Zootaxa 2096: 33–49 (2009)
www.mapress.com/zootaxa/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

Culexiregiloricus, a new genus of Nanaloricidae (Loricifera) from the deep sea of the Guinea Basin (Southeast Atlantic)*

GUNNAR GAD
Abt. DZMB, Forschungsinstitut Senckenberg, Südstrand 44, D-26382 Wilhelmshaven, Germany
E-mail: ggad@senckenberg.de

* *In*: Brökeland, W. & George, K.H. (eds) (2009) Deep-sea taxonomy — a contribution to our knowledge of biodiversity. *Zootaxa*, 2096, 1–488.

Abstract

A postlarva of Nanaloricidae (Loricifera) was found in the deep sea of the Guinea Basin. This postlarva belongs to a new species, *Culexiregiloricus trichiscalida,* which also represents a new genus. It inhabits clayish sediments with a high amount of calcitic multi-chambered shells of recent planktonic foraminiferans of 0.25 to 1.5 mm in size. This is the third report of a species of Nanaloricidae from a deep-sea habitat. The postlarva is characterized by a mouth cone divided in a short basal section and being drawn out terminally in to a long and slim mouth tube as second section. It also has distinct filiform and delicate clavo- and spinoscalis of the second and third rows all covered with minute trichoids, a lorica divided into eight plates (four broad and four narrow ones, some of which have two to eight transversal undulations) and eight wide intercalary plicae (six broad and two narrow ones, with distinct longitudinal folds), 14 lorica spikes of medium size along anterior rim of lorica. Other characters include eight dorsal papillated flosculi, of which six form clusters of three each on dorsolateral plates, and a caudal end with a broad ventral plate flanked longitudinally by massive elevated cuticular ridges. Together with the three species of the genus *Armorloricus* and one species of the genus *Phoeniciloricus*, the new species may form a specific species-group within Nanaloricidae, which is characterized by a long and slim mouth tube as the most obvious character.

Keywords: deep-sea meiofauna, southeast Atlantic deep-sea basins, Meteor Cruise M63/2, DIVA 2

Introduction

The DIVA 2 (Latitudinal Gradients of Deep-sea BioDIVersity in the Atlantic Ocean, Part 2) Expedition is the second in a series of expeditions dedicated to the study of benthic diversity in the deep-sea basins of the Atlantic Ocean. The material of the DIVA 1 Expedition hints at an unexpectedly diverse loriciferan fauna inhabiting the fine-grained clayish bottoms of the deep sea (Gad 2002; 2005a). These earlier observations have been confirmed so far by the results of examinations of the DIVA 2 material. Generally, the majority of all newly discovered loriciferans species found in deep-sea basins of the southeast Atlantic and elsewhere belongs to the Pliciloricidae (Kristensen & Shirayama 1988; Gad 2005 a, b). Nanaloricidae, however, are to be a regular part of the deep-sea meiofauna, because they are found sporadically and in extremely low densities even for Loricifera standards. However reports of deep-sea Nanaloricidae have increased with each expedition (Heiner & Neuhaus 2007). *Nanaloricus mysticus,* the first species discovered, and the first species described of *Armorloricus* Kristensen & Gad, 2004, inhabit the interstitial of shell-gravel (*Dentalium* sand) of sublittoral areas near the coast of Roscoff (France) (Kristensen 1983; Kristensen & Gad 2004). Other species of both genera have been described from similar shallow water habitats (Todaro & Kristensen 1998; Heiner 2004; Kristensen et al. 2007). Two additional species representing new taxa of Nanaloricidae have been

Accepted by K.H. George: 11 Mar. 2009; published: 11 May 2009

reported to be part of a diverse interstitial meiofauna of coarse calcareous sediment which covers the summits of seamounts (Gad 2004b). The only exceptions so far are *Phoeniciloricus simplidigitatus* Gad, 2004, and *Spinoloricus turbatio* Heiner & Neuhaus, 2007. These are both representatives of Nanaloricidae which have been discovered in the deep sea. *P. simplidigitatus* inhabits a mixed sediments covered by volcanic ashes at 1,813 m depth in the deep sea of the New Ireland Basin in the Pacific (Gad 2004a). This finding came as a surprise but could be explained by the presence of specific coarse sediment, offering exactly the right conditions for the occurrence of Nanaloricidae. In the case of *S. turbatio* no data of the inhabited sediment is mentioned in the literature (Heiner & Neuhaus 2007). The presumed preference of Nanaloricidae for interstitial habitats is supported by morphological features, which characterize them and which are not normally found in Pliciloricidae, which inhabit fine-grained clayish bottoms of the deep sea (Gad 2004a, b). The new species described here as also a new genus is represented by a single postlarva and is the third report of a Nanaloricidae species from the deep sea. Its occurrence in the deep sea of the Guinea Basin may be connected with sediments rich in calcareous shells of planktonic foraminiferans, which provide the coarse sediment suitable for interstitial life.

Material and Methods

The sample yielding the loriciferan for this study was taken in spring 2005 during the DIVA 2 Expedition (Cape Town–Mindelo) with R/V "Meteor" (M63/2) with a multicorer (MUC) at 4,141 m depth at station 76 MUC 05 (from the Guinea Basin). Sampling and sorting of the meiofauna was carried out by the staff of the DZMB (Deutsches Zentrum für Marine Biodiversitätsforschung, Wilhelmshaven).

The upper five centimetres of the sample were fixed together with the supernatant water, which was filtered through a 40 µm mesh. The whole sample was fixed and preserved with 4% buffered formalin to which Bengal Pink was added. The meiofauna was extracted from the sediment using the differential flotation method with the colloidal silica gel Levasil (density 1,299 g/ml, at a concentration of 40%, Bayer, Leverkusen, Germany) and centrifugation of the sample at 4,000 rpm. The Loricifera specimen was sorted together with the other meiofauna with the aid of an Irwin loop under a stereomicroscope (LEICA MZ8). Once sorted, the specimen was placed in a 70% ethanol medium, then transferred to glycerol and mounted in a glycerol-paraffin-beeswax preparation (adapted from Higgins & Thiel 1988), and sealed with Glyceel (recipe after Brown 1997).

Microscopic investigation was carried out with a LEICA interference microscope (DMLB with UCA condensor, IC prism and doubler x1,5 and x2 (Leica Microsystems GmbH, Wetzlar, Germany)). Illustrations were made using the DMLB microscope with the aid of a drawing tube (mirror technique and macro-apparatus LEICA FS25PE).

LM imaging: Photographs were taken using the same microscope fitted with a computerised digital camera (ColourView system).

CLSM imaging: The same specimen was used for confocal imaging without specific treatment because the cuticular structures of Loricifera have strong autofluorescence. The images were taken on a Leica TCS SP 5 (Leica Microsystems GmbH, Wetzlar, Germany) equipped with a Leica DM 5000 B microscope and three visible lasers (Ar 100 mW 458, 476, 488 and 514 nm; DPSS 10 mW 561 nm; HeNe 10 mW 633 nm). Excitation wavelengths of 476 nm, 488 nm and 561 nm were used and the emitted fluorescence was detected on two channels (ch1: 492 nm–540 nm; ch2: 570 nm–618 nm). To view the specimen a Leica HCX PL FLUOTAR L 40.0 x 0.75 DRY objective and a Leica HCX PL APO CS 63.0 x 1.40 OIL objective were used. To maximise quality of output, specific laser settings and image parameters were adjusted and optimised during the imaging process.

Species were differentiated morphologically. The terminology used in text and figures was adapted from Kristensen and Gad (2004). The type material is lodged at the Senckenberg Museum Frankfurt (SMF) under the series number (SMF 16897).

