Facetotectan larvae from the White Sea with the description of a new species (Crustacea: Thecostraca)

Gregory A. Kolbasov [a] & Jens T. Høeg [b]

[a] Department of Invertebrate Zoology, White Sea Biological
Station, Biological Faculty Moscow State University, Moscow,
119899, Russia E-mail:

[b] Department of Zoomorphology Zoological Institute, University
of Copenhagen, Universitetsparken 15, Copenhagen, DK-2100,
Denmark E-mail:

Version of record first published: 06 Nov 2010.

PLEASE SCROLL DOWN FOR ARTICLE

Facetotectan larvae from the White Sea with the description of a new species (Crustacea: Thecostraca)

Gregory A. Kolbasov & Jens T. Høeg

From a number of partial moult series obtained by laboratory culture of plankton-caught specimens, and based on drawings from whole-mounted material, we describe all the larval instars, including the y-cypris, of a new species of Facetotecta. The mid-length constriction of the antennulary aesthetasc and the shape of the head shield separate the y-cypris in our material from all other forms of y-cyprids previously assigned to species. The morphology of the present y-nauplii and y-cypris is compared with that of previously described facetotectan larvae.

Gregory A. Kolbasov, Department of Invertebrate Zoology, White Sea Biological Station, Biological Faculty, Moscow State University, Moscow 119899, Russia.
E-mail: kolbasov@soil.msu.ru
Jens T. Høeg*, Department of Zoomorphology, Zoological Institute, University of Copenhagen, Universitetsparken 15, DK-2100, Copenhagen, Denmark.
E-mail: jthoeg@zi.ku.dk
* Corresponding author

INTRODUCTION

Nauplii and cyprids of Hansen's enigmatic type y crustacean larvae occur in the marine plankton in almost all seas. Hansen (1899) originally illustrated five different naupliar types of y-larvae from West Indian and equatorial Atlantic waters and the Bay of Kiel. He suggested that they represented 10 or 12 different cirripede species belonging to Darwin's (1854) order Apoda, until then only represented by the species *Proteolepas bivincta* Darwin. Similar larvae were first observed by Hensen (1887) from the North Sea, and subsequently y-nauplii were reported from the North Sea, Norwegian Sea, and Baltic Sea (Apstein 1905; Lohmann 1908; Hoek 1909; Runnström 1931). Steuer (1904, 1905) proposed the new species *Proteolepas hanseni*, belonging to the Cirripedia Apoda, for a single instar of y-nauplius of type IV. After Bocquet-Védrine (1972) transferred *Proteolepas* in its original sense to the Isopoda and rejected the Apoda as a valid taxon, the taxonomic position of y-nauplii became *incertae sedis*, and Steuer's *Proteolepas hanseni* remains a dubious species.

McMurrich (1917) described three naupliar instars of y-nauplii of type IV from Passamaquoddy Bay, Canada. A revival of interest in the y-larvae occurred in the second half of the 20th century, when Bresciani (1965)

first found a post-naupliar larval instar and named it "y-cypris" due to its resemblance to the cypris of the Cirripedia and the cypris-like (ascothoracid) larvae of the Ascothoracida. Mileikovsky (1968) described an occurrence of "*Proteolepas*-larvae of Cirripedia" in plankton from the Norwegian and Barents seas, and they probably belonged to type IV. Since then, new descriptions of different y-larvae from the Atlantic, including y-cyprids, have been made by Schram (1970a, b, 1972), Elofsson (1971), Davis (1982, 1986), and Grygier (1987). Both Elofsson (1971) and Grygier (1987) studied the internal and external morphology of y larvae in detail and discussed their relationships with other maxillopodan taxa.

Y-larvae were also reported from the Pacific (Kurile Islands) by Mileikovsky (1970). More recently, several types of y-nauplii and y-cyprids were described from coastal waters of Japan (Itô & Ohtsuka 1984; Itô 1984, 1985, 1986a, b, 1987a, b, 1989, 1990, 1991; Itô & Takenaka 1988; Kikuchi & al. 1991; Grygier 1996; Watanabe & al. 2000).

Recently y-larvae were reported from the Gulf of Aqaba, Red Sea (Almeida Prado-Por & Por 1988), and from a marine cave in the Canary Islands (Ohtsuka & al. 1999).

Most authors used or extended Hansen's (1899) informal taxonomy for y-larvae until Itô (1985)

proposed the new genus *Hansenocaris* for his three new species (*H. pacifica*, *H. rostrata*, and *H. acutifrons*), described on the basis of characters of the respective y-cyprids. Two other new species were described later, *H. tentaculata* (Itô 1986b) and *H. furcifera* (Itô 1989). The work of Almeida Prado-Por & Por (1988) refers to an unpublished genus "*Ufocaris*" in a forthcoming publication that never appeared. This name is a *nomen nudum*, although Hulings (1989) cites this paper and uses "*Ufocaris*" again.

The position of y-larvae within Crustacea was until recently quite uncertain. Hansen (1899) and Elofsson (1971) suggested a close affinity to the Cirripedia, whereas Bresciani (1965) argued for a close relationship to the Ascothoracida. Grygier (1985) erected the new subclass Facetotecta to accommodate all larvae of type "y" and placed them inside the monophylum Thecostraca together with the Ascothoracida and Cirripedia. This move was seconded by Schram (1986). Grygier (1987) consolidated this taxonomy by characterizing the constituent groups of the Thecostraca as monophyla and performing a cladistic analysis of the entire taxon. Most recently, Høeg & Kolbasov (2002) added the presence of a special type of chemosensory organ (lattice organ) to the suite of apomorphies in support of the Thecostraca.

At present, the monophylum Facetotecta contains five nominal species, excluding the very dubious *Proteolepas hanseni* [*Hansenocaris hanseni* in Itô (1985)]. Thirteen naupliar series (types) are described to date within the taxon, including the recently described "Manazuru types" I and II (Watanabe & al. 2000), but only some of these have been correlated with y-cyprids and, hence, referred to formal species.

Dr N. M. Pertsova and Professor A. V. Tchesunov (pers. comm.) advised us on the presence of facetotectan larvae in the White Sea. In this paper we report for the first time on Facetotecta from this locality and describe a new species based on its complete larval development. Høeg & Kolbasov (2002) described the presence of lattice organs from y-cyprids of the new species and subsequent papers will deal with other details of larval ultrastructure.

MATERIAL AND METHODS

About 350 specimens of nauplii and cyprids were collected in June–July 1998–1999, off the White Sea Biological Station (66°34′N 33°08′E), with a 40 cm mouth opening, 72 µm mesh net at a depth of 15–35 m. Some field-collected larvae were preserved, while others were cultured to establish the larval sequence. Although the nauplii are planktotrophic, we did not feed

them and no single larva was cultured from instar 1 to the cypris. Instead, we cultured the individual larvae from instar 2 onwards until they moulted and thereafter preserved and examined both the empty exuviae of the previous instars and the resulting new larvae. Instar 1 larvae were very rare in the field and were not cultured into stage 2. In this way we could assemble the whole larval series by comparison of field-collected and cultured instars. Both live larvae and their shed exuviae were preserved in glutaraldehyde or in 4% formalin. The cultures were maintained in a cold room at 8–9 °C, but due to the culture method we naturally cannot give the developmental time with any confidence. Due to the thermocline in the White Sea and the fact that the larvae occur throughout a large depth range, we also cannot give the sea water temperature in their natural environment. All moult stages or their shed exuviae were examined as glycerine whole mounts using differential interference contrast (Nomarsky) optics with a Leica DM RXA light microscope. We tried to examine five or more specimens of each instar for our investigations and measurements, except the first instar (only one specimen and exuvium were collected). Although light microscopy was our principal instrument, we also used scanning electron microscopy to resolve some details, especially with respect to segmentation and setation of the appendages.

TAXONOMY

We refer all facetotectan nauplii found in the White Sea samples to type IV in Hansen's (1899) classification. In agreement with Itô (1990), we found five free-swimming naupliar instars followed by the y-cyprid. All naupliar instars have setiform maxillulary rudiments and are therefore formally metanauplii. The size of the naupliar instars increases gradually from instar 1 to 5. The larvae represent a hitherto unnamed species within the Facetotecta, presented here as the seventh formally described member of the group (including *H. hanseni*).

Both Schram (1972) and Itô (1987b) established nomenclatures for the dorsal plates of the naupliar head shield, and we try to use both systems for instar 1. Schram's system was made for the first instar only, so we attempt to use Itô's terminology for the following instars, but it breaks down after a few moults. This effectively means that we cannot reliably follow the plates on the naupliar head shield through the entire larval development.

