

**A NEW SPECIES OF THE Y-LARVA GENUS *HANSENOCARIS* ITÔ, 1985
(CRUSTACEA: THECOSTRACA: FACETOTECTA) FROM INDONESIA, WITH
A REVIEW OF Y-CYPRIDS AND A KEY TO ALL THEIR DESCRIBED SPECIES**

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ABSTRACT. – A y-cypris larva, representing a new species of *Facetotecta* from Indonesia, was found in the gut of the cardinalfish *Pterapogon kauderni*. Its external morphology was examined using scanning electron microscopy (SEM). Features such as the anterior papilliform protrusions, the short head shield and the lack of pointed posteroventral extensions of the third abdominal segment are the most distinctive attributes of the new species. The morphological character state distribution among the different species of this genus and recommendations for future descriptions are discussed. A key is provided for the species of *Facetotecta* that have been described from the cypris y stage.

KEY WORDS. – *Facetotecta*, y-cypris, SEM, taxonomy, morphology, description standards, key, Indonesia, Banggai cardinalfish.

INTRODUCTION

Enigmatic facetotectan nauplii and cyprids, often referred to as ‘y-larvae’, have been found in the plankton in many seas. Grygier (1996) and Ponomarenko (2006) provided a concise review of the group. Hensen (1887), who was the first to observe these nauplii from plankton in the Bay of Kiel, could not assign them to any known adult crustacean. The first illustrated report, by Hansen (1899), concerned five different “types” of nauplius y from widely scattered North and Equatorial Atlantic waters; he suggested that they may represent 10 or 12 cirripede species belonging to Darwin’s (1854) order Apoda (the genus *Proteolepas*). Subsequently, y-nauplii were reported from the North Sea, Norwegian Sea, Maritime Canada and the Baltic Sea (Apstein, 1905; Lohmann, 1908; McMurrich, 1917; Runnström, 1932; Fish & Johnson, 1937). Steuer (1904, 1905) attributed a single instar of nauplius y (Type IV of Hansen’s classification) that he found in the Gulf of Trieste to the new species *Proteolepas hanseni*, belonging to the Cirripedia, Apoda. 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 *Proteolepas hanseni* continues to remain a dubious species.

The finding of a post-naupliar larval instar, called ‘cypris y’ because of its resemblance to the cypridiform larvae of both the Cirripedia and the Ascothoracida (Bresciani, 1965), revived interest in these crustaceans. New records and descriptions of different y-larvae from the North Atlantic, Arctic and North Pacific, including y-cyprids, were made by Mileikovsky (1968, 1970), Schram (1970a, b, 1972), Elofsson (1971), Davis (1982, 1986), Grygier (1987) and Kolbasov & Høeg (2003). Several types of y-nauplii and y-cyprids were described or recorded from coastal waters of Japan (Itô & Ohtsuka, 1984; Itô, 1984, 1985, 1986a, b, 1987a, b, 1989, 1990, 1991; Kikuchi et al., 1991; Watanabe et al., 2000) and the Russian Far-East (Ponomarenko & Korn, 2006), from the Gulf of Aqaba and elsewhere in the Red Sea and Gulf of Aden (Almeida Prado-Por & Por, 1988; Böttger-Schnack, 1995), a marine cave in the Canary Islands (Ohtsuka et al.,

1999) and from around Rodrigues and the Seychelles, islands in the Indian Ocean (Conway et al., 2003). Elofsson (1971), Itô & Takenaka (1988) and Grygier (1987) studied various aspects of the internal morphology of y-larvae in detail and discussed their relationships with other maxillopodan taxa. Grygier (1985) erected a new subclass Facetotecta for all y-larvae, placing them inside the class Thecostraca together with the Ascothoracida and Cirripedia (Grygier, 1987). More recently, Kolbasov & Pegova (2001) discussed these relationships based on their finding of tetraploid somatic cells in one kind of y-larva and Høeg & Kolbasov (2002) confirmed the presence of special chemosensory lattice organs in various y-cyprids, thus demonstrating that these organs are an autapomorphy for all the Thecostraca.

Rejecting an informal taxonomy for y-larvae, Itô (1985) proposed the new genus *Hansenocaris* for his three new species (*H. pacifica*, *H. rostrata* and *H. acutifrons*) described on the basis of their respective y-cyprids. Three other new species were later described: *H. tentaculata* Itô, 1986 and *H. furcifera* Itô, 1989, from coastal waters of Japan, and *H. itoi* Kolbasov & Høeg, 2003 from the White Sea. Of these, both the cypris and naupliar stages have been described for *H. furcifera* (see Itô, 1990) and *H. itoi* (see Kolbasov & Høeg, 2003) but only the cypris for *H. tentaculata*. Most recently, Belmonte (2005) described four new species of *Hansenocaris* from Mediterranean coastal waters of southern Italy based on the nauplius y stage: *H. corvinae*, *H. leucadea*, *H. mediterranea* and *H. salentina*. There are a great many undescribed species of y-larvae in Japanese waters (e.g. Itô, 1991; Grygier, 1991, 1995; Høeg, 2005). We take this opportunity to describe a new species from Indonesia, based on its cypris-y stage found in the stomach of a coral reef fish endemic to the Banggai Archipelago of eastern Indonesia. Two of us (AAV and VNI) discovered the specimen, sorted and identified fish gut contents, and provided information about the fish. However, the description itself was prepared by the first two authors (GAK and MJG). The authorship of the new species described here should only contain the names of the first two authors.

MATERIALS AND METHODS

A single y-cypris was found in the stomach of the cardinalfish *Pterapogon kauderni*. The digestive tract of the fish was removed under a dissecting microscope. The stomach and intestines were opened using a scalpel and surgical needles and their contents were washed with alcohol into Petri dishes. Food items were cleaned using 70% ethanol and fine needles, and transferred with pipettes to clean Petri dishes for qualitative–quantitative analysis. The food items were then preserved in 70% ethanol in a labeled vial. A single y-cypris was found among them. The y-cypris was mounted on a slide in glycerol and studied with Olympus™ BX51 light compound microscope. For scanning electron microscopy (SEM) investigation it was dehydrated in acetone and critical-point-dried in CO₂. The dried specimen was sputter-coated with gold and examined with a 15 kV accelerating voltage with a HITACHI™ S405A in Moscow.

List of abbreviations. – *al* – antennules, *ab* – abdomen, *ae* – aesthetasc, *ba* – basis, *ce* – compound eyes, *co* – coxa, *en* – endopod, *ex* – exopod, *fr* – furcal rami, *ho* – antennular hook, *hs* – head shield/carapace, *lb* – labrum, *lo* (1–5) – lattice organs, *ne* – nauplius eye, *po* – cuticular pore, *te* – telson, *th* – thorax, *thp* – thoracopods, *ts* – terminal spines of telson.

