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NAUPLII AND COPEPODIDS OF THE CYCLOPOID COPEPOD *DIOITHONA OCULATA* (FARRAN, 1913) (OITHONIDAE) FROM A MANGROVE CAY IN BELIZE

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Abstract.—Somites, appendage segments and armament elements of 6 naupliar and 6 copepodid stages are described for *Dioithona oculata* (Farran, 1913) from Belize. *Dioithona oculata* were cultured on *Isochrysis galbana* from egg through naupliar stage 5 with some individuals growing as far as copepodid stage 3; copepodid stages were collected from daytime swarms. At 31°C, development time from 50% N1 to 50% N5 was 3.8 days. New information about morphological development is described for appendage segments and armament elements. Modified setae are present only on copepodids and are found on exopods of the mandible and maxillule, the endopod of swimming leg 4, and on the caudal ramus. The naupliar antennule is 2-segmented and the number of setae on this appendage is reduced from nauplius 6 to copepodid 1. Development of ramal segments for swimming legs follows the common pattern for copepods with identical patterns for legs 1 and 2. The pattern of addition of setae and spines is identical for swimming legs 2 and 3. A study of formation homology for swimming leg 3 suggests that new segments form proximally to the distal-most segment of each ramus; new armament elements usually appear first at the proximal edge of the distal-most segment and subsequently become incorporated onto the next newly formed segment at the next molt.

Oithonid copepods are among the numerically dominant copepod species in many estuarine, coastal, and oceanic ecosystems (Marshall 1949, Marlowe & Miller 1975, Peterson et al. 1979, Lonsdale 1981, Turner & Dagg 1983, Ambler et al. 1985, Roman et al. 1985, Paffenhöfer et al. 1987). Some developmental stages of oithonid species have been described for nine species belonging to *Oithona* and one species of *Dioithona* (Table 1). No descriptions are available for the remaining oithonid genera, *Paroithona* and *Limnoithona*. From our studies of swarms of *D. oculata,* we describe changes in the exoskeletal morphology for all naupliar and copepodid stages, present molting rates for naupliar stages, compare our findings to developmental information known for other cyclopoid copepods, and discuss homologies of several appendages and their armament.

Dioithona oculata is a tropical cyclopoid copepod with a circumglobal distribution in neritic areas (Nishida 1985). During the day, *D. oculata* often forms swarms, composed of copepodid stages, in coral reef and mangrove habitats (Emery 1968, Hamner & Carlton 1979, Ueda et al. 1983, Ambler et al. 1991). Along mangrove shores of cays off Belize, swarms of *D. oculata* among mangrove roots disperse at sunset to open water 3–5 m away, adjacent to shore. Before dawn the copepodids move back under the mangroves to form swarms during the day (Ambler et al. 1991). Females produce egg sacs at night, and approximately 24 hours later, nauplii hatch to join the plankton in the water adjacent to the mangroves (Am-

Table 1.—Sources of information about development of cyclopod copepods.

Name	Source
Oithonidae	
Dioithona rigida	Ramamohana Rao (1958) [as *Oithona*]
Oithona atlantica	Gibbons & Ogilvie (1933) [as *O. spinirostris*]
O. brevicornis	Goswami (1975)
O. davisae	Uchima (1979) [as *O. brevicornis*]
O. nana	Haq (1965) [as *Oithonina*]
O. nana	Murphy (1923)
O. oligohalina	Fonseca & Almeida Prado (1979)
O. ovalis	Fanta (1976)
O. similis	Gibbons & Ogilvie (1933) [as *O. helgolandica*]
O. hebes?	Goswami (1975) [*O. hebes* is neotropical]
Ascidicolidae	
Ascidicola rosea	Illg & Dudley (1980)
Enterocola fulgens	Canu (1892)
E. fertilis	Illg & Dudley (1980)
E. laticeps	Illg & Dudley (1980)
Enteropsis capitulatus	Illg & Dudley (1980)
Haplosaccus elongatus	Ooishi (1980)
Haplostoma albicatum	Ooishi (1980)
Haplostomella distincta	Ooishi (1980)
H. oceanica	Ooishi (1980)
Zanclopus cephalodisci	Calman (1908)
Cyclopidae	
Acanthacyclops viridus	Lucks (1927) [as *Cyclops*]
Allocyclops silvaticus	Rocha & Bjornberg [in litt.]
Apocyclops dengizicus	Valderhaug & Kewalramani (1979)
Bryocyclops caroli	Bjornberg (1984)
Cyclops strenuus	Gurney (1932)
Diacyclops bicuspidatus	Amores-Serrano (1978) [as *Cyclops*]
Ectocyclops rubescens	Carvalho (1971)
Eucyclops serrulatus	Auvray & Dussart (1966)
Graeteriella unisetigera	Lescher-Moutoué (1973)
Halicyclops neglectus	Candcias (1966)
Macrocyclops albidus	Defaye (1984)
Mesocyclops edax	Amores-Serrano (1978)
Speocyclops racovitzai	Lescher-Moutouć (1966)
Cyclopinidae	
Cyclopina longifera	Goswami (1977)
Lernaeidae	
Lamproglena chinensis	Kuang (1962)
Lernaea cyprinacea	Grabda (1963)
Notodelphyidae	
Doroixys uncinata	Canu (1892)
Doropygus seclusus	Dudley (1966)
Notodelphys affinis	Dudley (1966)
Pachypygus gibber	Hipeau-Jacquotte (1978)
Pygodelphys aquilonaris	Dudley (1966)
Scolecodes huntsmani	Dudley (1966)

bler et al. 1990). Nauplii remain in the plankton until they molt to the first copepodid stage (CI); CI's migrate horizontally to swarms among mangrove roots. Two other oithonid species are present with *D. oculata* in the plankton at night. *O. fonsecae* is found in tropical Atlantic lagoonal waters (Ferrari & Bowman 1980), and *O. nana* has a tropical oceanic and nearshore distribution (Nishida 1985).

Methods

Copepodid stages of *D. oculata* were sorted from preserved swarm samples collected at Twin Cays, Belize (16°50'N, 88°05'W), in May 1985, June 1988, and July 1990. Nauplii were cultured from eggs hatched from dropped egg sacs of females isolated from swarm samples collected in February and May 1989. Nauplii were kept in several 500 ml (February) or 50 ml (May) beakers of ambient seawater which were suspended with a styrofoam float in a water-bath cooler, and fed a chrysomonad, *Isochrysis galbana*. Temperatures varied from 20–25°C in February and 30–31°C in May. In February, 12–80 nauplii from several beakers were collected daily; during May, 30–70 nauplii were collected from a 50 ml beaker in 8–12 hr intervals. Specimens were fixed with 2.0% formaldehyde, preserved in 0.5% propylene phenoxytol/4.5% proplylene glycol/95.0% water, cleared in steps through 50.0% lactic acid/50.0% water to 100% lactic acid, and stained by adding a solution of chlorazol black E dissolved in 70.0% ethanol/30.0% water.

Table 2.—Development of *Dioithona oculata* nauplii reared in laboratory from May 18, 1989 experiment. Time from egg hatching to 50% of stage i (T50), instar duration (T), coefficient of determination (R2) for linear regression of angular transformed percent stage versus time. In parentheses is probability of rejecting Ho: Slope = 0, Slope, and Intercept. n = number of points in regression.

Stage	n	T_{50} (hours)	T (hours)	R^2	Slope	Intercept
N1	4	24.00	10.93	0.959 (0.0206)	0.225	−4.62
N2	3	34.93	34.89	1.000 (0.0105)	0.125	−3.57
N3	8	69.82	25.00	0.901 (0.0003)	0.0274	−1.13
N4	8	94.82	21.22	0.744 (0.0059)	0.0250	−1.59
N5	8	116.04	—	0.767 (0.0043)	0.0167	−1.15

Depending upon their availability, up to 30 specimens of each stage were measured to determine body length; caudal rami were included in body length measurements of copepodids. From 3 to 10 specimens of each stage were dissected; the number depended upon the degree of difficulty in determining structural morphology or variability of an appendage. Results consist of brief descriptions of changes in each appendage for each developmental stage. The ventral view of nauplii or lateral view of copepodids are shown for each developmental stage, and the appropriate appendages are illustrated. Descriptions of appendage segments or their armament elements are not repeated if they have not changed from the previous stage. Dense setules on a seta or spine are indicated in illustrations only over a short section of a seta and are not repeated for similar elements.

Developmental times for naupliar stages were determined from the experiment started on May 18, 1989. The time when 50% of the nauplii had molted to a particular stage was determined from linear regression of the angular transformation (Sokal & Rohlf 1969) of percent stage as a function of time. Developmental times were calculated as a difference of times between two successive stages for 50% of the specimens to molt. The angular transformation for each stage, which is the arcsine of the square root of the percent molted to the next stage, was used to meet the assumption of constant variance. Time was calculated from time zero (May 18, 0400) when females produce egg sacs (see Ambler et al. 1990).

Naupliar stages are abbreviated N1 to N6; copepodid stages CI to CVI; male = m, female = f. Appendages are A1 = antennule; A2 = antenna; Mn = mandible; Mx1 = maxillule; Mx2 = maxilla; Mxp = maxilliped; swimming legs = legs 1–4; posterior to these are two simple appendages = legs 5 and 6; caudal ramus = CR. Appendage segments are named following Boxshall (1985) with exopods = Re; endopods = Ri; medial lobes of a segment = li. Armament elements of appendages are spines and setae which are distinguished by apparent degree of flexibility (Dudley 1966); medial, terminal and lateral elements are si, st and se. Homology of appendages, their segments and elements in different developmental stages usually was established by position and occasionally by morphology. For a few appendages, homology by formation was determined if the developing appendage or element of a succeeding stage was visible within the skeleton of the preceding stage.

Results

For experiments in February and May 1989, *D. oculata* was reared from N1

Table 3.—Length range (mm), number of somites or complexes [two or more fused somites] (S + C), appendage buds and number of swimming legs (S1) on stages of *Dioithona oculata*. *n* = number of specimens.

Stage	*n*	Range	S + C	Buds	S1
N1	20	0.11–0.13	1	0	0
N2	18	0.12–0.14	1	0	0
N3	12	0.12–0.14	1	0	0
N4	10	0.15–0.16	1	mx1	0
N5	7	0.16–0.17	1	mx1	0
N6	20	0.19–0.21	1	mx1, legs1,2	0
CI	20	0.34–0.37	6	leg3	2
CII	20	0.39–0.42	7	leg4	3
CIII	30	0.43–0.49	8	leg5	4
CIV	30	0.52–0.60	9	legs5,6	4
CV	30	0.59–0.67	10	leg6	4
CVIf	30	0.73–0.80	10	leg6	4
CVIm	30	0.64–0.70	11	leg6	4

through CIII on unialgal cultures of *Isochrysis galbana*. During February when temperatures varied between 20–25°C, CI were present 8–11 days after egg hatching. In May, sufficient nauplii were raised at nearly constant temperature (30–31°C) to calculate development times for the first four naupliar stages (Table 2). N1 had the shortest development time (10.93 hr) and N2 the longest (34.89 hr). Durations of N3 and N4 were approximately one day. When the experiment was terminated 7.2 days after egg hatching, 56% of the animals had molted to at least N6, and 23% were copepodids.

