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

# A parthenogenetic, simplified adult in the life cycle of *Pliciloricus pedicularis* sp. n. (Loricifera) from the deep sea of the Angola Basin (Atlantic)

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## Abstract

A new species, *Pliciloricus pedicularis* (Pliciloricidae, Loricifera), is described inhabiting fine-grained clayish sediments in the deep sea of the Angola Basin. This is the first report of a *Pliciloricus*-species with a simplified parthenogenetic adult in its life cycle. The simplified adult is a non-free-living stage differing morphologically considerably from the free-living bisexual adults. It has a sack-like body without an introvert but with a persisting neck region covered with hooks or spiny pads. The sack-like body contains mainly the mature ovary. Large eggs are released into a shelter formed by the exuvium of the last or seventh instar Higgins-larva. Both types of adults, the parthenogenetic as well as the bisexual ones, are surrounded during metamorphosis by two exuviae: a simple inner one as rest of the postlarval stage and an outer one belonging to the seventh instar Higgins-larva. The bisexual adult of the new species is characterized by type B spinoscalids in the fourth row basally equipped with a ventral row of minute denticles; long rigid trichoscalids basally with numerous strong cross walls; small cuticular bars directly above the well-defined edge of the lorica, and a lorica consisting of 44 primary plicae. Distinguishing features of the Higgins-larva of the new species are: very long toes, and clavoscalids with a dorsal row of spinules and an additional fourth segment. The most conspicuous feature of the Higgins-larva is the stem-like basal part of the anterior setae called pedicels. Especially the enlarged pedicels of the posterolateral setae enable the larva to be determined even when the introvert is retracted. The study revealed new information about embryology and development, which have never been observed in any Loricifera-species so far. The great abundance of the new species in samples from the Angola Basin allows the identification of most life history stages and developmental instars.


***Keywords:*** Loricifera; Pliciloricidae; Parthenogenesis; Life history stages; Life cycles; Deep-sea meiofauna

## Introduction

There are only few reports of Loricifera from the deep sea so far (Soetaert et al. 1984; Kristensen and Shirayama 1988; Hubbard et al. 1988). The first and to date only species described from the deep sea belongs to the 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).

During the DIVA 1 (*Div*ersity of the deep sea in the *A*tlantic) expedition many new species of Loricifera were discovered in the deep sea of the Angola Basin indicating that Loricifera are more widely distributed in the deep sea than previously assumed (Gad 2001, 2004a). What is regarded as the basic life cycle of the Loricifera includes sexually dimorphic adults of both

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**Nomenclature Abbreviations**

| | |
|---|---|
| ac | anal cone |
| Ad | bisexual adult |
| Ad* | simplified (parthenogenetic) adult |
| af | anal field |
| cgl | caudal gland |
| an | anus |
| ap | anal plate |
| apl | anterior plate of prepharyngeal armature |
| apo | apodeme |
| bar | cuticular bar |
| bc | buccal channel |
| $bg_1$ | anterior cuticular bridge |
| $bg_2$ | posterior cuticular bridge |
| bl | blastula |
| bp | basal plate |
| $bp_{1–2}a$ | first to second row of type A basal plates |
| $bp_3a$ | third row of type A basal plates with single type A trichoscalid |
| $bp_{1–2}b$ | first to second row of type B basal plates |
| $bp_3b$ | third row of type B basal plates with double type B trichoscalid |
| br | brain |
| $bra_1$ | anterior double bracelet |
| $bra_2$ | posterior single bracelet |
| bt | basal plate of toe |
| bu | buccal tube |
| bug | buccal gland |
| cb | central body |
| clo | cloaca |
| co | collar |
| $cr_1$ | first row of clavoscalids |
| cs | clavoscalid |
| ct | claw-tip |
| cw | cross wall |
| d | dorsal |
| $do_1$ | primary double-organ |
| $do_2$ | secondary double-organ |
| ec | end cone |
| ed | anterior edge of lorica |
| eg | egg |
| egs | egg shell |
| em | embryo |
| fl | flosculus |
| fo | follicle |
| ga | gastrula |
| gu | midgut |
| ho | hook |
| ia | prepharyngeal armature |
| in | introvert |
| Lar I | first instar Higgins-larva |
| Lar VII | seventh instar Higgins-larva |
| lm | longitudinal muscle |
| lo | lorica |
| lr | longitudinal fold in larva |
| $lr_1$ | longitudinal (primary) ridge in adult |
| $ls_1$ | anterolateral seta |
| $ls_2$ | anteroventral seta |
| lw | lateral weal |
| mac | macromeres |
| mc | mouth cone |
| mca | mouth cone anlage |
| mcr | mouth cone retractor |
| $mcs_{1-3}$ | first to third section of mouth cone |
| mic | micromeres |
| mo | mouth opening |
| ms | midventral oral seta |
| muc | multicorer |
| nc | nucleus |
| ne | protonephridium |
| ngl | neck gland |
| nk | neck |
| oc | oocyte |
| oe | oesophagus |
| or | primary oral ridge |
| os | oral stylet |
| ost | oral stria |
| ot | oral tooth |
| ov | ovary |
| $p_{1-5}$ | first to fifth row of placoids |
| pa | papilla-like oral elements of postlarva |
| pb | pharyngeal bulb |
| pc | pharyngeal crown |
| pd | pad |
| ped | pedicel |
| $pl_1$ | primary plica |
| $pl_2$ | secondary plica |
| Pla | postlarva |
| plm | midventral transformed plica |
| por | gonopore |
| ps | protoscalid |
| pt | pore of tubular part of toe |
| ram | radial muscle |
| $re_1$ | retractor of scalids |
| $re_2$ | main retractor of introvert |
| $re_3$ | neighbouring retractor of introvert |
| rec | rectum |
| rim | ring muscle |
| $rim_1$ | ring muscle of thorax |
| $rim_2$ | ring muscle at end of midgut |
| ro | round structure |
| ru | ruff |
| $sbp_{4–8}$ | basal plates of fourth to eighth row of spinoscalids |
| sc | scalid |
| scm | scalid muscle |
| sca | scalid anlage |
| $se_1$ | posterodorsal seta |
| $se_2$ | posterolateral seta |

| | | | |
|---|---|---|---|
| $se_3$ | posteroterminal seta | th | thorax |
| ser | serration | $thp_{1-3}$ | first to third row of adult thoracic plates |
| $sg_{1-4}$ | first to fourth segment | $thr_{1-6}$ | first to sixth row of larval thoracic plates |
| $sip_{1-3}$ | scalid inserting point of first to third row | tm | transversal muscle |
| sk | stalk of mouth cone | to | toe |
| $sr_{2-9}$ | second to ninth row of spinoscalids | tr | trichoscalid |
| $sr_4a$ | type A spinoscalids of fourth row | $tr_1$ | lower primary ramus of trichoscalid |
| $sr_4b$ | type B spinoscalids of fourth row | $tr_2$ | upper secondary ramus of trichoscalid |
| $sr_5a$ | type A scalid of fifth row | tr a | type A single trichoscalid |
| $sr_5b$ | type B scalid of fifth row | tr b | type B double trichoscalid |
| $sr_6a$ | type A scalid of sixth row | tri | transversal ridge of lorica |
| $sr_6b$ | type B scalid of sixth row | trk | trunk of simplified adult |
| srs | dorsal row of spinules | trp | ornamental triangular plates above lorica rim |
| srt | ventral row of denticles | tu | tubular part of toe |
| ss | spinoscalid | Tv | transversal constriction of lorica |
| st | end spine of toe | V | ventral |
| tb | toe base | Wa | wart |
| te | testis | | |

sexes and seven larval instars (Kristensen 1991a; Kristensen and Brooke 2002). Pliciloricidae are characterized by complex life cycles which is one of the most astonishing characteristics of the Loricifera in general (Kristensen and Brooke 2002; Gad 2002). These life cycles are sometimes so complicated (Kristensen and Brooke 2002) that hardly ever all stages of the life cycle of one species are found at one locality even in large samples. Apart from the larval stages, a juvenile or postlarval stage occurs in most of the known life cycles, but sometimes as first noticed for the genus *Rugiloricus* Higgins and Kristensen, 1986 (Higgins and Kristensen 1986; Kristensen and Brooke 2002; Gad 2004a) this postlarva is transformed to a dormant stage with unfinished adult morphology. Many Pliciloricidae seem to have the ability to reproduce with specialized paedogenetic larvae. Such larvae are known from the life cycle of *Rugiloricus*-species (Kristensen 2003; Gad 2004a) and also from inside a giant larva discovered in the Angola Basin (Gad 2005).

## Material and methods

The samples yielding the specimens for this study were taken with a multicorer at stations 325, 342, and 346 at 5389–5427 m depth during the DIVA I expedition no. 48/1 of RV "Meteor" to the Angola Basin (Southeast Atlantic) in 2000. Sampling of the 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 upper 5 cm of the samples were fixed together with the remaining 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 and centrifugating the sample at 4000 rpm. The loriciferans were sorted with the aid of an Irwin loop under a stereomicroscope (LEICA MZ8). The sorted specimens were placed in a 70% ethanol medium, later transferred to glycerol and mounted in glycerol–paraffin–beewax preparations, sealed with glyceel (adapted from Higgins and Thiel 1988).

The microscopic investigation was carried out with an LEICA interference-microscope (DMLB with UCA condensor, IC prism and doubler ×1,5 and ×2). Photographs were taken with the DMLB microscope and a computerized digital camera (ColourView system). Illustrations were made with the same microscope and with the aid of a drawing tube (mirror technique and macro-apparatus LEICA FS25PE). Species are differentiated morphologically. The terminology used in text and figures is adapted from Higgins and Kristensen (1986). 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
***Pliciloricus pedicularis* sp. n.**

## Material examined

All 16 examined specimens (representing most life history stages including seven Higgins-larvae, two

mature males, two mature females, one adults in metamorphosis, and four simplified adults in different phases of maturity; except for the holotypic male all adults are enclosed into the exuvium of the postlarva and of the seventh instar Higgins-larva) of the new species were mainly collected at both stations with the largest number of multicorer hauls: Station 346 (eight hauls) and 325 (seven hauls); an additional specimen was found at station 342 (two hauls). Station data: station 325 (19° 58.3′ S/002° 59.8′ E) 5448 m depth, July 14, 2000; station 342 (17° 07.9′ S/004° 42.0′ E) 5415 m depth, July 24, 2000; station 346 (16°17.0′ S/005°27.0′ E) 5388 m depth, July 27, 2000.

*Type material*: Holotypic mature male: 325/6 muc 12 (slide UNIOL 2003.007); paratype I: Higgins-larva (with extended introvert), 325/1 muc 6 (slide UNIOL 2003.008); paratype II: mature female, 325/6 muc 4 (slide UNIOL 2003.009), paratype III: adult in metamorphosis, 325/6 muc 6 (slide UNIOL 2003.010); paratype IV: mature simplified parthenogenetic adult with eggs, 346/2 muc 8 (slide UNIOL 2003.011), paratype V: mature simplified parthenogenetic adult with embryos and young larva, 325/3 muc 9 (slide UNIOL 2003.012), paratype VI: immature simplified parthenogenetic adult, 325/3 muc 9 (slide UNIOL 2003.013), paratypes VII: simplified parthenogenetic adult in phase of disintegration with many eggs released into exuvium of seventh instar Higgins-larva, 346/2 muc 9 (slides UNIOL 2003.014). Additional type material including paratype VIII: mature female, 346/2 muc 9; and paratype IX: mature male, 346/8 muc 4 (mounted on slides UNIOL 2003.015, UNIOL 2003.016); paratypes X and XI: two Higgins-larvae (with retracted introvert) from station 325/4 muc 1 and muc 10 (slides UNIOL 2003.017, UNIOL 2003.018); paratypes XII–XV: two Higgins-larvae (with retracted introverts) from station 325/5 muc 2, 325/3 muc 2 (slide UNIOL 2003.019, UNIOL 2003.020); and another two Higgins-larvae from station 342/2 muc 4, 342/1 muc 11 (slide UNIOL 2003.021, UNIOL 2003.022), respectively.

## Type locality

Deep sea of the Angola Basin (Atlantic) near 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 mud contents in surface layer reaching 90–99% and decreasing towards 12 cm sediment depth; total carbon contents between 8% and 8,7%; with high amounts of globularian foraminiferans; sediments well oxygenated down to a depth of 20 cm; 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 *pediculus* (slender, foot-like or stemlike part) and refers to the large pedicels of the posterolateral setae of the Higgins-larva.

## Measurements

Measurements of holotypic male and paratypic Higgins-larva are presented in Table 1.

## General remarks

No adult specimens of *P. pedicularis* sp. n. with an extended introvert were available for this study. This is a common sampling artefact observed in loriciferans from the Angola Basin or from other material of not yet analysed deep-sea expeditions. More than 70% of the collected adults and Higgins-larvae in the samples of the Angola Basin have the introvert retracted when fixed with formalin only and when not having been treated before with freshwater to cause an osmotic shock. Fig. 2 shows the habitus of the holotypic male with withdrawn introvert, as is typical for most adults of Pliciloricidae found. It is unfortunate that in Loricifera the most important features for separating species are generally found on the introvert in contrast to the related Kinorhyncha, which have the characteristic features on their body plates. Fortunately, most life history stages of the species described here show very characteristic features, which allow species identification even with withdrawn introvert. In the case of the adults these characteristic features are: ornamentation of lorica, structure of type B scalids in the fourth row, and trichoscalids with cross walls (Figs. 1A–C); and in the case of the Higgins-larva: long toes together with pedicels of $se_2$-setae (Figs. 3A and 4B).

Fortunately, the cuticle of most life history stages is so transparent that it can be seen which stage or instar moults into which next one so that reconstruction of the life cycle is possible. In the case of mature males or females also the tissue is transparent (or made more transparent by adding lactic acid), so that the structure and arrangement of the withdrawn scalids is not obfuscated.

