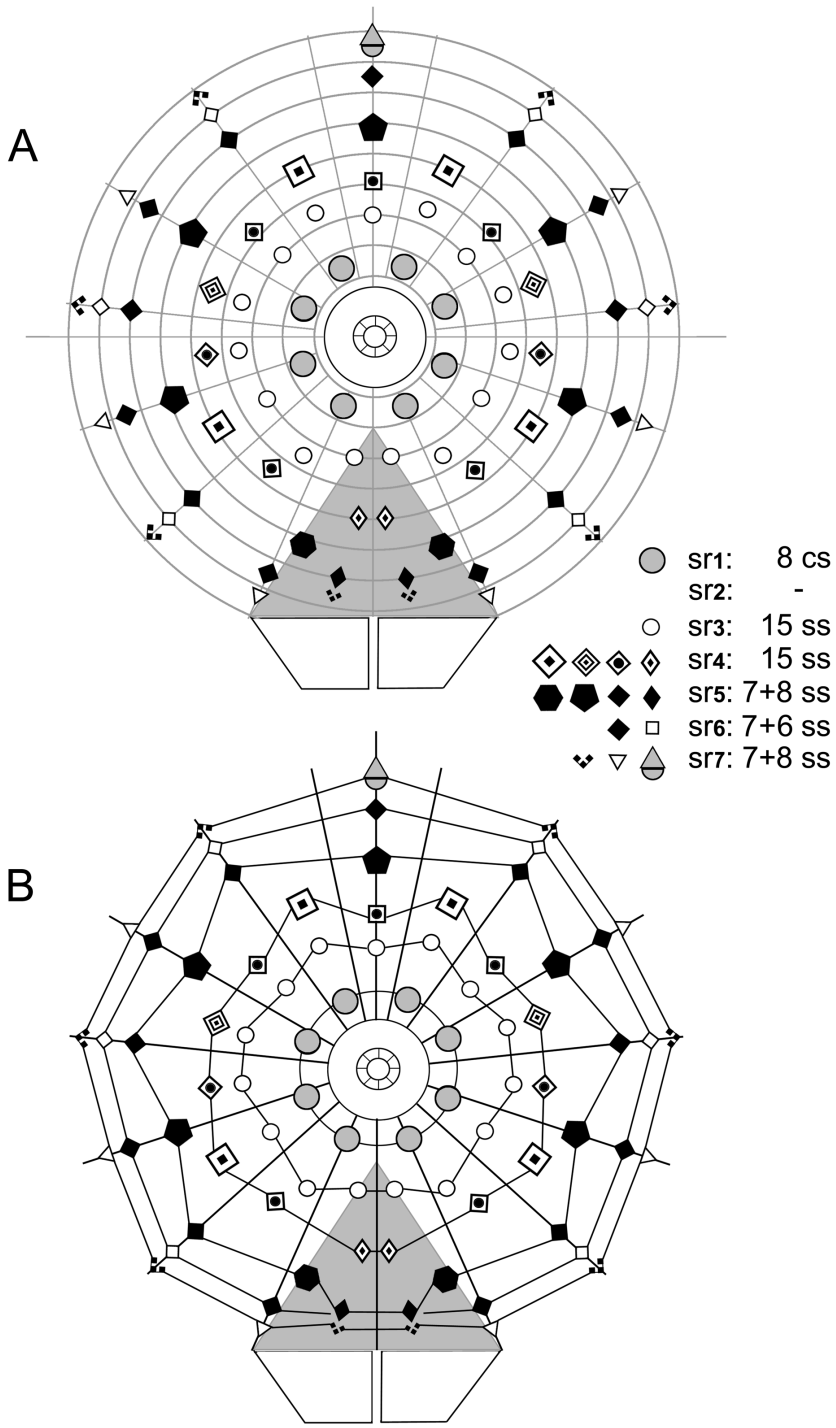


Figure 16. Scalid arrangement on the introvert of the Higgins-larvae of *Armorloricus* sp. I. ; the second row of scalids is missing. **A.** as polar coordinate diagram; **B.** as transformed diagram. Identical symbols = group of scalids which share the same structure.

Figure 16. Disposition des scalides sur l'introvert de la "Larve-Higgins" de *Armorloricus* sp. I ; la deuxième rangée de scalides manque. **A.** diagramme en coordonnées polaires ; **B.** diagramme transformé. Les symboles identiques représentent des groupes de scalides ayant la même structure.

located between the lorical spikes. Since the introvert is retracted in *A. elegans* sp. nov., the inverted scalids and the mouth cone are seen in the centre. The introvert is fully extended in *N. mysticus*; therefore the pharyngeal bulb (pb) is located in the posterothorax. The anterior region of the lorica is very different in the two genera. In *N. mysticus*, the dorsal lorica consists of a single plate (Fig. 19 D, F and H), while in *A. elegans* sp. nov. the dorsal plate (Fig. 19 C and E) is split into middorsal (dp_1) and laterodorsal plates (dp_2, dp_2'). The dorsoventral muscles (dv) are much more developed in *A. elegans* sp. nov. (Fig. 19C) than in *N. mysticus*, where these muscles are separated into two bundles (Fig. 19 F). The two dorsolateral plates of the lorica (lp_2) are different in the two genera. In *N. mysticus* the two plates are of medium size and concave (Fig. 19D, F and H), while in *A. elegans* sp. nov. these two plates are very large (about the same size as the unit of the three ventral plates) and first get concave in the posterior part of the lorica (Fig. 19C, E and G). Furthermore, the cuticular hinge (hi) of the lorica plates is located in a different way in the two genera (Fig. 19G and H).