TAXONOMY

Hansenocaris Itô, 1985

Hansenocaris papillata, new species (Figs. 1–4)

Material examined. – Holotype: One y-cypris in the gut of the fish *Pterapogon kauderni* Koumans, 1933 (Teleostei, Apogonidae) (size: SL = 24 mm, TL = 40.5 mm, sex = male), collected by A. A. Vagelli with hand nets using SCUBA and preserved immediately in alcohol. Collection date: 3 Feb. 2001. Type locality: off Masoni [=Island], Banggai [=Archipelago], eastern Indonesia (01°45'56.7"S 124°08'48.5"E), depth 2.2 m. The holotype mounted on an SEM stub is deposited in the Zoological Museum of Moscow State University (no. Mg. 1213). A CD-ROM containing all the digital SEM photographs that were taken of the specimen has also been deposited there for permanent reference.

Diagnosis. – Y-cyprid with short head shield, its anterior end slightly produced and its posteriolateral ends not reaching the abdomen; pair of conspicuous ventral papilliform protrusions at anterior end of head shield (the clearest autapomorphy of the species); antennules with conspicuous, curved claw; pleural extensions of thoracomeres 5 and 6 of trapezoidal shape; abdomen four-segmented, first three segments lacking pointed posteroventral extensions (square posteroventral corners in the first two) and third segment small; telson with serrate spines along posteroventral margin.

Etymology. – From the Latin *papillatus* – budlike, referring to the pair of papilliform protrusions at the anterior end.

Description. – General appearance: the body consists of a head, a six-segmented thorax and a four-segmented abdomen (Fig. 1). The total length is approximately 340 µm. The head shield (or carapace) covers the head and the anterior part of the thorax, although it is free from the latter. The small nauplius eye lies dorsally to the pair of large compound eyes. It was impossible to trace in detail the number and positions of the ommatidia of the compound eyes. The labrum and antennules are situated on the ventral side of the head, under the compound eyes. Each thoracic segment bears a pair of biramous thoracopods. The fourth abdominal segment or telson is the largest and it terminates in a pair of furcal rami.

Head shield (Figs. 1, 2, 3A, B): the short, univalved head shield only partially covers the dorsal and lateral sides of the larval body, with the shield's lateral sides extending to the fourth thoracic segment (Figs. 1, 2A, B). This shield resembles an inverted boat with the posteriolateral parts somewhat produced, about 215 µm long along the mid-

dorsal line and 240 μm along the lateral margins. Long longitudinal, short transverse and oblique cuticular ridges outline 'plates' that occupy the anterior and lateral sides of the head shield, whereas the mid-dorsal area possesses indistinct longitudinal ribs only. A conspicuous narrow groove, 18 μm long, is situated along the mid-dorsal line in the centre of the head shield (Fig. 2B). The surface of the head shield bears numerous pores and pore-like pits in a symmetrical pattern (Fig. 2B), comprising three major types. The first type has a slit-like, somewhat puckered opening enclosed by a conspicuous circular rim (Figs. 2E, 3A, B). The second type is a deep pit with a round mouth from which a single short seta protrudes (Figs. 2, 3A). The third type are small paired pores (including the terminal pores of the lattice organs) and bigger unpaired, so-called central pores (*cp*), all with round mouths and possessing neither a cuticular rim nor a seta (Fig. 2). There are at least three of these unpaired central pores in the mid-dorsal line, two situated anteriorly and one posteriorly (Figs. 2B–F). A pair of unusual papilliform protrusions is located at the anterior end of the cypris, arising ventrally from the lateral margins of the head shield (Figs. 1, 2A, 3A, B). They are about 7 μm long, converge slightly towards their distal ends and have a round opening at the tip.

Lattice organs (Figs. 2B–F): we found four pairs of lattice organs (*lo*) on the surface of the head shield, situated near the mid-dorsal line and grouped into two anterior and two posterior pairs. The anterior pairs (*lo1* and *lo2*) are demarcated from the general cuticle by a weak depression and as a group surround the most anterior of the unpaired central pores 30–40 μm from the anterior end of the head shield (Figs.

2B–D). The cuticle of the lattice organs is smooth and lacks any trace of small pores comprising a pore field. The first pair (*lo1*) have a teardrop-like form about 6.7 μm long and 2.7 μm wide; they converge strongly anteriorly and each narrows posteriorly towards the small terminal pore (Fig. 2D). The second pair (*lo2*) are elongate, 14 μm long and about 2 μm wide; they converge anteriorly and each narrows weakly towards the tiny, posterior terminal pore (Fig. 2D).

In our specimen we have not found the usual third pair of lattice organs, which in *H. itoi* normally sits in front of the posterior unpaired central pore (Høeg & Kolbasov, 2002). The posterior pairs of lattice organs (*lo4* and *lo5*) are situated near the most posterior central pore and lie within conspicuous, posteriorly tapered, cuticular ridges or keels (Figs. 2E, F). They do not possess visible terminal pores, but their shape indicates a posterior position for the pore of each. The *lo4*, each about 8 μm long and 2 μm wide, converge anteriorly whereas the *lo5*, each about 12 μm long and 3 μm wide, converge weakly anteriorly.

Antennules (Figs. 1, 3A, C, D, G): the antennules are covered by shrunken cuticle, which hides all traces of segmentation (Fig. 3C). Their distal parts bear a conspicuous curved hook ('claw'), a corrugated aesthetasc, and a single seta (Figs. 3C, D).

Other cephalic structures: the distal part of the labrum has one anterior and four posterior prominent hooks (Figs. 1, 2A, G). We did not find vestiges of antennae or mandibles, nor any trace of a pair of bifurcate paraocular processes associated with the compound eyes or a pair of postocular filamentary tufts situated more posteriorly.

Thorax and thoracopods (Figs. 1, 2A, 3A, E–G, 4A, B): the thorax consists of six segments (Figs. 1, 4A) with serrate posterior margins (Fig. 4B). We could not determine whether the tergites of the first two segments were dorsally fused (cf. Grygier, 1987). Each tergite is also equipped with two or three transverse, serrated cuticular ridges (Figs. 4A, B). The tergites of the fifth and sixth thoracic segments have trapezoidal pleural extensions with sharp posterior ends (Figs 3F, 4A, C). Each thoracomere bears a pair of biramous thoracopods.