**Table 1.** Measurements of holotypic male and paratypic Higgins-larva

| Male (holotype) | No. | Measure (μm) | Higgins-larva (paratype) | No. | Measure (μm) |
|---|---|---|---|---|---|
| *Length of* | | | *Length of* | | |
| Body | | — | Body | | 204 |
| Mouth cone (mc) | | 27 | Partly retracted mouth cone (mc) | | 35 |
| Introvert (in) | | — | Prepharyngeal armature (ia) | | 40 |
| Lorica (lo) | | 115 | Oral setae (ms) | | 20 |
| End cone (ec) | | 23 | Introvert (in) | | 45 |
| Primary double-organ ($do_1$) | | 98 | Lorica (lo) | | 105 |
| Secondary double-organ ($do_2$) | | 60 | Toes (to) | | 130 |
| Primary branch of type A and B | | 80 | Tubular part of toes (tu) | | 95 |
| Trichoscalid ($tr_1$) | | | End spine of toes (st) | | 35 |
| Secondary branch of type B | | 75 | Anterolateral seta ($Is_1$) | | 24 |
| Trichoscalid ($tr_2$) | | | Anteroventral seta ($Is_2$) | | 24 |
| Clavoscalids of first row ($cr_1$) | 8 | 125 | Posterodorsal seta ($se_1$) | | 40 |
| Spinoscalids of second row ($sr_2$) | 9 | 110 | Posterolateral seta ($se_2$) | | 30 |
| Spinoscalids of third row ($sr_3$) | 15 | 100 | Posteroterminal seta ($se_3$) | | 26 |
| Type A scalids of fourth row ($sr_4$a) | 15 | 95 | Clavoscalids of first row ($cr_1$) | 8 | 48 |
| Type B scalids of fourth row ($sr_4$b) | 15 | 50 | Spinoscalids of second row ($sr_2$) | 10 | 45 |
| Spinoscalids of fifth row ($sr_5$) | 30 | 100 | Spinoscalids of third row ($sr_3$) | 15 | 40 |
| Spinoscalids of sixth row ($sr_6$) | 30 | 108 | Spinoscalids of fourth row ($sr_4$) | 14 | 28 |
| Spinoscalids of seventh row ($sr_7$) | 30 | 112 | Type B scalids of fifth row ($sr_5$ b) | 7 | 15 |
| Spinoscalids of eighth row ($sr_8$) | 30 | 118 | Type A scalids of fifth row ($sr_5$ a) | 8 | 10 |
| Spinoscalids of ninth row ($sr_9$) | 30 | 8 | Type B scalids of sixth row ($sr_6$ b) | 7 | 6 |
| | | | Type A scalids of sixth row ($sr_6$ a) | 8 | 8 |
| Diameter of lorica: | | 73 | Diameter of lorica: | | 80 |

## Description of morphology of holotypic male

*Body* divided into mouth cone, introvert, neck, thorax, and loricate abdomen. Anterior body regions retracted into lorica, length of lorica 109 μm, width of lorica 73 μm (Fig. 1).

*Mouth cone* (mc, Fig. 1A) divided into three sections. First section ($mcs_1$) long, conical, and pointed; mouth opening (mo) located terminally; cuticle equipped with only eight primary oral ridges (or). Second section ($mcs_2$) being broadest part of mouth cone, consisting of flexible cuticle, which is divided into eight plates folded transversally together, and surrounding the base of the first section frill-like as a hyaline outer layer; first section slightly retracted into second one. Third section ($mcs_3$) narrowing posteriorly and forming a stalk (sk, Figs. 2 and 8F); stalk basally surrounded by a ruff (ru). Ruff, a ring-like structure composed of numerous well-developed cuticular fibres.

*Introvert* (in, Fig. 1A) retracted, with nine rows of scalids.

*First row* ($cr_1$) with eight long clavoscalids (Figs. 1A and 8B), which consist of narrow, stalk-like bases, and broad, flattened elements. Elements with reinforced dorsal margins, distally with many strong transversal cross walls (cw), elements ending bluntly, and with asymmetrical tips.

*Second row* ($sr_2$) with nine spinoscalids; seven free spinoscalids strong, composed of four segments; First segment broad and visibly enlarged, basally with narrow separate base, equipped with two dorsal thorns and lateral fringes of small spinules, tapering distally and ending in a swollen hinge joint; next three segments filiform, last segment ending in a pointed tip. Pair of ventral spinoscalids shorter and strongly sclerotized; forming primary double-organ of the *P. enigmaticus*-type. Double-organ ($do_1$, Fig. 1A) consisting of two branches, each branch being subdivided into an inner and an outer ramus. Basal parts of inner rami enlarged and fused; with transversal dorsal fringe of spinules; distal parts of inner rami free, long, rigid, and unsegmented; equipped over their entire length with ventral row of minute, stiff spinulae. Outer rami spinose, short, with a length of 35% of that of the inner rami, fused with them longitudinally.

*Third row* ($sr_3$) with 15 smaller, and filiform spinoscalids consisting of five segments; first segment broad, with round diameter and double base; second segment distally with swollen joint bearing two minute lateral spines; distal two segments bristle-like, last segment with spinose end; midventral pair of these spinoscalids below primary double-organ of second row modified as short secondary double-organ ($do_2$, Fig. 1A); both spinoscalids, united to double-organ, not fused, but standing

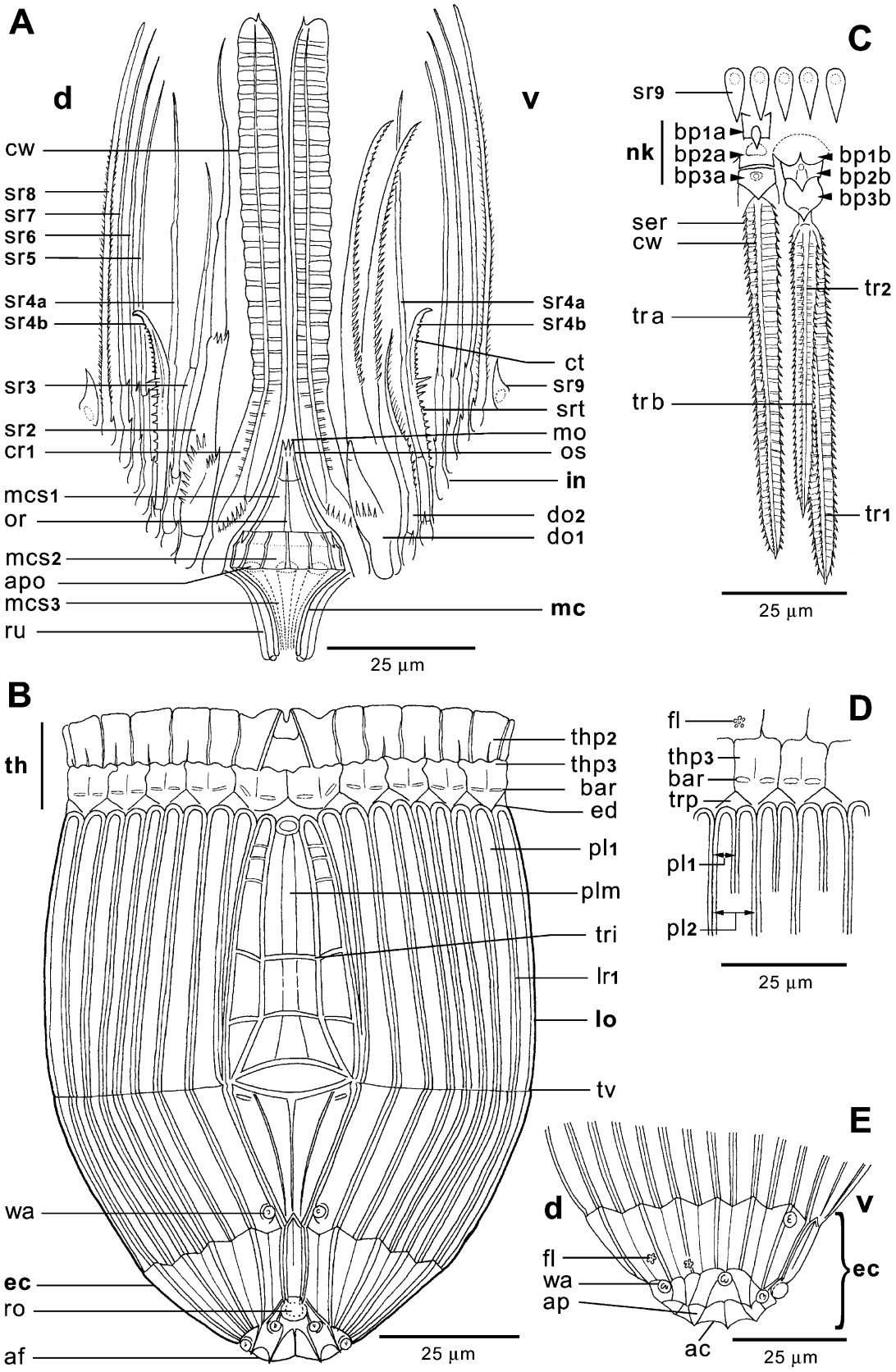



**Fig. 1.** *P. pedicularis* sp. n., holotypic adult, external features: (**A**) retracted introvert with details of scalid structure and mouth cone; (**B**) lorica, ventral view; (**C**) details of trichoscalids and associated basal plates; (**D**) details of anterior edge of lorica, ventral view; (**E**) end cone, lateral view.

close together, indistinctly segmented, and covered with fine long spinules.

*Fourth row* with 30 spinoscalids representing two different types in alternating arrangement. Type A ($sr_4a$) scalids long, filiform, consisting of four segments; first segment short and slightly swollen, second and third segments narrow, last segment seta-like. Type B ($sr_4$ b) scalids short, strongly sclerotized, consisting of two segments; first segment short, swollen; second segment long, basal part narrow with ventral row of minute denticles (srt), distal part enlarged, claw-like (ct); distal part starting with three larger ventral teeth, and continuing with fine ventral double serration; spinoscalid ending in hook-like tip.

*Fifth row* ($sr_5$) with 30 uniform spinoscalids of hair-like appearance, consisting of three filiform segments, first two segments short, third segment long and bristle-like.

*Sixth row* ($sr_6$) with 30 uniform spinoscalids, similar to spinoscalids of fifth row.

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

*Eighth row* ($sr_8$) with 30 uniform spinoscalids of more hair-like appearance, with slightly serrate or feathery margins.

All spinoscalids from the fifth row onwards insert on small arched basal plates (sbp, Fig. 2).

*Ninth row* ($sr_9$) with 30 uniform thorn-like scalids.

*Neck* (nk, Fig. 1C) covered with three rows of basal plates, and eight single type A (tr a) and seven double type B (tr b) trichoscalids. Row of basal plates standing closely together (Figs. 1C, 8C and D). Well-defined basal plates of the first row representing two types; eight small rectangular type A basal plates ($bp_1a$) alternating with seven larger type B basal plates ($bp_1b$). Type A basal plates with posteriorly directed spine lie above, type B basal plates elevated roof-like and rounded. Eight type A basal plates ($bp_2a$) of second row less developed, small, rectangular with round depression, alternating with seven larger type B basal plates ($bp_2b$), trapezoidal in shape and with posterior thorn. Basal plates of third row carrying a trichoscalid each, eight angular type A basal plates ($bp_3a$) with a round depression alternating with seven round type B basal plates ($bp_3b$). Round type B basal plates equipped with seven double trichoscalids with a common base; angular type A basal plates carrying eight single trichoscalids. Midventrally two single trichoscalids standing close together; middorsally one double trichoscalid.

*Trichoscalids* (Figs. 1C and 8D) long, broad, and basally with well-developed cross walls (cw) which become finer (hardly visible). Cross walls are supporting structures, giving trichoscalids rigidity. Trichoscalids with two undulated lateral margins with fine serration (ser), third margin also serrated, perpendicular to lateral ones. Channel running inside trichoscalids along median axis. All trichoscalids ending in simple but pronounced pointed tips. Double type B trichoscalids consisting of two rami originating from one common basal shaft. Upper or secondary ramus of double trichoscalids ($tr_2$) shorter than lower or primary one ($tr_1$), but identical with it in structure (Fig. 1C).

*Thorax* (th, Figs. 1B, D and 8E) flexible, with thin cuticle consisting of three transversal rows of plates ($thp_{1-3}$) divided by longitudinal and transversal ridges; last two rows not retracted into lorica; each plate of third row corresponding to two primary plicae of lorica, and equipped with a pair of small transversal bars (bar) in their centre and with triangular plates or fields (trp) posteriorly. A few flosculi (fl) scattered on the thoracic plates. Edge (ed, Fig. 1B) separating thorax and lorica well marked.

*Lorica* (lo, Figs. 1B and 8E) consisting of thick cuticle divided longitudinally into 44 identical narrow primary plicae ($pl_1$). Two plicae ($pl_2$) together forming 24 secondary units as indicated anteriorly by corresponding triangular fields and posteriorly by continuation into end cone; each primary plica framed by a strongly developed primary ridge (lr), adjacent plicae therefore separated by double ridges. No secondary ridges. Midventral transformed plicae (plm) broad: four primary plicae fused longitudinally, two of them totally along midventral axis (no easily detectable indications of fusion left), forming round ornament at their anterior end; next two plicae laterally partly fused, anteriorly equipped with three transversal ridges. Midventral unit of plicae with four strong transversal ridges (tri), restricted to this part of lorica only; pair of cuticular bars located directly behind last transversal ridge, additional secondary longitudinal ridges present but weakly developed; midventral plicae posteriorly flanked by a pair of small warts (wa). Lorica divided halfway into two halves by a transversal constriction (tv). Last part of lorica separated as end cone from remaining lorica by zigzag border.

*End cone* (ec, Figs. 1B and E) forming anal field at caudal end. Every second double ridge of plicae continuing as primary ridge (11 altogether) into end cone, other double ridges ending at zigzag border and continuing as simple folds; two pairs of flosculi (fl) located on both lateral sides of end cone (Fig. 1E). Midventral plicae of end cone region not modified and narrow, ending with a round structure (ro). Anal field (af) composed of many small anal plates (ap) surrounding terminal anal cone (ac) bearing anus; anal field equipped with six additional pairs of warts (wa).

