RESULTS OF THE DIVA-1 EXPEDITION OF RV "METEOR" (CRUISE M48/1)

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?

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Abstract

A new genus and species of Loricifera, *Titaniloricus inexpectatovus* (Pliciloricidae) represented by a new type of Higgins-larva is described from the deep sea of the Angola Basin. The new larva is characterized by its gigantic size which is unusual for larval Loricifera, by six rows of scalids on the unit of introvert and neck, by an additional transversal row of scales marking the anterior rim of the collar, by a high number of thoracic plates, by more than 160 longitudinal ridges forming plicae on the loricate abdomen, by tubular toes with a broad basal part and undulated cuticle, and by two pairs of long anterior setae. The exuvium of the presumable sixth instar Higgins-larva of *T. inexpectatovus* gen. et sp. n. functions as a shelter for several instars: a large simplified seventh instar larva which is paedogenetic and contains some rests of smaller Higgins-larvae, and rests of adult specimens. The paedogenetic or seventh instar larva is morphologically not identical with the sixth instar Higgins-larva from which it moults because of the following transformations: all body regions form a sack-like trunk on which only the scalids of introvert and neck persist as small protoscalids.

One of the smaller Higgins-larvae inside contains an adult ready to leave it. The large sixth instar Higgins-larva and the simplified seventh instar paedogenetic larva it contains seem to function together as a "mother larva" for a new larval generation, which has the ability to moult directly into a postlarva and then into an adult. These adults have a size not different from that of other adults of Pliciloricidae. It remains unclear whether these instars represent a new life cycle or just an additional phase in a more complex life cycle such as is often found in other taxa of Pliciloricidae especially from the deep sea. An adult specimen from the same locality as the giant larva is briefly described and assigned with caution to the same species *T. inexpectatovus* sp. n. The larval gigantism of a deep-sea loriciferan probably reflects adaptations to the deep-sea habitats they inhabit.
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Introduction

In the life cycles of most invertebrates there is a series of consecutive developmental stages leading from egg to adult as is also the case in Loricifera (Kristensen 1983, 1991a, 2003). Indirect development is characterized by

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Nomenclature

ac	anal cone
Ad	adult
af	anal field
ap	anal plate
bp_1a	type A basal plates of first row
bp_2a	type A basal plates of second row
bp_3a	type A basal plates of third row with trichoscalids
bp_2b	type B basal plates of second row
bp_3b	of type B basal plates of third row with trichoscalids
bt	basal plate of toe
co	collar
cr_1	first row of clavoscalids
cs	clavoscalid
do	double-organ
ec	end cone
ed	edge of lorica
eg	egg
egs	egg shell
ho	hook
ia	prepharyngeal armature
in	introvert
Lar	larva
Lar I-VI	first to sixth instar Higgins-larvae
Lar VII	seventh instar or paedogenetic larva
lo	lorica
lr_1	primary longitudinal ridge
lr_2	secondary longitudinal ridge
ls_1	anterolateral seta
ls_2	anteroventral seta
mc	mouth cone
mcs_{1-3}	first to third section of mouth cone
muc	multicorer
nk	neck
oc	oocyte
or	primary oral ridge
orv	oral valve
os	oral stylet
ot	oral tooth
ov	ovary
pcr	protoclavoscalids
pl	plica
Pla	postlarva
plm	midventral transformed plica
psc	protoscalids
psr	protospinoscalids
pt	gland pore of toe
ro	round structure
ru	ruff
sc	scalid
sca	scale
se_1	posterodorsal seta
se_2	posterolateral seta
se_3	posteroterminal seta
sr_{2-9}	second to ninth row of spinoscalids
sr_4a	type A scalids of fourth row
sr_4b	type B scalids of fourth row
sr_5a	type A scalids of fifth row
sr_5b	type B scalids of fifth row
sr_6a	type A scalids of sixth row
sr_6b	type B scalids of sixth row
ss	spinoscalid
st	end spine of toe
tb	toe base
th	thorax
thp_{1-3}	rows of adult thoracic plates
thr_{1-6}	rows of larval thoracic plates
to	toe
tr	trichoscalid
tri	transverse ridge of lorica
tu	tubular part of toe
tv	transversal constriction of lorica
wa	wart

larval instars which differ morphologically clearly from adults and may undergo metamorphosis to become adult (Young 2002). This normally involves new organogenesis or reorganization of the body plan. Larvae are generally characterized by "larval organs" which disappear during metamorphosis, whereas juvenile instars resemble mature adults in an unfinished form (Gilbert and Raunio 1997). Typical larval organs of pliciloricid Higgins-larvae are toes as caudal appendages assumed to play a role in locomotion (Kristensen 1991a), pairs of anterior and posterior setae on the trunk, a long thorax as a movable body region consisting of transversal plate rows resembling an accordion, and the cylindrical, hexaradial, internal prepharyngeal armature which supports the short buccal channel in front of the large pharyngeal bulb (Kristensen and Brooke 2002; Kristensen 2003). In Higgins-larvae the cuticle of the loricate abdomen is not much thicker than on the rest of the body. Instead of longitudinal ridges found in adults the abdomen of Higgins-larvae has deep primary longitudinal folds which allow increase of abdominal volume.

The life cycle assumed as basic for the Loricifera includes sexually dimorphic adults and a maximum number of seven instars of Higgins-larva. The Higgins-larva grows by a series of moults. Apart from the larval stages there also is a juvenile or postlarval stage in all life cycles, but sometimes this postlarva is reduced or modified to a dormant stage with unfinished adult

morphology, e.g. in *Rugiloricus* species (Kristensen, 1991a; Kristensen, 2003; Gad, 2004).

Not much is known about Loricifera from the deep sea (Gad 2001, 2002, 2005). The first and to date only species described from the deep sea belongs to Pliciloricidae. *Pliciloricus hadalis* Kristensen and Shirayama, 1988 was found inhabiting red clay at 8260 m depth in the Izu-Ogasawara Trench of the Western Pacific (Kristensen and Shirayama 1988). Material collected from south Atlantic deep-sea basins, the central Pacific, and Antarctica show that Loricifera are more frequent and more diverse in the deep sea than hitherto assumed (Gad 2001, 2002). Results of the DIVA expedition have shown that the population density of Loricifera is lower (they make up only 0.1% of the total meiofauna, on average each core of a multicorer contains one to four specimens), but less patchy than in shallow water habitats (Gad 2004). The 160 samples taken contained about 280 Loricifera belonging to the Pliciloricidae without exception, but many are so highly transformed that identification of all life stages is difficult. More than 95% of the specimens are Higgins-larvae. The high proportion of larval instars may be characteristic of the deep sea, and seems to be a result of their life cycle (Gad 2002). Nearly all Loricifera in the deep sea of the Angola Basin reproduce as parthenogenetic simplified adults (Gad 2005) or as transformed paedogenetic larvae (Gad 2002). In case of paedogenetic reproduction via larvae they seem to have the ability to skip the adult generation and produce large unfertilized eggs from which hatch the larvae of the next generation (Kristensen and Brooke 2002; Kristensen 2003; Gad 2002, 2004). The parthenogenetic, simplified adults are morphologically not identical with free-living females and males (Gad 2005).

Loricifera are described to be among the smallest metazoans (Kristensen 1991a, 2003). This is true for the first discovered Nanaloricidae. Adults of *Nanaloricus mysticus* Kirstensen, 1983 measure only 240–250 μm (Kristensen 1983). Some adults of Pliciloricidae measure not more than 180 μm (Higgins and Kristensen 1986), but they can have a larger body size, e.g. in the genus *Rugiloricus* Higgins and Kristensen, 1986 adults measure between 260–350 μm and the related Higgins-larvae have a maximal body size of 300–450 μm (Gad 2004). Compared with adults of Harpacticoida, Tardigrada or Nematoda found in the deep-sea meiofauna which can also measure below 150 μm (Giere 1993; Higgins and Thiel 1988) Loricifera can no longer be regarded as the smallest metazoans altogether. Especially the Higgins-larvae of Pliciloricidae can reach a size which is four to six times bigger than that of the adults they produce (Gad 2004). A Higgins-larva of an unusually large size with an increased number of longitudinal ridges on its lorica is reported here for the first time. The deep-sea meiofauna generally decreases in body size with

increasing depth (Giere 1993). Since food is limited on the deep-sea floor, most organisms are assumed to be small (Herring 2002). In fishes this seems to be the case. There are reports that species of some invertebrate groups, mainly crustaceans, attain a larger size in the cold deep waters than their relatives in warm shallow waters (De Broyer 1977; Childress and Price 1978; King and Butler 1985; Mauchline 1988, 1995; Chapelle and Peck 1999). The phenomenon of larger size with increasing depth is called abyssal gigantism (Herring 2002; Nybakken 2001). The reasons for abyssal gigantism are controversial and will be discussed here in connection with the gigantic Higgins-larva discovered in the deep sea of the Angola Basin.