Discussion

Occurrence of representatives of Nanaloricidae

To date only two species of Nanaloricidae have been described, *Nanaloricus mysticus* Kristensen, 1983 from Roscoff (Atlantic Ocean) and *Nanaloricus khaitatus* Todaro & Kristensen, 1998 from the Mediterranean Sea (Todaro & Kristensen, 1998). Other localities are known to be inhabited by *Nanaloricus* species, mainly in the Atlantic Ocean. New species still undescribed were collected off the coast of Florida (USA), the Faroe Bank, and also from the vicinity of the type locality of *N. mysticus*. With the description of two new species of *Armorloricus*, a second

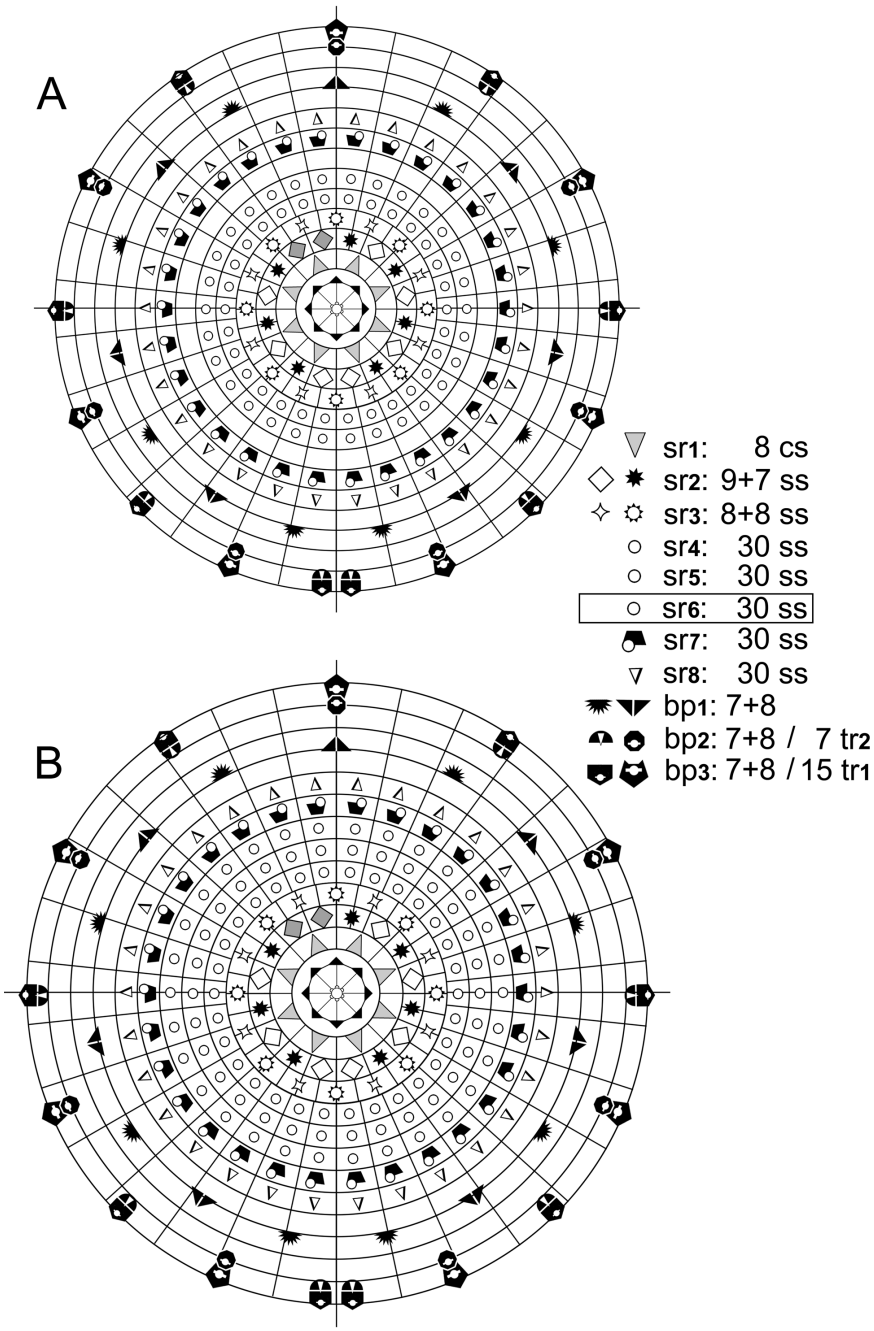


Figure 17. Scalid arrangements on the introvert of the postlarva and adult of *A. elegans* sp. nov. as polar coordinate diagram. **A.** postlarva; **B.** adult.

Figure 17. Disposition des scalides sur l'introvert de la post-larve et de l'adulte de *A. elegans* sp. nov., diagramme en coordonnées polaires. **A.** post-larve ; **B.** adulte.

genus within the Nanaloricidae is established. To our knowledge, Nanaloricidae are mainly distributed in the subtidal zone. Representatives of other new genera were found in samples from the plateau of the Great Meteor Seamount, at 280 m depth (Gad, 2003). Reports of Nanaloricidae from the deep sea do not exist, with one exception: one aberrant specimen was collected from deep-sea sediments of volcanic origin at 1500 m depth around Lihir Islands, Pacific (Gad, 2004).

