Journal of Natural History

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P. A. McLAUGHLIN [a]; K. Anger [b]; A. Kaffenberger [b]; G. A. Lovrich [c]

[a] Shannon Point Marine Center, Western Washington University, 1900 Shannon Point Road, Anacortes, WA 98221-9081B, USA; e-mail: patsy@sos.net.
[b] Alfred-Wegener-Institut für Polar- und Meeresforschung: Biologische Anstalt Helgoland, Meeresstation, D-27498 Helgoland, Germany.
[c] Centro Austral de Investigaciones Cientificas (CADIC-CONICET), CC 92, (9410) Ushuaia, Tierra del Fuego, Argentina.

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P. A. McLAUGHLIN†, K. ANGER‡, A. KAFFENBERGER‡ and
G. A. LOVRICH§

†*Shannon Point Marine Center, Western Washington University,
1900 Shannon Point Road, Anacortes, WA 98221-9081B, USA;
e-mail: patsy@sos.net*
‡*Alfred-Wegener-Institut für Polar- und Meeresforschung: Biologische
Anstalt Helgoland, Meeresstation, D-27498 Helgoland, Germany*
§*Centro Austral de Investigaciones Científicas (CADIC-CONICET),
CC 92, (9410) Ushuaia, Tierra del Fuego, Argentina*

Morphological variations in the two zoeal stages and megalopa of a lecithotrophic population of *Paralomis granulosa* (Jacquinot) reared under laboratory conditions are reviewed. Attention is also directed to certain aspects of their development not previously considered. More importantly, the first three juvenile stages are described and illustrated for the first time. Specific consideration is given to the structural changes in the abdominal tergites during the transformation from megalopa to third crab, and ancillary information on abdominal plate development in juvenile stages four and five is provided. Total pleopod loss in both sexes and subsequent reappearance in females is discussed.

Introduction

Larval development in the genus *Paralomis* consists, as far as is known, of two zoeal stages and a megalopal stage. Of the 46 species assigned to this genus, zoeal and megalopal stages have been described only for *Paralomis granulosa* (Jacquinot in Hombron and Jacquinot, 1846), by Campodonico and Guzmán (1981), for *P. japonicus* Balss, 1911, by Hayashi and Yanagisawa (1985), and for *P. hystrix* (De Haan, 1846), by Konishi and Taishaku (1994). Heretofore, no morphological information has been available for the early crab stages. In addition to describing and illustrating the structural attributes of the first three crab stages of *Paralomis granulosa*, we have paid particular attention to the changes occurring in the abdominal tergites between the megalopal and the early crab stages and to juvenile

pleopod loss. However, we also have had the opportunity to note some variations in the zoeal morphology from that reported by Campodonico and Guzmán (1981) for a population at Puerto Zenteno, Straits of Magellan. Variations observed in the structures of mandibles and maxillules may, at least in part, be correlated with the fact that larvae from our more southern population of *P. granulosa* are fully lecithotrophic, at least during the zoeal stages (Kaffenberger, 2001). Additionally, since the completion of the initial study, supplemental information on abdominal plate development has been become available from surviving juveniles that moulted to crab stages four and five.

Materials and methods

Females of *Paralomis granulosa* were collected in Beagle Channel, near Ushuaia, Tierra del Fuego, Argentina, and transported to the Helgoland laboratory aboard the RV *Polarstern*. These females were held in live tanks with running seawater (6°C, 32‰ salinity) until their larvae hatched. The larvae were provided with filtered (1 μm pore size) North Sea water at constant 6°C, a salinity of 32‰, and artificial light conditions with 12:12 h light: darkness. Sibling larvae were individually reared in 100-ml beakers under fed (freshly hatched *Artemia franciscana*; food density *ca* 10 nauplii per ml) and non-fed conditions. Water was changed every 2 days. Larval development from hatching through metamorphosis to the first juvenile crab instar was at least facultatively lecithotrophic; no significant differences between the two treatments occurred in the duration of development or in the rate of mortality; details of larval and early juvenile development, growth and changes in chemical composition will be published elsewhere. Samples for the morphological examination were taken from unfed cultures.

Five individuals from each zoeal, megalopal and first crab, two from the second and five from the third crab stages were preserved in 70% ethyl alcohol for morphological examination. Supplemental information on the second and third crab stages were obtained through the examination of exuviae. Additionally, five individuals and three exuviae of the fourth crab stage and five individuals of the fifth crab stage were reviewed for abdominal plate development. Specimens were stained in 1% chorazol black E for detailed examination. Zoeas were initially evaluated using a Wild M-5 dissecting microscope, then dissected and mounted in polyvinyl alcohol lactophenol and critically examined using a Wild M-20 compound microscope. Megalopal and early crab stage specimens were dissected in 70% ethyl alcohol, with non-calcareous appendages also mounted in polyvinyl alcohol lactophenol. All illustrations were made with the aid of camera lucidas mounted on these microscopes. One measurement, carapace length (cl), as measured from the tip of the anterior rostral projection to the mid-point of the posterior carapace, provides an indication of animal size. Terminology for the descriptions follows that of Crain and McLaughlin (2000a).