Material and methods

This publication is a result of the DIVA I (Diversity of the deep sea in the Atlantic) expedition no. 48/1 of RV "Meteor" to the Angola Basin (Atlantic) off the coast of Namibia (Africa) in 2000. Sampling of meiofauna on board was carried out by Dr. Elke Willen (C. v. O. University of Oldenburg, AG Zoosystematik und Morphologie) and Dr. Kai Horst George (DZMB, Deutsches Zentrum für Marine Biodiversitätsforschung, Wilhelmshaven).

The sample yielding the specimens for this study was taken with a multicorer (muc) at stations 325 and 346 at 5389–5427 m depth. The upper 5 cm of the substrate of the sample were fixed together with the supernatant water, which was filtered through a 40 μm mesh. The meiofauna was extracted using the differential flotation method with the colloidal silica gel Levasil 200 (40%, viscosity 20, density 1.29) and the sample was centrifugated at 4000 rpm (adapted from McIntyre and Warwick 1984; Higgins and Thiel 1988). The loriciferans were sorted with the aid of an Irwin loop under a stereomicroscope (LEICA MZ8) at magnifications 50–150 × (in dark-field illumination). The sorted specimens were placed in a 70% ethanol medium, later transferred to glycerol and mounted in glycerol–paraffin–beeswax preparations, sealed with glyceel (adapted from Higgins and Thiel 1988).

Microscopic investigation was carried out with LEICA interference-microscopes (DMLB with UCA condensor, IC prism and additional magnification × 1.5 and × 2). Photographs were taken with a computerized digital camera ColorView system adapted for the DMLB microscope. Illustrations were made with type DMLB and with the aid of a drawing tube (mirror technique and macro-apparatus FS25PE). The species was differentiated morphologically. Terminology used in text and figures is adapted from Higgins and Kristensen (1986) and Gad (2005). The type material

has been deposited in the type collection of the AG Zoosystematik and Morphologie of the Carl von Ossietzky University Oldenburg (UNIOL).

Description

Phylum: Loricifera Kristensen, 1983
Family: Pliciloricidae Higgins and Kristensen, 1986
Type genus: *Pliciloricus* Higgins and Kristensen, 1986
Type species: *Pliciloricus enigmaticus* Higgins and Kristensen, 1986
New genus: Titaniloricus
Type species: Titaniloricus inexpectatovus sp. n.

Genus diagnosis

Higgins-larva: sixth instar larva, containing seventh instar larva (being paedogenetic), are approximately six or more times larger than adults and characterized by the following features: (1) barrel-like, well-developed lorica characteristically sculptured with more than 160 narrowly standing longitudinal ridges forming narrow plicae; (2) long thorax consisting of a large number of thoracic plates, 28–40 of them arranged in transversal rows; (3) collar well developed, with additional transversal row of single and double scales along anterior rim; (4) strong, rigid toes consisting of enlarged tubular bases with undulated cuticle and long end spines; (5) anterior setae long, basally annulated and with a few scattered spinules; (6) mouth cone with six large oral valves; (7) unit of introvert and neck covered with six rows of short scalids, each row with full set of scalids; (8) three pairs of posterior setae present, posteroterminal setae long, standing close together between toes and located slightly dorsally; and (9) prepharyngeal armature slim anteriorly with strongly inversely arched bracelets.

Etymology

The genus name derives from the Latin *titanis* (giant) and *titanes* (rare) which refers, on the one hand, to the large size of the Higgins-larva which has a volume six times larger than that of the biggest Loricifera-larva known so far, and on the other hand to the rarity of this species of which only five specimens are known from one single locality of the Angola Basin, and which has not been found in other deep-sea sample series so far.

General remarks

The description of this species is based on the giant Higgins-larva. It is assumed here that a badly preserved exuvium in the same sample represents the respective adult. This indentification is based on the identical structure of the scalids of the second and fourth rows found as rests in the holotypic Higgins-larva (Figs. 2A and 5D). The structure of these scalids is used as a distinguishing character for separating adults of different species. However, most of the features of the single adult specimen are not clearly visible, and the indirect morphological evidence for uniting larva and adult is rather insecure. The following description of the adult is given in the hope that more specimens will be available in better fixation in the future.

Titaniloricus inexpectatovus gen. et sp. n.

Material examined

Five specimens of presumable sixth instar Higgins-larvae were collected at station 325: two Higgins-larvae from station 325/3, muc 2, (holotype slide UNIOL 2003.23, paratype I slide UNIOL 2003.24); two additional Higgins-larvae from station 325/4, muc 5 and muc 8 (paratype II slide UNIOL 2003.25, paratype III slide UNIOL 2003.26); and one Higgins-larva from station 325/6, muc 11 (paratype IV slide UNIOL 2003.27 respectively). One presumably adult specimen of unknown sex from station 325/3, muc 3, is mounted as paratype V (slide UNIOL 2003.28).

Type locality

Deep sea of the Angola Basin (Atlantic) off the coast of Namibia (Africa). Station 325 (19° 58.3′ S/002° 59.8′ E) 5448 m depth, July 14, 2000.

Type habitat

Oligotrophic to eutrophic environment; sediment type white to light beige; with carbon fixation, total carbon content between 8% and 8.7%; with mud contents in surface layer reaching 90–99% and decreasing towards 12 cm depth; with high amounts of globularian foraminiferans; sediment well oxygenated down to 20 cm depth, 94–171 mV measured in surface sediments; bottom temperature 2.48 °C; salinity 34.8‰ (Kröncke and Türkay 2003).

Etymology

The species name derives from the Latin *inexpectatus* (surprise) and *ovum* (egg). This is an allusion to the sweet "Surprise-Eggs". These chocolate eggs contain small containers with a surprise inside. Many Loricifera-larvae, especially the one described here, contain a surprising variety of instars or stages often of unexpected morphology.

Description first to sixth instar larvae (Lar I – Lar VI = Higgins-larvae) **Figs. 1, 2A, 5A and B**

The holotypic specimen (Figs. 2A and 5A) is a weakly preserved exuvium of a sixth instar Higgins-larva with
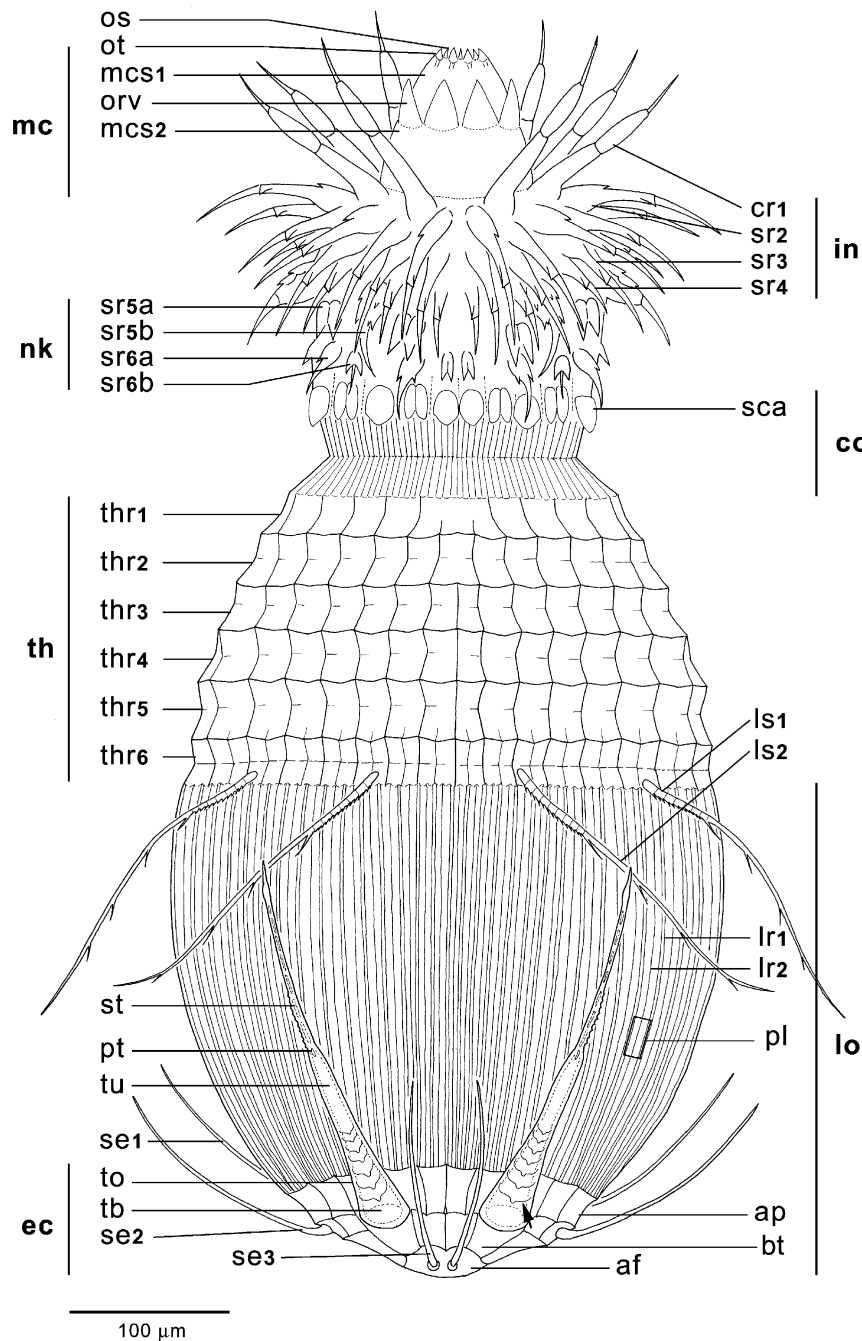
Fig. 1. *T. inexpectatovus* gen. et sp. n., paratypic sixth instar Higgins-larva (Slide UNIOL 2003, 19), ventral view, extended introvert reconstructed from withdrawn introvert.

