Two New Species of Lecithotrophic Nauplius y with Remarkable Labra from Okinawa, Japan, and a Family-Group Name for y-Larvae (Crustacea: Thecostraca: Facetotecta: Hansenocarididae fam. nov.)

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Two large (ca. 0.5 mm long), rare, and probably closely related species of Facetotecta (y-larvae), *Hansenocaris cristalabri* sp. nov. and *Hansenocaris aquila* sp. nov., are described on the basis of last-stage lecithotrophic nauplii reared from plankton at Sesoko Island, Okinawa, Japan. The two species resemble each other in having a labrum with a row of spines and a long, attenuate trunk region that terminates in a long, heavily spinose dorsocaudal spine. The labrum of *H. cristalabri* sp. nov. has an enormous, cockscomb-like ventral process that bears a row of distally directed, dagger-like spines along its anterior side, while the spine-bearing keel of the labrum of *H. aquila* sp. nov. extends posteriorly into a robust, eagle-like beak. The labral "crest" of *H. cristalabri* sp. nov. has no equivalent in any other described y-larva, nor in any other crustacean nauplius; its possible functions are discussed. Another diagnostic feature of *H. cristalabri* sp. nov., absent in *H. aquila* sp. nov., is a pair of shallow, rounded notches bounded by sharp spinules on the far posteriolateral margins of the cephalic shield. Both new species have longitudinal spine rows on the trunk dorsum, two rows in *H. cristalabri* sp. nov. and four in *H. aquila* sp. nov., something not previously documented for y-nauplii. The plate arrangement of the cephalic shield in *H. cristalabri* sp. nov. is described in detail, with an attempt to homologize the pattern with that of other y-nauplii (especially *Hansenocaris furcifera* Itô, 1989). The body surface of *H. cristalabri* sp. nov. has fewer setae and pores than any other late- or last-stage facetotectan nauplius described to date, suggesting paedomorphic development. A formal diagnosis is presented for the family-group taxon Hansenocarididae fam. nov.; this name, while already in use, has until now been nomenclaturally unavailable.

Key Words: Crustacean larvae, new family, inshore plankton, laboratory rearing, scanning electron microscopy, cuticular organs, larval holotype, lecithotrophy, Ryukyu Islands, paedomorphosis.

Introduction

The Facetotecta are marine planktonic crustacean larvae whose adult forms remain unknown (Grygier 1996; Glenner et al. 2008; Pérez-Losada et al. 2009; Høeg et al. 2014). Having at first been mistaken for nauplii of corycaeid copepods (Hensen 1887), their distinctness and likely affinity with the Cirripedia were first recognized by Hansen (1899) on the basis of his study of several forms of "Larven vom Typus y" (*Nauplius* I–V) from various parts of the Atlantic Ocean. Facetotectan larvae are thus often referred to as "Hansen's y-larvae." Later, a somewhat Ascothoracida-like subsequent larval phase comprising just one instar, the 'cypris y,' was added to the life-cycle (Bresciani 1965), and eventually a slug-like, putatively host-infective juvenile phase, the 'ypsigon,' was discovered as well (Glenner et al. 2008). The morphology of both the cypris y and ypsigon suggests that the still unknown adults are likely to be para-sitic (Scholtz 2008; Pérez-Losada et al. 2009; Høeg et al. 2014). Dreyer et al. (in press) provided a heavily illustrated comprehensive review of the different known phases of the facetotectan life cycle, partly based on new data, comparisons to the corresponding larval and juvenile stages of, especially, parasitic barnacles (Rhizocephala), and detailed profiles of the ecology and geographic distribution of y-larvae.

Taxonomic understanding of y-larvae has been built up only very slowly. The 15 formally named species are all based on naupliar and/or cyprid specimens; only three are known from both types of larva (Olesen et al. 2022). The only described genus, *Hansenocaris* Itô, 1985 (q.v.), was established with four nominal species, and more have been gradually added since (Itô 1986b, 1989; Belmonte 2005; Kolbasov and Høeg 2003; Kolbasov et al. 2007, 2021a, b; Swathi and Mohan 2019; Olesen et al. 2022). A para-taxonomy exists alongside the formal taxonomy, started already by Hansen (1899) as noted above, and continued by Schram (1970, 1972), Itô (1986a, 1987a, b), Grygier (1987), and

Watanabe et al. (2000), whereby distinct "types" of naupliar larvae have been assigned Roman-numeral designations.

For seven species of *Hansenocaris*, the type series consists solely of cypris y individuals (Itô 1985, 1986b, 1989; Kolbasov et al. 2007, 2021b). This has practical value as this stage is certainly homologous between species. However, evidence has long been available (Itô 1986a, 1987b) that the morphological diversity among facetotectan nauplii in certain geographical areas is large. Several workers have based formal descriptions solely on different forms of nauplius y (Steuer 1904; Belmonte 2005; Swathi and Mohan 2019), and the potential usefulness of this larval phase for taxonomy should be re-evaluated.

One of us (MJG) long ago began to explore the y-larva diversity at the marine laboratory of the University of the Ryukyus on Sesoko Island, Okinawa, Japan (see Grygier et al. 2019), and members of the present research team continued this work with renewed sampling there in 2018 and 2019 (Grygier et al. 2019; Olesen et al. 2022). These still largely unpublished surveys confirmed earlier reports (Itô 1990; Grygier 1991; Kikuchi et al. 1991; Watanabe et al. 2000; Glenner et al. 2008) of a large facetotectan diversity in various Japanese coastal waters. Among the several dozen unreported types of nauplius y that have thus been collected at Sesoko Island are two particularly rare and remarkable forms that have uniquely modified labra (either with a cockscomb-like process or an aquiline beak-like extension) that make them easily identifiable for a broader audience of carcinologists and thus worthy of formal description as new species.

Materials and Methods

Collection and preparation. Naupliar specimens of *Hansenocaris cristalabri* Olesen and Grygier, sp. nov. and *Hansenocaris aquila* Grygier and Olesen, sp. nov. were collected during surveys of y-larva diversity conducted at Sesoko Island (Okinawa) in 1996, 2004, and 2005 (see Grygier et al. 2019) and again in 2018 and 2019 (Olesen et al. 2022). One specimen of *H. cristalabri* sp. nov. (holotype) was collected from the surface plankton at 07:00 on 10 June 2019 by tossing a conical plankton net (30 cm mouth opening, 70 μm mesh) on a rope from the end of the pier at the Sesoko Station, Tropical Biosphere Research Center, University of the Ryukyus, on the semi-sheltered southeast coast of Sesoko Island, Okinawa Prefecture, Japan (26°38′09.4″N, 127°51′55.3″E). Two specimens of *H. aquila* sp. nov. (paratype and holotype respectively) were collected the same way at the same locality using a smaller net (20 cm mouth opening, NXX13-grade 100 μm mesh) sometime during 16–19 July 1996 and at 18:30 on 22 September 2005.

In the belief that species descriptions of facetotectans with lecithotrophic nauplii are best based on plankton-caught nauplii that are maintained in the laboratory through their entire molt sequence to the last-stage nauplius and/or the cyprid, Olesen et al. (2022) described a protocol suitable
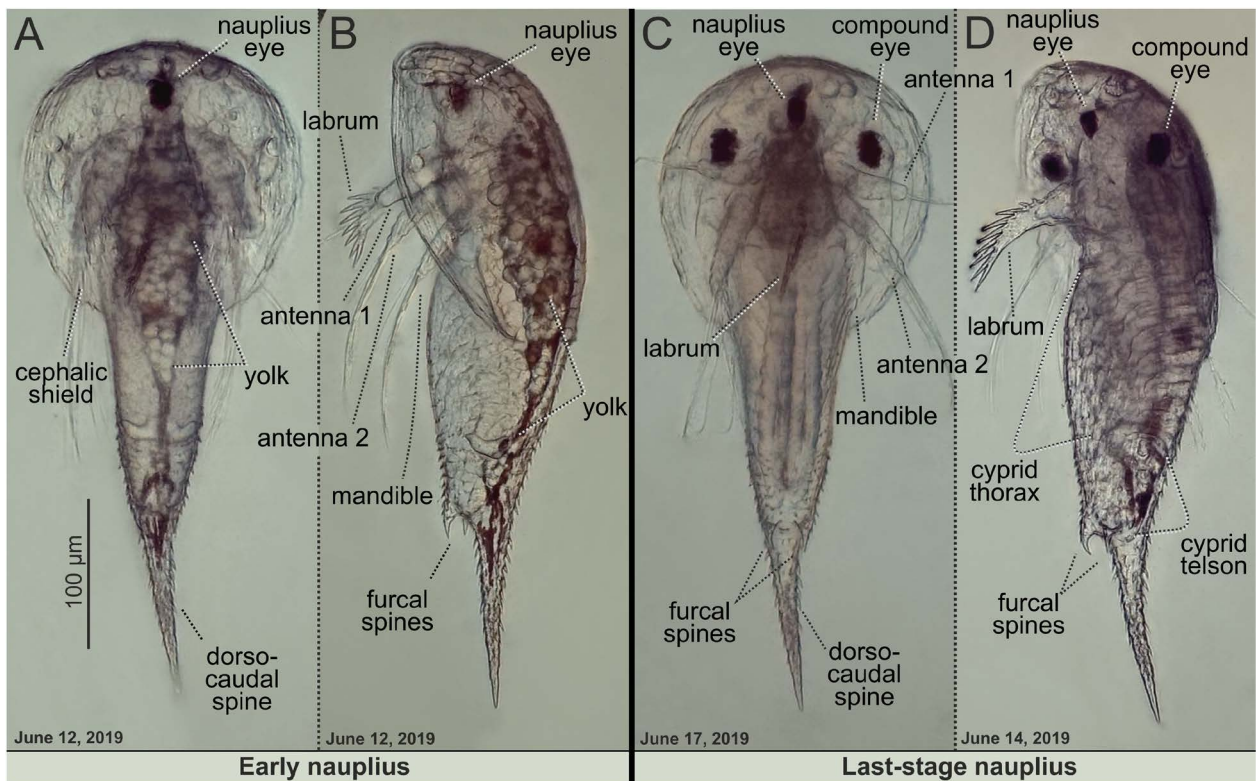

Fig. 1. *Hansenocaris cristalabri* sp. nov., holotype (NHMD-1174614), microphotographs of living nauplius at two different stages of development. A, B, nauplius in dorsal and lateral view, respectively; C, D, last-stage nauplius in ventral and lateral view, respectively. Live video of *H. cristalabri* sp. nov. can be seen here: https://youtu.be/SCskuhPTCXo and is also deposited at Figshare.com: https://doi.org/10.6084/m9.figshare.20430807.