Subclass Facetotecta Grygier, 1985
Genus *Hansenocaris* Itô, 1985
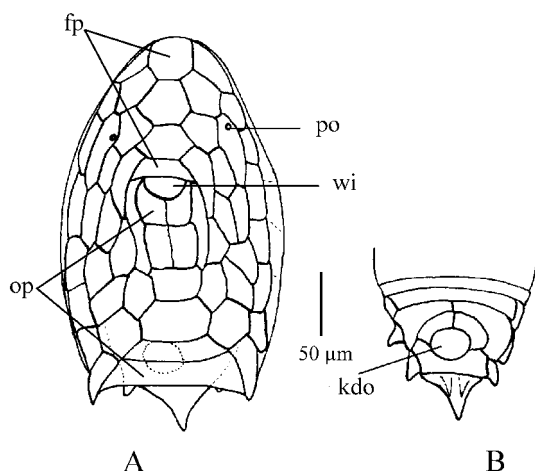*Hansenocaris itoi* Kolbasov and Høeg, sp. nov.
(Figs 1–7)

Fig. 1. *Hansenocaris itoi* sp. nov., nauplius instar 1 (exuvium). A. Whole larva, dorsal view. B. Hindbody, dorsal view. fp – Frontal plates; kdo – Knob of dorsocaudal organ; op – Occipital plates; po – Pore; wi – Window plate.

Holotype

A y-cyprid no. Mg 1203, deposited in the Zoological Museum of Moscow State University, and five para-types, no. Mg 1204, represented by nauplii of instars 1, 2, 3, 4, and 5 and deposited with the holotype.

Diagnosis

Y-cypris with antennulary aesthetasc constricted at mid-length and with elongated lateroposterior ends of head shield reaching telson.

Etymology

The new species is named in honour of the distin-guished Japanese carcinologist Tatsunori Itô, who made a great contribution to the study of the Facetotecta before his untimely death in 1990.

DESCRIPTION OF LARVAL INSTARS

The nauplii are planktotrophic. All instars are semi-transparent with a black nauplius eye and a brownish gut coloured by food particles. In culture they swim slowly forward in different directions, bobbing up and down.

NAUPLIUS 1 (Fig. 1A, B)

This instar is very similar to the type IV described by

Hansen (1899) and to the one described by McMurrich (1917) as "Hansen's y larva, stage I".

The body consists of an anterior part covered by the 282 μm long and 177 μm wide head shield and a triangular 114 μm long and posteriorly projecting hindbody. The latter represents the prospective thorax and abdomen. Cuticular ridges divide the head shield into 54 dorsal plates, including a small window plate, which are all arranged in a symmetrical pattern (52 plates if the split pairs mentioned below each count as only one). An axial row consists of 11 "axial plates" in Schram's (1972) terminology, or four unpaired "frontal plates", the semicircular "window plate", and six "occi-pital plates" in Itô's (1987b) terminology. The window plate is situated above the nauplius eye. The two axial (occipital) plates immediately behind the window are each separated (or split) by a very delicate median ridge just as in the Japanese y-nauplii of types IX, X, and XI (Itô 1987b). Hansen (1899) and McMurrich (1917) described neither a window plate nor a delicate median ridge splitting the first two occipital plates, but their nauplii have 11 plates in the axial row just as in nauplii from the White Sea. The head shield carries only a single pair of pores situated in elongated (polygonal) plates (Fig. 1A) just as in the specimens studied by Hansen (1899) and McMurrich (1917). Marginal plates project as sharp thorns at the posteriolateral end of the head shield, whereas Hansen's (1899) and McMurrich's (1917) specimens have smooth margins.

The dorsal side of the hindbody also has "plates" delineated by cuticular ridges (Fig. 1B). Anteriorly there are two long and narrow, unpaired plates traversing the body. A pair of large polygonal plates, a pair of smaller polygonal plates and an unpaired, posteriorly placed polygonal plate surround the round knob of the dorsocaudal organ (Elofsson 1971). The large posterior-most plate terminates in a conspicuous spine. Three pairs of small plates with sharp ends are inserted laterally. A pair of smaller ventral spines represents rudimentary furcal spines. The morphology of the ventral side (labrum, naupliar appendages) is similar to that of instar 2.

Unfortunately, we had only an exuvium and one specimen of this instar, and both were fouled with bacteria, which could hide some details, such as pores and setae.

NAUPLIUS 2 (Fig. 2A–E)