retracted introvert. The larval exuvium contains a thin cuticle belonging to a simplified paedogenetic larva which contains rests of disintegrated yellowish tissue of the ovary (ov), some young Higgins-larvae (Lar I), empty egg-shells (egs), and rests of an unclear number of larvae and adults. One of the young Higgins-larvae inside is not more than an exuvium either, containing a fully developed adult still surrounded by a cuticle (the only remnant of the postlarva) and ready to leave both exuviae.

The holotypic specimen and all additional paratypes represent sixth instar Higgins-larvae of large size with a stubby body, a retracted introvert (Fig. 2A), a long extendable thorax with many foldable cuticular plates, and a rounded barrel-like lorica. The first instar Higgins-larvae found enclosed into the large holotypic Higgins-larva have the same morphology, but the toes and pairs of setae seem to be slightly longer in relation to body size. The description of introvert and scalids (Fig. 1) is based also on paratype I because this
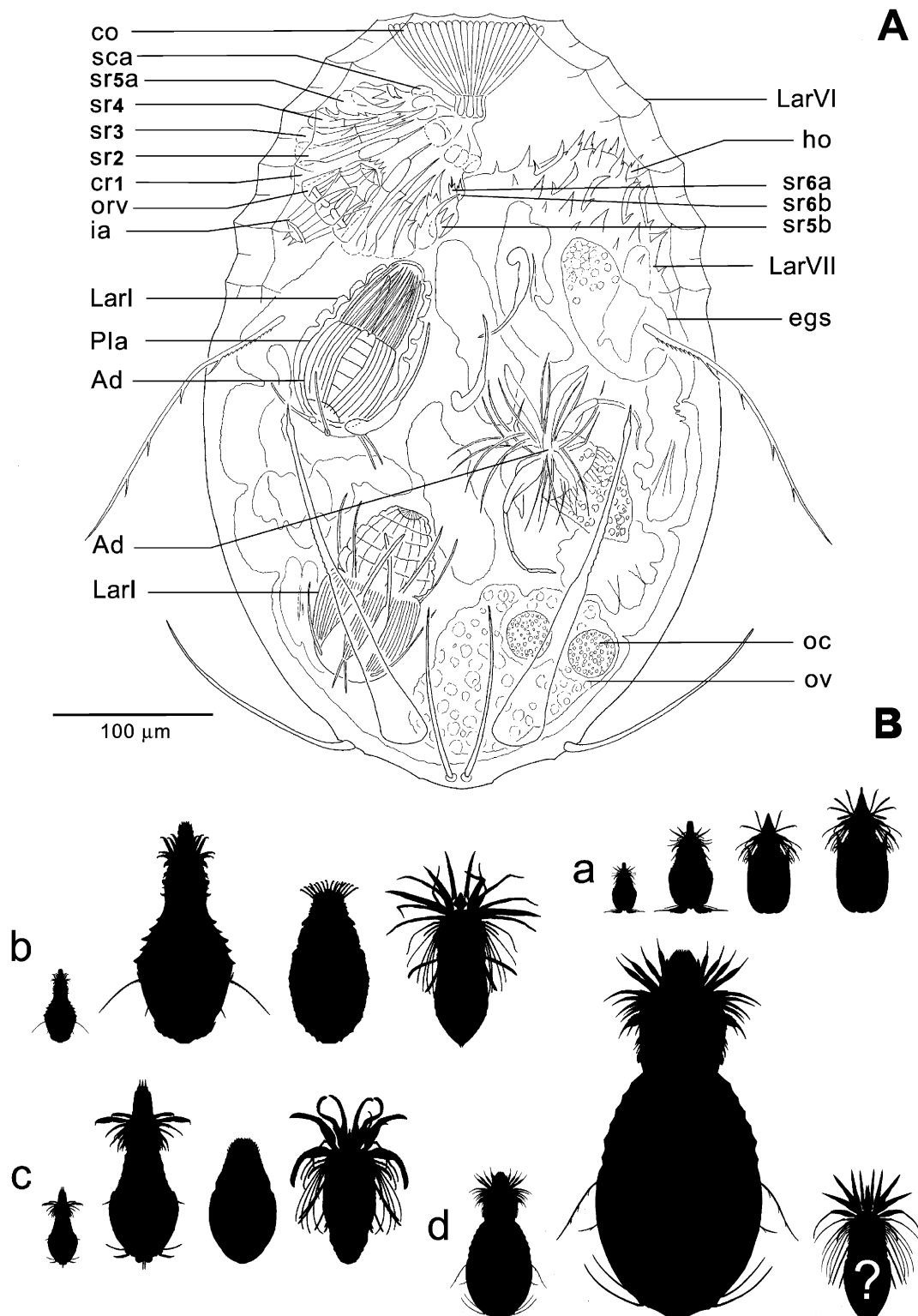
Fig. 2. *T. inexpectatovus* gen. et sp. n., (A) holotypic sixth instar Higgins-larva (slide UNIOL 2003,18; photographs Fig. 5A–F), ventral view, with withdrawn introvert, closed collar, and enclosed stages and instars; (B.a–B.d) comparison of the size of life history stages of different Loricifera taxa: (a) *Nanaloricus mysticus* Kristensen, 1983 (Nanaloricidae) from left to right: first instar Higgins larva (105 μm), fifth instar Higgins-larva (180 μm), postlarva (200 μm), and adult (240 μm); (b) *Rugiloricus* sp. (Pliciloricidae) from the Great "Meteor" Seamount from left to right: first instar Higgins-larva (120 μm), sixth instar Higgins-larva (500 μm), postlarva (330 μm), adult (320 μm); (c) *Pliciloricus* sp. from the Angola Basin from left to right: first instar Higgins-larva (130 μm), sixth instar Higgins-larva (350 μm), postlarva (280 μm), adult (300 μm); (d) *T. inexpectatovus* sp. n. from left to right: first instar Higgins-larva (approximately 250 μm), sixth instar Higgins-larva (approximately 800 μm), adult (approximately 230 μm).

specimen offers a better view on this part of the body which is retracted in all found Higgins-larvae, but less visible in the holotype.

Body divided into broad conical mouth cone, a unit consisting of introvert and neck, and collar, thorax, and loricate abdomen. The retracted body of the holotypic larva measures 510 μm (when the body is fully extended it should measure more than 800 μm); maximal body width 250 μm (in middle of the lorica).

Mouth cone (mc) broadly conical and blunt; divided into two sections. First section of mouth cone (mcs$_1$) narrowing slightly towards the terminal mouth opening which is surrounded by an outer circle of six small oral teeth (ot), and by an inner circle of six smaller oral stylets (os). First section assumed to be extendable from second section (mcs$_2$) which is large and broad, anteriorly equipped with six large and triangular oral valves (orv). Buccal channel short, smooth, and without anterior buccal tube; armed with well-developed pre-pharyngeal armature supporting the buccal channel over its entire length.

Prepharyngeal armature (ia, Fig. 2A) long and slim (more than two times longer than broad), hexaradially symmetrical, consisting of six single longitudinal brace-lets. Anterior half of armature with strongly inversely arched bracelets and covered by six short hyaline plates forming an outer cylinder. Bracelets being connected with each other by transversal bridges in the middle of the armature. In the posterior half of the armature bracelets converge on each other, and become fused at their posterior ends. Of the disintegrated pharyngeal bulb only the sclerotized anterior crown is preserved which is still fused with the prepharyngeal armature.

Introvert (in) united with neck region, densely covered with four scalid rows; scalids short in relation to large larval body.

First row (cr$_1$) with eight spinose clavoscalids (55 μm), consisting of three segments; first and second segments enlarged and flattened; first segment shaft-like, longer than second one; third segment spine-like, with sharply pointed tip; followed by three rows of spinoscalids.

Second row (sr$_2$) with 10 strong spinoscalids (60 μm), slightly longer than clavoscalids consisting of two segments; first segment beginning with broad base and tapering distally, with small dorsal thorn; lateral surfaces of first segment with longitudinal weal; second segment spine-like, shorter than first one.