## Description of anatomy of holotypic male

Adult Pliciloricidae show a typical habitus when the introvert is retracted, as can be seen in the holotypic

male of *P. pedicularis* sp. n. (Fig. 2). The scalids of the adults are too long to be retracted completely inside the lorica. This means that in contrast to the Higgins-larvae adults are always in contact with the surrounding medium via their scalids. In this position, the flexible thoracic region is folded and retracted. A large ring muscle ($rim_1$) closely behind the trichoscalids probably functions as a sphincter or closing apparatus to hold the retracted introvert in position. Another large ring muscle ($rim_2$) is located on the level of the end cone and surrounding the end of the hindgut. Outer trunk muscles directly under the epidermis appear as an outer layer of separated bundles of transversal muscles (tm) and as an inner loose grid of longitudinal muscles (lm). The bundles of transversal muscles attach to the cuticle via the epidermis only at the tip of the inward folds of the plicae. The longitudinal muscles are restricted to the anterior half of the trunk. They run from the third row of thoracic plates to the transversal constriction in the middle of the lorica. Each scalid row on the introvert has its own well-developed ring muscle in the introvert region. The scalids have separate diagonal retractors ($re_1$), which are attached to the posterior end of the thorax. A pair of large main retractors of the introvert ($re_2$) is located dorsally, these muscles run from the brain region to the caudal end. Neighbouring retractors of the introvert ($re_3$) are smaller and connected with the posterior ends of the cuticular ruff fibres (ru). The basal plates of the fourth to eighth row of spinoscalids ($sbp_{4–8}$) form a clearly visible inner cylinder supporting the cavity for the withdrawn scalids. They seem to be responsible for the high order in which the scalids are folded together.

The digestive system begins with the mouth cone (mc, Fig. 8F) which contains the small and round pharyngeal bulb, followed by the oesophagus (oe) occupying the stalk of the mouth cone, continuing as a short and sack-like midgut (gu) with large absorptive cells, and ending with a hindgut and a cloaca (clo) which opens dorsocaudally via the rectrum (rec). Ducts of protonephridia and testes seem to end together in the cloaca.

The opening of the mouth is surrounded by 4 min oral stylets (os, Figs. 1A and 2). Internally a narrow buccal channel runs through the first section of the mouth cone. Its smooth cuticle forms a straight buccal tube (bu). The buccal channel is supported by three small symmetrical prepharyngeal elements forming a weakly developed prepharyngeal armature (ia) which is basally also connected with the cuticular wall of the first section and the pharyngeal bulb. In front of these elements there are small clusters of buccal glands (bug).

The second section of the mouth cone contains the small and round pharyngeal bulb (pb), which has three transversal layers of radial muscles (ram). Where the radial muscles have contact with the buccal tube there are three transversal rows of small placoids ($p_1$–$p_3$). Each row consists of three placoids (see also Fig. 8D).

The apodemes (apo) of the mouth cone retractors are connected with the wall of the second section of the mouth cone. The eight mouth cone retractors (mcr) run through the stalk (sk) of the mouth cone and through the brain (br).

The thorax contains a series of neck glands (ng), which open into the basal plates above the trichoscalids ($bp_2b$, $bp_3a$) via pores. A cluster of caudal glands (cgl) is located near the caudal end. The large pair of testes (te) occupies the lateral sides of the lorica and indicates the sex. The testes are densely packed with fibroid spermatozoa. The terminal cells and ducts of the protonephridia are embedded in the testis.

## Description of female

Two females less preserved than the holotypic male have been found; in both, introverts are also retracted. Both females are still enclosed into two exuvia, one being the remnant of the postlarva, the other of the seventh instar Higgins-larva. Females seem to have the same morphology and size as males, without external sexual dimorphism. A large and single ovary occupies one side of the lorica. After metamorphosis of the female the ovary contains one large egg and a few small follicles (Fig. 3).

## Description of postlarva

*Postlarva* (*Pla*, Figs. 5C, 6A, 7A, B and 9A) has moulted to adult so that only its exuvium remains. This exuvium consists of a thin cuticle without ornamentation. Six papilla-like elements (pa) mark the oral end (Fig. 7B). Mouth cone, introvert with scalids or other appendages lacking. This postlarval exuvium often disappears when the adults become mature.

## Description of morphology of Higgins-larva

Paratypic Higgins-larva of unknown instar (judging from its size it could be the fifth one).

*Body* (Fig. 4A) divided into mouth cone, introvert, neck, collar, thorax, and loricate abdomen. Body extended, length 270 μm (from tip of mouth cone to caudal end); maximal body width (in middle of lorica) 80 μm.

*Mouth cone* (mc, Fig. 4A) divided into three sections. First section ($mcs_1$) slightly retracted and strengthened by eight cuticular bars; mouth opening (mo, Fig. 4C) terminally, surrounded by two circles of external armature: Outer circle with six small oral teeth (ot), inner circle with six large valve-like oral stylets (os) which close the mouth. Second ($mcs_2$) and third sections ($mcs_3$) forming a cylindrical unit, divided by a transversal constriction and with eight longitudinal oral striae

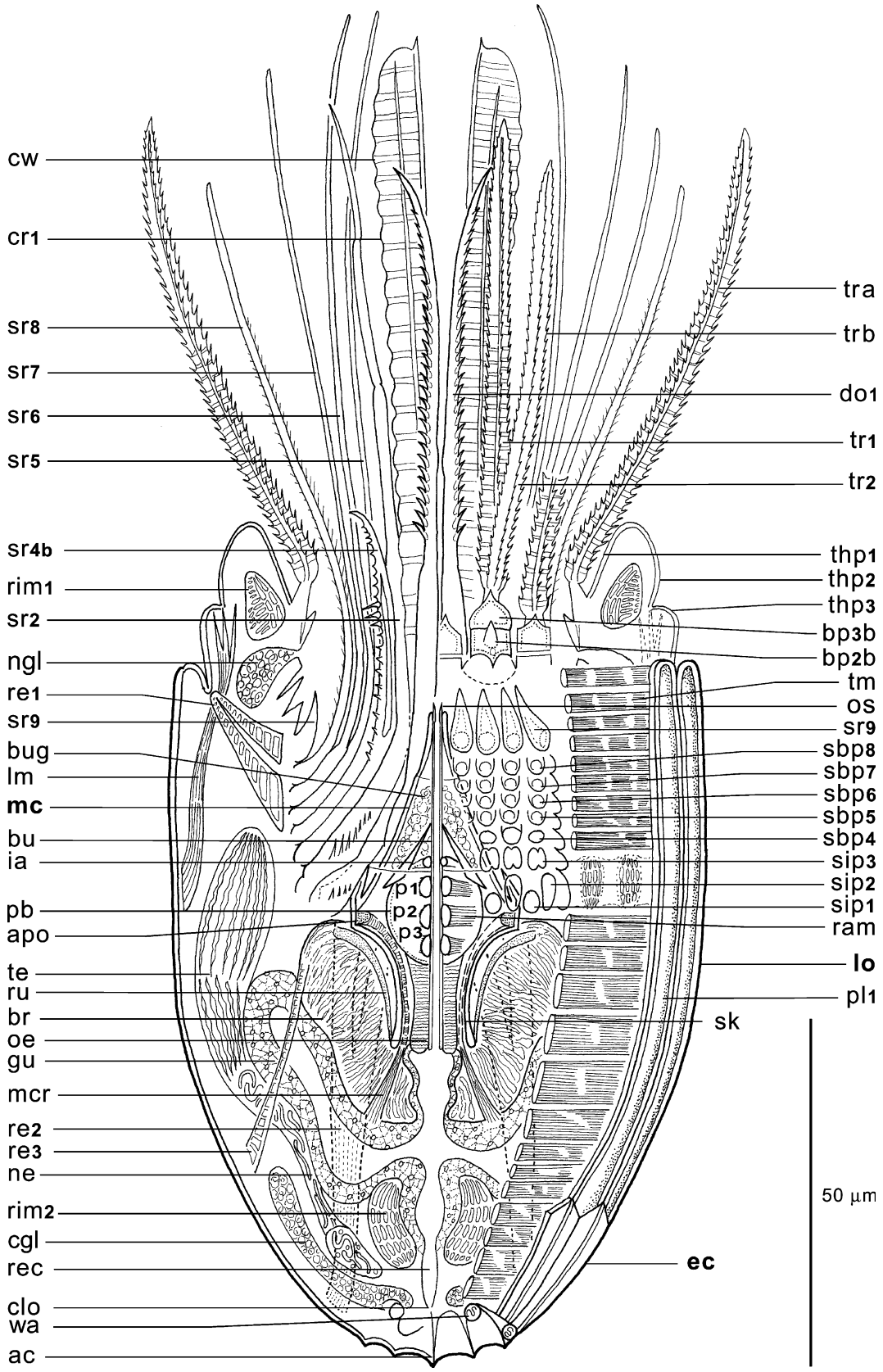



**Fig. 2.** *P. pedicularis* sp. n., anatomy of holotypic male; with details in three different optic layers.

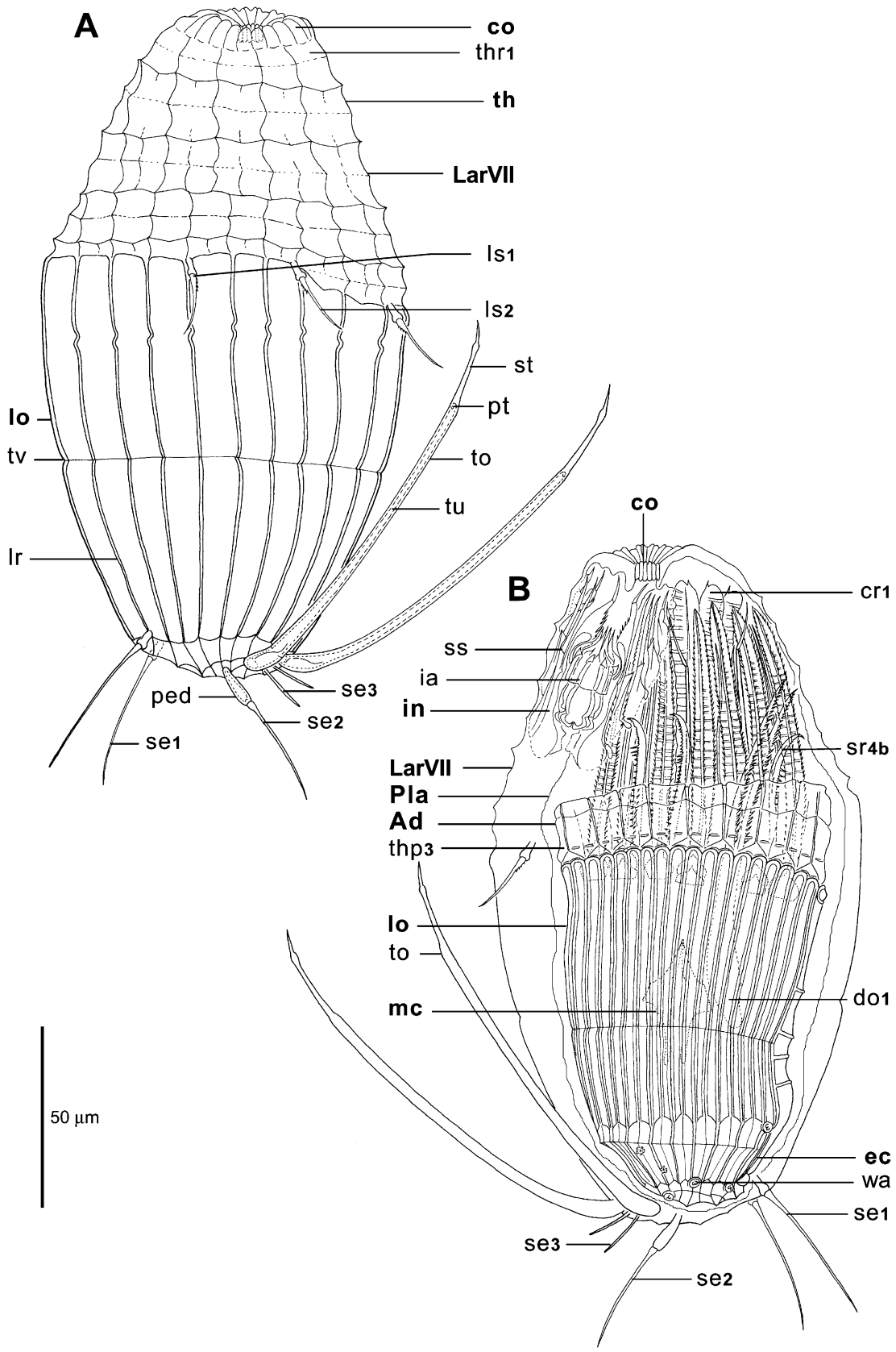



**Fig. 3.** *P. pedicularis* sp. n., paratype II: (**A**) exuvium of seventh instar Higgins-larva with closed collar (external view); (**B**) same exuvium containing retracted introvert and mature adult female into postlarval exuvium (Both in lateral views).

(ost, Fig. 4A) reaching down to base of mouth cone. Midventral oral seta (ms) marking transition from second to third section. Buccal channel (bc) smooth, without anterior buccal tube, armed with prepharyngeal armature (ia, Fig. 4C, see section anatomy) supporting buccal channel over its entire length. Six oral stylets together with posterior part of internal armature slightly extended through mouth opening in paratypic Higgins-larva.

*Introvert* (in, Figs. 4A, B) spherical, united with neck region, densely covered with four scalid rows.

*First row* ($cr_1$) with eight spinose clavoscalids, consisting of enlarged bases and four segments; first ($sg_1$) and second ($sg_2$) segments large and flat, both with dorsal, pectinated row of spinules (srs); third segment ($sg_3$) narrow, and smooth; fourth segment ($sg_4$) spinose, with sharply pointed tip.

*Second row* ($sr_2$) with 10 strong spinoscalids of same length as clavoscalids consisting of two segments; first segment arising with broad base from introvert, tapering distally, lateral surfaces with lateral weal (lw); second segment spine-like, as long as first one, with ventral saw-like serration (ser) and claw-tip.

*Third row* ($sr_3$) with 15 strong spinoscalids of same structure as scalids of second row, and reaching 80% of their length.

*Fourth row* ($sr_4$) with 14 strong spinoscalids of same structure as scalids of second row, and reaching 60% of their length.

