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Larval Development of the Hermit Crab *Diogenes nitidimanus* TERAO, 1913 (Crustacea : Anomura : Diogenidae) Reared in the Laboratory*

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The complete larval development of the hermit crab *Diogenes nitidimanus* from hatching to first crab stage was obtained by laboratory rearing. Four zoeal and one megalopal stages are described and illustrated. The pleopod buds appeared in the third zoea, the posterior lobe of the scaphognathite appeared in the second zoea, and the antenna in the megalopa showing a remarkable differentiation toward suspension feeding, all unique to *D. nitidimanus*, are discussed.

Introduction

The hermit crab genus *Diogenes* represented by about 46 species are sublittoral inhabitants, many species of which are known from the Indo West-Pacific. In spite of the recent increase of species descriptions the systematics of the genus requires revision from a view point of functional morphology relating especially to the feeding habits, which will be published elsewhere.

Knowledge of the larval development of this genus is very limited, restricted to thorough descriptions of *D. pugilator* by MACDONALD, PIKE and WILLIAMSON (1957), *D. bicristimanus* by SAROJINI and NAGABUSHANAM (1968), *D. avarus* by SANKOLLI and SHENOY (1975) and *D. diogenes* by NAYAK and KAKATI (1977). Planktonic material has also been described earlier for *D. pugilator* (MENON, 1937).

Diogenes nitidimanus is a typical suspension feeder and is one of the common shore hermit crabs in Kyushu, Japan ; when the tide recedes the animals are sometimes found buried partly on muddy sand substrates at low tide levels, but usually they are not exposed to the air. This paper describes the complete larval development of *D. nitidimanus* obtained by rearing in the laboratory. Herein discussed are some of the larval characters uniquely displayed by *D. nitidimanus*, which seem at variance with previous definitions especially of the infraorder Anomura and the developmental sequence of scaphognathites, or, which may expand the definition of *Diogenes*. Attention is also accorded to the functional morphology of the antenna in the postlarval stages, the flagellum with a row of long plumose setae being associated with net-casting or suspension feeding.

Methods and Materials

The ovigerous female was collected on 25 June 1979 from the intertidal zone in Amakusa, Kumamoto, the west coast of Kyushu, Japan. The first zoeas were obtained on 29 June 1979 and reared under laboratory temperatures of 26.0 - 29.0°C. The rearing techniques follow FUKUDA

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(1982). Length of carapace was measured at midline between the tip of the rostrum to the posterior end of the carapace in five specimens. Setae of appendages are formulated toward the distal end, unless otherwise mentioned.

Results

Diogenes nitidimanus passed through four zoeal and one megalopal stages before reaching the first crab stage. The number of days required to complete the larval development in the laboratory (filtered sea water, *Artemia* nauplii fed) was 20 days. The major characteristics are described below.

FIRST ZOEA

Carapace length. — 1.14 mm (average).
Duration of stage. — Four days.
Carapace (Fig. 1a). — About as long as abdomen, inclusive of rostral spine; smooth, dorsoanteriorly concave moderately, anterolaterally with tiny but distinct spine, posterolaterally rounded. Rostrum horizontal, only slightly shorter than remaining carapace when measured from postorbital margin, overreaching antennal scale but not its distal marginal setae. Eyes sessile.
Antennule (Fig. 1b). — Elongate rod, provided terminally with 4 aesthetascs and 2 plumose, shorter setae, subterminally with pronounced plumose seta.
Antenna (Fig. 1c). — Endopod not divided from peduncle, provided terminally with 2 well-developed plumose setae, subterminally with very short one. Peduncle with laterally serrate, spiniform process on ventral terminal margins. Antennal scale fully 1.5 times as long as endopod, provided with outer terminal spine, and fringed with 11 plumose setae on inner and distal margins; outermost seta directly inside terminal spine rather short and somewhat ventral in position.
Mandible (Fig. 1d). — Almost symmetrical. Incisor process acute, with serrate accessory process on dorsoproximal portion. Molar process with submarginal denticles.
Maxillule (Fig. 1e). — Palp 2-segmented, distal segment very short, provided with 2 simple terminal setae. Coxal endite with 6 plumose, bristle-like setae. Basal endite with 2 strong spines, each with row of marginal denticles.
Maxilla (Fig. 1f). — Palp unsegmented, with 2 terminal setae. Coxal endite also bilobed, with 7 setae on proximal lobe, 4 on distal lobe (formulated as 7, 4). Basal endite also bilobed, proximal lobe with 5 setae, distal lobe 3 setae (5, 3). Scaphognathite lacking posterior lobe, anterior lobe with 5 plumose setae.
First maxilliped (Fig. 1g). — Setation of basis, 1, 3, 2; endopod 5-segmented, with setal formula of 3-2-1-2-5. Exopod constricted at midlength, with 4 natatory setae.
Second maxilliped (Fig. 1h). — Setation of basis, 1, 1; endopod 4-segmented, its setation, 2-2-3-4. Exopod much like that of preceding appendage.
Third maxilliped (Fig. 1i). — Uniramous, elongate simple bud.
Abdomen. — Sixth segment not separated from telson. Fourth segment with middorsal spine posteriorly. Fifth segment with lateral and middorsal spines posteriorly.
Telson (Fig. 1j). — Triangular, posterior median sinus distinct. Telson processes, 7+7; first process spiniform, not articulated at base, second process hair-like and plumose; remainder seta-like but pronounced.