Only McMurrich (1917) has previously described this instar. He erroneously claimed that the third instar (a y-cyprid in the modern understanding) is located inside the body of instar 2. In fact, the y-cyprid is located
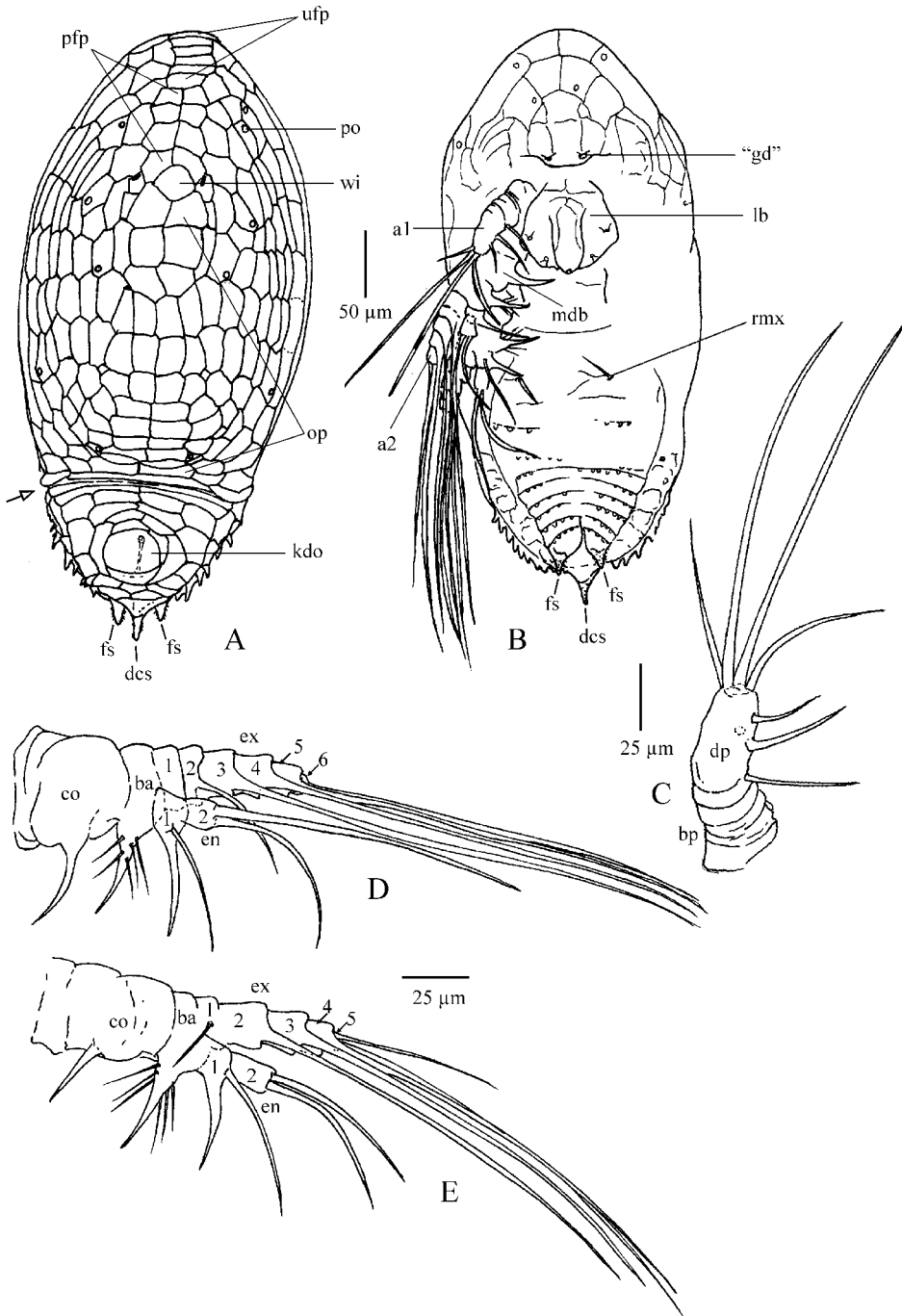
Fig. 2. *Hansenocaris itoi* sp. nov., nauplius instar 2 (exuvium). A. Dorsal view (the arrow on the left indicates the separation of the thorax and the hindbody). B. Ventral view. C. Antennule. D. Antenna. E. Mandible. 1–6 – Segments in endo- and exopods; a1 – Antennule; a2 – Antenna; ba – Basis; bp – Basal portion of antennule; co – Coxa; dcs – Dorsocaudal spine; dp – Distal portion of antennule; en – Endopod; ex – Exopod; fs – Furcal spines; "gd" – Gland ducts on head shield (or frontal filaments?, interpretation uncertain); kdo – Knob of dorsocaudal organ; lb – Labrum; mdb – Mandible; op – Opercular plates (all paired); pfp – Paired frontal plates; rmx – Setiform rudiments of maxillules; po – Pore; ufp – Unpaired frontal plates; wi – Window plate.
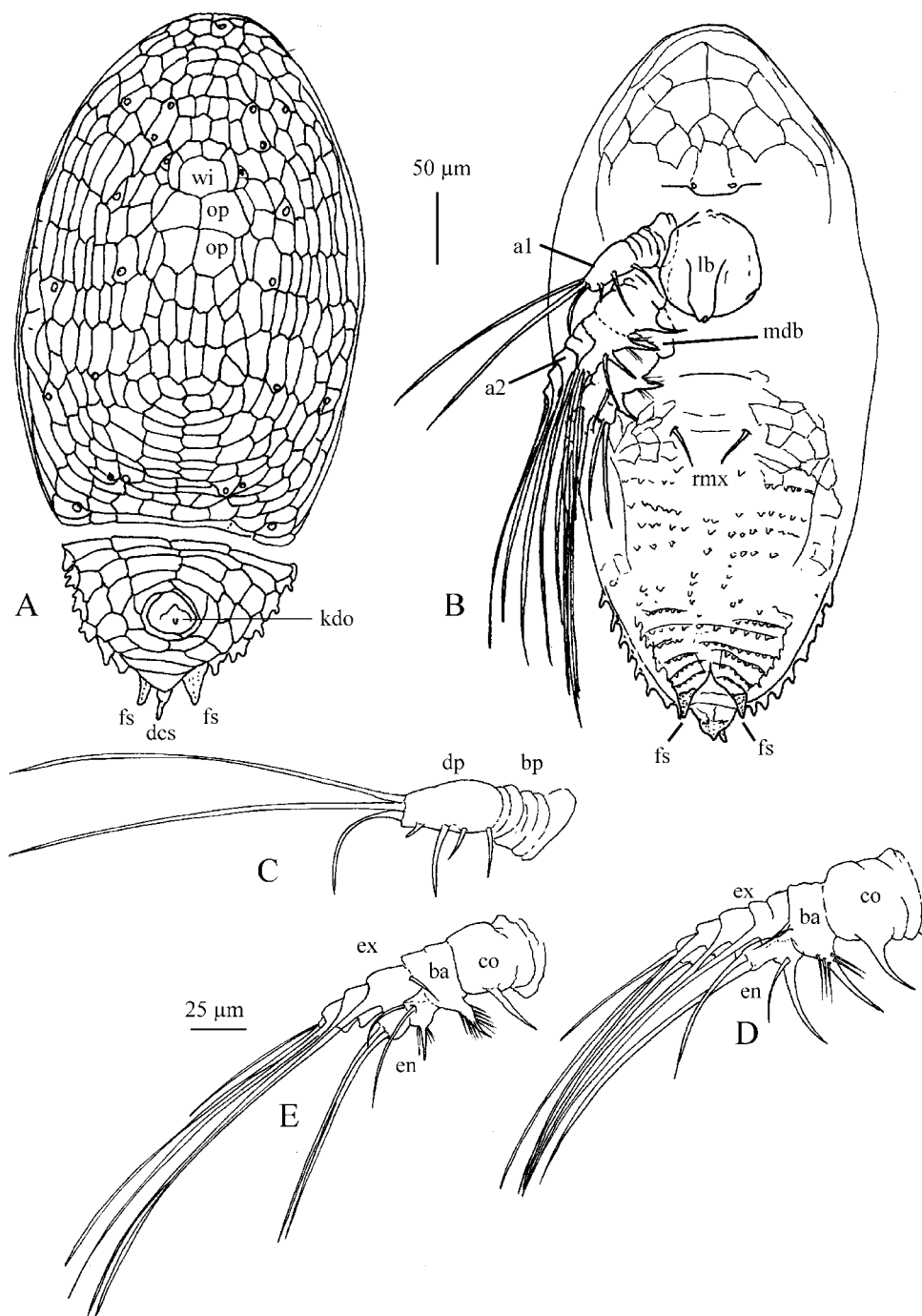
Fig. 3. *Hansenocaris itoi* sp. nov., nauplius instar 3 (exuvium). A. Dorsal view; only the window plate (wi) and two pairs of occipital plates behind it (op) can be compared with confidence with plates in other instars. B. Ventral view. C. Antennule. D. Antenna. E. Mandible (scanning electron microscopy has verified that the coxa normally carries a spine, but it may have broken off in this specimen). a1 – Antennule; a2 – Antenna; ba – Basis; bp – Basal portion of antennule; co – Coxa; dcs – Dorsocaudal spine; dp – Distal portion of antennule; en – Endopod; ex – Exopod; fs – Furcal spines; kdo – Knob of dorsocaudal organ; lb – Labrum; mdb – Mandible; op – Occipital plate; rmx – Rudimentary maxillule; wi – Window plate.

inside the body of nauplius 5. It was observed, but not described, by him.

The dimensions of the body are significantly greater than instar 1: the head shield measures 330–340 μm in length and 216–218 μm in width, while the hindbody is 120–122 μm long.

The number of dorsal plates has increased in both parts of the naupliar body. The head shield is divided into approximately 180 plates of different sizes (Fig. 2A). The axial row always includes five or six unpaired frontal plates followed by four additional pairs of frontal plates [the last frontal plate is unpaired in McMurrich's (1917) specimen], a rounded window, and 12 pairs of occipital plates. There is some slight individual variability in the numbers and shapes of the more laterally situated plates. McMurrich (1917) found only two pairs of pores (anterior and posterior), whereas we could observe at least seven symmetrically placed pairs, which differ in size and structure. As in instar 1, the posterior-most edge of the head shield is formed by a single, but now much narrower, plate.

The hindbody is divided by cuticular ridges into 33–35 dorsal plates. The anterior-most part of the hindbody bears a single narrow plate and, behind that, two similarly narrow plates formed by the splitting of a single plate in instar 1. Three or four curved plates surround the knob of the dorsocaudal organ. Three pairs of polygonal plates are situated between the above-mentioned narrow plates and the dorsocaudal organ. The lateral margins carry numerous sharp projections. Posteriorly the hindbody terminates in a conspicuous dorsocaudal spine and a pair of more ventrally placed furcal spines.

On the ventral surface (Fig. 2B) several chitinous ridges, more feeble than the dorsal ones, form anterior plates with a few pores. A pair of papillae with terminal pores (present in all naupliar instars) projects from a cuticular fold located a little anteriorly to the labrum ("gd", in Fig. 2B). The prominent labrum consists of a large, proximal, rounded part with two pairs of pores, and a smaller, distal, elongated part with a terminal pore. A slit-like mouth is hidden by the labrum. Three pairs of naupliar appendages surround the labrum (Fig. 2). The uniramous antennules (Fig. 2C) consist of two portions. The basal portion or "segment" lacks setae and has several circular annulations and therefore looks like a multi-segmental structure. The elongated distal portion or segment bears three small lateral setae on the inner margin and two long and two smaller terminal setae.

The biramous antennae (Fig. 2D) each consist of a coxa and a basis bearing the exopod and the endopod. The coxa bears a large, simple, curved spine on the
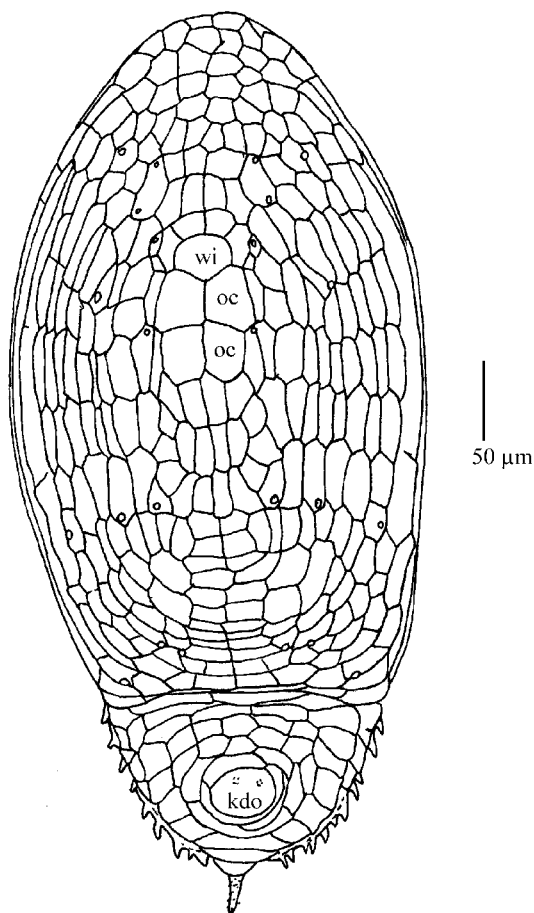

Fig. 4. *Hansenocaris itoi* sp. nov., nauplius instar 4 (exuvium). General view, dorsal. kdo – Knob of dorsocaudal organ; op – Occipital plate; wi – Window plate.

inner margin. A smaller curved spine on the basis carries several small setae (or denticles?). The endopod is two-segmented; its proximal segment carries a prominent curved spine with a seta at its base. The distal segment has two terminal setae. The exopod consists of six segments. The first, basal, segment is unsetated. Segments 2–5 each carry a single seta mediodistally, short in segment 2 and longer in the remaining ones. Segment 6 bears two apical setae, but this segment is always partly hidden by the penultimate one in whole-mounted specimens (Fig. 2D). The mandibles (Fig. 2E) look similar to the antennae but have an indistinctly five segmented exopod. The first segment is not separated completely from the basis and carries a single, small seta. As in the antenna, the apical, fifth segment bears two setae but is partially or completely hidden.