*Neck* (nk, Figs. 4A and B) not distinct from introvert, and carrying fifth and sixth rows of scalids.

*Fifth row* with 15 modified scalids of two different types arranged in two subcircles. Upper subcircle with seven larger type B scalids ($sr_5b$), consisting of double leaf-like basal plate and two segments, first segment covered elytra-like by protruding plates; first segment short and swollen, second segment rigid and spine-like. Lower subcircle with eight type A scalids ($sr_5a$), consisting of protruding double leaf-like plates only, each part with reinforced inner margin.

*Sixth row* with 15 protoscalids of two different types arranged in two subcircles. Seven double plates ($sr_6b$) forming upper subcircle and alternating with eight single spines ($sr_6a$) with slightly bulbous bases of the lower subcircle; ventral spines being double.

*Collar* (co, Fig. 4A) well-developed intermediate region between introvert and thorax. Cuticle of collar with many longitudinal folds and subdivided by transversal constriction; with seven pores or flosculi (not easily seen), collar with distinct borders anteriorly and posteriorly.

*Thorax* (th, Fig. 4A) a long, flexible, strongly retractable, accordion-like body region; divided into transverse rows of thoracic plates ($thr_{1–6}$), each row containing 16–26 plates, all plates can be folded transversally once, thorax ventrally with six and dorsally with five rows of thoracic plates. Transition zone between thorax and lorica with two pairs of short anterior setae; anterolateral ($ls_1$) and anteroventral setae ($ls_2$) having same structure: filiform, with strong basal part; arising from small protrusions, called pedicels (ped).

*Lorica* (lo, Fig. 4A) less armoured, with 22 deep longitudinal folds (lr); surface of cuticle with slightly papillate ultrasculpture. Ventrally, lorica half-way divided into two parts by transversal constriction (tv). Toes (to, Fig. 4A) very long, consisting of long hollow tubes (tu) proximally and solid end spines (st) distally; extending pairwise from caudal end and articulating with ball-and-socket joints on modestly developed basal plates (bt); toe bases (tb) slightly enlarged; tubular parts opening with single pore (pt) distally; solid spines with small bulge terminally. Other caudal appendages of lorica including three pairs of posterior setae. Posterodorsal setae ($se_1$) long, fine, with small pedicels, located dorsally at end of lorica; posterolateral setae ($se_2$) long, robust, and arising with enlarged bases from large pedicels (ped, 12 μm), posteroterminal setae ($se_3$) long, extremely robust, bristle-like, standing close together between toes. Ventrocaudal part of lorica triangular, shield-like, posteriorly with pair of flosculi (fl) of minute size; caudal end composed of numerous small anal plates forming anal field. Anal cone (ac) situated terminally with elevated lateral margins and central anus (an), adjacent plates of anal field dorsocaudally large with three flosculi composed of five papillae.

## Description of anatomy of Higgins-larva

Prepharyngeal armature (ia, Fig. 4C) surrounding weakly sclerotized buccal channel (bc) consists of six longitudinal bracelets arranged in two stories, an anterior and a posterior one. Anteriorly, the bracelets stand in pairs ($bra_1$), their bases being connected by anterior cuticular bridges ($bg_1$), their other ends bifurcating to make contact with different oral teeth. The bracelet pairs are covered by six hyaline anterior plates (apl) forming an outer cylinder and being connected with them via apodemes. Posteriorly, the bracelets ($bra_2$) continue as single, flexible, elements, which are connected with each other also by posterior cuticular bridges ($bg_2$). The single bracelets become broader posteriorly and converge towards the buccal channel, their ends being fused with the pharyngeal crown. The pharyngeal bulb (pb) is large, round, and slightly cylindrical. The anterior part of the bulb is sclerotized and called pharyngeal crown (pc). The parts of the crown have small apodemes functioning as attachment for longitudinal pharyngeal muscles. The bulb muscles are in longitudinal section arranged

in five layers of three radial muscles (ram) each in cross-section. Around the buccal channel there are five rows of placoids ($p_{1-5}$) each row containing three placoids, which form the sclerotized part of the inner pharyngeal walls. As a consequence, the lumen of the bulb is triangular in cross-section. The connection of the placoids with the inner cuticular layer of the pharyngeal bulb persists, even when bulb tissue disintegrates in larval exuvium (Fig. 8D).

The brain is a large round mass. The body muscles are visible under the cuticle as a grid of longitudinal and transversal bundles. Transversal muscles are well-developed in the abdominal region, and attached via the epidermis only to the tips of the inward folds of the 22 longitudinal plicae of the lorica. Many small pores, in a pattern that is not clearly distinguishable, perforate the trunk cuticle. Each pore belongs to a small subcuticular gland.

The trunk of the Higgins-larva contains a granular tissue. The gut is straight and densely filled with fine granules and storage cells. Two large caudal glands, which are connected with the toes, are located ventrally at the caudal end of the lorica (Fig. 4).

## Description of morphology of simplified adult ( = parthenogenetic stage)

Transformed, not free-living instar with sack-like trunk, lacking any buccal structures and introvert (see section "discussion"). Parthenogenetic, simplified adult generally enclosed by exuvium of postlarval stage and additionally by exuvium of last or seventh instar Higgins-larva. This instar generally with retracted introvert, thorax closed by the folding collar of spook-wheel-like appearance, and thus forming shelter for released eggs and developing embryos.

*Body* (Figs. 5B, C and 9C) with thin, weakly developed cuticle, surface partly and loosely covered with minute spinulae.

Introvert reduced; all scalids, clavoscalids and spinoscalids normally belonging to an introvert are lacking.

*Neck* (nk, Figs. 5A and B) barely distinct from the trunk by zone of wrinkled and spiny cuticle, bearing two transversal rows of basal plates transformed anteriorly into hooks and scalids, posteriorly into spiny pads (Figs. 5A and B; see section "Discussion").

First (anterior most) row with eight type A basal plates ($bp_1a$) transformed into eight large and strong hooks (ho) standing close together.

Second row of visible elements close beneath first row, with seven type B basal plates ($bp_1b$) transformed into seven scalids (sc) consisting of conical base covered with a few spinules and with long spine arising distally from conical base.

Third row consisting of eight small type A basal plates ($bp_2a$) transformed into eight spiny pads (pd) accompanying posteriorly eight large hooks of first row.

Fourth row with type B basal plates ($bp_2b$) also transformed into seven spiny pads (pd), three of them being less defined than the remaining four. Pads of fourth row accompanying posteriorly seven scalids of second row.

*Thorax* and *abdomen* united to form simple sack-like trunk (trk, Fig. 5B). Cuticle anteriorly with weakly developed plates. Caudal end with gonopore (por) located terminally or slightly ventrally (Fig. 6A) and surrounded by muscle bands (a sphincter?) for release of eggs. (In Figs. 5B and C gonopore displaced slightly to lateral side, presumably an artefact of fixation).

## Description of anatomy of simplified adult ( = parthenogenetic stage)

Musculature of trunk not fully developed, consisting of 12 longitudinal (lm) and four transversal bundles (tm). Anterior neck internally with clusters of round structures arranged in two circles, an outer and an inner one. Round structures of outer circle beneath $bp_1b$ and $bp_2a$ (Fig. 5B) containing dense tissue assumed to be neck glands (ng). Round structures of inner circle with less dense tissue and of unknown origin. Otherwise only mature ovary (ov, Fig. 6A) to be seen. When immature, body of simplified adult (Fig. 7A) filled with yellowish storage cells, when mature (Fig. 6A), with oocytes (oc) or a single large egg (eg). In phase of disintegration tissue of simplified adult completely transformed into eggs (Figs. 5–7).

## Moulting, metamorphosis, maturing, embryology, and development

Bisexual adults (Fig. 7B) in an early stage of metamorphosis are easy to distinguish from the simplified adult (Fig. 7A) and all adults are also easy to distinguish from Higgins-larvae in moult. In contrast to the moulting Higgins-larvae, which are only surrounded by the exuvium of the preceding instar Higgins-larva adults (males, females, and simplified ones) generally are found to be enclosed, not only into the exuvium of the seventh instar Higgins-larva (Lar VII), but also into the postlarval exuvium from which they have moulted (Figs. 3B, 7A and B). When moulting a Higgins-larva shows from the beginning a well-developed cuticle with all body appendages like scalids, setae and especially toes. The whole body is filled with coarse granules or cells. A central body with fine granules as found in adults during metamorphosis is lacking in moulting Higgins-larvae.

Adults becoming males or females have a stout pear-shaped appearance during the early phase of metamor-

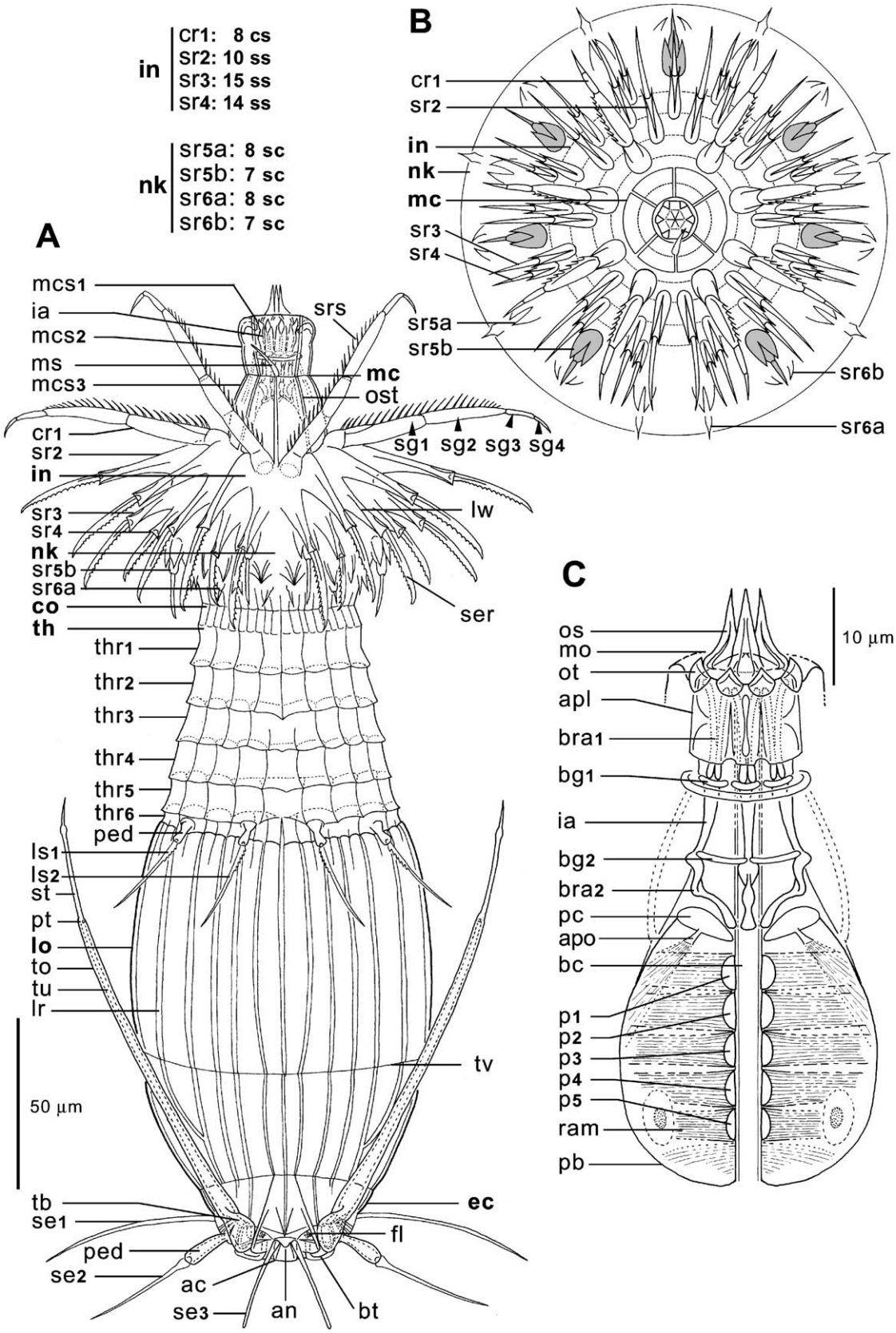



**Fig. 4.** *P. pedicularis* sp. n., paratype I, Higgins-larva with fully extended introvert: (**A**) habitus, ventral view; (**B**) half-schematic frontal view of larval introvert and neck to demonstrate scalid arrangement, (**C**) buccal channel with surrounding prepharyngeal armature and pharyngeal bulb, ventral view.