Comparison of Nanaloricus *and* Armorloricus *gen. nov.*

The species of *Armorloricus* gen. nov. can be distinguished from the species of *Nanaloricus* by many distinguishing features. The characters of both taxa are compared in table 3. The most obvious features separating both taxa are associated with the structure of the mouth cone and the lorica in the adults. *Armorloricus* gen. nov. possesses an extremely long mouth tube (Fig. 8A, F). External furcae as described for *Nanaloricus* (Kristensen, 1983, 1991a) are only present in the short conical basal section of the mouth cone of *Armorloricus* gen. nov. An accordingly longer, telescopically protrudable buccal tube reflects this extreme length of the mouth tube internally.

The differences in structure between the lorica of *Armorloricus* gen. nov. and *Nanaloricus* can be well demonstrated in cross-sections through the middle of the trunk (Fig. 19). In *Nanaloricus* the undivided dorsal and both dorsolateral plates of the lorica have nearly the same width. Additionally, the width range between dorsal and ventral plate does not differ much. The dorsal plate reaches 87% of the width of the ventral plate. This observation can be summarized in a relation of proportions: ventral plate > dorsal plate > dorsolateral plates. In *Armorloricus* gen. nov. the ventral plate and both dorsolateral plates are large and have identical dimensions. The dorsal plate is clearly narrower and reaches only 64% of the width of the ventral plate. Additionally, the dorsal plate is longitudinally entirely subdivided into three additional plates. The relation of proportions of the plates is summarized as followed: ventral

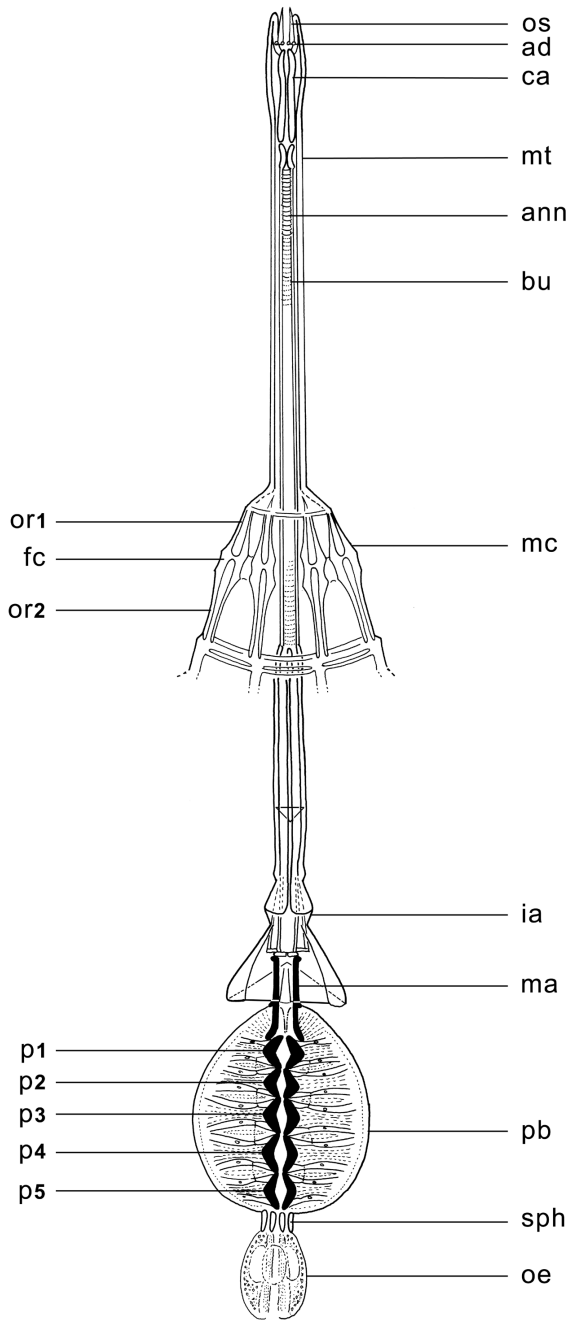


Figure 18. Mouth cone and associated internal structure of *Armorloricus* gen. nov.

