Naupliar Development of *Hansenocaris furcifera* Itô (Crustacea: Maxillopoda: Facetotecta) from Tanabe Bay, Japan

By

Tatsunori Itô

Seto Marine Biological Laboratory, Kyoto University,
Shirahama, Wakayama 649-22, Japan

With Text-figures 1–12

Abstract Five naupliar stages of *Hansenocaris furcifera* Itô, 1989, the first of which is Nauplius y Type IX *sensu* Itô, are described in detail, based upon specimens originally collected in Tanabe Bay on the Pacific coast of Honshu, Japan, and reared in the laboratory. The naupliar sequence was determined by connecting partial series of exuviae of separately cultured individuals. The five naupliar stages, which are planktotrophic, are all metanauplii with a pair of setiform maxillular rudiments, and no orthonauplius stage was found. The surface structure of the first naupliar stage was studied by SEM. In front of the first antennae lies a pair of small protuberances with central pores, which are identified as the termini of the head gland instead of frontal filaments. Most of the body surface has a very fine, mesh-like texture, but the dorsocaudal organ and at least part of the window do not. The dorsal plates are deliniated by prominent, chitinous ridges about 1 μm high. Some new terminology is introduced to describe the developmental changes of the plates. Remarkable alterations in the Elongate and Intercalary plates are noticed through naupliar development. The setal ornamentation of the antennule changes through the first four naupliar stages, but that of the antenna and mandible remains unchanged.

Hansenocaris furcifera Itô, 1989, was described from Tanabe Bay on the Pacific coast of Honshu, Japan, on the basis of five individuals at the cypris y stage, all raised from nauplii in the laboratory (Itô, 1989a). It has already been noted that Nauplius y Type IX, provisionally described by Itô (1987c), is a naupliar stage of this species. In the present paper, the five naupliar stages preceding the cypris y stage are described.

The nauplii of *H. furcifera* seemed planktotrophic, so I tried to feed them with *Isochrysis* sp., *Nannochloropsis* sp. and *Nitzschia* sp. in earlier, preliminary cultures. However, adding such algae to the cultures was unsuccessful because the animals readily accumulated organic debris on their setae and other parts of the body, which made microscopic observation of the animals and their exuviae very difficult. Moreover, such the debris apparently disturbed their continuous swimming acitivity and, in the worst cases, they did not molt and finally died in spite of repeated changes of culture dishes and medium. Hence, I did not feed the larvae used for the present study, but treated them in the same manner as lecithotrophic nauplii (Itô & Takenaka, 1988; Itô, in press). I have not yet succeeded in raising a first-stage nauplius of *H. furcifera* into its cypris y stage in the laboratory, although cypris y larvae of many species with lecithotrophic naupliar stages have already been obtained in this fashion from early naupliar larvae (Itô, 1984, 1986b, 1989b, Itô & Takenaka, 1988). The longest sequence

of molts exhibited by a single individual of *H. furcifera* in culture was from the third naupliar stage to the cypris y stage, namely three molts. Because of the difficulty in obtaining complete series of exuviae from a single individual, some naupliar stages described in this paper are based upon partial series of exuviae obtained from different individuals.

Most of the nauplius y larvae used for this study were collected from plankton samples taken in Tanabe Bay off the Seto Marine Biological Laboratory (33°42′N, 135°21′E) from May through July, 1986. Those larvae used for the observation of developmental stages were individually raised in glass dishes with paper-filtered sea-water (for details of rearing method, see Itô, in press). These dishes were kept at a constant temperature of 19°C. Nauplii were transferred into sterilized dishes with fresh sea-water twice a day. Exuviae left in dishes, if present, were pipetted out and fixed in 5% formalin-sea water. Fixed exuviae were mounted onto glass slides with anhydrous glycerin and sealed with balsam-paraffin. The exuvia illustrated in Fig. 9 is that of the holotype of *H. furcifera*.

For study by SEM, four individuals of the first naupliar stage were selected from a formalin-perseved sample of y-larvae collected at Toshima Rock in Tanabe Bay (9–VI–1989). As specimens for SEM are necessarily mounted on metal stubs, at least one side of their body is hidden from view. To avoid any misidentification due to this problem, the morphology of each specimen was carefully checked with a phase-contrast microscope before dehydration through a graded series of ethanol. Specimens were transferred into isoamyl acetate after dehydration, and were dessicated in a critical-point drier using carbon dioxide. Dried specimens were sputter-coated with gold and observed in an SEM (JEOL JSM T-220) at an accelerating voltage of 10 kv.

In this paper the word "nauplius" is used as a general term subsuming both "orthonauplius" and 'metanauplius." The terminology proposed by Itô (1987c) is used to describe the plates of the cephalic shield in first-stage nauplii. However, the plate names will be capitalized here to avoid confusion with ordinary adjectives, e.g., Polygonal vs polygonal, Marginal vs marginal. Some new terms and abbreviations will be introduced mainly to describe and lable the plates of later stages. The usage of some of them is illustrated in Fig. 1. When a plate becomes divided into two plates by a ridge extending toward the window, such a division is called "meridional" and the ridge is called a "meridional" ridge; the two plates formed by a meridional division are referred to as "anterior" and "posterior" plates (abbr: a and p, respectively). When a plate becomes divided into two plates by a rigde extending horizontally, such a division is called "latitudinal" division and the ridge is called a "latitudinal"
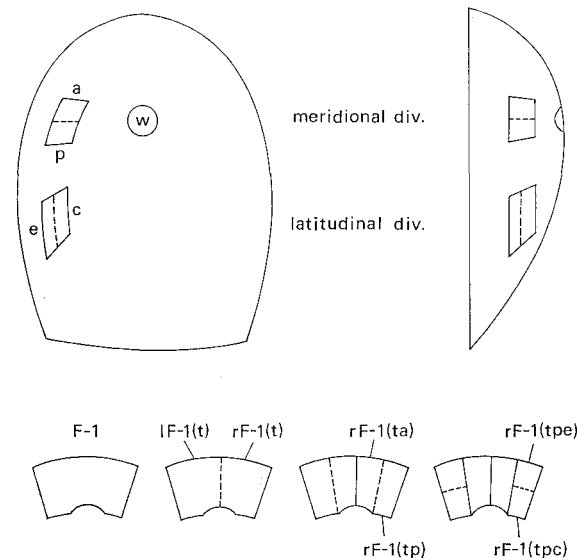

Fig. 1. Schematic explanation of additional terminology to describe differentiation of plates on cephalic shield.

ridge; the two plates formed by a latitudinal division are referred to as "central" and "external" plates (abbr: c and e, respectively).   If a plate becomes divided into three plates by two new latitudinal ridges, then the three plates so formed are referred to as "central," "external," and "medial" (abbr: m), where the medial plate is situating between the other two.   If a given division is not clearly either meridional or latitudinal, then it is categorized arbitrarily for convenience.   When an axial plate is divided originally or secondarily into two parts by a sagittal (=meridional) ridge, the two resulting parts combined are called a twin plate, e.g., twin F–1, and each part is labelled as F–1(t).   If an axial plate is divided at once into four parts by meridional ridges at once, those four parts combined are called a quadruple plate, e.g., quadruple O–4, and the two parts of each side are labelled O–4(qc) and O–4(qe).   When elements of twin or quadruple plates are specified as either right or left, then they are referred to as "right F–1(t)" or "left F–1(t)", etc.   The terms "right" and "left" are occasionally abbreviated as "r" and "l", respectively.   Some examples are given in Fig. 1: rF–1(t) means the right one of the two plates formed by a sagittal (=meridional) division of F–1; F–1(ta) means the anterior one of the two plates formed by a meridional division of one of two F–1(t) plates; F–1(tpe) means the external one of the two plates formed by a latitudinal division of F–1 (tp).

The new term "faciomarginal area" refers to the area of faciotrunk integument that encircles the labrum and the first three pairs of appendages.   The term "trunk" will refer to the rear portion of the body, situated posterior to the cephalic shield in dorsal view.   When a nauplius is viewed from the ventral side, the more or less swollen, rear portion of the body appears to border anteriorly upon a rather flat area.   Thus, the anterior border of the "trunk" in ventral view can be defined by tracing the contour of this swelling.

In the figures of cephalic shields, two types of arrows are used with separate maenings.   Facing arrows mark the site of a ridge that has disappeared by fusion of plates.   A two-headed arrow over a ridge indicates that the ridge is newly formed by plate division.

Description of Naupliar Stages

1.   General.

The body is almost colorless and transparent, but the gut usually appears brownish due to food material inside it.   Through all the naupliar stages a red nauplius eye is present in front of the labrum and below the window of the cephalic shield (Fig. 5B).   The number of eye cups is uncertain.

The borders of the plates on the cephalic-shield as well as on the dorsal half of the trunk are actually chitinous ridges (Fig. 2), measuring about 1 μm high.   The plates delineated by such ridges appear to have a mesh-like texture when viewed in the light microscope (Figs 4C, 6D, 8D, 9D).   The mesh-like texture is an external feature, due to surface wrinkles (Figs 2 and 3).   There is no such surface texture on the window or at least its central area, nor on the dorsocaudal organ (Fig. 3C, D).

The mouth is present at every stage, located a little anterodorsal to the apical edge of the labrum.   In exuviae, the mouth opening clearly leads into an anterodorsally extending, cuticle-lined duct (e.g., Fig. 9B, C).

The mode of molting is just as outlined by Itô (1987c, p. 914).   Exuviae are colorless and transparent.   The cephalic shield of earlier stages easily detaches from the faciotrunk integument either naturally or during handling.