for rearing and documenting large numbers of y-larvae at once. The present holotype of *H. cristalabri* sp. nov. was obtained by following this protocol. Briefly, immediately after sampling, facetotectan larvae (nauplius y and cypris y) were sorted from the live sample under a dissecting microscope using a Pasteur pipette. They were then resorted into coarsely filtered (63 µm) sea water in small plastic petri dishes, and any extraneous organisms were removed from the resulting stock cultures of generally four to six individuals, these being chosen to be mutually distinctive or, less often, mutually similar. The dishes were maintained on an open tabletop at about 25°C. Over the next several days, some living nauplii from these dishes, at different stages of development, were video-photographed in a depression slide without a cover glass using a Nikon ECLIPSE 80i compound microscope equipped with Nomarsky (DIC) optics and a Canon EOS 5D Mark IV digital camera, then returned to the culture dish. Surviving lecithotrophic nauplii, including the holotype nauplius of *H. cristalabri* sp. nov., were removed to individual culture dishes after they had reached the last naupliar instar, which could be recognized by the appearance of the cyprid larva's pair of dark compound eyes, and again video-photographed (Fig. 1). A final molt to the cypris y stage was awaited, but in some cases, including the holotype of *H. cristalabri* sp. nov., the last-stage nauplius was fixed in seawater-buffered 4% formaldehyde and later prepared for observation in a JEOL JSM-6335-F (FE) scanning electron microscope. In other cases, as with the type specimens of *H. aquila* sp. nov. (see below), the exuviae of last-stage nauplii were prepared as semi-permanent slide-mounts in glycerine jelly prepared according to standard recipes.

In 1996 and 2005, when the two present specimens of *H. aquila* sp. nov. were collected, rearing procedures up to the cyprid stage were much the same as described above, except that 1) each stock culture represented the entire y-larva catch from a single live sample or pooled catches from several samples, 2) last naupliar exuviae were routinely mounted in glycerine jelly, and 3) nauplii were not photographed. The free-swimming cyprids of the holotype and paratype of *H. aquila* sp. nov. were found along with their naupliar exuviae on 27 September 2005 (5 days after capture) and 22 July 1996 (3–6 days after capture), respectively. The former cyprid was used in an ypsigon rearing trial (see Glenner et al. 2008), during which it died and, therefore, was not saved. The latter cyprid was mounted on the same slide as its naupliar exuvium, but there are two cyprids on that slide and it is unclear which of them corresponds to *H. aquila* sp. nov.

The description of *H. cristalabri* sp. nov. is based on about 100 SEM micrographs of the holotype taken at an operating voltage of 5 kV, some of which have been trimmed and arranged into the present photo plates using CorelDraw graphics software (Figs 2–5). The description of *H. aquila* sp. nov. was based on the exuviae of the last-stage nauplii of the holotype and paratype, which were photographed with an inverted compound microscope (Olympus, IX83) using fully automated image-stacking techniques to obtain complete z-stacks of images (Fig. 6). In order to show selected parts of each exuvium in focus, subsets of the z-stack were exported for blending into single images in Zerene Stacker ver. 1.04.

Nomenclature of body parts. The morphological terms used herein usually follow Olesen et al. (2022), but also Kolbasov et al. (2021a) when necessary. There is no existing terminology for the few setae and many pores on the body surface of nauplius y. Here, as in Olesen et al. (2022), all setae and pores have been mapped and arbitrarily numbered (from 1 to 15), with the annotations "r" and "l" for the right and left sides if the structure is paired. We introduce a new term, 'primordial plates,' for the 50-odd facets of the cephalic shield that were first individually named by Schram (1972) in an early-instar planktotrophic nauplius, and later renamed in the equivalent instar in various other forms of nauplius y by Itô (1987b) (see Fig. 4A). The primordial plates are nearly constant in position, and thus likely homologous, among different y-larvae. In later instars, most of them become subdivided into 'subsidiary plates.' Because of a lack of knowledge of earlier instars, Itô's (1990) augmented system of nomenclature for the subsidiary plates is only tentatively applicable to the present nauplii. Instead, color-coding was used to trace the fate of the primordial plates of the earliest known nauplius of *Hansenocaris furcifera* Itô, 1989 through four molts to the last-stage nauplius of that species (Fig. 4A–E). Comparison of the holotype of *H. cristalabri* sp. nov., also a last-stage nauplius, with the corresponding stage of *H. furcifera* (Fig. 4E) and sometimes also with preceding instars (especially Fig. 4C), to some degree allowed us to infer which regions of the new species' shield reticulation correspond to the primordial plates of *H. furcifera* (Figs 3C, 4F). This approach was much less successful when applied to *H. aquila* sp. nov., as the examined exuviae provided limited information on "landmarks," such as pores and setae, that help to establish positional homologies.

Taxonomy

Class **Thecostraca** Gruvel, 1905
Subclass **Facetotecta** Grygier, 1985
Family **Hansenocarididae** Olesen and Grygier, fam. nov
[New Japanese name: Chou-kou-mushi-ka]

Diagnosis. Mostly agreeing with the diagnosis proposed for Subclass Facetotecta by Chan et al. (2021: 34), but with additional detail that is subject to change as more taxa are described. Known only from ortho- and metanauplii, cyprid larvae, and ypsigons; adults unknown or unrecognized.

Nauplii [based in part on Grygier (1991, 1996), thus also on M. J. Grygier's unpublished data]: cephalic shield posteriorly abutting on free, exposed trunk dorsum; frontolateral horns and frontal filaments absent. Common plan of cephalic shield ridges fully or partially outlining more-or-less stereotypical turtle-shell-like pattern of plates (facets) in early instars, plates commonly becoming complexly subdivided and/or re-fused in later instars. Common posi-

tions of 'window' plate and dorsal setae (of which no more than 4 pairs present) and certain pores on cephalic shield. Ventral side of cephalic region flat, round, with wide rim ('faciomarginal cuticle'). First antenna with up to 8 setae on distal segment only. Maximal second antennal armature of 1 coxal spine, 1 basal spine, 2-segmented endopod with spine and seta on proximal segment and 2 apical setae on distal, and 6-segmented exopod with short seta on second segment, 1 long seta each on next 3 segments, and long and short seta on distal segment. Maximal mandibular armature similar except basis maximally with 1 spine and 1 seta, and exopod 5-segmented with 1 seta each on first 4 segments, 2 setae on apical segment. Second antenna and mandible essentially unchanged in segmentation and armature from second through final instar except for rare loss of 1 protopodal spine. Paragnaths either absent or rudimentary and unarmed. No ventral setation except for rare occurrence of pair of setae representing first maxillae. Trunk region often complexly subdivided by ridges. Caudal end asetose, but usually with pair of furcal spines and terminal dorsocaudal spine, these being of various sizes and possessing various subsidiary spination depending on taxon. Round, knob-like 'dorsocaudal organ' of unknown function present posteriorly on dorsum of trunk region mainly in planktotrophic forms, possibly represented by similarly positioned pore in some lecithotrophic forms. Exuvium of last nauplius of lecithotrophic forms often containing fine, membranous trace ("ghost") of ventral thoracic parts of cyprid formerly held within, this being connected by internal struts to pair of anterioventral invaginations of trunk wall.

Cyprids [based in part on Itô (1985), Kolbasov et al. (2007), Høeg et al. (2014); also on J. Olesen's unpublished SEM data]: non-feeding, with boat-like, univalved head shield or carapace not covering whole body and free from thorax. Carapace with lattice organs and often with complex pattern of surface sculpturing featuring anterior meshwork and longitudinal ridges. Head with pair of prehensile first antennae bearing hook (occasionally absent) and uni- or usually bi-articulate palp on presumed third segment (proximal segmentation often obscure); knob-like vestiges of naupliar second antennae and mandibles sometimes present. Pair of sessile compound eyes, each composed of about 9 ommatidia with tripartite crystalline cones. Eyes often (not confirmed in some) flanked by 2 pairs of sensory organs ('bifurcate paraocular processes,' 'postocular filamentary tufts'). Large, ventrally produced labrum bearing apical and posterior hooks usually present, its form and armament taxon-specific to some degree. Thorax 6-segmented and bearing 6 pairs of biramous limbs, with first 2 tergites fused to each other dorsally (in at least some taxa), last 2 segments with pleural extensions. Coxa and basis of thoracopods separate or (in sixth pair) fused, exopods 2-segmented (rarely 1-segmented) with 3 apical natatory setae (2 setae in first pair), endopods 2- or 3-segmented with 2 apical and 1 subapical natatory setae (subapical seta absent in first pair). Abdomen consisting of 1 or, much more usually, 3 short somites with or without sharp ventrolateral extensions, and large, oblong telson, latter heavily ornamented with cuticu-

lar ridges defining 6 rows of dorsal and lateral plates, thus appearing pseudo-segmented. Telson similarly ornamented ventrally and bearing 0–6 serrate spines along posterioventral margin and pair of small, setose, unsegmented or (perhaps superficially) 2-segmented furcal rami on posterior face.

Ypsigon stage [based on Glenner et al. (2008), Chan et al. (2021), Dreyer et al. (in press)]: unsegmented, slug-like, slightly motile despite lacking appendages. Lined externally by extremely thin (epi)cuticle. Internal cellular contents comprising epithelium beneath cuticle, derivatives of former cyprid nervous system (including large anterior neuropile and degenerating compound eyes), muscle bands, and elongate mass of cells filled with lipid vesicles. No ovarial or testicular tissue present.

Type genus. *Hansenocaris* Itô, 1985.

Remarks. As reviewed by Dreyer et al. (in press), a putative family-group name "Hansenocarididae", with or without attribution to Itô (1985), has been cited in a few print and internet sources, but Itô never proposed such a name in any of his works. Our action herein is the first to make this family-group name available for y-larvae in accordance with the relevant provisions of Chapter 4 of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature 1999). The new Japanese name combines the existing Japanese name for Facetotecta ("chou-kou-rui", which refers to the faceted cephalic shield; Ohtsuka 2000), and "mushi", meaning "bug" or "worm."