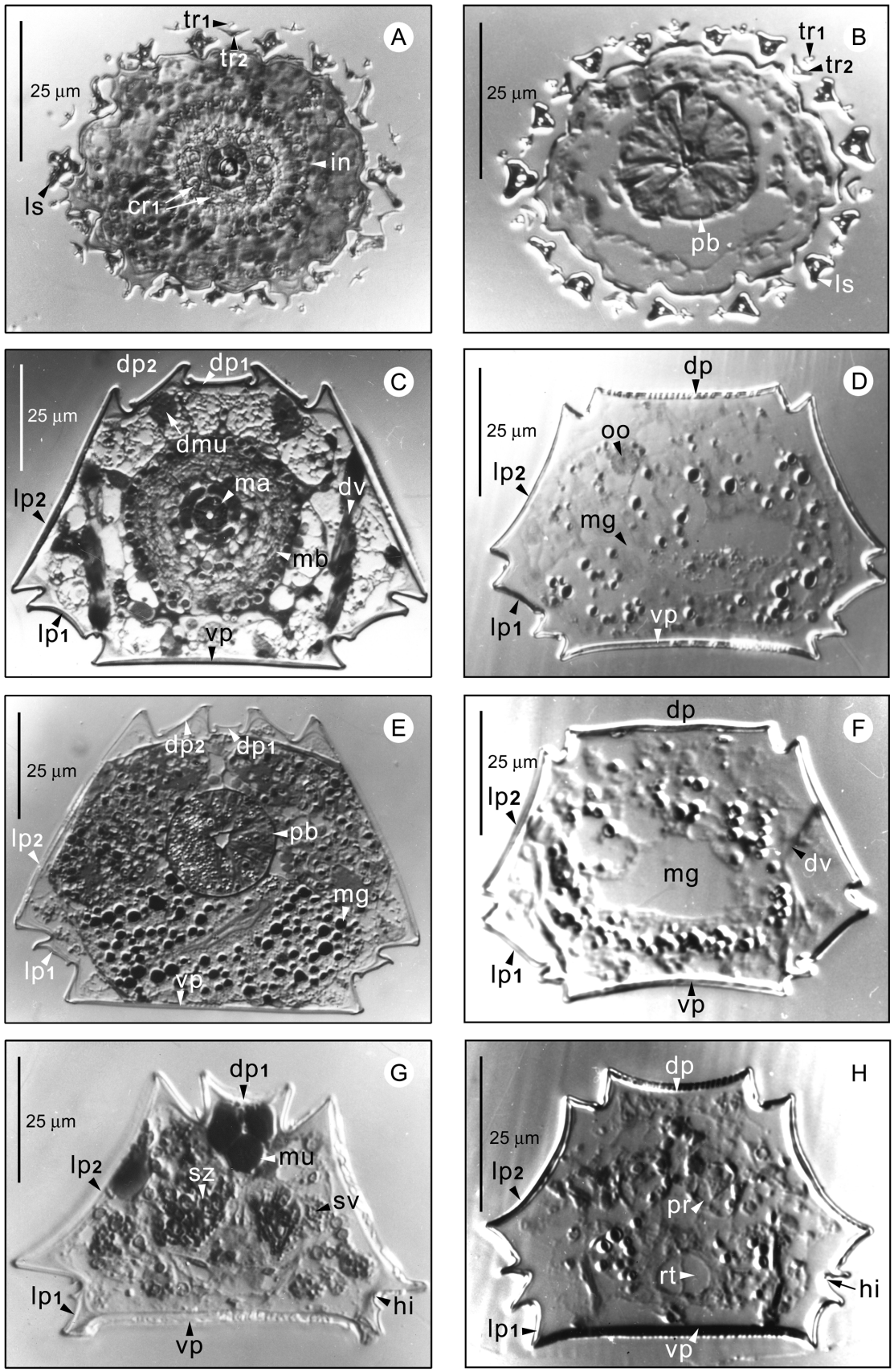
Figure 18. Cône buccal de *Armorloricus* gen. nov. et structures internes associées**.**

plate = dorsolateral plates > dorsal plate. The lateral upward folding of the inner margins of the dorsolateral plates, which cover the dorsal plates partly, is also a new character for *Armorloricus* gen. nov. The same phenomenon is apparent in the outer lateral margins of the laterodorsal plates, which also fold up and partly back and cover the same plates. The trunk cuticle of adults of *Armorloricus* gen. nov. lacks any ultrasculpture, which gives the surface of the cuticle a smooth and shiny appearance (Fig. 8). In contrast, in all adults of described and presently undescribed species of *Nanaloricus*, the cuticle of the lorica plates have a pronounced honeycomb ultrasculpture (Kristensen, 1983, 1991b; Todaro & Kristensen, 1998; Gad, 200).

Internally the adults of both taxa differ in the posterior part of the prepharyngeal armature. An additional part, the manubrium, exists in both species of *Armorloricus* gen. nov., exclusively (Figs 7E and 18). A cross-section through the middle of the trunk reveals that the muscles also differ in both taxa. The pair of dorsoventral muscle bundles, which connect the two dorsolateral plates with the ventral plates, insert directly in the middle of the ventral plate in *Nanaloricus* (Kristensen, 1991b), whereas these muscles are attached more laterally in *Armorloricus* gen. nov. They do not insert directly on the ventral plate, but on the articulate cuticle between the ventral and the ventrolateral plates instead. Furthermore, the large paired dorsal retractor of the introvert, which extends subdorsally through the whole trunk, is fused along its entire length in *Nanaloricus* (Kristensen, 1991b). The related retractor in *Armorloricus* gen. nov. is widely separated, and both main bundles (a small third bundle in the middle) are in a more dorsolateral position.

Other distinguishing external characters are less obvious, e.g. the difference in the fine structure of the scalids present in the second, third and eight row. The sensory flosculi of the posterior half of the lorica are reduced in size to microflosculi in *Armorloricus* species. They can easily be overlooked in light microscopy investigation. The position of the lateral locking element of the plate articulation clearly differs in both genera, but also differs between *Nanaloricus* species. The value of this character for separation on a higher taxonomic level is unclear. The same is true for the number and structure of internal glands of the lorica spikes, i.e. the glands of *Nanaloricus*-species always have basal reservoirs.