Each thoracopod consists of a basal array of sclerites, a coxa, a basis, and a pair of rami (exopod and endopod). The first limb has two-segmented endo- and exopods, each with a short proximal segment lacking armament and an elongate distal segment bearing two terminal setae (Figs. 3A, E, G). The distal segment of the exopod has a short outer seta and a long inner seta whereas the endopod bears two long setae (Fig. 3E). The exopods of the remaining thoracopods (2–6) are two-segmented as in the first pair, but they have three, instead of two, terminal setae: one short outer seta and two long middle and inner setae (Figs. 3E–G). The endopods are all three-segmented; the second segment has a single long inner seta on its distal end while the distal segment bears two long terminal setae. The protopod of thoracopod 6 is shorter than the others and appears unsegmented (Fig. 4A).

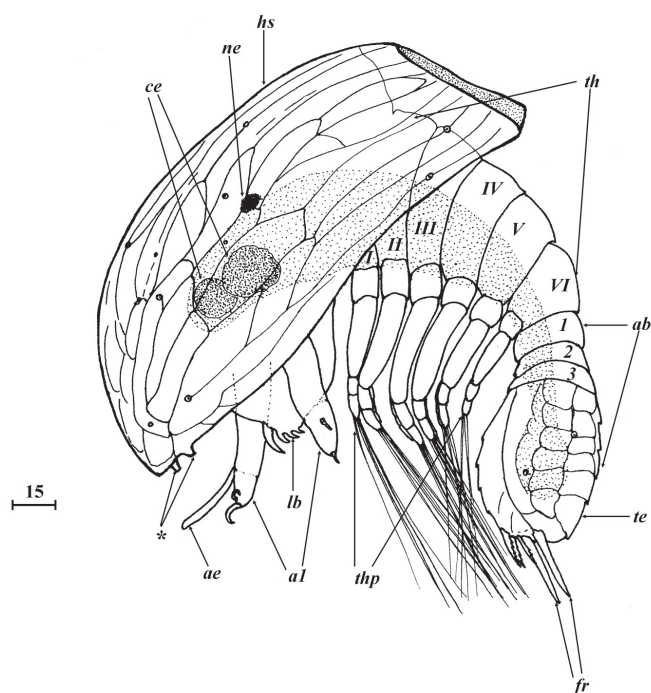


Fig. 1. *Hansenocaris papillata*, new species, habitus of holotype y-cypris, lateral view, with anterior papilliform protrusions indicated by asterisk, thoracic and abdominal segments numbered in Roman and Arabic numerals respectively. Scale bar = 15 μm .

Abdomen (Figs. 1, 2A, 4A, C–E): the abdomen consists of three short segments and a long telson with furcal rami. The third segment is the shortest, tapering ventrally and intercalated between the second segment and the telson (Fig. 4A). The abdominal segments have serrate margins, and the first and second segments have quadrangular pleural

extensions with sharp posteroventral corners. The telson is densely covered by serrate, ridges that outline two dorsal and two lateral longitudinal rows of ‘plates’, whereas the ventral face lacks such ridges (we did not notice any conspicuous sculpture on the ventral face). Four pairs of lateral pores are present on the telson, two at the anterior end (Fig. 4C)

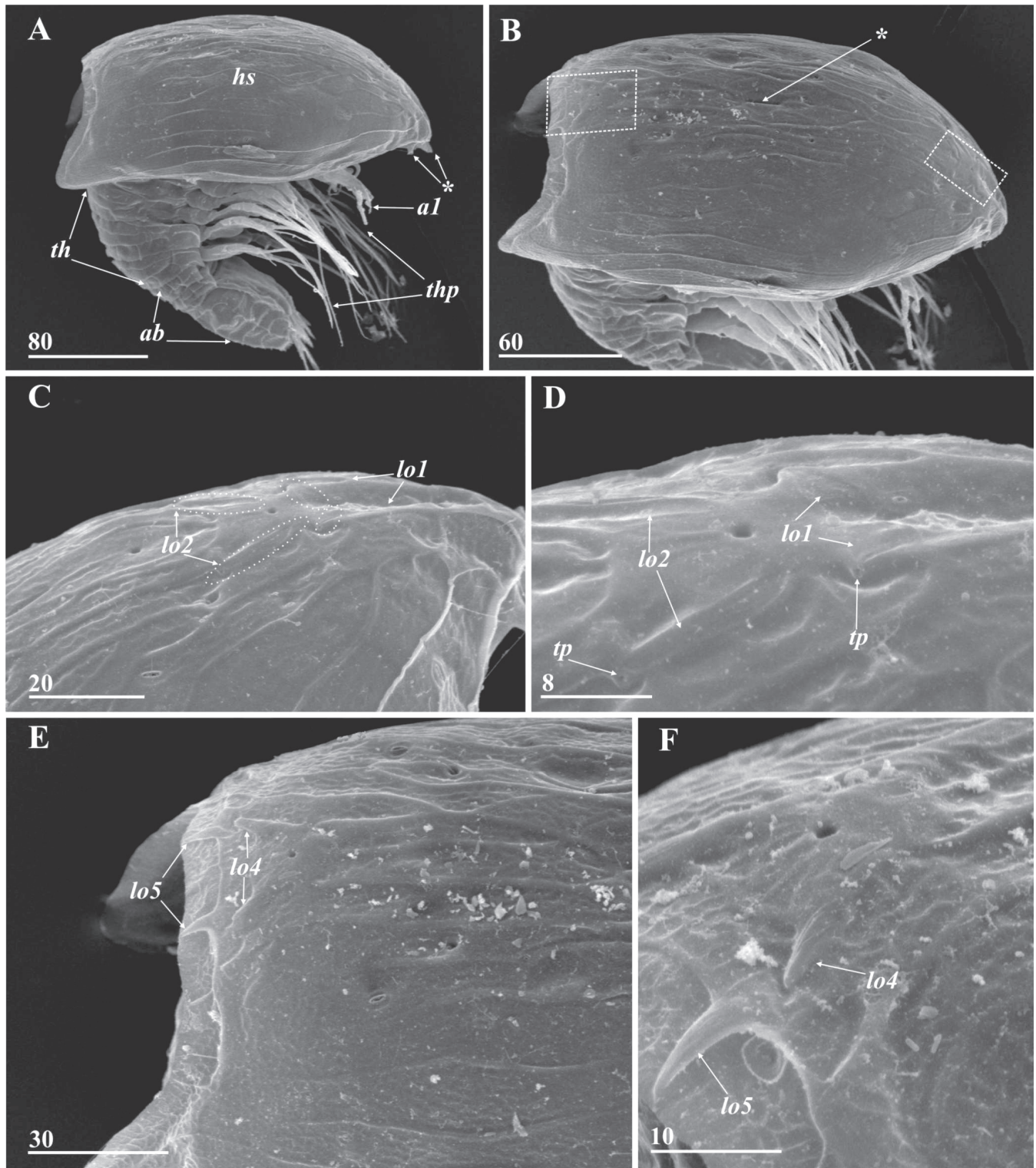


Fig. 2. *Hansenocaris papillata*, new species, general appearance and ultrastructure of head shield of holotype y-cypris, SEM: A – general appearance, lateral view, with anterior papilliform protrusions indicated by asterisk; B – head shield, dorsolateral view, with locations of anterior and posterior pairs of lattice organs indicated by rectangles, medial groove indicated by asterisk; C – anterior part of head shield, with anterior lattice organs surrounded by dotted ellipses; D – anterior pairs of lattice organs; E – posterior part of head shield; F – posterior pairs of lattice organs. Scale bars in μm .