There are 6 naupliar and 6 copepodid stages of *D. oculata*. Body length and somite number are given in Table 3 and Figs. 1A, E, 2A, D, 3A, E, 4A, 5A, 6A, 7A, 8A, E, and 9E. In N1–5 all cephalic somites are fused into a single complex segment; in N6 this complex includes the first 3 thoracic somites. In CI–CVI all cephalic and the first thoracic somites are fused into a complex, and in addition in CVIf the seventh thoracic and first abdominal somites are fused laterally and ventrally into a genital complex.

Posterior Armament and CR.—N1–N2 (Fig. 1A, E) 1 pair of setae. N3–N4 (Fig. 2A, D) 3 pairs of setae. N5–N6 (Fig. 3A, E) 5 pairs. CI CR (Fig. 4B) length 1.6× width, 1 lateral, 1 dorsal, 4 terminal setae; medialmost terminal seta with thick base and recurved medially. CII–CIII (Fig. 5B) no setae recurved. CIV–CV (Fig. 7B) length 1.8× width. CVIf (Fig. 8F) length 2.5× width. CVIm (Fig. 10E) length 2.0× width.

A1.—[* = count includes a small, pointed seta; a = count includes an aesthetasc] N1–N2 (Fig. 1B) 2 segments with 3 and 4 setae. N3 (Fig. 2B) segment 2 with 7 setae. N4 (Fig. 2E) segment 2 with 12 setae. N5 (Fig. 3B) segment 1 with 4 setae, segment 2 with 14 setae. N6 (Fig. 3F) segment 2 with 16 setae. CI (Fig. 4C) 4 segments with 3, 3, 1 and 9 setae. CII (Fig. 5C) 7 segments with 3, 3, 2, 1, 1, 1 and 10 setae. CIII (Fig. 6B) 9 segments with 3, 3, 2, 3, 4, 1, 2, 2, and 11 setae. CIV (Fig. 7C) 11 segments with 2, 3, 6, 3*, 4, 4, 2a, 3, 2, 3 and 7a setae. CV (Fig. 8B) 11 segments with 7, 8, 3, 4*, 4, 4, 2a, 3, 2, 3, and 7a setae. CVIf (Fig. 10A) 11 segments with 2, 5, 10, 6*, 4, 4, 2a, 3, 2, 3, and 7a setae. CVIm (Fig. 10F) 15 segments with 2, 5, 4, 3, 2, 2, 1, 1, 1, 2, 2, 2, 3, 2, and 9aa setae plus 3 sensilla.

A2.—N1 (Fig. 1C) coxa 2 si; basis 2 si; Re1 fused to basis; several indistinct segments and 6 setae; Ri1 4 setae. N2 (Fig. 1F) basis 3 si; Re 7 setae. N3 (Fig. 2C) coxa 3 si; Re 8 setae; Ri1 5 setae. N4 (Fig. 2F) Re 10 setae; Ri1 7 setae. N5 (Fig. 3C) Re 10 setae. N6 (Fig. 3G) Ri1 8 setae. CI (Fig. 4D) coxa and basis fused 2 si; Re1 wrinkled, 2 setae; Ri 10 setae. CII–CIII (Fig. 5D) Re 1 seta; Ri1 5 setae; Ri2 6 setae. CIV–CVIf (Fig. 6G) Ri2 7 setae. CVIm (Fig. 10G) Ri all segments more elongate.

Mn.—N1 (Fig. 1D) coxa 1 si; basis 2 si; Re1 1 si; Re2 1 si; Re3 2 setae; Ri1 2 si; Ri2 4 si. N2–N6 (Fig. 1G) Re3 1 si; Re4 1 st; Ri1 4 si. CI (Fig. 4E) coxa a gnathobase; basis 1 si; Re4 2 setae, lateral seta a brush; Ri1 fused with basis, 2 si; Ri2 4 setae. CII–CV (Fig. 5E) Ri2 5 setae. CVIf (Fig. 9A) Re4 1 si; Re5 1 seta a brush. CVIm (Fig. 9F) Ri1 2 setae; Ri2 5 setae.

Mx1.—N2–N3 (Figs. 1E, 2A) 1 seta, N4

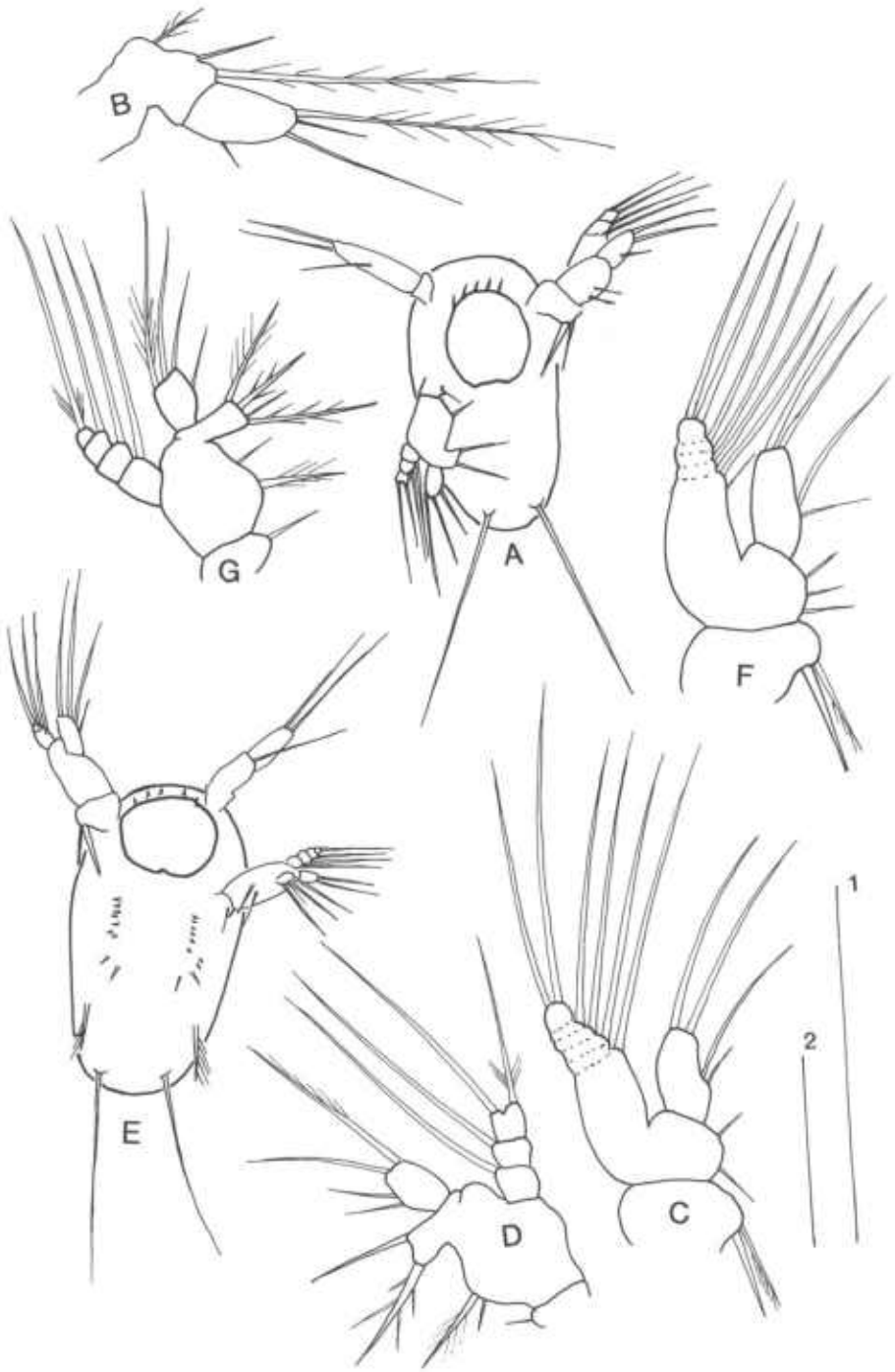

Fig. 1. *Dioithona oculata,* A–D nauplius 1: A, ventral; B, antennule; C, antenna; D, mandible. E–G nauplius 2: E, ventral; F, antenna 2; G, mandible. Scales 1 (B–D, F, G) and 2 (A, E) equal 0.10 mm.