Developmental descriptions

First zoeal stage (cl = 2.75–3.25 mm; N = 5)

Campodonico and Guzmán (1981) reported that the eyes of their first-stage zoeas were sessile. While anomuran eyes are sessile in typical Zoea I larvae (Fincham, 1992), Crain and McLaughlin (2000a) noted that the eyes in the lithodid, *Lopholithodes mandtii* Brandt, 1848, which has four, or rarely five zoeal stages,

varied from being partially fused to the carapace to being completely stalked. The eyes in our specimens of *Paralomis granulosa* (figure 1A) all are stalked, although the peduncles remain adjacent to the orbital walls of the carapace. The ocular peduncles each consists of a single 'segment' (cf. Powar, 1969), with delineated cornea.

Although development of the protopodal spines of the antenna and setation of the scaphocerite in our specimens (figure 2C) are comparable, the endopod lacks any trace of the incipient segmentation described and illustrated by Campodonico and Guzmán (1981: figure 1F) for their first-stage zoeas. A feature not mentioned by these authors in their description of the antenna is the prominence of the protrusion marking the orifice of the antennal gland that is present in our specimens.

Campodonico and Guzmán described the mandible as being strong, with a series of small teeth. In our sample, the mandibles (figure 2E) lack all traces of calcification. Although incisor and much-reduced molar processes are distinguishable, dentition on the incisor process consists of one prominent tooth, and a series of minute denticles; only a few very miniscule denticles can be seen on the molar process. A small, unsegmented palp bud is present.
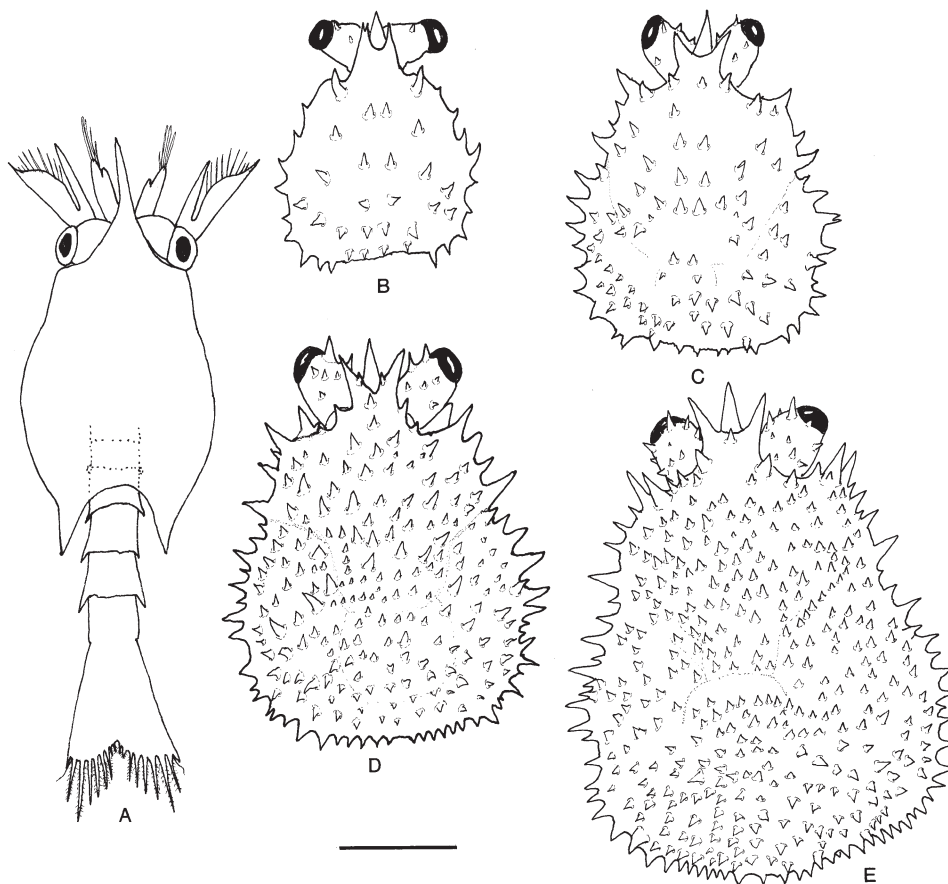