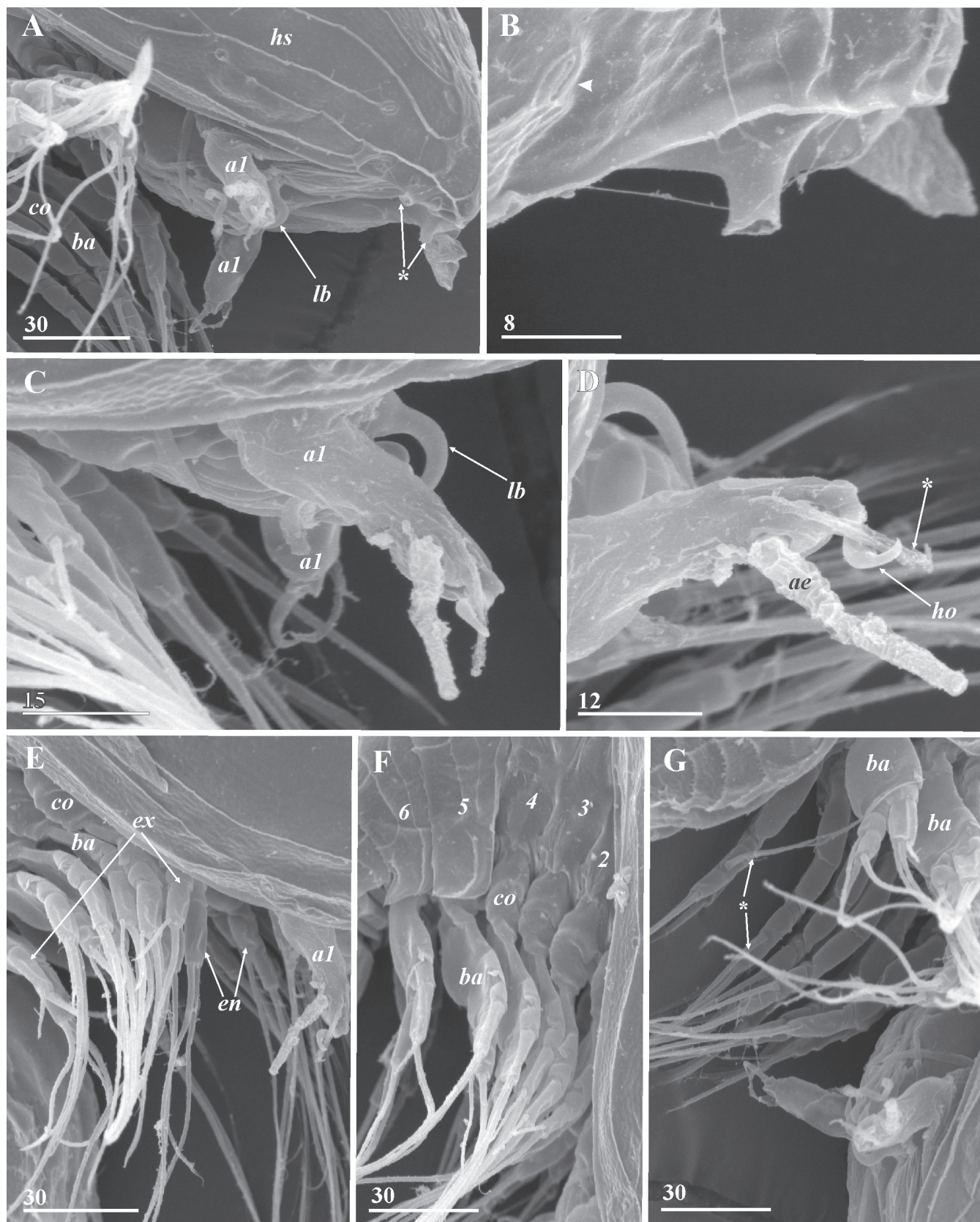


Fig. 3. *Hansenocaris papillata*, new species, holotype y-cypris, morphological details, SEM: A – anterior end, ventrolateral view, with papilliform protrusions indicated by asterisk; B – ventral papilliform protrusion at anterior end, with cuticular pore of head shield indicated by arrowhead; C – labrum, lateral view; D – antennule, distal part; E – thoracopods, anteriolateral view; F – thoracopods, lateral view, with thoracic segments numbered; G – thoracopods, rear view, with seta on inner margin of second segment of endopod indicated by asterisk. Scale bars in μm .