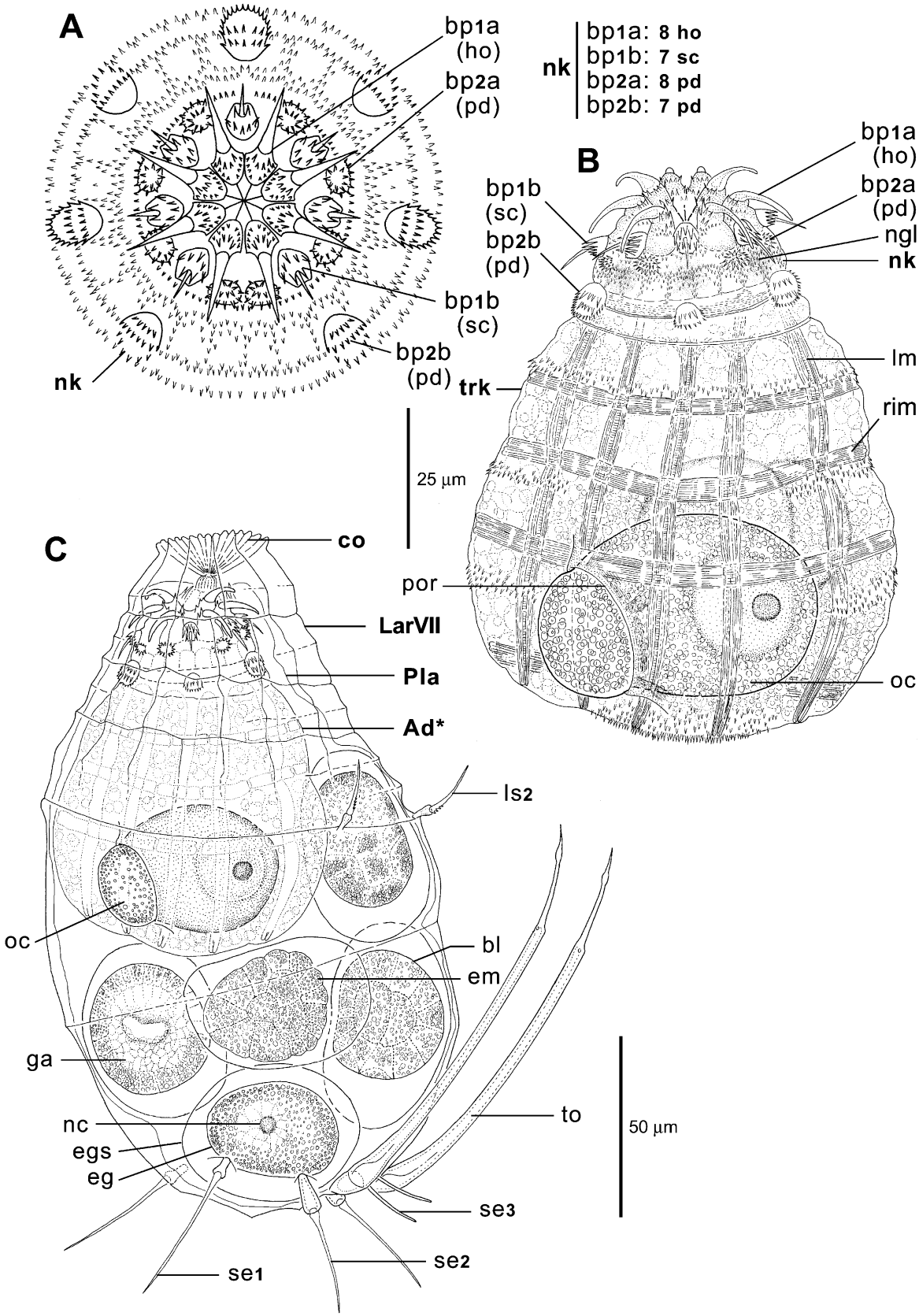



**Fig. 5.** *P. pedicularis* sp. n., paratype IV, simplified parthenogenetic adult being in late phase of maturity: (**A**) half-schematic frontal view of the neck to demonstrate scalid arrangement; (**B**) habitus of simplified parthenogenetic adult (same stage as in Fig. 5C and in different position in Fig. 9C), ventrolateral view; (**C**) and enclosed together with eggs inside exuvia of seventh instar Higgins-larva and of postlarva (retracted introvert and prepharyngeal armature of Higgins-larva covered by simplified adult).

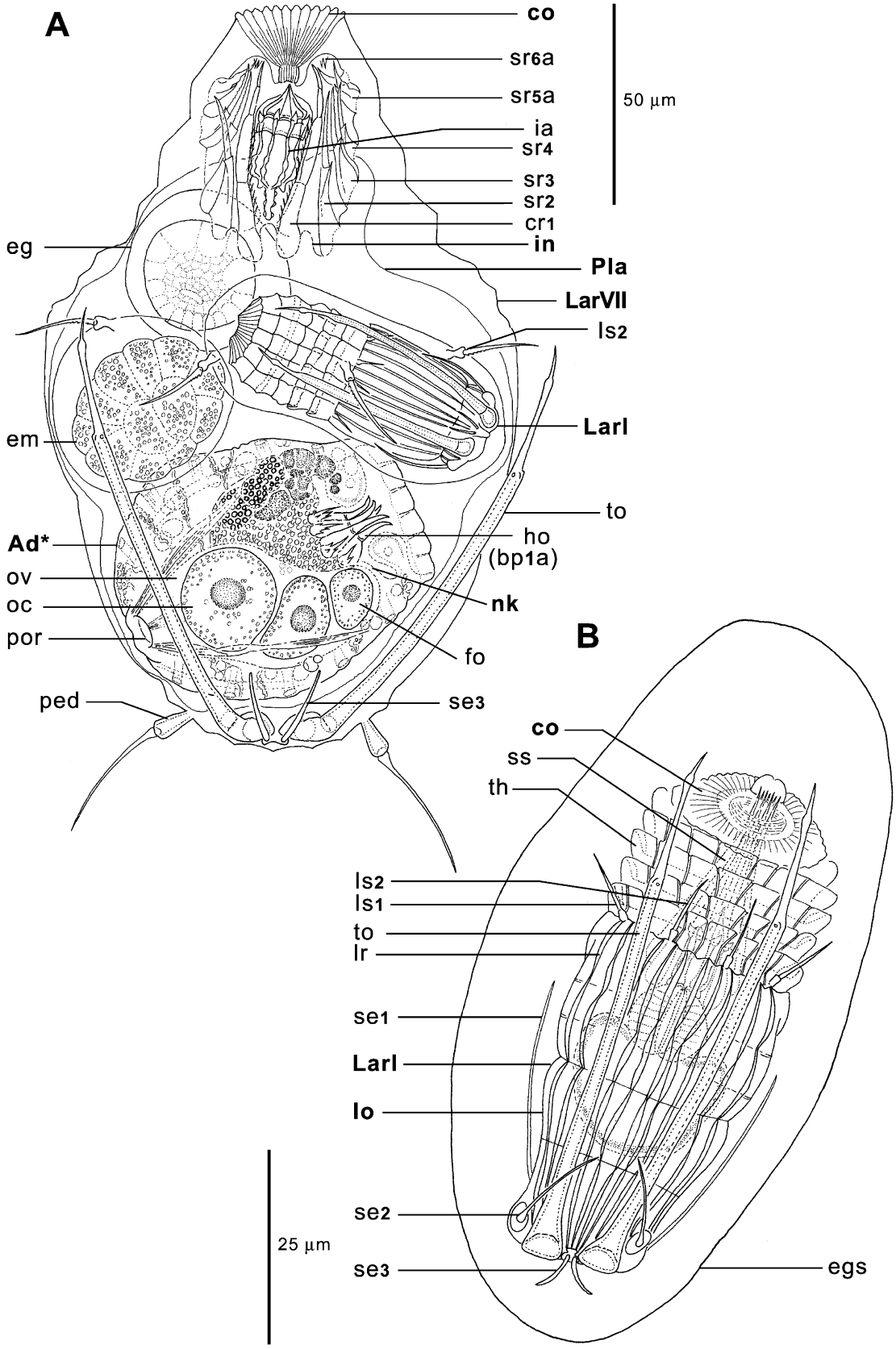



**Fig. 6.** *P. pedicularis* sp. n., paratype V (same specimen as in Fig. 9A): (**A**) simplified parthenogenetic adult in late stage of maturity enclosed together with egg, embryo and first instar larva inside exuvia of seventh instar Higgins-larva and of postlarva, ventral view; (**B**) first instar larva inside egg (same larva (Lar I) as in Fig. 6A), ventral view.

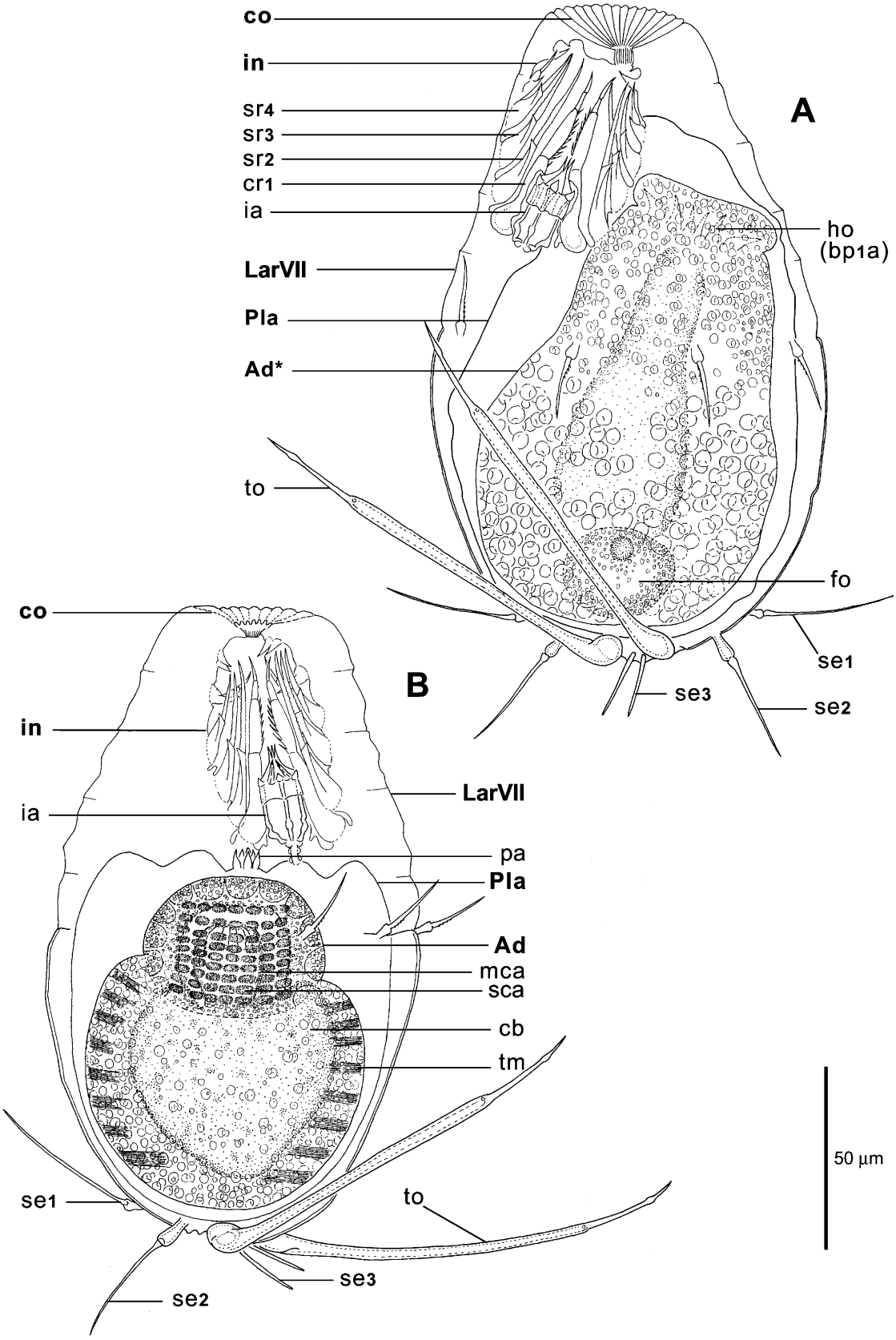



**Fig. 7.** *P. pedicularis* sp. n.:(**A**) paratype VI, immature simplified parthenogenetic adult in early stage of metamorphosis, ventrolateral view; (**B**) paratype III, bisexual adult in early stage of metamorphosis (becoming male or female), lateral view; both types of adults enclosed into exuvia of postlarva and of seventh instar Higgins-larva.

phosis (Fig. 7B). The anterior part of the trunk is more or less distinct from the remaining body and more transparent compared with that of the simplified adult in the early phase of metamorphosis (Fig. 7A). This allows to see the scalid anlagen (sca), which are strictly arranged in circles and surround a hollow cavity into which the conical mouth cone protoformation (mca) is projected (Fig. 7B). The posterior part of the trunk is round and filled with a dense central body (cb). Sometimes bundles of transversal muscles (tm) are visible in this phase of metamorphosis. After metamorphosis the anterior part with the mouth cone and introvert is located deeply inside the trunk and the characteristic shape of the loricate abdomen has developed (Fig. 8G). The transversal muscles (tm) form a thick layer beneath epidermis and cuticle.

The immature simplified adult looks a little bit like a Higgins-larva in moult, but instead of a strong cuticle and early forming toes, a soft cuticle appears and the trunk is filled with fine granules only. In the beginning, when the simplified adult is immature (Fig. 7A) the body is large ($120 \times 90\,\mu m$), sack-like and occupies almost the whole space inside the exuvium of the seventh instar Higgins-larva. The follicle of the developing ovary emerges at the caudal end and is embedded in a central cylinder consisting of dense yellowish tissue. This high density of the central cylinder in the posterior half is more pronounced in the simplified adult than in bisexual adults and the tissue does not disintegrate before the ovary is fully developed. The hook-like basal plates (see section "Discussion") of the neck region are retracted during this phase and cannot easily be traced in the dense tissue surrounding them. They become more and more visible in the course of maturity especially when they are finally protruded (Fig. 9C).

Mature simplified adults show four clearly detectable organs (Fig. 5B): (1) rows of hooks, of scalids, and of spiny pads with an own ring of muscles, (2) clusters of internal neck glands beneath the scalids together with additional inner loops of uncertain origin, (3) a loose grid of trunk musculature consisting of a few longitudinal and transversal muscle bands to expel the eggs through a terminal or ventral gonopore, (4) a large reproductive system occupying the whole trunk.