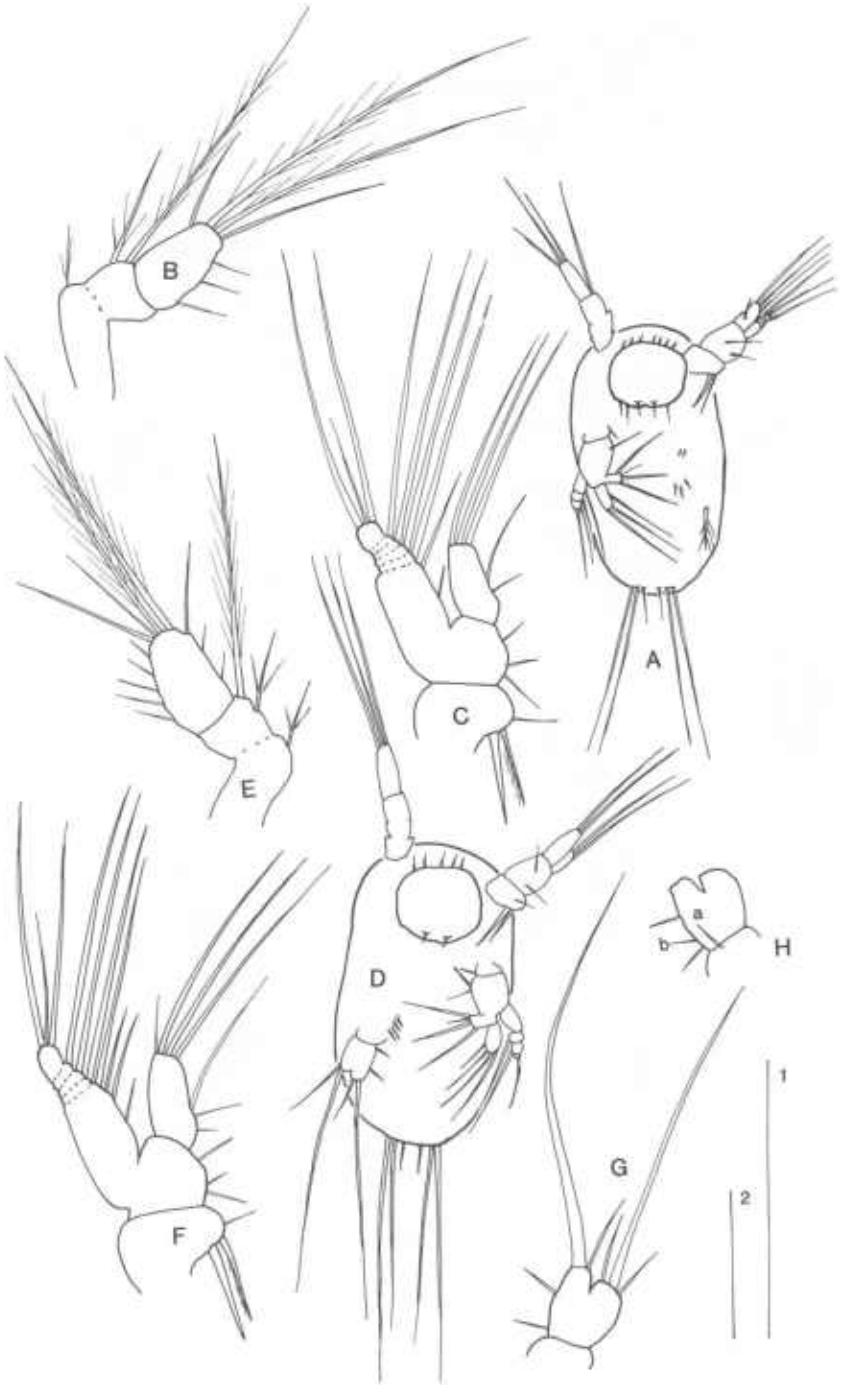

Fig. 2. *Dioithona oculata*. A–C nauplius 3: A, ventral; B, antennule; C, antenna. D–H nauplius 4: D, ventral; E, antennule; F, antenna; G, maxillule; H, maxillule variations (a = seta on 40% of May 1988 specimens and b = seta on one May 1988 specimen). Scales 1 (B, C, E–H) and 2 (A, D) equal 0.10 mm.

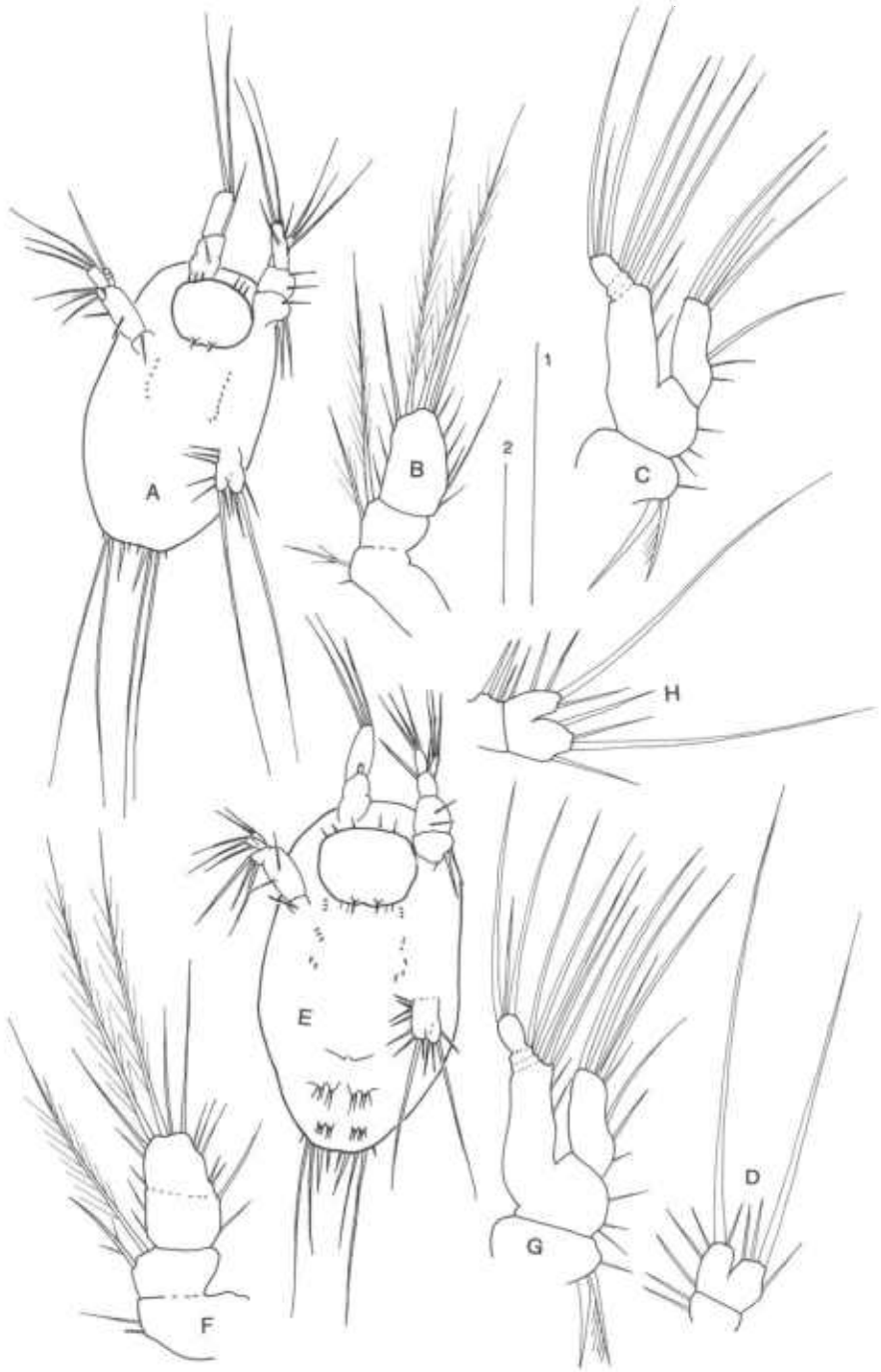

Fig. 3. *Dioithona oculata,* A–D nauplius 5: A, ventral; B, antennule; C, antenna; D, maxillule. E–H nauplius 6: E, ventral; F, antennule; G, antenna; H, maxillule. Scales 1 (B–D, F–H) and 2 (A, E) equal 0.10 mm.

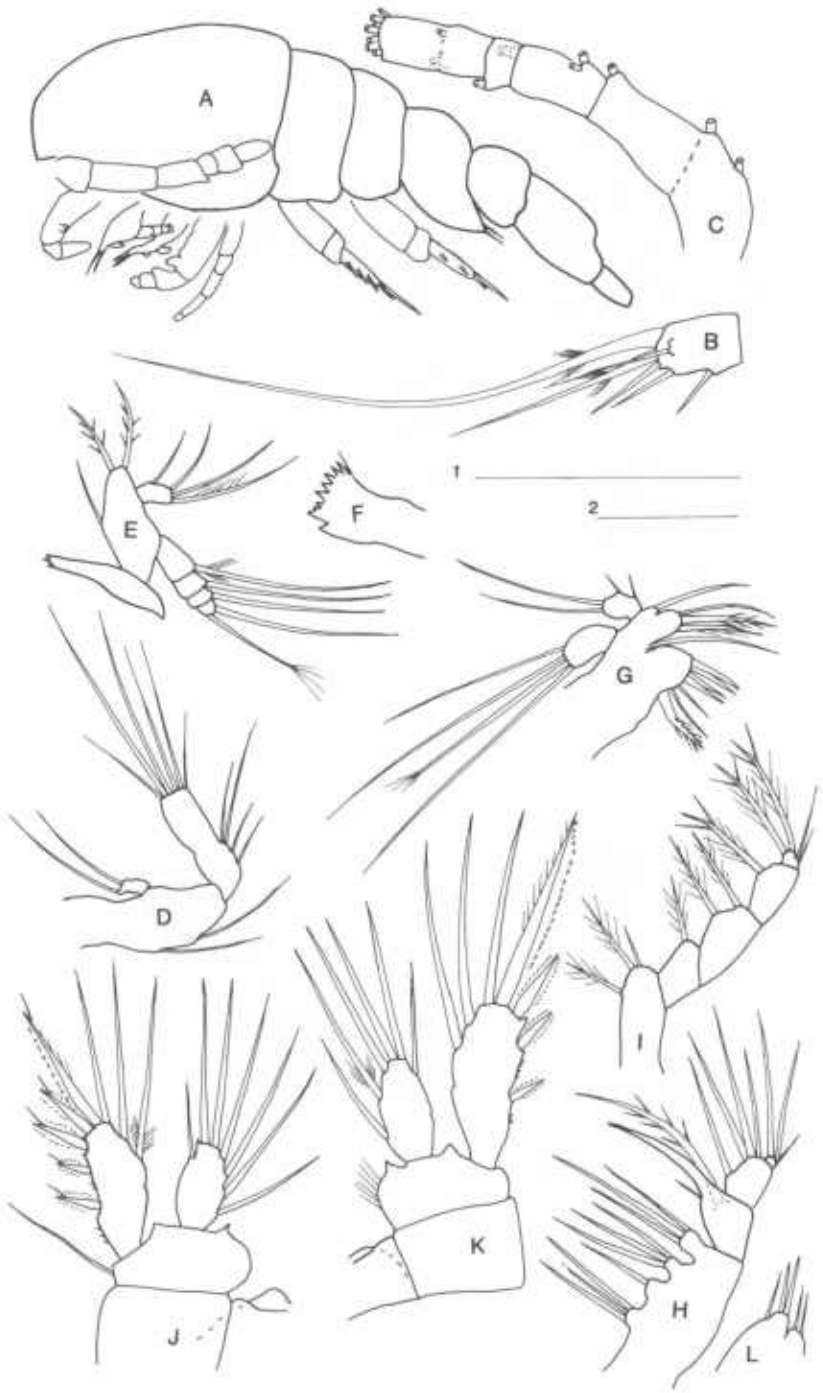

Fig. 4. *Dioithona oculata*, copepodid I: A, lateral; B, caudal ramus; C, antennule; D, antenna; E, mandible; F, mandibular gnathobase; G, maxillule; H, maxilla; I, maxilliped; J, leg 1; K, leg 2; L, leg 3. Scales (B–L) and 2 (A) equal 0.10 mm.

(Fig. 2G) a bilobed bud with basal segment; le 3 setae, li 4 setae [4 of 10 May specimens with an extra seta on basal segment; 1 other May specimen with li 5 setae]. N5 (Fig. 3D) basal segment 2 Si, le 4 setae; li 5 setae. N6 (Fig. 3H) basal segment 3 si. CI–CII (Fig. 4G) sympod li1 7 setae, li2 1 setae, li3 3 setae, li4 1 setae; Re1 4 setae, 2nd seta a brush; Ri1 4 setae, CIII-CVI (Figs. 6H, 9C) sympod li1 9 setae.