The duration of each stage is uncertain, but it may be assumed that the fourth naupliar stage lasts about three days, the fifth stage about four days, and earlier stages than the fourth last one to two days for each.
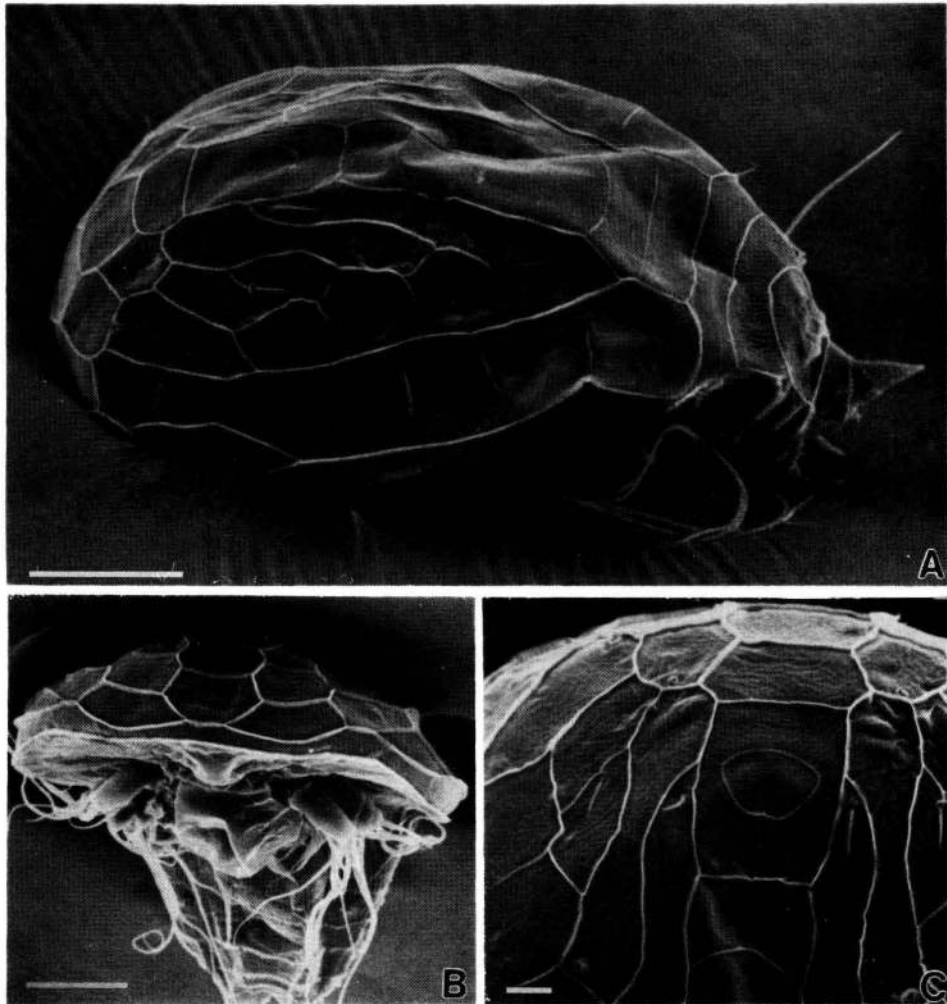
Fig. 2.   SEM photomicrographs of first naupliar stage of *Hansenocaris furcifera*. A.
Dorsolateral view; B. Frontal view; C. Plates around Window, showing mesh-
like texture.   Scales: 50 μm for A and B, 10 μm for C.

2.   First naupliar stage.

Body droplet-shaped in dorsal view, measuring about 280 μm long, 170 μm
wide across window, 60 μm high excluding labrum.   Faciomarginal area almost
flat, with very faint ridges anterior and posterior to labrum (Fig. 4D) and pair of
small protuberances, each with a central pore, in front of labrum.   Labrum well-
developed, almost rectangular, 70 μm long, 60 μm wide, with pair of lateral pores,
another pore on mid-apical edge; ventral (frontal) surface of labrum mostly smooth
except for narrow lateral and proximal areas (Fig. 3A).

In the light microscope, ventral surface of trunk appearing to have at least eight
transverse rows of spinules (Fig. 4D); each row of spinules actually a serrate ridge
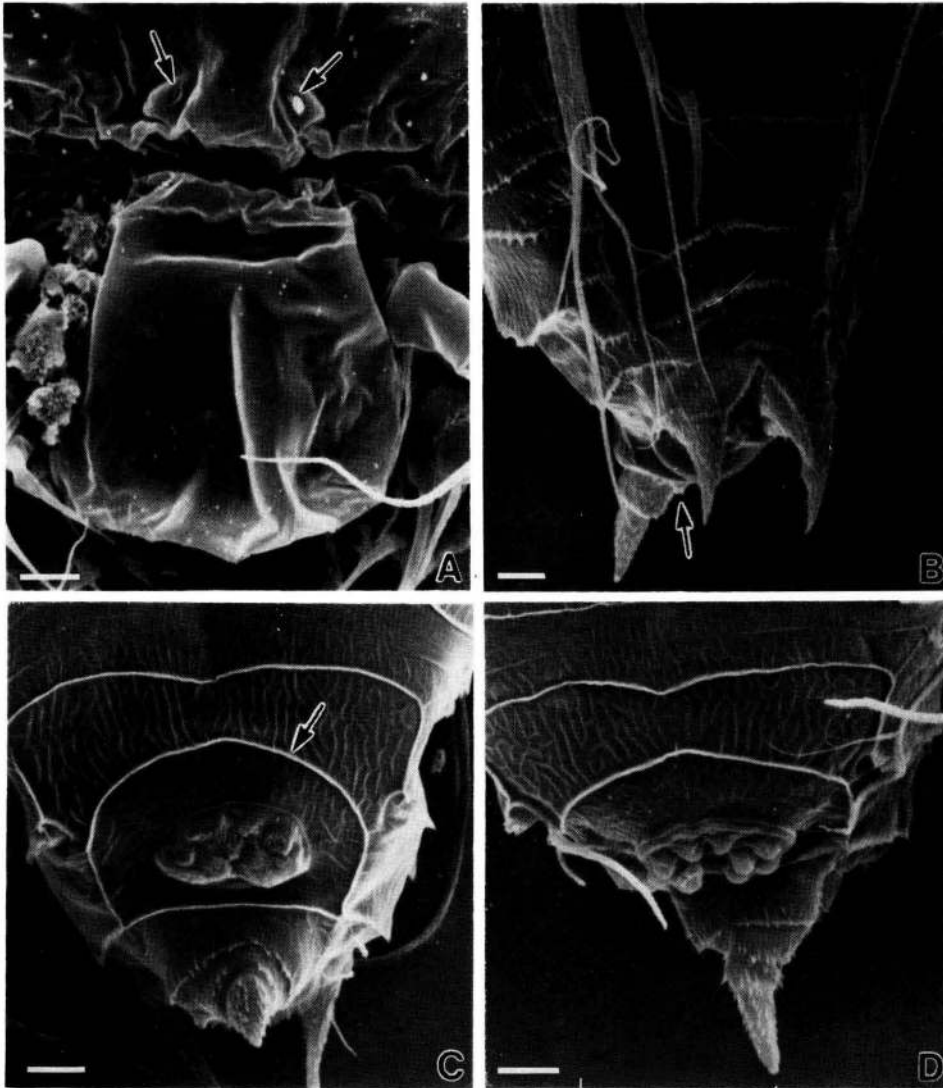
Fig. 3.   SEM photomicrographs of first naupliar stage of *Hansenocaris furcifera*. A. Paired openings of head gland (arrowed) in front of labrum; B. Ventrolateral view of trunk, showing maxillular rudiments and caudal area (arrow pointing a small protuberance with apical pore); C. Dorsal view of trunk (second dorsal ridge arrowed); D. Dorsal view of trunk, showing dorsocaudal organ with protuberances.   Scales: 10 μm.