Abbreviations used in figures and text:

‘	marks left side position of a structure; symmetrical ones (right side) unmarked
ac	anal cone
an	anus
ann	annuli (of buccal tube)
ba	hairy spinules of type sr$_2$b spinoscalids
bg	posterior bridge of lorica spikes
bp	basal plates
bp$_1$a	type A thoracic basal plates of first row (scale-like, on anterothorax)
bp$_1$b	type B thoracic basal plates of first row (scale-like, on anterothorax)
bp$_2$a	type A thoracic basal plates of second row (on interthorax, bearing tricoscalids)
bp$_2$b	type B thoracic basal plates of second row (on interthorax, bearing tricoscalids)
bp$_3$b	type B thoracic basal plates of third row (on interthorax, bearing tricoscalids)
bs	basal plate of spinoscalid
bu	buccal tube
ca	buccal closing apparatus (of buccal tube)
cr$_1$	first row of clavoscalid
cs	clavoscalid
dp	dorsal plate of lorica
dlp	dorsolateral plate of lorica
ea	lateral locking apparatus of lorica
fc	external furca of mouth cone
fl	papillate flosculus
gd	gland duct
gp	pore of subcuticular gland
in	introvert
ip	intercalary plica (numbered 1, 2, 3, 4, 1', 2', 3', and 4')
lo	lorica
lp	lateral plate of lorica (numbered 1, 2, 1', and 2')
lr$_1$	longitudinal primary fold of plicae
lr$_2$	longitudinal secondary fold of plicae
ls	lorica-spikes (along anterior margin)
mc	mouth cone
mo	mouth opening
mt	mouth tube
or	oral ridge
os	oral stylet
pr	protrusion
ps	protoscalid
rfl	reinforcement of lorica margin
sg$_{1-4}$	first to fourth segments of clavo- and spinoscalids
sr$_{4-8}$	fourth to eighth rows of spinoscalids
sr$_2$a	type A spinoscalid of second row
sr$_2$b	type B spinoscalid of second row
sr$_2$-ir	dorsal irregular asymmetrical arrangement in second row of spinoscalids
sr$_3$a	type A spinoscalid of third row
sr$_3$b	type B spinoscalid of third row

ss	spinoscalids
tc	trichoids of clavoscalids
th	unit of thorax
th_1	anterothorax
th_2	interthorax (= neck)
th_3	posterothorax
tr	trichoscalid
tr a	single type A trichoscalid
tr_1b	upper type B trichoscalid of paired ones
tr_2b	lower type B trichoscalid of paired ones
tu	transversal undulation
us	ultrasculpture of lorica
vp	ventral plate of lorica
ws	“window” of lorica spikes

Taxonomy

Loricifera Kristensen, 1983

Nanaloricidae Kristensen, 1983

Culexiregiloricus gen. nov.

Type species: Culexiregiloricus trichiscalida sp. nov.

Etymology: The generic name is composed of three words: *culex* (Lat. mosquito), *rex* (Lat. king) and *lorica* (Lat. corset), the first part means mosquito-king, referring to the characteristic long mouth tube of the new species which resemble the long piercing-sucking mouthparts of a mosquito.

Diagnosis of postlarva: Postlarva of small size, 285 µm length, posterior part of well-defined mouth cone divided in 2 sections. The first section is broad, bearing 8 elevated, external furcae and 8 oral ridges of identical length and structure, anterior second section being a narrow and long mouth tube. Inside of buccal channel begins with 6 oral stylets, of which the main part consists of a sclerotized but flexible buccal tube, which is long, narrow, and has a singly annulated inner cuticle layer. Connection of buccal tube and large round muscular pharyngeal bulb with triradiate internal prepharyngeal armature equipped with manubrium. Pharyngeal bulb, located (in fully extended holotype) at level of posterior half of thorax, internal pharyngeal layer sclerotized with 5 transversal rows of placoids. All 8 clavoscalids identical in structure, composed of 4 segments, basal segment enlarged, distal segments extremely slim, long, and fringed densely with fine trichoids. Long spinoscalids of 2nd to 6th rows are filiform and delicate; long type A spinoscalids of 2nd row basally enlarged and also covered densely with fine trichoids; type B spinoscalids of 2nd row short, indistinct, and covered with many fine hairy spinules; type A spinoscalids of 3rd row long, type B spinoscalids slightly stronger, distally claw-like, also covered with many fine hairy spinules. Long spinoscalids of 6th row missing, represented only by tiny protoscalids; scalids of 8th row in form of small beak-like protrusions. First row of basal plates of anterothorax consisting of 7 scale-like triangular protrusions alternating with 8 double tooth-like formations. Narrow interthorax bearing 2 circles of narrow but distinct trichoscalids which vary slightly in length but are identical in structure; paired trichoscalids separated basally. Lorica consisting of 8 plates and of 8 wide intercalary plica, plates with 2–8 transversal undulations (upwellings of cuticle), intercalary plica with thinner cuticle, defined by primary and secondary longitudinal folds, and without undulation; surface of lorica with distinct square-like as well as honey-comb ultrasculpture; ventral lorica-plate on both sides in anal region with locking apparatus flanked by 2 short, massive and longitudinal, cuticular protrusions; edge of lorica with 14 distinct spikes of moderate length; each spike with single indistinct window, transversal bridge, and single gland duct. Caudal half of lorica with 8 papillate flosculi, 3 of them forming clusters on both large lateral plates. Ventral anal region with small and slightly pointed anal cone located centro-caudally.

Culexiregiloricus trichiscalida sp. nov.

Figs. 1–4 (ventral view, dorsal view, photos of details)
Measurements in Table 1

Type material: Holotypic postlarva, DIVA 2 station 76, MUC 05 (mounted on slide SMF 16897).

Type locality: Guinea Basin I, 00°50’00’’ S, 05°35’00’’ E, depth 4,141 m, 19.03.2005.

Etymology: The species name *trichiscalida* means hairy scalids.

Description. Holotypic postlarva (Figs. 1; 2; 3A; 4A) being a fully extended specimen filled with granular tissue. Body length from tip of mouth tube to caudal end, sums up to 285 µm. Maximum diameter of trunk in middle of lorica, is 110 µm. Species of medium size with urn-shaped, rounded, and well-defined lorica. Body divided into mouth cone, introvert, subdivided thorax, and abdomen armoured with massive lorica. Abdomen not compressed dorsoventrally.

Anterior body part composed of non-extendable, unstalked, rigid mouth cone (Figs. 1; 3B, 4A), extruded and separated transversally from introvert by constriction and row of 8 cuticular plates.

Mouth cone divided into 2 parts (Fig. 1): mouth cone itself, as short proximal basal section (mc) with cuticle peeled off (as an artefact, see Figs. 3B, 4A) and mouth tube (mt) as long and narrow terminal section. Mouth cone basally surrounded by 8 oral furcae (fc) as supporting structures; 8 oral ridges (or) present, which frame each furca on both sides; furcae as well as oral ridges of identical structure. Mouth tube narrow, funnel-like and longer than proximal mouth cone. Mouth opening (mo) terminal on mouth tube. Internal buccal structures well visible starting with 6 small oral stylets (os) arranged ringwise inside mouth. All 6 oral stylets articulating with internal cuticular layer. Mouth cone with long, narrow buccal channel which starts with a closing apparatus behind ring of oral stylets and extending into long well-sclerotized buccal tube (bu), which is partly stiff and partly flexible. Buccal tube 12% longer than mouth cone and extending through brain down to large, round, and muscular pharynx bulb, its inner cuticular layer with characteristic fine transverse single striae or annulation (ann). Posterior part of buccal tube indistinctly triradiate in section, with extra sclerotized longitudinal edges. Buccal tube ends in triradiate prepharyngeal armature composed of 3 primary supporting elements longitudinally fused along their entire lengths with buccal tube. All primary elements also fused transversally forming 3 plates as outer pyramidal unit covering supporting elements of armature. Posteriorly armature with manubrium, anchored deeply inside pharyngeal bulb. In extended specimen (as in holotypic postlarva) pharyngeal bulb located deeply inside trunk at level of interthorax. The 3 corners of triradiate myoepithelial pharyngeal lumen paved with 5 rods of cuticular placoids, which are connected longitudinally with each other.

Spherical introvert (in, Figs. 1; 2A, B, 4A, 5) densely covered with 7 rows or circles of scalids (6th row of spinoscalids only developed as protoscalids). First row (cr_1) has 8 more anteriorly oriented clavoscalids, not stronger sclerotized than following spinoscalids.