Mx2.—CI (Fig. 4H) coxa li1 3 setae, li2 1 seta, li3 3 setae, li4 3 setae; basis with distal inner corner elongate as a curved claw, 2 si; Ri1 4 si; Ri2 3 setae. CII–CV (Fig. 7H) Ri2 2 setae; Ri3 3 setae. CVIf (Fig. 11A) Ri2 3 setae; Ri3 4 setae. CVIm (Fig. 11C) Ri2 5 setae.

Mxp.—CI–CII (Fig. 4I) praecoxa 3 si; coxa 1 si; basis 2 si; Ri1 1 si; Ri2 4 setae. CIII (Fig. 6C) praecoxa 4 si; coxa 2 si; Ri1 2 si. CIV–CVI (Fig. 9D, H) syncoxa 6 si; basis 2 si and inner row of hairs; Ri1 3 setae.

Leg 1.—N6 (Fig. 3E) a bilobed bud le 3 setae, li 2 setae. CI (Fig. 4J) coxa naked; basis 1 se; Re1 with 4 se, 3 si, 1 st; Ri1 7 setae. CII (Fig. 5F) coxa 1 si; basis 1 si; Re1 1 se; Re2 3 se, 4 si, 1 st; Ri1 1 si, Ri2 6 setae. CIII-CIV (Fig. 6I) Re1 1 se, 1 si; Re2 3 se, 4 si, 1 st; Ri1 1 si; Ri2 7 setae. CV–CVIf (Fig. 10B) Rel 1 se, 1 si; Re2 1 se, 1 si; Re3 3 se, 4 si, 1 st; Ri1 1 si; Ri2 1 si; Ri3 6 setae. CVIm (Fig. 9I) basis 1 si recurved medially.

Leg 2.—N6 (Fig. 3E) a bilobed bud le 3 setae, li 2 setae. CI (Fig. 4K) coxa naked; basis naked; Re1 with 3 se, 3 si, 1 st; Ri1 6 setae. CII (Fig. 5G) coxa 1 si; basis 1 se; Re1 1 se; Re2 2 se, 4 si, 1 st; Ri1 1 si, Ri2 6 setae. CIII–CIV (Fig. 6J) Re1 1 se, 1 si; Re2 3 se, 5 si, 1 st; Ri1 1 si; Ri2 7 setae. CV–CVI (Fig. 10C) Re1 1 se, 1 si; Re1 1 se, 1 si; Re3 3 se, 5 si, 1 st; Ri1 1 si; Ri2 2 si; Ri3 6 setae.

Leg 3.—CI (Fig. 4L) a bilobed bud le 3 setae, li 2 setae. CII (Fig. 5H) coxa naked; basis naked; Re1 with 3 se, 3 si, 1 st; Ri1 6 setae. CIII (Fig. 6D) coxa 1 si; basis 1 se; Re1 1 se; Re2 2 se, 4 si, 1 st; Ri1 1 si, Ri2 6 setae. CIV (Fig. 7D) Re1 1 se, 1 si; Re2 3 se, 5 si, 1 st; Ri1 1 si; Ri2 7 setae. CV–CVI (Fig. 10D) Re1 1 se, 1 si; Re2 1 se, 1 si; Re3 3 se, 5 si, 1 st; Ri1 1 si; Ri2 2 si; Ri3 6 setae.

Leg 4.—CII (Fig. 5I) a bilobed bud le 3 setae, li 2 setae. CIII (Fig 6E) coxa naked; basis naked; Re 1 segment with 3 se, 3 si, 1 st, Ri 1 segment with 6 setae. CIV (Fig. 7E) coxa 1 si; basis 1 se; Re1 1 se, 1 si; Re2 3 se, 5 si, 1 st; Ri1 1 si; Ri2 6 setae. CV (Fig. 7G) Re1 1 se, 1 si; Re2 1 se, 1 si; Re3 2 se, 5 si, 1 st. CVIf (Fig. 11B) Ri2 both and Ri3 proximal setae modified, slightly curved distally with hyaline flange along inner edge. CVIm (Fig. 11D) Ri2 both and Ri3 proximal setae modified, straight with hyaline flange smaller than in female.

Leg 5.—CIII (Fig. 6F) unilobed bud with 2 setae. CIV (Fig. 7F) bilobed bud with 3 setae. CV–CVI (Figs. 8D, H, 9J) basal lobe with 1 seta; 1 segment with 2 setae.

Leg 6.—CIV–CVIm (Figs. 7F, 8D, 9K) unilobed bud with point and 1 seta. CVIf (Fig. 8H) unilobed bud with seta recurved dorsally.

Discussion

Our specimens of *D. oculata* differ from those (as *Oithona oculata*) of Nishida (1985) in the following: (1) A1 of our females has two fewer segments; apparently our 3rd and 6th segments represent fused segments (Fig. 10A); (2) Mxp of the female has one fewer segment (Fig. 9D), i.e., praecoxa and coxa are fused, and medial spinules at base of segment 1 are absent; (3) modified setae on female and male Mn, Mx 1, leg 4, and male leg 1 are present (Figs. 9A, C, F, 10F, K). We believe that these modified setae are difficult to discern and may have been overlooked in earlier studies. Ferrari & Bowman (1980) described modified setae (previously noted for *O. plumifera* by Giesbrecht 1892, and for *O. brevicornis* and *O. hebes* by Wel-

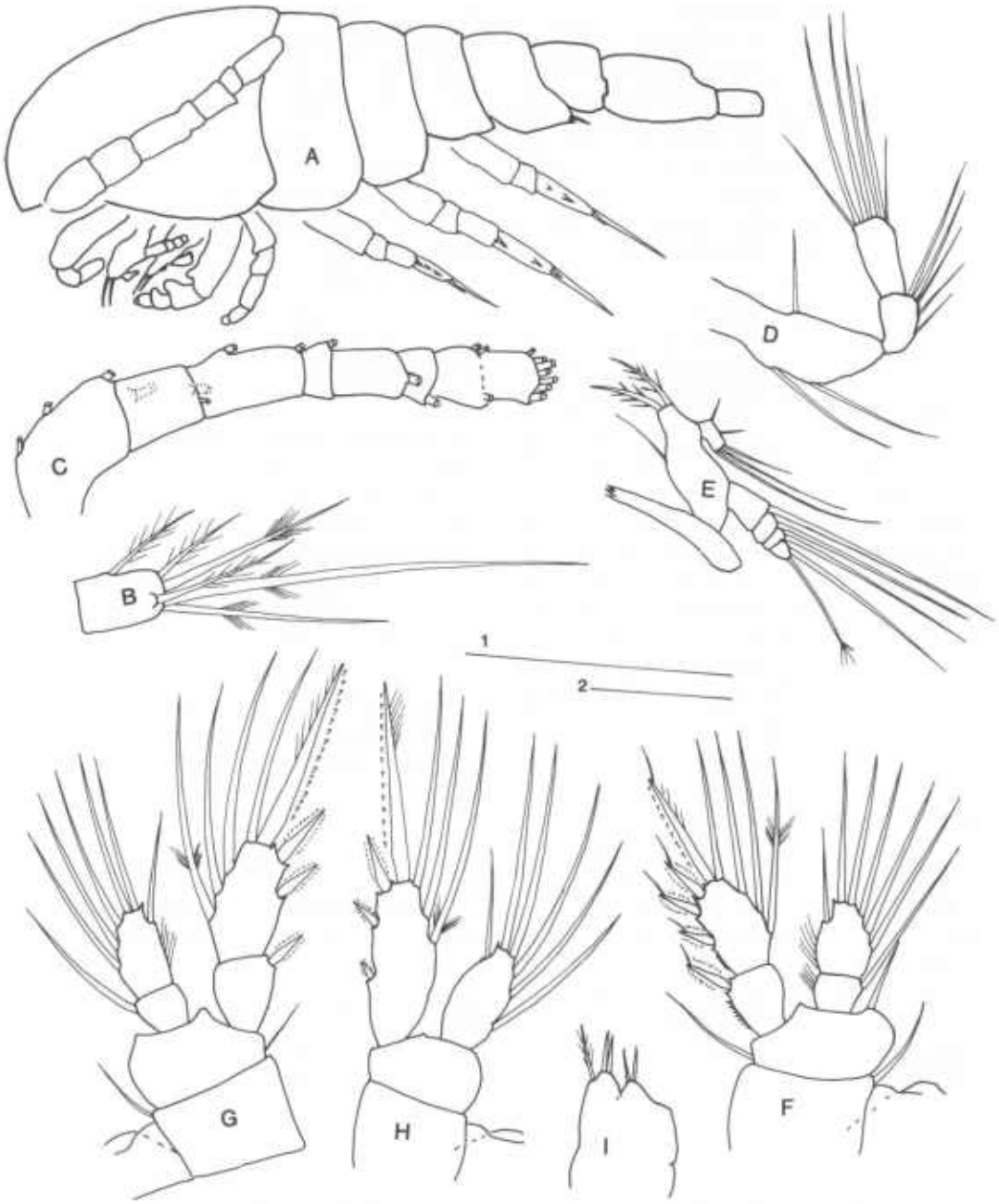

Fig. 5. *Dioithona oculata,* copepodid II: A, lateral; B, caudal ramus; C, antennule; D, antenna; E, mandible; F, leg 1; G, leg 2; H, leg 3; I, leg 4. Scales 1 (A) and 2 (B–I) equal 0.10 mm.

lershaus 1969) on leg 4 of many *Oithona* females, including *D. oculata,* but failed to detect these setae on males of *D. oculata.*

Oithonid species (*O. nana, O. similis, O. brevicornis, O. hebes*?, *O. colcarva,* and *O. davisae*) have been cultured on diets of chlorophyte flagellates, dinoflagellates, and chryptophyte flagellates (Haq 1965, Eaton