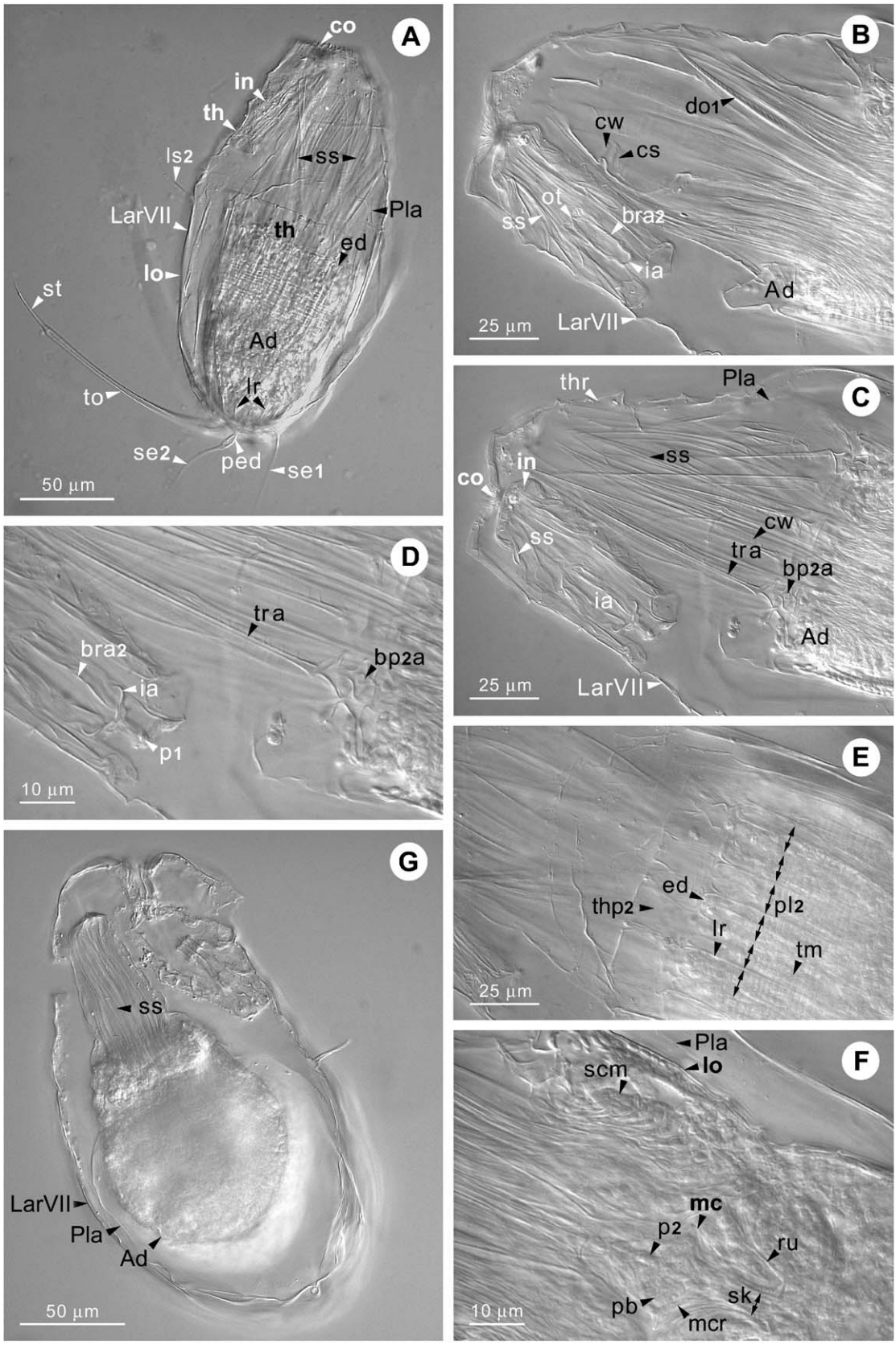
The reproductive system of the simplified adult consists of a single enlarged, clumpy ovary with a short zone with oogonia. The ovary contains a series of two or three clearly visible follicles and one large oocyte (Fig. 10D). The oviduct is a simple duct opening through a single terminal or ventral gonopore. The body of the simplified adult shrinks with every expelled egg and finally measures $70 \times 60\,\mu m$ only (Figs. 6A and 9A). This leaves enough space for the eggs in the extended exuvium of the seventh instar Higgins-larva to undergo embryological development. With depletion of the yolk reserves in the ovary the simplified adult becomes more and more transparent and the few remaining follicles and oocytes gain in visibility. After formation of the last egg the tissue of the ovary disintegrates leaving behind not much more than an empty cuticle.

To sum up the maturation process of the simplified parthenogenetic adult passes through four phases, which can be distinguished from one another:

(1) *Immature phase*: body densely filled with granules, apart from some follicles no other internal organs visible, no eggs in the exuvium of seventh instar Higgins-larva (Fig. 7A).
(2) *Phase of early maturity*: body densely filled with granules; ovary, hooks, and bundles of muscles visible; first eggs in the exuvium of seventh instar Higgins-larva.
(3) *Phase of late maturity*: body becoming transparent; internal structures like ovary clearly visible, exuvium of seventh instar Higgins-larva filled with eggs, embryos, and young larvae (Fig. 6A).
(4) *Phase of disintegration*: after all eggs have been shed body and tissue totally disintegrate leaving behind only a "rest body"; exuvium of seventh instar Higgins-larva contains eggs, embryos, and young larvae only (Fig. 9F).

The round eggs (eg) produced parthenogenetically by the simplified adult are large (Figs. 5C, 6A, 9A, F and G). They have a diameter of $40\,\mu m$. Fertilized eggs inside of mature females reach a diameter of just $28\,\mu m$ in all females of *P. pedicularis* sp. n. found and in all other studied females of *Pliciloricus*-species with a similar body size found in the Angola Basin.

Eggs inside the ovary before being shed contain dense yellowish yolk and a greyish nucleus. After being expelled the egg rounds up, the ovum retreats from the shell (egs), becomes slightly smaller with the yolk being condensed, and finally lies free in the middle of its shell. The holoblastic cleavage of the ovum is unequal and results in macromeres (mac) marking the vegetal pole as well as in micromeres (mic) concentrated at the animal pole (Fig. 9B). During gastrulation the eggs increase in size and reach a diameter of $50\,\mu m$. The observed gastrulae (ga) are filled with small cells and leave a narrow blastocoel (Figs. 6A and 9G). When embryo (em) and first instar larva develop the soft eggshell expands widely and becomes more oval in shape. The embryo of the first larval instar (Lar I) with retracted introvert measures $60–70\,\mu m$ (Figs. 6B, 9D and E). The young larvae develop, leave the egg shell and find their way to the outside one after the other through the cuticle of the seventh instar Higgins-larva (Lar VII). The first instar Higgins-larva has a size of $110–120\,\mu m$ with fully extended introvert. The proportions of the first Higgins-larva (Fig. 6B) differ slightly from those of the seventh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instar Higgins-larva, e.g. the anterior and posterior setae, scalids and toes are longer in relation to the rest of the body.

## Discussion

### Differential diagnosis

Characters separating the adult of *P. pedicularis* sp. n. from that of other *Pliciloricus*-species are: (1) lorica with characteristic ornamentation such as 44 identical narrow primary plicae of which two together form a unit, and with modified midventral plicae with a specific pattern of transversal and longitudinal ridges, (2) thin cuticle at the transition between thorax and lorica with triangular plates and small pairs of transversal bars, (3) claw-like type B scalids of fourth row with ventral row of minute denticles scattered over their entire length, (4) mid-ventral plicae of end cone not modified, flanked by two warts only, (5) trichoscalids long and extremely rigid basally with many cross walls, (6) basal plates of second row associated with type A trichoscalids with round and oval depressions.

The adults show a few similarities with *P. enigmaticus* Higgins and Kristensen, 1986, e.g.: (1) clavoscalids resembling leguminous pods with strong cross walls and club-shaped ends, (2) similar spinoscalids of the second row, and (3) a similar mouth cone. The long double-organ of *P. pedicularis* sp. n. is of the *P. enigmaticus*-type, but it is more sclerotized and has a more pronounced serration consisting of stronger spinules.

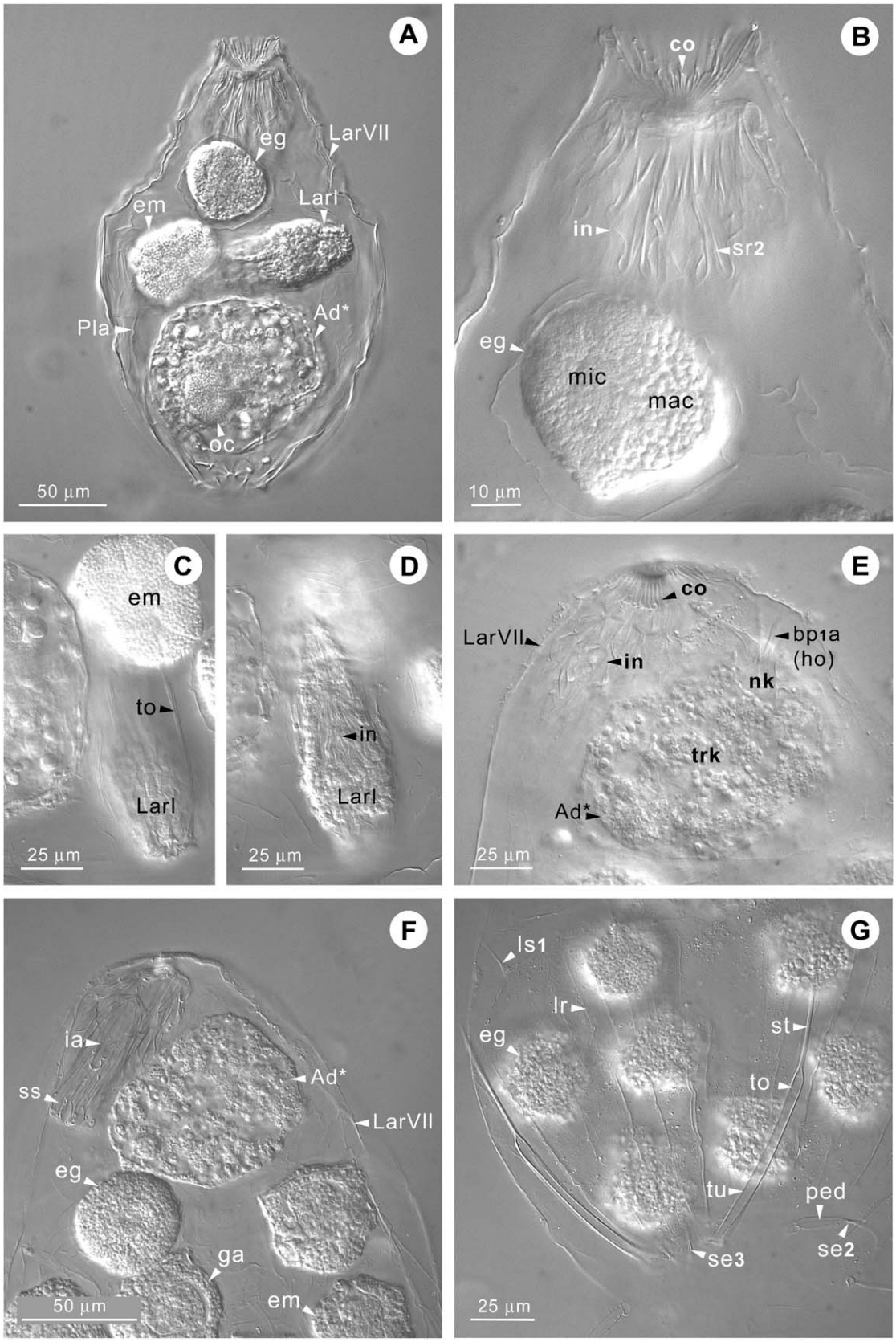
The Higgins-larva fits perfectly into the diagnosis of *Pliciloricus* (derived and extended from Higgins and Kristensen 1986): (1) well developed conical mouth cone, divided into three sections, small first section movable; (2) mouth cone basally with six longitudinal ridges and a single midventral oral seta; (3) mouth opening surrounded by outer circle of six small oral teeth and inner circle of six large more or less valve-like oral stylets; (4) buccal channel short, without buccal tube, supported by well developed prepharyngeal armature over its entire length; (5) prepharyngeal armature hexaradially symmetrical, short (proportion: as long as double width), in detail consisting of six long bracelets, anteriorly covered with six thin valves, posteriorly connected via two transversal bridges; (6) pharyngeal bulb large and round, anterior end with sclerotized crown attached to prepharyngeal armature of the buccal channel, lumen of bulb paved with five rows of placoids; (7) clavoscalids divided into three segments, first and second segment of nearly equal length; (8) second, third and fourth row consisting of spinous spinoscalids divided into two segments; (9) neck region with two transversal rows of small scalids or plates arranged in upper and lower subcircles; (10) first part of thorax modified as well developed collar with many longitudinal folds and seven flosculi; (11) two pairs of short anterior setae ventrally at transition of thorax and lorica; (12) abdomen with weakly developed lorica with 20–24 longitudinal folds; (13) caudal end with three pairs of posterior setae and spinose toes; (14) posteroterminal setae well developed and standing closely together between toe bases; (15) toes long, consisting of basal tubes and distal solid end spines.

As a new species, the Higgins-larva of *P. pedicularis* sp. n. is characterized by the following features: (1) clavoscalids with an additional small fourth segment, and a dorsal row of minute spinules; (2) distal segments of spinoscalids in second, third, and fourth row with clear ventral serration; (3) anteroventral and anterolateral setae short with small pedicels; (4) toes long, same length as or slightly longer than lorica, (5) posterodorsal and posterolateral setae long, of same size, (6) posterolateral setae with slightly enlarged bases and very large pedicels.

### New terminology

With the discovery of *P. pedicularis* sp. n., many new features have been revealed and new information about already known structures has turned up. According to Higgins and Kristensen (1986) this would require refinement and redefinition of the terminology, but they have mainly continued to use the terminology proposed in the original publication on the Loricifera (Kristensen 1983). The basis for the use of many terms was and still is the hypothesis that Loricifera have closest affinities with Kinorhyncha and Priapulida (Higgins and Kristensen 1986). However, many morphological features of Loricifera differ much more from those found in the two other taxa than so far assumed. It is therefore felt necessary to introduce new terms for newly revealed

**Fig. 8.** *P. pedicularis* sp. n., interference-contrast photographs of adults (Ad) enclosed into exuvia of the postlarva (Pla), and of seventh instar Higgins-larva (Lar VII), all in lateral view: (**A**) paratype II (same specimen as in Fig. 3A and B), mature female ready to leave the exuvium of seventh instar Higgins-larva (both with retracted introvert); (**B–F**) anterior details of paratype II, adult female and seventh instar Higgins-larva: (**B**) details of clavoscalids and double organ, (**C**) details of spinoscalids and prepharyngeal armature of Higgins-larva, (**D**) details of trichoscalids, (**E**) details of lorica edge and lorica, (**F**) details of retracted mouth cone, (**G**) paratype IX, adult in early phase of metamorphosis.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structures and to make established terminology more precise prior to further species descriptions.