Compared with the adults, the distinguishing characters of the Higgins-larvae of the two genera are much less pronounced (which is also known from the larvae of the genus *Rugiloricus* Higgins & Kristensen, 1986). They largely concern external features. The best feature consists of the short leaf-like and cut-off mucrones, which end in diverging, pointed tips in *Armorloricus*-larvae. There are further slight differences in the scalid modification between *Armorloricus*-larvae and *Nanaloricus*-larvae. In general, the scalids are shorter in *Armorloricus* species. A good character of the *Nanaloricus*-larvae is the four ventral spinoscalids arranged in a tight square. The upper pair originates from the second; the lower pair from the third row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of scalids. Each of them is more robust and has more hooklike tips than the other scalids belonging to these rows. Their distal segment is more clawlike. This tetrad of scalids is missing in *Armorloricus*-larvae. Generally shorter locomotory appendages on the ventral side are a questionable character for the Higgins-larva of *Armorloricus* gen. nov. The two *Armorloricus*-larvae show differences in the scalid number and arrangement on the introvert. The larva of *Armorloricus* sp. I has no scalids in the second row of scalids. The scalid formula is as follows: 8cs/0/15/15/7+8/6+7/7+8ss (Fig.16). In the sixth row, two scalids are lacking (s6a, s6a') in the ventral position. The scalids in the same location of the seventh row (s7a, s7a') are covered by the scalids of the fifth row (s5a, s5a'). As opposed to this, the larva of *Armorloricus* sp. II has five developed scalids in the second row: 8cs/5/15/15/7+8/6+7/5+8ss. So in this species only a part of the second scalid row is developed and both scalids of the sixth row (s6a, s6a') are lacking in the ventral position.

With the investigation of the species of *Armorloricus* gen. nov. many new details are presented and the Nanaloricidae are characterized more consequently. The new results concerning the *Armorloricus*-species will be discussed after the next paragraph listing the revised characters of the Nanaloricidae, because they are shared by the *Nanaloricus*-species, and will be elaborated in more detail in that context.

Characters of adult Nanaloricidae: (1) a big, non-eversible mouth cone with eight strong elevated, external furcae, (2) a mouth opening internally surrounded by six protrudable oral stylets, (3) an extremely long and anteriorly telescopically protrusible buccal tube, (4) a large pharyngeal bulb with placoids and a prepharyngeal armature representing a transformation of a primary hexaradial symmetric element, (5) the position of the pharyngeal bulb behind the brain, and the mouth cone and pharyngeal bulb being separated, (6) an introvert with eight rows of scalids, (7) branched clavoscalids in the males, segmented and spinose leglike scalids in the females, (8) two types of second row spinoscalids: nine long leglike spinoscalids alternating with eight shorter filiform spinoscalids resembling feathers, (9) a distinct dorsal asymmetry in the second row of scalids, where two big leglike scalids are situated closely together, (10) the anterothorax, a new thoracic region, as a secondary, flexible separation extended between the first and second row of the thoracic basal plate, (11) short trichoscalids, and double trichoscalids with separate bases, (12) a lorica covered with heavily sclerotized plates with strong glandular spikes located on the anterior edge, (13) the lorica is furthermore equipped with a regular pattern of pores, which correspond with subcuticular glands, (14) the posterior half of the lorica is provided with papillate flosculi dorsally arranged in a tight cluster.

Characters of postlarval Nanaloricidae: (1) the free-living postlarval instar is always present, and it is similar to female individuals, (2) the postlarva is about 80% smaller than mature adults, (3) the sixth row of spinoscalids is not developed or present in protoformations, (4) the midgut walls are filled by granular cells, and sexual organs are not developed.

Characters of larval Nanaloricidae: (1) the larval instars are conspicuously smaller than the postlarva or adults, (2) an eversible mouth cone, which is a long conical unit, (3) a large pharyngeal bulb, which is simply cylindrical and without any armatures, (4) an introvert with seven rows of modified scalids, (5) the arrangement of scalids in functional units which are not always ordered as simple rows, (6) spinoscalids in the subventral sector from row four to seven are highly modified into a grasping apparatus, (7) two big ventral closing plates in the weakly developed collar region, (8) the transition of thorax and lorica with three pairs of scalidlike, segmented appendages with locomotory or grasping function, (9) the honeycomb ultrasculpture of the cuticle, (10) toes with broad mucrones and long end spine, (11) the posterior terminal setae are

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Figure 19. Cross-sections of corresponding regions of *A. elegans* sp. nov. (A, C, E, G) and *N. mysticus* (B, D, F, H); interference-contrast photographs. Note that the introvert is retracted in *A. elegans* sp. nov. and fully extended in *N. mysticus*. **A.** thorax with trichoscalids, lorical spikes, the inverted scalids, and mouth cone in the centre; **B.** thorax with trichoscalids, lorical spikes, and the pharyngeal bulb; **C.** anterior region of lorica with retracted midbrain (*mb*), manubrium (*ma*) and both dorsiventral lorical muscles; **D.** anterior region of lorica with midgut and an oocyte; **E.** median region of lorica with retracted pharynx bulb surrounded by midgut; **F.** median region of lorica with midgut and dorso-ventral lorical muscles; **G.** posterior region of lorica with three dorsilongitudinal muscles and seminal vesicles with spermatozoa; **H.** posterior lorica with rectum and protonephridia.