Clavoscalids (Fig. 1) uniform in structure, but ventral pair slightly smaller; all of them divided into 4 segments; 1st segment (sg_1) enlarged, oval in section, short and united with swollen base, connected via joint with introvert; 2nd segment (sg_2) very long, flattened laterally, narrowing posteriorly and covered densely by tiny trichoids (tc); last 2 segments (sg_3, sg_4) small and narrow; terminal segment spine-like. Next rows have spinoscalids oriented posteriorly and with enlarged bases. Fully developed spinoscalids of third to 7th rows arise from small arched basal plates (bs).

Second row (sr_2) consists of 16 spinoscalids of 2 different types (Fig. 1). Nine being leg-like type A scalids (sr_2a), longer than clavoscalids and covered densely with trichoids. They consist of 4 segments; 1st segment (sg_1) enlarged, with separate base, and proximal fringe of small spinules; 2nd segment (sg_2) as long as

1st one, narrow and stalk-like; 3rd segment (sg_3) short end even narrower; 4th segment (sg_4) spine-like and of same length as third one; distinct hinge joint present between first and second segments. Type A spinoscalids alternat with 7 smaller and shorter type B spinoscalids (sr_2b) consisting of only 2 segments; 1st segment bulbous and with fringe of spinules; 2nd segment rigid, filiform and with numerous fine hairy spinules (ba) scattered over entire length like barbs of a feather. Alternating arrangement of sr_2-spinoscalids irregular ventrally at midline and dorsally beside midline (Figs. 2, 5), where 2 type A spinoscalids stand close together, and where 1 type B spinoscalid is lacking.

Third row (sr_3) of scalids also has 16 spinoscalids of 2 different types (Figs. 1, 2), but without irregularities in alternating arrangement, because they are equal in number. Both spinoscalid types of this row similar in appearance to type A spinoscalids of 2nd row but composed of 3 segments only. First segment of 8 type A spinoscalids (sr_3a) enlarged, with hinge joints at border to 2nd segment, this segment filiform, covered with trichoids, and 4 times longer than 1st segment; 3rd segment spine-like. Eight type B scalids (sr_3b) clearly shorter than type A spinoscalids; 1st segment bulbous with dorsal fringe of spinules; 2nd segment long, filiform, and equipped with tiny spinules; 3rd segment as long as 2nd one, sickle-like, basally with ventral tooth, and with numerous fine long hairy spinules scattered over entire length; hinge joints between 2nd and 3rd segments bearing 2 lateral spines.

Fourth (sr_4) and 5th (sr_5) rows each with circle of 30 uniform spinoscalids (Figs. 1, 3c) which are more filiform and hair-like than spinoscalids of 2nd and 3rd rows. All of these consist of 3 segments; basal segment short and slightly enlarged; 2nd and 3rd segments elongated, connected via indistinct hinge joints. Long spinoscalids of 6th (sr_6) row are missing (which is a characteristic feature of postlarvae in general, see discussion), only developed as 30 wart-like protoscalids located in distinct gap between 5th and 7th rows (marked with an arrow in Fig. 3C). 7th row (sr_7) has 30 bristle-like spinoscalids, which are not divided into segments, but with enlarged bases and long filiform distal parts which have lateral margins covered with fine trichoids. Eighth row of scalids with 30 small, distinct and posteriorly oriented sharply pointed, tooth-like protrusions.

Thorax (Figs. 1, 2) subdivided into 3 subregions: antero-, inter-, and posterothorax. Anterothorax (th_1) with 1st row of 15 thoracic basal plates, zone between this row of basal plates and the next with flexible cuticle. Basal plates of 1st row scale-like, located immediately behind 8th row of scalids of introvert, so that there is no clear separation between introvert and thorax. Seven triangular type A basal plates (bp_1a) of 1st thoracic row alternate with 8 type B basal plates (bp_1b) which have double tooth-like appearance.

The next 2 rows of basal plates (Fig. 1) constitute the interthorax (th_2) or neck, and carry 8 single and 7 paired trichoscalids arising from 2 rows of basal plates. Eight type A basal plates (bp_2a) are small in size, smooth, and shield-like carry single type A trichoscalids (tr a), which have enlarged angular bases (absent from the 2 midventral ones). Type A basal plates alternate with 7 type B basal plates. Upper basal plates of 2nd row (bp_2b) are large and trapeziform, whilst lower basal plates of 3rd row are hexagonal. All trichoscalids indistinct and similar in structure: narrow, flat, with finely serrated lateral margins and with capillary central channel running inside the median axis, indistinct erect margin present perpendicular to central channel equipped with spinules; tips ending indistinctly in 4 spinules.

Upper type B trichoscalids (tr_1b) connects with basal plates via small triangular shafts, lower type B trichoscalids (tr_2b) inserting directly on basal plates and being slightly shorter than upper ones. Upper and lower type B trichoscalids appear as “paired trichoscalids” with separate, not fused, bases. Third row has only 7 trapeziform type B basal plates (bp_3b), which carry trichoscalids. Midventrally, there are 2 single lower slightly smaller type A trichoscalids on both sides of central axis; middorsally, there is a pair of upper and lower type B trichoscalids.

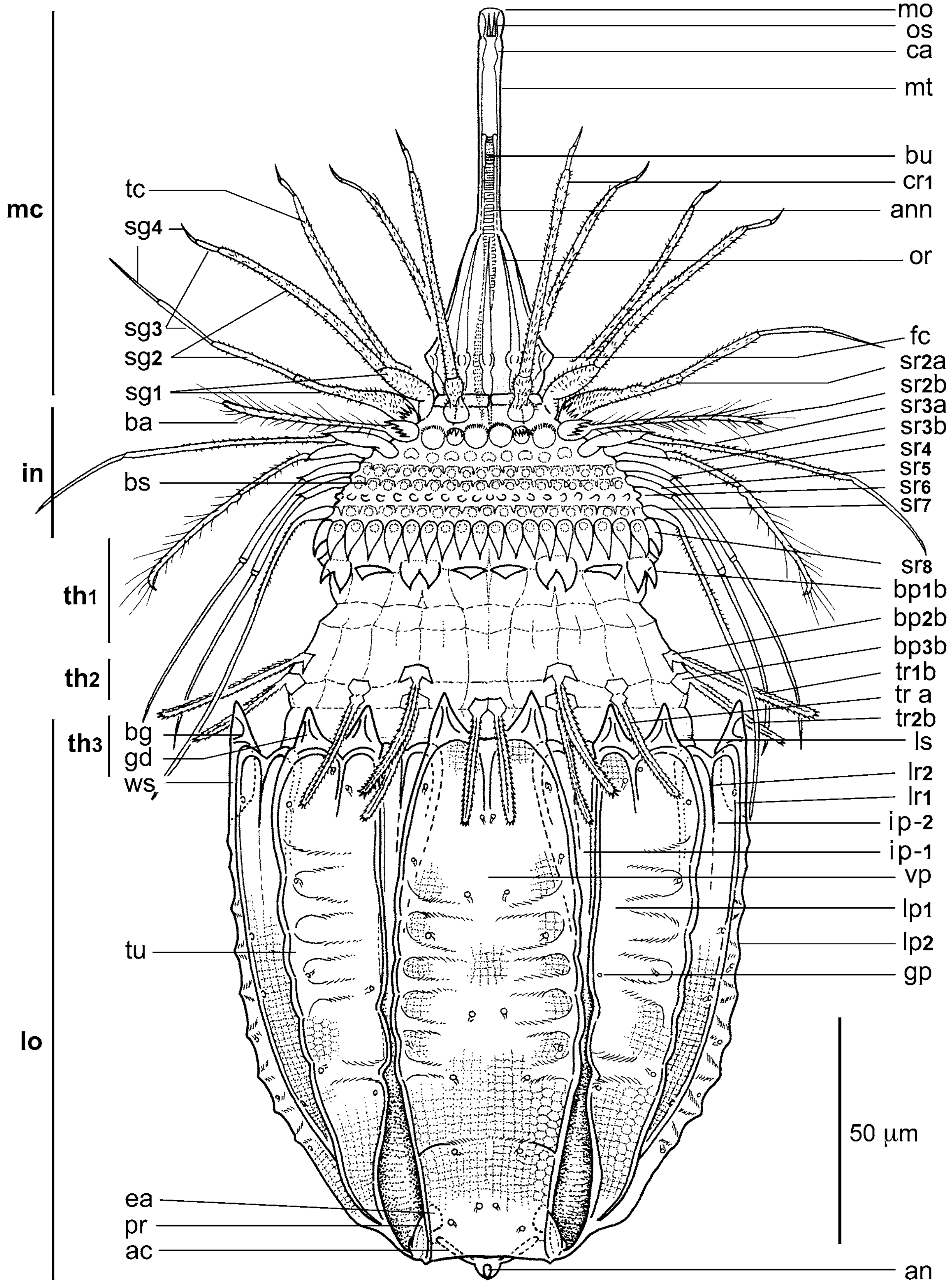

FIGURE 1. *Culexiregiloricus trichiscalida* gen. et sp. nov., holotypic postlarva, ventral view.