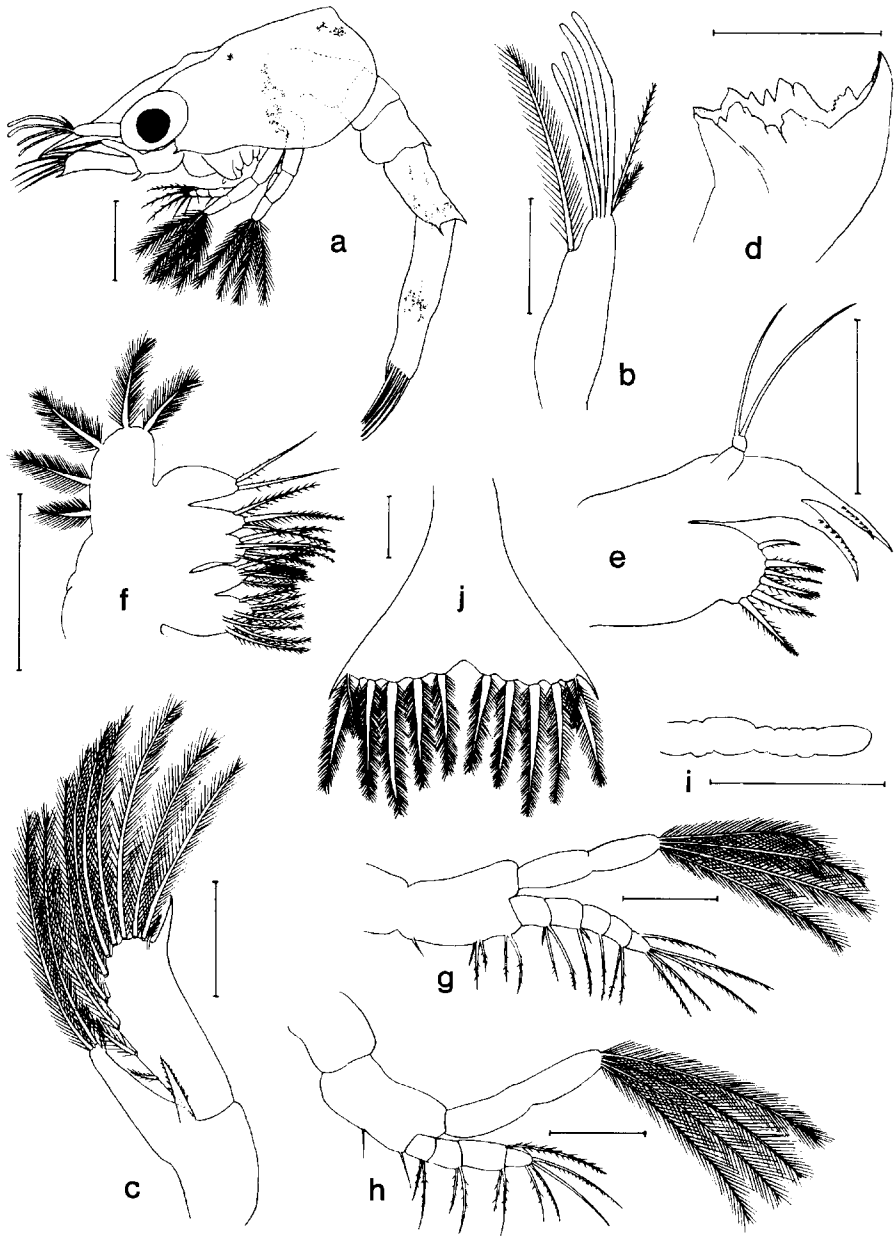

Fig. 1. *Diogenes nitidimanus* TERAO, first zoea : a, lateral view ; b, antennule ; c, antenna ; d, mandible ; e, maxillule ; f, maxilla ; g, first maxilliped ; h, second maxilliped ; i, third maxilliped ; j, telson. Scale for a, 0.2 mm ; for b-j, 0.1 mm.