(Fig. 3B).   Pair of prominent setae (maxillular rudiments) about 30 μm long arising near lateral ends of third serrate ridge from front (Figs 3B, 4D).   A prominent pore on both ventrolateral sides of trunk, 26 μm behind level of maxillular rudiments. Some ventral serrate ridges fusing to each other laterally and extending as three major, non-serrate ridges onto dorsal surface of trunk, referred to from front to rear as first, second, and third dorsal ridges (Fig. 3C).   First dorsal ridge and major por-
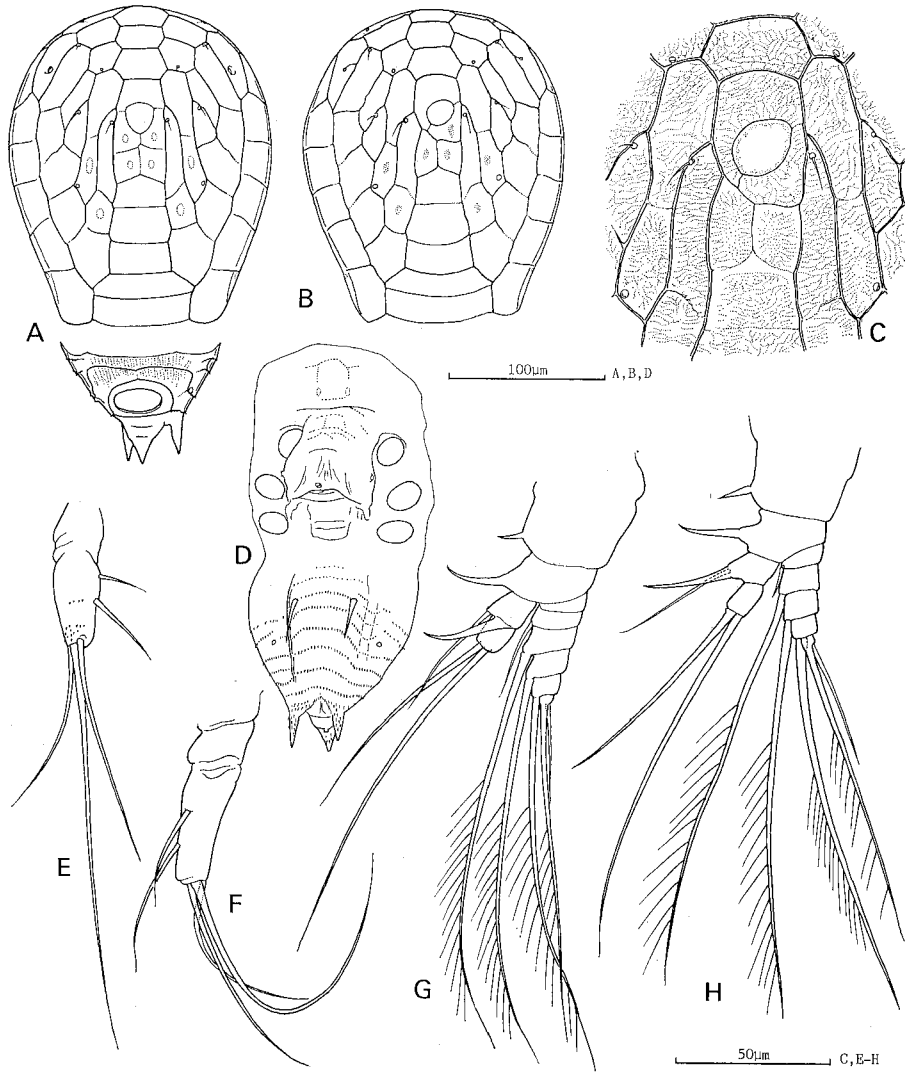
Fig. 4. First naupliar stage of *Hansenocaris furcifera*. A, C and E based upon a specimen, the rest on another. A. Cephalic shield (mesh-like texture omitted) and separated trunk; B. Cephalic shield (mesh-like texture omitted); C. Mesh-like texture of part of cephalic shield; D. Ventral view of faciotrunk integument; E and F. First antenna; G. Second antenna; H. Mandible.

tion of second one located anterior to dorsocaudal organ. Both sides of first dorsal ridge first turning toward rear, then toward ventum alongside prominent lateral pore, and extending farther as serrate ridge. Second dorsal ridge smoothly curving alongside dorsocaudal organ until it passed a little over the latter, then turning acutely toward ventum, and extending farther as serrate ridge. Third dorsal ridge located posterior to dorsocaudal organ, linking limbs of arc of second dorsal ridge. Dorsal surface of trunk, except for dorsocaudal organ, with prominent, mesh-like texture (Fig. 3C, D).

Dorsocaudal organ dome-like, elliptical in outline, 25 to 35 μm wide, about 20 μm along body axis; in one specimen examined with SEM, eight prominent, papillary protuberances apparent (Fig. 3D), though not in two other specimens examined with SEM (Fig. 3C).

Trunk armed with two furcal spines and one caudal horn posteriorly; all processes conical, almost the same in length, caudal horn thicker than furcal spines and bearing scattered spinules. Short tubule arising from ventral side of caudal horn (Figs 3B, 4D). Possible anus represented by a slit just dorsal to meeting point of furcal spines (Fig. 4D).

Cephalic shield (Figs 4A, 5E) 200 μm long, 170 μm wide. Four Frontals all clearly defined, though in some cases border between F–1 and O–1 indistinct. Window clearly delimited by circumambient ridge, deeply wedged into O–1. Seven Occipitals clearly defined; O–1 and O–2 both twin, splitted by very fine, sagittal ridge, with small, round, smooth area in center of each part; O–3 tapering anteriorly; O–6 markedly widening posteriorly; O–7 as wide as O–6, 1.5 times as wide as O–5.

C–1 twice as long as C–2, tapering anteriorly, with sensory hair close to border abutting O–1 near anterior end; C–2 with small, round, smooth area at its center.

E–1 and E–2 subequal in length, faintly demarcated from each other; E–2 with round, smooth area at its center and pore near corner bordering upon both P–4 and P–5.

I–1 hexagonal, with pore near boundary abutting E–1; I–2 extending anteroposteriorly, bordering on I–1 with its short anterior ridge, and widely bordering on I–3; ridge between I–2 and I–3 placed rather latitudinally; I–3 tapering anteriorly, wedged between E–1 and I–2, with sensory hair near its anterior end close to I–2.

Six Polygonals well defined; P–1 hexagonal; P–2 longest, 1.5 times as long as P–1, with sensory hair at anterior end; posterior four plates subequal in size, faintly demarcated from each other.

Seven Marginals well defined; M–1 almost trapezoidal, longer than P–1; M–2 longest, as long as P–2, tapering posteriorly, with prominent pore positioned almost centrally; posterior five plates subequal in size, faintly demarcated from each other.

Superlateral almost triangular, wedged between M–2 and M–3.

Brim clearly defined by ridges dorsally and ventrally (Fig. 2B), with a total of four pores, one located ventral to M–1 and near border between M–6 and M–7 on each side.

Abnormality of cephalic shield. In one specimen, W smaller and plates around it aberrant (Fig. 4B, C). Left part of F–1 markedly extending posteriorly alongside W. O–1 almost lacking area of lO–1(t), instead, rO–1 (t) appearing larger than normal; rO–2(t) shorter than usual.

First antenna (Fig. 4E, F) two-segmented; first segment unornamented; second segment at least twice as long as first, with delicate spinules on anterior surface, armed with two inner setae and three apical setae. In SEM all setae appearing to have very delicate, short hairs, although such hairs not seen in standard or phase contrast

microscopy. *Second antenna* (Fig. 4G).   Coxa as long as wide, with somewhat widened proximal part, armed with short inner spine near distal angle.   Basis shorter than coxa, armed with strong inner spine.   Endopod two-segmented; first segment armed with strong inner spine accompanied by seta near its anterior base; second segment as long as first one but a little slimmer, armed with two apical setae; all setae bearing very delicate, short hairs (seen in SEM; not illustrated in Fig. 4G).   Exopod six-segmented; first segment unarmed, with inner edge shorter than outer; second segment armed with short inner seta; third, fourth and fifth segments each armed with well-developed, hairy inner seta; sixth segment small, armed with two apical setae, one of them well-developed and hairy, other one small and almost naked. *Mandible* (Fig. 4H).   Coxa, basis and endopod as in second antenna.   Exopod five-segmented; first segment armed with short seta, with inner edge shorter than outer; second, third and fourth segments each armed with well-developed, hairy inner seta; seta of fourth segment more stout and rigid than other exopodal setae; fifth segment small, armed with two apical setae, one of them well-developed and hairy, other one small and almost naked. *Maxillular rudiments* already described (Figs 3B, 4D).

3.   Second naupliar stage.

Body (Fig. 5A–C) about 290 μm long, 190 μm wide across window; height undetermined.   Faciomarginal area and labrum almost as in previous stage (Fig. 5B). Ventral face of trunk ornamented with at least 10 transverse, serrate ridges, some of them extending onto lateral sides; two pairs of widely spaced, minute pores present, anterior pair located a little behind level of pair of prominent ventrolateral pores, posterior pair located near base of furcal spines.   Ventrolateral pores of trunk located 40 μm posterior to level of maxillular rudiments.   Dorsal face of trunk ornamented with two major, transverse ridges, which, together with sagittal ridges and anterior limit of dorsocaudal organ, form two rows of two plates before dorsocaudal organ; pair of big, almost trapezoidal plates flanking above-mentioned, paired plates. Lateral pore of previous stage now located below trapezoidal plate.

Dorsocaudal organ dome-like as in first stage; no papillary processes detected. shape and size of furcal spines and caudal horn as in first stage.

Cephalic shield (Figs 5A, C, F) 210 μm long, 190–200 μm wide.   W, F–1, and F–2 unchanged.   F–3 divided by sagittal ridge, forming twin F–3.   F–4 divided latitudinally, forming F–4(c) & (e).   O–1(t) and O–2(t) unchanged.   O–3 posteriorly tapering and wedged between twin plates of O–4; O–5 also now twin.   O–6 and O–7 now quadruple, i.e., O–6(qa) & (qp) and O–7(qa) & (qp) on each side, but border between rO–7(qp) and lO–7(qp) indistinct.   Behind plates of O–7 group, one new, narrow, transverse, belt-like plate occurring, with two widely spaced hairs. Narrow zone present behind this belt-like plate, its posterior margin being actual posterior end of cephalic shield and resembling a hyaline frill due to lack of any posterior ridge.