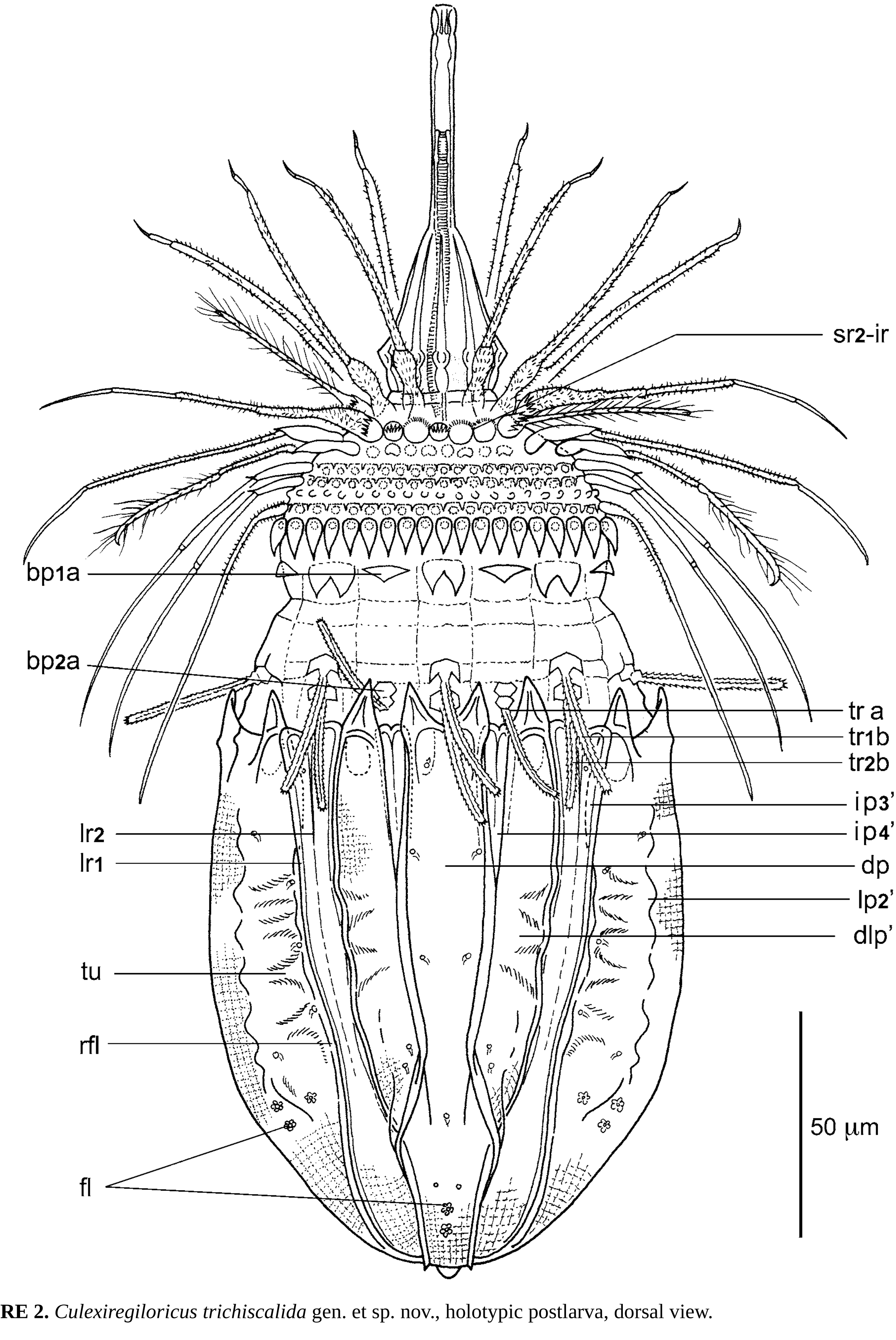

FIGURE 2. *Culexiregiloricus trichiscalida* gen. et sp. nov., holotypic postlarva, dorsal view.

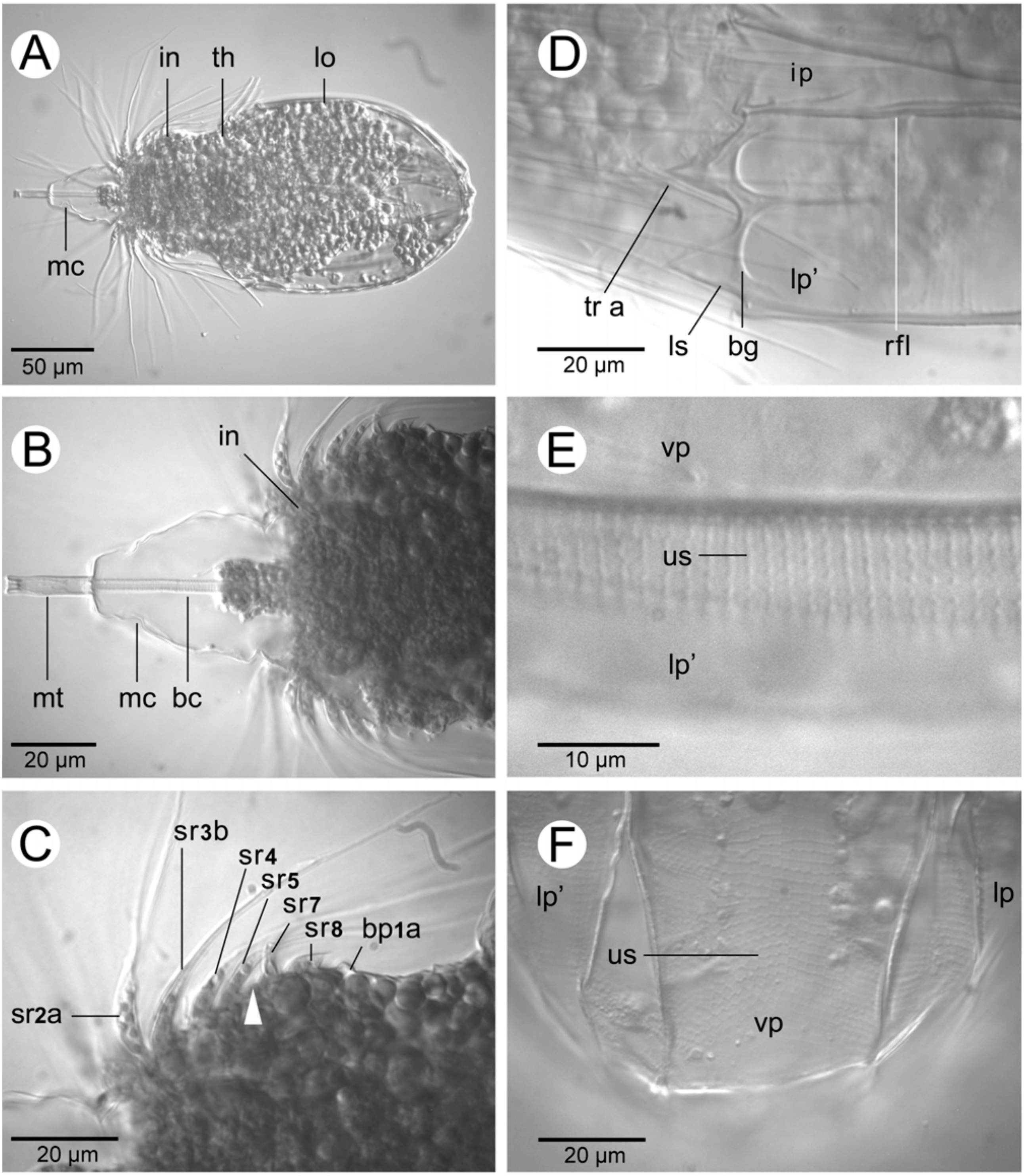

FIGURE 3. LM images (interference-contrast) of *Culexiregiloricus trichiscalida* gen. et sp. nov., holotypic postlarva, A habitus; B introvert and mouth cone which has become artificially more swollen and lost cuticle during fixation and preparation treatment; C rows of scalids on introvert (arrow points to gap between spinoscalids of fifth and seventh row where long spinoscalids of the sixth row are present as tiny protoscalids only); D lorica composed of plates and intercalary plicae, anterior rim of plates with lorica spikes; E lateral plate of lorica with distinct square-like ultrasculpture; F caudal end of lorica with distinct honeycomb ultrasculpture. All photographs from ventral view.