Higgins and Kristensen (1986) distinguished tow types of flosculi ( = lat. small flowers). The *Nanaloricus*-flosculi or *N*-flosculi were studied with TEM (Kristensen 1991b) and consist of a pore in the cuticle out of which arises a single kinocilium. This is surrounded by of up to nine small papillae or microvilli, which together belong to the same sensory cell. Similar looking sensory structures are also known from Priapulida and Kinorhyncha (Lemburg 1999; Neuhaus and Higgins 2002). Such papillate flosculi are also known from several larval and adult Pliciloricidae (Higgins and Kristensen 1986; Kristensen 1991b) including *P. pedicularis* sp. n. (Figs. 1C and 4A). The other type of flosculi was called *Pliciloricus*-flosculi or P-flosculi (Higgins and Kristensen 1986) which have not so far been studied with TEM. Studies with LM have shown that these structures are large round papilla-like formations which are according to Kristensen (1991b) overlaid by a very thin and delicate cuticle. It is not known for sure whether P-flosculi have a sensory function like *N*-flosculi. Apart from *Pliciloricus*-species P-flosculi have been observed in adults of *Rugiloricus* (Higgins and Kristensen 1986), but so far truly not in Nanaloricidae. It is therefore recommended to separate these structures terminologically from their occurrence in certain taxa and from an assumed but unknown function. Therefore "*N*-flosculi" are suggested to be called just flosculi ( = fl) and the "P-flosculi" to be called warts ( = wa) according to their characteristic shape in LM and REM.

In *P. enigmaticus* a large rosette structure has been discovered by Higgins and Kristensen (1986) which is located ventrally in the end cone region and consists of six cells surrounding a large pore. This structure is confined to this species (Higgins and Kristensen 1986; Kristensen and Shirayama 1988). Apart from *P. pedicularis* sp. n. also other adults from the Angola Basin or from the Great Meteor Seamount (Gad 2004a) have instead a simple round structure in the same body region without a pore surrounded by cells. To distinguish these two similar but different structures the new term round structure ( = ro) is used here for the first time while the other is called rosette structure.

The terms anal cone, anal plates and anal field have been used sometimes unspecifically (Higgins and Kristensen 1986). The anal cone can be found in adult as well as in larval Loricifera and bears the anus. The anal cone ( = ac) is located on a more or less distinct anal field ( = af) composed of anal plates (ap) differing in size and number depending on the species. The term end cone ( = ec) is used here for the caudal part of the lorica in adult Pliciloricidae, which is separated from the rest of the lorica by a distinct zigzag border. Often the double ridges of the lorica become single in the end cone. An end cone composed of two transversal rows of plates is observed in most Higgins-larvae of Pliciloricidae, except for some *Rugiloricus*-larvae where it is indistinct (Higgins and Kristensen 1986). Adult and larval Nanaloricidae lack the end cone but not the anal cone (Kristensen and Gad 2004), especially the nanaloricid Higgins-larvae have a large anal field with many well-defined anal plates (Kristensen 1983; Kristensen and Gad 2004; Gad 2004b).

The terminology for the internal buccal structures is derived from Kristensen and Gad (2004). Adult Nanaloricidae have a triradially symmetrical prepharyngeal armature and a round pharyngeal bulb paved with rows of placoids whereas the Higgins-larvae do not (Kristensen 1991a, b; Kristensen and Gad 2004). In pliciloricid Higgins-larvae a hexaradially symmetrical prepharyngeal armature is known (Higgins and Kristensen 1986; Kristensen 1991b) but its details have not been described before. New is the observation made on *P. pedicularis* sp. n. that placoids (Fig. 4C) can also occur in the pharyngeal bulb of adults and larvae of *Pliciloricus*-species. The term pharyngeal crown for the sclerotized anterior part of the larval pharyngeal bulb is used here because it looks different from the placoids. Additional new terms concerning the structure of the prepharyngeal armature of the Higgins-larvae are cuticular bridges (bg) and anterior plates (apl). These structures have not been observed in the armature of adult Nanaloricidae (Kristensen and Gad 2004).

**Fig. 9.** *P. pedicularis* sp. n., interference-contrast photographs of simplified parthenogenetic adults (Ad*) in different stages of maturity and enclosed together with their offspring in the exuvia of the postlarva (Pla) and of the seventh instar Higgins-larva (Lar VII), all ventral views: (**A**) paratype V (same specimen as in Fig. 6A), habitus of simplified parthenogenetic adult in a late stage of maturity (containing oocytes) together with instars in advanced stages of development: egg, embryo, and young larva, (**B**) details of retracted introvert of seventh instar Higgins-larva and an egg at early stage of development, (**C**) details of embryo and posterior end (marked by toes) of hatching young larva, (**D**) details of anterior end of hatching young larva, marked by scalids of retracted introvert; (**E**) paratype IV (same specimen as in Fig. 5C), simplified parthenogenetic adult, habitus, with view on hooks of the neck region, (**F**) paratype V, simplified parthenogenetic adult in late stage of maturity together with shed eggs in early stage of development, (**G**) paratype VII, simplified parthenogenetic adult in phase of disintegration after which only eggs in the same developmental phase remain in the exuvium of the seventh instar Higgins-larva.

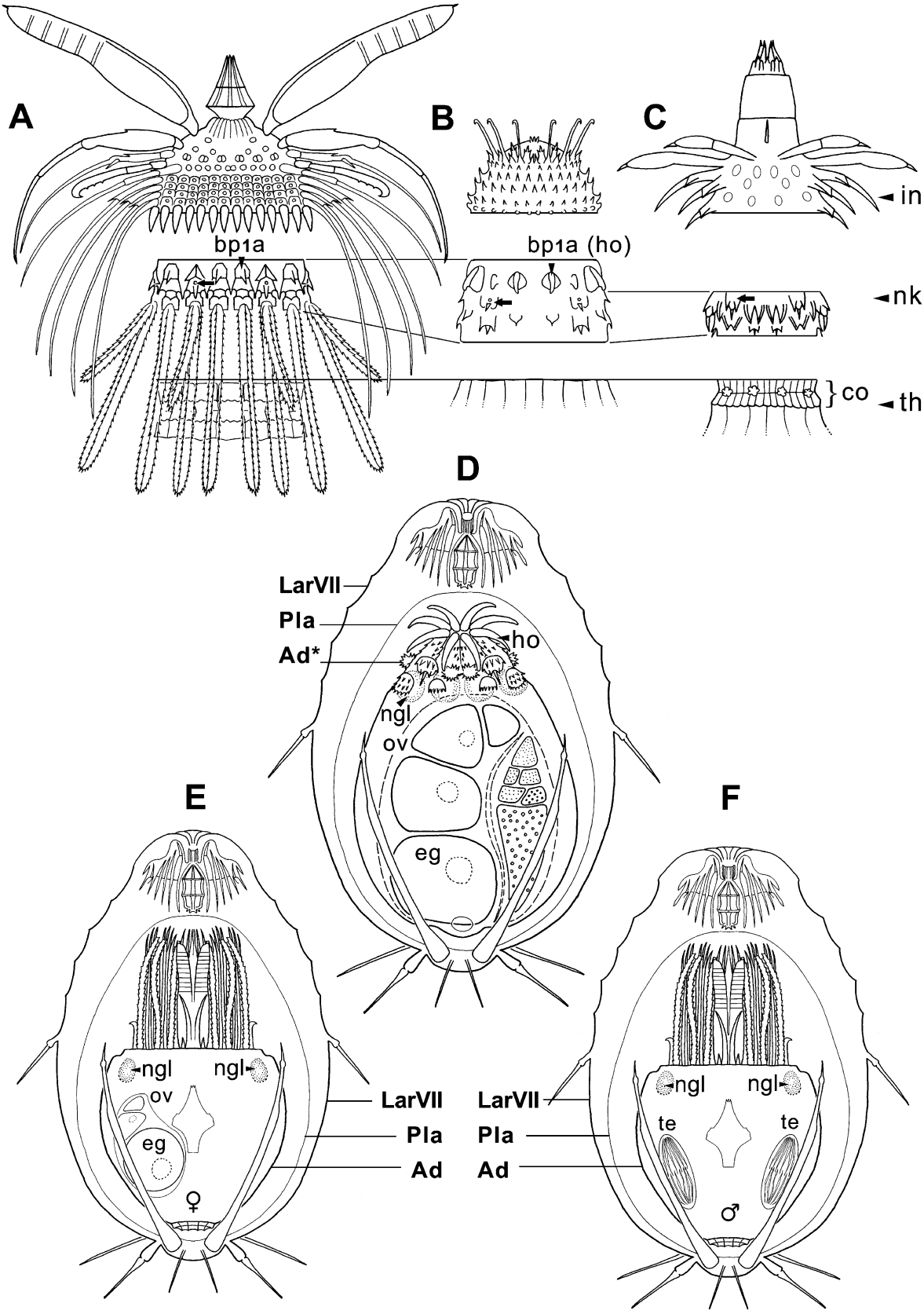


**Fig. 10.** (**A–C**) Comparison of the anterior body region in three different pliciloricid life history stages, schematized drawings, ventral views: (**A**) adult of *Pliciloricus* sp., (**B**) Postlarva of *Rugiloricus* sp., (**C**) Higgins-larva of *Pliciloricus* sp.; (**D–F**), schematized comparison of adults (Ad, Ad*) of *P. pedicularis* sp. n. which all have finished metamorphosis and are enclosed in the exuvia of the postlarva (Pla) and of the seventh instar Higgins-larva (Lar VII), all ventral views: (**D**) newly discovered mature parthenogenetic simplified adult, (**E**) mature female, (**F**) mature male.

## The occurrence of a neck region in different life history stages of Loricifera

The body of larval and adult Loricifera has been divided into five regions so far: (1) mouth cone, (2) introvert, (3) neck or collar, (4) thorax, and (5) abdomen (Kristensen 1983, 1991a, 2002; Higgins and Kristensen 1986; Kristensen and Brooke 2002). According to this subdivision a neck region is confined to adults where it is clearly distinguishable form the introvert, because it is covered with basal plates and equipped with trichoscalids (Fig. 10A). In Higgins-larvae the respective region is assumed to be the collar (Fig. 10C) which lacks basal plates and appendages (Kristensen 2002; Kristensen and Brooke 2002).

Comparison with the most closely related taxa Priapulida and Kinorhyncha reveals slight differences in the body division of these three taxa. In Kinorhyncha the body consists of a mouth cone, a head or an introvert with up to seven rows of scalids, a very short neck with up to 16 cuticular placids, and a trunk divided into eleven zonites or "segments" in the adults (Neuhaus and Higgins 2002). Juveniles have the same body regions but reach the full number of zonites successively during postembryonic development (Neuhaus and Higgins 2002). In Priapulida only the larvae have a short neck region directly behind the introvert together with a thoracic region and a loricate abdomen, whereas adults have an introvert, a thorax and a vermiform abdomen (Lemburg 1999). The neck of Priapulida larvae lacks basal plates and appendages (Lemburg 1999). The collar of loriciferan Higgins-larvae, the neck of Kinorhyncha and larval Priapulida seem to be similar because they close the opening formed by the retracting introvert. The neck of adult Loricifera is unique because it is covered with basal plates (not similar in structure with the placids of Kinorhyncha) and carries appendages like trichoscalids (also not comparable with the trichoscalids found in Kinorhyncha) at its anterior border (Higgins and Kristensen 1986).

In the present description of *P. pedicularis* sp. n. mention is made for the first time of a neck region also in the Higgins-larva. Indications for the existence of such a larval neck region, which is rather indistinct from the introvert, result from recent observations made on *Rugiloricus*-larvae from the Antarctic deep sea (Gad, unpubl.). These larvae have a row of 15 short but fully developed trichoscalids, similar in structure to those found in adults, arising from the last row of scalids found on the larval "introvert". In the same position small formations can be seen on the "introvert" of the Higgins-larva of *Rugiloricus carolinensis* Higgins and Kristensen, 1986 which have already been discussed by Higgins and Kristensen (1986) as probable "prototrichoscalids" which are assumed to become fully developed later in the adults.

An additional indication for the existence of a neck region also in Higgins-larvae are the seven large scalids called here upper type B scalids of the fifth row (marked grey in Fig. 4B; marked with an arrow in Fig. 10C; see also Fig. 11B, and scalid formula below). These scalids can be found in Higgins-larvae of all known species of Loricifera (Higgins and Kristensen 1986; Kristensen and Shirayama 1988; Kristensen and Gad 2004; Gad 2004a, 2005). In the *Rugiloricus*-larvae from the Antarctic deep sea these scalids bear the large pores of seven internal neck glands. Neck glands are known form adults of *P. enigmaticus* and open via large pores located on basal plates above the trichoscalids (Kristensen 1991b). These neck glands are known so far from all adults of *Pliciloricus- and Rugiloricus*-species discovered in the deep sea of the Angola Basin and of the Antarctic (Gad, unpubl.), and consequently also from the adult of *P. pedicularis* sp. n. (ng, Figs. 2, 10E and F).

In summary the number and arrangement of scalids (cs = clavoscalids, do = double-organ, sc = scalids, ss = spinoscalids) and basal plates ( = bp) belonging to the introvert and neck of the new *Rugiloricus*-species together with accessory elements of the neck like neck glands ( = ng) and trichoscalids ( = tr) can be expressed in the following scalid formulas:

Adult of *Rugiloricus* sp.:
introvert: 8cs/2(do)7ss/15ss/15a + 15b ss/30ss/30ss/20ss/30ss/30ss

neck : 8a + 7b bp/8a + 7b bp/8a + 7b bp
(8 + 7 ngl, 8a + 7b tr)

Higgins-larva of *Rugiloricus* sp.:
introvert: 8cs/10ps/15ss/8a + 7b ss

neck : 8a + 7b sc/8a + 7b sc
(7 ngl, 8a + 7b tr)

Number and arrangement of scalids as well as the presence of trichoscalids and neck glands allow the conclusion that the last two rows on the larval "introvert" belong to an indistinct neck region (Figs. 10C and 11B) which becomes distinct later in the adults. According to this hypothesis the larval neck lies behind the fourth row of scalids of Higgins-larvae and starts with the seven large and well-developed type B scalids of the fifth row on which there are the pores of the seven internal neck glands. Their equivalents on the adult neck region (Figs. 10A and 11A) are believed to be the seven type B basal plates of the second row because of their number, arrangement, structure, and association with neck glands.