Genus *Hansenocaris* Itô, 1985
[New Japanese name: Chou-kou-mushi-zoku]
Hansenocaris cristalabri Olesen and Grygier, sp. nov
[New Japanese name: Tosaka-chou-kou-mushi]
(Figs 1–5)

Diagnosis. In last-stage nauplius, labrum produced ventrally as three-sided pyramidal base topped with elongate, cockscomb-like process bearing row of 9 dagger-like spines along anterior side. Cephalic shield clearly and nearly completely reticulated, divided into discrete facets except for a few continuous submarginal belts in posteriolateral sector, and with pair of rounded, spine-bounded marginal notches far posteriolaterally. Cephalic shield with fewer pores than any other described late-stage facetotectan nauplius: 1 unpaired anterior pore, 6 pairs of simple pores elsewhere, and 3 pairs of pores with emerging setae (2 obvious dorsal pairs, 1 minute anterior pair). Faciotrunk with broad keel along about half of dorsum, bounded by 2 rows of spines. First antenna with 3 apical setae and preaxial spine. Second antenna and mandible devoid of feeding structures (lecithotrophic); setal formulae of their exopods $0:1:1:1:1:2$ and $0:1:1:1:2$ respectively, their endopods 2 and 2, respectively. First maxillae and dorsocaudal organ (or corresponding pore) absent. Dorsocaudal spine nearly as long as trunk dorsum preceding it, armed along most of length with about 10 irregular rings of large, pointed subsidiary spines.

Type locality. Off pier at the University of the Ryukyus Tropical Biosphere Research Center, Sesoko Station, on

Sesoko Island, Okinawa Prefecture, Japan (26°38′09.3″N 127°51′55.2″E).

Type material. Holotype, last-stage nauplius mounted on SEM stub, Natural History Museum of Demark. NHMD-1174614. Originally collected 10 June 2019, first photographed 12 June 2019, again photographed 14 June 2019 after molt to last-stage nauplius, again photographed 17 June 2019 and fixed same day. Live video of this specimen in these two naupliar instars viewable at https://youtu.be/SCskuhPTCXo, also deposited at https://doi.org/10.6084/m9.figshare.20430807. Specimen collected and processed by D. Eibye-Jacobsen, M. J. Grygier, and J. Olesen.

Etymology. The Latin name is a genitive compound noun, from Latin "*crista*", for a comb or plume on an animal's head, and "*labrum*", for lip (Brown 1956), glossed as "crest of the labrum" and referring to the labrum's extraordinary, cockscomb-like ventral process. The new Japanese name combines the Japanese noun "tosaka", meaning "cockscomb", with an existing Japanese name for Facetotecta ("chou-kou-rui", which refers to the faceted cephalic shield), and "mushi", meaning "bug" or "worm."

Description (holotype). A last-stage nauplius larva (Figs 1C, D, 2, 3, 4F, 5).

Habitus (Figs 1C, D, 2A, B, 3A). Cephalic portion of body slightly oblate-oval; trunk portion long and attenuate, resembling champagne glass in outline in dorsal or ventral view. Total length 434–445 μm as measured in different photographs; length, width, and height of domelike cephalic shield 223, 182, and 73 μm, respectively; post-shield length of trunk in dorsal view 240 μm, anterior width and post-labral length of trunk in ventral view 87 μm and 317 μm, respectively; trunk height at posterior end of shield 102 μm. Length (measured from midventral pore) and basal diameter of dorsocaudal spine 123–129 μm and 31–35 μm, respectively, as measured in different photographs. Long axis of trunk, extending from midheight at anterior end of trunk to midheight at base of dorsocaudal spine, downturned 20° with respect to long axis of cephalic shield as defined by its lateral margins (Fig. 2B); dorsocaudal spine then upturned 18° with respect to long axis of trunk.

Cephalic shield (Figs 3A–C, 4F). Ornamented with dense, nearly symmetrical pattern of reticulate ridges outlining many so-called plates, or facets, as well as 4 pairs of submarginal elongate belts in posteriolateral sectors. Limited numbers of setae (2 obvious dorsal pairs and 1 minute anteriolateral pair) and simple pores (6 pairs, 1 unpaired, plus posteriolateral pair of pits) situated within these plates or along ridges delimiting them (Figs 2B, I, 3A, C–M; Table

1). Ridges obvious but not especially prominent in SEM photos, some fainter ones perhaps representing new plate divisions compared to preceding instar (cf. Itô 1990). Faint and extremely fine vermiculation evident within plates, but plate surfaces essentially smooth. Pair of shallow, triangular indentations present in anterolateral margins (probably artifact associated with adjacent crosswise fold in ventral cuticle). Pair of shallow, rounded notches present in far posterolateral margins, each flanked anteriorly and posteriorly by a spine, and with posteriorly-facing pit on shield margin immediately behind posterior spine (Figs 2E, N, 3N).

Cephalic shield's plates or facets centered on rounded-quadrangular 'window' (W) at about one-third length along midline. Remainder of plate description based on homology assumptions indicated by color-coding in Fig. 4. Among 'frontal' plates (labelled in Figs 3C, 4F; see also Fig. 3A), primordial plate F-1 represented by pair of small pentagonal plates flanking W and by transverse row of 4 small plates preceding these and W. Primordial plate F-2 possibly represented by array of 6 small plates preceding F-1 region, including transverse central pair and 2 longitudinally oriented lateral pairs. Primordial plate F-3 possibly represented by next more anterior 2×2 array of plates, and F-4 by next more anterior 2 or 3 transverse plates (site of boundary between original F-4 and original 'Brim' unknown). Unpaired, ridge-encircled pore *1** present on midline anteriorly.

Among 'occipital' plates (labeled in Fig. 3C, 4F; see also Fig. 3A, B), large O-1 and O-2 pairs present successively behind W. Set of 20 small plates with clear lateral boundaries but somewhat asymmetrical internal arrangement (presumably derived from primordial plates O-3, O-4, and O-5) present behind O-2 pair, with pair of small, ridge-bounded pores (*9r* and *9l*) externally near anterior ends of lateral bounding ridges (Fig. 3H). These plates succeeded by well-defined rectangular array of small quadrilateral or pentagonal plates in 4 longitudinal rows of 6 plates each (presumably derived from axial parts of primordial plates O-6 and O-7), with third pair of outer plates distinctly smaller than rest. These followed by middle 4 of 6 plates in transverse row along shield's posterior margin, an area not included in Itô's (1990) nomenclature.

Among identifiable 'intermediate,' 'polygonal,' and 'marginal' plates (labeled in Figs 3C, 4F; see also Fig. 3A), plate pair I-1 heptagonal, maintaining its primordial identity and not subdivided, each member of pair with large, ridge-bounded pore (*4r* and *4l*) posteriorly. Each I-1 plate preceded by 2 rows of sometimes bisected plates, evidently derived from primordial P-1 and, more anteriorly, from primor-

Table 1. Overview of distribution of 28 cuticular surface structures (pores, sensilla, setae) on different body regions of last-stage nauplius (LSN) of *Hansenocaris cristalabri* sp. nov., holotype (NHMD-1174614) from Sesoko Island (Japan: Okinawa). Numbers refer to individual structures as indicated on Figs 2–4. All structures paired except when asterisk (*) indicates unpaired structure found only in midline.

	Large, slit-like pore (~2 μm diam.)	Pore with large seta	Small, circular pore (1–2 μm diam.)	Pore with small seta	Total
Cephalic shield	1*, 2, 4, 7, 8, 10, 11	5, 6	9	3	21
Faciotrunk	12, 13, 15*		14		7
Total	18	4	4	2	28

dial M-1 plates (most anterior plates possibly derived from Brim, not M-1), with large, ridge-bounded pore (*2r* and *2l*) at anteriolateral corner of each array (Fig. 3L). Small anteriolateral pair of pores each containing minute seta (*3r* and *3l*; Fig. 3J) present along ridges extending posteriorly from middle of lateral sides of putative P-1 regions, these ridges evidently dividing regions corresponding to plates P-2(a) and M-2(a) of *H. furcifera* (cf. Fig. 4B). Large, ridge-bounded submarginal pore (*7r* and *7l*) present near outer posterior corner of putative M-2(p) area (if not in Brim-derived area; see Fig. 3L). Putative derivatives of primordial 'intercalary,' 'elongate,' and 'crescentic' (I-, E-, and C-) plates all quite narrow and long; anterior ends of primordial C-1 and (laterally adjacent) I-3 plates marked by 2 obvious pairs of setae (*5r* and *5l*, *6r* and *6l*) flanking primordial F-1 region (Fig. 3E). Two other pairs of large, ridge-encircled pores present on shield, including 1 pair (*8r* and *8l*) situated posteriolaterally within primordial plates E-2 (Fig. 3F) and another more posterior and slightly more lateral pair (*10r* and *10l*) of uncertain positional homology (P-5 or P-6 area) (Fig. 3G).

Cephalic part of faciotrunk (Figs 2A, B, 5A, B). Three pairs of limbs (uniramous first antennae, biramous second antennae and mandibles; Fig. 5) all arising from single large pair of rounded-crescentic or reniform areas of arthrodial membrane (Figs 2A, B, 5A, B). These limbs flanking labrum and surrounded externally by flat faciomarginal area with 3 or 4 concentric cuticular ridges joined by sparse connecting ridges (Figs 2A, 5A); ridge pattern most regular anteriorly (2 rows of lozenges) and posterolaterally (similar to but fainter than that of adjacent dorsal surface). No obvious pair of pores between first antennae and anterior cephalic margin, but pair of ventral pores (*11r* and *11l*) immediately adjacent to faciomarginal area's posteriolateral margins (Fig. 2A).

Labrum (Figs 1D, 2A–D, 5A, B). Proximal part expressed as narrow, triangular pyramid, posterior width 27 µm, lateral diagonal length 44 µm, height 35 µm, with large unpaired pore *16** situated proximally on midline of posterior face slightly distal to transverse slit-like depression (Fig. 2F, G). Pyramid encircled with cuticular ridge near base, leading to possibly paired slit-like depression across front (Fig. 5B), also with cuticular ridge defining its entire anterior midline. Pyramid topped with 79 µm long, ventrally directed, tapered, and somewhat rounded in cross-section cockscomb-like process (Figs 2C, 5A); inclined circular ridge delimiting it from pyramidal base leading to weak, slit-like furrow posteriorly (Fig. 5A). This process armed with single row of 9 distally directed dagger-like spines arising from within shallow longitudinal groove along anterior face. Proximal 2 spines ≤7 µm long, others considerably longer, up to about 19 µm as measured along distal side, and apical 2 spines sharing common base. Pyramidal base flanked by faint ridges on facial cuticle, forming 2 elongate lozenges on each side, these being connected to several wedge-shaped ridge arrays present farther anteriorly out to innermost of above-mentioned concentric ridges (Figs 2A, 5B).