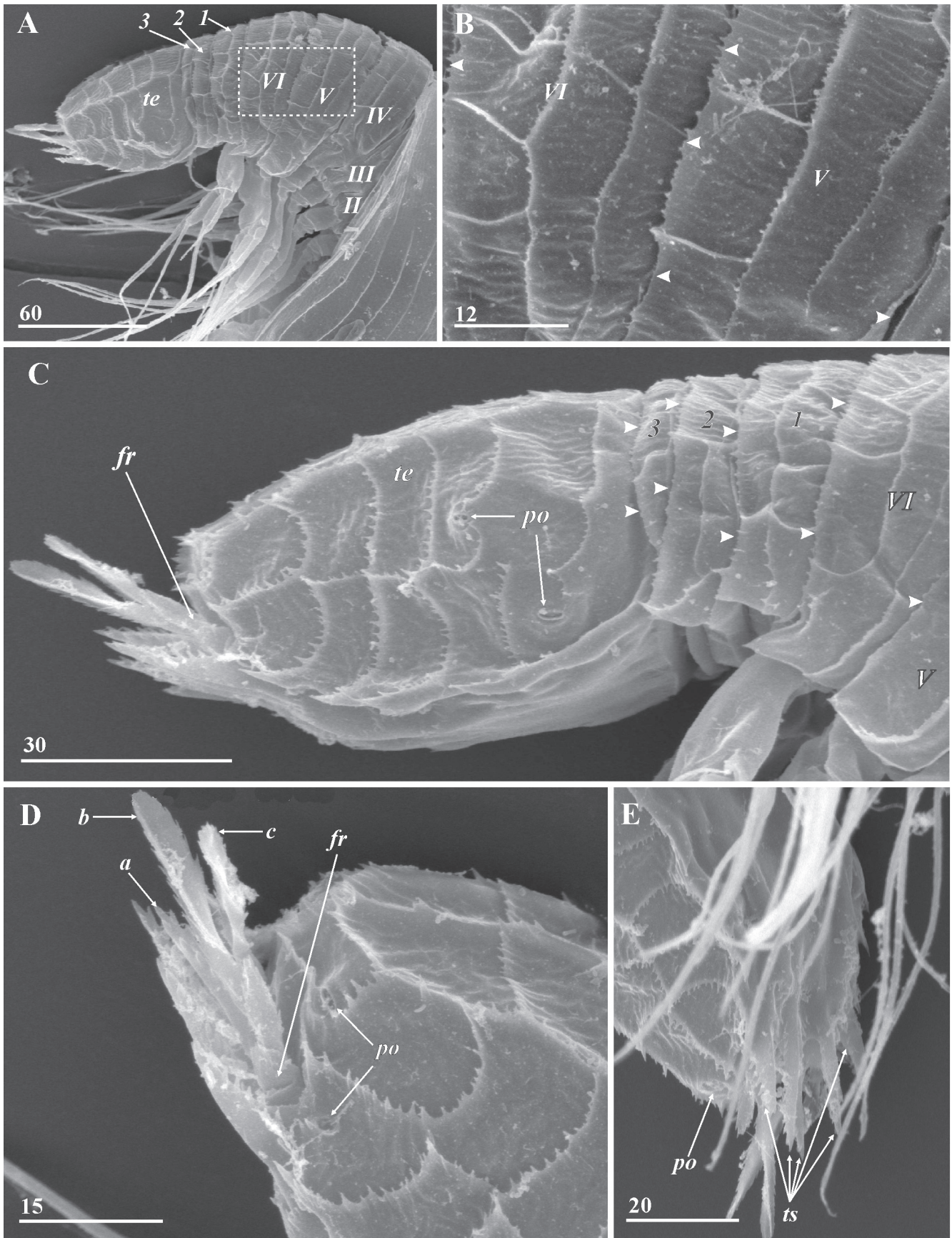


Fig. 4. *Hansenocaris papillata*, new species, holotype y-cypris, morphology of thorax and abdomen, SEM: A – trunk, lateral view, with thoracic and abdominal segments numbered in Roman and Arabic numerals, respectively; B – close-up of rectangle in Fig. 4A showing cuticle of fifth and sixth thoracic segments, with borders of segments indicated by arrowheads; C – posterior part of trunk, with thoracic and abdominal segments numbered in Roman and Arabic numerals respectively, borders of segments indicated by arrowheads; D – posterior part of telson, dorsolateral view, with furcal setae designated as “a”, “b” and “c”; E – posterior part of telson, ventrolateral view. Scale bars in μm .

and two near the furcal rami (Fig. 4D). Five conspicuous and serrate terminal spines project along the posteroventral border of the telson (Figs. 4C–E).

A pair of short, unsegmented furcal rami is inserted in the posterior end of the telson (Figs. 4C, D). Each ramus carries three wide, lanceolate setae of different lengths, with serrate margins.

Comparison. – The anterior papilliform protrusions, the short head shield, and the lack of pointed posteroventral extensions of the first three abdominal segments are the most distinctive characteristics of *H. papillata*.

Six of the 11 previously described facetotectan species were established on the basis of y-cypris characters (Table 1), the other five on the nauplius y phase. The first of the latter, *Proteolepas hanseni*, was described from the Adriatic Sea based only on a single instar (Steuer, 1905). Later, Itô (1985) referred to this species as *Hansenocaris hanseni* (Steuer, 1905), new combination. It displays characters of both naupliar types I and IV of Hansen (1899), and therefore *H. hanseni* remains a species of dubious recognition (Kolbasov & Høeg, 2003). Recently, four more facetotectan species were described on the basis of naupliar instars from Mediterranean coastal waters of the Salento Peninsula in southeastern Italy (Belmonte, 2005): *H. corvinae*, *H. leucadea*, *H. mediterranea*, and *H. salentina*. Although these species are readily distinguishable from one another, none are linked to any form of cypris y and none can be compared directly to previously described nominal species of *Hansenocaris* that are based on the cypris stage. Along with *H. hanseni*, these Mediterranean y-nauplii represent the beginning of a parallel nomenclature, which, although perhaps inevitable given the availability of material, may in time prove to be an impediment.

All the main characters of the described facetotectan species for which the y-cypris stage is known are listed in Table 1. *Hansenocaris papillata* differs distinctly from all the other species by the presence of a pair of conspicuous, ventrally-directed, papilliform protrusions at the anterior end. It also can be easily distinguished from the Atlantic y-cyprids, including *H. itoi*, and some of the Pacific species (i.e. *H. pacifica* and *H. furcifera*) in having a relatively shorter head shield, which does not reach the abdominal segments, as well as a shorter total length, approximately 340 µm for the new species instead of 425–590 µm for the other species (Itô & Ohtsuka, 1984; Itô, 1989; Kolbasov & Høeg, 2003). The three unpaired central pores along the mid-dorsal line of *H. papillata* may represent gland openings and correspond to pores *cp2*, *cp3* and *cp4* found in the cypris y larva of *H. itoi* (Høeg & Kolbasov, 2002; Kolbasov & Høeg, 2003). The most anterior of these pores is surrounded by the anterior two pairs of lattice organs in our specimen, as is true for *cp2* in *H. itoi*. The single posterior central pore in both of these forms of cypris y is presumably mutually homologous. *Hansenocaris papillata* is comparable in length with *H. rostrata*, *H. acutifrons* and *H. tentaculata* (335–375 µm) (Itô, 1984, 1985, 1986b). These species also have a rather

short head shield, but differ from the new species in other characters. They all reportedly lack an antennular claw or hook, whereas *H. papillata* has a well developed antennular claw. In most other forms of cypris y the antennules consist of four segments, the second segment being armed with a hook and sometimes with a minute lateral seta, the third segment bearing one or two lanceolate setae, and the small fourth segment carrying a subterminal aesthetasc and one long and one short terminal setae (Grygier, 1987; Kolbasov & Høeg 2003). Not all of the elements of the distal two segments were confirmed as being present in our specimen.

The anterior end of the head shield of *H. rostrata* and *H. acutifrons* is strongly produced in comparison with the slight elongation in *H. papillata*. In addition, *H. acutifrons* has six serrate spines along the posteroventral border of the telson (five in *H. papillata*) while *H. tentaculata* lacks such spines.

