Zootaxa 1693: 1–26 (2008)
www.mapress.com/zootaxa/

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

A reexamination of adults and larval stages of *Diogenes nitidimanus* (Crustacea: Decapoda: Anomura: Diogenidae)

OLGA M. KORN[1], ELENA S. KORNIENKO[1] & TOMOYUKI KOMAI[2]

[1]*A.V. Zhirmunsky Institute of Marine Biology, Far East Division, Russian Academy of Sciences, 17 Pal'chevskogo Str., Vladivostok, 690041, Russia. E-mail: okorn@mail.primorye.ru; kornielena@mail.ru*

[2]*Natural History Museum and Institute, Chiba, 955-2 Aoba-cho, Chuo-ku, Chiba, 260-8682, Japan. E-mail: komai@chiba-muse.or.jp*

Abstract

A redescription of adult and larval stages of diogenid hermit crab *Diogenes nitidimanus* Terao, 1913 is presented. Morphological similarities suggest that *D. nitidimanus* is allied to *D. avarus* Heller, 1865, *D. granulatus* Miers, 1880, *D. ovatus* Miers, 1881, *D. pugilator* (Roux, 1838) and *D. rectimanus* Miers, 1884. *Diogenes nitidimanus* can be distinguished from the latter four species by different armature or ornamentation of the left chela and/or the shape of the ambulatory dactyli. Zoeal and megalopal stages of this species are described from laboratory-reared material hatched from parental individuals collected from Peter the Great Bay, Russian Far East. Larval development in the Russian population is compared with that described for a population of this species from southern Japan. The developmental morphology between the two populations is generally similar, but some minor differences, which might be attributable to variability, are found. Larvae of *D. nitidimanus* are morphologically closest to those of *D. avarus* among eight species of *Diogenes* for which larval descriptions are available.

Key words: Crustacea, Decapoda, Anomura, Diogenidae, *Diogenes nitidimanus*, morphology, adult, larva, zoea, megalopa, Sea of Japan

Introduction

The diogenid hermit crab genus *Diogenes* Dana, 1851 is represented by about 60 species chiefly occurring in temperate and tropical waters in the Indo-West Pacific region and the eastern Atlantic Ocean. In spite of recent studies (Morgan & Forest 1991; Rahayu & Forest 1995; McLaughlin & Haig 1996; Rahayu 1996; McLaughlin & Clark 1997; McLaughlin & Dworschak 2001; McLaughlin & Holthuis 2001; Rahayu & Hortle 2002; McLaughlin 2002, 2004, 2005; Siddiqui & McLaughlin 2003; Asakura 2006; Asakura & Goodwin 2006) the taxonomy of the genus remains inadequate. The taxonomic status of several species is unclear and discovery of new species is continuing. Morphology of larvae of *Diogenes* has been described for only eight species (MacDonald *et al*. 1957; Pike & Williamson 1960; Sarojini & Nagabushanam 1968; Sankolli & Shenoy 1975; Nayak & Kakati 1977; Nayak 1981; Nayak & Neelkantan 1983; Baba & Fukuda 1985; Siddiqui & Tirmizi 1988; Shenoy & Sankolli 1993).

The aim of this paper is a reexamination of adults and larval stages of *Diogenes nitidimanus* Terao, 1913 chiefly on the basis of material from waters from Far East Russia. *D. nitidimanus* was found in Peter the Great Bay for the first time in 2002 and it is possible that this species was introduced from southern Japan (Korn *et al.* 2007). The rather wide latitudinal range (Peter the Great Bay to Kyushu, Japan, see Asakura (2006)) and commonness in intertidal to subtidal zones of *D. nitidimanus* have made it one of the most extensively studied hermit crabs, particularly in its ecologicy (Asakura & Kikuchi 1984a, 1984b; Asakura 1987a, 1987c, 1991,

Accepted by S. Ahyong: 10 Dec. 2007; published: 31 Jan. 2008

1992, 1995a). Despite the well studied ecology and rather numerous faunal records (Kim 1973; Miyake 1978, 1982; Miyake & Imafuku 1980; Asakura 1987b, 1995b, 2006), the adult morphology of *D. nitidimanus* is surprisingly poorly known and comparisons with other congeneric species are insufficient. Variations in the morphology of the left cheliped were briefly described by Asakura (1987b). A brief account showing characters for discriminating three local species, *D. nitidimanus*, *D. edwardsii* (De Haan, 1849) and *D. spinifrons* (De Haan, 1849), was presented by Asakura (1995b). Although Asakura (2006) published photographs of selected body parts of *D. nitidimanus*, he did not provide a description. As a result, at the time of the capture, the first and second authors had difficulty in identifying the adult specimens to the specific level. Consequently, we give a full description of adults to facilitate positive recognition of the species in the East Asian fauna.

Larval stages of *D. nitidimanus* were described by Baba & Fukuda (1985) on the basis of material hatched from parental specimens collected from the west coast of Kyushu, Japan. Their description, however, does not fully meet modern standards, especially with regard to the megalopal stage. Furthermore, paguroid larvae are known to show considerable variation throughout their geographical ranges (Pike & Williamson 1960). Therefore, we provide descriptions of larvae obtained from females from the Russian coast of the Sea of Japan in order to fully document their morphology and to show the morphological variability of the species.

Material and Methods

Adults of *D. nitidimanus* used in this study were collected from Vostok Bay (Peter the Great Bay, Sea of Japan). Supplemental specimens from Japan were also examined to verify their identification. For detailed observation of the surface structure of the integument, specimens (including removed appendages) were stained with methylene blue. Terminology used in the description follows McLaughlin (2003), with the exception of the numbered thoracic sternites, dactylus for dactyl, dactyli for dactyls and “pleon” instead of “abdomen”, which follows Schram & Koenemann (2004).

Three ovigerous females were collected on 10 August 2006 at a depth of 2 m, at 22ºC and 32‰. After hatching occurred the same day, larvae were concentrated at the edge of aquarium using a point-light source and transferred to 250-ml plastic vessels with filtered and UV-sterilized seawater. They were then reared at a temperature of 22–25ºC. The density of the larvae was about 1 specimen per 10 milliliters. The larvae were fed newly hatched nauplii of *Artemia salina*. The water in the vessels was changed daily. The larvae of each stage were fixed in 4% formaldehyde for light microscopic studies. The chromatophore patterns were determined by observing the live larvae. Preserved larvae were dissected under a MBS-10 stereomicroscope using fine entomological needles. The outlines of the larvae and their appendages at the different developmental stages were drawn using a camera lucida attached to a binocular Ergaval microscope (Carl Zeiss, Jena); measurements were made with an ocular micrometer. Methods of measurement, descriptions of setal arrangements and basic terminology followed that of Clark *et al*. (1998) and Konishi & Shikatani (1998). The size of adults is indicated by shield length (SL), measured from the tip of the rostral lobe to the posterior midpoint of the shield. The carapace length (CL) of zoeas and megalopas was measured from the tip of the rostrum to the posterior midpoint of the carapace. The count of the telsonal posterior processes followed that of Pike & Williamson (1960). The setal arrangements are listed from endopod to exopod, from proximal to distal segments, and from anterior to posterior pleonal somites.

Material used in this study is deposited in the Museum of the Institute of Marine Biology, Russian Academy of Sciences, Vladivostok, Russia (MIMV), the Natural History Museum and Institute, Chiba, Japan (CBM), and the Musée Zoologique, Strasbourg (MZS), France.

For comparison, the following adult specimens were examined:

Diogenes avarus Heller, 1865 — Thailand: CBM-ZC 4793, 13 males (SL 2.0–3.9 mm), 1 female (SL 1.7 mm) and 1 ovigerous female (SL 2.7 mm), Ao Nam Bor, Phuket, intertidal mudflat, 15 November 1995, coll.

T. Komai; CBM-ZC 4795, 12 males (SL 1.6–2.9 mm) and 3 females (SL 1.5–1.6 mm), Ao Tang Khen, Phuket, intertidal, sea grass bed on sand flat, 10 November 1995, coll. T. Komai; CBM-ZC 4807, 8 males (SL 1.9–3.4 mm), Ban Pa Khlok, Phuket, tidal flat, 20 November 1995, coll. T. Komai.

Diogenes pugilator (Roux, 1838) — Greece: CBM-ZC 6539, 2 males (SL 5.8, 5.9 mm), Lesvos, subtidal sand bottom, July 1992, coll. S. De Grave.

Results

Family Diogenidae Ortmann, 1892

Genus *Diogenes* Dana, 1851

Diogenes nitidimanus Terao, 1913

Diogenes edwardsii. — Ortmann, 1892: 295. [Not *Diogenes edwardsii* (De Haan, 1849)].
Diogenes nitidimanus Terao, 1913: 363, fig. 1 [type locality: Province Sagami, Japan]; Gordan, 1956: 317 (bibliography); Kim, 1973: 208, fig. 40, pl. 68, fig. 22; Miyake & Imafuku, 1980: 3, pl. 1, fig. 5; Miyake, 1982: 194 (list), 213 (key); Asakura, 1987b: 34–37, fig. 1, pl. 6, figs 1–6; 1995b: 352, fig. 21; 2006: 28, figs 9, 10.
Diogenes spinifrons. — Komai *et al*., 1992: 196. Not *Diogenes spinifrons* (De Haan, 1849).

Description of Adult
(Figs 1–3)

Material examined. *Russia*. CBM-ZC 8618, 1 male (SL 5.8 mm) and 1 female (SL 3.7 mm), Volchanka River estuary, Vostok Bay, Peter the Great Bay, 3 m, silt bottom, 12 August 2005, coll. O. Korn; CBM-ZC 8618, 5 males (SL 3.6–5.2 mm) and 2 females (SL 2.4, 3.4 mm), same data.

Japan. CBM-ZC 607, 2 males (SL 2.9, 3.4 mm) and 1 female (SL 3.0 mm), Takeoka, Futtsu, Chiba Prefecture, 5–10 m, 29 August 1994, lobster net, coll. T. Komai; CBM-ZC 1961, 4 males (SL 2.6–2.8 mm), Banzu, Obitsu-gawa estuary, Kisarazu, Tokyo Bay, intertidal sand flat, 27 July 1995, hand, coll. T. Komai; CBM-ZC 8734, 1 male (SL 3.8 mm), Kan'non-ji, Kagawa Prefecture, Shikoku, intertidal sand flat, 8 May 2005. MZS 455 (spirit), 1 male (not measured), Tokyo Bay, 1880–1881, coll. L. Döderlein; MZS 475, 4 specimens (not measured), Tokyo Bay, 1880–1881, coll. L. Döderlein.

Description. Shield slightly broader than long; anterior margin between broadly rounded rostral lobe and lateral projections weakly concave and sometimes with few minute or tiny tubercles; anterolateral angles spinulose, lateral margins each usually cut by few transverse, spinulose or tuberculate ridges and extending onto lateral surface of shield; posterior margin truncate; dorsal surface with additional short transverse rows of spinules and tufts of short stiff setae. Lateral projections triangular, each with small marginal spine. Dorsal margin of branchiostegite with 5–8 small spines.

Ocular peduncles 0.6–0.8 SL, moderately stout, broadened distally, each with rows of tufts of short setae dorsomesially and mesially; corneal diameter 0.2–0.3 peduncular length. Ocular acicles subtriangular, anterior margin with 5–8 spines increasing in size, innermost spine distinctly larger than others and often slightly curved laterally. Intercalary rostral process stout proximally, usually drawn out into long slender terminal spine, but not overreaching apices of innermost acicular spine; no ventral spine.

Antennular peduncles moderately slender, when fully extended, overreaching corneas by 0.2–0.4 lengths of ultimate segments. Ultimate and penultimate segment each with few tufts of moderately long setae. Basal segment with few shorter setae.