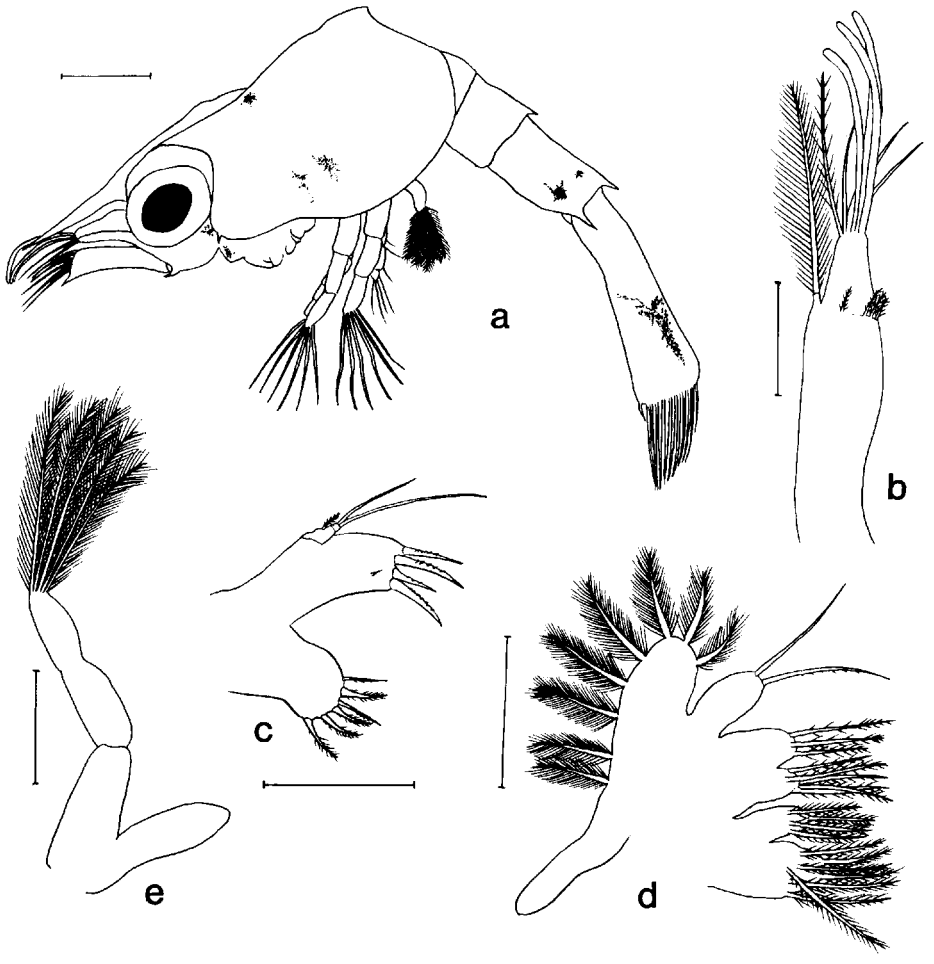

Fig. 2. *Diogenes nitidimanus* TERAO, second zoea: a, lateral view; b, antennule; c, maxillule; d, maxilla; e, third maxilliped. Scale for a, 0.2 mm; for b–e, 0.1 mm.

SECOND ZOEA

Carapace length. — 1.24 mm (average).

Duration of stage. — Four days.

Carapace (Fig. 2a). — Little larger than in previous stage, retaining anterolateral spine. Rostral spine about as long as remaining carapace. Eyes movable.

Antennule (Fig. 2b). — Terminally with 3 aesthetascs, 3 simple and 1 plumose setae; pronounced subterminal plumose seta accompanying few fine, plumose setae directly dorsal to it.

Antenna. — Almost as in first zoea, endopod articulate basally.

Mandible. — Marginal denticles of molar process more numerous.

Maxillule (Fig. 2c). — Short plumose seta newly appeared on proximal segment of palp. Setation of coxal endite unchanged; basal endite with 4 strong marginal spines and 1 tiny seta slightly ventral to margin.