C–1 almost latitudinally divided about mid level of O–2(t) and forming C–1 (c) and shorter C–1(e); C–1(c) retaining sensory hair.   C–2 undivided, somewhat
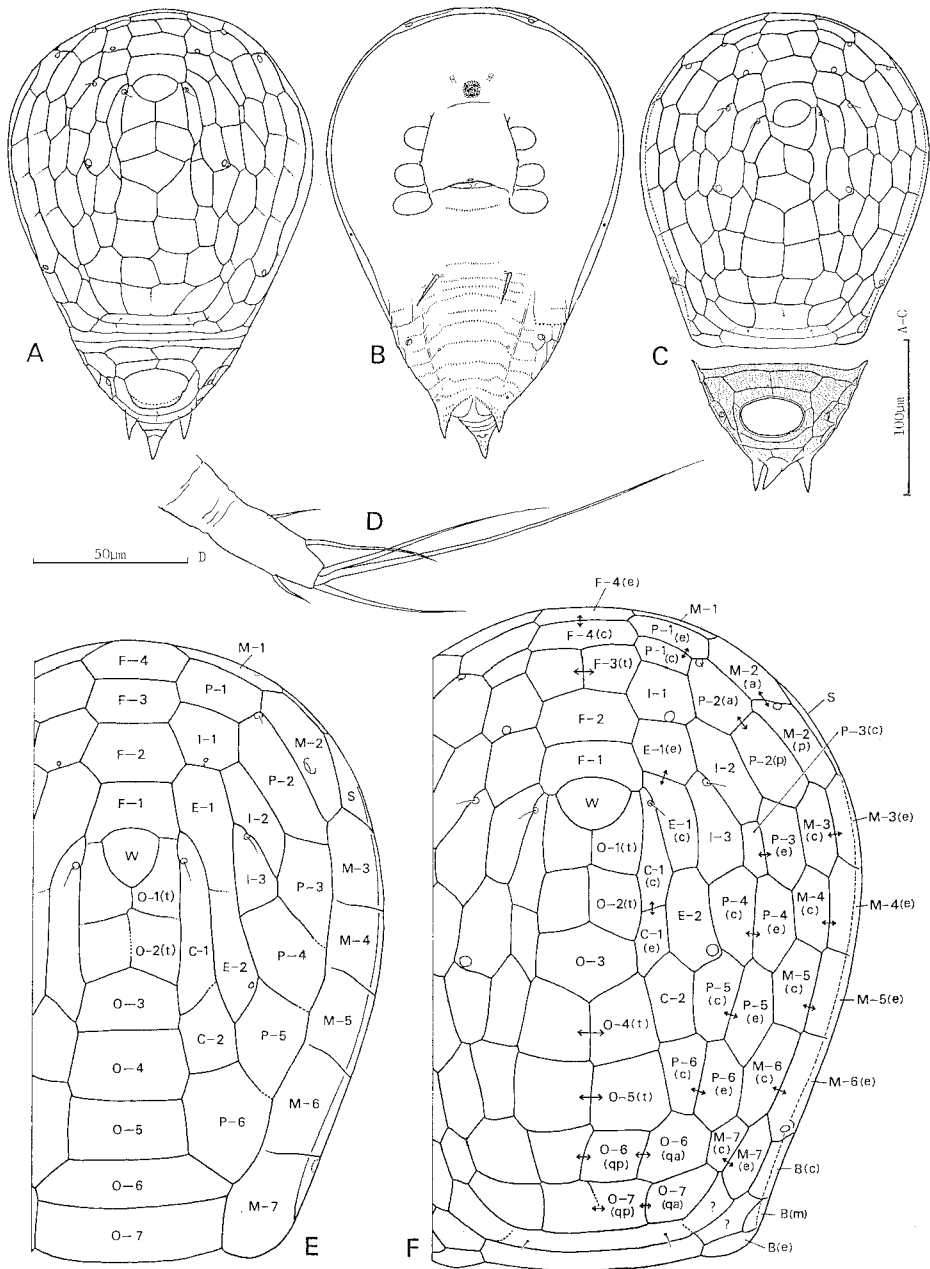
Fig. 5. A-D, second naupliar stage of *Hansenocaris furcifera*. A and B based upon one specimen, appearing unusually short due to tilted orientation on slide glass, the rest on another. A. Dorsal view of body (mesh-like texture omitted); B. Ventral view of body; C. Dorsal view of cephalic shield (mesh-like texture omitted) and separated trunk; D. First antenna. E and F, schematic explanation of cephalic shield's plates of first (E) and second (F) naupliar stages.

narrower than before.

E–1 divided by almost latitudinal ridge extending from mid level of F–1 to anterior portion of I–3, forming hexagonal E–1(e) and long E–1(c). E–2 undivided, retaining pore.

I–1 retaining pore. Border between I–1 and I–2 shortened. I–2 and I–3 transformed into higher-level polygons than previously. I–3 retaining sensory hair.

P–1 divided by latitudinal ridge connecting borders of previous F–4 and previous P–2, forming P–1(c) & (e). P–2 meridionally divided to form P–2(a) & (p); P–2(a) retaining sensory hair. P–3, P–4, P–5, and P–6 divided latitudinally; P–3 (c) distinctly smaller than others.

M–1 not clearly seen due to its marginal situation, but probably undivided, or at least not divided meridionally. M–2 divided almost meridionally by ridge arising from point near posteroventral end of P–2(a) and extending ventroposteriorly; prominent pore previously almost at middle of M–2 now located close to anterior border of M–2(p). M–3, M–4, M–5, and M–6 equally divided by strong, continuous, latitudinal ridge. Meridional ridges separating these plates (ridges between M–3 and M–4, M–4 and M–5, etc.) all becoming faint. M–6(e) bearing prominent pore close to ventroposterior border; this pore previously located just below ventral border of M–6 and then not seen from dorsal side. M–7 divided latitudinally into at least two plates, M–7(c) & (e), but area occupied by these two plates smaller than previous M–7. Two latitudinally arranged plates (Fig. 5F, question marks) behind M–7(c) & (e) likely also derived from M–7.

Situation of previous Superlateral suggested by shallow bend in outer ridge bounding M–2(p) and M–3(e), but presence of ridge delimiting its ventral margin uncertain.

Because no specimen could be observed laterally, exact condition of brim is unknown. However, at least two new, latitudinal ridges extending through area bordered by M–plates and ventral extremity of cephalic shield, dividing it into three zones called B(c), B(m) and B(e). In dorsal view, posterior end of B(c) appearing behind M–6(e), curving a little dorsally along M–6(e) and bordering M–7(e). Posterior part of B(m) similarly curved and visible dorsally just behind above-mentioned part of B(c). Posterior end of B(e) not clear, apparently partially confluent with above-mentioned, posterior, frill-like zone. Anterior ends of B(c), B(m) & B(e) undetermined. B(e) bearing small pore below M–5(e)/M–6(e) level on each side.

Variation of cephalic shield. Fig. 5C showing cephalic shield of second stage of nauplius, whose first stage cephalic shield shown in Fig. 4B. Asymmetrical nature of some axial plates (F–1, W, O–1, O–2) in the previous stage still persisting in second stage. In specimen illustrated in Fig. 5A, size difference between C–1(e) and C–1(c) unusually big. In specimen in Fig. 5C, ridge between rC–1(c) and rC–1(e) unusually faint. Right I–3 of specimen illustrated in Fig. 5A lacking sensory hair near anterior tip of I–3.

First antenna (Fig. 5D). Segmentation unchanged. Short outer seta added

about one third of way from apex of second segment. Setal armature otherwise unchanged. Spinules undetected. *Second antenna* and *mandible* unchanged in principal ornamentation. *Maxillular rudiments* located at about 50 μm behind labrum (Fig. 5B).

4. Third naupliar stage.

Body (Fig. 6A–C) about 320 μm long, 200 μm wide across window, 110 μm high excluding labrum. Faciomarginal area bearing two prominent pores, each
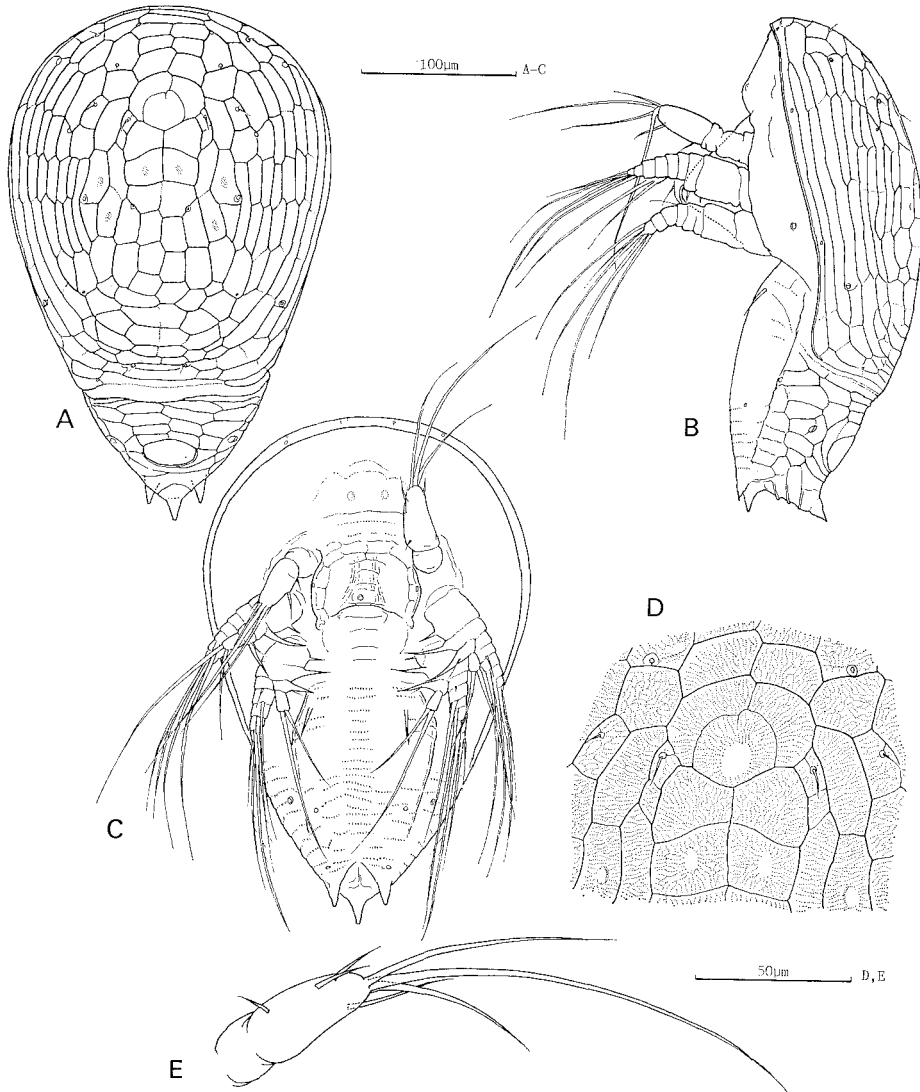