The ventral area behind the mandibles is fairly smooth except for the setiform maxillulary rudiments and perhaps two rather indistinct cuticular ridges (Fig. 2B). More posteriorly, the ventral area of the hindbody is ornamented by seven or eight closely spaced, quite prominent, ridges armed with minute spines, and it terminates in the furcal spines.

Nauplius 3 (Fig. 3A–E)

The head shield is 360–370 µm long and 235–240 µm wide, while the hindbody is 128–130 µm long. The head shield consists of approximately 280 plates of different size and form. About 12 pores, some with seta like structures arising from within them, are scattered on the dorsal surface. Unlike instar 2, there are no unpaired frontal plates. We can single out about nine pairs of frontal plates, an unpaired window plate, and 17 pairs of occipital plates, but surrounding plates may also be the derivatives of frontal and occipital plates of the previous instars. The two conspicuous pairs of plates immediately behind the window plate are undoubtedly homologous with the similarly situated ones in nauplii 1 and 2 and in all succeeding naupliar instars. Otherwise we refrain from entering into an uncertain comparison of plates.

The hindbody (Fig. 3A) differs from that in instar 2 and has approximately 35 dorsal plates, excluding the small lateral plates with sharp protrusions. Two anterior rows including four narrow plates each, are derivatives of the two single narrow plates of instar 1. They are followed by three pairs of central plates and two narrow, semicircular plates surrounding the knob of the dorsocaudal organ. The hindbody terminates with a single, large dorsocaudal spine and a conspicuous pair of furcal spines (Fig. 3B).

The ventral surface (Fig. 3B) is similar to that of instar 2, but the longer hindbody now has a total of 10–11 transverse spine rows and ridges.

The "two segmented" antennules (Fig. 3C) bear four setae along the inner margin (only three in instar 2) and three terminal setae (reduced from four in instar 2). The antennae (Fig. 3D) have almost the same structure as in instar 2. So do the mandibles, except the spine on the basal segment of the endopod (Fig. 3E) is armed with minute setae.

Nauplius 4 (Fig. 4)

This instar differs from instar 3 only in the morphology of the hindbody and the dimensions of the body, but its existence is certain as we obtained it from plankton samples and by the moulting of nauplius 2 in our cultures.

The head shield is about 430–436 µm long and 264–265 µm wide and consists of about 290 dorsal plates with at least 12 pores. The number, form, and distribution of the dorsal plates are almost as in instar 3. The 143 µm long hindbody possesses about 40 irregular plates, and the three pairs of central plates found anteriorly to the knob of the dorsocaudal organ in instar 3 seem to have split into a total of nine smaller plates.

The structure of the ventral side and of the appendages is very similar to that of instar 3.

Nauplius 5 (Figs 5A, B, 6A–E)

This instar is larger than all the preceding ones and can be easily distinguished from them by the distinct compound eyes of the cypris larva forming inside the nauplius (Fig. 6B). Similar nauplii, differing in the structure of the hindbody, were described by Schram (1972) and Grygier (1987). The head shield is 482–507 µm long and 293–303 µm wide and the hindbody is 171–200 µm long. The head shield consists of 290–312 dorsal plates. The frontal and some occipital plates form rather asymmetrical patterns of distribution. One specimen (Fig. 5A) had 17 pairs of pores, whereas another one (Fig. 5B) had only 10 pairs of pores scattered on the dorsal surface. It is noteworthy that there are two pairs of large occipital plates behind the window plate, just as in all preceding instars.

The elongated hindbody (Fig. 5A, B) differs strongly from that in all previous instars. Heralding the condition in the ensuing y-cypris, it carries four longitudinal rows of rectangular plates. The rear part is variable and may bear either several single narrow plates (Fig. 5B) or about 10 irregular plates (Fig. 5A). The external part of the dorsocaudal organ is papilliform. The lateral margins carry numerous sharp spines. The dorsocaudal spine and the two furcal spines, having a different shape in each nauplius, carry small, sharp denticles.

The ventral side (Fig. 6A) has several sharp projections on the anterior-most margin. Some indistinct cuticular ridges form plate-like structures under and behind the labrum. A pair of small papillae with terminal pores projects just anteriorly to the labrum. The labrum consists of a larger, rounded, proximal part and an elongated distal part with a terminal pore.

The ventral part of the hindbody is long, with 12–15 transverse rows of small spines. The trunk segments of
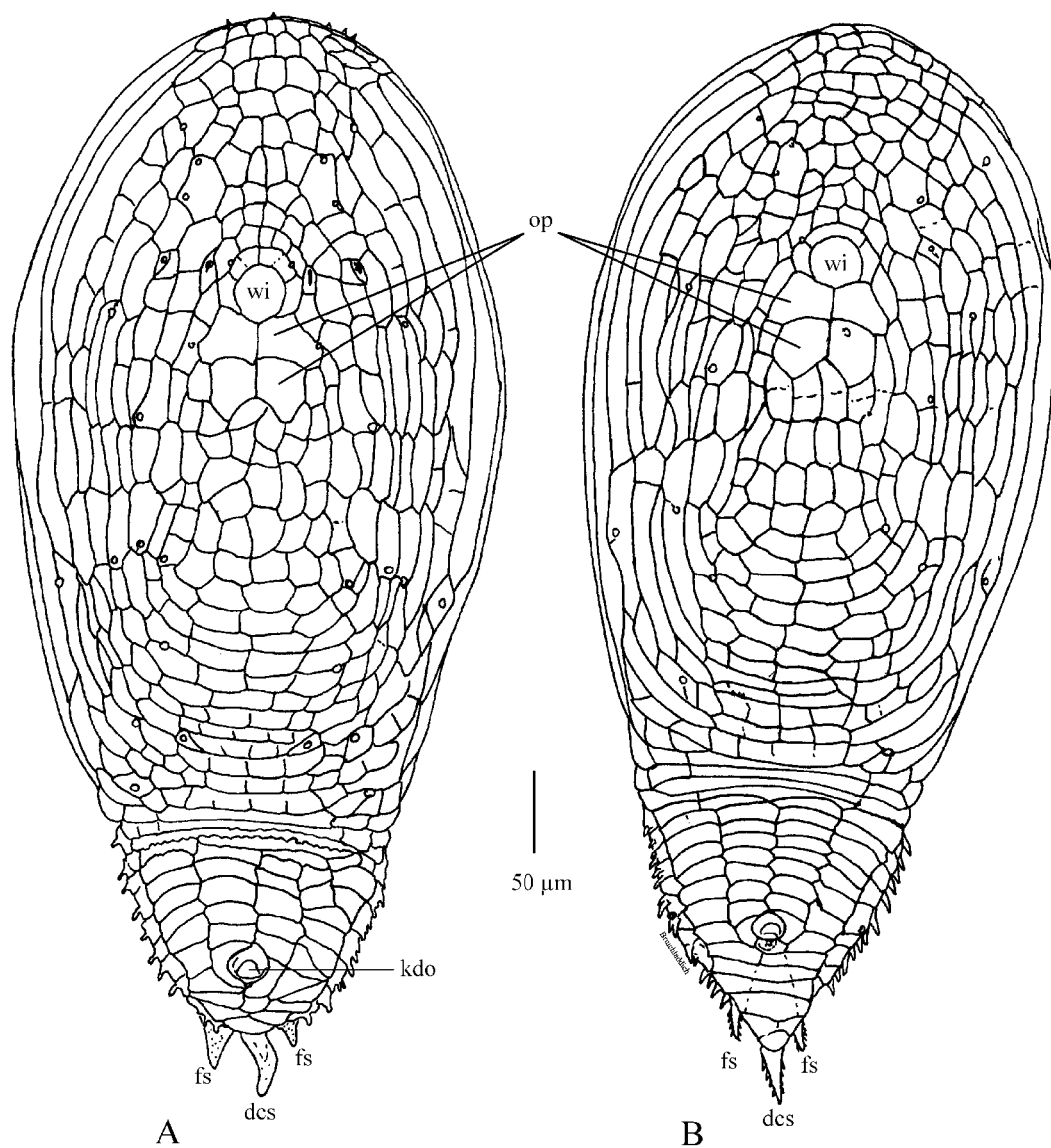
Fig. 5. *Hansenocaris itoi* sp. nov., nauplius instar 5 (exuviae). A, B. Two larvae with slightly different morphology, dorsal view; only the window plate (wi) and two pairs of occipital plates (op) behind it can with confidence be identified with specific plates in previous instars; the homology of the remaining head shield plates is uncertain. dcs – Dorsocaudal spine; fs – Furcal spines; kdo – Knob of dorsocaudal organ; op – Occipital plate; wi – Window plate.

the y-cypris are visible through the semitransparent naupliar cuticle.