FIG. 1. *Paralomis granulosa* (Jacquinot, 1846). (A) Whole animal (dorsal view); (B–E) carapace and ocular peduncles (dorsal view). (A) First zoeal stage; (B) megalopa; (C) first crab stage; (D) second crab stage; (E) third crab stage. Scale = 1 mm.
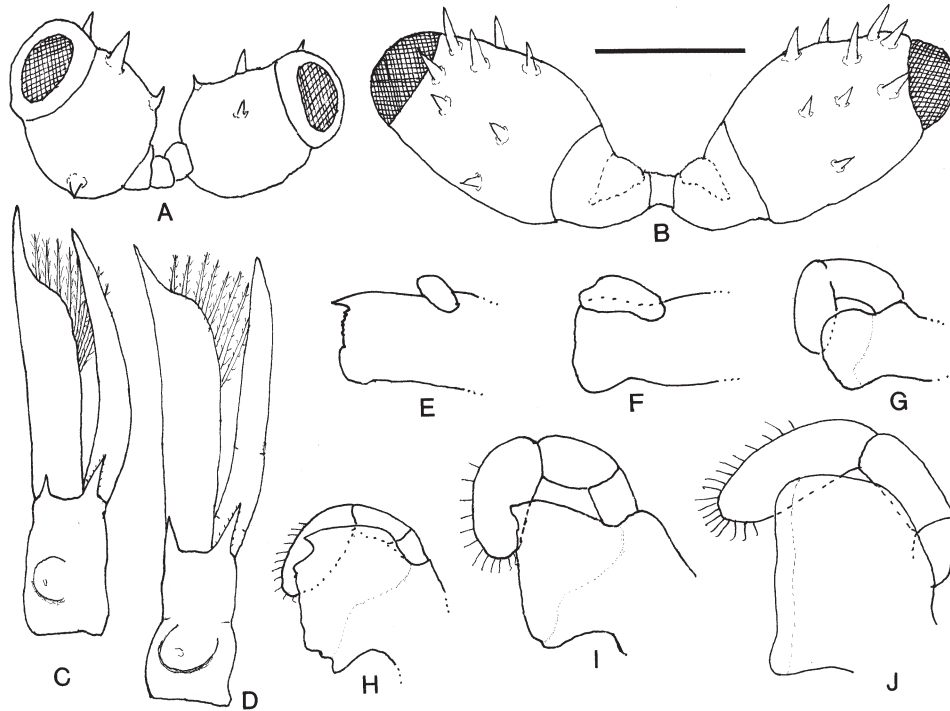
FIG. 2. *Paralomis granulosa* (Jacquinot, 1846). (A, B) Ocular peduncles (dorsal view); (C, D) antennae (ventromesial view); (E–J) mandible (left, external view). (A) Megalopa; (B) crab stage 3; (C), first zoeal stage; (D) second zoeal stage; (E) first zoeal stage; (F) second zoeal stage; (G) megalopa; (H) first crab stage; (I) second crab stage; (J) third crab stage. Scale = 0.5 mm (A, B), 0.4 mm (C, D) and 0.25 (E–J).

The endopod of the maxillule (figure 3A) is three-segmented in our specimens rather than two-segmented, as reported by Campodonico and Guzmán; only one or two short terminal setae are present. In both populations, the basial endite of this appendage has two quite small, weakly denticulate teeth. Development of the coxal endite appears similar.

In our specimens, the proximal lobe of the scaphognathite of the maxilla (figure 3E) is not delineated, whereas this lobe is described as forming a pointed lobe in Campodonico and Guzmán's specimens. Our specimens also had fewer setae on the distal lobe. Similarly, the endopod and both lobes of the coxal and basial endites are provided with fewer setae in our material.

Konishi and Taishaku (1994) reported 'regressive' mouthpart morphology for *Paralomis hystrix*, and suggested that the main mouthparts might not be functional during the zoeal stages. The reductions in the mouthparts, particularly in the mandibles and maxillules, observed in our population of *P. granulosa* are consistent with their full lecithotrophy. When viewed *in situ*, the mandibles and maxillules of all our specimens are not only markedly reduced but widely separated by the labrum and paragnaths. This is in significant contrast to the structure and position of these appendages as described and illustrated by Crain (1999) for *Placetron wosnessenskii* Schalfeew, 1892 first-stage zoeas, which are known to feed actively.