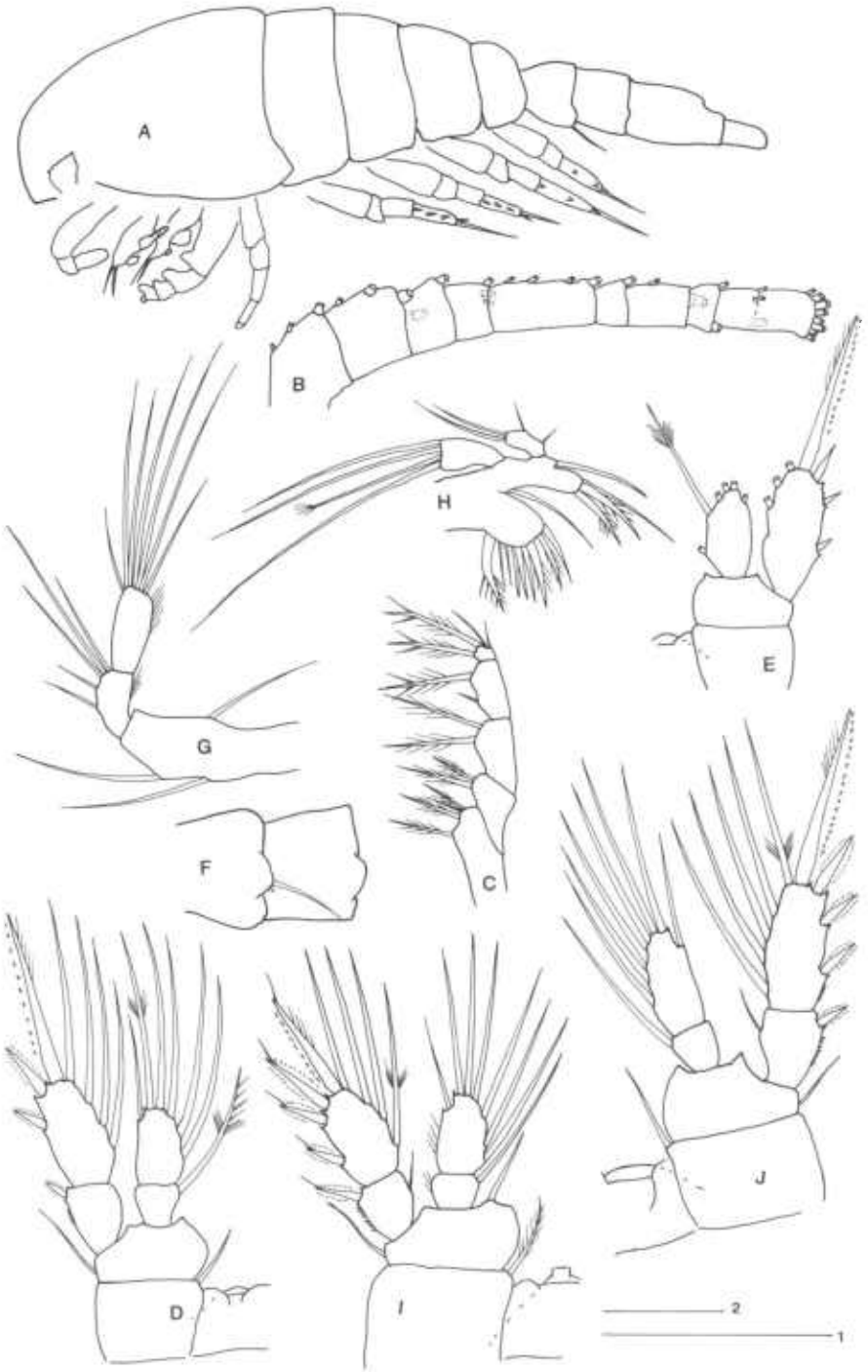

Fig. 6. *Dioithona oculata,* A–F copepodid III: A, lateral; B, antennule; C, maxilliped; D, leg 3; E, leg 4; F, leg 5. G–J copepodid IV: G, antenna; H, maxillule; I, leg 1; J, leg 2. Scales 1 (B–J) and 2 (A) equal 0.10 mm.

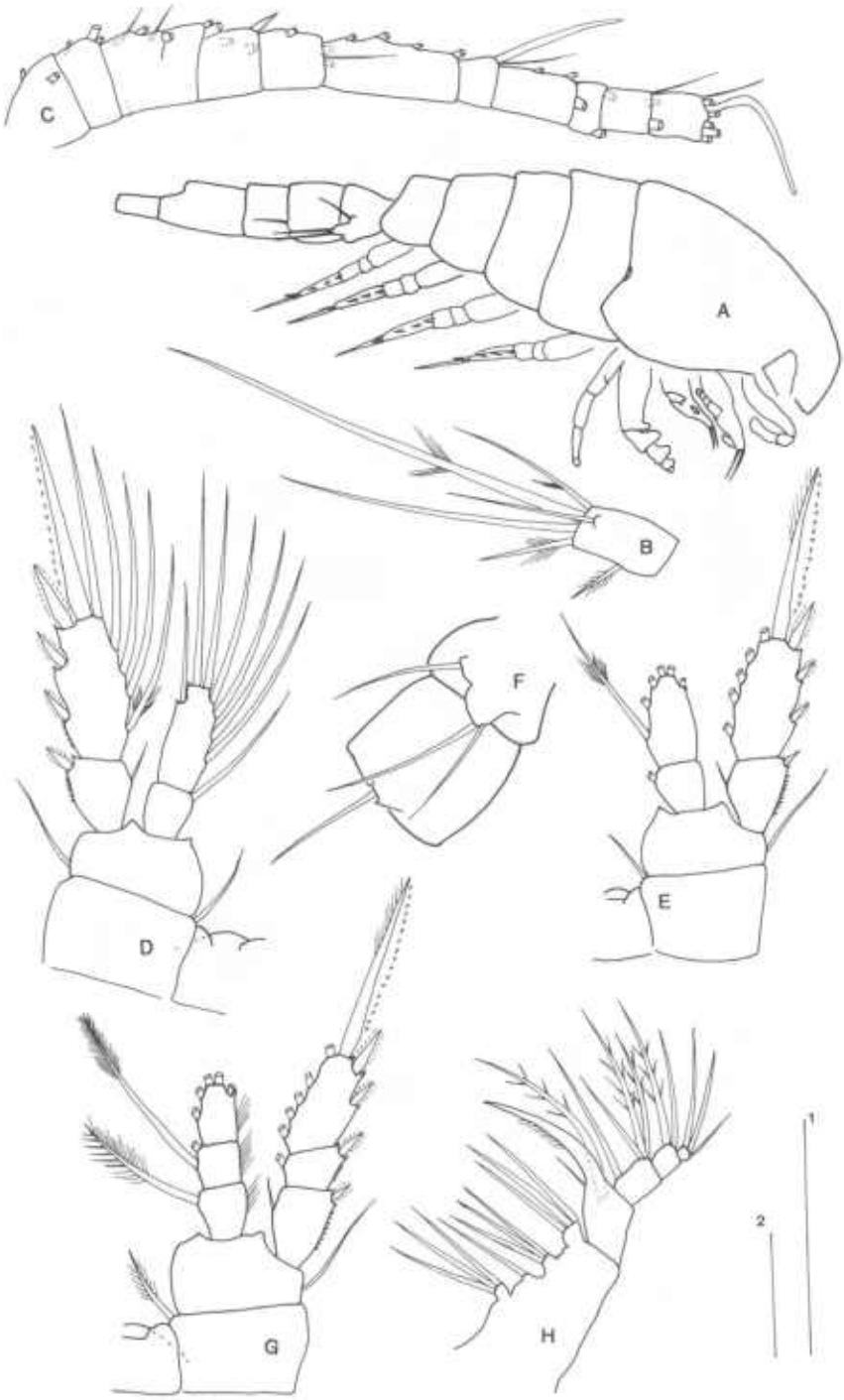

Fig. 7. *Dioithona oculata,* A–F copepodid IV: A, lateral; B, caudal ramus, C, antennule; D, leg 3; E, leg 4; F, legs 5–6. G–H copepodid V: G, leg 4; H, maxilla. Scales 1 (B–H) and 2 (A) equal 0.10 mm.

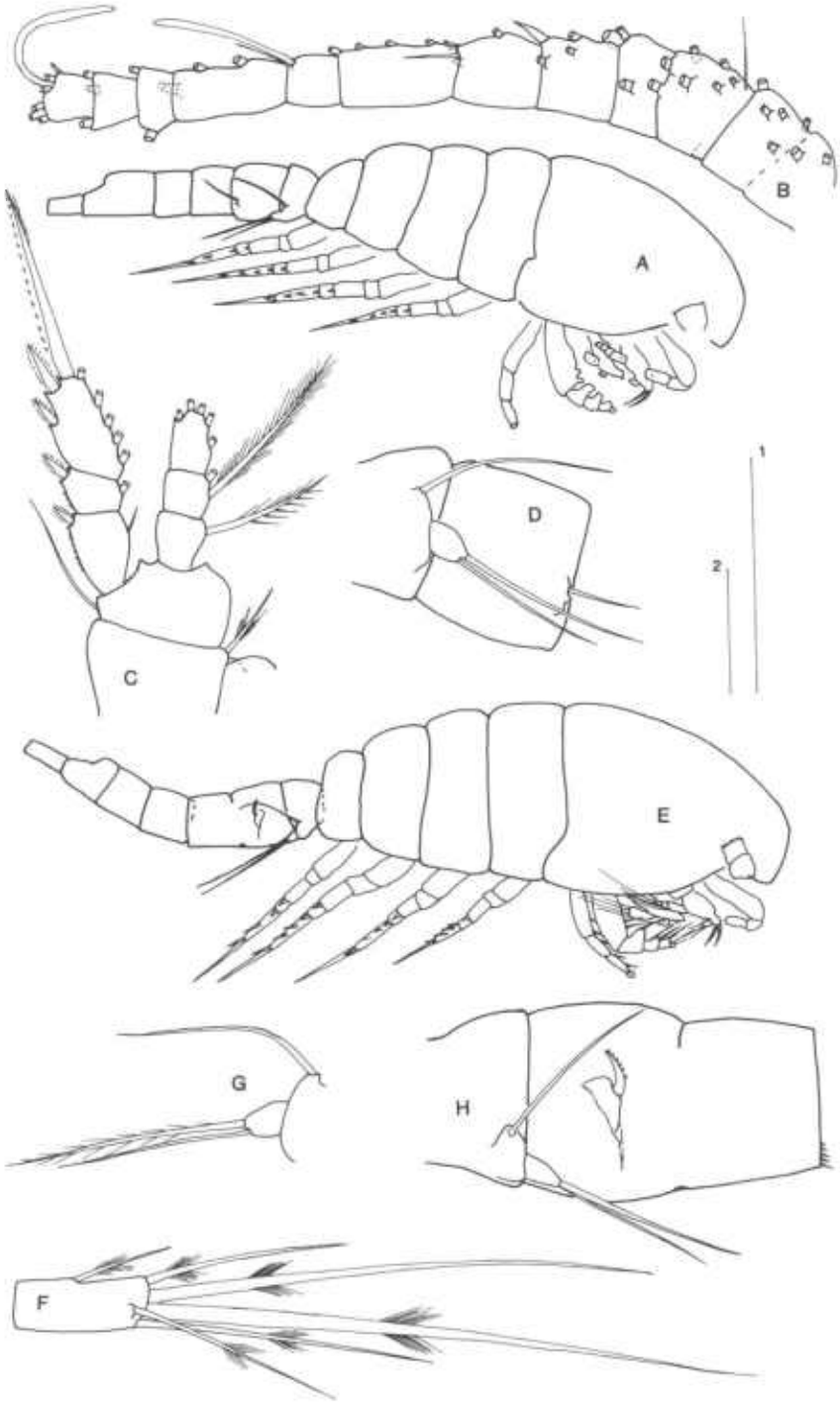

Fig. 8. *Dioithona oculata*. A–D copepodid V: A, lateral; B, antennule; C, leg 4; D, legs 5–6. E–H copepodid VI female: E, lateral; F, caudal ramus; G, leg 5 ventrolateral; H, legs 5–6. Scales 1 (B–D, F–H) and 2 (A, E) equal 0.10 mm.