Third row (sr$_3$) with 15 strong spinoscalids of same structure as scalids of second row, reaching 75% of their length (46 μm).

Fourth row (sr$_4$) with 15 strong spinoscalids (32 μm), of same structure as scalids of second row, reaching 40% of their length.

Neck (nk) not distinct from introvert, carrying two additional rows of scalids arranged in two alternating subcircles.

Fifth row with 15 modified scalids of two different types. Upper subcircle with seven larger type B scalids (sr$_5$b), strongly arched, spinous, and divided into conical bases equipped with few dorsal thorns and distally with long solid spine which is arched claw-like. Lower subcircle with eight type A scalids (sr$_5$a) consisting of paired plate-like elements.

Sixth row with 15 modified scalids of two different types. Eight type B scalids in shape of paired plates (sr$_6$b) with posterior spine, similar to the lower subcircle of the fifth row but smaller; midventrally two of these plates stand close together, both are smaller and without spine. Type B scalids alternating with seven single type A scalids (sr$_6$a), strongly arched, and dorsally with two protrusions. Scalid formula of unit comprising introvert and neck assumed to be: 8cs/10ss/15ss/15ss (in) 8a + 7b sc/8a + 7b sc (nk).

Collar (co) well-developed closing apparatus of the thorax; when closed, of typical spoke-wheel-structure (Fig. 5E). Collar with many longitudinal folds and with transversal constrictions in the middle; anterior border of collar with transversal row of 15 conspicuous scales (sca), seven double scales alternate with eight single scales.

Thorax (th) a long (195 μm), flexible, and accordion-like body region with thin cuticle; divided into transverse rows of many small thoracic plates (thr$_{1-6}$), all plates can transversally be folded once. Thorax ventrally with six, dorsally with five rows of thoracic plates. In the sixth row each thoracic plate is secondarily divided longitudinally, thus corresponding with the plicae of the lorica. In the anterior rows the plates are broader and fewer in number: 28–40 per row. The maximum number of 40 thoracic plates is reached in the fifth row. Transition zone between thorax and lorica with two pairs of long, flexible setae; anterolateral setae (ls$_1$) and anteroventral setae (ls$_2$) having same length (185 μm) and structure: filiform, basal parts annulated and rough. Four spinules scattered over their entire length.

Lorica (lo) of abdomen (315 μm) less armoured but well-developed, sculptured with about 160 longitudinal ridges (Fig. 5B). Ridges standing narrowly together and delineating 160 plicae (pl) of about 10 μm width. Adjacent plicae separated by primary ridges (lr$_1$). A finer secondary ridge (lr$_2$) divides each plica in its middle longitudinally. Caudal end with well-developed end cone.

End cone (ec) consisting of three transversal rows of anal plates (ap) and a few additional intercalate plates and forming an anal field (af) terminally. A small anal cone arises from the anal field and bears a terminal anus. Toes (to) extending pair-wise from end cone and articulating via ball-and-socket joints on moderately developed basal plates (bt). They are rigid, long (220 μm) and distinctly arched (Fig. 5C); consisting of

hollow tubes (tu) opening with gland pore (pt) at beginning of end spine and having enlarged and conical basis (tb, 95 µm) with undulated cuticle (see arrow Fig. 1), and drawn out distally into long end spine (st, 125 µm). Each end spine without inner duct, but with a series of seven inner small hallow spaces. Basal parts of spine rough, terminally with small bulge, and sharply pointed tip.

Other caudal appendages of lorica include three pairs of setae. Posterodorsal setae (se_1) long (94 µm), located dorsally on anal field; posterolateral setae (se_2) long (88 µm); posteroterminal setae (se_3) long (75 µm), robust, and bristle-like standing close together between toes. Posteroterminal setae as well as anal field slightly displaced dorsally.

Description of seventh instar larva (Lar VII = paedogenetic stage) Figs. 2A and 4A

Not free-living instar, enclosed in sixth instar Higgins-larva having the introvert retracted (as seen in all five specimens found, e.g. Fig. 2A) and the thorax closed by the folding collar. The exuvia of both larvae together form a shelter for eggs (eg) and developing embryos. Seventh instar larva with simplified body; mouth cone, buccal channel with adjunctive prepharyngeal armature, toes, and all setae lacking.

Body with thin, smooth, and weakly developed cuticle.

Introvert and *neck* forming a unit, with a similar number and arrangement of scalids as found in the sixth instar Higgins-larva, but reduced to small protoscalids. Some protoscalids modified to hooks (ho). Scalid formula of unit comprising introvert and neck seems to be: 8 pcr/10 psr/15 psr/15 psr (in) 7 + 8 psc/7 + 8 psc (nk).

Thorax and *abdomen* united to form simple sack-like trunk.

Description of postlarva (Pla) Fig. 2A

Body reduced to a simple exuvium as only remnant of this stage containing adults during metamorphosis and consisting of one layer of pure cuticle without any ornamentation. External appendages or buccal structures totally lacking.

Description of adult (Ad) Fig. 3

Body divided into introvert, neck, thorax, and loricate abdomen. Anterior body regions slightly contracted, therefore size measurements restricted to the inflexible lorica, length of lorica 140 µm; width of lorica 80 µm.

Mouth cone (mc) long (55 µm), narrow, stalked, divided into three sections. First section (mcs_1) long, conical, and pointed; mouth opening located terminally surrounded by four oral stylets (os) originating form the four elevated, longitudinal, primary oral ridges (or) which sculpture the cuticle of the first section. Second section (mcs_2), the broadest part of mouth cone, consisting of flexible cuticle, which is divided into four (eight ?) plates folded transversally together, and enveloping base of first section like a well developed hyaline frill; first section slightly retracted into second one. Third section (mcs_3) narrowing posteriorly and forming long stalk; stalk basally surround by a ruff (ru). Ruff, a formation composed of numerous well-developed fibers which surround the base of the stalk. The ring-like arranged fibers are part of the cuticle, and run from the anterior end of the introvert down to the insertion of clavoscalids.

Introvert (in) slightly retracted, spherical and covered with nine rows of scalids.

First row (cr_1) with eight short (80 µm) hyaline clavoscalids, which consist of a narrow, stalk-like shaft, and broad, flattened elements. Elements tapering distally and ending in pointed tips; with reinforced dorsal margins, but without transversal cross walls.

Second row (sr_2) with nine long spinoscalids (96 µm); seven dorsal and lateral ones free, strong, and composed of four segments; first segment large and broad, with a few dorsal spinules; remaining segments slim, last segment spine-like. Pair of mid-ventral spinoscalids somewhat transformed, but resembling free scalids of this row in structure. They are slightly shorter, composed of only three segments, stand close together (fused basally?), and possibly form a double-organ (do).

Third row (sr_3) with 15 filiform spinoscalids (86 µm) consisting of three segments; first segment with double base; distally with swollen joint bearing two minute lateral spines; last two segments bristle-like, last segment rigid and spine-like.

Fourth row with 30 spinoscalids representing two different types in alternating arrangement. Type A (sr_4a) scalids long (80 µm), filiform, consisting of three segments; first segment short and broadest, second and third segment narrow, last segment spine-like. Type B (sr_4b) scalids short (50 µm), strongly sclerotized, unsegmented, consisting of one large element. Scalid with bulbous and spiny base; distal part drawn out, massive, smooth, slightly arched, and ending claw-like. All spinoscalids from the fourth row onwards insert on small arched basal plates.

Fifth row (sr_5) with 30 uniform spinoscalids (95 µm) of hairy appearance, consisting of three segments, first two segments short with slightly developed joints, third segment very long and filiform.

Sixth row (sr_6) with 30 uniform spinoscalids (100 µm), similar to spinoscalids of fifth row.

Seventh row (sr_7) with 30 uniform spinoscalids (120 µm), also similar to spinoscalids of fifth row.