It is not clear whether the conclusions derived from the Antarctic *Rugiloricus*-species can also be applied to all *Pliciloricus*-species, but they can at least in the case of *P. pedicularis* sp. n. The scalid formula given above for

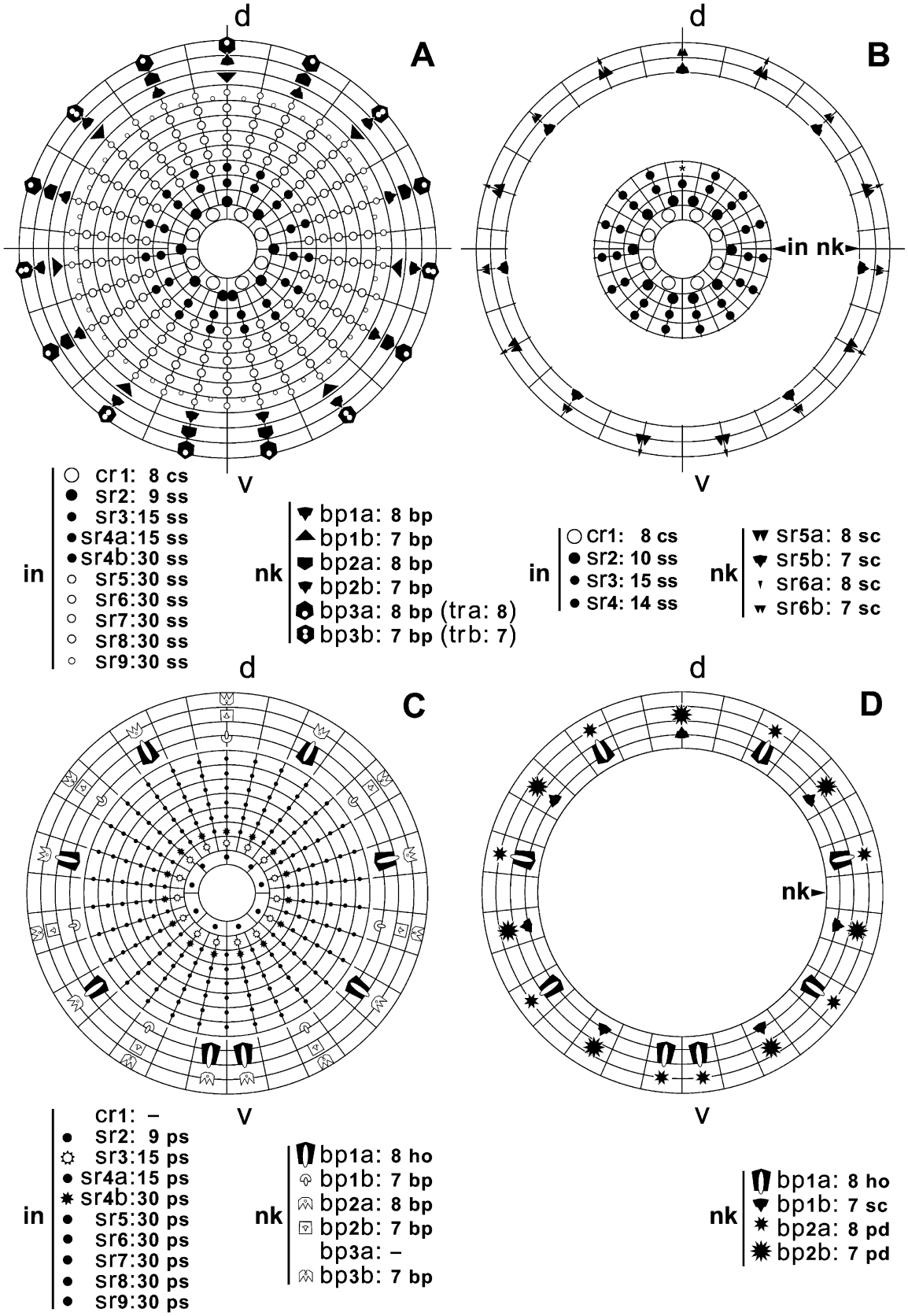


**Fig. 11.** Comparison of scalid diagrams demonstrating structure and arrangement of scalids and basal plates on introvert and neck: (**A**) adult of e.g. *P. pedicularis* sp. n., (**B**) Higgins-larva of e.g. *P. pedicularis* sp. n., (**C**) Postlarva of e.g. *R. cauliculus* Higgins and Kristensen, 1986), (**D**) parthenogenetic simplified adult of *P. pedicularis* sp. n.

the adult of the Antarctic *Rugiloricus*-species is identical with that for the holotypic adult of *P. pedicularis* sp. n., except that the type B trichoscalids are double ones. Although trichoscalids or neck glands have not been observed in the Higgins-larva of *P. pedicularis* sp. n. (and not as yet in any other *Pliciloricus*-larva) the scalid formula agrees with that of the Antarctic *Rugiloricus*-larva except for the fact that there are only 14 instead of 15 spinoscalids in the fourth row of spinoscalids of the larval introvert. Here is the scalid formula:

Higgins-larva of *P. pedicularis* sp. n.:
introvert: 8cs/10ss/15ss/14ss
neck: 8a + 7b sc/8a + 7b sc

It is not yet known for certain what these "scalids" on the presumable neck of pliciloricid Higgins-larvae really are. Some of them may be basal plates instead of scalids whereas others may be protrichoscalids. To sum up it can be said:

(1) Pliciloricid Higgins-larvae are assumed do have a neck region which is, however, indistinct from the introvert (Figs. 10C and 11B).
(2) The larval collar region does not seem to be the equivalent of the neck of the adults; instead it may be a separate region or the anterior part of the thorax (Fig. 10C).
(3) Larvae of Loricifera and Priapulida seem to have a collar whereas adults of both taxa do not.
(4) The loriciferan head of adults *and* larvae seems to consist of an anterior part called introvert (comparable with what is found in Priapulida and Kinorhyncha) and a posterior part called neck (which may not be equivalent to the part called "neck" in Priapulida and Kinorhyncha).

The hypothesis about the neck region within Loricifera also explains to which body region the anterior end of the simplified adult is equivalent. The structure of its "scalid-like" formations seems to be unique because nothing similar is observed in bisexual adults or Higgins-larvae. The "scalid-like" formations, however, match perfectly well the arrangement of basal plates (with trichoscalids) found on the neck region of adults (Figs. 10A, C, 11A and B) as it follows the formula: 8 ho + 7 pd, 8 sc + 7 pd.

The introvert as anterior part of the head is therefore assumed to be lacking in the simplified adult. Instead the neck region persists (Figs. 10D and 11D) as is evidenced also internally by the neck glands (Fig. 10D). The postlarva of some *Rugiloricus*-species (Kristensen and Brooke 2002; Kristensen 2003; Gad 2004a) shows that the neck region together with its structures (Fig. 10B), the hooks, can be more developed and different in structure than the neck region of the adult moulting from it. The eight type A basal plates of the first row which are small and barely hook-like in the adults (ho, in Fig. 10A) have their precursors in the eight large well-developed hooks observed in the postlarva (ho, in Figs. 10B and 11C). Comparison of the simplified adult of *P. pedicularis* sp. n. with the *Rugiloricus*-postlarva shows that the introvert can be simplified or totally lacking while the neck region is strongly developed. One indication that the simplified stage is an aberrant adult (Figs. 5B and 10D) is derived from the structure of the conserved neck region. A second indication lies in its position in the life-cycle as discussed in the following section.

## Simplified instar: larva or adult?

Paedogenetic larvae are known in *Rugiloricus* species (Kristensen and Brooke 2002; Gad 2004a), and the newly discovered giant larva of *Titaniloricus inexpectatovus* Gad, 2004 which is also part of the Loricifera-fauna of the Angola Basin (Gad 2005) belongs to this category. These paedogenetic larvae are assumed to be the *seventh* instar larvae and have been found not to be morphologically identical with the *sixth* instar Higgins-larva from which they moult (Gad 2005). Although the exact number of larval instars is not yet known of any species of Pliciloricidae, the number of seven instars of Higgins-larvae is assumed to be prevalent in most life cycles (Kristensen and Brooke 2002; Gad 2005). This assumption is based on extrapolation of the sizes of Higgins-larvae found, and from that it is concluded that the last instar Higgins-larva which contains adults moulting from a postlarva must be the seventh one in *Pliciloricus*- and *Rugiloricus*-species. This presupposition may not be wholly satisfactory but it is the best basis for the moment for the comparison of life cycles and morphological transformations of life history stages (Gad 2005).

The known paedogenetic larvae are simplified such that all body regions form a sack-like trunk on which the scalids of introvert and neck persist as small protoscalids. This is quite similar to what is assumed here as being a simplified adult, the main difference being that the simplified adult is surrounded by an extra layer of thin cuticle (Fig. 10D) whereas the paedogenetic larvae are not. In some *Pliciloricus*-species from the Angola Basin such an extra cuticle, which is surrounding adults after their metamorphosis, could clearly be identified as a postlarva (Gad, unpubl.) because not all of its particular features are lost. Additionally in the postlarva of a new *Pliciloricus*-species the lorica is already fully developed as though it were the lorica of the adult moulting from it. Considering all *Pliciloricus*-species found in the Angola Basin a complete series can be arranged along which the postlarvae lose more and more of their particular features to finally become a simple and thin cuticle without any structures left to

guess at their origin. The hypothesis derived from this series is that the thin and delicate cuticle surrounding the adults of both sexes during their metamorphosis in *P. pedicularis* sp. n. (Figs. 10E and F) is the remnant of the postlarval stage.

It remains open whether this simplified stage can be called a simplified *female* reproducing parthenogenetically although this seems to be a plausible conclusion. To clarify this question hermaphroditic adults have to be studied which have been observed in the Antarctic deep sea (Gad, unpubl.). In the simplified adults of *P. pedicularis* sp. n. or in other *Pliciloricus*-species discovered in the Angola Basin no clear indications of testes have been found, whereas a large and well-developed ovary could clearly be identified.

## Observations on remaining life history stages, life cycle, and development

In the Higgins-larvae the collar looks like a wheel with spokes when it is folded together over the retracted introvert. A closed collar is very common in seventh instar Higgins-larvae of *Pliciloricus*-species from the Angola Basin, especially when they contain adults during metamorphosis, mature adults, young larvae or eggs (e.g. Figs. 3A, 6A, 8A and 9A). The well-developed collar region in these larvae seems to function as a closing apparatus for the retracted introvert (Higgins and Kristensen 1986) and seems to work mechanically even when only the larval exuvium is left. The last or seventh instar Higgins-larva is visibly larger than the adults it generates. Its volume is approximately one-third bigger than that of the adults. Measurements of material of *P. pedicularis* sp. n. indicate that there is the tendency that a Higgins-larva moulting into a parthenogenetic simplified adult is slightly larger than that moulting into a male or a female.

Study of parthenogenetic simplified adults of *P. pedicularis* sp. n. revealed that development of eggs and embryos is either consecutive or synchronous:

(1) The eggs start cleavage shortly after they have been shed. As a result a whole series of eggs, embryos and young larvae in different phases of development can be found (Fig. 9A). The highest number of such instars enclosed in an exuvium of a seventh instar Higgins-larva was five first instar larvae and four embryos plus the three eggs found inside the nearly disintegrated parthenogenetic simplified adult.
(2) All eggs start development simultaneously, but not before all eggs are shed and the parthenogenetic simplified adult has totally disintegrated.

Five to eight eggs were found in the exuvium of the seventh instar Higgins-larva of *P. pedicularis* sp. n., all in the same phase of development (Fig. 9F).

In the first case, a first instar Higgins-larva can be ready to hatch and leave the shelter of the seventh instar Higgins-larva e.g. before the last egg is formed. To become free the larva makes an opening into the exuvium of the seventh instar Higgins-larva normally somewhere in the thoracic region where the cuticle is thinnest leaving behind the eggshells, which fill up the exuvium of the seventh instar Higgins-larva.

In the second case, there must be the possibility of the development of eggs being somehow postponed until the last one of them has been shed. In this case, no larva leaves the exuvium of the seventh instar Higgins-larva before the others as all eggs develop simultaneously. This allows to measure the reproductive success of the simplified adults. Differences in number of produced eggs seem to depend on the nutritional state of the seventh instar Higgins-larva. This state is important for the direction of further development: bisexual reproduction (moulting to males or females) or unisexual reproduction (moulting to parthenogenetic simplified adults). The conditions which trigger a life cycle with paedogenetic larvae (Gad 2004a, 2005) are assumed to be linked to food availability or other changing environmental conditions and may also play a role in life cycles with parthenogenetic simplified adults as in the case of *P. pedicularis* sp. n.

The expedition to the Angola Basin yielded 160 samples, which contained 280 specimens of Loricifera. Every fourth specimen of them belongs to *Pliciloricus*. Despite these numbers Loricifera make up only 0.1% of the total meiofauna found in the deep sea of the Angola Basin. More than 95% of the specimens obtained are larval instars. This high proportion of larval instars may be characteristic for the deep sea because of the complex life cycles. Nearly all Loricifera found in the deep sea of the Angola Basin seem to have the ability to reproduce unisexually (Gad 2002). They skip the bisexual phase and produce large, unfertilized eggs from which the larvae of the next generation hatch. Larvae developing from unfertilized eggs produced unisexually are morphologically identical with larvae hatched from fertilized eggs. Whether larvae hatching from the bigger eggs of parthenogenetic origin are bigger than larvae hatching from the smaller eggs produced by mature females remains unclear.

The reproductive success of paedogenetic or parthenogenetic stages seems to make them outnumber sexual adults by more than one hundred to one (Kristensen 2002). This may be the reason why adults are found so rarely in the deep sea of the Angola Basin. The presence or absence of Loricifera seems to indicate a rather patchy distribution in the samples, which most likely is not a sampling artifact, but rather a reflection of the population dynamics of deep-sea Loricifera with unisexual reproduction.

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