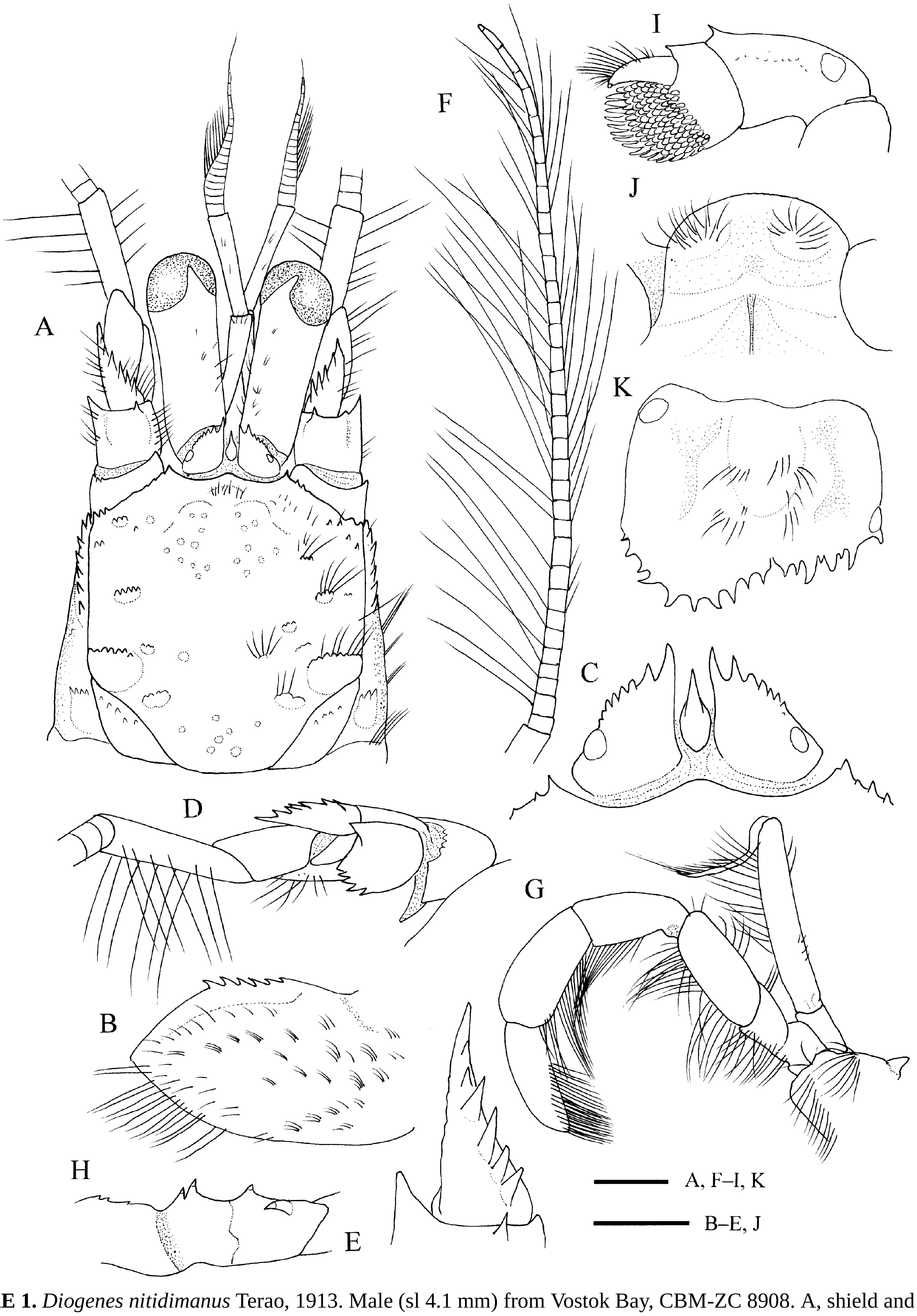

FIGURE 1. *Diogenes nitidimanus* Terao, 1913. Male (sl 4.1 mm) from Vostok Bay, CBM-ZC 8908. A, shield and cephalic appendages, dorsal view; B, anterior part of branchiostegite, lateral view; C, intercalary rostral process and ocular acicles, dorsal view; D, left antenna, lateral view; E, antennal acicle of left antenna, dorsal view (setae omitted); F, left antennal flagellum, dorsal view; G, left third maxilliped, lateral view; H, coxa to ischium of left third maxilliped, ventral view; I, dactylus, propodus and carpus of left fourth pereopod, lateral view; J, sixth thoracic sternite, ventral view; K, telson, dorsal view. Scale bars: A, B, D, F, G = 1 mm; C, E, H–K = 0.5 mm.

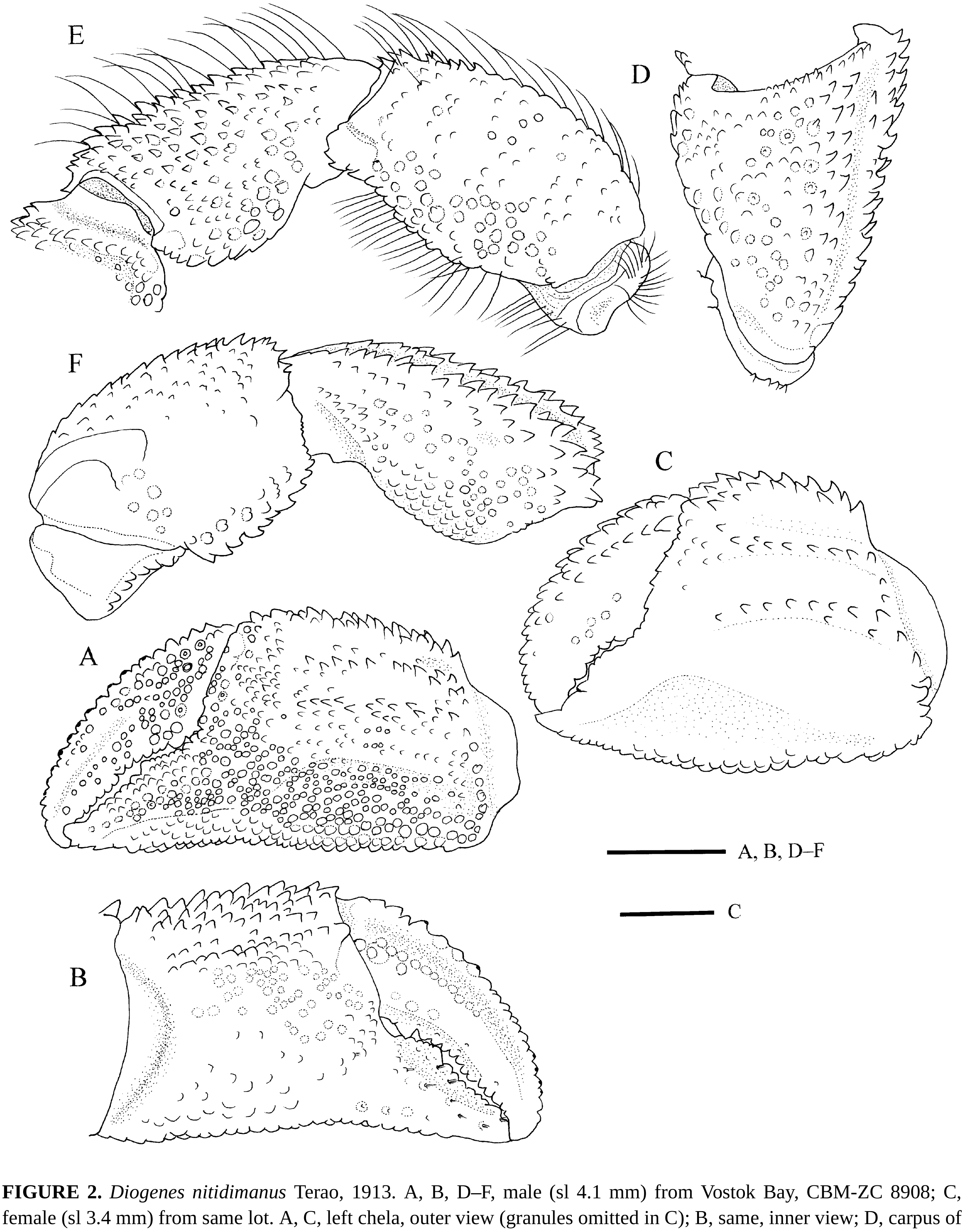

FIGURE 2. *Diogenes nitidimanus* Terao, 1913. A, B, D–F, male (sl 4.1 mm) from Vostok Bay, CBM-ZC 8908; C, female (sl 3.4 mm) from same lot. A, C, left chela, outer view (granules omitted in C); B, same, inner view; D, carpus of left cheliped, outer view (setae omitted); E, carpus to ischium of left cheliped, lateral view; F, same, mesial view. Scale bars: A, B, D–F = 2 mm; C = 1 mm.

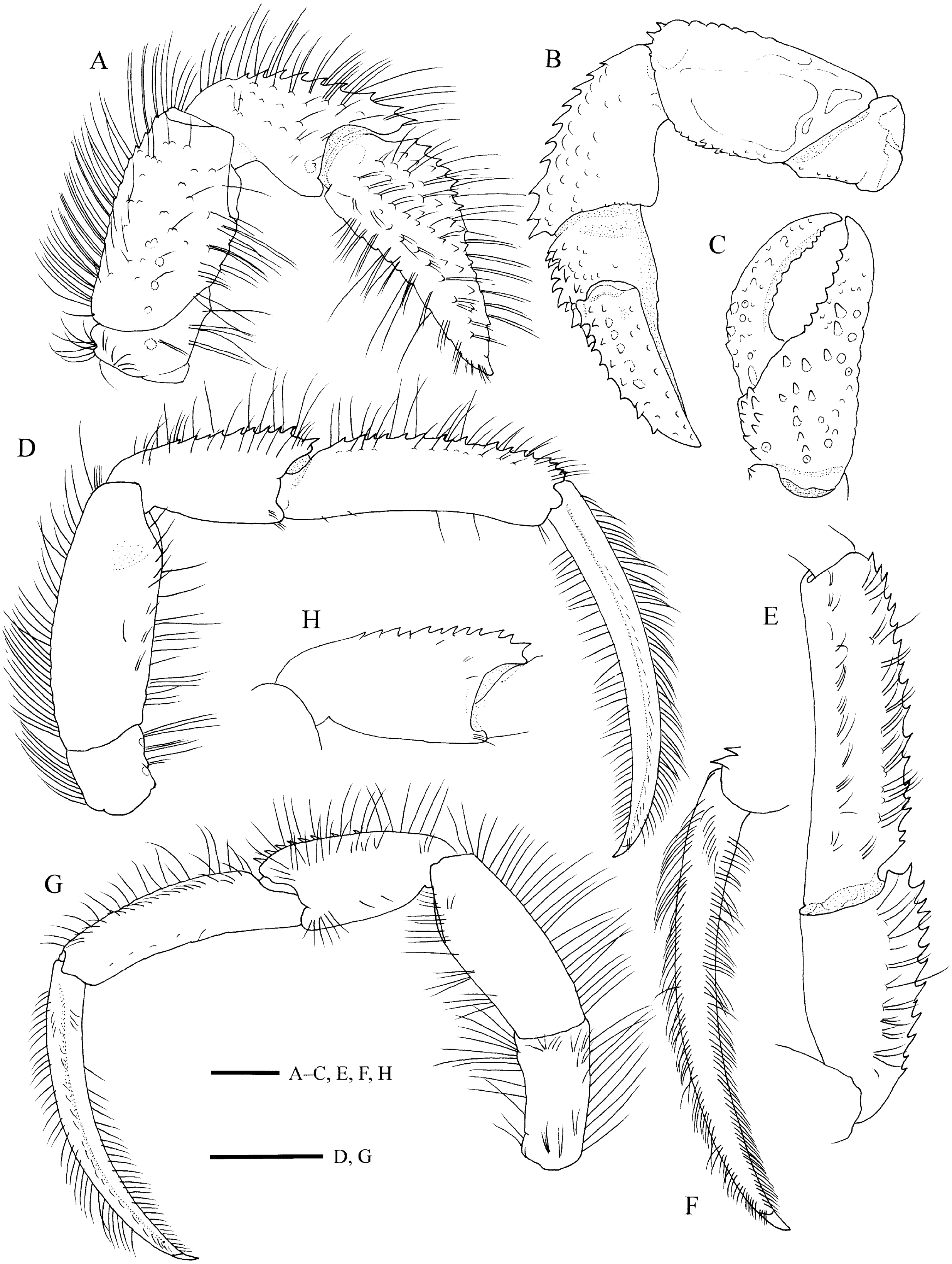

FIGURE 3. *Diogenes nitidimanus* Terao, 1913. Male (sl 4.1 mm) from Vostok Bay, CBM-ZC 8908. A, right cheliped, lateral view; B, same, mesial view (setae omitted); C, right chela, dorsal view (setae omitted); D, right second pereopod, lateral view; E, propodus and carpus of right second pereopod, mesial view (setae partially omitted); F, dactylus of right second pereopod, mesial view (setae partially omitted); G, left third pereopod, lateral view; H, carpus of left third pereopod, mesial view (setae omitted). Scale bars: D, G = 2 mm; A–C, E, F, H = 1 mm.

Antennal peduncles overreaching distal margins of corneas by 0.3–0.5 length of fifth segment; with supernumerary segmentation. Fifth segment with 2 rows of long setae ventrally. Fourth segment unarmed, but with several setae dorsally and laterally. Third segment with short setae on ventral surface. Second segment with dorsolateral distal angle produced into prominent spine, 3–6 small additional spines on laterodistal margin ventrally, dorsomesial distal angle with small spine, mesial margin with row of short setae. First segment with 1–4 tiny spinulose tubercles at dorsolateral distal margin. Antennal acicle moderately long and stout, with 4–6 spines and short stiff setae on mesial margin. Antennal flagellum exceeding twice length of shield, reaching base of dactylus of left cheliped, each article with pair of long, pinnate setae.

Maxillule with endopod lacking external lobe. Third maxilliped with moderately slender endopod; inner margin of coxal plate smooth; 2 or 3 small spines on basis; ischium with crista dentata poorly developed, with 2 or 3 corneous tipped spines (distal spine strongly curved proximally).

Left cheliped with dactylus slightly longer to approximately as long as upper margin of palm, arched; cutting edge with row of small calcareous teeth and sometimes 1 larger tooth proximally; terminating in large calcareous claw, sometimes overlapping fixed finger; outer surface generally flattened, armature varying from longitudinal row of moderately small, subacute to blunt, tuberculate spines to covering of small spinulose tubercles; upper margin with single or double row of subacute or blunt spines over full length of margin; inner surface weakly elevated in midline, usually with row of blunt spines at least in proximal half. Fixed finger with lower margin not distinctly delimited, with 2 or 3 rows of rounded tubercles extending onto palm; outer surface flat or slightly concave, with covering of small blunt or subacute tubercles; inner surface with few low tubercles and 2 rows of tufts of very short setae. Palm with outer surface convex and with covering of small tubercles (shape quite variable from flattened to spinulose), often larger near upper margin, 2 median rows of small spines usually evident; upper margin with irregular single or double row of small to moderately large, subacute or blunt spines; ventral margin not delimited, no prominent spines or tubercles at ventroproximal angle; inner surface with covering of tubercles, tubercles of upper side more prominent, those of lower side low, rounded. Carpus slightly longer than palm and approximately equal to length of merus; armature of upper margin varying from irregular double row of small, tuberculate spines to similarly double row of prominent acute or subacute spines; upper margin with moderately long setae; outer face angularly convex, upper 0.2–0.3 relatively flat and with few small spines or tubercles, lower remainder with covering of small spines or spinulose tubercles; lower margin not delimited, but with larger, low, blunt tubercles; inner surface with covering of small tubercles. Merus subtriangular; distal margin with row of small spines often extending laterally and mesially; dorsal surface with row of tubercles becoming shaper distally or with short, transverse, spinulose ridges and moderately long setae; lateral face tuberculate, tubercles larger near ventral margin, ventrolateral margin tuberculate; mesial face weakly tuberculate in upper 0.3–0.4, with row of low, often spinulose tubercles near ventral margin, ventromesial margin with row of small spines or spinulose tubercles; ventral surface tuberculate. Ischium short, with row of small tubercles on ventromesial margin.