Eighth row (sr_8) with 30 uniform spinoscalids (130 µm) of rigid and bristle-like appearance and with hairy margins.
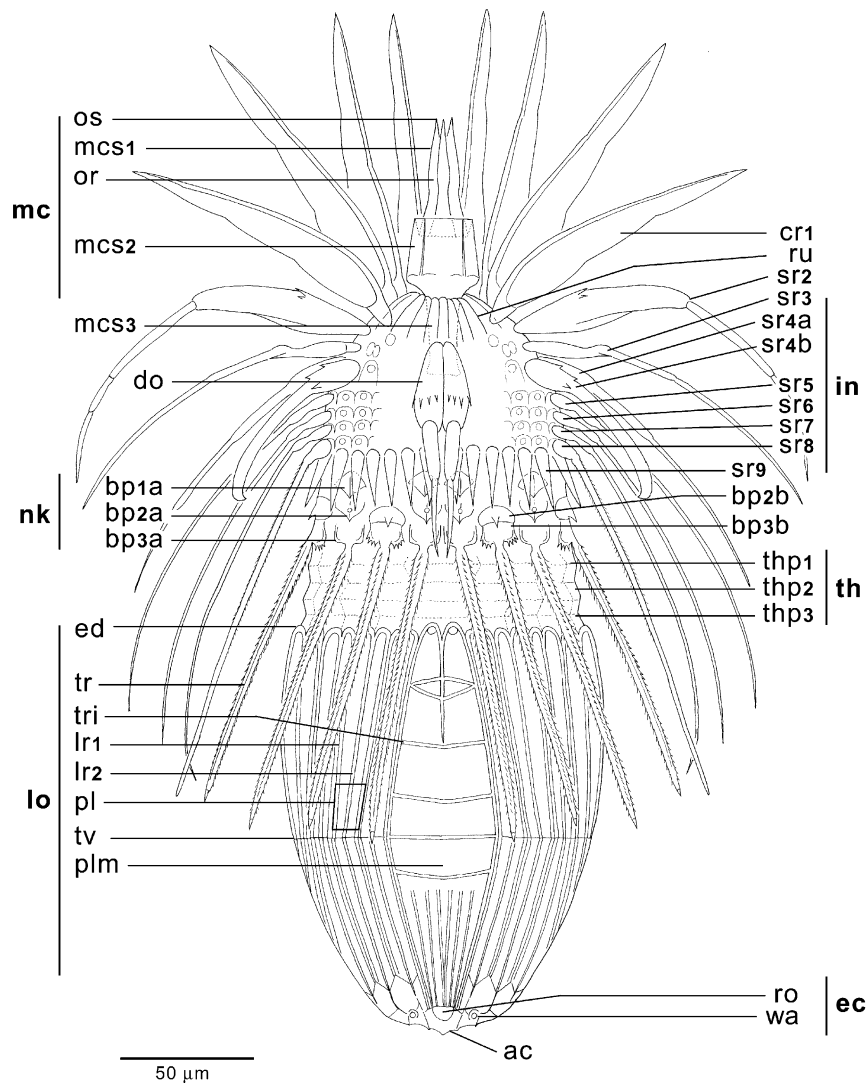
Fig. 3. *T. inexpectatovus* gen. et sp. n., paratypic adult of unknown sex, ventral view.

Ninth row (sr$_9$) with 30 uniform, long (15 μm), and thorn-like scalids.

Neck (nk) covered with rows of basal plates, and 15 single trichoscalids (tr). First row consisting only of eight rhomboid type A basal plates (bp$_1$a) with median keel. Second row with eight type A basal plates (bp$_2$a) alternating with seven type B basal plates (bp$_2$b); upper type A basal plates leaf-like, and with a peak pointing posteriorly; lower type B basal plates scale-like, oval, with a minute thorn. Both types of basal plates of second row equipped with a pore. Third row also with eight type A basal plates (bp$_3$a) alternating with seven type B basal plates (bp$_3$b); type A basal plates rectangular; type B basal plates similar, but more rounded and with fine serration. All basal plates of third row posteriorly with trichoscalids.

Trichoscalids (tr) long (85 μm), slim, and with narrow shaft. Both lateral margins with fine serration and third margin, perpendicular to lateral ones also serrated. All trichoscalids with simple pointed tips.

Thorax (th) flexible, with thin cuticle consisting of three transversal rows of plates (thp$_{1-3}$) divided by longitudinal and transversal folds. Edge (ed) between thorax and lorica distinct and marked by crescent-like ornamentation of lorica.

Lorica (lo) with moderately thick cuticle. Cuticle divided longitudinally into 20 uniform plicae. Each plica (pl) framed by a primary ridge (lr$_1$), hence adjacent plicae separated by double ridges. Weakly developed secondary ridge (lr$_2$) in the middle of each plica. Midventral plicae (plm) transformed: two plicae with round ornament at their anterior end are fused longitudinally, forming broad unit. Lorica divided halfway into two halves by a transversal constriction (tv). Anterior part of midventral unit of plicae with six transversal ridges (tri) which are restricted to this part of

the lorica; posterior part with six longitudinal ridges. Caudal part of lorica separated as end cone (ec) from remaining lorica by transversal zigzag border; only secondary ridges of plicae continue into end cone. A round structure is located at caudal end of midventral plicae.

End cone (ec) with 10 ridges, forming an anal field at the end. Anal field composed of many small anal plates surrounding a terminal anal cone (ac) bearing the anus. Midventral plicae continue into end cone ending with a round structure (ro) flanked by a pair of small warts (wa). In addition there are four pairs of warts and six small papillate flosculi laterally on the end cone (not visible in Fig. 3 because it is a ventral view).

Discussion

Differential diagnosis

The sixth instar Higgins-larva of *Titaniloricus inexpectatovus* gen. et sp. n. shares some characters with the Higgins-larvae of the genus *Pliciloricus* which indicates a close relationship with this taxon and consequently with Pliciloricidae: (1) well developed conical mouth cone, divided into sections; (2) short buccal channel supported over its entire length by well developed hexaradially symmetrical prepharyngeal armature; (3) clavoscalids divided into three segments; (4) second, third and fourth rows of scalids as part of the introvert consisting of spinous spinoscalids; (5) neck region with two transversal rows of small scalids of two different types arranged in upper and lower subcircles; (6) collar well-developed with many longitudinal folds, when closed looking like spoke-wheel; (7) ventral side at the transition of thorax and lorica with two pairs of anterior setae, which carry a few scattered spinules; (8) abdomen not armoured, only with slightly thicker cuticle and with straight longitudinal folds (or longitudinal ridges); (9) end cone with three pairs of posterior setae, and (10) long spinose toes, divided into basal tubular part and end spine.

The following distinguishing characters of Higgins-larvae separate *T. inexpectatovus* sp. n. from species of *Pliciloricus* and characterize it as a new genus: (1) second segment of clavoscalids visibly shorter than first one, length ratio 1.5:2 (in *Pliciloricus* length ratio of segments nearly 1:1); (2) upper subcircle of fifth row with large hook-like spinoscalids, consisting of a swollen, spiny base and a strongly arched spine (in *Pliciloricus*: first segment dorsally with double plates or two protrusions, second segment small and third segment like a small spine); (4) well developed collar with numerous folds, anterior border with transversal row of seven double and eight single scales (in

Pliciloricus row of scales not present), (5) thorax with 28–40 thoracic plates in first to fifth transversal row (in *Pliciloricus* not more than 24 thoracic plates per row); (6) lorica with around 160 longitudinal ridges, including primary and secondary ones (in *Pliciloricus* not more than 24 lorica folds, real plicae lacking); (7) anterior pair of setae long (in *Pliciloricus* anterior sensory setae short); (8) posteroterminal setae standing close together between toe bases but inserting more dorsally on anal field (in *Pliciloricus* inserted more ventrally, directly between bases of toes); (9) tubular part of toes basally enlarged, conical, and with basal undulation, end spine of toes longer than tubular part (in *Pliciloricus* tubular part of toes basally not enlarged, without undulation, end spine generally shorter or as long as tubular part).

The six large oral valves at the beginning of second section of the mouth cone of *T. inexpectatovus* sp. n. are lacking in Higgins-larvae of *Pliciloricus* but can be observed in Higgins-larvae of the genus *Rugiloricus* (Higgins and Kristensen 1986). Furthermore, the six small oral teeth and the six oral stylets surrounding the mouth are similar in both taxa. The anterior setae are also long in *Rugiloricus* but covered with more spinules.

Numerous primary longitudinal ridges delineate an increased number of plicae, a finer median secondary longitudinal ridge divides each plica. This kind of lorica sculpture resembles the one found in adult *Rugiloricus* species (see Higgins and Kristensen 1986).

A new life cycle?

As observation of live specimens is not possible, the life cycles of Loricifera have to be reconstructed on the one hand from moulting specimens, and on the other hand from size classes that indicate the number of larval instars. The basic life cycle of Loricifera is assumed to include five (Nanaloricidae) or seven (Pliciloricidae) instars of Higgins-larvae, a juvenile or postlarval stage, and sexually dimorphic adults of both sexes (Kristensen and Brooke 2002; Kristensen 2002, 2003; Gad 2004). This basic life cycle without any simplified or transformed life history stages is probably realized in Nanaloricidae (Kristensen 1991a).