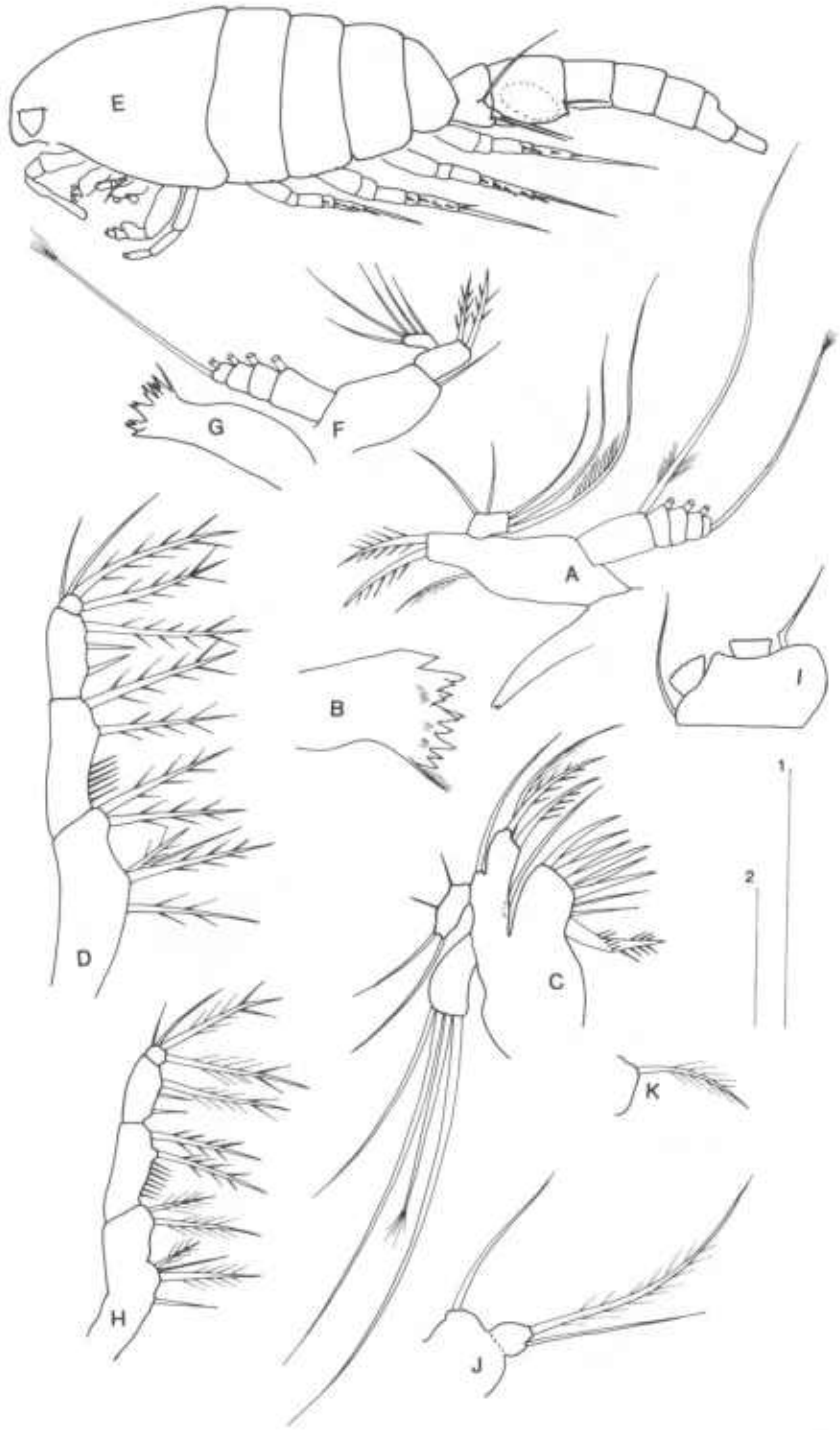

Fig. 9. *Dioithona oculata,* A–D copepodid VI female: A, mandible; B, mandibular blade; C, maxillule; D, maxilliped. E–K copepodid VI male: E, lateral; F, mandible; G, mandibular blade; H, maxilliped; I, leg 1 basis; J, leg 5; K, leg 6. Scales 1 (A–D, F–K) and 2 (E) equal 0.10 mm.

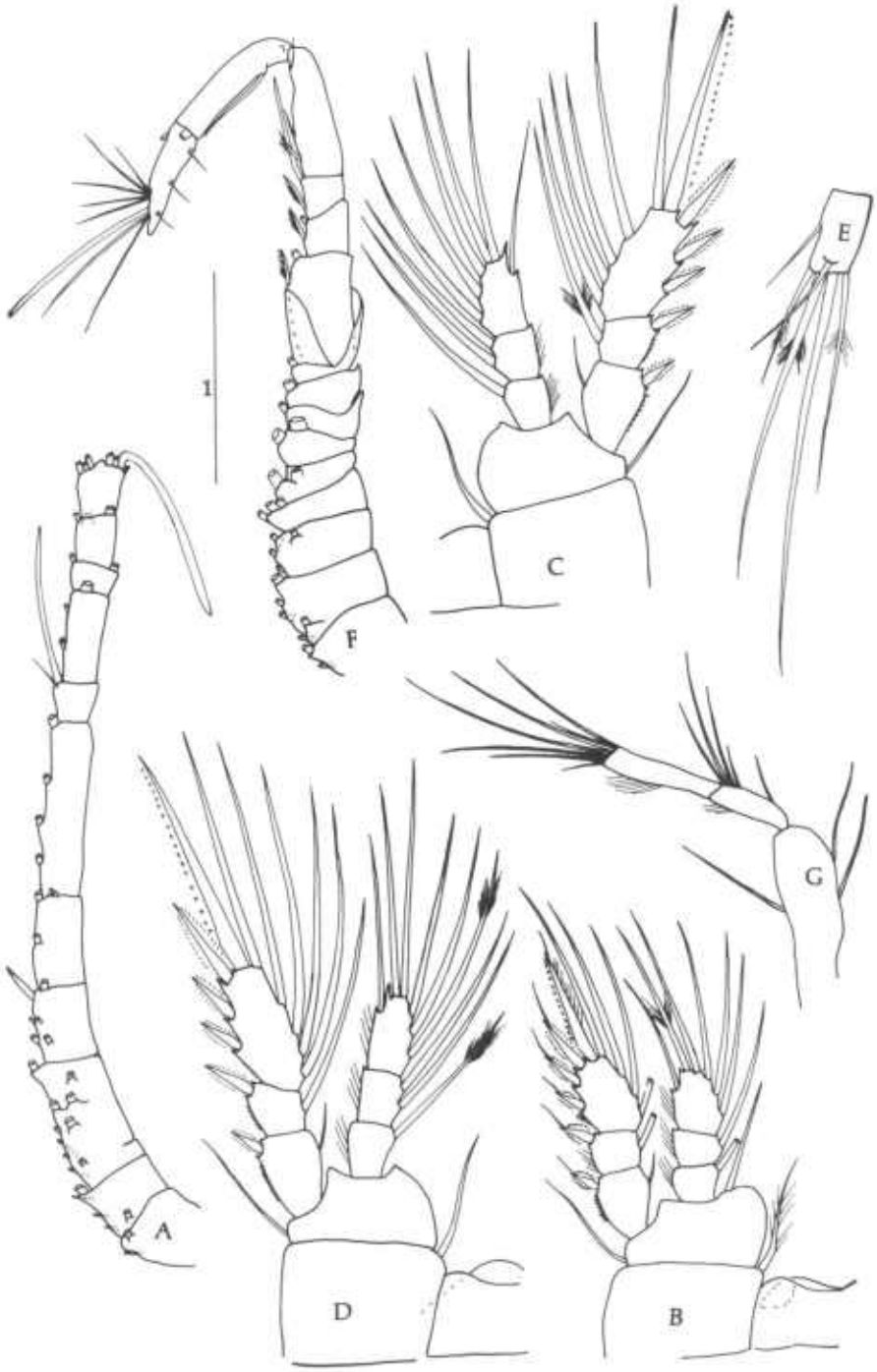

Fig. 10. *Dioithona oculata,* A–D copepodid VI female: A. antennule; B, leg 1; C, leg 2; D, leg 3. E–G copepodid VI male: E, caudal ramus; F, antennule; G, antenna. Scale 1 equals 0.10 mm.