Right cheliped appreciably shorter than left, usually not reaching proximal margin of palm of left. Dactylus and fixed finger with prominent hiatus, both terminating in small calcareous claws. Dactylus more than 3.0 times as long as palm, noticeably arched; dorsal surface with row of small spines or tubercles on midline and tufts of long setae; mesial surface with row of tiny tubercles or spines dorsally; ventral surface with 2 rows of tufts of long setae; cutting edge with row of tiny tubercles at least proximally. Palm with irregular rows of spinulose tubercles or small spines on convex dorsal surface (lateral rows extending onto fixed finger) and obscured by tufts of long setae; dorsolateral and dorsomesial margins not delimited; mesial face tuberculate in dorsal half, nearly smooth in ventral half; ventral surface weakly tuberculate, with numerous tufts of long setae. Cutting edge of fixed finger with row of small, subacute calcareous teeth at least proximally. Carpus with row of small to moderately large spines on dorsal margin, dorsolateral and dorsomesial faces with low tubercles and numerous tufts of long setae; ventral surface nearly smooth. Merus with tufts of long setae arising from low protuberances or tubercles on dorsal margin; dorsodistal margin with few small spines; lateral surface weakly tuberculate, ventrolateral margin weakly delimited and unarmed; mesial face nearly smooth, ventromesial margin with row of tiny tubercles; ventral surface with few tiny tubercles and several tufts of long setae. Ischium with tuberculate ventromesial margin.

Second and third pereopods moderately slender. Dactyli 1.1–1.3 times longer than propodi, weakly curved, but not twisted; terminating in moderately small corneous claws; dorsal surfaces unarmed, but with numerous long, simple setae, ventral surfaces each with row of less numerous, shorter setae; lateral surfaces each with shallow longitudinal sulcus medially and row of short setae dorsally; mesial surfaces each with 2 rows of simple stiff setae flanking midline. Propodi each with dorsal margin bearing row of small spines (second) or smooth (third), and with row of short to long stiff setae; lateral surfaces each with longitudinal row of setae arising from tiny low protuberances near dorsal margin; mesial surfaces each with 2 rows of tufts of stiff setae; ventral margins faintly tuberculate (second) or smooth (third), and with few short setae. Carpi each with dorsal row of small spines increasing in size distally and with row of sparse setae dorsally; lateral and mesial surfaces each with row of moderately long setae dorsally; ventral surfaces naked. Meri with tufts of long plumose setae on dorsal surfaces; ventral surfaces unarmed, but with less numerous tufts of setae. Ischia with long setae dorsally and ventrally.

Fourth pereopods semichelate; dactylus short, only reaching distal margin of propodus (including rasp); propodus suboval, with small spine dorsodistally; propodal rasp consisting of numerous rows of small corneous scales increasing in length distally. Carpus with small dorsodistal spine.

Fifth pereopods chelate.

Anterior lobe of sixth thoracic sternite divided by faint median groove, each half with tuft or cluster of short setae.

Male unpaired left pleopods uniramous, marginally setose. Female with paired gonopores; unpaired left second to fourth pleopods well developed, biramous; fifth pleopod as in male.

Telson with very small median cleft, left lobe distinctly larger than right; left terminal margin with row of small spines, 1–4 much larger spines at or near outer angle and several smaller spines extending onto lateral margin; right terminal margin with row of relatively large spines often interspersed by spinules, usually not extending onto lateral margin.

Coloration in life. Body and appendages generally sand gray or grayish brown, darker markings on chelipeds and ambulatory legs. Shield mottled, with pair of spots. Ocular peduncles light gray or brown. Carpi of chelipeds each with brown transverse line across at midlength; meri with large brown patch on upper or dorsal surface. Propodi of ambulatory legs each with indistinctly defined brown band proximal to midlength, often with longitudinal branch extending distally; carpi and meri each with narrow brown band at about midlength. Pleon transparent.

Variation. Asakura (1987b) showed that this species exhibited a considerable degree of polymorphism in the shape and armature of the male left cheliped. The present material shows similar variations to those reported by Asakura (1987b). Furthermore, as Asakura (1987b) noted, the female left cheliped is less elongate than that of male; the armature of the chela is rather constant in females.

Distribution. Japan southward from Hakodate Bay, southern Hokkaido to Kyushu; Korea; Peter the Great Bay, Russian Far East (Asakura 2006; this study); intertidal to subtidal.

Description of Larval Stages

(Figs 4–10)

Diogenes nitidimanus hatched at a prezoeal stage, which lasted a few minutes before molting to the first zoeal stage. It then passed through four zoeal stages. The minimal time required to reach the megalopal stage was 22 days at a temperature of 22–25ºC.

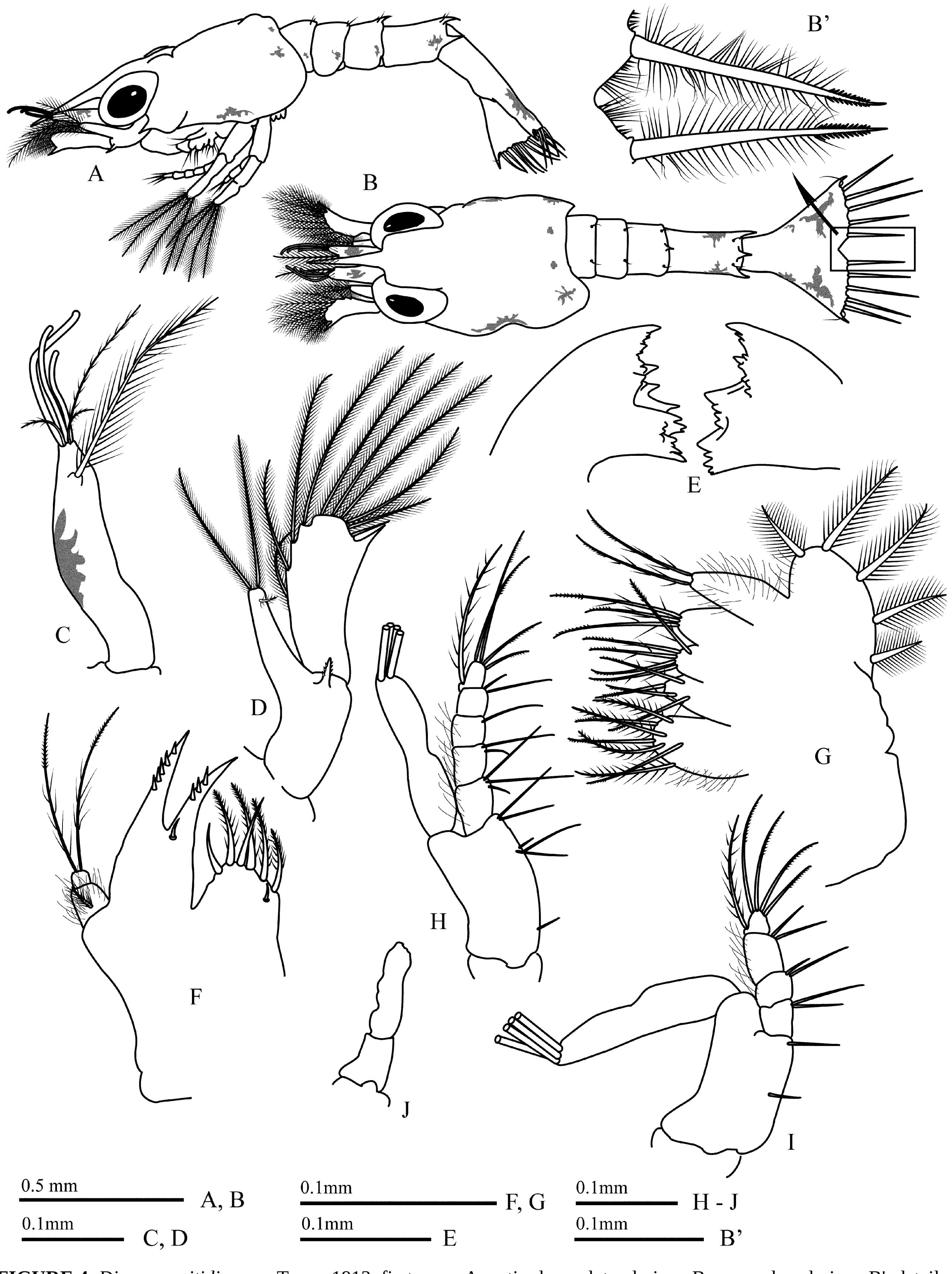

FIGURE 4. *Diogenes nitidimanus* Terao, 1913, first zoea. A, entire larva, lateral view; B, same, dorsal view; B', details of telson; C, antennule; D, antenna; E, mandibles; F, maxillule; G, maxilla; H, first maxilliped; I, second maxilliped; J, third maxilliped.

First zoea (Fig. 4).

Material examined. CL = 0.80 ± 0.02 mm (0.76–0.82 mm), N = 13.

Duration. Five to seven days.

Description. Carapace (Fig. 4A–B) without setae on surface, with low keel anteriorly in dorsal midline; rostrum short, not exceeding half length of carapace, tapering and slightly overreaching distal spine of antennal scaphocerite; small anterolateral marginal spines present; posterolateral spines absent; eyes sessile.

Antennule (Fig. 4C) uniramous, endopod absent. Exopod unsegmented, with 3 terminal aesthetascs of different lengths, 3 terminal plumose setae (1 long and 2 short), and 1 long subterminal plumose seta.

Antenna (Fig. 4D) biramous; endopod fused with protopod, with 2 long terminal and 1 short subterminal plumose setae; protopod with strong serrate spine at the base of endopodal junction; scaphocerite about 2.5 times longer than wide, curved, with 1 short distal spine, outer margin unarmed, inner margin with 10 long plumose setae.

Mandibles (Fig. 4E) asymmetrically dentate; incisor process with single strong tooth and few small teeth; molar process with serrate ridges and small acute denticles; no palp bud.

Maxillule (Fig. 4F) with endopod 2-segmented; proximal segment covered with fine microtrichiae and with 1 short pappose seta; distal segment with 2 terminal long plumodenticulate setae. Coxal endite with 6 marginal setae (4 plumodenticulate and 2 simple) and 1 submarginal short simple seta. Basial endite with 2 marginal elongate spinous teeth and with 1 submarginal short simple setae.

Maxilla (Fig. 1G) with endopod unilobed, covered with fine microtrichiaes and with 2 terminal plumodenticulate setae. Coxal and basial endites each bilobed; coxal endite with 2 marginal and 4 + 1 submarginal setae on proximal lobe and with 1 marginal and 3 submarginal setae on distal lobe. Basial endite with 4 marginal and 1 submarginal setae on proximal lobe and 3 marginal setae on distal lobe. All setae plumodenticulate except for 4 submarginal plumose setae on proximal lobe of coxal endite. Proximal part of scaphognathite fused with protopod, distal part with 5 marginal plumose setae.

First maxilliped (Fig. 4H) with endopod 5-segmented, setal formula progressing distally 3, 2, 1, 2, 4 + I plus numerous microtrichiae on first to third segments. Coxa unarmed; basis with setal formula 1, 3, 2. Exopod incompletely 2-segmented, with 4 terminal plumose natatory setae.

Second maxilliped (Fig. 4I) with endopod 4-segmented, setal formula progressing distally 2, 2, 2, 4 + I plus numerous microtrichiae on second and third segments. Coxa unarmed; basis with setal formula 1, 1. Exopod as in first maxilliped.

Third maxilliped (Fig. 4J) uniramous, unarmed.

Pereopods visible as small buds.

Pleon (Fig. 4A, B) consisting of 5 somites and telson. Second through fifth somites each with pair of posterodorsal simple setae; fourth somite with 1 mediodorsal spine; fifth somite with 1 mediodorsal and 1 pair of lateral processes.

Telson (Fig. 4A, B) fan-shaped, slightly wider than long; posterior margin with triangular median cleft covered with long hairs and with 7 + 7 processes: outermost process showing a short smooth seta, second process an anomuran hair, third to seventh processes plumodenticulate articulated setae; posterior margin between processes with row of short spinules; anal spine absent.

Coloration in life. Body generally transparent. Tip of rostrum red. Carapace with a pair of brown chromatophores on the lateral margins and 2 black chromatophores adjacent to the posterodorsal margin; 2 additional yellow-brown chromatophores appearing near posterodorsal margin a few days after hatching. Antennule dorsally with reddish orange branching chromatophores in the middle part and black rounded chromatophores in the basal part; ventrally with red chromatophores at the bases of antennules and antennae. Labrum with red chromatophores. Pleon with lateral brown chromatophores on second to fifth somites; telson with 2 dorsal brown chromatophores. Coxae of first maxillipeds with red chromatophores.