In Pliciloricidae the life cycle seems to be much more complicated. The free sexual phase is still present (Fig. 4B) but an additional unisexual phase may occur (Kristensen and Brooke 2002; Kristensen 2002, 2003; Gad 2004). For a better understanding of the discussion concerning life cycles and their different phases the life history stages found in *T. inexpectatovus* sp. n. are depicted in Fig. 4A together with the reconstructed hypothetical life cycle drawn in Fig. 4B. Although the exact number of larval instars of *T. inexpectatovus* sp. n. is not known seven instars are assumed like in all other species of Pliciloricidae. This presupposition is necessary
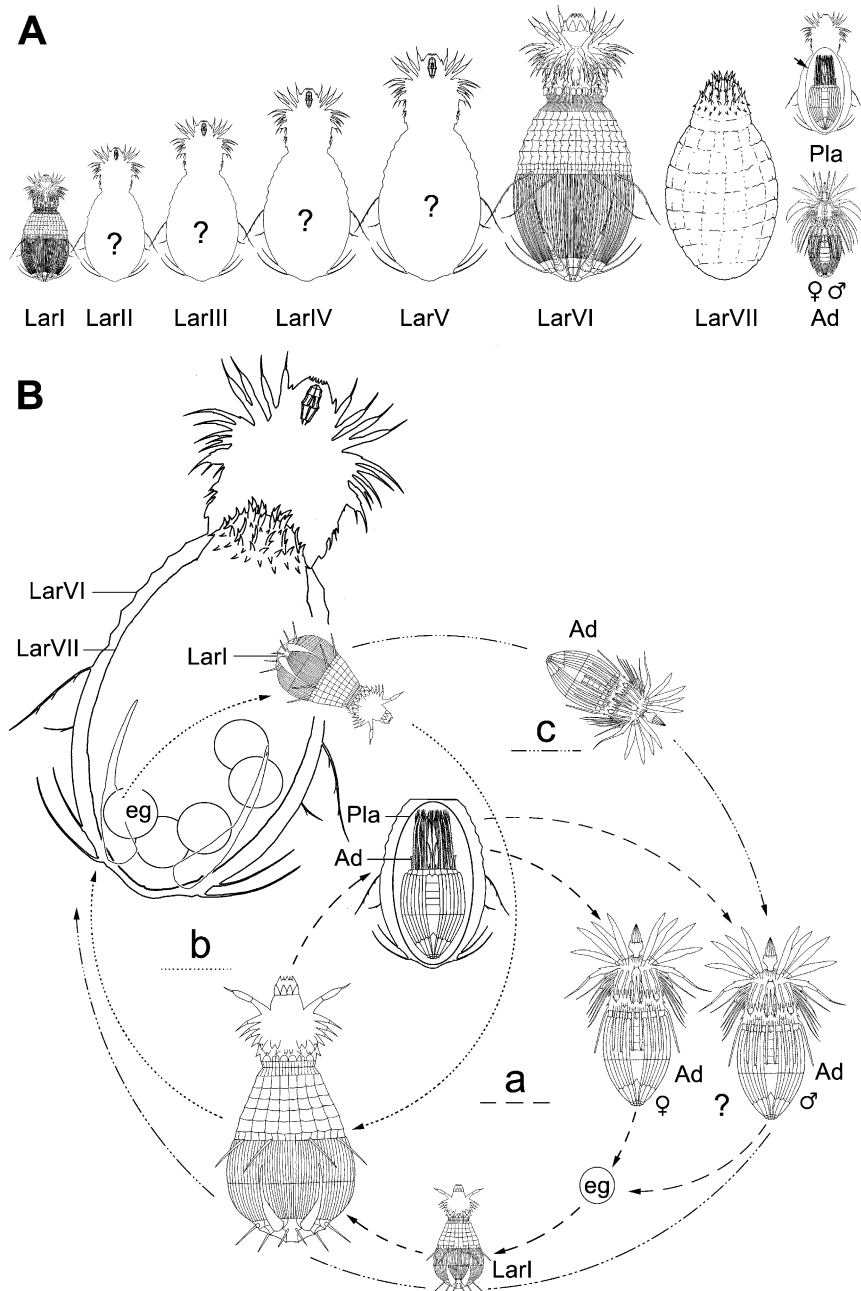
Fig. 4. Life history stages and hypothetical life cycle of *T. inexpectatovus* gen. et sp. n., (A) life history stages, Ad = adult, Lar I— Lar VI = first to sixth instar Higgins-larva (Lar II–V not found), Lar VII = simplified seventh instar or paedogenetic larva, Pla = postlarva (reduced to a simple cuticle (see arrow) surrounding adult during metamorphosis); (B) hypothetical life cycle: (a) free phase of the life cycle with mature males and females, single laid eggs, and reduced postlarva as common in other species of Pliciloricidae, (b) paedogenetic phase only with larvae as is common in some other species of Pliciloricidae but in this case with giant sixth instar Higgins-larva being involved, (c) similar phase as in Fig. (B.a) but adult developing inside a shelter formed by giant sixth and seventh instar larvae and emerging from paedogenetically produced Higgins-larva.

to allow comparison of the life cycles without using confusing terms like: last instar Higgins-larva, penultimate larva, non modified larva (see Gad 2004).

The first noticeable modification in life cycles of Pliciloricidae relates to the postlarva, which becomes modified as a dormant stage or reduced to a simple

exuvium as the only remnant of it. Such a postlarva modified to a free dormant stage with unfinished adult morphology can be found in species of the genus *Rugiloricus*, especially of the *R. cauliculus*-group (Kristensen and Brooke 2002; Kristensen 2003; Gad 2004). In many species of the genus *Pliciloricus*, e.g. in

Pliciloricus pedicularis Gad, 2004, the postlarva is reduced to a simple layer of cuticle but still contains the adults after they have moulted form it (Gad 2004, 2005).

A high proportion of eggs containing larval instars is characteristic for Pliciloricidae of the deep sea because they have unisexual phases in their life cycles. This allows them to skip the sexual generation with males and females and to produce large eggs parthenogenetically or paedogenetically from which hatch the Higgins-larvae of the next generation. Inside its body the large sixth instar Higgins-larva produces an additional larval instar which is the transformed seventh instar and at the same time a paedogenetic stage, discovered in the life cycle of *Rugiloricus* species (Kristensen and Brooke 2002; Gad 2004) and now also of *T. inexpectatovus* sp. n. This paedogenetic instar is not a free larva and is totally different morphologically from the free-living sixth instar Higgins-larva preceding it. The transformation of this instar is remarkable. In contrast to all other instars of Higgins-larvae which are uniform morphologically, the paedogenetic instar larva has a simplified body in which the different regions like introvert, neck, collar, thorax, and abdomen can no longer be distinguished. The trunk is sack-like; locomotory, sensory, and feeding organs like toes, setae, and mouth cone are lacking in this instar of *Rugiloricus* species as well as of *T. inexpectatovus* sp. n. Only the unit comprising introvert and neck can be identified by the number and arrangement of scalids as found in the Higgins-larva which are retained, but are merely small protoscalids of which some are modified to spiny pads or small hooks (Figs. 4A and B, see Gad 2004).

This instar differs from the also simplified parthenogenetic adults of *P. pedicularis* (Gad 2005) which can be mixed up with it because both have a sack-like trunk without appendages, but in the simplified adult the scalids of the introvert are lacking while basal plates of the neck region persist as modified spiny pads or large hooks. Additionally, the simplified adults are surrounded by the thin exuvium of the postlarval stage which obviously is lacking in the case of the paedogenetic larvae (Gad 2005). All this indicates that these parthenogenetic reproducing adults or larvae are reduced life history stages, which both produce eggs they sometimes release into the shelter formed by the sixth instar Higgins larva which generally has the introvert retracted and the collar closed (Lar VI in Fig. 2A; see also Gad 2005).

The unisexual development of paedogenetic larvae of *Rugiloricus* species (Gad 2004) and of *T. inexpectatovus* sp. n. ends when the tissue of the ovary disintegrates after formation of the last unfertilized egg and when the cuticle remains as the only rest of the body. Sometimes also this cuticle disappears so that eggs come to ly in the sixth instar Higgins-larva. The same happens with the simplified parthenogenetic adults known from *P. pedicularis* (Gad 2005). This is the reason why earlier the untransformed Higgins-larva was assumed to be egg-producing and therefore neotenic (Kristensen 2002, 2004a).

The first instar Higgins-larvae develop, hatch, and leave the shelter of the empty exuvium of the sixth instar Higgins-larva (Gad 2004). The large sixth instar Higgins-larva (Lar VI) and the simplified paedogenetic larva (Lar VII) it contains, seem to form a developmental unit for the protection of the new larval generation. This larval generation, which is unique in the case of *T. inexpectatovus* sp. n., seems to have the ability to moult directly into reduced postlarvae and then into adults (Figs. 2A and 4B).

All five studied specimens of Higgins-larvae of *T. inexpectatovus* sp. n. represent sixth instar Higgins-larvae containing a seventh instar paedogenetic larva. The young Higgins-larvae of the next generation were discovered in only two of them (holotype and paratype II). In the remaining specimens the young Higgins-larvae must already have left the exuvium of the sixth instar Higgins-larva leaving behind their empty egg shells and also the cuticle of the paedogenetic seventh instar larva. There are indications that the development of a whole generation from the first instar Higgins-larva to the metamorphosis of the adults can take place inside the large sixth instar Higgins-larva which then is virtually a "mother larva" (Fig. 4B). This is concluded from the observation that young Higgins-larvae developing inside it already contain matured adults (Fig. 5F) and that there are rests of additional adults (Fig. 5D) that must have been unable to leave the shelter of the "mother larva" (Fig. 2A).