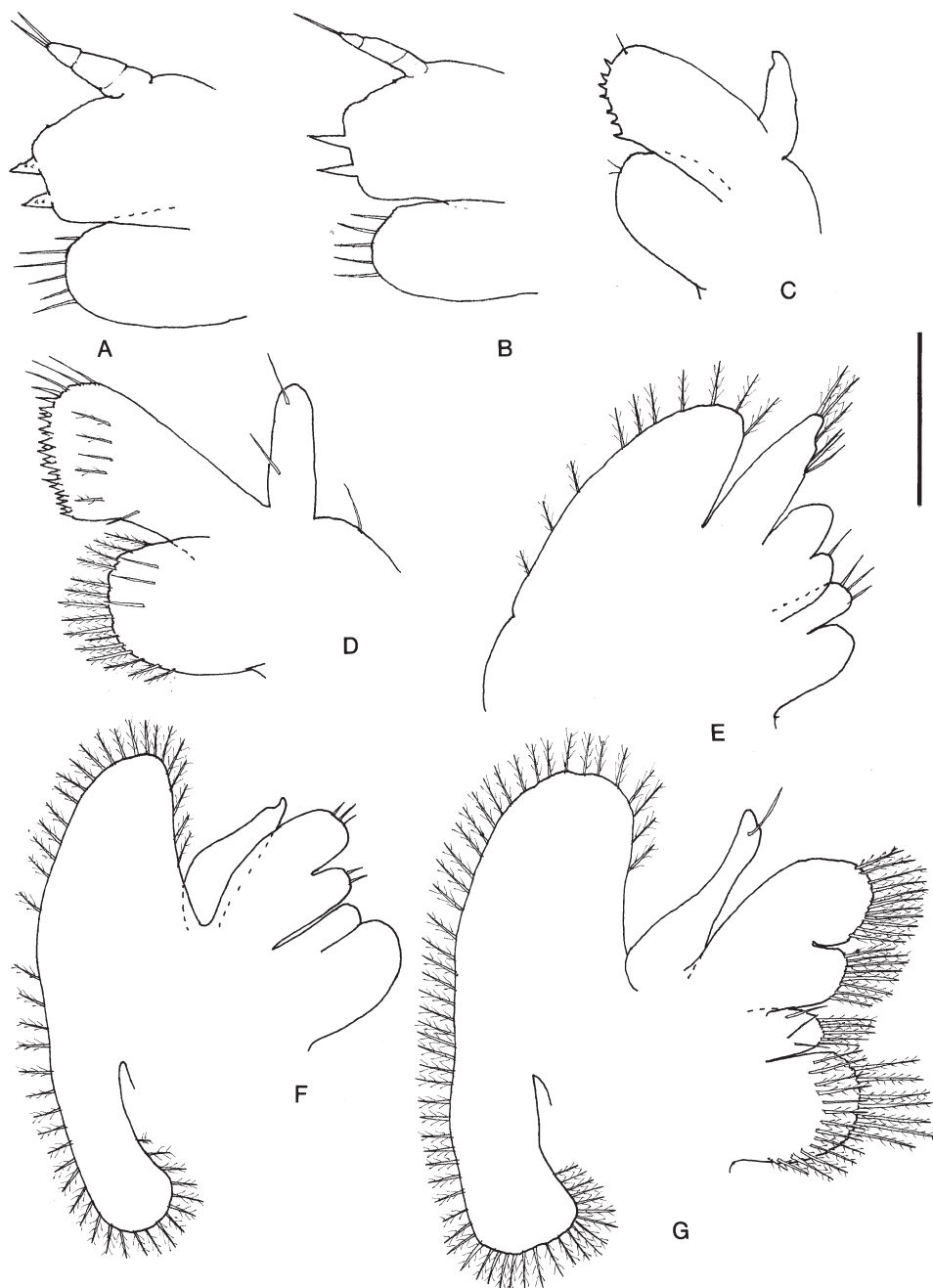Gills were not mentioned by Campodnico and Guzmán (1981); however, in all

FIG. 3. *Paralomis granulosa* (Jacquinot, 1846). (A–D) Maxillule (left, external view); (E–G) maxilla (right, external view). (A) First zoeal stage; (B) second zoeal stage; (C) megalopa; (D) first crab stage; (E) first zoeal stage; (F) megalopa; (G) first crab stage. Scale = 0.25 mm.

of our first-stage zoeas arthrobranchial buds were present at the bases of the developing chelipeds and ambulatory legs.

Campodonico and Guzmán described abdominal somites 2–5 as each bearing a pair of strong lateral spines, usually an additional two to four spines on the posterodorsal margins, and a pair of dorsal hair-like setae. In our specimens (figure 1A) the posterodorsal margins exhibit nothing more than weak crenulations or minute protuberances; no dorsal hair-like setae have been observed. Paired abdominal pleopods 2–5 were described by the earlier authors as present, with rudimentary endopods developed. In three of our five specimens, the pleopods are represented only by incipient, uniramous buds. In the other two, uniramous, but moderately well-developed pleopod buds are present. The telson, while not distinctly separated from the sixth somite, does show indications of potential separation. No anal spine has been observed in any of our material.

Second zoeal stage (cl=2.87–3.22 mm; N=5)

Campodonico and Guzmán (1981) gave no measurements for their specimens, but judging from their illustrations (1981: figures 1A, B, 2A, B), their specimens, like ours, showed no noticeable growth from the first stage to the second. Variations in the second-stage development of zoeas from the two populations includes segmentation of the antennules and antennae, and differences in the mandibles and maxillules.

The incipient segmentation of neither the antennular peduncle nor its endopod and exopod is as advanced in our second-stage zoeas as described by Campodonico and Guzmán. The peduncle in our specimens shows only slight indications of division into two segments, as does the exopod. No impending segmentation of the endopod can be detected.

Only two or three incipient segments have been observed on the endopod of the antenna (figure 2D); however, the first segment of the peduncle shows partial delineation and the protrusion of the antennal gland is more prominent than in the preceding stage.