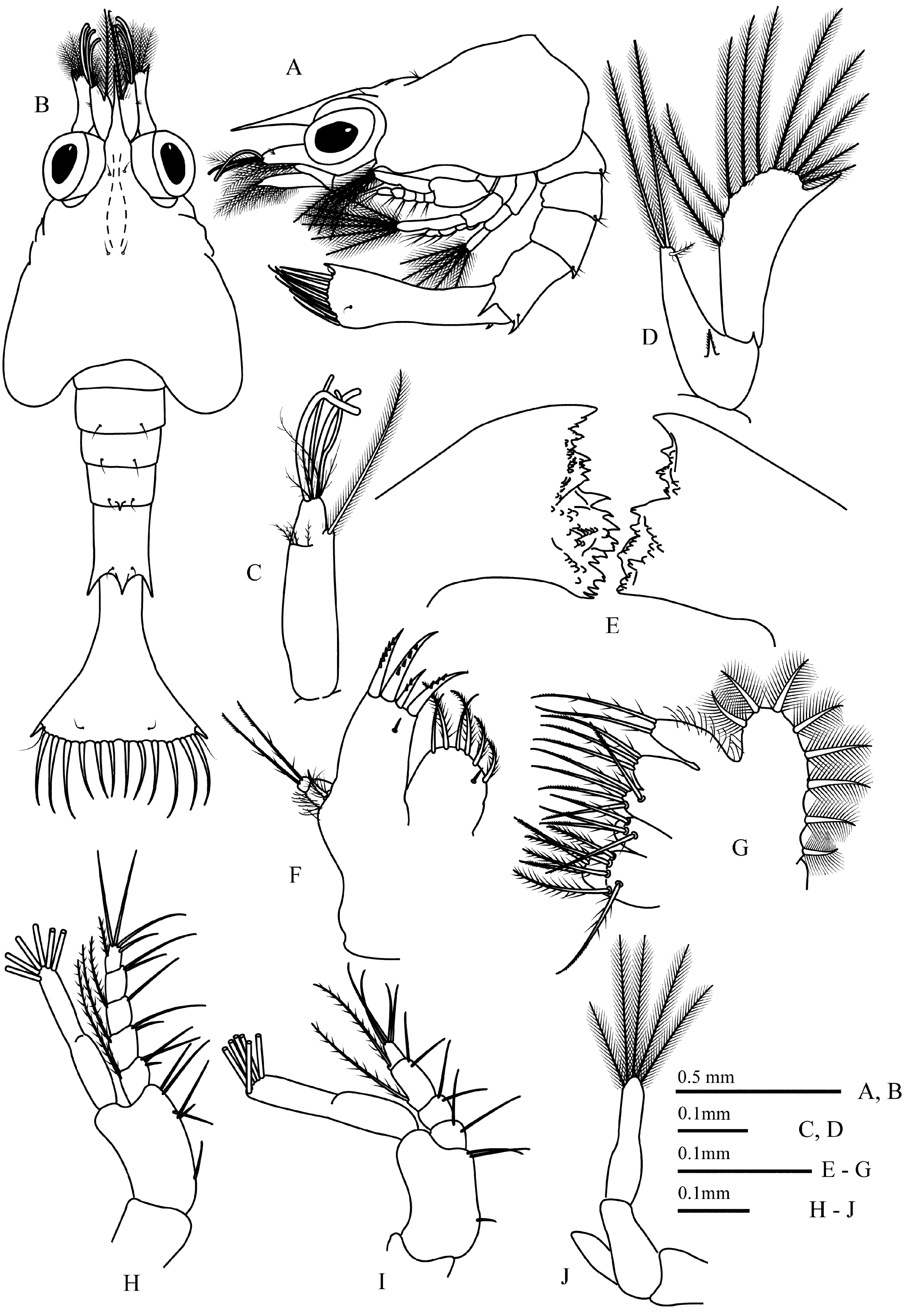

FIGURE 5. *Diogenes nitidimanus* Terao, 1913, second zoea. A, lateral view; B, dorsal view; C, antennule; D, antenna; E, mandibles; F, maxillule; G, maxilla; H, first maxilliped; I, second maxilliped; J, third maxilliped.

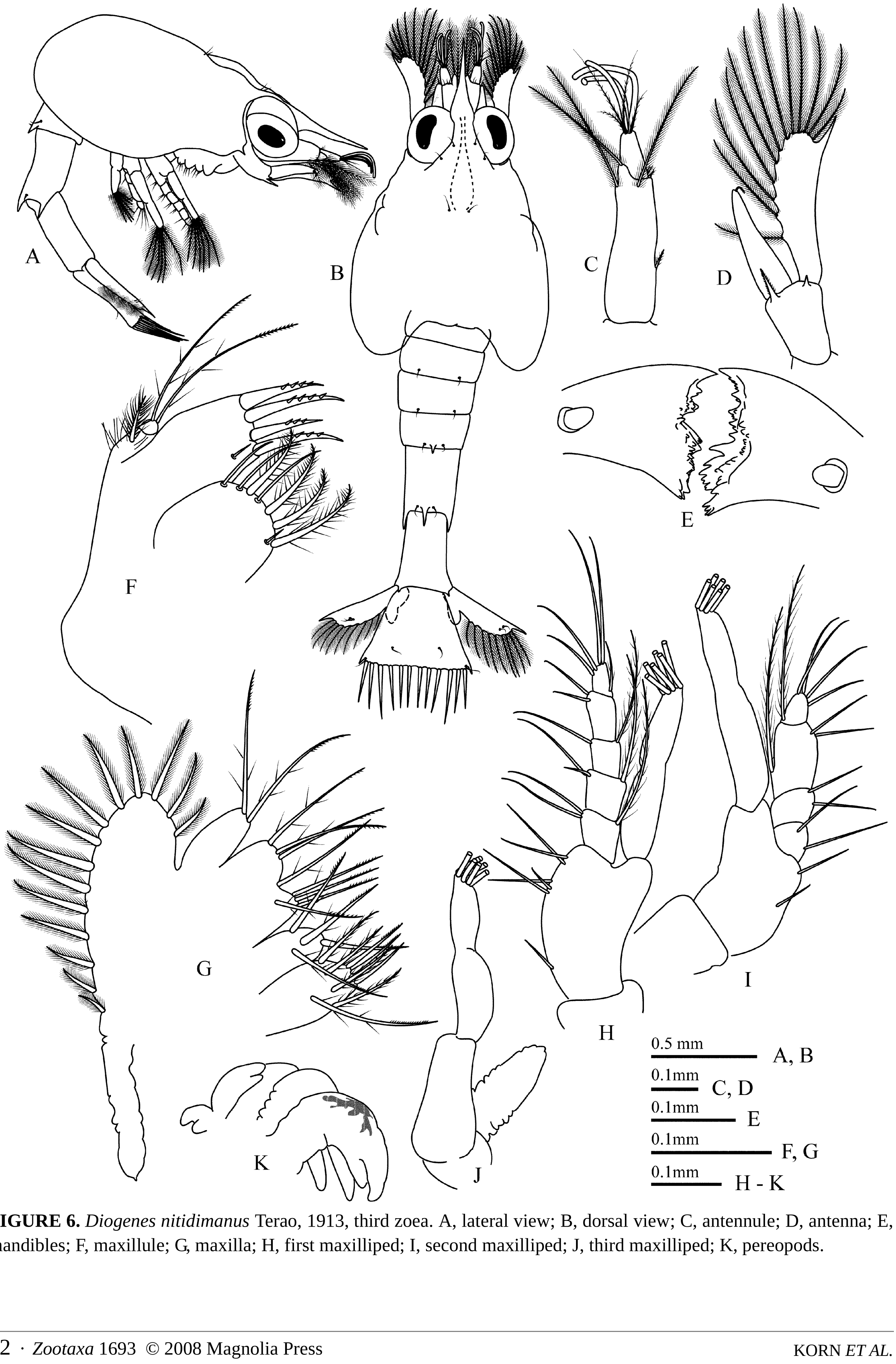

FIGURE 6. *Diogenes nitidimanus* Terao, 1913, third zoea. A, lateral view; B, dorsal view; C, antennule; D, antenna; E, mandibles; F, maxillule; G, maxilla; H, first maxilliped; I, second maxilliped; J, third maxilliped; K, pereopods.

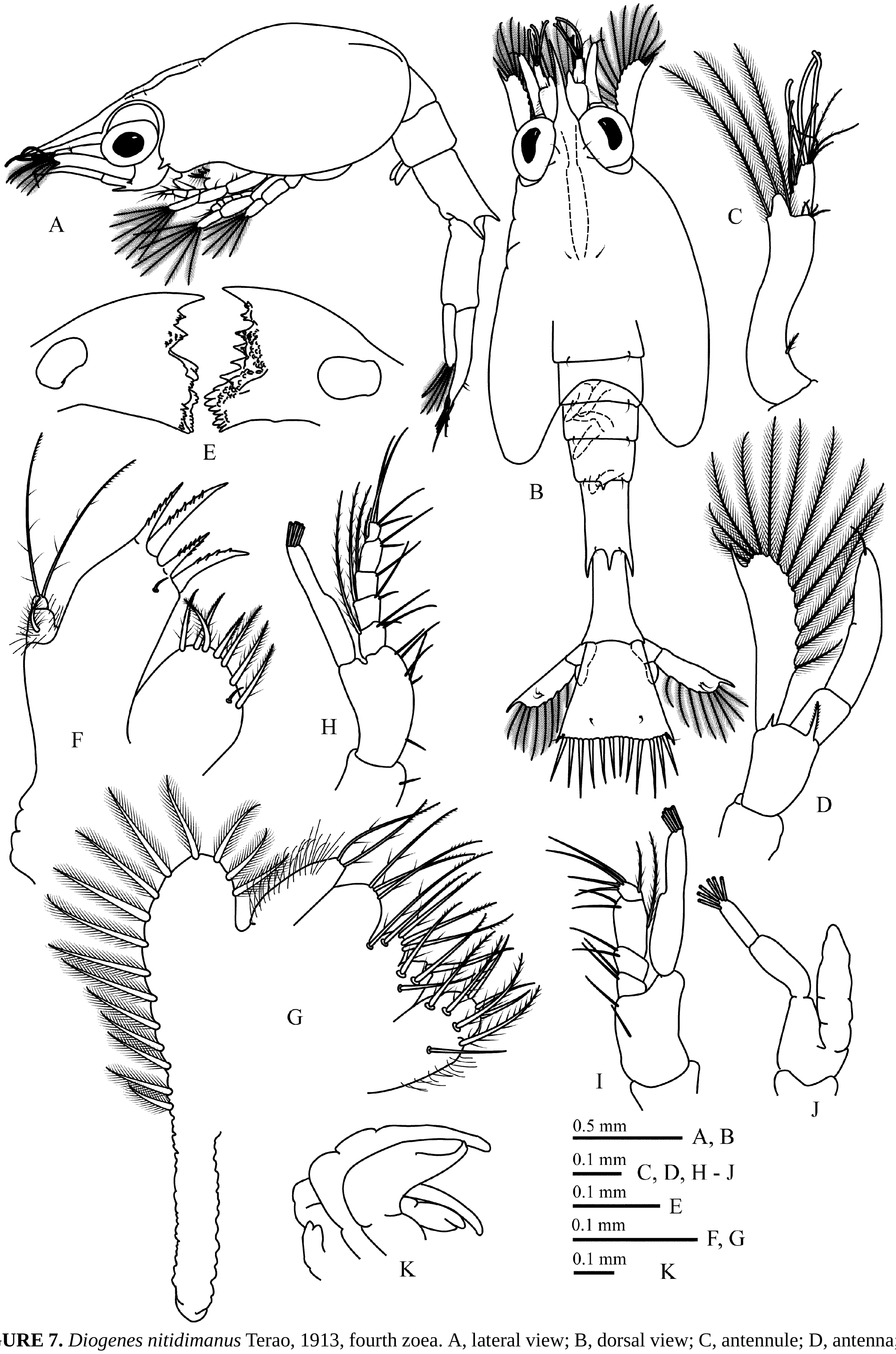

FIGURE 7. *Diogenes nitidimanus* Terao, 1913, fourth zoea. A, lateral view; B, dorsal view; C, antennule; D, antenna; E, mandibles; F, maxillule; G, maxilla; H, first maxilliped; I, second maxilliped; J, third maxilliped; K, pereopods.