Fig. 6. Third naupliar stage of *Hansenocaris furcifera*. A–C. Dorsal, lateral and ventral views of body (mesh-like texture omitted); D. Mesh-like texture of part of cephalic shield; E. First antenna.

located near base of mandible (Fig. 6B). Labrum as in previous stage, with pro-
minent sculpture of ridges. Ventral face of trunk ornamented with at least 17 trans-
verse, serrate ridges forming longitudinal zone with dense serration; most serrate
ridges not extending onto lateral sides. Pores on ventral side of trunk arranged as
in previous stage. Dorsal side of trunk bearing two longitudinal rows of four lateral-
ly extended plates before dorsocaudal organ. Each lateral side of trunk bearing
about 15 complete plates, with lateral pore as prominent as in previous stage. Dorso-
caudal organ a little smaller than in previous stage. Shape and size of furcal
spines and caudal horn as in previous stage.

   Cephalic shield 240 μm long, 210 μm wide (Figs 6A, 7). Mesh-like texture ex-
tending inside W except for small central area (Fig. 6D). F–1 and F–2 now twin;
F–1(t) extending somewhat posteriorly alongside W. F–3(t) divided into F–3(tc)
& (te). F–4(c) & (e) probably unchanged (not clearly seen). Twin O–1 and O–2
unchanged. O–3 no longer wedged between posterior plates, but divided sagittally
to form posteriorly truncated twin O–3. Twin O–4 and O–5 all divided meridional-
ly to form, e.g., O–4(tp) & (ta) from O–4(t); O–4(ta) bearing pore close to anterior
border. Plates of O–6 and O–7 groups all divided at least latitudinally, but some
lacking clear borders and not readily traceable; some posterior ones appearing to be
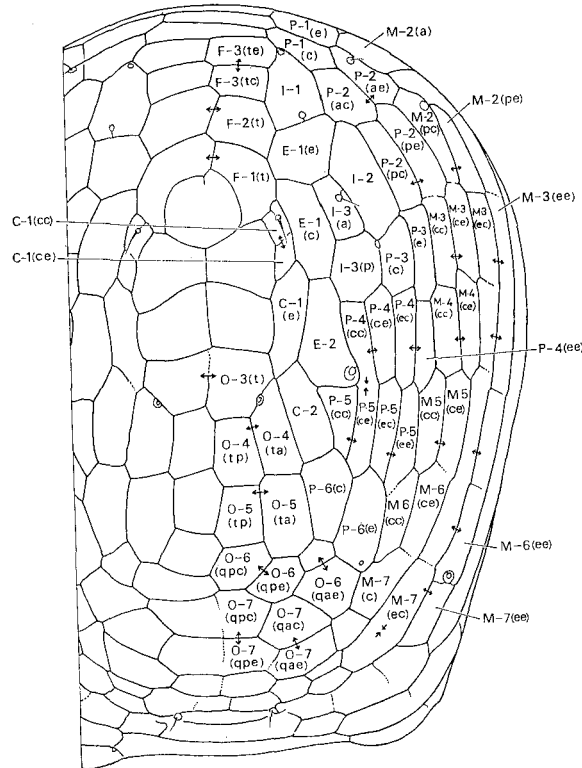

Fig. 7. Third naupliar stage of *Hansenocaris furcifera*. Schematic explanation of ce-
       phalic shield's plates.

arranged latitudinally. Small, latitudinally arranged plates added behind O–7 group plates. Pair of widely spaced, fine hairs persisting in front of posterior hyaline zone.

C–1(c) divided into C–1(cc) with sensory hair and C–1(ce). C–1(e) and C–2 as in previous stage.

E–1(e) enlarged, extending between I–1 and I–2 to border against P–2(ac). E–1(c) and E–2 somewhat enlarged, otherwise unchanged.

I–1 now bearing two pores, one of them added to its anterior limit (see Variation). I–2 completely separated from I–1 by intervening E–1(e), somewhat enlarged. I–3 divided into I–3(a) & (p); I–3(a) retaining hair near anterior border.

P–1(c) & (e) probably unchanged. P–2(a) latitudinally divided; P–2(ae) retaining sensory hair. P–2(p) latitudinally divided. P–3(c) now bearing small pore close to its inner border. P–3(e) undivided. P–4(c) & (e) and P–5(c) & (e) all latitudinally divided, but previous ridge between P–4 and P–5 partially disappeared, so P–4(cc) and P–5(ce) represented by portions of long, continuous plate. P–6(c) undivided. P–6(e) now bearing a small pore near posterior limit.

M–1 undetermined due to its marginal situation. M–2(a) probably undivided. M–2(p) latitudinally divided; M–2(pc) retaining pore near its anterior limit. Plates of M–3, M–4, M–5, and M–6 groups all divided latitudinally, and their meridional ridges becoming very faint; presumed area of M–6(ee) retaining prominent pore. M–7(c) probably undivided. M–7(e) latitudinally divided, with M–7(ec) probably fused to a posterior plate. Some untraceable plates behind M–7 group splitting into smaller plates arranged almost latitudinally.

Superlateral untraceable, but probably incomplete plate below M–2(pe) representing it (Fig. 6B, hatched area).

B(c), B(m), and B(e) clearly seen laterally. Two ridges alongside B(m) meeting near supposed area of S. B(e) bearing small pores, though exact number unknown.

Variation of cephalic shield. Specimen illustrated in Fig. 6A lacking anterior pore on left I–1; this missing pore actually located at meeting point of lP–1(c), lF–3(te), and F–4(c).

First antenna (Fig. 6E). Distal one of two inner setae already present in previous stage somewhat reduced. Short seta added onto subapical inner face. Otherwise as in previous stage. *Second antenna* and *mandible* as in previous stage. *Maxillular rudiments* (Fig. 6C) loacted at about 60 μm behind labrum.

5. Fourth naupliar stage.

Body (Fig. 8A) about 350 μm long, 200 μm wide across Window; height undetermined. Faciomarginal area and labrum almost as in previous stage. Ventral face of trunk ornamented with sagittal band of at least 26 short, transverse, serrate ridges (Fig. 8C). Ventrolateral faces of trunk ornamented with variously interrupted, serrate ridges, some posterior ones of which extending onto lateral faces. One pair of small pores added posterior to the pair of small pores existing since previous stage. Furcal spines and caudal horn as in previous stage. Dorsal face of trunk ornamented with

two longitudinal rows of at least five laterally extended plates in front of dorsocaudal organ (Fig. 8A). Dorsocaudal organ as in previous stage. Lateral faces of trunk ornamented with more plates than in previous stage, but exact number and characteristics undetermined.

Cephalic shield (Fig. 8A, E) 350 μm long, 210 μm wide. Window filled with mesh-like texture except for small central area as in previous stage (Fig. 8D). F–1(t), F–2(t), F–3(tc) & (te) all divided almost meridionally, thus, e.g., F–1(t) forming
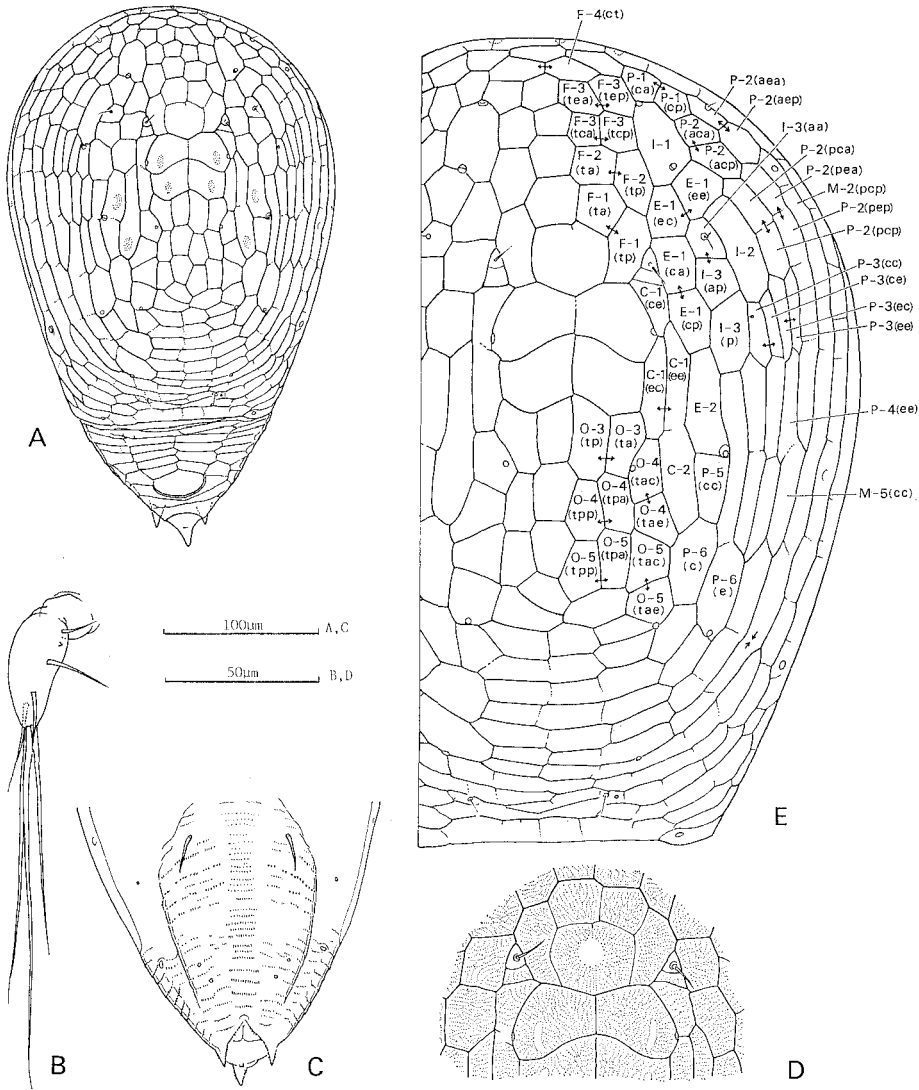