The molar process of the mandible (figure 2F) is no longer distinguishable in the present material, although both processes are illustrated by Campodonico and Guzmán (1981: figure 2G). The mandibular palp has enlarged in our specimens, but no incipient segmentation is detectable.

Like the maxillules in the earlier study, the coxal endite has only a few short setae, and the basial endite has only two small spine-like teeth. However, while Campodonico and Guzmán illustrate a still two-segmented endopod with three terminal setae, the endopods of our specimens are three-segmented, but with only a single terminal seta (figure 3B).

The proximal lobe of the scaphognathite is now separated from the protopod; however, setation is not as abundant as indicated by Campodonico and Guzmán for their specimens.

Arthrobranchs are better developed at bases of the chelipeds and ambulatory legs.

Well-developed, unequally biramous pleopod buds are now present on abdominal somites 2–5; however there is no indication of setae. As in Campodonico and Guzmán's population, there is still nothing more than a faint hint of separation of the telson and sixth somite. No uropods are developed.

Megalopa (cl=2.06–2.18 mm; N=5)

The carapace lengths of the megalopas of the two populations are practically identical. Development of the anterior process (rostral spine of Campodnico and Guzmán) and carapace spines (figure 1B) is also quite similar in the two populations, although it is more variable in ours. In our specimens, the dorsal rostral spines (anterolateral spines of Campodonico and Guzmán) are simple or bifid, and nearly as long as the anterior process The *linea anomurica* is only weakly delineated anteriorly at the carapace margin.

Segmentation of the ocular peduncles was not addressed by Campodonico and Guzmán. In our specimens, the ocular peduncles (figure 2A) at this stage are clearly three-segmented, the third (distal) and second (subdistal) segments are separated by a median ocular plate, representing the fused first (proximal) segments. Each distal peduncular segment is provided with three or four spines, as it is in Campodonico and Guzmán's specimens.

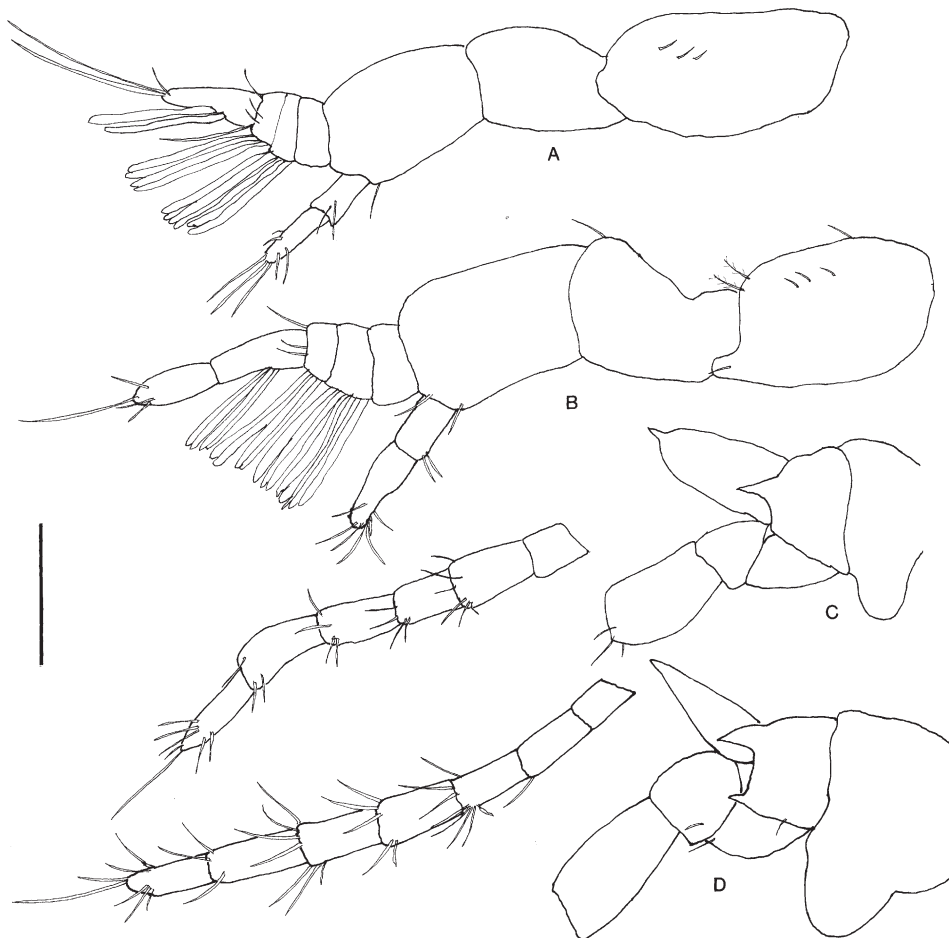Development in the megalopal antennule (figure 4A) is comparable between the

FIG. 4. *Paralomis granulosa* (Jacquinot, 1846). (A, B) Antennule (lateral view); C, D, antennal peduncle (lateral view) and flagellum (detached). (A) Megalopa; (B) first crab stage; (C) megalopa; (D) first crab stage. Scale=0.25 mm.