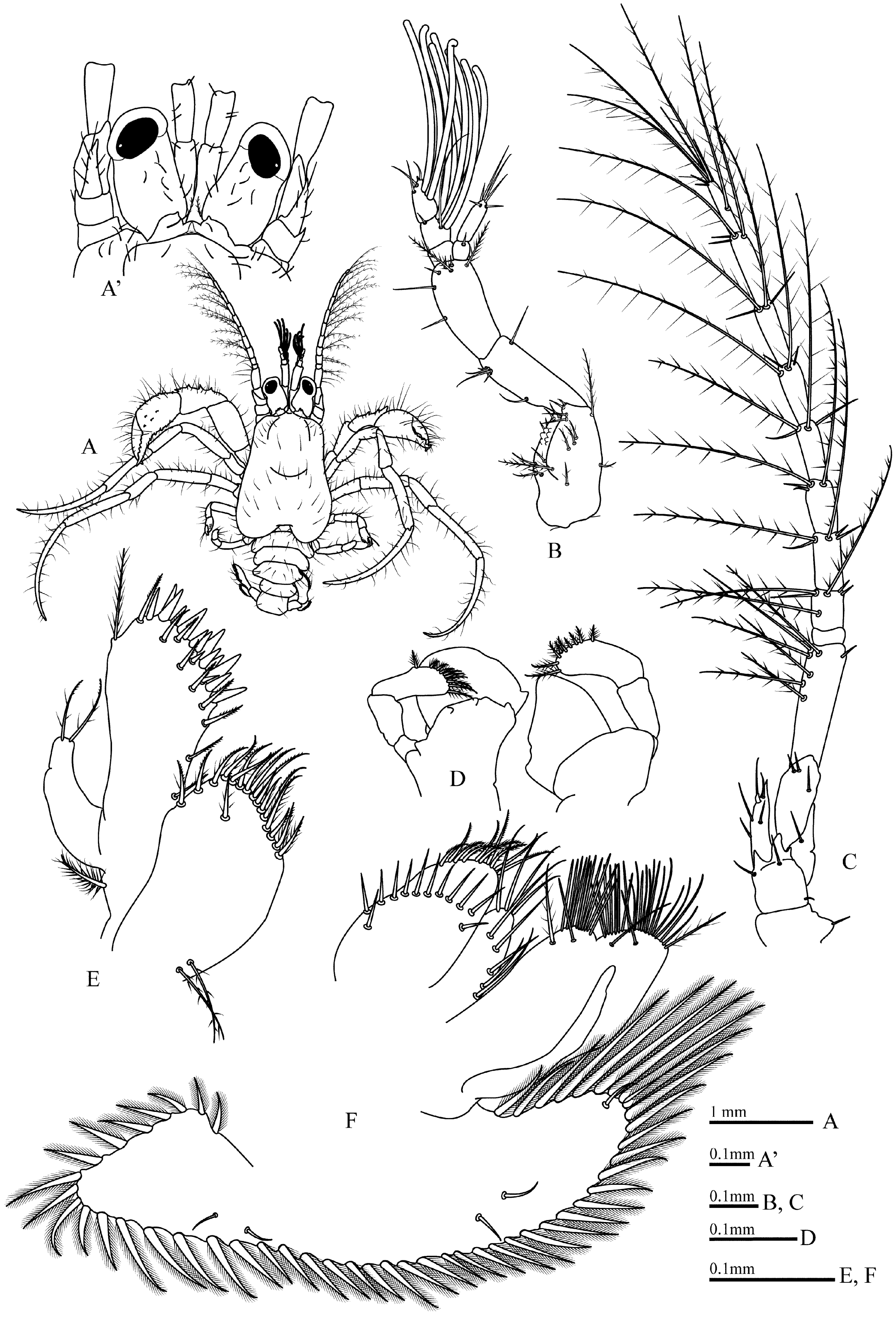

FIGURE 8. *Diogenes nitidimanus* Terao, 1913, megalopa. A, dorsal view; A', details of frontal part of the body; B, antennule; C, antenna; D, mandibles; E, maxillule; F, maxilla.

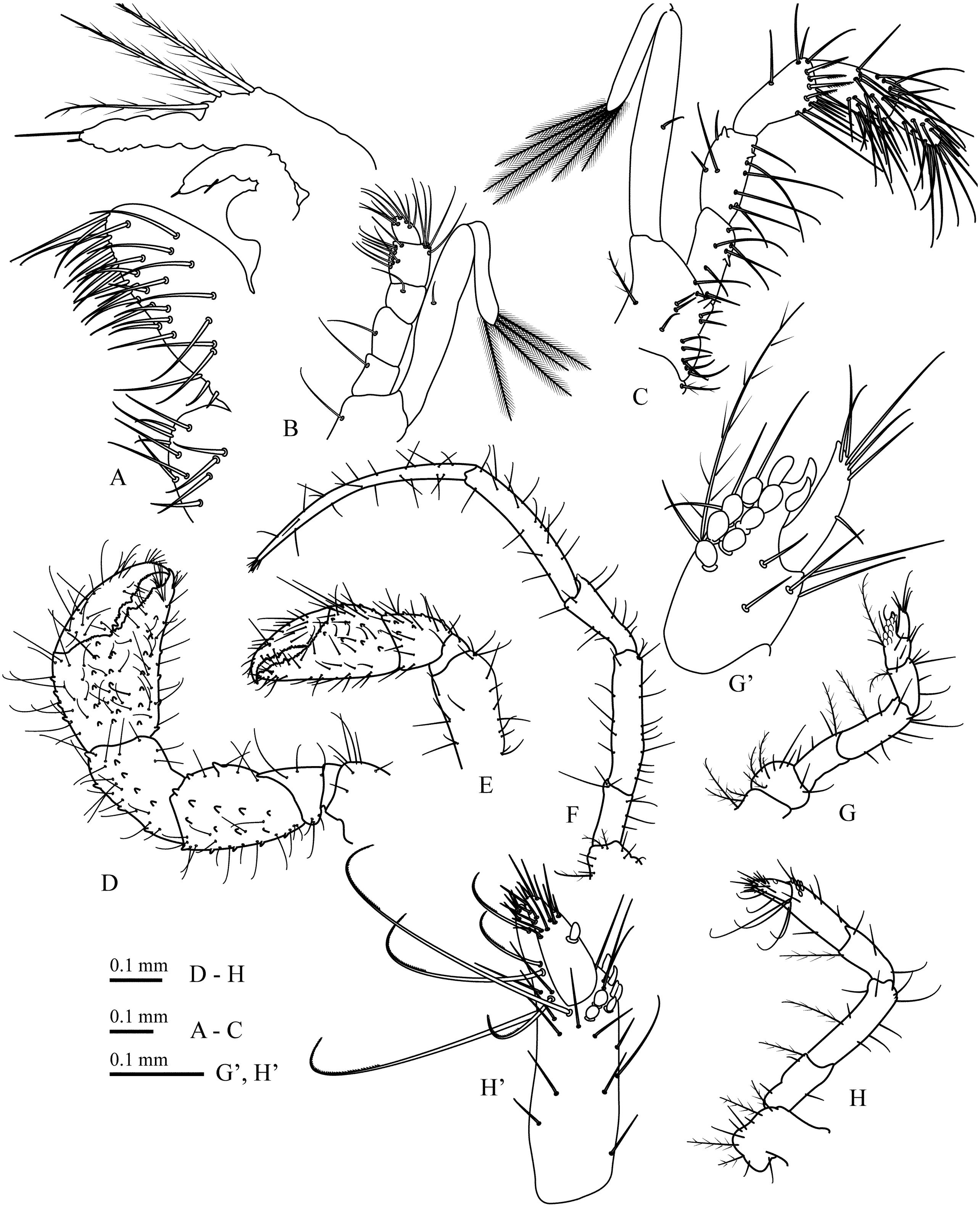

FIGURE 9. *Diogenes nitidimanus* Terao, 1913, megalopa. A, first maxilliped; B, second maxilliped; C, third maxilliped; D, left cheliped; E, right cheliped; F, pereopod II; G, pereopod III; G', details of pereopod III; H, pereopod IV; H', details of pereopod IV.

Duration. Three to six days.

Description. Carapace (Fig. 5A, B) with 1 pair of small simple setae behind eyes and 1 pair of setae near distal part of median keel; eyes stalked.

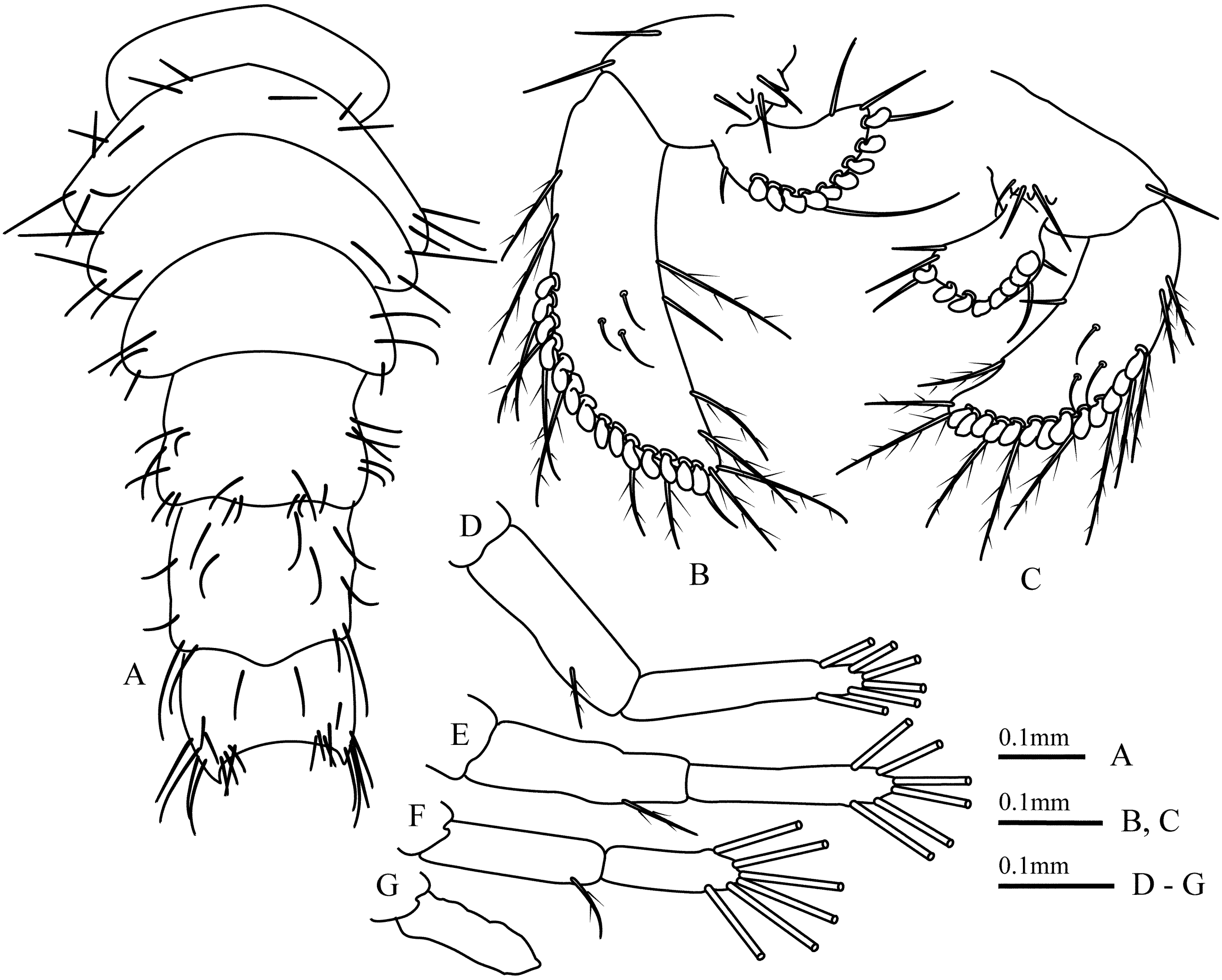

FIGURE 10. *Diogenes nitidimanus* Terao, 1913, megalopa. A, dorsal view of abdomen; B, left uropod; C, right uropod; D–G, pleopods I–IV**.**

Second zoea (Fig. 5)

Material examined. CL = 0.93 ± 0.04 mm (0.89–1.00 mm), N = 12.

Antennule (Fig. 5C) biramous; endopod as bud with 1 long terminal plumose seta; protopod with 4 short plumose setae; exopod with 4 (rarely 5) terminal aesthetascs and 4 terminal plumose setae.

Antenna (Fig. 5D) biramous; endopod and scaphocerite unchanged; protopod with 2 spines near junction with endopod; scaphocerite about 3.0 times longer than wide.

Mandibles (Fig. 5E) with more numerous teeth than in first stage, but otherwise unchanged.

Maxillule (Fig. 5F) with endopod and coxal endite unchanged; basial endite with 4 marginal elongated teeth each bearing small denticles and with 1 submarginal short simple seta.

Maxilla (Fig. 5G) with endopod, coxal and basial endites unchanged; distal lobe of scaphognathite with 8 marginal plumose setae.

First maxilliped (Fig. 5H) with endopodal setal formula progressing distally 3 + I, 2 + I, 1 + I, 2, 4 + I; coxa and basis unchanged; exopod with 6 terminal plumose natatory setae.

Second maxilliped (Fig. 5I) with endopodal setal formula progressing distally 2, 2, 2 + I, 4 + I; coxa and basis unchanged; exopod with 6 terminal plumose natatory setae.

Third maxilliped (Fig. 5J) biramous; endopod, coxa and basis unarmed; exopod with 5 terminal plumose natatory setae.

Pereopods still appearing as buds, but larger than in first stage.

Pleon (Fig. 5A, B) unchanged.

Telson (Fig. 5A, B) with proximal part increased in length; median cleft absent; posterior margin with 8 + 8 processes, of them fourth longest; distal part of telson with 1 pair of simple setae on dorsal surface.

Third zoea (Fig. 6)

Material examined. CL = 1.30 ± 0.09 mm (1.12–1.42 mm), N = 14.

Duration. Three to seven days.

Description. Carapace (Fig. 6A, B) with 2 pairs of small simple setae behind eyes and 1 pair near distal part of keel.

Antennule (Fig. 6C) biramous; endopod with 1 terminal plumose seta; protopod with 2 long plumose setae at base of endopod, 4 short plumose setae at base of exopod, and 1 short lateral plumose seta; exopod with 3 long terminal aesthetascs and 4 terminal plumose setae.

Antenna (Fig. 6D) biramous; endopod with 1 terminal short plumose seta; scaphocerite with 12 long plumose setae, about 4.0 times longer than wide; endopod length 2/3 of scaphocerite length.

Mandibles (Fig. 6E) increased in size; palps present as buds.