Figure 19. Coupes transversales des mêmes régions chez *Armorloricus elegans* (A, C, E, G) et *Nanaloricus mysticus* (B, D, F, H) ; photographies en contraste interférentiel. Noter que l'introvert est rétracté chez *A. elegans* sp. nov. et complètement étendu chez *N. mysticus*. **A.** Thorax avec trichoscalides, pointes de la lorica, scalides rentrées et cône buccal au centre ; **B.** Thorax avec trichoscalides, pointes de la lorica, et bulbe pharyngien ; **C.** région antérieure de la lorica avec région moyenne du collier nerveux (*mb*) rétractée, manubrium (*ma*) et les deux muscles dorso-ventraux de la lorica ; **D.** région antérieure de la lorica avec intestin moyen et un ovocyte ; **E.** région médiane de la lorica avec bulbe pharyngien rétracté entouré de l'intestin moyen ; **F.** région médiane de la lorica avec intestin moyen et muscles dorso-ventraux de la lorica ; **G.** région postérieure de la lorica avec trois muscles longitudinaux dorsaux et des vésicules séminales avec spermatozoïdes ; **H.** région postérieure de la lorica avec rectum et protonéphridies.

Table 3. Characters of *Nanaloricus* compared to *Armorloricus* gen. nov.
Tableau 3. Caractères comparés de *Nanaloricus* et *Armorloricus* gen. nov.

Nanaloricus	***Armorloricus*** gen. nov.
Adults:	Adults:
• Mouth cone broad, with long furcae of unequal length	• Mouth cone slim, only basal part with short identically furcae, with extrem long mouth tube
• Internal prepharyngeal armature without posterior manubrium	• Internal prepharyngeal armature with fully developed posterior manubrium
• Second row with long, spiny, leglike spinoscalids, alternating with short, filiform, and hairy spinoscalids, ending in pointed tips	• Second row with long, smooth, leglike spinoscalids, flattened, broad and strongly sclerotized, alternating with short, filiform, and hairy spinoscalids with club-shape tips
• Third row with long, spiny, leglike spinoscalids with spinose tips, alternating with slightly shorter, trichoid-covered, and leglike spinoscalids with claw-tips	• Third row with long, spiny spinoscalids alternating with slightly shorter, trichoid- covered, leglike spinoscalids, both with spine-tips
• Scalids of the seventh row tricruspidate	• Scalids of the seventh row toothlike
• Double trichoscalids of one type	• Double trichoscalids of two different types
• Lorica with honeycomb ultrasculpture	• Lorica smooth, lacking ultrasculpture
• Laterodorsal and middorsal plates nearly of the same width, middorsal plate one unit and planar	• Laterodorsal plates wider than dorsal plate, dorsal plate longitudinally subdivided into three additional plates
• (Lateral locking elements of plate articulation in ± 25% distance from caudal end)	• (Lateral locking elements of plate articulation on the level of caudal end)
• Lorica spikes with gland reservoirs; midventral spine ± reduced	• Lorica spikes without reservoirs of glands; midventral spine not reduced
• Flosculi well-developed	• Flosculi reduced in size to micro-flosculi
• Dorsoventral muscles attached median directly on ventral plate; paired dorsal retractor of introvert fused longwise	• Dorsoventral muscles attached laterally between ventral and venterolateral plates; paired dorsal retractor of introvert widely separated
Higgins larva:	Higgins larva:
• Four spinoscalids tightly arranged in a quadrat in ventral position, strongly sclerotized and with hook-tips	• Two spinoscalids in tight paired arrangement in ventral position, without extra modification
• Six elements of last scalid row duplicate and spiny	• Six elements of last scalid row singular and dental
• Ventral pair of locomotory appendages spinelike, 30 % of the length of lateroventral pair	• Ventral pair of locomotory appendages hooklike, 20% of the length of lateroventral pair
• Toes with long mucrones, with distinct serrated lateral margins	• Toes with short cut-off mucrones, ending in two diverging pointed tips, with ± undulate lateral margins

reduced in length and situated in the centre of the anal cone, (12) three well developed flosculi on the anal plates, (13) the four adhesive glands of the toes are sacklike and of the same size, (14) the larval cuticle of the lorica has an obvious ultrasculpture in a honeycomb pattern.

Comparison of Nanaloricidae and Pliciloricidae

One of the obvious adult characters of the Nanaloricidae is the presence of a non-eversible mouth cone. Internally the mouth cone is a cuticularized and telescopic buccal tube (Kristensen, 1991a, 1991b). Also unique for the Nanaloricidae is the separation between the mouth cone and the large triradiate myoepithelial pharyngeal bulb. The long buccal tube connects the external mouth cone with the internal pharyngeal bulb. The pharyngeal bulb is located deep inside the trunk behind the brain. This is in contrast to the Pliciloricidae, where the mouth cone is basally eversible and the small pharyngeal bulb is fused internally with the mouth cone. Furthermore, the pharyngeal bulb of the Pliciloricidae also lacks the extremely long, annulated, and well-cuticularized buccal tube and the five rows of placoids forming a sclerotized layer of the lumen walls. The complex prepharyngeal armature is another characteristic feature of the Nanaloricidae and is not so obvious developed in the Pliciloricidae. This special modification of the feeding apparatus seems to allow a basic feeding strategy by external digestion and ingestion of liquefied food or small particulate material (bacteria). Bigger particles cannot pass the narrow buccal tube.