First antenna (Figs 2A, B, 5A–C). Two-segmented, excluding narrow, arcuate sclerite at base upon which proximal end of first segment articulates and very thin, hemi-

annular sclerite with tapered ends present within postaxial half of articulation between two main segments (best visible in Fig. 5C). Unarmed first segment short and cylindrical (11 µm long, 15 µm in diameter) with rounded slight protrusion of distal half of preaxial side. Distal segment 42 µm long, digitiform with proximal 60% of preaxial side moderately swollen, showing faint indications of subdivision at 20% and 70% length, and bearing arrays of minute spinules mostly on distal half. This segment thickest (19 µm) at one third length, half as thick distally, with 3 apical setae: 1 extremely short seta and 1 simple seta of medium length (32 µm) arising adjacent to each other on postaxial rim (shorter one outer), and 1 long seta (60–70 µm) with single(?) row of very short setules arising mid-apically. Additional spine present on preaxial face at distal end of swollen region, associated with distal subdivision trace.

Second antenna (Fig. 2A, B, 5A, B, D). With unarmed, ring-like sclerite at base (precoxa?), unarmed cylindrical coxa slightly thicker than long (16×12 µm), shorter unarmed basis 8 µm long, and 2 rami. Six-segmented exopod 31–32 µm long, bearing 6 setae. All segments fully annular: first segment short and unarmed; second a little longer with 1 minuscule seta; next 3 segments again longer and equal in size among themselves, bearing 1 long seta each; apical segment minute and bearing 1 long inner and 1 short (28 µm) outer seta. Endopod 1-segmented, cylindrical, 6 µm long and 3 µm thick, thus slightly longer than first 2 exopodal segments combined, bearing 2 long and nearly equal apical setae. At least some setae of antenna 2 setulate, but precise distribution of setules unclear.

Mandible (Fig. 2A, B, 5A, B, E, F). Similar to second antenna but smaller, with no clear pre-coxa; coxa longer (13 µm) than basis (8 µm) and of slightly greater diameter (14 µm); articular facet of basis with exopod beveled. Exopod 31–33 µm long, 5-segmented, bearing 5 setae: 1 each (all long) on second to fourth segments and 2 unequal setae on tiny apical segment, shorter one (21 µm) outer. Endopod 1-segmented, 6 µm long and 4 µm thick, reaching to mid-length of second exopodal segment, bearing 2 long apical setae. At least some mandibular setae setulate, but precise distribution of setules unclear.

Hind part of faciotrunk. Trunk divisible into long, sparsely ornamented anterior part, heavily and concentrically ornamented posterior part, and heavily armed dorsocaudal spine. Anterior two thirds of venter with short and sparse transverse ridges, 3 of them at front end being more obvious and longer; in posterior third, ridges well expressed and bearing small spinules; in between, somewhat swollen and rounded area largely unornamented, but with several paired clusters of spinules possibly representing thoracopodal setae of next-instar cypris y (Fig. 2A). Anterior-most ridges flanked by pair of narrow but thick-lipped, slightly arcuate, transverse invaginations (Figs 2A, 5A), these at least 12 µm long but partly obscured in all photographs and presumably related to anterior struts of internally developing cypris y's "ghost" (presence of which not confirmed, requiring examination of shed last naupliar exuviae; see Grygier et al. 2019). Anterolateral part of trunk below distinct longitu-

dinal ridge ornamented with weak, parallel, dorsoventrally oriented ridges (Fig. 2B). Area dorsal to posterior part of same longitudinal ridge together with remainder of dorsal side of trunk with about 15 slightly produced, obviously but irregularly and sparsely denticulate transverse ridges (Figs 2B, 5A), posterior 10 or so of which encircling whole body although to some degree discontinuous ventrally. Most of posterior half of trunk dorsum slightly compressed to form low dorsal "keel" bounded by 2 rows of spines (Fig. 3A, B, O). Longest ridge spines on trunk about half as long as distance between successive ridges. Two presumably paired (right side not visible), ridge-encircled pores (*12l* and *13l*) present laterally below "keel", associated with fifth and seventh ridges anterior to furcal spines (Fig. 2B, K, L); additional tiny pore (*14l*) present between and below them. Dorsocaudal organ (or positionally equivalent mid-dorsal trunk pore) absent.

Pair of somewhat upcurved, sharply pointed, and proximally spinose furcal spines arising anterioventrally to midventral (anal?) pore below base of dorsocaudal spine, each furcal spine 15 μm long along its central axis (Figs 1C, D, 2A, B, O, P, 3B). Midventral (anal?) pore *15** itself situated on slightly raised transverse oval, with weak, arcuate transverse ridge behind it (Fig. 2P). Dorsocaudal spine (Figs 1C, D, 2A, B, L, M, 3A) armed along entire length, except for its sharply pointed tip, with about 10 irregular rings of large, pointed spines up to about 11 μm long, proximal ones slightly curved, distal ones straight. Pair of faint ridges extending out from base of each spine, all such ridges together imparting embossed scale-like appearance to surface of spine (Fig. 2O, P).

Earlier and later developmental stages. General appearance of holotype specimen as photographed alive 5 days prior to fixation (Fig. 1A), and again before molt to last-stage naupliar instar (Fig. 1B), much like that of last-stage nauplius (e.g., labrum with large, cockscomb-like process), but lacking pigmented pair of developing compound eyes or any other internally developing cyprid structures such as thoracopods, and having significantly more internal yolk-like material than last-stage nauplius. Within last-stage nauplius (Fig. 1C, D), compound eyes of internally developing cyprid about 8.8 μm long, 6–6.5 μm wide in ventral view (Fig. 1C), presumptive labrum of cyprid with small distal knob but no evidence of any unusual structure (Fig. 1D).

Hansenocaris aquila Grygier and Olesen, sp. nov.
[New Japanese name: Washi-chou-kou-mushi]
(Fig. 6)

Diagnosis. In last-stage nauplius, labrum wine-glass-shaped in ventral view with rounded posteriolateral corners, median keel carrying 3–4 small spines, and robust, sharply pointed posterior spine reminiscent of eagle's beak. Labral surface with characteristic ridge pattern described below. Cephalic shield clearly and completely reticulated. Dorsum of faciotrunk with 4 longitudinal spine rows, inner pair of rows longer than outer pair. Second antennae and mandibles devoid of feeding structures (lecithotrophic), segmentation of their exopods and endopods 6/5 and 1/1, respectively. First maxillae and dorsocaudal organ absent. Dorsocaudal spine nearly as long as trunk dorsum preceding it, armed with robust spines. Furcal spines small.

Type locality. Off pier at the University of the Ryukyus Tropical Biosphere Research Center, Sesoko Station, on Sesoko Island, Okinawa Prefecture, Japan (26°38′09.3″N 127°51′55.2″E).

Type material. Holotype: exuvium of last-stage nauplius prepared as semi-permanent glycerine jelly slide-mount, Natural History Museum of Denmark. NHMD-1174615; collected alive as young nauplius on 22 September 2005, last stage isolated from batch culture on 25 September, its empty molt retrieved on 27 September. Paratype: exuvium of last-stage nauplius prepared as semi-permanent glycerine jelly slide-mount, Natural History Museum of Demark. NHMD-1174616; collected alive as young nauplius on 16–19 July 1996, final exuvium recovered on 22 July; unclear which of 2 cyprids mounted on same slide corresponds to this nauplius. Both type specimens collected and processed by M. J. Grygier.

Etymology. The Latin name is a noun in apposition, "*aquila*" (="eagle"), referring to the large, strongly pointed, eagle-beak-like extension of the posterior margin of the labrum. The new Japanese name combines "washi" (Japanese for "eagle," again referring to the labrum) with an existing Japanese name for Facetotecta ("chou-kou-rui") plus "mushi," meaning "bug" or "worm."

Description (holotype). A last-stage nauplius larva (Fig. 6).

Habitus (Fig. 6A, B). Cephalic portion slightly oblate-oval, trunk portion long and attenuate. Total length 500 μm; length and width of cephalic shield 265 and 210 μm, respectively; anterior width and post-labral length of trunk in ventral view 105 μm and 350 μm, respectively. Length (measured from furcal spines) and basal diameter (at position of furcal spines) of dorsocaudal spine 100 μm and 30 μm, respectively. No lateral view available but long axes of cephalic shield, trunk, and dorsocaudal spine apparently nearly in same plane (no significant bending).

Cephalic shield (Fig. 6C). With dense, nearly symmetrical pattern of reticulate ridges outlining many so-called plates, or facets. Setation and pore pattern of shield not clearly visible, but posteriolateral corners lacking *H. cristalabri*-like pair of spine-bounded notches. Plates or facets centered on rounded-quadrangular 'window' (W) at about one-third length along midline, but only those near W (Fig. 6C) easily identifiable with those of *H. cristalabri* sp. nov. and *H. furcifera*. Namely, region of primordial 'frontal' plate F-1 represented by pair of small pentagonal plates flanking W and by transverse row of 4 small plates preceding these and W; region of primordial 'frontal' plate F-2 possibly represented by array of 6 small plates preceding F-1 region, including transverse central pair and 2 longitudinally oriented lateral pairs; and primordial 'occipital' plates O-1 and O-2 represented by 2 successive pairs of large plates posterior to W. Configuration of all other plates, including more anterior F-plates, more posterior O-plates, and most non-ax-

ial plates, differing from those in *H. cristalabri* sp. nov. and *H. furcifera* (cf. Fig. 4E) and, owing to lack of information about important "land-mark" pores and setae, also difficult to homologize with any other species' primordial plates; therefore, detailed description omitted.

Labrum (Fig. 6A, B, D, E). Excluding its robust, sharply pointed, 35 μm long posterior extension, main portion of labrum obovate or rounded-spatulate in ventral view, 80 μm long and 60 μm wide, with median keel bearing row of 3 small but distinct and equal distal spines preceded by another minute spine. Labral surface divided by ridges into facets as follows: 2 elongated and overlapping facets along each lateral margin, with more anterior pair meeting in anterior midline; paired diagonal rows of 4 facets situated medial to these, extending from anterior midline to posteriolateral margin; 1 pair of posteriomesial facets preceding 2 small pairs flanking spine at posterior margin; and keel-bearing facet(s) along labrum's posterior midline.