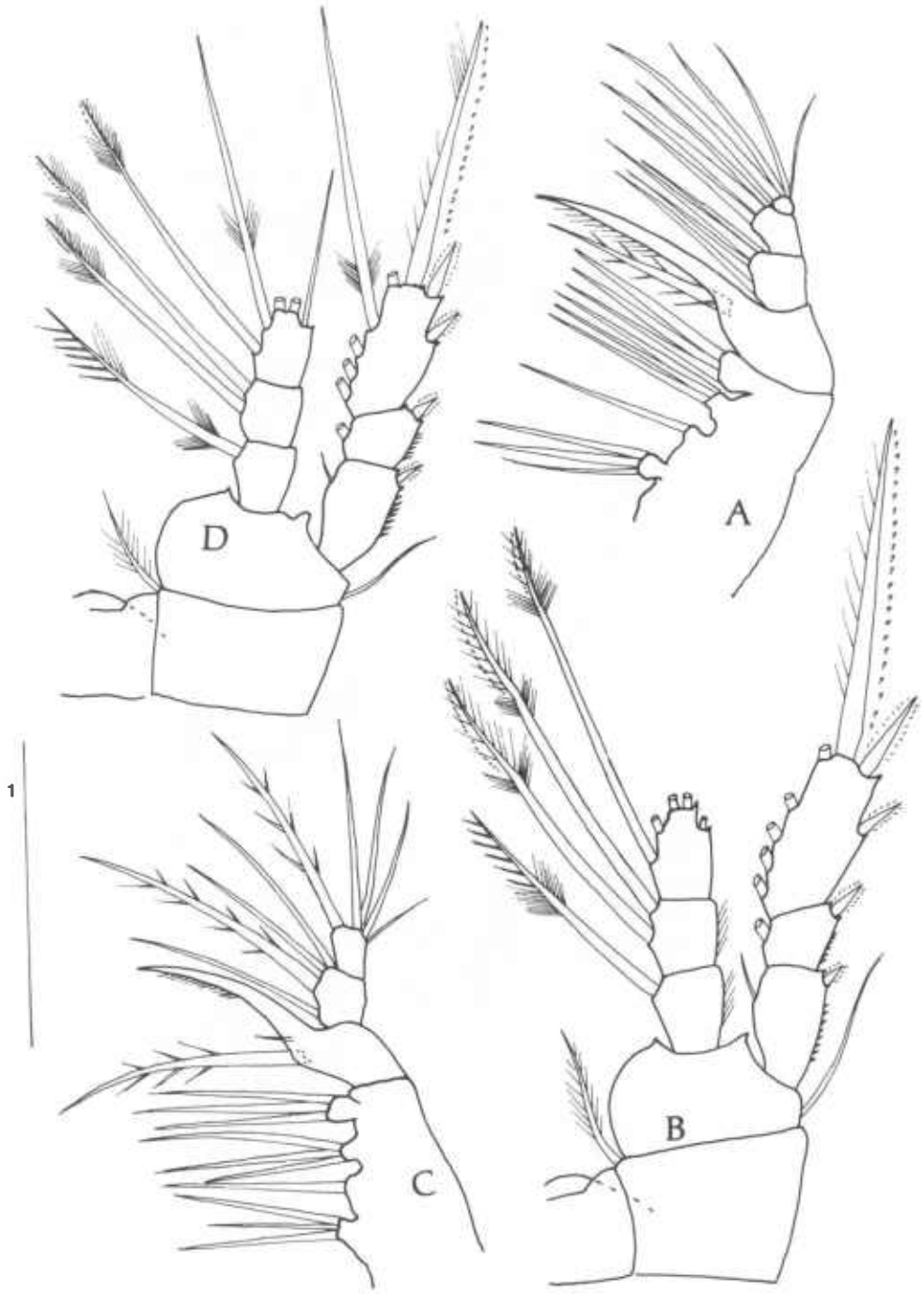

Fig. 11. *Dioithona oculata*, A–B copepodid VI female: A, maxilla; B, leg 4. C–D copepodid VI male: C, maxilla; D, leg 4. Scale 1 equals 0.10 mm.

1971 referenced in McLaren (1978), Goswami 1975, Lonsdale 1981, Uchima 1979). Protozoans such as oligotrichines are ingested by all stages of *O. davisae* (Uchima & Hirano 1986), and Murphy's (1923) kelp detritus for *O. similis* included protozoans. Diatoms are not as readily ingested by oithonids, but several species (*O. similis, O. nana,* and *O. davisae*) have been reported to ingest at least one species (Murphy 1923, Haq 1965, Uchima & Hirano 1986). *Isochrysis galbana* was sufficient for growth for most of the naupliar stages of *D. oculata* but growth of N5 and N6 may have been retarded. Growth of older nauplii and copepodids probably depends on diets of larger protists such as the dinoflagellate *Amphidinium klebsii,* which was fed to adult females for egg production (unpublished data). Females did not produce new egg sacs when offered other species such as newly hatched *Artemia salina,* the rotifer *Asplancha* sp., and *Dunaliella salina.* Older nauplii and copepodids may also need larger food species.

The first feeding stages varies with copepod species, but it is usually the naupliar stage of longest duration (Landry 1983). For *O. similis* and *O. davisae,* N1 is the first feeding stage (Uchima & Hirano 1986). Orange droplets, probably yolk, were observed in the guts of N1 of *D. oculata*; its first feeding stage is probably N2 because it is the naupliar stage of longest duration (Table 3).

The development time for growth between egg hatching and CI has been determined for several oithonid species with varying precision. For most published studies it is difficult to determine from methods if time from N1 to CI is the time to the first appearance of CI, or to the time of 50% CI which is used in the present study. Development time as a function of temperature (Fig. 12), however, shows a classical Bělehrádek function which has been observed for egg development rates (McLaren 1966). Goswami (1975) determined that *O. brevicornis* and *O. hebes*? developed from N1 to CI in 8–10 and 10–14 days, respectively, at 24–27°C. Several species of calanoid copepods raised at 15°C developed from hatching to CI in 6.5–9.8 days (Landry 1983), which was much faster than oithonid species (Fig. 12). Development time for *D. oculata* to 50% N5 was 3.83 days, and development to 50% CI probably is in the range of the other oithonid species. Since ambient temperatures near the Belizean mangroves are typically near 30°C, *D. oculata* probably is adapted to growth at maximal rates at these high temperatures.

Dioithona oculata possesses a 2-segmented naupliar A1 (Figs. 1B, 2B, E, 3B, F), a brush-like seta on the exopod of both Mn and Mx1 of all copepodids (Figs. 4E, F, 5E, 6H, 9A, C, F), and modified setae on the basis of the male leg 1 (Fig. 9I). These structures have not been described for other cyclopoid copepods. A reduction (from 20 to 16) of setae on A1 from N6 to CI (Figs. 3F, 4C) has been reported only for *O. similis* and *O. atlantica.* Presence on male leg 4 of three endopodal setae modified with a hyaline flange similar to female leg 4 is unique to *D. oculata* (Fig. 11B, D).

Development of exopodal and endopodal segments of the swimming legs of *D. oculata* follows the common pattern described by Ferrari (1988, 1991) with the segmentation pattern of legs 1 and 2 identical, while legs 3–6 are similar but one copepodid stage each out of register. The addition of armament elements to each ramus is a more complex process. Six conditions of appendage development (Table 4) can be defined: (A) a leg bud, (B) a reorganized swimming leg with 1-segmented exopod and endopod, (C) an early 2-segmented exopod and endopod, (D) a later 2-segmented exopod and endopod, (E) a final 2-segmented exopod and endopod, (F) a 3-segmented exopod and endopod. Conditions A–F occur in legs 1–2, conditions A–D, and F occur in leg 3, and conditions A, B, D, and F occur in leg 4. Addition of armament elements on legs 1–

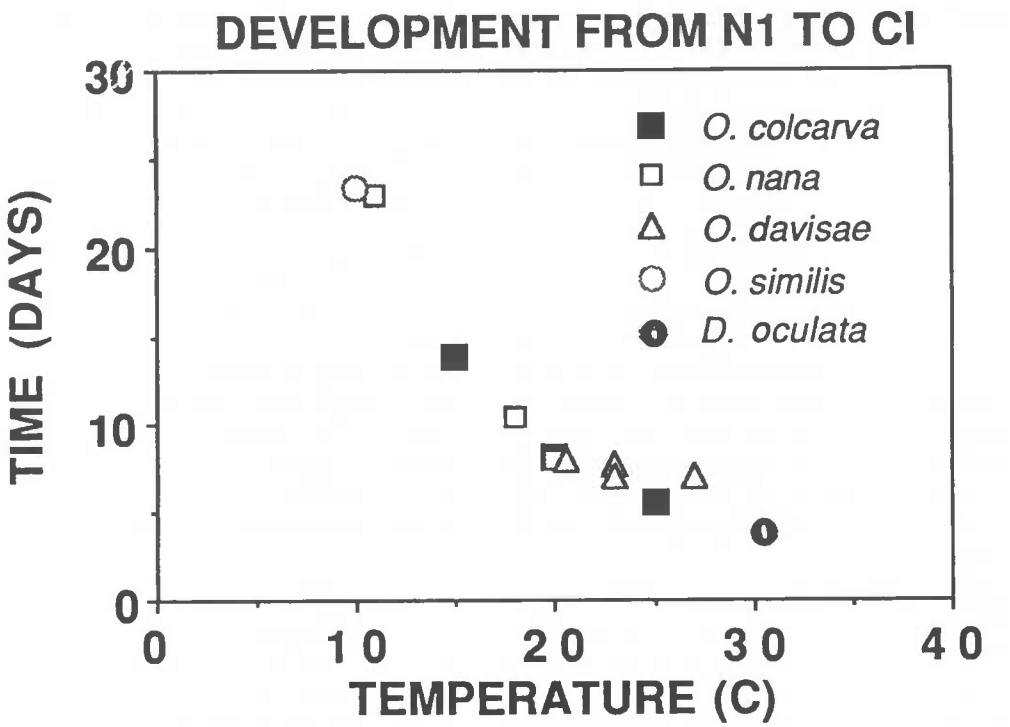

Fig. 12. Development time (days) as a function of temperature from egg hatching to CI for oithonid species. Only mean values are plotted. When means are not given, the middle value of the range is plotted. Literature values of development time given as mean and standard deviation (*O. colcarva* by Lonsdale 1981), mean and range (*O. davisae* by Uchima and Hirano 1986), range (*O. davisae* by Uchima 1979), range (*O. nana* by Haq 1965), and overall mean and range of means (*O. similis* by Eaton 1971 as referenced in McLaren 1978). *Dioithona oculata* development time from 50% N1 to 50% N5 from Table 3. Standard deviation or range from means was 1.2 at most, except for *O. similis* with a range of 2.0.

3 occurs prior to conditions B, C, D, and F. Addition of elements for leg 4 occurs prior to conditions in B, D, and F.

For swimming legs 2 and 3, identical numbers of elements are present on the exopod and endopod segments for each leg condition (Table 4). For leg 1 there are more elements present early in development and fewer present later in development than for legs 2 and 3. We have assumed that the early 2-segmented condition (condition C) is skipped for leg 4 so that numbers of exopodal elements are identical to legs 2 and 3 but the endopod of leg 4 has fewer elements later in development.

Inferences about homologies of several appendages of *D. oculata* can be drawn from the development of their segments by comparing morphology, position, or formation. Homology by morphology suggests that the Re1 of naupliar A2 is fused to the basis, and that the medial recurved seta of CR on CI may become the second from medial seta on CR of CII–CVI.

In *D. oculata* the elongate lateral extension of the basis of A2 (e.g., Fig. 1C) is a fused exopodal segment, and not an extension of the basis as has been described as a part of the basis for *Haplosaccus elongatus, Doropygus seclusus, Notodelphys affinis, Pygodelphys aquilonaris,* and *Scolecodes huntsmani,* because several inner setae are added to it in later naupliar stages (Fig. 3G). Armament additions such as this have not been reported for the basis of other copepod appendages. In most descriptions of cyclo-

Table 4.—Number of armament elements for *Dioithona oculata* of the exopod (Re) and endopod (Ri) of legs 1–4. Six leg conditions: (A) leg bud, (B) reorganized swimming leg with 1-segmented exopod and endopod, (C) early 2-segmented exopod and endopod, (D) later 2-segmented exopod and endopod, (E) final 2-segmented exopod and endopod, (F) 3-segmented exopod and endopod are listed on the left; the number of setae plus spines present on each ramus are given to the left of the slash and the stage of development is given to the right. C = copepodid; n = nauplius; nc = no change from previous stage in number of elements; np = condition not present for that leg.