two populations, although the second article of the upper ramus has six to eight aesthetascs rather than the four reported by Campodonico and Guzmán. Differences in terminology are attributed, in part, to the apparent variation seen in the antenna (figure 4C). Campodonico and Guzmán (1981: 279, figure 3F) refer to the three distal segments of the antennal peduncle and the antennal flagellum collectively as the endopod; the first and second peduncular segments are reported as the 'basal peduncle'. In our specimens, the antennal flagellum consists of six articles, which is consistent with the flagellar portion of the earlier authors' 'endopod'. Only one of the 'two short ventral spines' of their 'basal peduncle' is present in our examples, and that spine is on the dorsolateral distal angle of the second peduncular segment. A supernumerary segment is apparent above the third segment.

Some variation is discernible in the feeding appendages, which now include the three maxillipeds. Only the palp of the mandible is described by Campodonico and Guzmán, and they report that it is well developed and three-segmented. They do, however, illustrate the mandible (1981: figure 3G) as having a denticulate medial margin. The mandibular palp in our specimens is moderately well developed, but only two-segmented and lacking all setae. The mandible (figure 2G) has a smooth, unarmed medial margin or may have one or two miniscule denticles, the exterior surface is similarly smooth; however, the inner surface is deeply concave and partially divided by a ridge that might be interpreted as a vestige of the molar process.

The maxillule is again reported by Campodonico and Guzmán to have a two-segmented endopod; the basial endite (their basipodite) bears three or four setae and several small teeth; the coxal endite (their coxopodite) is provided with two or three setae and a few lateral teeth. In contrast, the maxillules (figure 3C) of our specimens have an unsegmented, naked endopod. The basial endite is provided with seven to ten marginal small teeth and one or two submarginal short setae; the coxal endite has only two to four very short setae.

The megalopal maxillas (figure 3F) in our material, like their zoeal counterparts, lack much of the setation of the coxal and basial lobes described by Campodonico and Guzmán for their specimens. However, the scaphognathites in our sample have 42–47 marginal setae. The earlier authors recorded from 45 to 54 setae.

The primary differences seen in the maxillipeds between the two populations is in the setation of the first and the segmentation of the third. Whereas the coxal and basial endites of the first maxilliped (figure 5A) are provided with marginal setae in Campodonico and Guzmán's megalopas, these endites completely lack setae or at most have only one or two extremely short setae in our sample. The earlier authors also report that the endopod of the third maxilliped is four-segmented, and illustrate (Campodonico and Guzmán, 1981: figure 3L) a large basal protuberance on the protopod. Our specimens have five-segmented endopods (figure 5D) and completely lack any unusual protuberance on the protopod. There is a slight indication of the developing crista dentata that was not mentioned for their population, and a strong spine is present on the ventromesial distal surface of the ischium in our specimens.

As in the earlier study, the megalopal chelipeds and ambulatory legs all are provided with slender, acute spines. The fifth pereopod is reduced and already carried under the carapace. A pair of small arthrobranchs are now present at bases of the third maxillipeds; larger and better-developed arthrobranchs are seen at bases of chelipeds and ambulatory legs; a pleurobranch bud is present on the thoracic wall above the fourth pereopod.