First antenna (Fig. 6F). Apparently 3-segmented, excluding narrow sclerites between 3 main segments. Unarmed first segment short, cylindrical (15 μm long, 20 μm in diameter). Unarmed second segment short, cylindrical (20 μm long, 17 μm in diameter). Distal segment 45 μm long, digitiform with moderate preaxial swelling of proximal 50%. This segment thickest (19 μm) at 1/3 length, with 3 apical setae: 2 long and 1 short.

Second antenna (Fig. 6G). Biramous with unclear proximal segmentation. Unarmed coxa about as thick as long (25 μm), unarmed basis shorter (20 μm long). Exopod 50 μm long, 6-segmented with rudimentary (perhaps not fully annular) proximal segment and further segments gradually becoming smaller distally, apparently bearing 5 setae in all. Endopod 1-segmented, cylindrical, 15 μm long and 7 μm thick, bearing 2 long apical setae.

Mandible (Fig. 6). Similar to second antenna but smaller, again with unclear proximal segmentation. Coxa longer than basis (16 μm vs. 14 μm) and of slightly greater diameter (16 μm). Exopod 40 μm long, 5-segmented, apparently bearing 4 setae. Endopod 1-segmented, 10 μm long and 3–4 μm thick, bearing 2 long apical setae.

Hind part of faciotrunk (Fig. 6A, B, J). Trunk divisible into long, sparsely ornamented anterior part, heavily and concentrically ornamented posterior part, and heavily armed dorsocaudal spine. Anterior 15% or so of venter with short and sparse transverse ridges, followed by somewhat swollen and rounded middle region with short transverse ridges along midline and, more laterally, paired rows of bumps evidently representing future thoracopodal setae; in posterior third, concentric ridges well expressed and bearing small spinules (Fig. 6A, B). Trunk dorsum with 2 dorsal rows of spines along nearly whole length from first or second transverse ridge to base of dorsocaudal spine, with slight discontinuity posterior to midlength, and additional shorter dorsolateral pair of spine rows reaching only to dorsal rows' points of discontinuity (4 spine rows in total) (Fig. 6B). Dorsocaudal organ (or positionally equivalent mid-dorsal trunk pore) absent. Dorsocaudal spine (Fig. 6A, B) armed with large subsidiary spines along entire length, except at sharply

pointed tip. Pair of small (7 μm long), pointed furcal spines arising anterioventrally to base of dorsocaudal spine (Fig. 6J). Midventral (anal?) pore not observed.

No "ghost" of cyprid thorax (see Grygier et al. 2019) detected inside slide-mounted exuvium.

Description (Paratype). Trunk region rotated on slide relative to cephalic region, and posteriolateral part of one side of cephalic shield distorted; therefore, some of following measurements probably different in life. Total length 530 μm; cephalic shield length along midline 277 μm, maximal width 215 μm, posterior width 147 μm; dorsal trunk length 257 μm including 97 μm long dorsocaudal spine. Dorsocaudal spine similarly spiny to that of holotype. Labrum 113 μm long including posterior medial spine, maximal width 70 μm; main portion with same rounded-spatulate or obovate shape as that of holotype and with row of small spines preceding robust, beak-like posterior extension, latter relatively shorter (23 μm) than that of holotype; cuticular ridge pattern of labrum resembling that of holotype. Four longitudinal rows of spines on trunk dorsum: 2 inner rows extending from about fourth transverse ridge to base of dorsocaudal spine, 2 outer rows extending from anterior margin only half this distance posteriorly. Limb setation as follows: first antenna with 1 long and 1 medium-long apical setae; second antenna with unarmed coxa and basis, 2 apical setae on 1-segmented endopod, and 5 setae on 6-segmented exopod (0-0-1-1-1-2); mandible similar but exopod 5-segmented with 1-1-1-2 setal arrangement. No cyprid "ghost" visible within exuvium, but pair of oval (19.5×5.5 μm), purportedly "ghost"-related anterioventral invaginations present on trunk (Fig. 6B).

Discussion

Taxonomic comparison. Although crustacean y-larvae (Facetotecta) have been known for more than a century (Hansen 1899) and are now known from all over the world while occasionally being abundant (Kolbasov and Høeg 2003; Glenner et al. 2008; Olesen et al. 2022; Dreyer et al. in press), the corresponding adult crustaceans are unknown. This has not prevented the formal description of 15 species, but these have been based on different larval stages (early nauplii, late nauplii, cyprids) with uneven quality of description, which sometimes makes comparison difficult. Since the life cycle of y-larvae is yet not understood, it would probably be the best practice to base species descriptions on a combination of nauplii and cyprids, and also to accompany descriptions with molecular data in order to match eventually discovered or newly recognized adults with larvae bearing taxonomically available names (Olesen et al. 2022). The descriptions herein of *H. cristalabri* sp. nov. and *H. aquila* sp. nov. seem to flout this recommendation, being based only on last-stage nauplii, but both have an exceptional morphology that prevents confusion with any other species. Also, among the ca. 10000 y-larvae sampled and collected during field work in 2018 and 2019 at its type locality, Sesoko Island (Olesen et al. 2022), *H. cristalabri* sp.

Fig. 2. *Hansenocaris cristalabri* sp. nov., holotype (NHMD-1174614), scanning electron micrographs of last-stage nauplius. A, B, habitus, ventral and lateral views, respectively; C, D, cockscomb-like labral process, left (enlarged from B) and right-posterior views, respectively; E, detail of spine-flanked notch in posteriolateral margin of cephalic shield, indicated by dotted arrow (cf. Fig. 3N); F, G, successively enlarged details of pore in A on posterior face of labral base, indicated by dotted arrows; H, detail of pore in A indicated by dotted arrow; I–M, details of pores in B indicated by dotted arrows; N, same as E; O, detail of dorsocaudal spine in B, left lateral view; P, detail of region of furcal spines, slightly oblique ventral view. Abbreviations: invag, cuticular invagination; pores and setae numbered as described in text and Table 1.

nov. was apparently represented by only a single specimen. The two specimens of *H. aquila* sp. nov. were each unique in their year of collection among a large number of laboratory-reared specimens. It appears that both types of y-nauplii are extremely rare, and their cyprids will most likely not be recognized and described anytime soon.

Neither *H. cristalabri* sp. nov. nor *H. aquila* sp. nov. can

be mistaken for any other described species of y-larva. Most notably, the remarkable cockscomb-like process extending from the labrum of *H. cristalabri* sp. nov. and the aquiline extension of the labrum in *H. aquila* sp. nov. are unique to these forms, as are the spine-bounded posteriolateral notches of the cephalic shield in *H. cristalabri* sp. nov. Both species share a very long, attenuate trunk region terminat-
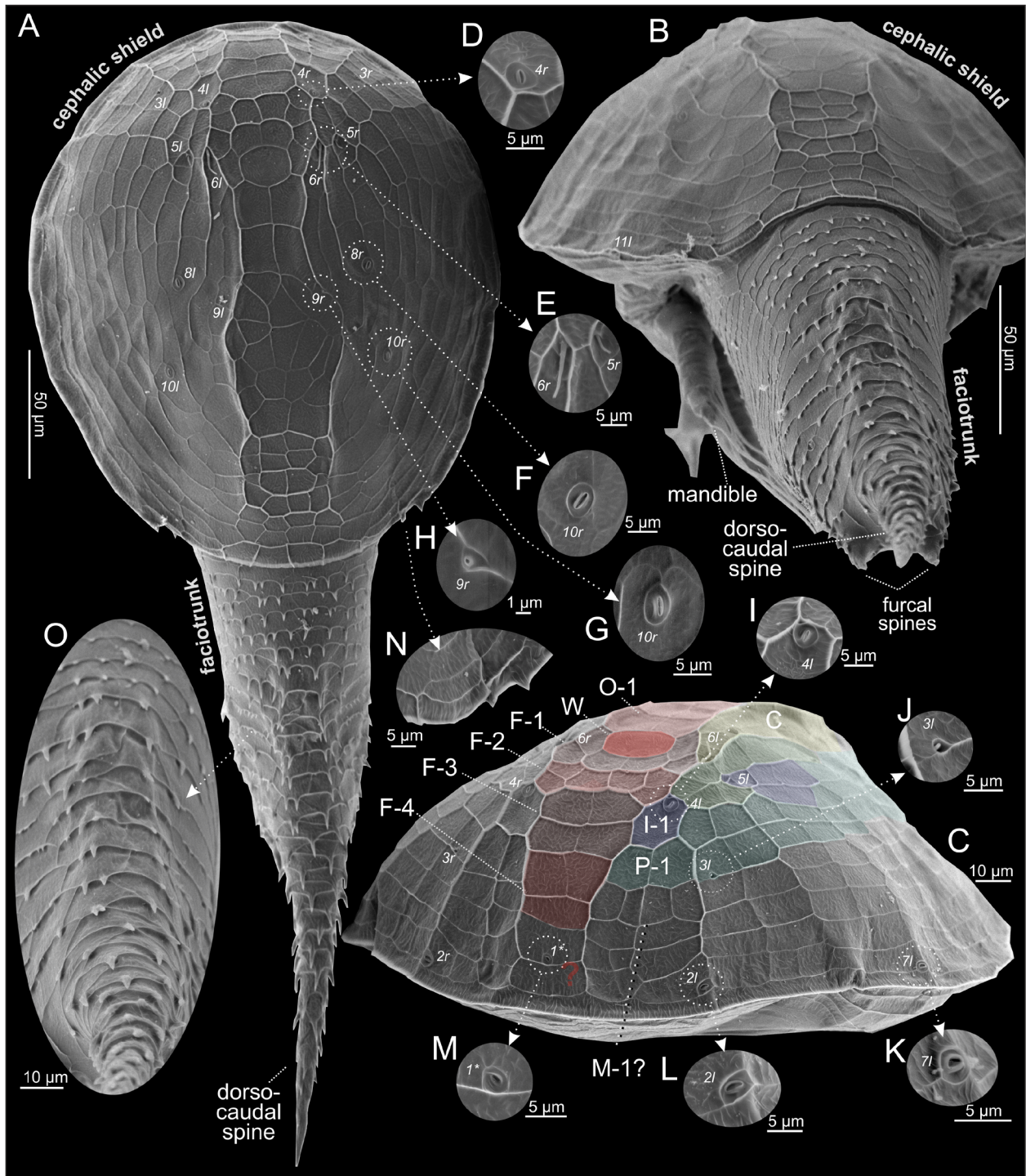
Fig. 3. *Hansenocaris cristalabri* sp. nov., holotype (NHMD-1174614), scanning electron micrographs of last-stage nauplius. A, B, habitus, dorsal and posteriodorsal view respectively; C, cephalic shield, slightly oblique frontal view, with 'primordial plates' differentiated by colors and abbreviations following Itô's (1987b, 1990) system (see Fig. 4); D–M, details of pores and setae of cephalic shield in A and C, indicated by dotted arrows; N, detail of spine-flanked notch in posterolateral margin of cephalic shield, indicated by dotted arrow (cf. Fig. 2E); O, two orderly spine-rows defining dorsal "keel" of trunk and contrasting with otherwise irregularly arranged spinules of transverse ridges. Abbreviations: C, crescentic plate; F-1–F-4, derivatives of primordial frontal plates 1–4; I-1, intercalary plate 1; O-1, occipital plate 1; P-1, derivatives of primordial polygonal plate 1; W, window; pores and setae numbered as described in text and Table 1.