The distal segment of the "two-segmented" antennules (Fig. 6C) carries ornaments of different types. A conspicuous spine projects at the base of the inner margin, and a small seta is inserted in the middle of the segment. There are two long subterminal setae,

one each on the inner and outer margins, and three terminal setae. The antenna and mandible (Fig. 6D, E) have the same segmentation as in the previous instars, although the segments of the endopod seem to be fused. As in previous instars, the coxa, basis and basal endopodal segment each carry a conspicuous spine. Those on the coxae are always without

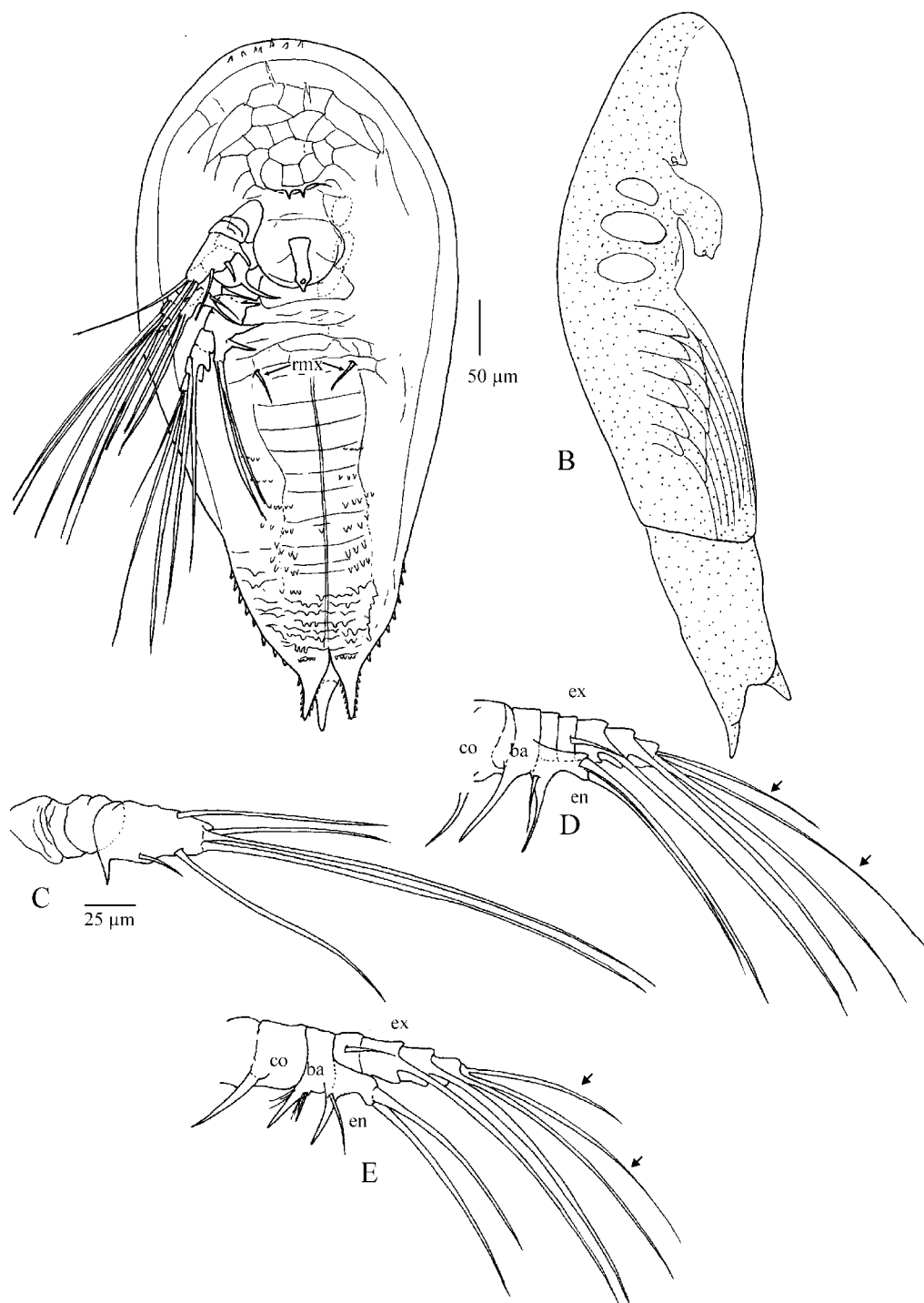Fig. 6. *Hansenocaris itoi* sp. nov., nauplius instar 5. A. Exuvium, ventral view of larva in Fig. 5B. B. Outline of y-cypris inside naupliar body, lateral view. C. Antennule. D. Antenna. E. Mandible. The setae marked with arrows in (D) and (E) sit on the apical but hidden sixth (antenna) and fifth (mandible) exopodal segments, see text. ba – Basis; co – Coxa; en – Endopod; ex – Exopod; rmx – Rudimentary maxillule.
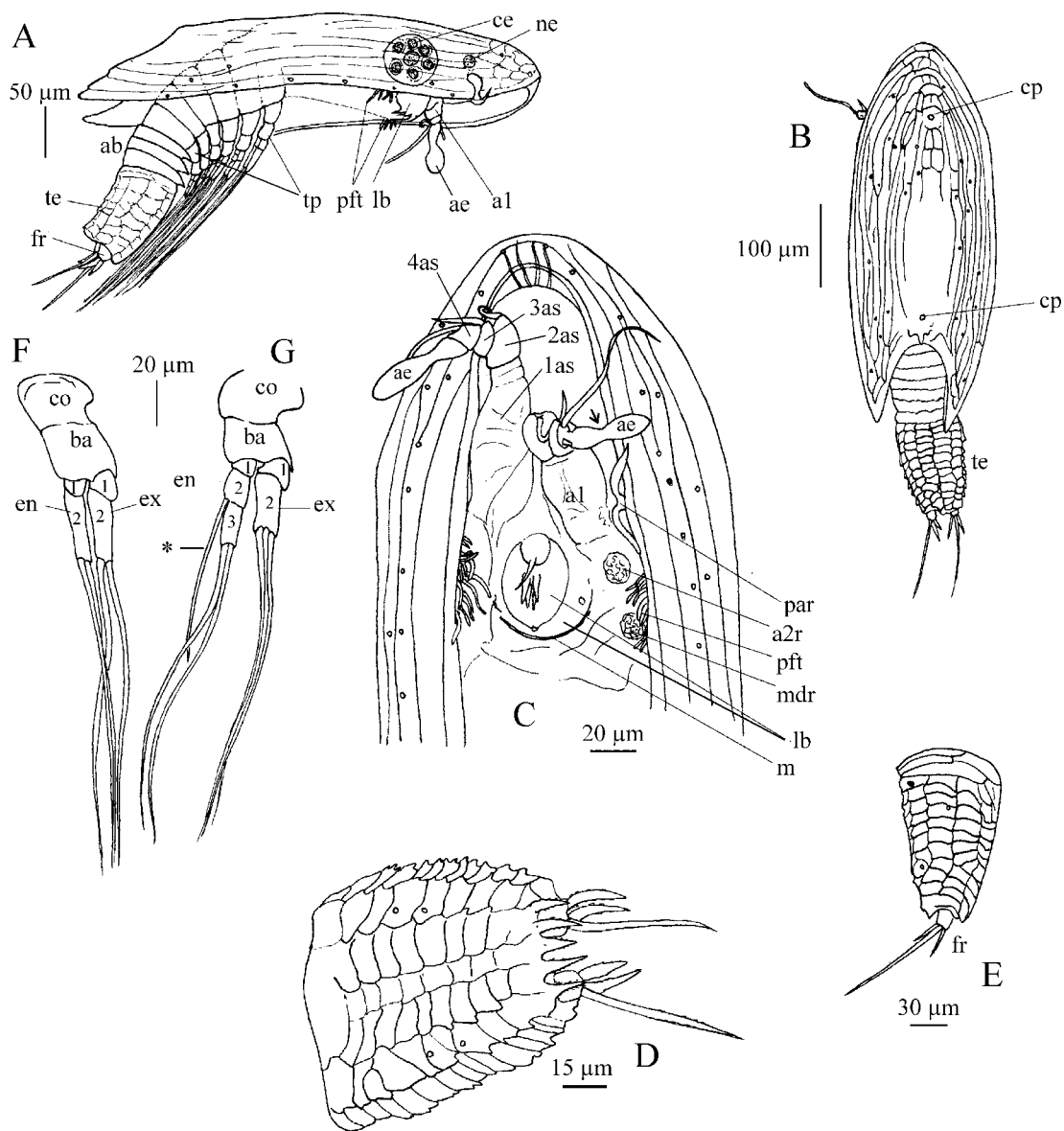
Fig. 7. *Hansenocaris itoi* sp. nov., y-cypris. A. Lateral view. B. Dorsal view. C. Anterior end, ventral view; species diagnostic constriction in aesthetasc shown by arrow. D. Telson, ventral. E. Telson, lateral. F. Thoracopod 1. G. Thoracopod 5; for the asterisked seta, see text. 1–3 – Segments of thoracopodal endo- and exopods; a1 – Antennule; 1as–4as – Antennulary segments 1–4; ab – Abdomen; ae – Aesthetasc; a2r – Rudiment of antenna; ba – Basis; ce – Compound eye; co – Coxa; cp – Central pore (in dorsal midline); en – Endopod; ex – Exopod; fr – Furcal rami; lb – Labrum; mdr – Rudiment of mandible; m – Slit with mouth; ne – Nauplius eye; par – Para-ocular process; pft – Post-ocular filamentary tuft; te – Telson; tp – Thoracopods.