In summary, the number and arrangement of scalids (cs = clavoscalids, ss = spinoscalids) in rows (cr = row of clavoscalids, sr = row of spinoscalids) on the introvert and of basal plates (= bp) together with trichoscalids (= tr) on the thorax can be expressed in the following formula:

	Introvert							
Scalid row:	1cr	2sr	3sr	4 sr	5 sr	6 sr	7 sr	8 sr
Number:	8cs	9 ss+7ss	8 ss+8ss	30ss	30ss	— (30ps)	30ss	30ss

	Anterothorax	Interthorax	
Formation row:	1	2	3
Number:	8 bp a+7 bp b	7 bp b 7 tr b	8 bp a+7 bp b 8 tr a+7tr b

Figure 5 demonstrates the arrangement of scalids on the introvert as a polar coordinate diagram.

Transition zone between interthorax and loricate abdomen (Fig. 1) formed by short and flexible posterothorax (th_3) not having any appendages or plates, but having thin cuticle and being as wide as interthorax.

Abdomen (Figs. 1, 2) massively armoured with sclerotized lorica (lo), divided longitudinally into 8 plates and 8 intercalary plicae (ip). Lorica slightly depressed dorsoventrally, surface of cuticle completely covered with distinct square-like (Fig. 3E) as well as honeycomb (Fig. 3F) ultrasculpture (us). Plates with reinforced lateral margins (rfl, Fig. 2). Plicae have distinct reinforced and folded lateral margins as primary folds and longitudinally subdivided along median axis by weakly developed secondary fold. Anterior margins of intercalary plicae form 2 crescents in some of their corners they are folded so tightly together that it appears as additional small “spikes” (see Fig. 3D and in Fig. 4A, but proof of their absence is given in Fig. 4B). Plates and plicae penetrated by small pores (gp), which connect with unicellular subcuticular epidermal glands. Each plate with 2–8 transversal undulations (upwellings of cuticle, tu, Fig. 1; 2, 4B) and armed with lorica spikes (ls, Figs. 3D) of medium size along anterior edge.

Schema of lorica structures of 1 body half, from ventral plate (vp) to middorsal plate (dp), other body half identical because of bilateral symmetry (dlp = dorsolateral plate, lp = lateral plate, ip = intercalary plica).

No. of element: Designation:	**1** **vp**	**2** **ip-1**	**3** **lp1**	**4** **ip-2**	**5** **lp2**	**6** **ip-3**	**7** **dlp**	**8** **ip-4**	**9** **dp**
Element structure	plate	plica	plate	plica	plate	plica	plate	plica	plate
Max. width of element	45 µm	6 µm	22 µm	10 µm	20 µm	10 µm	10 µm	5 µm	12 µm
No. of undulations	5	none	5	none	8	none	4	none	2
No. of spikes	2	—	2	—	2	—	1	—	2
Length of spikes	6 µm		6 µm		5 µm		10 µm		8 µm
Position and no. of flosculi	—	—	—	—	3	—	—	—	2

All spikes of same structure and length (Figs. 1, 3D); with 1 indistinct window (ws, part of thin translucent cuticle), lateral and transversal reinforcements of thicker cuticle (bridge of lorica spikes, bg); internally along their entire length spikes equipped with 1 long duct (gd) of subcuticular epidermal gland. Large, shield-like, ventral plate (Fig. 1) laterocaudally with indistinct locking apparatus (ea), caudal end of plate flanked by massive cuticular longitudinal ridge-like protrusion (pr). Eight distinct papillate flosculi (fl) present on dorsal lorica (Fig. 2) near caudal end, 3 of them forming a cluster on both dorsolateral plates (lp2, lp2'). Dorsal plate narrow anteriorly becoming wider posteriorly and ends as though cut off, bearing two additional papillate flosculi (fl, Fig. 2); in caudal half lateral margins folded up and extending over remaining portion of plate. Well-defined, small, and pointed anal cone (ac) with terminal anus (an).

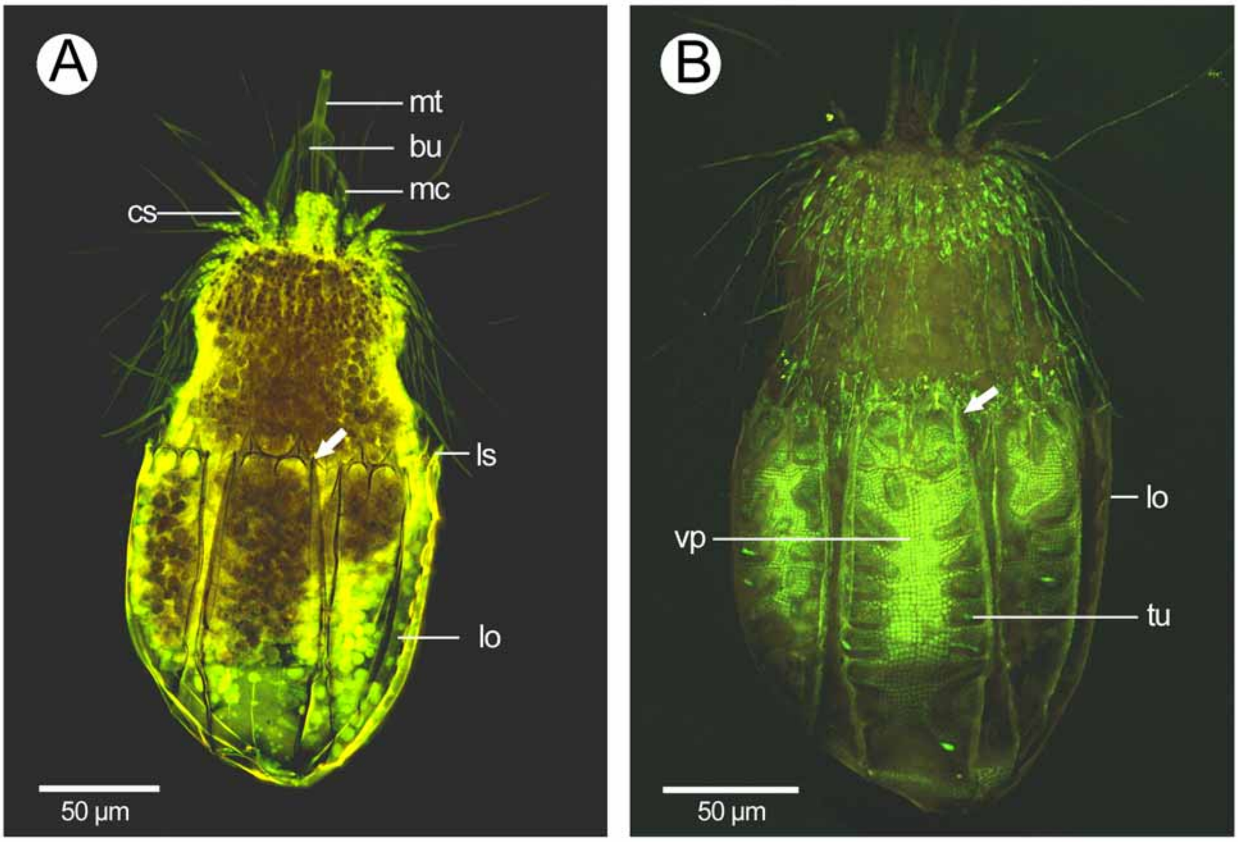

FIGURE 4. CLSM images of *Culexiregiloricus trichiscalida* gen. et sp. nov., holotypic postlarva, with distinct autofluorescence (green-yellow spectrum) of all cuticular structures, A habits, clearly visible are mouth cone, insertion of scalids, and lorica plates inclusive of the spikes of the anterior margin (arrow point to tightly folded corners of intercalary plica giving a “spike-like” impression); B structure of lorica, the lorica plates are highly visible with undulated parts inclusive of anterior margin, and the squarish ultrasculpture of the cuticle (arrow point to tightly folded corners of intercalary plica demonstrating that there are no additional spikes). Both photographs from ventral view.