ing in a long, heavily spinose dorsocaudal spine as well as longitudinal rows of spines on the trunk dorsum (two rows in *H. cristalabri* sp. nov., four in *H. aquila* sp. nov.). The presence of such common features suggests that the two new species are closely related. Total lengths of 445–530 μm

make the last-stage nauplii of these two species, especially *H. aquila* sp. nov., among the longest formally named y-nauplii known, matching the last naupliar stage of the lecithotrophic *Hansenocaris mediterranea* Belmonte, 2005 (506 μm: Belmonte 2005) but considerably shorter than
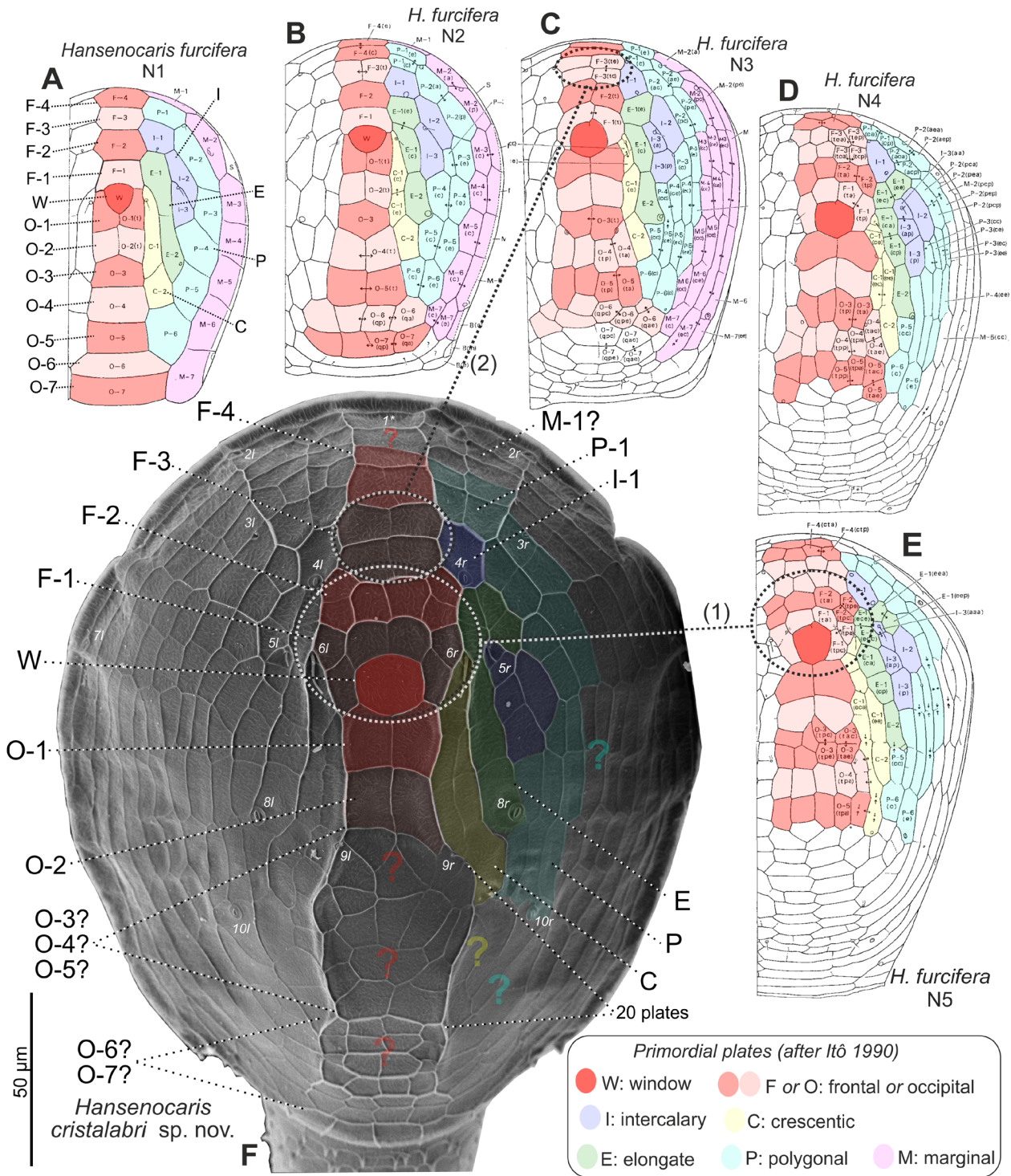
Fig. 4. Comparison of cephalic shield plates of *Hansenocaris furcifera* Itô, 1989 and *Hansenocaris cristalabri* sp. nov., holotype (NHMD-1174614). A–E, cephalic shields of last five naupliar instars [N1–N5 respectively according to Itô (1990)] of *H. furcifera* with color-zone indications (key at lower right) showing successive stages of subdivision of shield plates (facets) starting with 'primordial' plates in N1 (after Itô 1987a, 1990: figs 5E–F, 7, 8E, 10B; used with permission of the editor, Publications of the Seto Marine Biological Laboratory); F, last-stage nauplius of *Hansenocaris cristalabri* sp. nov. with presumed plate homologies to *H. furcifera* indicated by color-coding and alpha-numeric labels. Putatively homologous regions in C, E, and F marked by linked dotted ellipses.

the last naupliar stage of the planktotrophic *Hansenocaris itoi* Kolbasov and Høeg, 2003 (670–700 μm: Kolbasov and Høeg 2003; Kolbasov et al. 2021a). Some longer forms have also been described under Roman-numeral para-taxonomy, e.g., planktotrophic Type IV, up to 595 μm (Schram 1972), and

Type VI, 619 μm (Grygier 1987).

The nauplii of *H. cristalabri* sp. nov. and *H. aquila* sp. nov. sp. nov. are clearly non-feeding lecithotrophs, as shown by the lack of both feeding spines on the naupliar appendages and, at least in *H. cristalabri* sp. nov., a posteriorly ex-
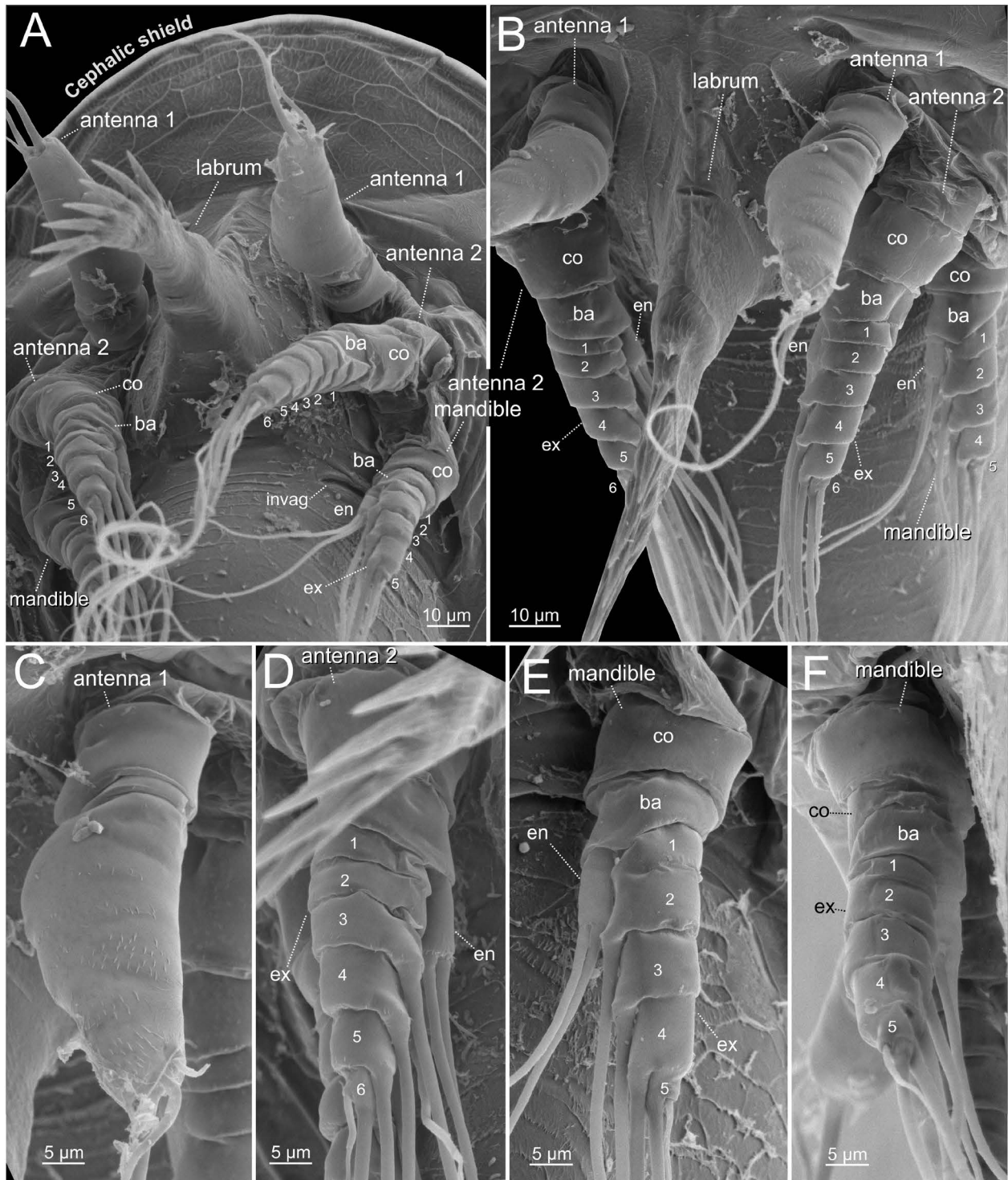
Fig. 5. *Hansenocaris cristalabri* sp. nov., holotype (NHMD-1174614), scanning electron micrographs of last-stage nauplius. A, naupliar appendages (first antennae, second antennae, and mandibles) and labrum with cockscomb-like process, ventral view; B, same, anterior view; C, left first antennae, outer side; D, right second antenna, inner side; E, F, left mandible, viewed from two different angles. Abbreviations: ba, basis; co, coxa; en, endopod; ex, exopod; invag, cuticular invagination. Arabic numerals 1–6, exopodal segments 1–6, numbered from proximal to distal.