Maxillule (Fig. 6F) with endopod and basial endite unchanged; coxal endite with 7 marginal plumodenticulate and 1 submarginal simple setae.

Maxilla (Fig. 6G) with endopod, coxal and basial endites usually unchanged (sometimes number of setae on proximal lobe of coxal endite increased up to 8); proximal lobe of scaphognathite unarmed, now well separated from protopod, distal lobe with 13–14 marginal plumose setae.

First maxilliped (Fig. 6H) unchanged from previous stage.

Second maxilliped (Fig. 6I) unchanged from previous stage.

Third maxilliped (Fig. 6J) with exopod incompletely 2-segmented, with 6 terminal plumose natatory setae; otherwise unchanged.

Pereopods (Fig. 6K) increased in size; first, fourth and fifth pereopods chelate; first pereopod with large orange chromatophore.

Pleon (Fig. 6A, B) with the sixth pleonal somite now delineated, posterodorsal margin with 1 pair of small processes.

Uropod (Fig. 6B) with endopod (as a small bud) and exopod fused with protopod; exopod with 9 plumose setae along inner margin and smooth terminal spine; ventral uropod surface with 2 small sparsely plumose setae.

Telson (Fig. 6B) with posterior margin nearly straight, armature unchanged.

Fourth zoea (Fig. 7)

Material examined. CL = 1.52 ± 0.09 mm (1.44–1.66 mm), N = 5.

Duration. Eleven to fifteen days.

Description. Carapace (Fig. 7A, B) with no noticeable changes.

Antennule (Fig. 7C) with endopod and protopod unchanged; exopod with 7 aesthetascs in three tiers (3 terminal, 2 and 2 subterminal) and 4 terminal plumose setae.

Antenna (Fig. 7D) with endopod 2-segmented, nearly equal to scaphocerite; distal segment with 1 subterminal short plumose seta; otherwise as in the third zoea (sometimes the number of marginal setae on scaphocerite increased up to 13).

Mandibles (Fig. 7E) with palp buds increased in size.

Maxillule (Fig. 7F) unchanged.

Maxilla (Fig. 7G) with endopod, coxal and basial endites unchanged; distal lobe of scaphognathite with

13–24 marginal plumose setae.

First maxilliped (Fig. 7H) unchanged from previous stage.

Second maxilliped (Fig. 7I) unchanged from previous stage.

Third maxilliped (Fig. 7J) with endopod increased in length; exopod unchanged.

Pereopods (Fig. 7K) increased in size, incompletely segmented.

Pleon (Fig. 7A, B) with uniramous pleopods on second to fourth somites.

Uropod (Fig. 7B) with endopod and exopod articulated with protopod; endopod usually unarmed (rarely with 1 or 2 terminal simple setae); otherwise unchanged.

Telson (Fig. 7B) unchanged.

Megalopa (Figs 8–10)

Material examined. CL = 1.14 ± 0.04 mm (1.06–1.20 mm), N = 9.

Duration. Undetermined.

Description. Carapace (Fig. 8A) generally pear-shaped in dorsal view; rostrum small; numerous fine plumose setae on surface; more than 20 plumose setae along each posteroventral margin. Ocular acicles present. Ocular peduncles moderately short, corneas slightly dilated.

Antennule (Fig. 8B) biramous; peduncle 3-segmented, slightly overreaching ocular peduncles; setal arrangement as shown. Endopod (inner flagellum) 2-segmented; proximal segment with 1 or 2 short simple setae; distal segment with 6 simple setae of different lengths. Exopod (outer flagellum) 3-segmented; proximal segment unarmed; second segment with 5 aesthetascs + 1 long and 1 or 2 short simple setae; distal segment with 3 subterminal aesthetascs and 3–5 short simple setae.

Antenna (Fig. 8C) longer than first pereopods (chelipeds). Peduncle 5-segmented; first to fourth segments each with 1–3 simple setae, fifth segment with 6 long plumose and 1 short simple setae. Flagellum 9-segmented; first segment unarmed; second to eighth segments each with 2 or 3 long plumose and some short simple setae; distal segment with 3–6 long plumose setae and some short simple setae. Antennal acicle terminating acutely, with 1 subterminal spine and 4 or 5 subterminal simple setae.

Mandibles (Fig. 8D). Armature now simplified; palp 3-segmented, terminal segment with 9 or 10 short plumose setae.

Maxillule (Fig. 8E) with endopod unsegmented, with 1 or 2 terminal simple seta. Coxal endite with 17 plumodenticulate setae; basial endite with 1 marginal plumose seta and 16–17 teeth, 6 submarginal and 2 lateral plumodenticulate setae. One plumose seta at base of endopod, 2 plumose setae at base of coxal endite.

Maxilla (Fig. 8F). Endopod reduced, unarmed; coxal and basial endites bilobed; proximal lobe of coxal endite with 9–12 marginal and 12–15 submarginal setae, distal lobe with 4 marginal and 5 submarginal setae; proximal and distal lobes of basial endite with 12–14 and 22–26 setae, respectively; scaphognathite with 44–49 marginal plumose setae and 5 simple setae on surface.

First maxilliped (Fig. 9A) with endopod and exopod reduced; endopod with 0–2 simple setae in distal part. Coxa with 10 or 11 plumose and plumodenticulate setae; basis with 32–36 simple and plumodenticulate setae. Exopod with 3 subterminal plumose and 1 or 2 terminal simple setae.

Second maxilliped (Fig. 9B) with endopod 5-segmented, with setal formula 1, 1, 1, 13–14 and 9–11; basis with 1 seta. Exopod incompletely 2-segmented, proximal part with 1 short simple seta, distal part with 3 or 4 terminal plumose setae.

Third maxilliped (Fig. 9C) with endopod 5-segmented; first segment with 6–8 plumodenticulate setae and 1 blunt tooth; second segment with 9 setae and 2 spines; following three segments with 15 or 16, over 20 and about 25 simple and plumodenticulate setae, respectively. Basis with 13–15 plumose and simple setae and 1 spine. Exopod incompletely 2-segmented; proximal part with 1 simple seta, distal part with 5–6 terminal plumose setae.

Pereopods (Fig. 9D–H) covered with scattered simple setae of different lengths. Chelipeds unequal, left larger than right. Cutting edges of dactyli and fixed fingers of both chelipeds with small teeth, terminating in corneous claws. Left cheliped palm bearing several longitudinal rows of spines on outer surface, upper and lower margins; carpus and merus with blunt spines on outer surfaces and upper margins, merus with 1 spine on inner surface. Right cheliped with palm and carpus bearing some blunt spines. Ambulatory legs generally similar. Dactyli of second and third pereopods longer than propodi, weakly curved, terminating in moderately small corneous claws. Carpi each with a small blunt spine at dorsomesial distal angle. Propodus of the fourth pereopod with rasp of 9 corneous scales and 9 or 10 simple and plumose setae; tip of dactylus as a small claw, distal part of dactylus with 5 or 6 simple setae. Propodus of the fifth pereopod with rasp of 6 or 7 corneous scales on dorsal surface, 6 subterminal long curved serrate setae on ventral surface and numerous terminal stiff simple setae; dactylus with 1 corneous scale and about 10 simple setae. Fourth and fifth pereopods with long plumose setae on ventral margins of all segments except ultimate and penultimate. Dactyli of fourth and fifth pereopods articulated with propodi subterminally.

Pleon (Fig. 10A) consisting of six somites; dorsal surface of all somites covered with numerous simple setae; second through fifth somites each with pleopods; sixth somite with uropods.

Pleopods (Fig. 10D–G) uniramous; first to third pleopods 2-segmented, each proximal segment with 1 sparsely plumose seta, each distal segment with 6 terminal plumose natatory setae; fourth pleopods as small buds.

Uropod (Fig. 10B, C) asymmetrical with left slightly larger than right, biramous, endopod and exopod clearly separated from protopod. Endopods each with 8 or 9 corneous scales and 3–5 simple or sparsely plumose setae. Protopods each with 3 or 4 spines and some simple setae at base of endopod. Left exopod with 14 corneous scales and 13–15 marginal sparsely plumose setae, right exopod with 13 corneous scales and 12–13 marginal rarely plumose setae, both with 3 simple setae on ventral surface.

Telson (Fig. 10A) asymmetrical, left lobe larger than right lobe; with numerous small simple setae on dorsal surface; terminal margin separated by deep median cleft without setae; posterolateral processes with numerous long simple setae.

Coloration in life. Reticulate pattern of red-orange chromatophores on ocular peduncles, antennular and antennal peduncles, on frontal and lateral carapace surfaces, on chelas and on margins of segments in second and third pereopods. One or several black chromatophores on central part of carapace.

Discussion

Taxonomy

Diogenes nitidimanus was originally described on the basis of a single male specimen (Terao 1913). The type locality was indicated in the original description as “Prov. Sagami”, corresponding to the Sagami Bay area of central Japan. It was suspected that the holotype was deposited in the Faculty of Science or University Museum of the University of Tokyo (formerly Tokyo Imperial University), where A. Terao was working at the time he published his paper (Terao 1913). However, despite the efforts by the third author, the holotype has not been located. The holotype is presumably no longer extant. The present identification was verified by comparison with material from Tokyo Bay, very close to Sagami Bay.

Morphological similarities suggest that *Diogenes nitidimanus* is closely allied to the following four congeneric species: *D. granulatus* Miers, 1880, *D. ovatus* Miers, 1881, *D. pugilator* (Roux, 1838), and *D. rectimanus* Miers, 1884. Shared characters include: intercalary rostral process not reaching terminal spines of ocular acicles and marginally unarmed; antennular peduncles distinctly overreaching distal margins of corneas; antennal peduncles also overreaching distal margins of corneas by more than half lengths of fifth segments; antennal acicle moderately long, not bifid; antennal flagellum slightly longer than carapace, with long pinnate setae; outer surface of palm of left cheliped convex, usually with 2 rows of small spines clearly differentiated from other tubercles or granules, but without conspicuous ridges extending onto fixed finger or to articulation with dactylus; dactyli of second and third pereopods lacking dorsal row of spinules but each bearing 2 rows of stiff setae on mesial surface; propodi of second pereopods each with a dorsal row of spines; and carpi of second and third pereopods each with a dorsal row of spines. We have tried to assess characters useful in discriminating *D. nitidimanus* from the four allied species through a comparison with literature or actual specimens.

Diogenes granulatus, represented only by the holotype from Shark Bay, Western Australia (Davie 2002), appears to be distinguishable from *D. nitidimanus* by the shorter dactyli of the left second and third pereopods. Miers (1880) specifically noted that those dactyli scarcely exceeded the propodi in the lengths. In *D. nitidimanus*, the dactyli of the second and third pereopods are distinctly longer than the propodi (1.20–1.30 times as long).

Diogenes ovatus, known from the West African coast, appears distinctive in having a large depression on the upper surface of the carpus of the left cheliped (Forest 1955).

Diogenes pugilator from the eastern Atlantic, including the Mediterranean (Ingle 1991), and *D. rectimanus* known from the Indo-West Pacific (McLaughlin & Clark 1997; McLaughlin 2002; McLaughlin *et al.* 2007) are very similar to *D. nitidimanus*. *Diogenes pugilator* is separated from *D. nitidimanus* by the ornamentation of the left chela and the structure of the fourth pereopod. In *D. pugilator*, the outer surface of the left chela is regularly convex, without a trace of rows of spines or longitudinal ridges; the upper surface is armed with numerous small tubercles; the dactylus of the fourth pereopod distinctly overreaches the distal margin of the propodus (including the rasp). In *D. nitidimanus*, the outer surface of the left chela is usually provided with two differentiated rows of small spines in the upper half; the upper surface of the left palm bears more coarse tubercles; and the dactylus of the fourth pereopod only reaches the distal margin of the propodus (including the rasp). *Diogenes rectimanus* differs from *D. nitidimanus* in having a prominent row of spines on the lower margin of the left chela. In spite of the strong variability in the armature of the left cheliped, such prominent spines are not seen in *D. nitidimanus*.

Diogenes avarus Heller, 1865 is also generally similar to *D. nitidimanus*, although the armature of the ambulatory legs is substantially variable in the former (Rahayu & Komai 2000). It occurs in the Ryukyu Islands in southern Japan (Komai, unpublished data), and it is worth comparing it with *D. nitidimanus*. Although variability diminishes the diagnostic value, the left palm with a proximally strongly elevated midline, often forming a spinulose crest, will be easy to use in distinguishing the two species. Furthermore, the armature of the second and third pereopods is usually less pronounced in *D. avarus* than in *D. nitidimanus*. The second and third pereopods are slenderer in *D. avarus* than in *D. nitidimanus*, and particularly the dactyli are more elongate in the former than in the latter. Furthermore, although both species occur in tidal flats of inshore waters, they appear geographically separated. *Diogenes avarus* is widespread in the tropical waters in the Indo-West Pacific (McLaughlin & Clark 1997), while *D. nitidimanus* appears restricted to temperate East Asia.

Three congeneric species, *Diogenes edwardsii* (De Haan, 1849), *D. penicillatus* Stimpson, 1858 and *D. spinifrons* (De Haan, 1849), are included in the distributional range of *D. nitidimanus* in temperate regions in East Asia. In many respects, *D. edwardsii* and *D. spinifrons* are similar to *D. nitidimanus*, but as Asakura (1995) noted, they are readily distinguished from *D. nitidimanus* in having a dorsal row of spinules on each ambulatory dactylus, as well as by the armature of the left palm. *Diogenes penicillatus* is immediately distinguished from the other three species by having dense setation on the left chela.