An additional characteristic of the Nanaloricidae is the scalid dimorphism of the second and third row. In the Pliciloricidae, dimorphic scalids in alternating arrangement are only present in the fourth row. Even the number of scalids in the first three rows of spinoscalids differs between both taxa. The number and arrangement of scalids on the introvert are expressed in a scalid diagram and in the scalid formula: 8cs//9+7/16/30/30/30/30/30ss in adults of Nanaloricidae (Fig. 17). The nanaloricid scalid formula differs from that for adults of all described species of Pliciloricidae : 8cs//9/15/15+15/30/30/30/30/30ss. For the

procedure of mapping the scalids on the introvert, a standardized polar diagram was used, created by Higgins and Brown for the Kinorhyncha (Brown, 1985, 1989; Higgins, 1990). The diagram demonstrates the alternating arrangement formed by two different types of scalids in the second and third row. The distinct dorsal asymmetry in the second circle of scalids is even best visualized in this kind of diagram. This asymmetry is common and identical in all studied adult and postlarval specimens belonging to the Nanaloricidae, but has not been observed in the Pliciloricidae. This allows the conclusion that the Nanaloricidae have only eight rows of scalids on the introvert, whereas the Pliciloricidae have nine. The structure and number of spinoscalids in the second row of the Nanaloricidae suggest that the second and the third scalid row of the Pliciloricidae are fused in the Nanaloricidae. The nine strong segmented and leglike scalids of the second row present in the Pliciloricidae are also developed in the Nanaloricidae. Only seven instead of the original fifteen scalids remain from the united third row. The special featherlike structure of these seven scalids may not be a result of high modification. Instead, these scalids are unlikely to be fully developed. They could represent protoscalids similar to those investigated in the Kinorhyncha, where every scalid appears as a spinose "Anlage" in one juvenile instar to be fully differentiated and developed in the next following instar (Neuhaus, 1995). If this mechanism for the development of scalids holds true in an ad-hoc way during the metamorphosis of the adult Loricifera as well is unclear.

In the Higgins-larvae of *Armorloricus* gen. nov., as a representative of the Nanaloricidae, the scalid modification are now investigated more carefully and worked out in finer details than described for *N. mysticus* (see Kristensen, 1983, 1991a, 1991b). The separation and arrangement of scalids in certain rows are simple in all adult Loricifera. The same result will be obtained in most larval types occurring in the Pliciloricidae. However, scalid mapping of nanaloricid larvae with the standardized polar diagram simplifies too much. Additionally, it does not reflect the high modification of scalids and their row structures. The spinoscalids lack the strict arrangement in rows and do not display a regular order. In Fig. 16 A-B a conventional polar diagram is compared with a transformed diagram to reflect the dislocation of scalids in a more realistic way. Groups of scalids become functional units and they are combined longitudinally or transversally to comply their function. This phenomenon is best recognized in the ventral sector, where scalids form an apparatus for grasping. The dislocation of scalids is explained by the fact that scalids or groups of scalids are enlarged to fulfil their special function. The restricted space on the introvert may cause other scalids to be consequently reduced in size.

A systematic numbering of scalids is introduced here to allow an easy comparison of scalids between different species and taxa. It shows that the scalids in the larval type of Nanaloricidae differ in number and pattern of arrangement from those of the larvae of Pliciloricidae. The latter have seven rows of scalids in contrast to six to seven rows in the Nanaloricidae. The maximum number of 15 scalids per row is identical in both taxa and is assumed to be a basic pattern found in all Higgins-larvae. Additionally, the investigation shows that the larva of *Armorloricus* sp. I lacks the second row of scalids in contrast to the larva of *Armorloricus* sp. II. In the former only four fully developed scalids remain from the second row.

In the adults, the first row of basal plates mediates a structure between the scalids of the introvert and the following rows of basal plates in the Nanaloricidae. The last row of introvert scalids is not clearly separated from the first row of basal plates. Instead, the first and second rows of basal plates are well separated by a broad and flexible region divided by weak folds. This is in contrast to the Pliciloricidae, where the three rows of basal plates are united and a comparable flexible region does not exist in this position. Moreover, the pliciloricid last scalid row and the first row of basal plates are well separated. Their flexible region behind the "neck", which contains all three rows of basal plates, is responsible for the movement of the introvert instead. Consequently the thoracic region is splitted into three subregions in the Nanaloricidae. The additional region has evolved as a secondary flexible apparatus for locomotory movements of the introvert and is called anterothorax. The posterior region of the "neck" carries two rows of basal plates, but all trichoscalids are located on the interthorax. Finally, the flexible and less sculptured transition zone connected with the lorica is called posterothorax and is shared by both taxa. Double and single trichoscalids in alternating arrangement are present in the Nanaloricidae as well as in the genus *Pliciloricus* Higgins & Kristensen, 1986. The double trichoscalids of *Pliciloricus* are fused basally. In the Nanaloricidae, the "double" trichoscalids are separated. This can easily be seen in SEM and TEM investigations.