tending free labrum. There is also much internal yolk in *H. cristalabri* sp. nov., especially in its earliest photographed nauplius (Fig. 1A, B). Among the 15 formally named species of y-larvae, remarkably few have lecithotrophic nauplii, so far only *H. mediterranea* (see Belmonte 2005) and *Hansenocaris demodex* Olesen, Dreyer, Palero, and Grygier,

2022 in Olesen et al., 2022 (q.v.). Of the seven with apparently planktotrophic nauplii, all are morphologically very different from *H. cristalabri* sp. nov. and *H. aquila* sp. nov., being somewhat shield-shaped with obvious lateral spination of the posterior trunk region. Among the lecithotrophs, *H. mediterranea* was based on nauplii of somewhat elongate
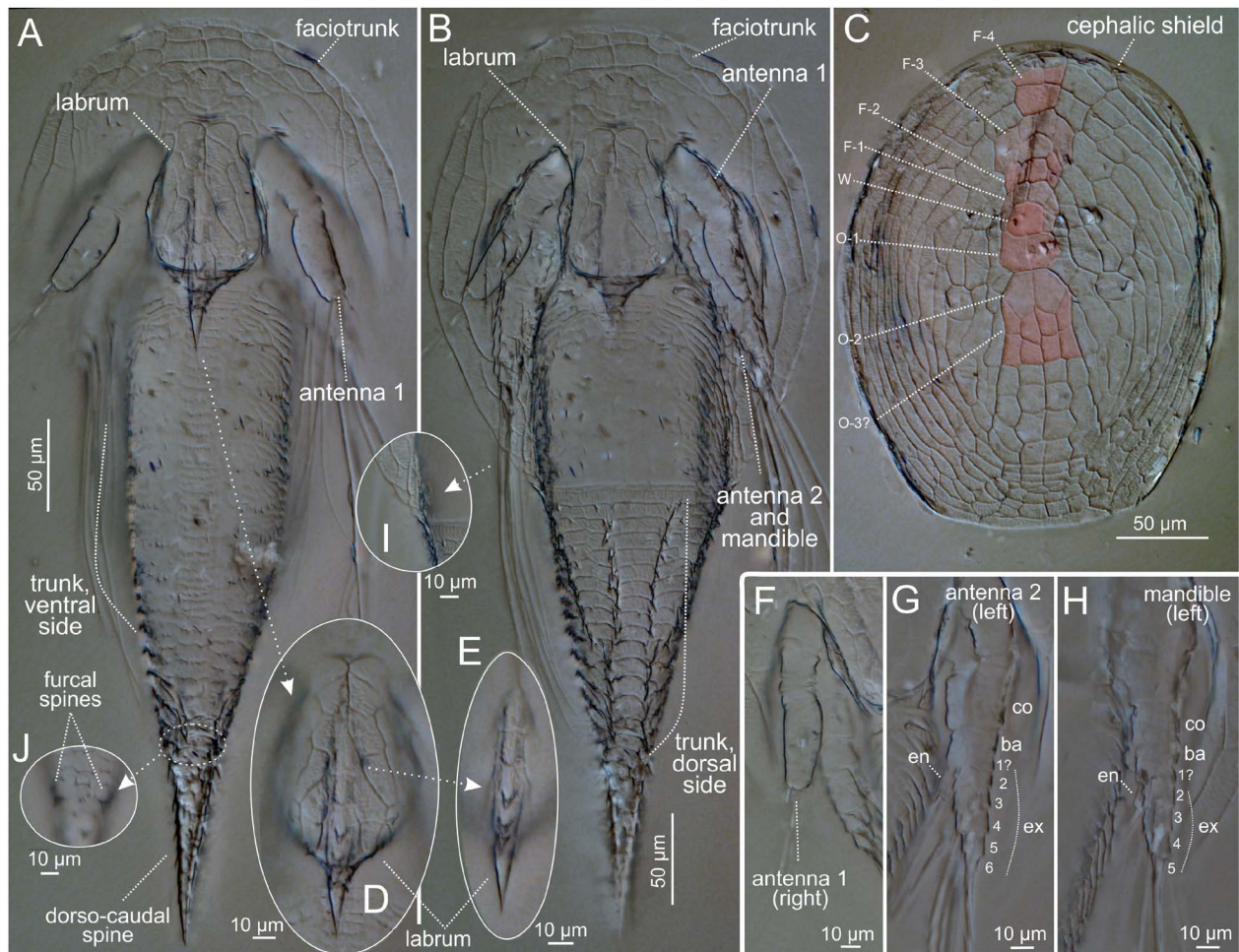
Fig. 6. *Hansenocaris aquila* sp. nov., holotype (NHMD-1174615), light microscopy of exuvium of last-stage nauplius, comprising subsets of full z-stack at different focus levels exported and fused into single images to increase depth of focus. A, habitus, with labrum, ventral side of faciotrunk, and dorsocaudal spine in focus; B, habitus, with dorsum of faciotrunk in focus; C, cephalic shield; D, labrum; E, spine-row of keel on labrum; F, right first antenna; G, left second antenna; H, left mandible; I, posteriolateral corner of cephalic shield showing no notch or spines; J, furcal spines. Abbreviations: ba, basis; co, coxa; en, endopod; ex, exopod; Arabic numerals 1–5, exopodal segments 1–5, numbered from proximal to distal; F-1–F-4 (red overlay), derivatives of frontal plates 1–4; O-1–O-3 (red overlay), derivatives of occipital plates 1–3; W, window.

shape but is readily distinguishable from *H. cristalabri* sp. nov. and *H. aquila* sp. nov. by the lack of all the more specific features of the latter that were mentioned above (labral form and processes, attenuate trunk, etc.). The semi-vermiform nauplii of *H. demodex*, with their lack of dorsal reticulation of the cephalic shield, rather thick body, short and blunt dorsocaudal spine, and reduced furcal spines (Olesen et al. 2022), are even more different from *H. cristalabri* sp. nov. and *H. aquila* sp. nov.

In addition to the 15 (17, including this paper) formally named species, the y-larva literature includes an extensive para-taxonomy as well as papers that present, for various purposes, illustrations of assorted y-larvae. Among these are some clearly lecithotrophic nauplii with remote similarities to *H. cristalabri* sp. nov. and *H. aquila* sp. nov., sharing for example a distinct cephalic region and a ventrally swollen but posteriorly attenuate trunk terminating in prominent dorsocaudal spine (e.g., Itô 1991), None of these, however, share any more specific characters with *H. cristalabri* sp. nov. and/or *H. aquila* sp. nov.

Plate arrangement of last-stage nauplius. One of the most visible characteristics of y-larvae is that the cuticular surface of the cephalic shield, and sometimes the surface of other body parts, is ornamented with a complicated reticular arrangement of plates, or facets, in both nauplii and cyprids, a fact that gave rise to their higher-level taxonomic name Facetotecta (Grygier 1985). Most authors, starting already with Hansen (1899), have meticulously depicted the arrangement of the plates of the cephalic shield when describing y-larvae. Itô (1990) tried to follow the subsequent development of the plate pattern through later planktotrophic nauplii of *H. furcifera*, especially with respect to the anterior and mid-dorsal regions. Besides a gradual and often eventually extensive subdivision of primordial plates into subsidiary plates, for which he proposed a nomenclature based on the precise course of plate division, Itô also found in later development a fusion of more marginally positioned subsidiary plates into long, continuous elongate belts (Fig. 4A–E). Apart from a briefly reported study of the development of an unnamed laboratory-reared form-taxon

from Japan (Itô 1991), the only detailed information on this topic for lecithotrophic y-larvae is the recent description of *H. demodex* (see Olesen et al. 2022) from Okinawa and Taiwan. Comparisons with that species are hampered by the absence of cuticular ridges over a wide dorsal and dorsolateral expanse of its cephalic shield.

Despite the fact that *H. cristalabri* sp. nov. and *H. furcifera* are otherwise not very similar, comparison of the plate pattern of the cephalic shield of the last-stage nauplius of both (Fig. 4E, F) revealed considerable similarity between them, enough that we could describe the former's shield in terms of the latter's in the species description above. However, at the detailed level there are also many differences in the plate arrangement. The plates at the center of the cephalic dome, i.e. the 'window' and the plates derived from primordial plates F-1 and F-2, which occur in a distinct pattern, can be identified rather precisely in the last-stage nauplius of both species [Fig. 4E, F: dotted circles (1)], and most of the plates formed by primordial plate series C, E, I, P, and M in the anterior half of the shield are identifiable. The situation is different, however, in the anterior and posterior parts of the axial row of primordial F and O plates. The anterior F-3 and F-4 plates in *H. cristalabri* sp. nov. are less subdivided than their counterparts in the last-stage nauplius of *H. furcifera*, showing more resemblance to the arrangement in the latter species' earlier nauplius 3 [Fig. 4C, F: dotted circles (2)]. This suggests that heterochrony (paedomorphosis) has played a role in the evolution of the plate arrangement in this part of the naupliar cephalic shield of *H. cristalabri* sp. nov. On the other hand, the posterior part of the shield in *H. cristalabri* sp. nov., corresponding to the primordial O-3 to O-7 plates, has no specific resemblance to the corresponding part of the cephalic shield in any naupliar stage of *H. furcifera*. Finally, putative primordial plate boundaries in the posteriolateral quadrants of the shield of *H. cristalabri* sp. nov. were not determinable.