Remarks: The body cavity of the holotypic postlarva investigated is filled with granular cells and tissue, which is strongly coloured by Bengal Pink so that no clear view can be gained on the internal organs, except for the highly dense buccal structures and the strong and muscular pharyngeal bulb.

Differential diagnosis. The lorica of *Culexiregiloricus trichiscalida* gen. et sp. nov. strongly resembles the lorica of *Spiniloricus turbatio* (Heiner & Neuhaus 2007). In both species the lorica is composed of 8 mostly narrow plates plus 8 intercalary plicae. Apart form this similarity the lorica of *S. turbatio* is equipped with short spikes and additional spikes in each corner in the anterior part of the plates (Heiner & Neuhaus 2007), which are lacking in *C. trichiscalida* gen. et sp. nov. In *C. trichiscalida* the reinforced anterior margins of most intercalary plicae are folded so tightly together that it appears to have additional small ’spikes’ as demonstrated in Figs. 3D and 4A. However, the CLSM image with higher solution and slight 3D effect (Fig. 4B) shows that this impression of small ‘spikes’ is an artefact. The intercalary plicae as thinner, wide, and loose parts of cuticle between the plates may be a general feature of postlarvae belonging to the Nanaloricidae (Heiner & Neuhaus 2007), because the adults developing inside have a larger body size than the postlarvae they moult from (Gad 2004a, b; Kristensen & Gad 2004, Heiner & Neuhaus 2007). Despite the lorica, *S. turbatio* share more similarities with *Nanaloricus*-species (see genus diagnosis in Heiner & Neuhaus 2007) than *C. trichiscalida* gen. et sp. nov., which is more closely related to *Armorloricus*-species (see Table 3).

TABLE 1. Morphometric data of the holotypic postlarva of *Culexiregiloricus trichiscalida* gen. et sp. nov. (all measurements in µm). Length of lorica plates include anterior spikes. Measurements of scalids take into consideration the average length of most scalids per row.

Length of:		Length of:		Length of:	
Body (total)	285	Lorica	135	tr1	30
Mouth cone	85	Lorica spikes	6	tr2	30
Mouth tube	40	cr_1	67	tr3	25
Buccal tube	95	sr_2a / sr_2b	75 / 50	Maximum width of:	
Oral stylets	7	sr_3a / sr_3b	80 / 66	Buccal tube	2
Internal armature	12	sr_4	75	Lorica	110
External furca	15	sr_5	70	Ventral plate	45
Introvert	30	sr_6	–	Other plates	22–30
Thorax (unit of)	50	sr_7	65	Plicae	8–13
Anterothorax	22	sr_8	7	Diameter of:	
Interthorax	13			Pharynx bulb	30
Posterothorax	15				

There are 3 genera of Nananloricidae known so far which contain species that all have a short basal section of the mouth cone with 8 oral furcae and oral ridges of identical size and structure. Furthermore the terminal section of the mouth cone is drawn out to a long and slim mouth tube (in species of the genera *Nanaloricus* and *Spinoloricus* the mouth cone itself is long and the mouth tube very short, nearly as if not present; additionally the oral furcae and oral ridges are of different length and in the case of *Nanaloricus*-species also of different structure, compare Kristensen & Gad 2004 and Heiner & Neuhaus 2007). Apart from this most obvious character, the genera *Armorloricus*, *Phoeniciloricus*, and *Culexiregiloricus* gen. nov. share the following features:

(1) prepharyngeal armature equipped with manubrium
(2) lorica spikes with single gland ducts lacking reservoirs (and with “windows”)
(3) ventral lorica plate narrow and outer lateral margins of ventrolateral plates folded up.

A differential diagnosis on generic level is given for all “long-mouth-tube species” in the form of a comparison of the distinguishing features in Table 2.

TABLE 2. Comparison of adult or postlarval characters respectively, of genera of Nanaloricidae — the "long-mouth-tube species-group".

Features	Genera		
	Culexiregiloricus gen. nov.	*Phoeniciloricus* Gad, 2004a	*Armorloricus* Kristensen & Gad, 2004
basal mouth cone	broad	narrow	narrow
mouth tube	long, slim	extremely long and slim	extremely long and slim
paired trichoscalids	upper ones longer	upper ones slightly shorter	nearly equal in length, or lower ones longer
lorica	composed of 8 small to large plates and 8 plicae	composed of 10 medium to large plates	composed of 6–8 large plates
surface of cuticle	with honeycomb or square pattern	with honeycomb pattern	smooth
no. of lorica spikes	14	15	15
size of lorica spikes	medium	small	large
windows of lorica spikes	present/large	very small	present/large
gland ducts of lorica spikes	single, instinct	single, indistinct	single, distinct
flosculi on lorica			
dorsally	8	10	9
ventrally	0	8	(sometimes 4)
size of flosculi	normal	normal	micro

TABLE 3. Diagnostic characterisation of Nanaloricidae.

Diagnostic traits for	Nanaloricidae*					
	mouth cone rigid, basally broad, not stalked, and not retractable buccal tube long, sclerotized, and with distinct annulation separation between mouth cone and large round pharyngeal bulb, which is located deeply inside trunk spinoscalids of second and third row reduced in number and united to one (sr2a + sr2b) long flexible thorax subdivided into antero-, inter- and postero parts anterior rim of lorica with distinct spikes papillated flosculi forming caudal groups on dorsolateral part (plates) of lorica					
	Culexiregiloricus	*Phoeniciloricus*	*Armorloricus*	*Nanaloricus*	*Spinoloricus*	gen. et sp. II
	spinoscalids of third row reduced in number (8 sr3a + 8 sr3b) some elements of lorica sclerotized and enlarged to distinct plates					15 sr3a + 15 sr3b lorica without plates
	Culexiregiloricus	*Phoeniciloricus*	*Armorloricus*	*Nanaloricus*	*Spinoloricus*	
	extremely long mouth tube oral furcae and ridges of same length prepharyngeal armature with manubrium single gland ducts of lorica spikes lacking reservoirs (and with one large "window") outer lateral margins of ventrolateral plates of lorica arising or folded up			short or absent mouth tube oral furcae and ridges of different length prepharyngeal armature without manubrium		
		Phoeniciloricus	*Armorloricus*			
		3th segment of clavoscalids enlarged ventral lorica plate with caudal locking apparatus				
Genera of Nanaloricidae	*Culexiregiloricus* gen. nov.	*Phoeniciloricus* Gad, 2004	*Armorloricus* Kristensen & Gad, 2004	*Nanaloricus* Kristensen, 1983	*Spinoloricus* Heiner & Neuhaus, 2007	gen. et sp. II (sensu Gad, 2004)
Species per genera:	*C. trichiscalida*	*P. simplidigitatus*	*A. davidi* *A. elegans* *A. kristenseni*	*N. mysticus* *N. khaitatus* *N. gwenae*	*S. turbatio*	sp. II
Specific characters of genera:	thin cs covered with tricoids		4th segment of sr4a spinoscalids enlarged	oral furcae and ridges of different structure	mouth cone with pleat oral ridges of same structure (?)	15 sr3a + 15 sr3b all tr are double
	lorica composed of 8 plates and 8 intercalary plicae (?) group of 3 flosculi on dorsolateral plates	lorica composed of 10 plates anal plates fused to large shield plates with additional corner spikes (?)	lorica composed of 8 plates only smooth cuticle micro-size flosculi	lorica composed of 6 plates only locking apparatus in middle of ventrolateral plates scalids of eight row tricuspid	lorica composed of 8 plates and 8 intercalary plicae plates with additional corner spikes (?) leaf-like smooth secondary tr additional row of alternating plates	lorica composed of 24 partly fused plicae with rounded lorica spikes equipped with 5–7 small "windows" and double gland ducts