There is a certain amount of disagreement in the armature of the abdominal
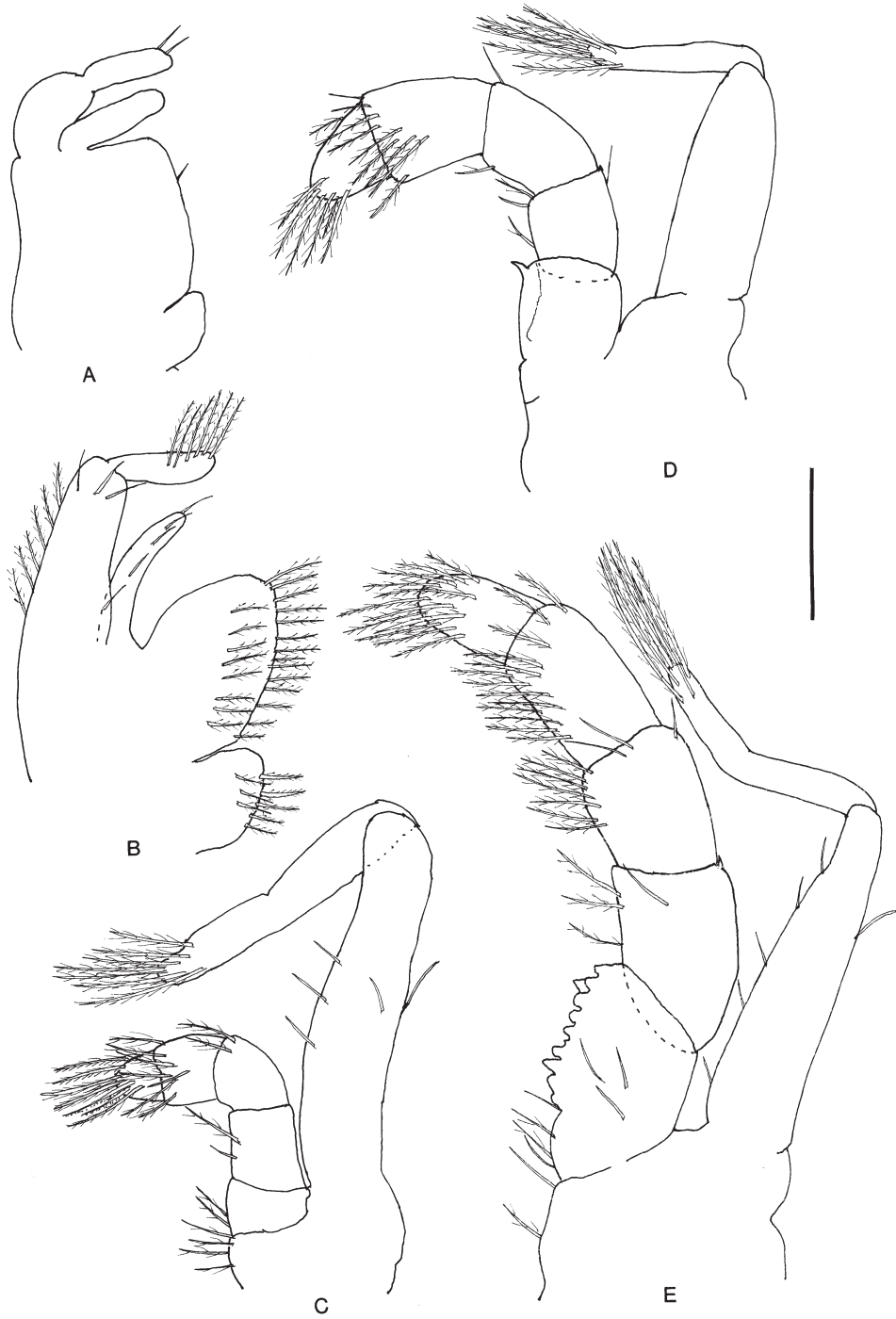
FIG. 5.   *Paralomis granulosa* (Jacquinot, 1846). (A, B) First maxilliped (right, external view); (C) second maxilliped (left, external view); (D, E) third maxilliped (left, external view). (A) Megalopa; (B) first crab stage; (C) first crab stage; (D) megalopa; (E) first crab stage. Scale = 0.25 mm.

tergites in Campodonico and Guzmán's megalopas and ours. These same tergal spines generally can be traced in the elements of the tergites in subsequent crab stages. All megalopal tergites (figure 6A) are well calcified. The first is appreciably smaller than the second and armed with a pair of prominent, median, dorsal spines and a smaller pair of spines dorsolaterally. The tergite of the second somite is broad, convex, and armed with an anterodorsal row of four spines, the median pair being appreciably larger than the lateral pair, a posterodorsal row of four spines, and a
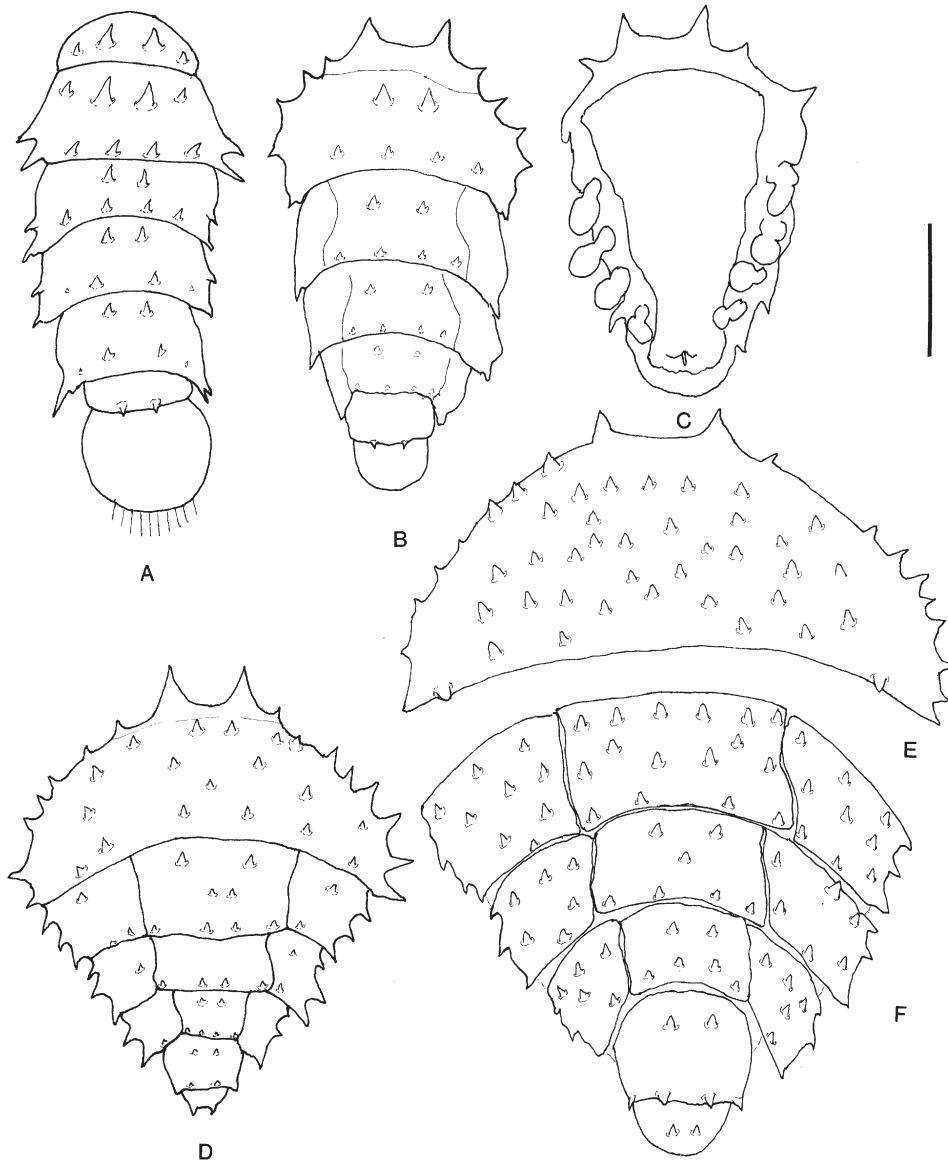