All this seems to be possible only because of the large size of the sixth instar Higgins-larva, which allows the storage of enough food reserves to feed the growing young larvae. Comparison of the size of stages and instars in different Loricifera (Fig. 2B) shows that only in Nanaloricidae the last instar Higgins-larvae seem to be smaller than the adults. In species of Pliciloricidae the sixth instar Higgins-larvae are much larger than the adults they produce. Especially in some species of *Rugiloricus* the large sixth instar Higgins-larvae measure about 350–500 µm. In well-nourished larvae of these species the thorax and lorica can be swollen balloon-like so that they were the largest Higgins-larvae known until *T. inexpectatovus* sp. n. was discovered (Gad 2004). The ability of the sixth instar Higgins-larva to store great amounts of food reserves is important for the mode of reproduction: sexual reproduction (little food = adults) or unisexual reproduction (much food = paedogenetic larva). This was shown in recent experiments which have established the importance of food quality and quantity
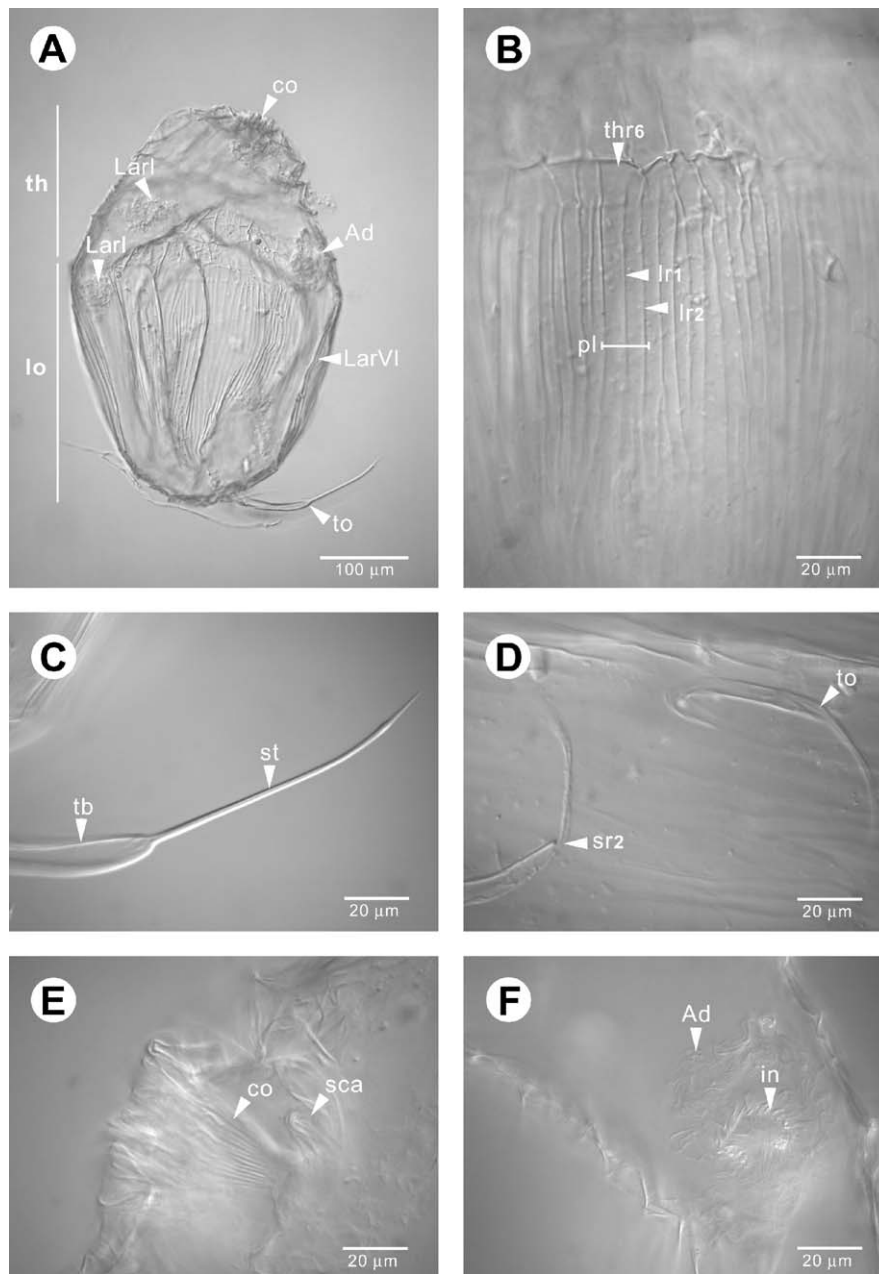
Fig. 5. *T. inexpectatovus* gen. et sp. n., interference-contrast photographs of holotypic sixth instar Higgins-larva (slide UNIOL 2003,18; drawing Fig. 2A). (A) Habitus, (B) details of lorica sculpture, (C) lateral view of a toe, (D) parts of enclosed instars e.g. second-row-spinoscalid (sr2) of adult and toe (to) of young Higgins-larva, (E) details of collar region, and (F) view of enclosed adult with retracted introvert.

for triggering the paedogenetic phases in the life cycles of e.g. gall midges (Hodin and Riddiford 2000).

The main question resulting from the study of *T. inexpectatovus* sp. n. and its life history stages is: Is this a new life cycle in which the two separate phases of sexual and unisexual reproduction are united into one and which takes place inside a giant Higgins-larva? Or does the giant Higgins-larva represents an additional phase (Figs. 4B.b and B.c) belonging to the complex life cycle already known form other Pliciloricidae (Fig. 4B.a)? If

so, a free life cycle without a giant larva may also exist. This question cannot be answered clearly because the conclusions presented here are based on only few specimens.

However, there is the curious fact that the young Higgins-larvae which develop inside the giant Higgins-larva of *T. inexpectatovus* sp. n. as well as the resulting adults have more or less the same size as the respective stages/instars in *Pliciloricus*-species without giant larvae (Figs. 2B.b–B.d). Measurements of sclerotized body

parts, like toes and scalids which cannot contract or shrink like other body parts were used to extrapolate the final size of the extended larval instars. The result is that the young instar Higgins-larva of *T. inexpectatovus* sp. n. produced inside the giant sixth instar Higgins-larva could have a size of 250–290 µm and the appertaining adult of 190–250 µm. This is a size which matches with the one found in the sixth instar Higgins-larva and mature adults of most *Pliciloricus*-species (Higgins and Kristensen 1986; Gad 2004, 2005). This indicates that the adults of *T. inexpectatovus* sp. n. have no unusual size and that they are not subject to miniaturization. The putative first instar Higgins-larva developing inside the giant "mother larva" seems already to have the size of the probable sixth instar Higgins-larva generally found in most *Pliciloricus*-species. If so, this would mean that the first instar Higgins-larva hatching from eggs produced by adult females is smaller than the Higgins-larva hatching from the larger paedogenetically produced eggs.

Paedogenesis or neoteny in Loricifera?

The occurrence of paedogenetic larvae, which differ morphologically from the preceeding Higgins-larvae, is one of the astonishing discoveries made on the life cycles of pliciloricid Loricifera. The term paedogenetic is used to describe the reproduction of larval Loricifera and is preferred here over neotenic (derived from neoteny) used by Kristensen (2003). Paedogenesis as defined by Gould (1977) or Chapman (1998) means that larval instars have functional ovaries, the eggs of which develop parthenogenetically. Paedogenesis is a special case of parthenogenesis and describes functionally the role of a stage/instar in its life cycle and its kind of reproduction. This does not exclude the occurrence of adults of both sexes in the same life cycle which then have different phases as found in pliciloricid Loricifera. Examples of paedogenesis according to this definition are otherwise known only from some insects such as gall midges of the genera *Heteropeza* and *Mycophila* (Diptera: Cecidomyiidae) (Hodin and Riddiford 2000), flower flies of the genus *Eristalis* (Diptera: Syrphidae) (Ibrahim and Gad 1975), and wood boring beetles of the genus *Micromalthus* (Scott 1938, 1941).

Neoteny together with progenesis are subcategories of paedomorphosis, a morphological term which is generally used in connection with evolutionary processes. Paedomorphosis according to Gould (1977) is the retention of ancestral juvenile characters by a later ontogenetic stage of descendants. Paedomorphosis means precocious development of the reproductive structures before completion of the development of all the nonreproductive (somatic) structures. The result is a reproductively functional animal retaining what in the

ancestor were certain embryonic, larval or juvenile characters. According to Gould (1977) this condition can result form two different processes: (1) neoteny, in which somatic development is retarded; or (2) progenesis, in which reproductive development is accelerated. These two terms are frequently used interchangeably in much of the literature, because it is certainly not always possible to know which process has given rise to a particular paedomorphic condition. Recognition of paedomorphosis often plays a significant role in examining phylogenetic hypotheses concerning the origin of certain taxa across the animal kingdom, e.g. in Bathynellacea (Crustacea) (Schminke 1981), *Ambystoma* (Urodela) (Sprules 1974), *Psammodrilus* (Polychaeta) (Swedmark 1964; Struck et al. 2002). Using neoteny according to the definition preferred here means that the "morphological adults" do no longer exist as part of the life cycles, but that despite the "larval morphology" the separation into both sexes is still conserved. This is clearly not the case in Loricifera.