*compare Kristensen and Gad, 2004

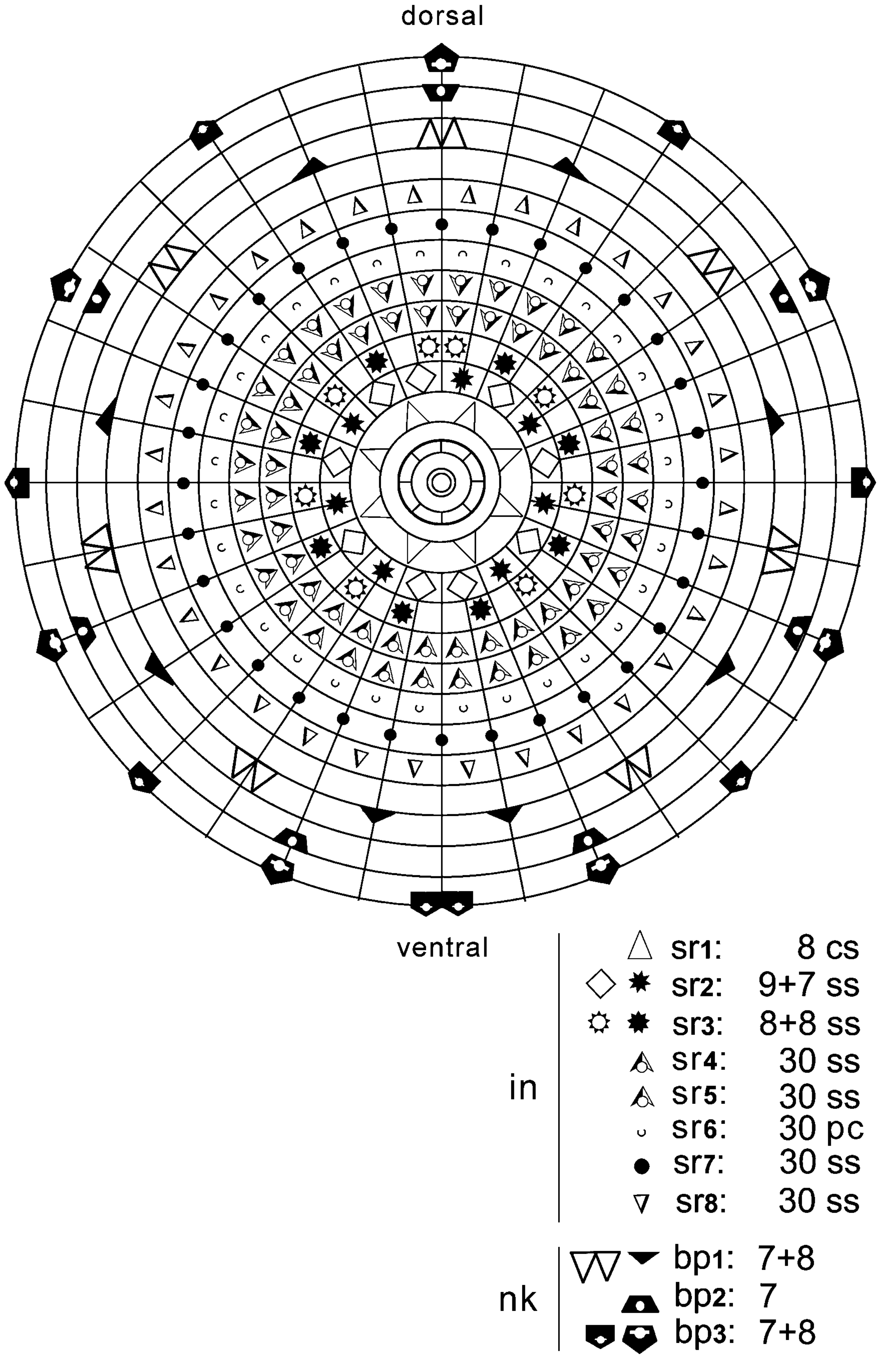

FIGURE 5. Scalid arrangements on the introvert of the postlarva of *Culexiregiloricus trichiscalida* gen. et sp. nov. as polar coordinate diagram.

Discussion

Notes on the postlarval stage

Postlarval stages of Nanaloricidae resemble juveniles and have rarely been reported since Kristensen (1991a) identified them as a part of their life cycle. Single postlarvae are known from seven of the ten known species of Nanaloricidae, i.e. from *Armoloricus elegans*, *A. kristenseni*, *Nanaloricus mysticus*, *N. gwenea*, *Phoeniciloricus simplidigitatus*, *Spiniloricus turbatio* (Kristensen 1983; Gad 2004a; Heiner 2004; Kristensen & Gad 2004; Kristensen et al. 2007; Heiner & Neuhaus 2007) and gen. et sp. II *sensu* Gad, 2004 (see Gad 2004a). Postlarvae, including the one of the new species described here, generally show most of the features found in adult females. As previously shown, postlarvae of Nanaloricidae are easily distinguished from adults by one lacking, or not fully developed, row of spinoscalids, i.e. the sixth row in *A. elegans* and *C. trichiscalida* sp. nov. There are two other differences (Gad 2004a; Kristensen & Gad 2004; Kristensen 2003; Kristensen et al. 2007): (1) Postlarvae reach only 80% of the size of adults; mouth cone, lorica spikes and scalids are slightly shorter in relation to total body size; (2) the body cavity of postlarvae is filled with granular tissue and the reproductive organs are not yet developed. Any sexual dimorphism, as e.g. expressed in the branched clavoscalids of males, is not recognisable in postlarval stages. Because of the nearly identical morphology of postlarvae and adults in Nanaloricidae postlarval features can be used to infer features of unknown adults (see Kristensen 1991a; Heiner 2004; Kristensen & Gad 2004; Kristensen et al. 2007; Heiner & Neuhaus 2007).

Notes on relationships within Nanaloricidae

The growing number of new described species of Loricifera, particularly Nanaloricidae, calls for phylogenetic analysis. It is, and likely to remain, a problem that not enough specimens of a new species are found, even in the large sample series from the deep sea, to get excellently preserved and extended material of all life history stages. However, with the growing number of species known, the characters which have to be chosen for any phylogenetic analysis are getting more evident. A first attempt to identify the potential autapomorphies of Nanaloricidae has been made in the discussion in Kristensen and Gad (2004). There is at present many indications that the Nanaloricidae are a monophyletic group within the Loricifera because of their specific characters (Higgins & Kristensen 1986; Nielsen 1995; Lemburg 1999; Ax 2001; Kristensen & Gad 2004). Since no phylogenetic analysis of the Loricifera as a whole is available, the Nanaloricidae can only be separated by diagnostic traits, which are summarized in Table 3.

The structure of the lorica differs distinctly between species of Nanaloricidae and has become one of the key characters for genus separation. That is why the undescribed representative of a new taxon (sp. et gen. II) from the Great Meteor Seamount is also included in the overview of diagnostic characters (Table 3), because postlarva and adults of this species have a lorica composed totally of plicae (not plates) like species of Pliciloricidae (Higgins & Kristensen 1986; Gad 2004b). Despite this peculiarity this species (sp. et gen. II) clearly shows all features which characterize the Nanaloricidae (Table 3), e.g. the unique rigid mouth cone equipped with all specific internal buccal structures (Kristensen 1983; 1991a, b; 2003; Gad 2004a, b; Heiner 2004; Kristensen & Gad 2004; Heiner & Neuhaus 2007).

There are indications for a specific species-group within Nanaloricidae characterized mainly by the long mouth tube as the anterior section of the mouth cone (versus a short or no mouth tube in e.g. *Nanaloricus*), mentioned earlier in the differential diagnosis. Even so the following characters (compare also Table 3) unite the species of three genera to a specific species-group: (1) oral furcae and ridges of same length, (2) prepharyngeal armature with manubrium, (3) single gland ducts of lorica spikes (if present in *Nanaloricus*) lacking reservoirs (and with one large "window"), and (4) outer lateral margins of ventrolateral plates of lorica arising or folded up.