The segmentation and setation of the thoracopods in *H. papillata* correspond completely with the situation in the Atlantic y-cyprids, including *H. itoi* (see Bresciani, 1965; Schram, 1970a; Grygier, 1987; Kolbasov & Høeg, 2003) and *H. furcifera* (cf. Itô, 1989). All have a two-segmented endopod in thoracopod 1 and three-segmented endopods in thoracopods 2–6. In contrast, all thoracopods of *H. acutifrons*, *H. pacifica* and *H. rostrata*, and thoracopods 3–6 of *H. tentaculata* possess only two-segmented endopods (Itô, 1985, 1986b), with a seta in the middle of the distal endopodal segment. The segment boundaries are all clear and represent movable articulations. Following Schram (1970a), Grygier (1987) and Kolbasov & Høeg (2003), we agree that this seta corresponds to the seta on the second endopodal segment in y-cyprids with three-segmented endopods and that either the two distal segments of the endopod are fused in Itô's specimens or he missed an imperfectly displayed segment border.

The two posterior pairs of pores on the telson have not been reported before in other species, but they may have been overlooked.

Hansenocaris papillata is the first facetotectan species reported from the tropical waters of Indonesia. All earlier named species of cypris y have been described from warm-temperate (Kuroshio Current-influenced) waters of Japan (*H. pacifica*, *H. rostrata*, *H. acutifrons*, *H. tentaculata* and *H. furcifera*) or boreal waters of the White Sea (*H. itoi*). Other unnamed y-cyprids have been found in boreal waters of the North Atlantic (Bresciani, 1965; Grygier, 1987), tropical waters of the Bahamas (Schram, 1970a), tropical waters of the Gulf of Aqaba (Eilat, Red Sea) (Almeida Prado-Por & Por, 1988) and in Japan including Okinawa (Grygier, 1997; unpublished data).

In total length and in terms of the size and form of the head shield, *H. papillata* is similar to the abovementioned y-cypris from the Gulf of Aqaba (Almeida Prado-Por & Por, 1988). Unfortunately, these authors did not describe the morphology of their specimen, providing only a single

Table 1. The main characters of y-cyprids of the described species (after Kolbasov & Høeg, 2003 with modifications).

Species of <i>Hansenocaris</i>	Length of head shield	Anterior end of head shield	Papilliform protrusions at anterior end	Paraocular process compared with head shield	Nf	Acl	Endopods of thoracopods 3-6	Nas	Size and shape of third abdominal segment	Nts
<i>H. acutifrons</i>	Not reaching abdomen	Produced	Absent	Much shorter	9	Absent	Two-segmented	4	Developed, with sharp pleural extensions	6
<i>H. furcifera</i>	Reaching abdominal segments	Rounded	Absent	Much shorter	9	Present	Three-segmented	4	Developed, with sharp pleural extensions	5
<i>H. itoi</i>	Reaching abdominal segments	Rounded	Absent	Much shorter	15	Present	Three-segmented	4	Developed, with sharp pleural extensions	5
<i>H. pacifica</i>	Reaching abdominal segments	Rounded	Absent	Much shorter	10-14	Present	Two-segmented	4	Developed, with sharp pleural extensions	3
<i>H. papillata</i>	Not reaching abdomen	Slightly produced	Present	Presence not confirmed	0?	Present	Three-segmented	4	Short, intercalated, without pleural extensions	5
<i>H. rostrata</i>	Not reaching abdomen	Produced	Absent	Much shorter	0	Absent	Two-segmented	4	Developed, without sharp pleural extensions	5
<i>H. tentaculata</i>	Not reaching abdomen	Slightly produced	Absent	About as long	0	Absent	Two-segmented	2	Absent	0

Acl - antennular claw; Nas - number of abdominal segments; Nf - number of filaments in the postocular filamentary tuft; Nts - number of serrate spines along the posteroventral margin of the telson.

light micrograph. Itô (1991) presented a drawing in dorsal view of an undescribed cypris y he raised though its naupliar series in the laboratory. As in *H. papillata*, the head shield is short and ornamented with a preponderance of longitudinal cuticular ridges. The visible dorsal ornamentation of the posterior thorax and abdomen is also consistent with that of *H. papillata*, but in the absence of information concerning its cephalic structures, appendages, etc., we can only suggest that Itô's form may be related to our new species. A relatively short-shielded, undescribed cypris y from Japan shown in side view by SEM by Grygier (1997) is, despite the small size of the image, readily distinguished from *H. papillata* by several features: a considerably greater length to height ratio of the head shield, rounded rather than protruding and pointed posteroventral corners of the shield, no sharp posteroventral protrusion of the pleural expansions of thoracomere 5, and at least one more 'plate' in each lateral plate row on the telson.

Remarks. – As mentioned before, the description of this species was done by the first two authors and this species

should be cited hereafter as *Hansenocaris papillata* Kolbasov & Grygier, 2007.

DISCUSSION

Taxonomic prospectus

Two informal morphological groups of facetotectan y-cyprids were recognized recently (Kolbasov & Høeg, 2003). The first, the '*Hansenocaris pacifica* group', includes y-cyprids with a long head shield with a round anterior end and sharp, laterally elongate posterior margins, and curved antennular hooks. This group includes all the Atlantic y-cyprids, including *H. itoi*, as well as *H. pacifica* and *H. furcifera*. Y-cyprids of the other group have a shorter head shield, often with an elongate and sharp anterior end, and supposedly lack curved antennular hooks. *Hansenocaris rostrata*, *H. acutifrons* and *H. tentaculata* belong to this group. This latter grouping has hardly any taxonomic value because of the very distinct morphology of *H. tentaculata* (e.g. the two-segmented

abdomen, instead of a four-segmented one) compared to other facetotectans. The new species *H. papillata* shares characters of both groups.

Characters of y-cyprids that need to be compared among species for phylogenetic purposes include gross morphological features, ultrastructural features such as details of the cuticular organs and ornamentation over the entire surface of the head shield and trunk, and appropriate gene sequences. Among the relevant gross morphological features of the head shield are its relative length (i.e. to which trunk segment its posteriolateral corners and mid-dorsal line reach) and length to height ratio, the shape of the posteriolateral corners, the degree and type of any anterior protrusion, and the presence or absence of anterior papilliform protrusions. Other cephalic features include paraocular process size relative to that of the head shield and details of the morphology of these processes, similar data (including presence or absence) for the postocular filamentary tufts, presence or absence of an antennular claw or hook, details of shape and positioning of antennular seta and aesthetascs, and the form and distal armature of the labrum, if present. Limb segmentation and setation must be mentioned, along with the shape of the pleural extensions of thoracomeres 5 and 6. The number of abdominal segments should be included, along with the shape of the pleural regions of all segments but the telson, as well as the presence or absence and number of spines on the posteroventral part of the telson and the shape and armature of the furcal rami. This is not an exhaustive list of morphological features of y-cyprids that might be compared and scored for cladistic analysis, and it does not even touch on features that are best investigated by SEM, but it does give an indication of the precision of description that will be needed in future descriptions for them to be useful in any comparative regard.