Fig. 8. Fourth naupliar stage of *Hansenocaris furcifera*. A. Dorsal view of body (mesh-like texture omitted); B. First antenna; C. Ventral view of trunk; D. Mesh-like texture of part of cephalic shield; E. Schematic explanation of cephalic shield's plates.

F–1(ta) & (tp), F–3(tc) forming F–3(tca) & (tcp).   F–4(c) probably divided sagit-
tally, forming two F–4(ct).   F–4(e) probably divided meridionally, but not exactly
determined due to its marginal situation.   Twin O–1 & O–2 as in previous stage,
but small pore added to outer limit of O–1(t).   O–3(t) divided into O–3(ta) &
(tp).   O–4(tp) divided meridionally to form O–4(tpp) & (tpa).   O–4(ta) divided
latitudinally to form O–4(tac) & (tae); O–4(tac) retaining pore close to border of
O–3(ta).   Plates of O–5 group divided as in O–4 group, namely, O–5(tp) divided
meridionally, O–5(ta) divided latitudinally; O–5(tae) bearing small pore close to its
posterior border.   Most plates of O–6 and O–7 groups probably divided latitudinal-
ly but exact divisions untraceable.   Pair of widely spaced, fine hairs persisting in
front of hyaline zone fringing posterior end.   Pair of small pores added before these
hairs.

    C–1(cc) & (ce) as in previous stage, but border between them shifted somewhat
anteriorly.   C–1(e) divided latitudinally; posterior limit of C–1(ee) faint, almost con-
tinuous with C–2.   C–2 undivided.

    E–1(e) divided latitudinally; E–1(ee) seeming to shove I–2 toward the rear.
E–1(c) divided meridionally.   E–2 as in previous stage, retaining prominent pore.

    I–1 as in previous stage, retaining two pores.   I–2 undivided, widely separated
from I–1 by intervening E–1(ee).   I–3(a) divided meridionally; I–3(aa) retaining
hair.   I–3(p) unchanged.

    P–1(c) divided meridionally.   P–1(e) undetermined due to its marginal situa-
tion.   P–2(ac) & (ae) divided meridionally; P–2(aea) retaining hair.   P–2(pc) &
(pe) divided meridionally, but new ridges very faint.   P–3(c) & (e) divided latitu-
dinally; formed P–3(cc) retaining pore close to inner border.   All plates of P–4 and
P–5 groups as in previous stage, but borders between P–4 group plates and P–5 group
plates becoming faint, and P–4(ee) almost fused to M–5(cc).   P–6(c) & (e) as in
previous stage; P–6(e) retaining pore.

    Superlateral undetermined, probably fused to externalmost plate of M–2 group.

    Fate of M–1 and M–2(a) undetermined.   M–2(pc) meridionally divided by
faint ridge, but M–2(pcp) lacking posterior boundary and continuing as long, latitu-
dinal plate back to M–5 level.   Plates of M–3, M–4, and M–5 groups as in previous
stage, but many meridional ridges disappearing.   Most plates of M–7 group probably
divided latitudinally, but untraceable with precision.

    Brim undetermined, but at least B(c), (m) & (e) still present.

    Variation of cephalic shield.   Fig. 6A and Fig. 8A showing third and fourth stages,
respectively, of single individual.   In fourth stage of this specimen, left I–1 with
only one pore as in third stage, while two pores present on right I–1.   Missing pore
of left I–1 still mislocated at wrong place.

    First antenna (Fig. 8B).   Rudimentary seta added to space between first two
inner setae, otherwise unchanged.   *Second antenna* and *mandible* as in previous stage.
Maxillular rudiments (Fig. 8C) located 55 μm behind labrum.

6.   Fifth naupliar stage.

    Body (Fig. 9A, B, C) 400 μm long, about 220 μm wide across window, 220 μm

high.   Paired pores in front of labrum prominent.   Labrum bearing granulated zone across anterior base (Fig. 9B).   Chitinous lining of pharynx extending from wide mouth about 80 μm into body.   Lateral pores of labrum each apparently connected to internal chitinous duct.   Pore on faciomarginal area near each mandible prominent; other, more posteriorly located pore also prominent (not illustrated in Fig. 9—
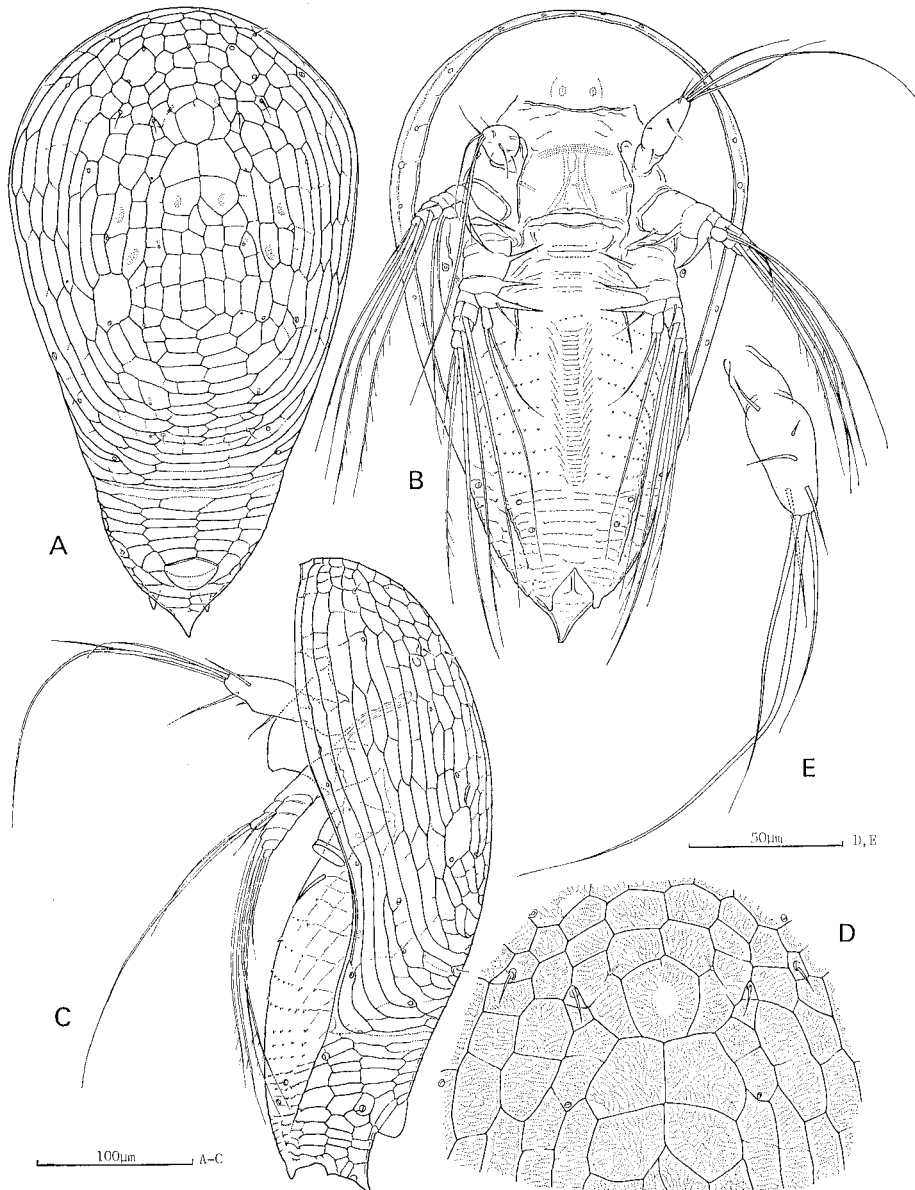

Fig. 9.   Fifth naupliar stage of *Hansenocaris furcifera*.   A, B and C.   Dorsal, ventral and lateral views of body (mesh-like texture omitted); D. Mesh-like texture of part of cephalic shield; E. First antenna.

hidden by second antenna). More than anterior half of ventral face of trunk ornamented with seven or eight transverse rows of spinules, all rows interrupted by a sagittally extended, special zone with internally sculptured cuticle as well as many external serrate ridges, rest of ventral face ornamented with serrate transverse ridges, among which two pairs of prominent pores occur. Furcal spines each accompanied by a small pore near base as in previous stage. In dorsal view, furcal spines almost hidden under basal portion of caudal horn. Dorsal face of trunk bearing two longitudinal rows of six laterally extending plates before dorsocaudal organ. Dorsocaudal organ well-developed. Each lateral side of trunk bearing two prominent pores as previously, with more plates than in previous stage.