ornaments. In nauplius 5 the spine on the antennary basis is also smooth, whereas the one on the mandibulary basis has numerous minute setae or denticles as in previous instars. Also as in previous instars, the basal endopod segment of both appendages carries a single seta.

Y-CYPRIS (Fig. 7A–G)

Species descriptions in the Facetotecta are usually based on characters of this instar. Unlike a cirripede cypris, the univalved dorsal head shield of the y-cypris only partially covers the larval body and extends

laterally rather than ventrally (Fig. 7A, B). The shield resembles an inverted boat, but with elongated and sharp posterior ends. Long longitudinal cuticular ridges ornament the lateral sides. Several plates occupy the anterior end and the posterior processes, whereas the medioposterior area of the shield lacks any ridges (Fig. 7B). The surface of the shield bears numerous pores forming a symmetrical pattern (Fig. 7A–C). The two large pores situated in the dorsal midline (cp in Fig. 7B) seem to represent gland openings and probably correspond to the large central pores 3 and 4 (cp3, cp4) described by Høeg & Kolbasov (2002). The small nauplius eye lies anteriorly to the large paired compound eyes (Fig. 7A). In lateral view we could only distinguish seven ommatidia (six smaller ones in a circle and a larger central one), but Grygier (1987) found two additional ommatidia pointing medioventrally in his specimens. Using the terminology of Itô & Takenaka (1988), a complex of organs including the antennules, labrum, para-ocular process, post-ocular filamentary tuft, and two pairs of rudiments of antennae and mandibles is situated under the compound eyes (Fig. 7A, C).

The antennules (Fig. 7C) consist of four segments, although the large, first segment may actually consist of several partially fused ones, as already suggested by Bresciani (1965) and Schram (1970a). The first segment resembles the basal segment of the naupliar antennule in lacking any armament and having circular cuticular folds. The second segment resembles the third, bell- or horseshoe shaped attachment segment of the antennule in cirripede cyprids. It is armed with a conspicuous curved hook ("claw") at the distal margin. We did not find the minute lateral seta described by Grygier (1987). The third, short segment bears only one lanceolate seta on the distal margin, in contrast to two such setae found by Grygier (1987). The fourth segment is small and armed terminally with one long and one very short seta. Subterminally it also carries a prominent aesthetasc, which has bulbous proximal and distal parts separated by a very characteristic constriction.

Like previous authors (Itô 1984, 1989; Itô & Ohtsuka 1984; Grygier 1987), we found two pairs of small wrinkled hillocks (Fig. 7C) just behind the antennules and lateral to the labrum. They probably represent the vestiges of the antennae and mandibles. A pair of bifurcate para-ocular processes is connected with the compound eyes (Fig. 7C) and may represent the external portion of the organs of Bellonci (Itô & Takenaka 1988). A pair of post-ocular filamentary tufts is situated posteriorly to the para-ocular processes; the tufts were shown by Itô & Takenaka (1988) to have a secretory nature (Fig. 7A, C). Each tuft consists of at least 15 setiform protrusions. The wider basal part of the labrum covers a slit with a mouth, the labrum has an ordinary structure with five prominent curved hooks, a pair of lateral pores, and an unpaired posterior pore (Fig. 7C).

The thorax consists of six segments with serrate dorsal margins, and each of them bears a pair of biramous thoracopods. The first thoracopod has two-segmented endo- and exopods sitting on a protopod consisting of a coxa and a basis. The basal segment of each ramus is short and lacks armament, but the elongated distal segment of each carries two long, terminal setae (Fig. 7F). The endopods of the remaining thoracopods (2–6) are all three-segmented. The medial, second segment bears a single long setae on the inner margin of its distal end. The distal segment bears two long, terminal setae (Fig. 7G). The exopods are two-segmented as in the first pair, although they bear three, instead of two, terminal setae. The protopod of thoracopod 6 is shorter than in the preceding ones and looks unsegmented, but a constriction indicates the coxa–basis division.

The abdomen consists of three short segments and a long telson with furcal rami (Fig. 7A). Just as in other facetotectan cyprids, each tergite of the abdominal somites has sharp pleural extensions. The telson is densely covered by chitinous ridges forming dorsal, lateral, and ventral rows of plates (Fig. 7B, D, E). Five longitudinal rows (three central and two lateral) of rectangular plates (nine to 12 in each) cover the dorsal surface of the telson (Fig. 7B). The lateral plates are grouped into four longitudinal rows, and three pairs of pores were observed on the lateral surfaces of the telson (Fig. 7E). The ventral surface consists of seven longitudinal rows of plates, and we found two pairs of pores there (Fig. 7D). Five conspicuous, serrate spines project along the posterioventral border (Fig. 7D).

A pair of unsegmented furcal rami is articulated to the telson (Fig. 7A, D, E). Each of them carries one long seta and two short, wide, and lanceolate setae with serrate margins.

COMPARISON

The features listed in the diagnosis have not been recorded from any other y-cypris assigned to species. They therefore represent autapomorphies for *H. itoi* sp. nov. The combination of several other features in the y-cypris is also diagnostic for the species. *Hansenocaris itoi* could be conspecific with the Øresund specimens studied by Bresciani (1965) and possibly also with other Atlantic y cyprids still unassigned to species. Judging from the morphology of the head shield, *H. itoi* may

Table 1. The main characters of y-cyprids of the described species.

Species	Anterior end of head shield	Para-ocular process compared with head shield	Np	Constriction of antennulary aesthetasc	Antennulary segment 2	Endopods of thoracopods 3–6	Nts
H. acutifrons	Elongated	Much shorter	9	No constriction	Without claw	Two-segmented	6
H. furcifera	Round	Much shorter	9	No constriction	With claw	Three-segmented	5
H. itoi	Round	Much shorter	15	Distinct constriction	With claw	Three-segmented	5
H. pacifica	Round	Much shorter	10–14	No constriction	With claw	Two-segmented	3
H. rostrata	Elongated	Much shorter	0	No constriction	Without claw	Two-segmented	5
H. tentaculata	Elongated	About as long	0	No constriction	Without claw	Two-segmented	0

Np – Number of protrusions of the post-ocular filamentary tuft; Nts – Number of serrate spines along the posterioventral margin of the telson.

also be conspecific with the y-cyprid from Norwegian waters studied with scanning electron microscopy by Høeg & Kolbasov (2002), but they could not adequately describe the antennule and its aesthetasc because their single specimen was mounted with the ventral side down. The main differences between the y-cyprids of the described species are listed in Table 1.

The White Sea y cyprids can easily be distinguished from *H. rostrata*, *H. acutifrons*, and *H. tentaculata* by the different shape and structure of the head shield and the para-ocular processes. Our specimens share a series of characters (structure of the head shield and head appendages, etc.) with all specimens known from the Atlantic (Bresciani 1965; Schram 1970a; Grygier 1987) and also with *H. pacifica* and *H. furcifera*. The y-cypris of *H. itoi* sp. nov. differs from them, as from other known y-cyprids, in having an antennulary aesthetasc with medial constriction and elongated lateroposterior ends of the head shield that reach the telson. It is also distinguished from the Bahamanian specimens (Schram 1970a) and from *H. pacifica* by the absence of dorsal cuticular ridges on the medioposterior part of the head shield. Contrary to that, *H. furcifera* has even more reduced cuticular ridges than seen in *H. itoi*. The naupliar instars of *H. itoi* also differ from those known for *H. furcifera,* which have a more rounded anterior margin. As one example of the detailed differences in plate arrangement, instar 2 of *H. furcifera* has several unpaired frontal plates in front of the window plate, whereas instar 2 of *H. itoi* possesses paired frontal plates.