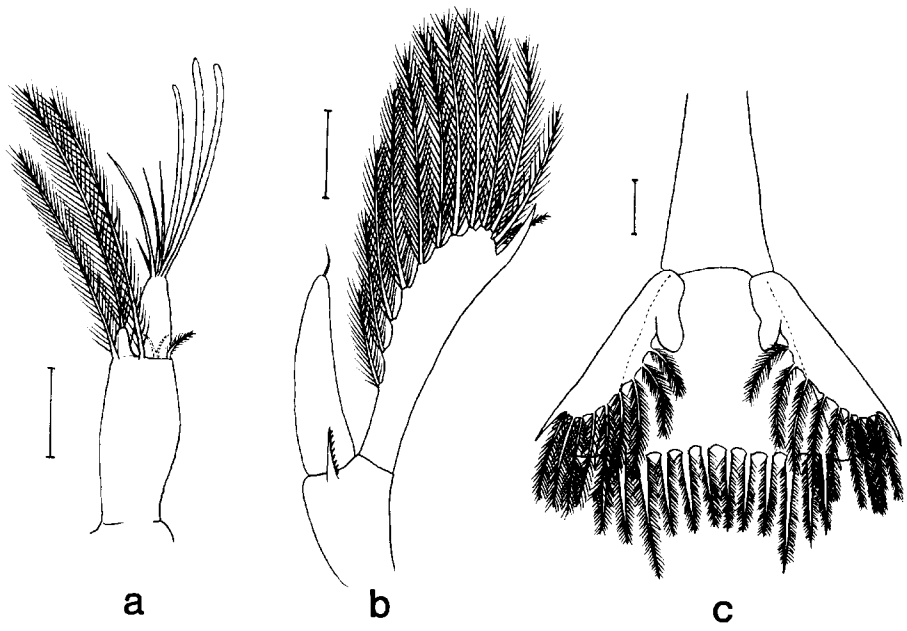

Fig. 3. *Diogenes nitidimanus* TERAO, third zoea : a, antennule ; b, antenna ; c, telson. Scales, 0.1 mm.

Maxilla (Fig. 2d). — Setae on coxal and basal endites and on palp as in first zoea. Scaphognathite with setaless posterior lobe ; marginal setae of anterior lobe increased to 8.
First maxilliped. — Endopod setae, 4-3-2-2-5 ; natatory setae increased to 6 ; otherwise unchanged.
Second maxilliped. — Setation of basis unchanged ; midventral seta added to penultimate segment of endopod ; 6 natatory setae.
Third maxilliped (Fig. 2e). — Biramous ; endopod simply rod-like ; exopod with 5 natatory setae.
Abdomen and telson. — Unchanged morphologically except size.

THIRD ZOEA

Carapace length. — 1.42mm (average).
Duration of stage. — Five days.
Carapace. — Nearly as in preceding stage.
Antennule (Fig. 3a). — Terminally with group of 3 aesthetascs and 4 setae. Inner ramus short, ending in pronounced plumose seta, flanked by pair of long plumose setae, and accompanying 3 fine setae directly outside to it.
Antenna (Fig. 3b). — Endopod with rudimentary terminal seta. Antennal scale relatively narrowed, with 12 marginal setae. Terminal process of basis reduced in size.
Mandible. — Nearly as in second zoea.
Maxillule. — Mostly as in second zoea, but coxal endite setae increased to 7.