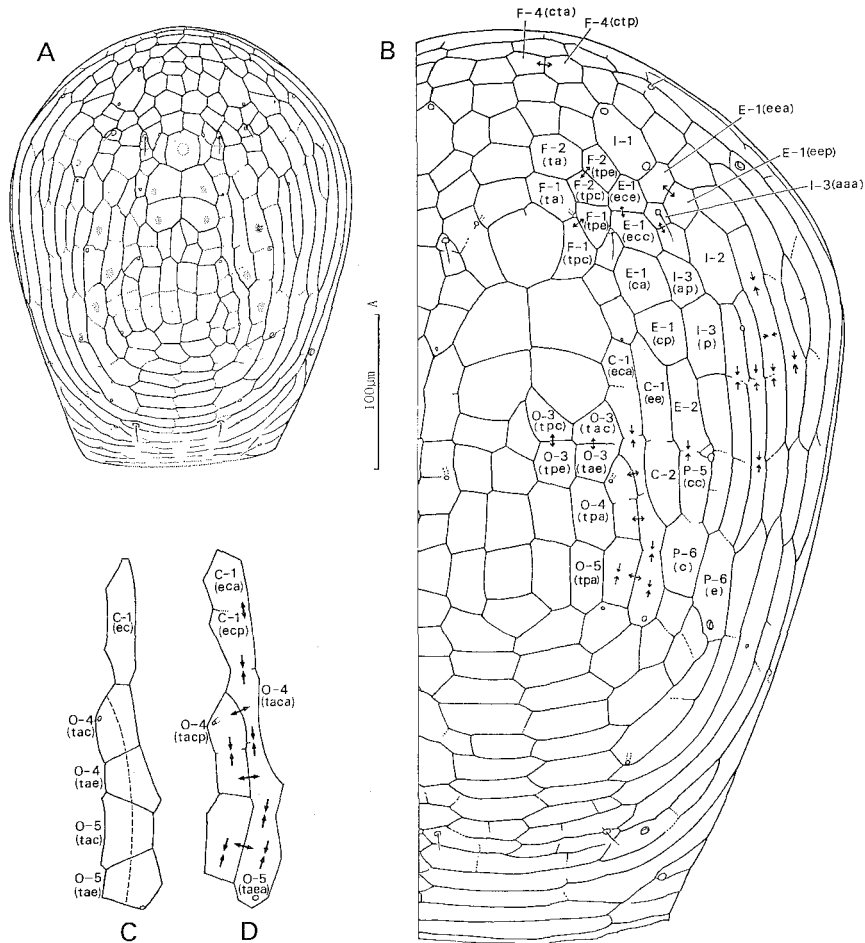*Cephalic shield* (Figs 9A, 10) 310 μm long, 225 μm wide. Window filled with

Fig. 10. A and B, fifth naupliar stage of *Hansenocaris furcifera*. A. Cephalic shield; B. Schematic explanation of cephalic shield's plates. C and D, schematic explanation of the development of some C-1, O-4 and O-5 group plates from fourth naupliar stage (C) to fifth naupliar stage (D); dotted line indicating where new ridge appearing in fifth naupliar stage.

mesh-like texture except for small central area as in previous stage (Fig. 9D). F–1 (ta) as in previous stage, but somewhat narrowed. F–1(tp) now divided almost latitudinally; posterior limits of F–1(tpc) situating closer to each other than counterparts in previous stage. F–1(ta) now bearing very fine tube opening at juncture with F–1(tpe) and F–1(tpc). F–2(ta) undivided, but F–2(tp) divided latitudinally. Plates of F–3 group as in previous stage. Plates of F–4 group not clearly determined, but F–4(ct) probably divided meridionally. Twin O–1 & O–2 as in previous stage. Plates of O–3 group all divided latitudinally. O–4(tpp) & (tpa) and O–5(tpp) & (tpa) as in previous stage. O–4(tac) & O–4(tae) and O–5((tac) & (tae) all divided by meridional (somewhat latitudinal) ridge continuously extending through them (Fig. 10C); O–4 (tacp) and O–5(taea) each retaining pore; ridges between newly formed plates in anteroposterior direction more or less faint, so two very long plates with indistinct subdivisions now appearing in this region (Fig. 10A). Plates of O–6 and O–7 groups untraceable, but most of them appearing to be enlarged in anteroposterior direction, and number of plates of this region before pair of widely spaced hairs not evidently increasing. Some latitudinal ridges inserted into the space behind above-mentioned pair of hairs, and this region markedly enlarged toward rear.

Plates of C group almost unchanged. C–1(ec) divided by incomplete meridional ridge; C–1(ecp) lacking clear posterior border and confluent with O–4(taca).

E–1(ee) divided meridionally, E–1(ec) divided almost latitudinally. Other plates of E group as in previous stage.

I–3(aa) divided by faint meridional ridge; I–3(aaa) retaining hair. Other plates of I group as in previous stage. Space between I–1 and I–2 widened by intervening E–1(eea) & (eep).

Plates of P and M groups probably not further divided; instead, their meridional ridges disappearing in various places, and fusion of P/M plates occurring in anteroposterior direction.

Superlateral probably involved in ventralmost (externalmost) one of M group plates, but not exactly traceable (Fig. 9C).

B(c), (m) & (e) all extending along almost whole lateral margin of cephalic shield. Their bounding ridges branching posteriorly to form some additional plates. Many pores arranged as in Fig. 9B.

Variation of cephalic shield. In specimen illustrated in Fig. 9, left P–6 abnormally remaining undivided, and some plates around it also unusual. In another specimen (Fig. 10A), left O–3(tp) abnormally divided meridionally instead of latitudinally. Fifth naupliar stage of yet another specimen, of which earlier exuviae are shown in Figs 6A and 8A, still with only one pore on left I–1.

Fifth naupliar stage showing strong tendency toward fusion of plates, especially in anteroposterior direction. Many meridional ridges disappearing, or expressed faintly and differently among specimen or even between right and left sides of a single specimen. Pore-like structures, not previously mentioned and apparently lacking internal ducts, occurring at various places, their distribution being different among individuals.

First antenna (Fig. 9E).   Rudimentary seta first appearing in previous stage now somewhat better developed.   Otherwise as in previous stage.   *Second antenna* and *mandible* as in previous stage.   *Maxillular rudiments* located 50 μm behind labrum.

Discussion

It still is uncertain whether facetotectans have six naupliar stages or not (Schram, 1970, p. 66).   Five is the maximum number of naupliar stages that have so far been confirmed by individual culture (Itô, 1987a, in press).   Since Itô & Grygier (1990) found that an ascothoracidan species has a special, probably non-planktonic stage with very delicate cuticle before five, typical, apparently planktonic naupliar stages, it is likely that facetotectans also have such a stage before the five planktonic naupliar stages so far known.   Nevertheless, I prefer to call the five stages before the cypris y stage the first through fifth naupliar stages until the true first stage, if present, is discovered.

Facetotectan nauplii hitherto described from Tanabe Bay, Japan, are as follows; Nauplius y Pacific Type I, Types VII, VIII (a, b, c), IX, X, and XI (Itô, 1986a, 1987b, 1987c).   Among them, Type IX, namely the first nauplius stage of *H. furcifera* here described, is the sole example of a facetotectan nauplius that has a pair of maxillular rudiments.   The only other reliable example of such maxillular rudiments is a single individual described by Grygier (1987) from Disko Bay, West Greenland, under the name of Type VI.   Although Grygier (1987) suggested that other authors may have overlooked them because "they [setiform maxillular rudiments] are small and could have been missed," actually maxillular rudiments are very rare among facetotectans.   They do not occur in numerous nauplii of more than 20 undescribed species of facetotectans from Tanabe Bay either (Itô, unpublished data).   It may be concluded that most facetotectans have no metanauplius stage, but have at least five orthonauplius stages before the cypris y stage.

The type VI larva accords with the nauplii of *H. furcifera* in having maxillular rudiments, and corresponds to the fifth naupliar stage because of the reported presence of a cyprid body within it (Grygier, 1987).   Type VI differs from the fifth naupliar stage of *H. furcifera* in not having two longitudinal rows of laterally extended plates before the dorsocaudal organ, but instead a mosaic of polygonal plates arranged rather irregularly.   The ornamentation of this area of the Type VI larva is evocative of the same region in a Type IV larva described from Spro, Norway, by Schram (1972), though, by some morphological differences to be discussed later, there is little doubt that they are distinct species.

The larval development of *H. furcifera* shows that some characters are available for the identification of naupliar stages, even though it is impossible to identify all stages by changes in a single character (Itô, 1989b).   For example, the presence of four Frontals and seven Occipitals before and behind the window, respectively, can be used to identify the first nauplius stage.   The nauplii illustrated in Fig. 2 of Itô (1987c) are all of this stage.   Other nauplii identifiable as first stage by this charac-

teristic are found in papers by Steuer (1905, Fig. 1), McMurrich (1917, Fig. 7) and Schram (1972, Fig. 3A). On the other hand, the absence of a complete set of these axial plates does not necessarily mean that a given nauplius belongs to some other stage than the first, because F–1 may fuse with W and/or O–1 (Itô, 1987b). Hansen's original type IV larva is also a case in point (Hansen, 1899, Taf. III, Fig. 5).