To what extent do the outlined similarities between cephalic plate arrangements in the planktotrophic *H. furcifera* and the lecithototrophic *H. cristalabri* sp. nov. illustrate a general pattern for y-larvae? Clearly, more studies on especially lecithotrophic y-larvae are needed, since a large undescribed variation among these is known to exist. Preliminary information provided by Itô (1991) on the plate development of an unnamed lecithotrophic species shows that asymmetry in the arrangement of the central plates may increase profoundly the older the nauplius becomes, which is true to a much lesser extent in *H. furcifera* and *H. cristalabri* sp. nov. The limited information available on cephalic plate arrangement in different species of y-larvae seems to suggest a large variation among taxa, possibly allowing its use as a taxonomic "fingerprint" for delineating species. Future species descriptions will surely benefit from having the plate arrangement mapped in detail. Since dozens of species remain to be described, however, it would be overly tedious to illustrate and describe complete molt series for more than a few, as Itô (1990) attempted. For the rest, priority should be put on establishing the primordial plate pattern in the appropriate early instar—nauplius 2 according

to Kolbasov et al. (2021a)—and the last-stage nauplius, in which interspecific variation seems greatest. We again draw attention to the plate arrangement of the cephalic shield in the holotype of *H. aquila* sp. nov., which is rather different from that of *H. cristalabri* sp. nov. (cf. Figs 4F, 6C) despite other morphological similarities between these two species.

Pore and setal patterns of cephalic shield and trunk region. As described above and summarized in Table 1, the cephalic shield of the last-stage nauplius of *H. cristalabri* sp. nov. bears one unpaired anterior pore, six pairs of simple pores elsewhere, and three pairs of pores from which setae emerge (the most anterior setal pair being minute). Compared to the other two SEM-described species of *Hansenocaris* (*H. itoi* and *H. demodex*), these numbers are remarkably low. Perhaps a similarly low number of pores is present in *H. aquila* sp. nov.*,* but the exuvium studied with DIC optics did not reveal such details. Including pores on the 'Brim,' the cephalic shield of the last (supposedly seventh) naupliar stage of *H. itoi* has 15–17 pairs of simple pores and four pairs of seta-bearing pores (Kolbasov et al. 2021a; most being mapped in their fig. 11c), whereas *H. demodex* has one unpaired anterior pore, 10 other pairs of simple pores, three pairs of seta-bearing pores, and one other pair of minute sensilla (Olesen et al. 2022). Published SEM photographs of *H. itoi*, including those of the supposed second through sixth naupliar instars (Kolbasov et al. 2021a: figs 3c, d, 4d, 5b–e, 7b, 8b–d, 10b, c) allow tentative hypotheses of correspondence of some pores and setae in *H. itoi* with those of *H. cristalabri* sp. nov. (Table 2). Of the structures so treated, the I-1, E-2, both B-2 (anterior and far posteriodorsal), P-2, C-1, and I-3 pores/setae originate in nauplius stage 2 of *H. itoi*, the B-1/F-4' (?) pore is sporadically present in nauplius 3 but consistently present thereafter, and the P-6″ pores originate in nauplius 4. The remaining pores of *H. itoi* and the pair of posteriolateral setae that first appear on facet O-7″ in its nauplius 4 have no equivalents in *H. cristalabri* sp. nov. The fact that all of the pores and setae of the cephalic shield of the last-stage nauplius of *H. cristalabri* sp. nov. correspond to features that first appear in supposed naupliar stages 2–4 (mostly stage 2) in *H. itoi*, while none of those that first appear in supposed naupliar stages 5–7 of *H. itoi* is present at all in *H. cristalabri* sp. nov., suggests heterochrony (paedomorphosis) in the latter species, perhaps connected with lecithotrophy.

The cephalic shield of the last stage nauplius of *H. demodex*, as described by Olesen et al. (2022), has an unpaired anterior pore, 11 pairs of other pores, two pairs of dorsal setae, and one pair of minute, setiform posteriolateral sensilla. Of these, no more than 10 structures appear to have potential homologues in *H. cristalabri* sp. nov. (Table 2), and a few of these are doubtful. Pore 1 is distinctly farther from the shield margin in *H. demodex* than in the other two species, and pore 14 or 15 could correspond to the posteriolateral pit in the shield margin of *H. cristalabri* sp. nov. (Fig. 2E) only if the latter is actually a pore and not a pit. Posteriolateral sensilla pair 16 has an equivalent in *H. itoi*, but not *H. cristalabri* sp. nov. Olesen et al. (2022) did not have all the naupliar stages of *H. demodex* at hand, but they

Table 2. Possible homologies of cuticular pores/setae of cephalic shield (nos. 1*–11 and pit) and faciotrunk (nos. 12–15*) of last naupliar stage of *Hansenocaris cristalabri* sp. nov. (see Figs 2–4 herein) with those of last naupliar stage of *H. demodex* (see Olesen et al. 2022) and second and later naupliar stages of *H. itoi* (see Kolbasov et al. 2021a), based on SEM data. Asterisks (*) indicate unpaired pores in the midline; all other structures are paired. Minus signs denote absence; question marks denote doubt.

H. cristalabri sp. nov.	*H. demodex*	*H. itoi*
Pore/seta no.	Pore/seta no.	Plate position of correspondingpore/seta when first present
1*	1* (?)	posterior in B-1 or F-4 (plate identity unclear)
2	2	anterior in B-2
3	4	anteriolateral in P-2 (later, in P-2′ and P-2″)
4	6	posterior in I-1
5	7	anterior in I-3 (later, I-3′)
6	8	anterior in C-1 (later, in C-1′ and C-1″)
7	10	—
8	9	posteriolateral in E-2
9	12	—
10	11	posterior in P-6″
11	—	—
12	17	—
13	21	—
14	19	—
15*	20*	anus (?)
posteriolateral pit	14 or 15 (?)	far posteriodorsal in B-2 (?)
—	16	present

nonetheless attempted to identify corresponding pores and setae in some earlier instars. Of the pores suggested here as common to *H. cristalabri* sp. nov., nos. 2, 4, 6 (perhaps), 9, and (if correctly homologized) 14 were present in the earliest available instar of *H. demodex* (i.e., the fifth or perhaps sixth instar preceding the last nauplius), pore no. 1 at least two instars later, and nos. 10, 11, and 12 in the antepenultimate naupliar instar. In contrast to the results for *H. itoi*, the lower ultimate number of shield pores in *H. cristalabri* sp. nov. compared to *H. demodex* is not established as early in development and, therefore, cannot as easily be attributed to paedomorphosis.

It is hard to compare the pore patterns of the differently shaped trunk regions in these three species (flat in *H. itoi*, tapered-cylindrical in *H. demodex*, attenuate-conical in *H. cristalabri* sp. nov.), also because detailed information is lacking for certain naupliar instars of the former two species. Briefly (see Kolbasov et al. 2021a), nauplius 2 of *H. itoi* has a pair of pores at the base of the dorsocaudal spine, another pair just anteriolateral to the furcal spines, and one pair each in the ventrolateral and ventromedial regions; the nauplius 3 stage seems to have a (new?) ventrolateral pair—nothing is mentioned of the two pre-existing ventral pairs—as well as a lateral pair positioned posteriorly in facet pair G-1. *Hansenocaris demodex* (see Olesen et al. 2022) has an unpaired posterior pore between the caudal spines (#26) and 10 other pairs of trunk pores (#17–#25 and #27) In contrast, the last-stage nauplius of *H. cristalabri* sp. nov. merely has an unpaired posterior (anal?) pore, which may correspond to unpaired pore #26 of *H. demodex*, and three pairs of lateral trunk pores (Table 1). These latter cannot easily be homologized positionally with any trunk pores of *H. itoi* but they do appear to correspond to pairs 19–21 of *H. demodex*.

Light-microscopic information has been published con-

cerning the distribution of pores and setae of the cephalic shield in a few other kinds of nauplius y, most notably in the five final instars of both *H. furcifera* (Itô 1990) and an unnamed lecithotrophic species (Itô 1991: fig. 1), and the penultimate naupliar stage of another lecithotroph (Grygier 1985: fig. 3). The last-mentioned specimen had four pairs of setae and 10 pairs of pores (including three pairs in the 'Brim') on its cephalic shield, an arrangement characterized by Grygier as a "stereotypical pattern" but clearly exceeding what is found in *H. cristalabri* sp. nov. The last-stage nauplius of *H. furcifera* (Itô 1990: figs 9, 10) has four pairs of setae and at least 22 pairs of pores (including at least seven pairs in the 'Brim'); it pores greatly exceed in number those of both *H. cristalabri* sp. nov. and Grygier's (1995) stereotype, as well as *H. demodex* and *H. itoi*. While some commonality of pore distribution clearly exists, especially among ontogenetically early-appearing pores, the compilation of a complete set of positionally homologous pores across species, and the formulation of a simple, perhaps facet-based nomenclature for them, will require detailed knowledge of many more y-nauplius forms. The process of establishing the veracity of these homologies would require knowledge of the ultrastructure of each different sort of cuticular organ, but taxonomic progress would benefit from even a provisional common nomenclature.

Function of labral process. The single most striking features of the two new species are the distinct shapes of their labra with spinose processes, not least the remarkably large, cockscomb-like labral process of *H. cristalabri* sp. n. We assume that such a significant structure must have a function, but it is not obvious what that might be. Dense rows of marginal labral setae or denticles are common in many crustacean larvae (e.g., Martin et al. 2014) and clearly play a role during larval feeding, but such setae are small

and fine, not large and dagger-like, as here. Furthermore, the labral process in *H. cristalabri* sp. nov. is not involved in feeding at all; its nauplii are lecithotrophic, and the process is directly away from the putative mouth region. Another explanation may be related to hydrodynamics, as the labral process increases the surface area of the larval specimen significantly. Its orientation perpendicular to the anterio-posterior body axis means that it must inevitably increase drag while swimming, although its backward curve suggests it may simultaneously increase lift. It may also serve as a stabilizing keel, as seen in sailing yachts. On the other hand, Reynolds number considerations may obviate such hydrodynamic explanations. Another possibility is that, together with the very spiny posterior end of the body, it may serve to ward off predators. Labral extensions of the size seen in *H. cristalabri* sp. nov. are extremely rare. Some examples exist among the planktotrophic larvae of spinicaudatan and laevicaudatan branchiopods (clam shrimps), in which the posterior margin of the large, free labrum is frequently extended into one to four sometimes huge spines (Olesen and Grygier 2003, 2004, 2014; Olesen and Martin 2014), but also here the precise function has been difficult to determine.

Acknowledgements

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