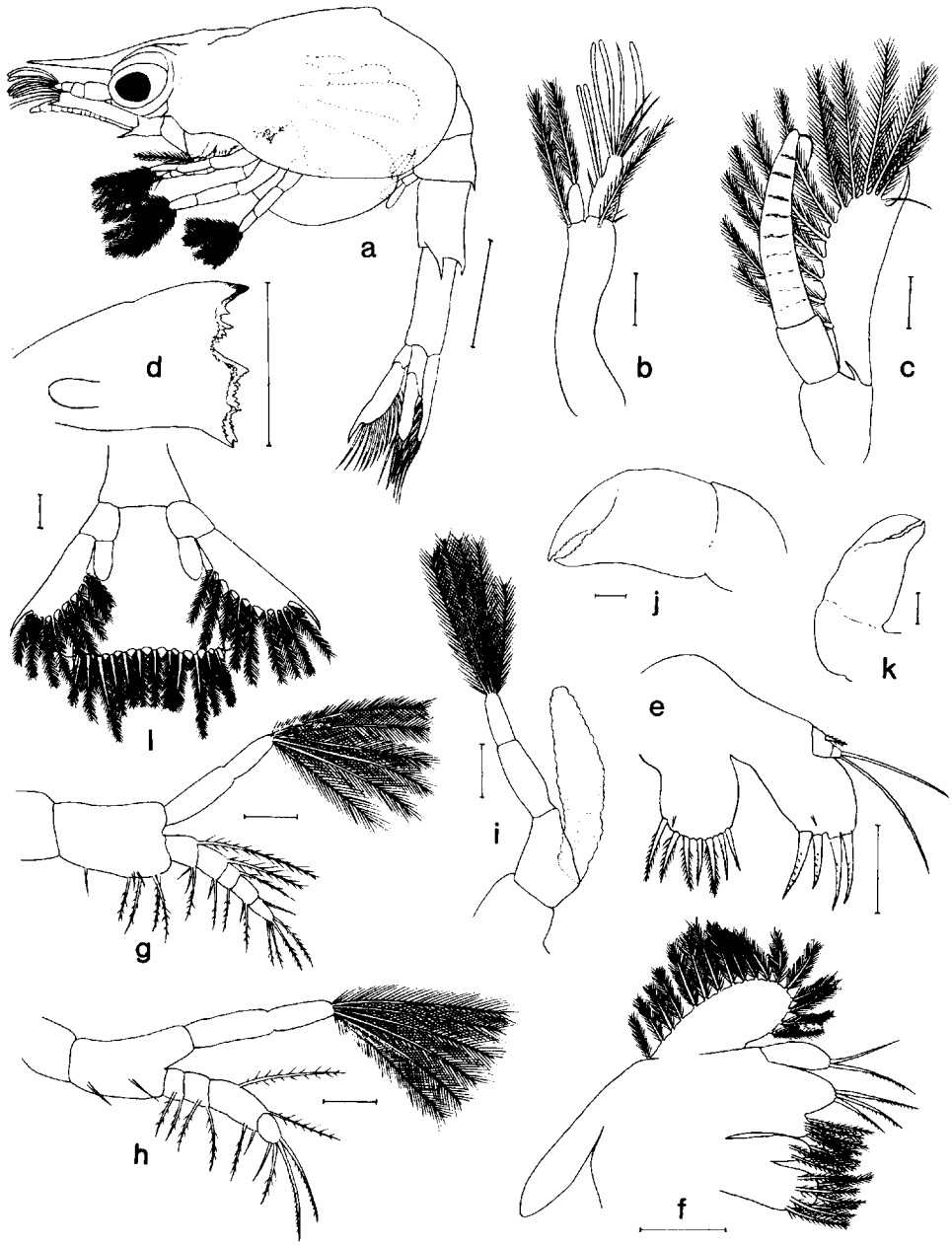

Fig. 4. *Diogenes nitidimanus* TERAO, fourth zoea: a, lateral view; b, antennule; c, antenna; d, mandible; e, maxillule; f, maxilla; g, first maxilliped; h, second maxilliped; i, third maxilliped; j, right cheliped; k, left cheliped; l, telson. Scale for a, 0.5 mm; for b-l, 0.1 mm.

Maxilla. — Posterior lobe of scaphognathite more elongate than in second zoea. Marginal setae of anterior lobe increased to 13. Setations of palp and endites unchanged.
First and second maxillipeds. — Nearly as in preceding stage.
Third maxilliped. — Endopod arising from proximal portion of basis, not overreaching end of basis ; 6 natatory setae.
Pereopods. — Only first pereopod appeared as bud, biramous, suggesting chela.
Abdomen. — Buds of pleopods on second through fourth abdominal segments. Sixth segment separated from telson. Uropod appeared, rami unarticulated, inner ramus (endopod) bud-like, setaless ; outer ramus (exopod) with elongate terminal spine and fringed with 9 plumose setae on inner margin.
Telson (Fig. 3c). — Posterior margin feebly concave, without distinct sinus, provided with 7+7 processes.

FOURTH ZOEA

Carapace length. — 1.93mm (average).
Duration of stage. — Three days.
Carapace (Fig. 4a). — Rostrum 0.92 as long as remaining carapace. Carapace relatively high posteriorly.
Antennule (Fig. 4b). — Peduncle much elongate, distally with 2 plumose setae, one at base of inner ramus, other at base of outer ramus ; and also 3 short setae near junction with outer ramus ; outer ramus with 2 aesthetascs and single short seta at midlength of inner margin, and 4 aesthetascs and 3 shorter setae terminally.
Antenna (Fig. 4c). — Basis with slender spine near base of antennal scale. Endopod subdivided into 10 segments, all bare but ultimate segment with reduced terminal seta ; antennal scale much like that of preceding stage.
Mandible (Fig. 4d). — Incisor process acute, basally with many denticles ; unsegmented bud of palp distinct.
Maxillule (Fig. 4e). — Setae on coxal endite increased to 7+1 (7 pronounced and 1 fine setae) ; other portions unchanged.
Maxilla (Fig. 4f). — Setation of palp and endites as in preceding stage. Posterior lobe still bare, anterior lobe fringed with 17 setae.
First maxilliped (Fig. 4g). — Setation of basis, 1, 4, 2 ; endopod with setation of 4-3-2-2-5 as in 2 preceding stages. Natatory setae neither increased nor decreased.
Second maxilliped (Fig. 4h). — As in preceding stage.
Third maxilliped (Fig. 4i). — Endopod not segmented, barely reaching end of exopod. Natatory setae not increased.
Pereopods (Fig. 4j, k). — Chelipeds distinct but small, left one larger.
Abdomen. — Biramous pleopods on second through fourth abdominal segments. Endopod and exopod of uropod (Fig. 4l) articulated with protopod ; other features as in third zoea.
Telson (Fig. 4l). — Nearly as in preceding stage, but not very wider posteriorly.