Paedogenesis which is additionally characterized by the precocious differentiation of the ovary and subsequent parthenogenetic reproduction in a larval form is identical in the examples known from insects and from *Rugiloricus* species as representatives of Loricifera (Kristensen and Brooke 2002; Gad 2004). In the gall midges *Heteropeza pygmaea* and *Mycophila speyeri* the paedogenetic phase of the life cycles is known in some detail (Hodin and Riddiford 2000). The ovaries differentiate and grow precociously in the early larval instar and the eggs develop unfertilized so that the embryos are brooded inside a large "mother larva". When the young larvae hatch they consume the histolyzing tissues of the "mother larva" and emerge from its empty cuticle. This is called viviparous paedogenesis (Ulrich et al. 1972; Hodin and Riddiford 2000) which also occurs in *Eristalis tenax* (Ibrahim and Gad 1975). In the wood boring beetles *Micromalthus debilis* viviparous as well as oviparous paedogenesis occurs. In *Rugiloricus* species and *T. inexpectatovus* sp. n. the paedogenetic seventh instar larva is generally filled with eggs. The tissue, at least the one of the ovary, of the egg-producing larva has already disintegrated before the first instar larvae hatch from the large eggs in which they undergo development, so it seems that in the case of Loricifera a oviparous paedogenesis occurs.

According to Gould (1977) paedogenetic life cycles are an adaptation to unstable, unpredictable habitats with frequent density-independent mass mortality. Rapid maturation of larvae along with dormant stages/instars is a good insurance against any crisis and allows a rapid recolonization after such an event. Observations on gall midges have confirmed that this may be the most plausible explanation for paedogenesis (Hodin and Riddiford 2000). It may also be a good explanation for the evolution of the complex life cycles

of deep-sea Loricifera. Paedogenesis or other modes of unisexual reproduction (Gad 2005) would allow deep-sea Loricifera to adapt to patchy distribution of food resources.

Large Higgins-larva an example of abyssal gigantism?

A lot has been written about body size paradoxes of deep-sea organisms. Despite the fact that deep-sea invertebrates show a broad spectrum of size classes similar to those found in shallow waters some species have been regarded as "giants" or "dwarfs" (Murray and Hjort 1912; Herring 2002). In the deep sea there are conflicting options for either becoming smaller in order to reduce nutritional requirements or for becoming larger to improve foraging ability, and these options tend to correlate with the reproductive strategy.

Abyssal gigantism is not a general trend of the deep-sea benthic fauna. It rather relates to some invertebrate groups such as in particular crustaceans like mysids, amphipods, isopods, and ostracods (De Broyer 1977; De Broyer et al. 1997; Childress and Price 1978; King and Butler 1985; Mauchline 1988, 1995). Taking into consideration macrobenthic invertebrates low food supply in the deep sea contributes to an overall decline in body size. In waters below 400 m there is much less food available than above. The same applies to the bottoms of the great deep-sea basins. Own observations show that the many meiofauna taxa, which inhabit the oligotrophic fine-grained clayish sediments of the Angola Basins, do not have larger representatives than elsewhere. On the contrary, the deep-sea meiofauna decreases in body size with increasing depth so that meiobenthologists started to use a smaller sieve with 36 μm mesh whereas 63 μm sieves are the rule in shallow water (Giere 1993). There is a general trend in deep-sea meiofauna to become smaller, especially in the dominating taxa Nematoda and Harpacticoida which together often make up more than 90% of the total meiofauna (Soetaert and Heip 1989; Giere 1993). What does this mean for the giant Higgins-larva of *T. inexpectatovus* sp. n.? Is it an exceptional example of abyssal gigantism in the meiofauna?.

One main argument for abyssal gigantism is that the combination of low temperature and food scarcity reduces growth rates and increases longevity as well as the time to reach sexual maturity (Nybakken 2001). Large size, long life, and delayed sexual maturity confer certain advantages to animals in the deep sea. In the case of the giant larva of Loricifera increased longevity means a longer period of sexual maturity and the production of larger eggs. A large larva with many food reserves could be an advantage for dispersal by being able to drift over long distances in the water column for a long time. In contrast to the macrofauna members, the meiofauna lack planktic larvae (Young 2002), dispersal being achieved by all life history stages such as juveniles, adults, and eggs by drifting in bottom currents (Palmer 1988).

In deep-sea Loricifera it seems that paedogenetic larvae and parthenogenetic adults are rather common and not an exception (Gad 2002, 2005). Bigger larvae hatching from large eggs are an advantage for rapid development and colonization. Through paedogenesis Loricifera would be able to colonize new habitats rapidly with a single drifting larva.

The generation of young larvae inside the giant well-nourished larva e.g. of *T. inexpectatovus* sp. n. may profit from the food reserves stored in the large ovary. This may be regarded as a case of brood care in Loricifera. In deep-sea mysids the large-sized females invest as much as 75% of the energy accumulated during their life time in brooding (Childress and Price 1978, 1983). The investment may be similar in large paedogenetic larvae of Loricifera, because they produce 8–40 eggs simultaneously with the consequence that all internal organs of the larva totally disintegrate after formation of the last egg, whereas adult females are just able to produce one large egg after the other (Kristensen and Brooke 2002; Kristensen 2003; Gad 2004, 2005). As the number of eggs produced by females during their life-time is not yet known, nothing can be said about their reproductive success.

Deep-sea Loricifera may have a second survival strategy by producing dormant stages/instars with postponed development. An example for both dormancy and larval gigantism has also been discovered in the Angola Basin. Apart from the large Higgins-larvae of *T. inexpectatovus* sp. n. there are many large cysts which contain around 40 eggs (Gad 2002). Similar but not identical instars are also known from the Faroer Bank (Kristensen and Brooke 2002) which like the Angola Basin (Gad 2002, 2004) is an extreme low nutrient habitat for meiofauna (Kröncke and Türkay 2003).

The Higgins-larvae of Pliciloricidae seem to have many functions and in this respect are quite unlike any larva of other invertebrates. Apart from postembryonic growth, dispersal, recolonization of unpredictable habitats, and storage of food reserves, the larvae of Loricifera can have two additional functions: Unisexual reproduction, either parthenogenetically or paedogenetically, allowing rapid development to build up large populations in short time and dormancy to survive unsuitable environmental conditions over long periods of time through delayed development. Furthermore, the Higgins-larva of *T. inexpectatovus* sp. n. is an example for the combination of low water temperature and food scarcity resulting in larger body size of parental animals and in this special case also of a larva.

Folding of the lorica

The structure of the loricate abdomen differs between adults and Higgins-larvae of Pliciloricidae. In adults of *Pliciloricus* the thick cuticle of the loricate abdomen is divided into 20–22 longitudinal plicae (Higgins and Kristensen 1986; Kristensen 1991b). A ridge of thickened cuticle frames each plica. These ridges are called primary ridges. A double primary ridge separates two neighbouring plicae from each other. In addition each plica can be folded longitudinally once in the middle. These folds are visible as fine median lines which are called secondary ridges. In the appertaining Higgins-larvae the cuticle of the loricate abdomen is not much thicker than that of the rest of the body. Instead of ridges 20–22 deep primary longitudinal folds divide the cuticle of the lorica. Sometimes secondary folds are present which generally do not reach the caudal end. Bundles of muscles which form a transversal layer attach at the tips of inward folds of the cuticle in adults as well as in larvae. This allows the abdomen to extend widely and to contract depending on the nutritional state of the specimens. The lorica will also widen when the introvert is withdrawn and narrow when it is extended. A lorica with longitudinal ridges usually does not occur in Higgins-larvae. Similar structures like in *T. inexpectatovus* sp. n. with an increased number of ridges and plicae (Fig. 5B) are found sometimes in adults of *Rugiloricus*, e.g., in adults of the *R. cauliculus*-group (Gad 2004) where the lorica has about 30 plicae and 60 ridges. The increased number of plicae goes together with a thinner cuticle of the abdomen. Adults of the *R. cauliculus*-group often have a more swollen, barrel-like abdomen than other pliciloricid adults. The Higgins-larvae of *Rugiloricus* species do not have a greater number of longitudinal folds which are less straight and deeper than in *Pliciloricus* larvae.

The lorica structure of adults of *Rugiloricus* and larvae of *T. inexpectatovus* seem to be the solution to the same problem: to gain flexibility of the lorica with the help of a thinner cuticle without losing strength. The increased number of plicae and the presence of real ridges instead of ordinary folds in the Higgins-larva of *T. inexpectatovus* seems to be an expression of this solution.

Acknowledgements

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