Provisionally, and with no judgements about character state polarity, we note that *H. furcifera*, *H. itoi* and *H. pacifica* all have an elongate head shield with a round anterior end. They also share, along with *H. papillata*, the presence of an antennular claw, but this last species is distinctive on account of its anteriorly-situated and conspicuous, ventral papilliform protrusions. Two other species, *H. rostrata* and *H. acutifrons*, share a strongly produced anterior end of the head shield; along with *Hansenocaris tentaculata* they also are reported to lack the antennular claw. This last species is particularly distinctive in other respects, having very long paraocular processes, a two-segmented abdomen, and no posteroventral telsonic spines. Based on the cypris y stage, at least, *H. tentaculata* may be the best candidate at present to serve as the type species for an additional genus in the Facetotecta. On the other hand, it shares with *H. rostrata* and *H. papillata* a relatively short head shield.

Only a cladistic analysis of all cyprid characters may establish true taxa within the subclass Facetotecta. We consider it premature to attempt such an analysis here because the number of described forms of cypris y is still small, and over 40 undescribed forms have been reared recently from nauplii collected in Okinawan waters alone (Grygier, unpublished

data). These latter forms are regarded provisionally as additional species based on their distinctive last naupliar stages, the morphological range of which greatly surpasses that of the hitherto described kinds of nauplius y, as hinted at by Grygier (1991). Another consideration is that a priori judgments about the polarity of alternative states, if desired, should be based on outgroup comparisons that refer to both the ascothoracid-larvae ("a-cyprids") of the Ascothoracida and the true cypris larvae of the Cirripedia. There is as yet insufficient information, either histological or ultrastructural, to compare certain features this way. No sure judgement can yet be made, for example, about a possible homology of the anterior papilliform protrusions of *H. papillata* with the frontolateral pores of cirripede cyprids, which are situated on the lateral faces of head shield, usually flush with the valve surface but sometimes on a pair of marked protrusions (Elfimov, 1995).

Relationship with fish

The endemic Banggai cardinalfish, *Pterapogon kauderni* Koumans, 1933 (Teleostei, Apogonidae), has a very restricted natural geographic range in the Banggai Archipelago and an adjacent site in mainland Sulawesi, eastern Indonesia. It is sedentary and inhabits mainly protected bays, on shallow reefs and seagrass beds, where it uses living benthic substrates as microhabitats, including sea urchins, sea anemones, and soft and hard corals. Its depth range is between about 0.8 and 4.5 m, usually between 1.5 and 2.5 m. It feeds principally upon benthic, epibenthic and symbiotic copepods, but it is also a generalist and opportunistic feeder that preys upon a variety of planktonic, demersal and benthic organisms (Vagelli, 1999, 2004, 2005; Vagelli & Erdmann, 2002; Bernardi & Vagelli, 2004). The present y-cypris was found in the fish stomach along with the remains of three polychaete larvae and assorted crustaceans: a cirripede cypris, two epicaridean isopods, five amphipods, a cumacean, a tanaidacean, one ostracod and many copepods (83 calanoid individuals, about 60 harpacticoids of various families including the Peltidiidae, two cyclopoid individuals and a siphonostomatoid). We consider it probable that the present y-cypris was simply eaten by the fish like all the other invertebrates found in its stomach. The opportunistic feeding of *P. kauderni* does not allow us to speculate about its being a possible host of parasitic facetotectans.

Key to the species of Facetotecta described from the cypris y stage

1. Abdomen two-segmented *H. tentaculata*
– Abdomen four-segmented 2
2. Anterior end of head shield strongly produced, antennular hook absent 3
– Anterior end of head shield round or slightly produced, antennular hook present 4
3. Anterior end of head shield sharp, six telsonic spines
..... *H. acutifrons*

- Anterior end of head shield blunt, five telsonic spines
..... *H. rostrata*
- 4. Head shield elongate, its posterior ends reaching abdomen,
anterior end lacking papilliform protrusions 5
- Head shield short, its posterior ends not reaching abdomen,
anterior end with ventral papilliform protrusions
..... *H. papillata*
- 5. Antennular aesthetasc constricted at mid-length, posterior ends
of head shield reaching telson *H. itoi*
- Antennular aesthetasc not constricted at mid-length, posterior
ends of head shield not reaching telson 6
- 6. Entire surface of head shield covered by cuticular ridges, three
telsonic spines *H. pacifica*
- Cuticular ridges absent in dorsal part of head shield, five telsonic
spines *H. furcifera*

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LITERATURE CITED

Almeida Prado-Por, M. S. & F. D. Por, 1988. "Y" Crustacean larvae (order Facetotecta) in the plankton of the Gulf of Aqaba (Eilat), Red Sea. *Rapports et procès-verbaux des réunions. Commission internationale pour l'exploration scientifique de la mer Méditerranée*, **31**(2): 302.

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

Belmonte, G., 2005. Y-nauplii (Crustacea, Thecostraca, Facetotecta) from coastal waters of the Salento Peninsula (south eastern Italy, Mediterranean Sea) with descriptions of four new species. *Marine Biology Research*, **1**: 254–266.

Bernardi, G. & A. A. Vagelli, 2004. Population structure in Banggai Cardinalfish, *Pterapogon kauderni*, a coral reef fish that lacks a pelagic larval phase. *Marine Biology*, **145**: 803–810.

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

Böttger-Schnack, R., 1995. Summer distribution of micro- and small meso-zooplankton in the Red Sea and Gulf of Aden, with special reference to non-calanoid copepods. *Marine Ecology Progress Series*, **118**: 81–102.

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

Conway, D. V. P., R. G. White, J. Hugues-Dit-Ciles, C. P. Gallienne & D. B. Robins, 2003. Guide to the coastal and surface zooplankton of the south-western Indian Ocean. *Occasional Publication of the Marine Biological Association of the United Kingdom* **15**: 1–354.

Darwin, C., 1854. *A monograph on the subclass Cirripedia, with figures of all the species. The Balanidae (or sessile cirripedes); the Verrucidae, etc., etc., etc.* Ray Society, London. 684 pp.

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

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

Elfimov, A. S., 1995. Comparative morphology of the thoracican cyprid larvae: studies of the carapace. In: Schram, F. R. & J. T. Høeg (Eds.), *New frontiers in barnacle evolution. Crustacean Issues*, **10**, Balkema, Rotterdam. Pp. 137–152.