In contrast to the Pliciloricidae where the trichoscalids have the same structure, the two lateroventral trichoscalids of the upper circle are modified into claspers in males in Nanaloricidae. This additional sexual dimorphism was first observed by Kristensen (1991b) in *N. mysticus*, and is common in all other investigated nanaloricid species. The claspers are assumed to function during copulation to hold the females.

The new observations described here verified the conclusions previously summarized by Lemburg (1999), i.e. that the Nanaloricidae have a higher modified morphology compared to the Pliciloricidae. However, their life cycle

with the occurrence of an unmodified free-living postlarva seems to be relatively basic (Kristensen, 1991a, Kristensen & Brooke, 2002). In the more modified life cycle of the Pliciloricidae, the postlarval instar is reduced or modified, and additional paedogenetic larval instars may be present (Kristensen,1991a, 2002a, 2002b).

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References

Brown R. 1985. *Developmental and taxonomic studies of Sydney Harbour Kinorhyncha*. Ph.D thesis, Macquarie University, Sidney, Australia. 193 pp.

Brown R. 1989. Morphology and ultrastructure of the sensory appendages of a kinorhynch introvert. *Zoologica Scripta*, **18**: 471-482.

Gad G. 2003. The Loricifera fauna of the plateau of the Great Meteor Seamount. *Archives of Fishery and Marine Research*. (in press).

Gad G. 2004. A new genus of Nanaloricidae (Loricifera) from deep-sea sediments of volcanic origin in the Kilinailau Trench north of Papua New Guinea. *Helgoland Marine Research*, **58**: 40-53.

Higgins R. P. 1990. Zelinkaderidae, a new family of cyclorhagid Kinorhyncha. *Smithsonian Contributions to Zoology*, **500**: 1-26.

Higgins R. P. & Kristensen R.M. 1986. New Loricifera from Southeastern United States coastal waters. *Smithsonian Contributions to Zoology*, **438**: 1-70.

Hubbard G.F., Howard R.L. & Gallaway B. J. 1988. Loricifera, a recently described phylum, occurring in the northern Gulf of Mexico. *Northeast Gulf Science*, **(10) 1**: 49-50.

Kristensen R.M. 1983. Loricifera, a new phylum with Aschelminthes characters from the meiobenthos. *Zeitschrift für Zoologische Systematik und Evolutionsforschung*, **21**: 163-180.

Kristensen R.M. 1991a. Loricifera - A general biological und phylogenetic overview. *Verhandlungen der Deutschen Zoologischen Gesellschaft*, **84**: 231-246.

Kristensen R.M. 1991b. Loricifera. In: *Microscopic Anatomy of Invertebrates 4: Aschelminthes*. (F. W. Harrison & E. E. Ruppert eds), pp. 351-375. Wiley-Liss: New York.

Kristensen R.M. 2002a. Loricifera. *Encyclopedia of Life Sciences*, **11**: 153-156, (www.els.net.) Macmillan Reference: London.

Kristensen R.M. 2002b. An introduction to Loricifera, Cycliophora and Micrognathozoa. *Integrative & Comparative Biology*, **41**: 134-144.

Kristensen R.M. 2003. Kapitel 18. Loricifera. In: *Das Mittelmeer, Fauna, Flora, Ökologie, II/1 Bestimmungsführer* (R. Hofrichter ed.), pp. 638-645. Spektrum Akademischer Verlag: Heidelberg, Berlin.

Kristensen R. M. & Brooke S. 2002. Phylum Loricifera. In: *Atlas of marine invertebrate larvae*. (C. M. Young, M. A. Sewell & M. E. Rice eds.) pp. 179-182. Academic Press: London, New York.

Kristensen R.M. & Meier T. 1986. Oppdagelsen av en ny dyrerekke, korsettdyrene. *Fauna*, **39**: 47-52. Oslo.

Kristensen R.M. & Shirayama Y. 1988. *Pliciloricus hadalis* (Pliciloricidae), a new loriciferan species collected from the Izu-Ogasawara Trench, Western Pacific. *Zoological Science*, **5**: 875-881.

Lake P. S. 1973. Trialdehyde fixation of crustacean tissue for electron microscopy. *Crustaceana*, **38**: 73-81.

Lemburg C. 1999. *Ultrastrukturelle Untersuchungen an den Larven von Halicryptus spinosus und Priapulus caudatus (Hypothesen zur Phylogenie der Priapulida und deren Bedeutung für die Evolution der Nemathelminthes).* Dissertation, Cuvillier Verlag: Göttingen, 393 pp.

Neuhaus B. 1995. Postembryonic development of *Paracentrophyes praedictus* (Homalorhagidae): neoteny questionable among the Kinorhyncha. *Zoologica Scripta*, **24**: 179-192.

Neuhaus B., Kristensen R.M. & Peters W. 1997. Ultrastructure of the cuticle of Loricifera and demonstration of chitin using gold-labelled wheat germ agglutinin. *Acta Zoologica*, **78**: 215-225.

Shirayama Y. & Kristensen R. M. 1988. Taxonomy, ecology und biogeography of Loricifera. *Benthos Research*, **32**: 18-20.

Todaro M. A. & Kristensen R.M. 1998. A new species and first report of the genus *Nanaloricus* (Loricifera, Nanaloricidae) from the Mediterranean Sea. *Italian Journal of Zoology*, **65**: 219-226.