Notes on the occurrence of Nanaloricidae in the deep sea

As the samples of the DIVA 2 Expedition have shown, the calcareous multi-chambered shells of planktonic foraminiferans are one additional component of the sedimentary material mixed into the otherwise fine-grained clayish bottoms of the deep-sea basins of the southeast Atlantic. The distributional pattern of planktonic foraminiferans in this part of the Atlantic Ocean is well known (Kemle von Mück & Hemleben 1999). The species assemblage which was found reflects quite well our actual knowledge about food availability in the upper regions of the euphotic zone, temperature of the surface water, and current systems and the seasonal impact on them (Kemle von Mück & Hemleben 1999). As can be seen on a map by Bé and Tolderlund (1971) of the general density of foraminiferans in the upper 10 m of the water column, the sampling sites of the DIVA 2 expedition, mainly in the Cape and Guinea Basins, less so in the Angola Basin, are located in an area of high productivity with seasonal blooms of planktonic foraminiferans. The first data of semi-quantitative analyses of the planktonic foraminiferans in the sediments of the investigated deep-sea basins were reported by Müllegger and Piller (2006). They found that mainly warm-water species occur in the Guinea and Angola Basins, whereas in the northern Cape Basin, those are replaced by transitional or cold-water species. Shells of the following species occur in the sediments of the Guinea Basin (Müllegger & Piller 2006): *Globorotalia cultrata*, *G. crassaformis*, *G. inflata*, *G. tumida*, *Globigerinoides sacculifer*, *Gl. ruber*, *Neogloboquadrina dutertrei*, *Pulleniatina obliquiloculata*, and *Sphaeroidinella dehiscens*. A clear overlap can be observed between the planktonic foraminiferan assemblages of the northern Angola and the Guinea Basins (Müllegger & Piller 2006). All species so fat known to occur in the Guinea Basin are also present, albeit at low density, in the Angola Basin with the exception of *G. inflata*, *Gl. ruber*, *P. obliquiloculata*, and ancillary *Gl. sacculifer*, which are confined to the Guinea Basin and have not yet been found from the Angola and the Cape Basins. In agreement with the general condition of planktonic foraminiferan assemblages of the South Atlantic as summarized by Bé and Tolderlund (1971), the species *Gl. sacculifer*, *Gl. ruber*, and *N. dutertrei* are tropic warm water species. Especially *N. dutertrei* is a strong indicator species characterizing the shallow thermocline along the African coast which has its broadest extension over the Guinea Basin. As such *N. dutertrei* is the most common species in the deep-sea sediments of this area and comprises more than 50% of the foraminiferan individuals found there (pers. Obs.). The Cape Station is influenced by the upwelling zone close to the coast of Namibia, which is indicated by cold-water species or transitional species like *Gl. truncatulinoides*.

According to Müllegger and Piller (2007), foraminiferan shells make up about 50 % of the sediment fraction > 250 µm and are still a substantial proportion in the sediment fraction 250–125 µm in some of the DIVA2 stations of the Guinea and Angola Basins. These shells may increase the coarseness of the sediment that allows species of Nanaloricidae to colonize it even if their occurrence in the deep sea is local and patchy. Finding Nanaloricidae in the deep sea may therefore not be as surprising as assumed when describing *P. simplidigitatus* (Gad 2004a). It has to be considered that the sediment even with a high amount of foraminiferan shells has predominantly no interstitial character because the space between the shells may filled with the clayish sediment. However, the specific crawling of Loricifera, a pushing of the body through the sediment by using the scalids of the introvert, probably similar to that of Kinorhyncha, is considered to need (in the case of Nanaloricidae) the sedimentary grid of grains as solid support. It is unclear if free interstitial space is therefore essential for their occurrence or not.

If sediments with a high content of foraminiferan shells are widespread in the deep-sea then it may raise habitat diversity for inhabitant meiofauna, and some taxa normally found in interstitial habitats may be common in the deep sea also. This conclusion would become even more compelling, if the respective samples contained not only Nanaloricidae but also other meiofauna taxa known to frequently occur in such habitats.

Acknowledgements

I am grateful to Prof. Dr. Pedro Martínez Arbizu for support of this project and to Prof. Dr. H. Kurt Schminke for helpful remarks and a critical review of the manuscript. Thanks are also due to the staff of the DZMB for helping with the collection of samples on board and in sorting the meiofauna and Marco Büntzow for his kind help by making the confocal images. This work was supported by a grant of the Deutsche Forschungsgemeinschaft (Ma-2557/7-1).

References

Ax, P. (2001) *Das System der Metazoa III*. Spektrum Akademischer Verlag, Heidelberg, 283 pp.

Bé, A.W.H. & Tolderlund, D.S. (1971) Distribution and ecology of living planktonic Foraminifera in surface waters of the Atlantic and Indian Oceans. *In*: Riedel, B.M. & Funnell, B.M. (Eds), *The micropalaeontology of oceans*. Cambridge University Press, Cambridge, pp. 105–149.

Brown, P.A. (1997) A review of techniques used in the preparation, curation and conservation of microscope slides at the Natural History Museum, London. *Biology Curator*, 10 (suppl.), 1–33.

Gad, G. (2002) New light on deep-sea Loricifera. *Deep-Sea Newsletter*, 32, 4–5.

Gad, G. (2004a) 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.

Gad, G. (2004b) The Loricifera fauna of the plateau of the Great Meteor Seamount. *Archive of Fishery and Marine Research*, 51 (1–3), 9–29.

Gad, G. (2005a) A parthenogenetic, simplified adult in the life cycle of *Pliciloricus pedicularis* sp. n. (Loricifera) from the deep sea of the Angola Basin (Atlantic). *Organisms, Diversity & Evolution*, 5 (suppl. 1), 60–77.

Gad, G. (2005b) Giant Higgins-larvae with paedogenetic reproduction from the deep sea of the Angola Basin - evidence for a new life cycle and for abyssal gigantism in Loricifera? *Organisms, Diversity & Evolution*, 5 (suppl. 1), 44–59.

Heiner, I. (2004) *Armorloriucs kristenseni* (Nanaloricidae, Loricifera), a new species from the Faroe Bank (North Atlantic). *Helgoland Marine Research*, 58, 198–205.

Heiner, I. & Neuhaus, B. (2007) Loricifera from the deep sea of the Galapagos Spreading Center, with a description of *Spinoloricus turbatio* gen. et sp. nov. (Nanaloricidae). *Helgoland Marine Research*, 61, 167–182.

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

Higgins, R.P. & Thiel, H. (eds.) (1988) *Introduction to the study of meiofauna*. Smithsonian Institution Press, Washington DC., 488 pp.Kemle von Mück, S. & Hemleben, C. (1999) Foraminifera. *In*: Boltovskoy, D. (Ed), *South Atlantic Zooplankton*, Backhuys Publishers, Leiden, pp. 43–73.

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*: Harrison, F.W. & Ruppert, E.E. (Eds), *Microscopic Anatomy of Invertebrates, vol. 4: Aschelminthes*, Wiley-Liss, New York, pp. 351–375.

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

Kristensen, R.M. & Gad, G. (2004) *Armorloricus*, a new genus of Loricifera (Nanaloricidae) from Trezen ar Skoden (Roscoff, France). *Cahiers de Biologie Marine*, 45, 121–156.

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.

Kristensen, R.M., Higgins, R.P., Heiner, I. (2007): Morphology and life cycle of a new loriciferan form the Atlantic coast of Florida with an emended diagnosis and life cycle of Nanaloricidae (Loricifera). *Invertebrate Biology*, 126 (2), 120–137.

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)*. PhD Thesis, Cuvillier Verlag, Göttingen, 393 pp.

Müllegger, S. & Piller, W.E., (2006) Latitudinal and sediment depth gradients in foraminiferal assemblage of the southeast Atlantic. *Anuário do Instituto de Geociências - UFRJ*, 26, 552–553.

Nielsen C. (1995) *Animal evolution - Interrelationships of the living phyla*. Oxford University Press, New York, 467 pp.

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.