	Leg Re				Leg Ri			
Leg condition	1	2	3	4	1	2	3	4
bud	3/n6	3/n6	3/CI	3/CII	2/n6	2/n6	2/CI	2/CII
1 + 1	8/CI	7/CI	7/CII	7/CIII	7/CI	6/CI	6/CII	6/CIII
2 + 2 (early)	9/CII	8/CII	8/CIII	np	7/CII	7/CII	7/CIII	np
2 + 2 (late)	10/CIII	11/CIII	11/CIV	11/CIV	8/CIII	8/CIII	8/CIV	7/CIV
2 + 2 (final)	nc/CIV	nc/CIV	np	np	nc/CIV	nc/CIV	np	np
3 + 3	12/CV	13/CV	13/CV	13/CV	8/CV	9/CV	9/CV	8/CV

poid naupliar development, a similarly elongate Re1 articulates with a simple, unextended basis. Other cyclopoid species in which this segment is described correctly as fused include *Ascidicola rosea* and *Lernaea cyprinacea.*

The long, thick, recurved, medial seta on the distal edge of the CR of CI (Fig. 4B) of *D. oculata* may be the homologue of the long, thick, second-from-medial seta of CII (Fig. 5B). A distinctively modified medial seta like that of *D. oculata* also is known for CI of *Haplosaccus elongatus, Haplostoma albicatum,* and *Lernaea cyprinacea.* Like *D. oculata,* CII of the first two species has a small, simple medial seta, and a longer thicker, second-from-medial seta. In CII–VI of *L. cyprinacea,* a distinctively modified seta of similar morphology to the modified medial seta of CI is present at the second-from-medial position. The medial seta in CII–VI is small and simple. Given these morphological data, an hypothesis that the medial seta of CI is the homologue of the second-from-medial seta in CII–VI of *D. oculata* seems reasonable. The identity of the seta on CI that is homologous to the medial seta on CII remains unresolved, although Dahms (1990) has described the transposition of two setae in similar positions during the development of an harpacticoid copepod.

Homology by position suggests that the endopod of Mxp is 2-segmented in all copepodids of *D. oculata,* and that the mandibular Ri1 is fused to the basis except in CVI male in which it is an articulating segment.

In determining homologies for the 5-segmented Mxp of CI–II (Fig. 4I) of *D. oculata,* we compared the position of groups of medial setae to similarly positioned groups of *Archimisophria discoveryi* (Boxshall 1985: fig. 34). Boxshall reviewed various proposed segment homologies of copepod postmandibular appendages and, basing his argument on the origin and insertion of muscles, he designated the proximal two segments of Mx2 and Mxp, each with two setiferous lobes, as the praecoxa and coxa. Based on positions of similar setal groups, we have interpreted segmental homologies for Mxp of *D. oculata* as a praecoxa, coxa, basis and a 2-segmented endopod. Although praecoxa and coxa are fused later in development (Fig. 9D), the endopod of *D. oculata* remains 2-segmented throughout its development, an inference which supports Ho's (1986) description of the oithonid maxilliped.

The mandible of the CVI male of *D. oculata* possesses two articulating endopodal segments, while the first of these segments is fused to the basis in all other nauplii and

eopepodids (Figs. 2G, 4E). Homologies of mandibular segments are somewhat problematieal; Izawa (1987) has suggested that the naupliar mandible of all cyelopoids has a 2-segmented endopod and a basis without medial lobes. Applying this definition, Ri1 (Fig. 2G) of *D. oculata* is fused to the mandibular basis, so that Ri1 with its two to four prominant spines forms a distal medial lobe of the basis. The artieulating segment is Ri2. In CI the seeond mandibular segment is eomprised of the basis and fused Ri1 with only two of the four prominent naupliar spines remaining; the artieulating segment is Ri2. This eondition also is found in CII–V and CVI female (Fig. 9A). We believe that an alternate hypothesis, i.e., that the naupliar inner lobe is a true lobe of the basis and not the fused Ri2, provides no unambiguous interpretation of the two free segments of CVI male.

Itô (1989) hypothesized that the basis of eopepod appendages originated by fusions of proximal segments of the exopod and endopod. Our information about fusion of Re1 of A2 and Ri1 of Mn of *D. oculata* supports that hypothesis.

Homology by formation suggests that the outer seta on segment 1 of A2 on CII–CVI is the remnant of the naupliar exopod, and that the addition of segments and armament of leg 3 usually oeeurs proximally on the distal-most segment.

We observed seven specimens of N6 with a small, wrinkled lobe bearing two setae whieh was visible within the long, fused Re1 of the nauplius. We believe that the wrinkled lobe is the exopod of CI. In a speeimen of CI, we observed the proximal section of a single, outer seta on segment 1 of the antennal exopod of CII whieh had formed within the wrinkled-lobe exopod of CI. However, we eould not determine in which one of the terminal distal setae of CI the distal seetion of this seta of CII seta was formed. This seta is the homologue of an exopodal seta and the seta is a remnant in copepodids of the naupliar exopod.

Lueks (1927), Hulsemann & Fleminger (1975), and Hulsemann (1991b) have used formation homology during eopepodid development, rather than positional or morphological homology, to determine segment or setal homologies of eopepod appendages. We used this method to determine the fate of swimming leg armament elements. Our findings are illustrated in Fig. 13. We studied three speeimens of CI in which the reorganized leg 3 of CII was visible within the leg 3 bud of CI, and one specimen of CII in whieh the reorganized leg 4 of CIII was visible within the leg 4 bud of CII. From these speeimens we infer that the three setae on the outer lobe of these leg buds beeome the distal-most outer spine, the terminal spine and the distal-most inner seta of the exopod (Fig. 13B); two outer spines and two inner setae are newly added. Two setae on the inner lobe of the leg bud beeome the middle two of six setae on the endopod; one terminal seta, the outer seta, and two proximal inner seta are new.

We studied one specimen of CII in whieh leg 3 of CIII was present within leg 3 of CII. The new segment of both exopod and endopod formed proximally to the distal ramal segment (Fig. 13C). On this new exopodal segment is the older, proximal-most, outer spine, and on the new endopodal segment is the older, proximal-most, inner seta. New setae of CIII not formed within a seta of CII are the inner seta of the coxa, outer seta of the basis, and the proximal-most, inner seta on eaeh distal ramal segment.

We examined two speeimens of CIII in whieh leg 3 of CIV was visible within leg 3 of CIII. No new segments are added but the proximal-most, inner seta of the distal segment of the endopod and proximal-most, inner seta and outer spine of the distal segment of the exopod were not formed within an element of CIII. These elements are presumed new (Fig. 13D).

We studied one specimen of CIV in which leg 3 of CV was present within leg 3 of CIV. The new segment on each ramus formed

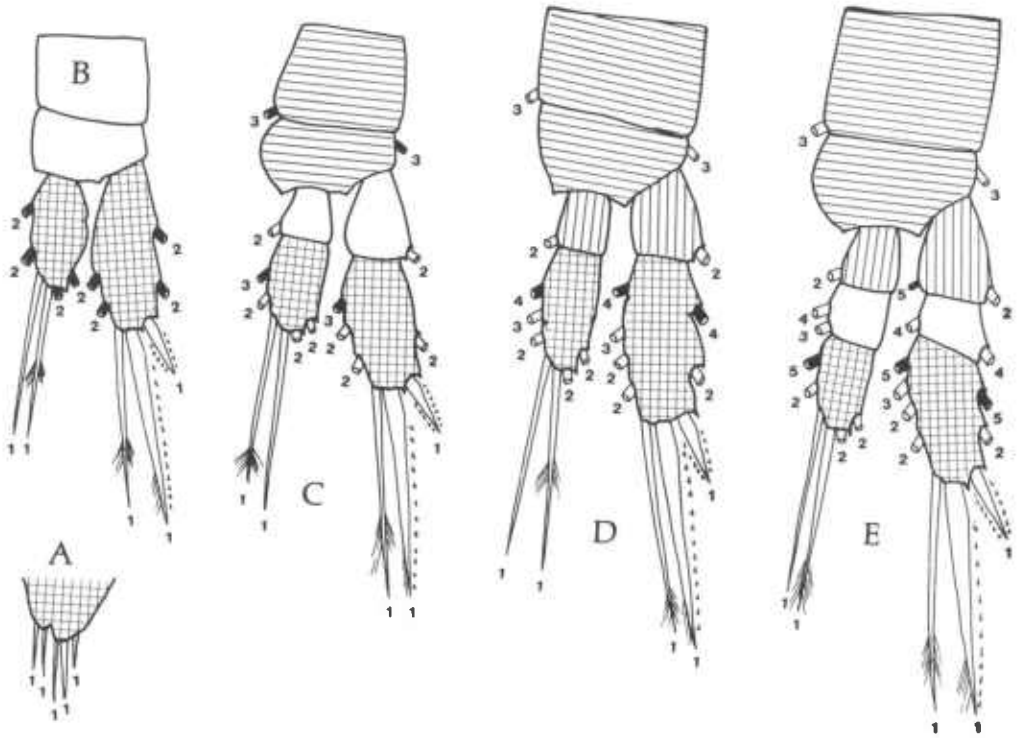

Fig. 13. *Dioithona oculata*, development of leg 3: A, primary bud of copepodid I with 3 setae on outer lobe and 2 setae on inner lobe. B–E, reorganized legs of copepodids II–V respectively. Oldest segment cross-hatched, youngest segment clear, oldest intermediate segment horizontally-hatched, youngest intermediate segment vertically-hatched. Oldest setae from copepodid I (#1's) are long; all others are cropped and new setae are black. New setae added to copepodids II–V are labeled #2–#5 respectively.

proximal to the distal ramal segment. On this new exopodal segment are the older, proximal-most, outer spine and inner seta, and on this new endopodal segment are two older, proximal-most, inner setae of differing ages (Fig. 13E). New setae of CV not formed within a seta of CIV are the small thin inner seta of Re1, the proximal-most inner seta on the distal endopodal segment, and the proximal-most inner seta and outer spine of the distal segment of the exopod.

Thus, for *D. oculata*, new leg segments appear to divide proximally from the distal-most, and oldest, segment of each ramus. Beginning at this distal-most and oldest segment, each more proximal, successive segments are younger than distal neighbors. New armament elements usually are formed at the proximal edge of the distal-most ramal segment. Older elements may be found both proximally and distally to this proximal edge. Changes in genetic regulation of element addition could produce the pattern reported by Von Vaupel Klein (1984) for *Euchirella messinensis*. In *D. oculata* a linear, symmetrical sequence of youngest-to-oldest armament elements may develop if new segments are added, continuously, one molt out of register and later than the newly added armament elements.

The addition of ramal segments described above agrees in general with the pattern described by Hulsemann (1991a) for *Drepanopus forcipatus*. A brief discussion of the pattern of development for segments and armament elements of leg 3 of *D. oculata* appears in Ferrari (1991).

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