Other differences between *H. itoi* and other faceto-tectans concern the number of protrusions in the post-ocular filamentary tuft and the segmentation and setation of the thoracopods. In *H. itoi*, the post-ocular filamentary tuft consists of at least 15 setiform protrusions. In comparison, there are 10–14 such protrusions in *H. pacifica*, nine in *H. acutifrons* (Itô 1985), 13 in Grygier's (1987) specimen, 16 in the undescribed y

cypris studied by Itô & Takenaka (1988), and nine in the paratype of *H. furcifera* (Itô 1989). The segmentation and setation of the thoracopods in *H. itoi* correspond completely with the situation in y-cyprids from Øresund (Bresciani 1965), the Bahamas (Schram 1970a), Greenland and Øresund (Grygier 1987), and *H. furcifera* (Itô 1989). They all have a two-segmented endopod in thoracopod 1 and three-segmented endopods in thoracopods 2–6. In contrast, all thoracopods of *H. pacifica*, *H. rostrata*, and *H. acutifrons*, and thoracopods 3–6 of *H. tentaculata,* possess only two-segmented endopods (in the last-mentioned species, thoracopods 1 and 2 have one-segmented endopods) (see Itô 1985, 1986b). In these four species, the position of a seta in the middle of the distal endopodal segment corresponds to a seta on the second endopodal segment in the y-cyprids with three-segmented endopods (seta marked by asterisk in Fig. 7G). We therefore agree with Schram (1970a) and Grygier (1987) in suspecting that the two distal segments are fused in Ito's specimens or that he missed an indistinct segment border.

Almost all y-cyprids possess serrate spines along the posterioventral border of the telson: three spines in *H. pacifica*; five in Bresciani's (1965), Schram's (1970a), and Grygier's (1987) specimens and in *H. rostrata*, *H. furcifera*, and *H. itoi*; six spines in *H. acutifrons*; none in *H. tentaculata*. The furcal rami of all previously described y-cyprids (except perhaps *H. acutifrons*) have a setation similar to the one described for *H. itoi*.

Steuer (1905) established a new species, *Proteolepas hanseni*, based only on a single naupliar instar of type IV from the Adriatic Sea. Itô (1985) referred to this species as *H. hanseni* (Steuer, 1905) comb. nov. It is extremely unlikely that the White Sea facetotectans belong to this species. Such characters as undivided frontal plates and others indicate that Steuer (1905) described a first naupliar instar and it differs from instar 1 of *H. itoi* in the following characters: it has a rounded anterior end and a different form of the frontal plates; it

possesses at least nine occipital plates instead of eight as in *H. itoi*; and the knob of the dorsocaudal organ is but feebly developed. It is well known that closely related species can possess very similar larvae, especially of such an early stage, and we need to obtain all larval instars to estimate the relationships between different species. Schram (1972) indicated that y-nauplii of type IV may represent different species, and Steuer's species shares characters of both types I and IV.

DISCUSSION

Hansenocaris itoi is only the second facetotectan species for which the larval development has been described. Because our instar 1 occurs very rarely in plankton, we did not observe it moulting into the next one. It is therefore possible that we have missed a stage, but against this is the fact that all of the 350 facetotectan nauplii collected from plankton could be assigned to the five instars described above. Formally, our instar 1 might also belong to another facetotectan species, but we find this very unlikely because the numerous specimens from the plankton sampled during 3 years contained no instars other than those obtained in cultures of *H. itoi*.

Grygier (1987) interpreted our "gland duct" papillae in the nauplii ("gd" in Fig. 2B) as the incipient frontal filaments, but Itô & Takenaka (1988) considered this interpretation as uncertain. Itô (1990) showed that the papillae each have a pore and probably represent the exit ducts of the "head gland", described by Elofsson (1971). The increasing number of transverse ridges developing on the ventral side of the naupliar hindbody most probably correspond to future body segments, but the exact correlation is difficult to establish without sagittal sections. The same is true for the thoracic tergites in the y-cyprid. Grygier (1987) used sections to show that thoracic segments 1 and 2 are covered by a single, joined tergite in his y-cyprids, but our whole mounts did not allow us to verify whether this is also true in *H. itoi*. Several authors have described two-segmented/bi-annulated furcal rami for some y-cyprids (Schram 1970a; Itô 1985, 1989). Kolbasov & al. (1999) showed that one-segmented furcal rami are a ground pattern feature (plesiomorphy) for the Thecostraca, but that the arms of a deeply cleft telson can masquerade as a pair of basal ramal segments. We therefore suspect that all y-cyprids will eventually be shown to have one-segmented furcal rami.

Five naupliar instars, as found in *H. itoi*, are most probably a general characteristic of the Facetotecta. They may retain the previous (really first) naupliar

instar inside the egg, but it is also possible that the first instar is very short-lived, as is seen in some rhizocephalan and many thoracican cirripedes (Costlow & Bookhout 1958; Walossek & al. 1996; Newman & Ross 2001), and so has remained unobserved. Itô (1990) also found five naupliar instars in *H. furcifera*, whereas the single naupliar instar assigned to *H. pacifica* (Itô 1986a) was later (Itô 1987b) reconsidered by him and redescribed as type XI of "… a separate species, the cypris y stage and the naupliar development of which are to be described elsewhere". Itô (1991, in Japanese without an English abstract) also illustrated the dorsal shields of several naupliar instars and a y-cypris larva for an undefined species *Hansenocaris* sp.

All the described naupliar types of the Facetotecta may be united into at least two groups. The first group consists of nauplii with a rather elongated body and numerous, well-developed plates. Nauplii described as type IV, including those of *H. itoi*, should be referred to this group, along with the nauplius of type VI (Grygier 1987), the nauplius of type VII (Itô 1986a), the nauplii of types IX, X, and XI (Itô 1987b), both "Manazuru" types I and II (Watanabe & al. 2000), and the nauplii of *H. furcifera*.

The second group comprises nauplii with a rather rounded form and a dorsal shield with fewer, often indistinct, plates and sometimes with smooth areas. Nauplii of types I, II, and III represent different instars of a single species (Schram 1970b); Pacific type I nauplii (Itô 1986a) and nauplii of type VIII (Itô 1987a) also belong to this group.

These groups have no present taxonomic value, especially when it remains unknown which y-cyprids correspond to which naupliar types. But their existence testifies to the morphological diversity of known facetotectan nauplii, which we suspect belong to different species, and most likely different higher categories.

The diversity of the Facetotecta is seen best in the y-cypris, which fall into two morphological groups. We name the first the "*H. pacifica* group". The y-cyprids of this group have a head shield with a rounded anterior end and sharp, laterally elongated posterior margins, with different degrees of ornamentation with cuticular ridges, and a second antennulary segment with a curved hook. Where studied with scanning electron microscopy, the head shield also carries the five pairs of lattice organs (Høeg & Kolbasov 2002). All the Atlantic y-cyprids, including those of *H. itoi*, and also *H. pacifica* and *H. furcifera*, belong to this group. Its representatives differ with respect to thoracopod segmentation.

Other y-cyprids have an elongated, often sharp, anterior end, a head shield shorter than in the "*H.*

pacifica group" and almost lacking well-developed cuticular ridges, and a second antennnary segment without a curved hook. *Hansenocaris rostrata*, *H. acutifrons*, and *H. tentaculata* belong to this group, which has hardly any taxonomic value because the very distinct morphology of *H. tentaculata* (the two segmented abdomen) makes this species different from other facetotectans.

Character state differences, such as supposedly unsegmented or two segmented caudal rami in different y cyprids and the position of the antennnary aesthetasc on the third or subterminally on the fourth segment, seem to be misinterpretations and need to be critically reinvestigated by means of transmission and scanning electron microscopy.

We have indicated how the morphological diversity of y-cyprids allows the known facetotectans to be placed into some informal groups. Only a cladistic analysis of these characters, perhaps also including naupliar traits, can establish true monophyletic taxa. Even then, the erection of formal supraspecific categories within the Facetotecta should probably await the discovery of the adult stages.

REFERENCES

Almeida Prado-Por MS, Por FD. 1988. "Y" Crustacean larvae (order Facetotecta) in the plankton of the Gulf of Aqaba (Eilat), Red Sea. *Rapport et procès-verbaux des réunions. Commision internationale pour l'explorations scientifique de la Mer Méditerranée* 31(2):302.

Apstein C. 1905. Plankton in Nord und Ostsee auf den deutschen Terminfahrten. *Wissenschaftliche Meeresuntersuchungen der Kommission zur wissenschaftlichen Untersuchung der deutschen Meere Abt. Kiel* 9:1–26, Anhang:1–58.