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

Fish, C. J. & M. W. Johnson, 1937. The biology of the zooplankton population in the Bay of Fundy and Gulf of Maine with special reference to production and distribution. *Journal of the Biological Board of Canada*, **3**(3): 189–322.

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

Grygier, M. J., 1991. Facetotecta ('y-larvae'): one day's catch in Okinawa, Japan (Crustacea: Maxillopoda). *Memoirs of the Queensland Museum*, **31**: 335.

Grygier, M. J., 1995. An unusual barnacle nauplius illustrating several hitherto unappreciated features useful in cirripede systematics. In: Schram, F. R. & J. T. Høeg (Eds.), *New frontiers in barnacle evolution. Crustacean issues*, **10**, Balkema, Rotterdam. Pp 123–136.

Grygier, M. J., 1996. Sous-classe des Facetotecta (Facetotecta Grygier, 1985). In Forest, J. (Ed.), *Traité de Zoologie: Anatomie, Systématique, Biologie. Tome VII, Crustacés. Fascicule 2, Généralités (suite) et Systématique*, Masson, Paris, Pp. 425–432.

Grygier, M. J., 1997. Y-yōsei [Y-larvae]. *Umindo*, **2**(1) [whole no. 3]: 5 [in Japanese].

Hansen, H. J., 1899. Die Cladoceren und Cirripeden der Plankton-Expedition. *Ergebnisse der Plankton-Expedition der Humboldt-Stiftung*, **2**(G, d): 1–58, pls. 1–4.

Hensen, V., 1887. Ueber die Bestimmung des Plankton's oder des im Meere treibenden Materials an Pflanzen und Thieren; nebst Anhang. *Bericht der Commission zur wissenschaftlichen Untersuchung der deutschen Meere, in Kiel*, **5** (für die Jahre 1882 bis 1886): 1–108, pls. I–VI.

Høeg, J. T., 2005. Y-larver, Okinawa og Hansens høje hat – mod løsningen af en 100 år gammel gåde i havbiologi. *Dyr i Natur og Museum*, **2005**(1): 17–20.

Høeg, J. T. & G. A. Kolbasov, 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.

- 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): 367–374.
- 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: Maxillopoda: 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.
- Itô, T. & S. Ohtsuka, 1984. Cypris y from the North Pacific (Crustacea: Maxillopoda). *Publications of the Seto Marine Biological Laboratory*, **29**(1/3): 179–186.
- Itô, T. & M. Takenaka, 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.
- Kikuchi, T., K. Takahashi & S. Gamô, 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 English summary].
- Kolbasov, G. A. & J. T. Høeg, 2003. Facetotectan larvae from the White Sea with the description of a new species (Crustacea: Thecostraca). *Sarsia*, **88**: 1–15.
- Kolbasov, G. A. & A. N. Pegova, 2001. Chromosome set in crustaceans of the subclass Facetotecta (Crustacea, Thecostraca) from the White Sea. *Zoologicheskii Zhurnal*, **80**(12): 1444–1451 [in Russian with English summary].
- Koumans, F., 1933. On a new genus and species of Apogonidae. *Zoologische Mededelingen (Leiden)*, **16**(1–2): 78–79.
- Lohmann, H., 1908. Untersuchungen zur Feststellung des vollständigen Gehaltes des Meeres an Plankton. *Wissenschaftliche Meeresuntersuchungen der Commission zur wissenschaftlichen Untersuchung der deutschen Meere Abt. Kiel*, **10**: 131–370.
- McMurrich, J. P., 1917. Notes on some Crustacean forms occurring in the Plankton of Passamaquoddy Bay. *Transactions of the Royal Society of Canada, Series 3*, **11** (Section 4): 47–61.
- Mileikovsky, S. A., 1968. Distribution of pelagic larvae of bottom invertebrates of the Norwegian and Barents Seas. *Marine Biology*, **1**(3): 161–167.
- Mileikovsky, S. A., 1970. [Distribution of pelagic larvae of bottom invertebrates in the Kurile–Kamchatka area]. *Trudy Instituta Okeanologii*, **86**: 117–133 [in Russian].
- Ohtsuka, S., M. J. Grygier & K. Torigoe, 1999. The phylogeny, zoogeography, and ecology of marine cavernicolous crustaceans. *Taxa*, **6**: 3–13 [in Japanese with English abstract].
- Ponomarenko, E. A., 2006. Facetotecta – an undecided riddle of marine biology. *Biologiya Morya*, **32**(3): 163–173 [In Russian with English abstract; English translation in *Russian Journal of Marine Biology*, **32**(Supplement): S1–S10].
- Ponomarenko, E. A. & O. M. Korn, 2006. The first record of a facetotectan crustacean in plankton of Peter the Great Bay, the Sea of Japan. *Biologiya Morya*, **32**(5): 355–357 [in Russian with English abstract; English translation in *Russian Journal of Marine Biology*, **32**(5): 299–301].
- Runnström, S., 1932. Eine Uebersicht über das Zooplankton des Herdla- und Hjeltefjordes. *Bergens Museums Årbok 1931. Naturvidenskapelig Rekke*, **7**: 1–67.
- Schram, T. A., 1970a. Marine biological investigations in the Bahamas. 14. Cypris y, a later developmental stage of nauplius y Hansen. *Sarsia*, **44**: 9–24.
- Schram, T. A., 1970b. On the enigmatical larva nauplius y type I Hansen. *Sarsia*, **45**: 53–68.
- Schram, T. A., 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 Cirripedenlarve aus dem Golfe von Triest. *Arbeiten aus den Zoologischen Instituten der Universität Wien und der Zoologischen Station in Triest*, **15**(2): 113–118.
- Vagelli, A. A., 1999. The reproductive biology and early ontogeny of the mouthbrooding Banggai cardinalfish *Pterapogon kauderni* (Perciformes, Apogonidae). *Environmental Biology of Fishes*, **56**: 79–92.
- Vagelli, A. A., 2004. Ontogenetic shift in habitat preference by *Pterapogon kauderni*, a shallow water coral reef apogonid, with direct development. *Copeia*, **2**: 364–369.
- Vagelli, A. A., 2005. *Reproductive biology, geographic distribution and ecology of the Banggai Cardinalfish Pterapogon kauderni Koumans, 1933 (Perciformes, Apogonidae), with considerations on the conservation status of this species on its natural habitat*. Ph.D. Dissertation. University of Buenos Aires. 276 pp.
- Vagelli, A. A. & M. Erdmann, 2002. First comprehensive ecological survey of the Banggai cardinalfish, *Pterapogon kauderni*. *Environmental Biology of Fishes*, **63**: 1–8.
- Watanabe, H., K. Takahashi, T. Toda & T. Kikuchi, 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 English abstract].