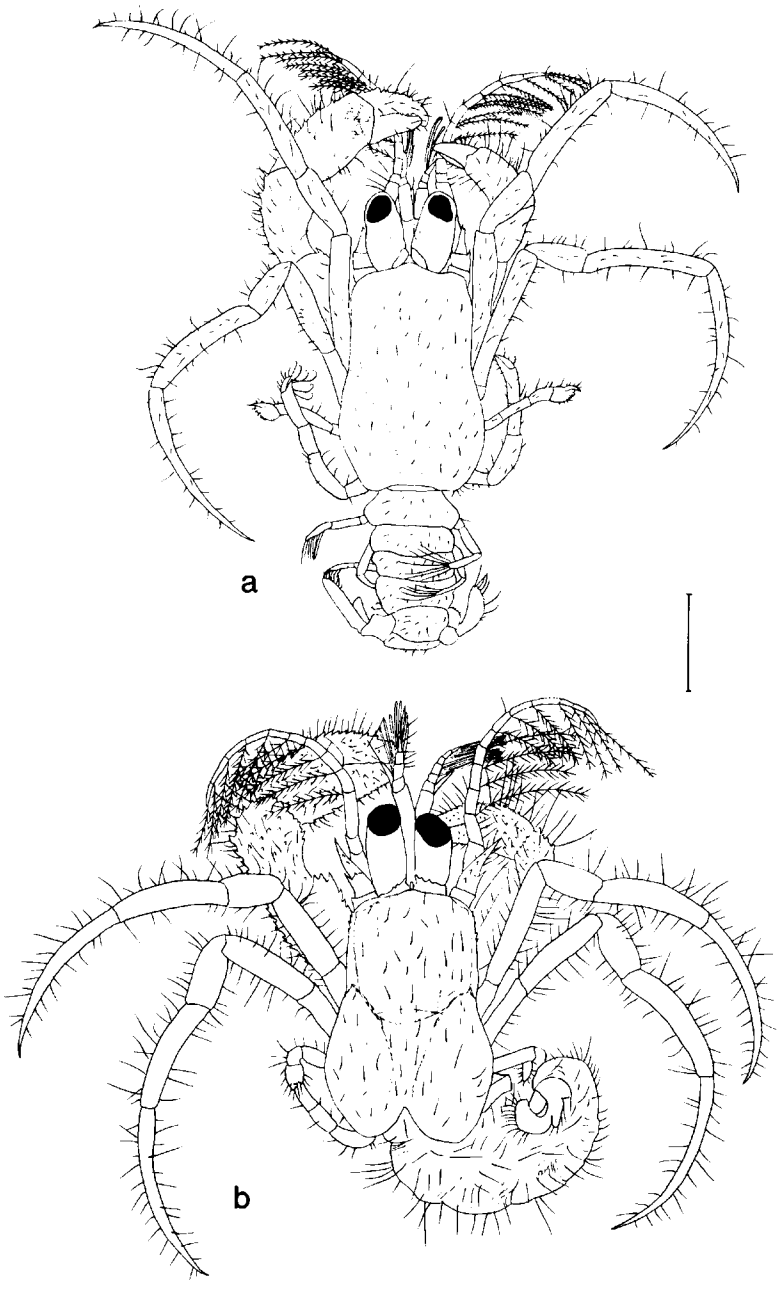

Fig. 5. *Diogenes nitidimanus* TERAO : a, megalopa, dorsal view ; b, first crab, dorsal view. Scale, 0.5 mm.

Fig. 6. *Diogenes nitidimanus* TERAO, megalopa : a, antennule ; b, antenna ; c, mandible ; d, maxillule ; e, maxilla ; f, first maxilliped ; g, second maxilliped ; h, third maxilliped ; i, fourth pereopod ; j, fifth pereopod ; k, second pleopod ; l, telson and uropod. Scales, 0.1 mm.