In the first nauplius stage, the first two Occipitals may or may not be twin, probably depending on species, while the posterior five Occipitals are single. In *H. furcifera*, O–1 and O–2 are both twin even in the first naupliar stage, and these twin Occipitals remain unchanged through all the later stages even though the more posterior Occipitals become divided into smaller plates. Twin O–1 and O–2 are easily identifiable in other kinds of nauplii as well (Schram, 1972, Fig. 3A, C, Fig. 4A, B; Grygier, 1987, Fig. 1), and are available as a marker for the identification of other plates.

I–1 remains undivided through all the stages, and is easily identifiable by the possession of either one or two pores. I–2 is never divided either and retains its original size very well. Hence, I–1 and I–2 are available as good markers for plate identification. I–1 and I–2 are readily identifiable in Schram's (1972) and Grygier's (1987) nauplii.

In the present species, I–1 is in contact with I–2 in the first stage, but later these plates become separated by intervening plate(s) originally derived from E–1 (Fig. 11). A similar phenomenon is noticed in other kinds of nauplii, too. A nauplius illustrated by Schram (1972, Fig. 4B) is a case in point, which appears to have two successive small plates between I–1 with two pores and the long I–2. These two small plates are the equivalents of E–1(eea) and E–1(eep) of the fifth naupliar stage of *H. furcifera* (Fig. 10B). In fact, the same nauplius illustrated by Schram has a set of seven plates of the E group completely identical to the set in the fifth stage of *H. furcifera*; in addition to E–1(eea) & (eep), it has E–1(ece) & (ecc), E–1 (ca) & (cp), and E–2 bearing a prominent pore. Grygier's (1987) nauplius is another case where I–1 is separated from I–2. However, between I–1 and I–2 there is a single plate, probably identical to E–1(ee) of the fourth stage in *H. furcifera*, and
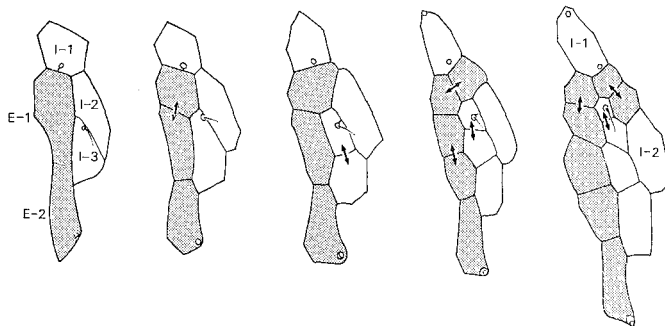

Fig. 11.   Schematic representation of the differentiation of Intercalary and Elongate plates in *Hansenocaris furcifera* through five naupliar stages (left to right).

the possible counterparts of E–1(ece) & (ecc) are represented by a single plate identifiable as E–1(ec), which again is a feature of the fourth stage in *H. furcifera*. In Grygier's nauplius, there is a very long plate in front of E–2 and there is little doubt that it is equivalent to E–1(c) in the third stage of *H. furcifera*. Although these characteristics of Grygier's nauplius might appear to represent those of earlier stages than the fifth stage of *H. furcifera*, they, or at least some of them, could be due to secondary fusion of previously divided plates.

Fusion to different degrees happens among various plates in some of the later molts in *H. furcifera*. According to the present observations, plate fusion seems to happen often among marginal plates such as the Polygonals and Marginals, and more often among latitudinally arranged ones (Fig. 10). Such fusion, probably together with the latitudinal division of Brim, makes latitudinal ridges dominant in later stages. Nauplii of type III (Hansen, 1899), type VI (Grygier, 1987), and type VII (Itô, 1986a) all show this tendency.

In relation to the latitudinal ridges that dominate the marginal area of the cephalic shield in later stages, it is noteworthy that similar latitudinal ridges have recently been discovered to occur also in other thecostracan taxa than the Facetotecta. These include the lepadomorph Cirripedia (Anderson, 1987) and Ascothoracida (Itô & Grygier, 1990). It is interesting that a predominance of latitudinal ridges appears at earlier stages in these groups than in facetotectans. This phenomenon will be discussed later in the relation to the development of the first antenna.

Some kinds of plates on the cephalic shield exhibit interesting behavior through their development (Fig. 11). For example, plates derived from E–1 extend between and completely separate the originally contiguous I–1 and I–2. Similar behavior of the Intercalaries/Elongates can easily be supposed in other kinds of facetotectan nauplii such as "type IV" described by Schram (1972) and type VI *sensu* Grygier (1987). In contrast to such dynamic plates, it is noteworthy that there are quite stationary ones too. The window, the anterior two Occipitals, I–1, E–2, and C–2 may be listed as examples. I feel such a prominent change in the distribution pattern of plates such as the Intercalaries/Elongates shown in different species is a reflection of some change in the underlying tissues or organs through their development. Furthermore, the difference between the dynamic plates and stationary ones might also reflect something underlying. Since more or less similar plates delimited by ridges have been reported to occur even in a trilobite and some nauplius-like arthropods from the Upper Cambrian (Müller & Walossek, 1986, 1987), knowledge of these plates, especially data obtainable through studies of exact plate homologies, if present, as well as from microanatomical studies, may shed light on the evolution of the Crustacea, not just within the Maxillopoda. I feel that the prominent, ridged plates of facetotectans might be an expression of an ancient characteristic that occurred among primitive crustaceans or even pre-crustacean arthropods.

All the naupliar stages of *H. furcifera* have a pair of small protuberances in front of the first antennae. Similar structures were described in Pacific Type I by Itô (1986a) and in Type VI by Grygier (1987), who called them "papilliform frontal

filaments." It seems likely that these structures have a certain relation with the frontal filaments known to be situated similarly in some cirripedian, ascothoracidan, and rhizocephalan nauplii, but these facetotectan structures are not frontal filaments *per se*. The frontal filament is now known to be part of the organ of Bellonci in cirripedes (Walker, 1974), and, for facetotectans the structure previously called the paraocular process of the cypris y stage (Itô, 1985) is known to actually be part of the same organ (Itô & Takenaka, 1988). The present study with SEM revealed that the small "papilliform frontal filaments" of facetotectan nauplii actually have prominent apical pores (Fig. 3A). They would be better described as swollen rims encircling the openings of internal ducts. Elofsson (1971) reported that his nauplius y larvae had a large "head gland" with two outlets extending to the ventum of the head. He also mentioned that "these openings [of the two outlets] are situated on each side and slightly anterior to the nauplius eye," the same situation as that of the "papilliform frontal filaments." In fact, he found elements of the organ of Bellonci elsewhere inside the head, and stated that "no outer frontal filament has been found in the nauplius y." There can be little doubt that the "papilliform frontal filaments" are not frontal filaments as external parts of the organs of Bellonci, but the terminal parts of ducts originating from what Elofsson called the head gland.

The development of the first antenna through the five naupliar stages is summarized schematically in Fig. 12. Differences in the number of setae and in their relative lengths are available to identify naupliar stages in *H. furcifera*. However, this scheme should not be used to try to identify the stages of other species' larvae. It is already known in various lecithotrophic larvae that degeneration of setae may take place together with the addition of new setae through antennular development and no simple increase of setae as observed in the present species can always be presumed (Itô, 1989b). The number of setae in the fifth naupliar stage of *H. furci-fera* accords with that in the first two naupliar stages of an ascothoracidan species
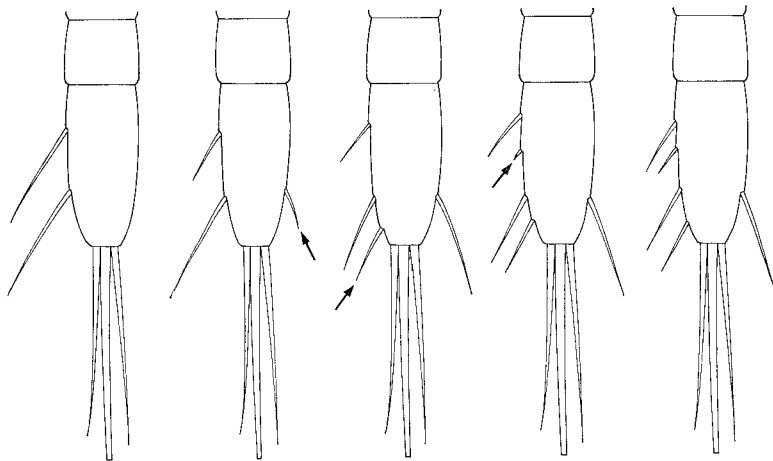

Fig. 12. Schematic representation of the development of first antennae of *Hansenocaris furcifera* through five naupliar stages (left to right).

described by Itô & Grygier (1990); moreover, the arrangement of these setae is also closely similar if differences in segmentation are not taken into consideration. As previously described, this ascothoracidan species has latitudinal ridges on the marginal area of naupliar cephalic shield (=dorsal shield in the sense of Itô & Grygier, 1990) as early as the second stage, though such ridges appear much later in facetotectan larvae. Thus, in both antennular setation and cephalic shield ornamentation, earlier stages of the ascothoracidan appear to resemble later stages of the facetotectan, instead of corresponding stages. With respect to these two characters, the larvae of that ascothoracidan species may be interpreted as exhibiting a relatively more advanced developmental condition than the larvae of *H. furcifera* at the corresponding stages. The meaning of this phenomenon is another open question in the study of facetotectan and ascothoracidan relationship.

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Dr. Tatsunori Itô died on April 8th, 1990.   The Laboratory.