Specimens referred by Ortmann (1892) to *Diogenes edwardsii* have been reexamined. One of the 11 specimens indicated as material “a” (MZS 455) was found to actually represent *D. nitidimanus*, instead of *D. edwardsii*. Komai & Mishima (2003) noted that four specimens of *D. nitidimanus* were mixed in the syntypes of *Pagurus dubius* (Ortmann, 1892) [= *Pagurus minutus* (Hess, 1865)].

McLaughlin *et al.* (2007) reported *Diogenes* aff. *nitidimanus* from Taiwan. The specimens from Taiwan, however, are different from those examined in this study in having a row of sharp spines on the lower margin of the left chela and the nearly horizontal terminal margins of the telson. Future study may eventually reveal that the Taiwanese specimens represent an undescribed species closely allied to *D. nitidimanus*.

Larval development

The morphological characters of zoeas and megalopas of *Diogenes nitidimanus* are generally similar between samples from Russian waters of the Sea of Japan and from the west coast of Kyushu, Japan (Baba & Fukuda 1985). Differences between the present zoeas and those described by Baba & Fukuda (1985) are summarized in Table 1. Zoeas are smaller in the Russian specimens than in Japanese specimens throughout the stages, but the size of megalopas is similar between the two populations (CL = 1.15 and 1.14 mm, respectively). The palp buds of mandibles appear in the third zoea in the Russian specimens and increase in size in the following stage, but in Japanese larvae they appear only in the fourth zoea. The antennal endopod of the fourth zoea is 2-segmented in the Russian larvae, but Baba & Fukuda (1985) described that it was 10-segmented in Japanese larvae. The 10-segmented endopod is quite unusual for diogenid species, and it is possible that Baba & Fukuda (1985) were in error. It is quite possible that the specimen they illustrated was approaching the metamorphic molt, and they were seeing the incipient segments of the megalopa through the integument of the zoea. It is remarkable that the developmental pattern of the pleopods appears different between the two populations. In the Russian larvae, uniramous pleopods appear only at the fourth zoea. Whereas in Japanese larvae, pleopod buds already appear in the third zoea and become biramous in the fourth zoea. The pleopods are uniramous in megalopas from both regions. The other, less significant, differences are found in the armament of the antennular exopod and protopod, the antennal protopod, the rami of the maxillule, and the basis of the first maxilliped (Table 1).

It is not easy to compare our megalopas with the description of that stage by Baba & Fukuda (1985), because the latter description is not fully detailed. Nevertheless, in the Russian larvae, the antenna overreaches the left cheliped, whereas in Japanese larvae the antenna just reaches the tip of the left cheliped. Differences are also seen in the segmentation and the setation of all rami of the antenna and the exopod of the maxillule (Table 2).

Descriptions of larval morphology are now available for eight *Diogenes* species, viz., *D. pugilator* (see MacDonald *et al*. 1957; Pike & Williamson 1960); *D. bicristimanus* (see Sarojini & Nagabushanam 1968), *D. avarus* (see Sankolli & Shenoy 1975; Siddiqui & Tirmizi, 1988), *D. alias* (as *D. diogenes*) (see Nayak & Kakati 1977), *D. planimanus* (see Nayak 1981), *D. violaceus* (see Nayak & Neelkantan 1983), *D. nitidimanus* (see Baba & Fukuda 1985; this study), and *D. miles* (see Shenoy & Sankolli 1993). The larvae of *D. nitidimanus* agree with those of other congeneric species in the principal generic characters (MacDonald *et al*. 1957; Pike & Williamson 1960; Sankolli & Shenoy 1975). These characters include: in zoeas, the posterolateral margins of the carapace are rounded; the fourth and fifth pleonal somites each has a mediodorsal spine; the antennal endopod is provided with three plumose setae in the first and second zoeas, and is 2-segmented in the last zoeal stage; the endopod of the maxillule is 2-segmented in all stages; the third telsonal process is not thickened and is not fused with the telson; the exopod and endopod of the uropod are articulated to the protopod in the fourth zoea; in megalopas, the left cheliped and left uropod are larger than the right ones; ocular acicles are present**.** The most remarkable discrepancy between the present larvae and the previous descriptions of *Diogenes* species is that bud of the mandibular palp already appears in the third zoea in our samples. In larvae of other species, including those of *D. nitidimanus* described by Baba & Fukuda (1985), the mandibular palp appears only in the last stage. This suggests that the development of the mandibular palp could be precocious in *Diogenes* species.

It is remarkable that in contrast to pagurids, which normally have not more than four zoeal stages (MacDonald *et al.* 1957; Gore & Scotto 1983) and rarely undergo an abbreviated development (Provenzano 1968), the number of zoeal stages in diogenids is considerably variable and abbreviated development in this group is widespread (Rabalais & Gore 1989). The larvae in the genus *Calcinus* usually pass through five to seven zoeal stages (Pike & Williamson 1960; Provenzano 1962). However, a *Calcinus* species with extremely abbreviated development that includes only one zoeal stage has recently found (Calado *et al*. 2006). The number of zoeal stages in the genus *Clibanarius* ranges from four (Tirmizi & Siddiqui 1979; Ajmal Khan *et al.* 1981; Siddiqui *et al*. 1993) to five (Lang & Young 1977; Brossi-Garcia 1987). The pattern of larval development in the genus

TABLE 1. Summary of morphological differences of zoeas of *Diogenes nitidimanus* Terao, 1913, found between our study and Baba & Fukuda (1985).

Character	First zoea		Second zoea		Third zoea		Fourth zoea	
	present data	Baba & Fukuda (1985)	present data	Baba & Fukuda (1985)	present data	Baba & Fukuda (1985)	present data	Baba & Fukuda (1985)
Carapace length, mm	0.80	1.14	0.93	1.24	1.30	1.42	1.52	1.93
Antennule								
exopod	3 aesthetascs + 3 plumose setae	4 aesthetascs + 2 plumose setae	4 (rarely 5) aesthetascs + 4 plumose setae	3 aesthetascs + 1 plumose and 3 simple setae			7 aesthetascs + 4 plumose setae	6 aesthetascs + 4 simple setae
protopod					4 short and 2 long plumose + 1 lateral seta	3 short and 2 long plumose setae	4 short and 2 long plumose + 1 lateral seta	3 short and 2 long plumose setae
Antenna								
endopod							2-segmented	10-segmented
protopodal spine			2	1	2	1	2	1
Mandible								
palp					bud	absent		
Maxillule								
endopod	1, 2	0, 2	6 + 1	6	7 + 1	7		
coxal endite	6 + 1	6						
basial endite	2 + 1	2						
First maxilliped								
basis							1, 3, 2	1, 4, 2
Pleon								
pleopods					absent	buds	uniramous	biramous

Paguristes includes five zoeal stages in *P. ortmanni* (Quintana & Iwata 1987), three (rarely four) zoeal stages in *P. spinipes* (see Provenzano 1978), two zoeal stages in *P. sericeus* (see Rice & Provenzano 1965), and direct development in *P. abbreviatus* and *P. frontalis* (see Dechancé 1963; Morgan 1987).

In the genus *Diogenes*, larval development varies from five to three zoeal stages. Sarojini & Nagabushanam (1968) recorded five zoeal stages for *D. bicristimanus* from the east coast of India. Mandibular palps and pleopods appear in the fifth zoea of this species. MacDonald *et al*. (1957) described four zoeal stages and megalopa in *D. pugilator* from British waters. They obtained the first zoea in the laboratory, remaining stages being collected from the plankton. These authors mentioned the possibility of a fifth zoea in British waters, as their fourth zoea lacked a mandibular palp and pleopod buds. However, Pike & Williamson (1960) believed that four was the normal number of zoeal stages for this species in Mediterranean and Indian waters. Four zoeal stages are known in *D. nitidimanus* (see Baba & Fukuda 1985; this study) and for *D. avarus* (see Sankolli & Shenoy 1975). Only three zoeal stages were described for *D. alias* (see Nayak & Kakati 1977), *D. miles* (see Shenoy & Sankolli 1993), *D. planimanus* (see Nayak 1981) and *D. violaceus* (see Nayak & Neelkantan 1983). Materials of the latter five species were all obtained from Indian waters.

TABLE 2. Summary of morphological differences of megalopas of *Diogenes nitidimanus* Terao, 1913, found between our study and Baba & Fukuda (1985).

Character	Present data	Baba & Fukuda (1985)
Antenna		
peduncle	5-segmented	4-segmented
endopod	1 spine	without spines
exopod	9-segmented	8-segmented
Maxillule	3 marginal plumose setae	without marginal setae

Five or four zoeal stages seems to be a primitive or plesiomorphic condition for larval development in *Diogenes*, whereas three zoeal stages are derived or apomorphic (Gore & Scotto 1983). It is interesting to note that three zoeal stages are recorded more often in species occurring tropical waters, but four and five stages occur in species of temperate waters. The third zoea in species with abbreviated development is advanced in antennular, mandibular, pleopodal and telsonal characters over those of the third zoea in species with longer development (Rabalais & Gore 1989). The existence of the abbreviation of the larval development makes it difficult to compare detailed larval morphology among species, because many characters are affected by ontogenetic change.

Among the species of *Diogenes* for which larval morphology is known, *D. nitidimanus* is similar to *D. pugilator* and *D. avarus* in adult morphology. All three species pass through four zoeal stages, but the larvae of *D. nitidimanus* and *D. avarus* are more advanced in the following attributes: the fourth zoea of *D. nitidimanus* and *D. avarus* possesses a mandibular palp and pleopod buds, whereas the fourth zoea of *D. pugilator* lacks them**.** In fact, zoeas of *D. nitidimanus* and *D. avarus* are morphologically more similar to each other than those of any other congener. The main differences between these two species are summarized as follows: the fourth and fifth pleonal somites bear mediodorsal spines in *D. nitidimanus,* whereas in *D. avarus*, only the fifth somite has a mediodorsal spine; the proximal lobe of the maxilla appears already in the third zoea of *D. nitidimanus*, but it is absent even in the fourth zoea of *D. avarus*; the number of marginal plumose setae on the scaphognathite of the maxilla in the fourth zoea reaches 24 in *D. nitidimanus*, but only 12 in *D. avarus*; the exopod of the uropod bears nine plumose setae in *D. nitidimanus,* only seven plumose setae in *D. avarus*. The endopod of the maxillule is two-segmented in *D. nitidimanus*, two-segmented in *D. avarus* according to Siddiqui and Tirmizi (1988), but unsegmented according to Sankolli & Shenoy (1975).

Acknowledgements

We thank Dr. Sammy De Grave of the Oxford Museum of Natural History and Mr. E. Myorin of Kanazawa City for donating specimens used in this study. We are also grateful to Dr. P.A. McLaughlin for offering valuable comments on the manuscript. The project was partially supported by the Far East Branch of Russian Academy of Sciences (grants no. 06-III-A-06-164, 06-III-A-06-161 and 06-I-П-11-034) and by the grant of Foundation APN ARCP2006-FP14.

References

Ajmal Khan, S.A., Sundaramoorthy, S., Thomas, M., Kannupandi, T. & Natarajan, R. (1981) Laboratory reared larval stages of the marine hermit crab *Clibanarius clibanarius* (Herbst) (Decapoda: Anomura). *Proceedings of Indian Academy of Sciences (Animal Sciences),* 90(2), 225–236.

Asakura, A. (1987a) Population ecology of the sand-dwelling hermit crab *Diogenes nitidimanus* Terao. 3. Mating system. *Bulletin of Marine Science*, 41, 282–288.

Asakura, A. (1987b) Polymorphism in chelae of *Diogenes nitidimanus* Terao (Decapoda: Anomura: Diogenidae). *Researches on Crustacea*, 16, 29–33.

Asakura, A. (1987c) Preliminary observations on the offshore mass migration of the sand dwelling hermit crab, *Diogenes nitidimanus* Terao. *Journal of Ethology*, 5, 207–209.

Asakura, A. (1991) Population ecology of the sand-dwelling hermit crab *Diogenes nitidimanus* Terao. 4. Larval settlement. *Marine Ecology Progress Series*, 78, 139–146.

Asakura, A. (1992) Population ecology of the sand-dwelling hermit crab *Diogenes nitidimanus* Terao. 5. Ecological implications in the pattern of molting. *Journal of Crustacean Biology*, 12(4), 537–545.

Asakura, A. (1995a) Sexual differences in life history and resource utilization by the hermit crab. *Ecology*, 76(7), 2295–2313.

Asakura, A. (1995b) Anomura. *In*: Nishimura, S. (Ed.), *Guide to Seashore Animals of Japan with Color Pictures and Keys, Vol. II*. Hoikusha Publishing Co., Ltd., Osaka, pp. 347–377, pls 93–100.

Asakura, A. (2006) Shallow water hermit crabs of the families Pylochelidae, Diogenidae and Paguridae (Crustacea: Decapoda: Anomura) from the Sea of Japan, with a description of a new species of *Diogenes*. *Bulletin of the Toyama Science Museum*, 29, 23–103.

Asakura, A. & Goodwin, S. (2006) *Diogenes patae* n. sp., a new species of hermit crab (Crustacea, Decapoda, Anomura, Diogenidae) from American Samoa. *Zoosystema*, 28(2), 457–463.

Asakura, A. & Kikuchi, T. (1984a) Population ecology of the sand-dwelling hermit crab *Diogenes nitidimanus* Terao. 1. Shell utilization. *Publications from the Amakusa Marine Biological Laboratory*, 7, 95–108.

Asakura, A. & Kikuchi, T. (1984b) Population ecology of the sand-dwelling hermit crab *Diogenes nitidimanus* Terao. 2. Migration and life history. *Publications from the Amakusa Marine Biological Laboratory*, 7, 109–124.