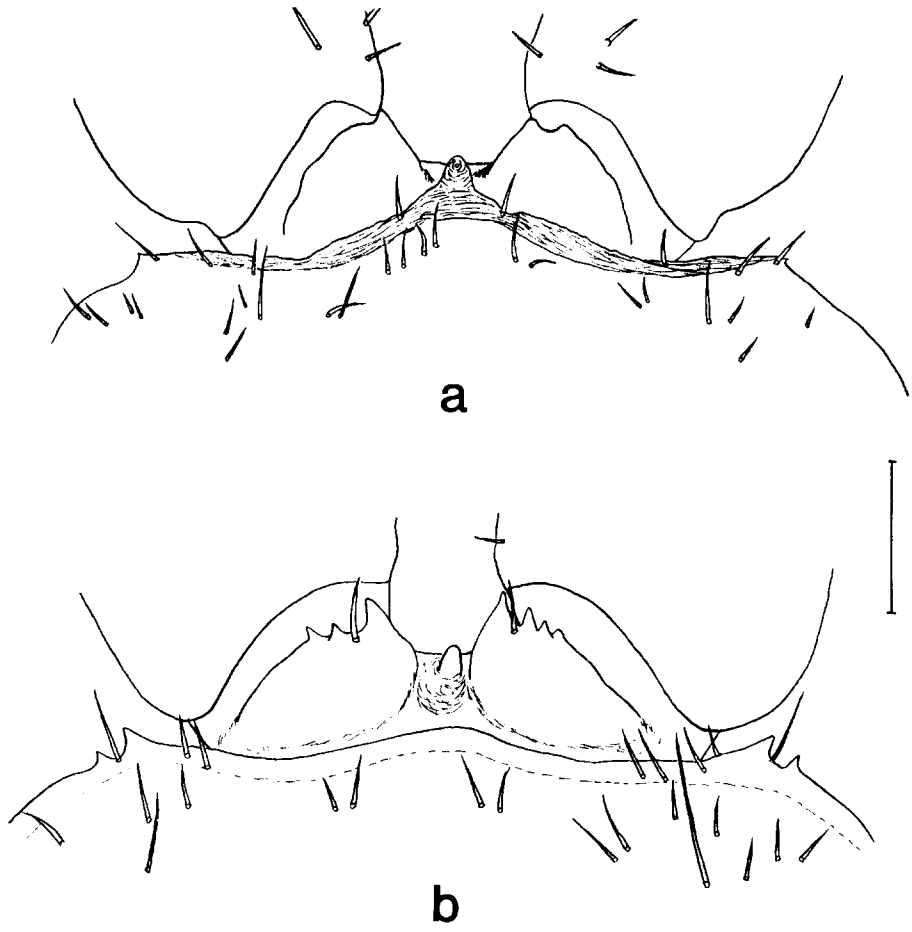

Fig. 7. *Diogenes nitidimanus* TERAO, anterior parts of carapaces: a, megalopa; b, first crab. Scale, 0.1 mm.

MEGALOPA

Carapace length. — 1.15 mm (average).

Duration of stage. — Four days.

Carapace (Fig. 5a). — About 1.5 times as long as wide, sparsely covered with coarse setae. Lateral margins spineless, subparallel in anterior half, convex in posterior half. Shield not fully calcified, but distinctly circumscribed by median depression from remaining carapace. Posterior branchial region well defined. Anterior margin roundly convex medially, anterolaterally minutely produced (Fig. 7a). — Rostriform process as uncalcified bud. Eyescale present, but lacking anterior denticles.

Antennule (Fig. 6a). — Peduncle 3-segmented, segments subequal; outer ramus 3-segmented, distal 2 segments with aesthetascs as illustrated; inner ramus 2-segmented, distal segment about twice as long as proximal one, overreaching median segment of outer ramus, distally provided with several short setae.

Antenna (Fig. 6b). — Peduncle 4-segmented, ultimate segment about twice as long as penultimate segment; acicle distally sharp, without spination. Flagellum composed of 8 segments, each distally provided with pair of long plumose setae and few other fine setae.
Mandible (Fig. 6c). — Much like that of adult. Palm 3-segmented.
Maxillule (Fig. 6d). — Palp with simple terminal seta. Coxal and basal endite setae as illustrated.
Maxilla (Fig. 6e). — Terminal setae lost in palp. Scaphognathite functional, fringed with setae on entire margin.
First maxilliped (Fig. 6f). — Coxal and basal endites as illustrated. Endopod curving, distally with reduced seta. Relatively broad proximal part of exopod bearing 3 plumose setae on distal margin, distal part slender with obtuse end.
Second maxilliped (Fig. 6g). — Endopod 5-segmented, relatively short, about half as long as exopod; distal 2 segments more setose. Exopod with 6 short plumose setae.
Third maxilliped (Fig. 6h). — Five-segmented endopod well developed, overreaching exopod; setose, especially on distal 3 segments. Exopod with 6 plumose setae.
Pereopods. — Chelipeds (Fig. 5a) asymmetrical, left one larger; left cheliped dorsally provided with tubercles on movable finger, palm and carpus; fingers crossing distally; right cheliped smooth, also sparsely setose. Second through fifth pereopods as figured (Figs. 5a, 6i, j).
Abdomen. — Segmentation distinct. Pleopods (Fig. 6k) present on second through fifth abdominal segments, endopod absent, exopod 2-segmented, each provided distally with 6 setae, but that of fifth segment bare and much reduced in size. Uropods (Fig. 6l) dissimilar, right one reduced in size; posterior margin of exopod with 13 (left) or 12 (right) closely arranged, short spines; outer margin of endopod with 9 (left) or 8 (right) similar spines.
Telson (Fig. 6l). — Asymmetrical, more or less diminutive on right side, posterior margin deeply concave, without posterolateral spine.