Bocquet Védrine J. 1972. Supression de l'ordre des Apodes (Crustacés, Cirripèdes) et rattachement de son unique représentant, *Proteolepas bivincta*, à la famille des Crinoniscidae (Crustacés, Isopodes, Cryptonisciens). *Comptes Rendus de l'Académie des Sciences Paris Série D* 275:2145–2148.

Bresciani J. 1965. Nauplius "y" Hansen: its distribution and relationship with a new cypris larva. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening* 128:245–258.

Costlow JD Jr, Bookhout CG. 1958. Larval development of *Balanus amphitrite* var. *denticulatus* Broch reared in the laboratory. *Biological Bulletin* 114:284–295.

Darwin CR. 1854. *A monograph on the subclass Cirripedia, with figure of all the species*. London: Ray Society. 684 p.

Davis CC. 1982. A preliminary quantitative study of the zooplankton from the Conception Bay, insular Newfoundland, Canada. *Internationale Revue gesamten Hydrobiologie* 67(5):713–747.

Davis CC. 1986. A comparison of the zooplankton in two Newfoundland bays with differing influences from major currents. *Internationale Revue gesamten Hydrobiologie* 71(1):11–47.

Elofsson R. 1971. Some observations on the internal morphology of Hansen's nauplius y (Crustacea). *Sarsia* 46:23–40.

Grygier MJ. 1985. Comparative morphology and ontogeny of the Ascothoracida, a step toward a phylogeny of the Maxillopoda. *Dissertation Abstracts International Section B* 45(8):2466B–2467B.

Grygier MJ. 1987. New records, external and internal anatomy, and systematic position of Hansen's Y larvae (Crustacea: Maxillopoda: Facetotecta). *Sarsia* 72:261–278.

Grygier MJ. 1996. Classe des Thécostracés (Thecostraca Gruvel, 1905): Sous-classe des Facetotecta (Facetotecta Grygier, 1985). In: Forest J, editor. *Traité de zoologie: anatomie, systématique, biologie, tome VII, Crustacés, fascicule 2*. Paris: Masson. p 425–432.

Hansen HJ. 1899. Die Cladoceren und Cirripedien der Plankton Expedition. *Ergebnisse der Plankton Expedition der Humboldt Stiftung* 2 (G, d):1–58, pl. 1–4.

Hensen V. 1887. Über die Bestimmung des Planktons oder des im Meere treibenden Materials an Pflanzen und Thieren. *Bericht der Kommision zur wissenschaftlichen Untersuchung der deutschen Meere* 5, XII bis XVI Jahrgang:1–108, pl. 1–6.

Høeg JT, Kolbasov GA. 2002. Lattice organs in y-cyprids of the Facetotecta and their significance in the phylogeny of the Crustacea Thecostraca. *Acta Zoologica (Stockholm)* 83:67–79.

Hoek PPC. 1909. Die Cirripedien des nordischen Planktons. *Nordisches Plankton* 8:265–331.

Hulings NC. 1989. A review of marine science research in the Gulf of Aqaba. *Publications of the Marine Science Station Aqaba, Jordan* 6(xix). 267 p.

Itô T. 1984. Another cypris y from the North Pacific, with reference to the bending behavior exhibited by a cypris y specimen of the formerly described type (Crustacea:

Maxillopoda). *Publications of the Seto Marine Biological Laboratory* 29(4/6):201–224.

Itô T. 1985. Contributions to the knowledge of cypris y (Crustacea: Maxillopoda) with reference to a new genus and three new species from Japan. *Special Publication of the Mukaishima Marine Biological Station* 1985:113–122.

Itô T. 1986a. Three types of "nauplius y" (Maxillopoda: Facetotecta) from the North Pacific. *Publications of the Seto Marine Biological Laboratory* 31(1/2):63–73.

Itô T. 1986b. A new species of "cypris y" (Crustacea: Maxillopoda) from the North Pacific. *Publications of the Seto Marine Biological Laboratory* 31(3/6):333–339.

Itô T. 1987a. Three forms of nauplius y type VIII larvae (Crustacea: Facetotecta) from the North Pacific. *Publications of the Seto Marine Biological Laboratory* 32(1/3):141–150.

Itô T. 1987b. Proposal of new terminology for the morphology of nauplius y (Crustacea: Maxillipoda: Facetotecta), with provisional designation of four naupliar types from Japan. *Zoological Science* 4:913–918.

Itô T. 1989. A new species of *Hansenocaris* (Crustacea: Facetotecta) from Tanabe Bay, Japan. *Publications of the Seto Marine Biological Laboratory* 34(1/3):55–72.

Itô T. 1990. Naupliar development of *Hansenocaris furcifera* Itô (Crustacea: Maxillopoda: Facetotecta) from Tanabe Bay, Japan. *Publications of the Seto Marine Biological Laboratory* 34(4/6):201–224.

Itô T. 1991 (dated 1990). Observation of the larval development of nauplius y (Crustacea: Facetotecta) in the laboratory. *Annual Report of the Seto Marine Biological Laboratory* 4:55–60 (in Japanese).

Itô T, Ohtsuka S. 1984. Cypris y from the North Pacific (Crustacea: Maxillopoda). *Publications of the Seto Marine Biological Laboratory* 29(1/3):201–224.

Itô T, Takenaka M. 1988. Identification of bifurcate paraocular process and postocular filamentary tuft of facetotectan cyprids (Crustacea: Maxillopoda). *Publications of the Seto Marine Biological Laboratory* 33(1/3):19–38.

Kolbasov GA, Høeg JT, Elfimov AS. 1999. Scanning electron microscopy of acrothoracican cypris larvae (Crustacea, Thecostraca, Cirripedia, Acrothoracica, Lithoglyptidae). *Contributions to Zoology* 68(3):143–160.

Kikuchi T, Takahashi K, Gamo S. 1991. Nauplius y (Crustacea: Maxillopoda: Facetotecta) from Manazuru, Sagami Bay, Central Japan. *Reports of the Manazuru Marine Laboratory for Science Education, Faculty of Education, Yokohama National University* 7:67–75 (in Japanese with an English summary).

Lohmann H. 1908. Untersuchungen zur Feststellung des vollständigen Gehaltes des Meeres an Plankton. *Wissenschaftliche Meeresuntersuchungen der Kommission zur wissenschaftlichen Untersuchung der deutschen Meere Abt. Kiel* 10:131–370.

McMurrich JP. 1917. Notes on some Crustacean forms occurring in the plankton of Passamaquoddy Bay. *Transactions of the Royal Society of Canada Series 3* 11(4):47–61.

Mileikovsky SA. 1968. Distribution of pelagic larvae of bottom invertebrates of the Norwegian and Barents Seas. *Marine Biology* 1(3):161–167.

Mileikovsky SA. 1970. [Distribution of pelagic larvae of bottom invertebrates in the Kurile–Kamchatka area]. *Trudy Instituta Okeanologii* 86:117–133 (in Russian).

Newman WA, Ross A. 2001. Prospectus on larval cirriped setation formulae, revisited. *Journal of Crustacean Biology* 21(1):56–77.

Ohtsuka S, Grygier MJ, Torigoe K. 1999. The phylogeny, zoogeography, and ecology of marine cavernicolous crustaceans. *Taxa* 6:3–13 (in Japanese with an English abstract).

Runnström S. 1931. Eine Übersicht über das Zooplankton des Herdla und Hjeltefjordes. *Bergens Museums Årbok. Naturvidenskabelig Række* 7:1–67.

Schram FR. 1986. *Crustacea*. Oxford: Oxford University Press. 606 p.

Schram TA. 1970a. Marine biological investigations in the Bahamas 14. Cypris Y, a later developmental stage of nauplius Y Hansen. *Sarsia* 44:9–24.

Schram TA. 1970b. On the enigmatic larva nauplius Y type I Hansen. *Sarsia* 45:53–68.

Schram TA. 1972. Further records of nauplius Y type IV Hansen from Scandinavian waters. *Sarsia* 50:1–24.

Steuer A. 1904. Mitteilungen aus der k.k. zoologischen Station in Triest. Nr. 9. Über zwei interessante Larvenformen aus dem Plankton des Triester Golfes. *Zoologischer Anzeiger* 28(7):228–230.

Steuer A. 1905. Über eine neue Cirripedienlarve aus dem Golfe von Triest. *Arbeiten aus dem Zoologischen Institut der Universität Wien u. der Zoologischen Station in Triest* 15:113–118.

Walossek D, Høeg JT, Shirley TC. 1996. Larval development of the rhizocephalan cirripede *Briarosaccus tenellus* (Maxillopoda: Thecostraca) reared in the laboratory: a scanning electron microscopy study. *Hydrobiologia* 328:9–47.

Watanabe H, Takahashi K, Toda T, Kikuchi T. 2000. [Distribution and seasonal occurrence of nauplius y (Crustacea: Maxillopoda: Facetotecta) in Manazuru Port, Sagami Bay, Central Japan]. *Taxa* 9:4–12 (in Japanese with an English abstract).