Baba, K. & Fukuda, Y. (1985). Larval development of the hermit crab *Diogenes nitidimanus* Terao, 1913 (Crustacea: Anomura: Diogenidae) reared in the laboratory. *Memoirs of the Faculty of Education Kumamoto University Natural Science*, 34, 5–17.

Brossi-Garcia, A.L. (1987) Morphology of the larval stages of *Clibanarius sclopetarius* (Herbst, 1796) (Decapoda, Diogenidae) reared in the laboratory. *Crustaceana*, 52(3), 251–275.

Calado, R., Nogueira, N. & dos Santos, A. (2006) Extended parental care in a hermit crab of the genus *Calcinus* (Anomura: Diogenidae). *Journal of the Marine Biological Association of the United Kingdom*, 86, 121–123.

Clark, P.F., Calazans, D.K. & Pohle, G.W. (1998) Accuracy and standartization of brachyuran larval descriptions. *Invertebrate Reproduction and Development*, 33, 127–144.

Davie, P.J.F. (2002) Crustacea: Malacostraca: Eucarida (Part 2): Decapoda – Anomura, Brachyura. *In*: Wells, A. & Houston, W.W.K. (Eds), *Zoological Catalogue of Australia*. Vol. 19.3B. CSIRO Publishing, Melbourne, xiv + 641 pp.

Dechancé, M. (1963) Développement direct chez un paguride, *Paguristes abbreviatus* Dechancé, et remarques sur le développement des *Paguristes*. *Bulletin du Muséum national D'Histoire naturelle*, 35(5), 488–495.

Forest, J. (1955) Crustacés Décapodes, Pagurides. Expédition océanographique Belge dans les eaux côtières africaines de l'Atlantique Sud (1948–1949), 3 (4), 23–147.

Gordan, J. (1956) A bibliography of pagurid crabs, exclusive of Alcock, 1905. *Bulletin of the American Museum of Natural History,* 108, 253–352.

Gore, R.H. & Scotto, L.E. (1983) Studies on decapod Crustacea from the Indian River region of Florida XXVII. *Phimochirus holthuisi* (Provenzano, 1961) (Anomura: Paguridae): the complete larval development under laboratory conditions, and the systematic relationships of its larvae. *Journal of Crustacean Biology*, 3(1), 93–116.

Ingle, R. (1991) *Hermit Crabs of the Northeastern Atlantic Ocean and the Mediterranean Sea*. Chapman & Hall, London, Glasgow, New York, Tokyo, Melbourne, Madras, 495 pp.

Kim, H.S. (1973) *Anomura and Brachyura*. *Illustrated Encyclopedia of Fauna and Flora of Korea*, Vol. 14. Ministry of Education, Seoul, 694 pp., 112 pls.

Komai, T. & Mishima, S. (2003) A redescription of *Pagurus minutus* Hess, 1865, a senior synonym of *Pagurus dubius* (Ortmann, 1892) (Crustacea: Decapoda: Anomura: Paguridae). *Benthos Research*, 58, 15–30.

Komai, T., Maruyama, S. & Konishi, K. (1992) A list of decapod crustaceans from Hokkaido, northern Japan. *Researches on Crustacea*, 21, 189–205.

Konishi, K. & Shikatani, N. (1998) Identification manual for larvae of commercially important crabs in Japan. I. Practical techniques for observation in identification of larvae. *Bulletin of the National Research Institute of Aquaculture*, 27, 13–26.

Korn, O.M., Kornienko, E.S. & Zvyagintsev, A.Yu. (2007) Naturalization of *Diogenes nitidimanus* Terao, 1913 (Decapoda: Anomura) in Vostok Bay (Sea of Japan). *Izvestiya TINRO*, 150, 291–297 (in Russian).

Lang, W.H. & Young, A.M. (1977) The larval development of *Clibanarius vittatus* (Bosc) (Crustacea: Decapoda: Diogenidae). *Biological Bulletin*, 152, 84–104.

MacDonald, J.D., Pike, R.B. & Williamson, D.I. (1957) Larvae of the British species of *Diogenes, Pagurus, Anapagurus* and *Lithodes* (Crustacea, Decapoda). *Proceedings of the Zoological Society of London*, 128(2), 209–257.

McLaughlin, P.A. (2002) *Diogenes pallescens* Whitelegge, *D. gardineri* Alcock and *D. serenei* Forest (Decapoda: Anomura: Diogenidae): morphological variants or distinct species? *Raffles Bulletin of Zoology*, 50, 81–94.

McLaughlin, P.A. (2003) Illustrated keys to families and genera of the superfamily Paguroidea (Crustacea: Decapoda: Anomura), with diagnoses of genera of Paguridae. *Memoirs of Museum Victoria*, 60(1), 111–144.

McLaughlin, P.A. (2004) A description of the first complete specimen of *Diogenes guttatus* Henderson, 1888 (Decapoda: Anomura: Paguroidea: Diogenidae). Zootaxa, 466, 1–8.

McLaughlin, P.A. (2005) The "*Troglopagurus* group" of *Diogenes* (Decapoda: Anomura: Paguroidea: Diogenidae) revisited. *Journal of Crustacean Biology*, 25(4), 598–619.

McLaughlin, P.A. & Clark, P.F. (1997) A review of the *Diogenes* (Crustacea, Paguridea) hermit crabs collected by Bedford and Lanchester from Singapore, and from the 'Skeat' Expedition to the Malay Peninsula, with a description of a new species and notes on *Diogenes intermedius* De Man, 1892. *Bulletin of the Natural History Museum, London (Zoology)*, 63, 33–49.

McLaughlin, P.A. & Dworschak, P. (2001) Reappraisal of hermit crab species (Crustacea: Anomura: Paguridea) reported by Camill Heller in 1861, 1862 and 1865. *Annalen Naturhistorisches Museum Wien*, 103B, 135–176.

McLaughlin, P.A. & Haig, J. (1996) A redescription of *Diogenes senex* Heller, 1865, sensu stricto (Decapoda: Anomura: Paguridae: Diogenidae). *Pakistan Journal of Marine Science*, 4(2), 115–126.

McLaughlin, P.A. & Holthuis, L.B. (2001) In pursuit of J. F. W. Herbst's species of *Diogenes* (Anomura: Paguridea: Diogenidae). *Journal of Crustacean Biology*, 21, 257–273.

McLaughlin, P.A., Rahayu, D.L., Komai, T. & Chan, T.-Y. (2007) *A Catalog of the Hermit Crabs (Paguroidea) of Taiwan*. National Taiwan Ocean University, Keelung, 375 pp.

Miers, E.J. (1880) On a collection of Crustacea from the Malaysian Region. Part III. Crustacea Anomura and Macrura (except Penaeidea). *Annals and Magazine of Natural History*, 5(29), 370–384, pls. 6–8.

Miyake, S. (1978) *The Crustacean Anomura of Sagami Bay*. Biological Laboratory, Imperial Household, Tokyo, ix + 200 pp. [In English], 161 pp. [In Japanese]

Miyake, S. (1982) *Japanese Crustacean Decapods and Stomatopods in Color, Volume 1: Macrura, Anomura and Stomatopoda*. Hoikusha, Osaka, viii + 261 pp., 56 pls. [In Japanese]

Miyake, S. & Imafuku, M. (1980) Hermit crabs from Kii Peninsula, II. *Nankiseibutu, the Nanki Biological Society*, 22, 59–64. [In Japanese]

Morgan, G.J. (1987) Abbreviated development in *Paguristes frontalis* (Milne Edwards, 1836) (Anomura: Diogenidae). *Journal of Crustacean Biology*, 7(3), 536–540.

Morgan, G.J. & Forest, J. (1991) Seven new species of hermit crabs from northern and western Australia (Decapoda, Anomura, Diogenidae). *Bulletin du Muséum national d'Histoire naturelle* (4) A, 12, 649–689.

Nayak, V.N. (1981) Larval development of the hermit crab *Diogenes planimanus* Henderson (Decapoda, Anomura, Diogenidae) in the laboratory. *Indian Journal of Marine Sciences*, 10, 136–141.

Nayak, V.N. & Kakati, V.S. (1977) Metamorphosis of the hermit crab *Diogenes diogenes* (Herbst) (Decapoda, Anomura) in the laboratory. *Indian Journal of Marine Sciences*, 6, 31–34.

Nayak, V.N. & Neelkantan, B. (1983) Zoeal stages of an Indian hermit crab, *Diogenes violaceus* Henderson, reared in the laboratory. *Mahasagar–Bulletin of the National Institute of Oceanography*, 16(4), 435–442.

Ortmann, A. (1892) Die Decapoden-Krebse des Strassburger Museums, mit besonderer Berücksichtigung der von Herrn Dr. Döderlein bei Japan und bei den Liu-Kiu-Inseln gesammelten und zur Zeit im Strassburger Museum aufbewahrten Formen, IV. Die Abtheilungen Galatheidea und Paguridea. *Zoologischen Jahrbücher, Abtheilung für Systematik*,

Geographie und Biologie der Thiere, 6, 241–326, pls. 11, 12.
Pike, R.B. & Williamson, D.I. (1960) Larvae of decapod Crustacea of the families Diogenidae and Paguridae from the Bay of Naples. *Publicazioni della Stazione Zoologica di Napoli*, 31, 493–552.
Provenzano, A.J.Jr. (1962) The larval development of *Calcinus tibicen* (Herbst) (Crustacea, Anomura) in the laboratory. *Biological Bulletin*, 123(1), 179–202.
Provenzano, A.J.Jr. (1968) *Lithopagurus yucatanicus*, a new genus and species of hermit crab with a distinctive larva. *Bulletin of Marine Science*, 18, 627–641.
Provenzano, A.J.Jr. (1978) Larval development of the hermit crab, *Paguristes spinipes* Milne-Edwards, 1880 (Decapoda, Diogenidae) reared in the laboratory. *Bulletin of Marine Science*, 28(3), 512–526.
Quintana, R. & Iwata, F. (1987) On the larval development of some hermit crabs from Hokkaido, Japan, reared under laboratory conditions (Decapoda: Anomura). *Journal of Faculty of Sciences of Hokkaido University. Ser. VI. Zoology*, 25(1), 25–85.
Rabalais, N.N. & Gore, R.H. (1989) Abbreviated development in decapods. *Journal of Crustacean Biology*, 9(2), 278–296.
Rahayu, D.L. (1996) Notes on littoral hermit crab (excluding Coenobitidae) (Crustacea: Decapoda: Anomura) mainly from Singapore and peninsular Malaysia. *Raffles Bulletin of Zoology*, 44, 335–355.
Rahayu, D.L. & Forest, J. (1995) Le genre *Diogenes* (Decapoda, Anomura, Diogenidae) en Indonésie, avec la description de six expèces nouvelles. *Bulletin du Muséum national d'Histoire naturelle, Paris*, (4) 16(A), 383–415.
Rahayu, D.L. & Hortle, K.G. (2002) The genus *Diogenes* (Decapoda, Anomura, Diogenidae) from Irian Jaya, Indonesia, with description of a new species. *Crustaceana*, 75, 609–619.
Rahayu, D.L. & Komai, T. (2000) Shallow water hermit crabs (Crustacea: Decapoda: Anomura: Diogenidae and Paguridae) of Phuket, Thailand. *Phuket Marine Biological Center Research Bulletin*, 63, 21–40.
Rice, A.L. & Provenzano, A.J.Jr. (1965) The zoeal stages and the glaucothoe of *Paguristes sericeus* A. Milne Edwards. *Crustaceana*, 8, 239–254.
Sankolli, K.N. & Shenoy, S. (1975) Laboratory culture of the hermit crab *Diogenes avarus* Heller (Crustacea, Decapoda, Anomura). *Bulletin of the Department of Marine Sciences, University of Cochin*, 7(2), 293–308.
Sarojini, R. & Nagabushanam, R. (1968). Larval development of *Diogenes bicristimanus* in the laboratory. *Journal of Marine Biological Association of India*, 10(1), 71–77.
Schram, F. & Koenemann, S. (2004) Developmental genetics and arthropod evolution: on body regions of Crustacea. *In:* Scholtz, G. (ed.) Evolutionary developmental biology of Crustacea. *Crustacean Issues*, 15, 75–92.
Shenoy, S. & Sankolli, K.N. (1993) Larval development of the hermit crab *Diogenes miles* (Herbst, 1791) (Decapoda, Anomura, Diogenidae) in the laboratory. *Crustaceana*, 65(2), 253–264.
Siddiqui, F.A., McLaughlin, P.A. & Crain, J.A. (1993) Larval development of the hermit crab *Clibanarius albidigitus* (Crustacea: Anomura: Diogenidae) reared under laboratory conditions. *Marine Biology*, 116, 603–613.
Siddiqui, F.A. & McLaughlin, P.A. (2004) Review of the Pakistan species of *Diogenes* Dana, 1851 (Decapoda: Anomura: Paguridea: Diogenidae). *Tropical Zoology*, 17, 155–200.
Siddiqui, F.A. & Tirmizi, N.M. (1988) Early developmental stages of *Diogenes avarus* Heller (Crustacea, Diogenidae) reared in the laboratory. *Karachi University Journal of Science*, 10(1&2): 73–80.
Terao, A. (1913) A catalogue of hermit-crabs found in Japan (Paguridae excluding Lithodidae), with descriptions of four new species. *Annotationes Zoologicae Japonenses*, 8, 355–391.
Tirmizi, N.M. & Siddiqui F.A. (1979) The larval development of *Clibanarius signatus* Heller and *C. virescens* (Krauss) (Decapoda: Diogenidae) under laboratory conditions. *Pakistan Journal of Zoology*, 11(2), 239–261.