First Crab

Carapace length. — 1.13mm (average).
Gross morphology as figured (Fig. 5b). Rostriform process (Fig. 7b) distinct, calcified. Eyescale with anterior dentition. Flagellar segments increased, bearing more numerous setae than in megalopa. Antennal acicle with spinules. Segmentation of abdomen indistinct.

Discussion

In the key to the Mediterranean species of the Diogenidae, PIKE and WILLIAMSON (1960) stressed as zoeal characters for distinguishing five genera the presence or absence of posterior carapacial spines, dorsal spines on the fifth abdominal segment and the terminal spine of the antennal scale. Based on available information, it seems constant in *Diogenes* that the marginal spines of the basal endite in the maxillule increase from two to four in number when the larvae molted into the second zoea, and that no such additional increase occurs until the megalopa stage.

It is apparent that the setations of the palp and coxal and basal endites in the maxilla are constant through all zoeal stages in both *D. bicristimanus* (see SAROJINI and NAGABUSHANAM, 1968) and *D. nitidimanus*. According to the figures prepared for *D. avarus* (see SANKOLLI and SHENOY, 1975), the setation of the coxal endites is unusual; it is 14, 3 in the first zoea, while in the third and fourth stages it is 8, 3; also unusual is the number of the palpal setae in the third zoea,

which is represented by three instead of two as in the first, second and fourth stages. Similarly, the figures for *D. diogenes* (see NAYAK and KAKATI, 1977), which however do not accurately correspond to the descriptions, indicate that the increase of setae occurred on the coxal endites in the third or last zoea. For these variabilities careful reexamination is greatly needed. Inasmuch as available information especially as to developmental sequences of larval appendages in the *Diogenes* species do not seem accurate or complete, comparison of larval characters in a specific level is not practical at the present time.

In *Diogenes nitidimanus*, pleopod buds appear first in the third zoea, and they become distinctly biramous in the following stage. This fact seems at variance with PIKE and WILLIAMSON (1960) who stated that in the Anomura, pleopods do not appear until the last zoeal stage, except in cases of *Paguristes, Galathodes* [=*Munidopsis*] and Lithodidae, all having abbreviated larval developments. We do not believe that the larvae here obtained by laboratory rearing showed an abnormal development. And, it is suggested that the definition of the Anomura may be expanded.

Van DOVER *et al.* (1982) found that there is a unique developmental sequence of larval scaphognathites in the Diogenidae as well as in the Paguridae, Coenobitidae and Lithodidae, i.e., the posterior lobe appears first in the last zoea or in the first postlarval stage. This may be applicable for *D. avarus* and *D. diogenes* ; however, in this species, such a lobe appears in the second zoea, and it remains naked through the fourth zoea ; the normal scaphognathite is nearly completed in the megalopa stage. The appearance of the posterior lobe in the penultimate zoeal stage was noted earlier in *D. bicristimanus* (see SAROJINI and NAGABUSHANAM, 1968). Thus, the minor amendment for the explanation of that sequence is needed.

The first pereopods appear as buds in the third zoea ; they become chelate in the fourth zoea, the left one being distinctly larger. This asymmetry becomes more distinct in the subsequent stage. Undoubtedly the handedness in the genus *Diogenes* is genetic, not caused by the case as in *Uca lactea* (YAMAGUCHI, 1977).

Of the four species previously known of the larval development, three Indian species are deposit feeders ; the British *D. pugilator* seems to be an antennary net-caster. According to PIKE and WILLIAMSON (1960), the differentiation toward the eating use of the antenna is still indistinct in the megalopa of *D. pugilator*, for the antennal flagellum bears relatively short setae ; in *D. nitidimanus*, on the other hand, a row of long plumose setae are fully developed on each segment of the antennal flagellum, suggesting that this appendage may be more functional than in *D. pugilator* for suspension feeding.

A spine anterior to the midfront margin and between the eyescales, which is distinct in the adult, and the presence of which is one of the important characters of *Diogenes*, is sometimes called a "rostral spine" (BARNARD,1950 ; LEWINSOHN, 1982) or "rostrum" (WANG and DONG, 1977) ; in early descriptions, however, ALCOCK (1905) used the term "rostriform process" for it. In the strict sense, we would like to follow ALCOCK, because, as illustrated in Fig. 7, the process arose first in the megalopa stage as a soft tiny process between the bases of the eye peduncles and distinctly anterior to the midfront margin of the carapace, and it then became calcified in the first crab stage.

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