FIG. 6.   *Paralomis granulosa* (Jacquinot, 1846). (A, B, D–F) Abdomen (dorsal view); (C) abdomen (ventral view). (A) Megalopa; (B) first crab stage; (C) first crab stage; (D) second crab stage; (E) third crab stage fused first and second tergites; (F) third crab stage tergites 3–6 and telson. Scale = 0.5 mm.

pair of simple or bifid spines on each lateral surface, strongest at the posterior angle. The tergites of the third to fifth somites are each slightly narrower than the preceding; each is armed with a pair of anterodorsal spines and a row of four posterodorsal spines; the lateral pair of this row often are tiny, and sometimes represented only by slight protuberances. Paired lateral spines are present on these somites; those at the posterolateral angles are larger and increase in size distally, whereas the more anterior spines decrease in size distally, and may even be lacking on the fifth tergite. The tergite of the sixth somite, now clearly delimited, is armed with a small pair of posteromedian spines. Frequently, each tergal spine is accompanied by a single seta. The telson is roundly subquadrate and provided with setae on the rounded or slightly indented terminal margin.

First crab stage (cl=2.42–2.87 mm; N=5)

Carapace (figure 1C). Elongate and roundly subrectangular in outline, globular; with gastric and cardiac regions faintly delineated, spines varying in strength and number; anterior projection moderately long, basally moderately narrow to moderately broad, terminally acute and slightly curved upward, dorsal spines prominent, simple or bifid, dorsal and ventral rostral surfaces unarmed; external orbital and antero-external spines small to large, hepatic spine prominent; gastric region with two or three pairs of small to moderately large spines medially and few to several additional small spines laterally; cardiac region with three or four pairs of small to moderately large median spines and few to several smaller spines laterally; branchial regions each with several small and few larger, simple and bifid spines; marginal carapace spines numerous, prominent and frequently bifid. Ocular peduncles with distal peduncular segments each with four to six spines. *Linea anomurica* now clearly delineating branchostegial portion of carapace.

Antennule (figure 4B). Basal peduncular segment with three to several short setae on upper margin of statocyst lobe, one or two plumose setae distally; one to four short setae distally on penultimate segment; distal segment with one or two short setae ventrally; upper ramus of flagellum with five articles, groups of 0, 6–8, 4–6, 4 aesthetascs, progressing distally, distal article with one long terminal seta and two to four shorter setae subterminally, often one moderately long seta in proximal half; lower ramus still with two articles, basal article usually with two or three short setae distally, distal article with four to six subterminal and two or three terminal setae.

Antenna (figure 4D). Peduncle with well-developed spine at dorsolateral distal angle of segment second and smaller spine at dorsomesial distal angle; scaphocerite subtriangular, with acute terminal spine-like projection; flagellum with seven distinct articles, setal formula progressing distally, 0, 0–1, 2–8, 2–5, 2–7, 2–3, 4–7 terminal and/or subterminal.

Mandible (figure 2H). Well calcified; incisor process with few blunt to subacute small teeth on medial margin; remnant of molar process appearing as one large blunt tooth basally, inner surface with lower half developed as prominent ridge; palp indistinctly three-segmented, terminal segment with 10–12 short setae.

Maxillule (figure 3D). Coxal endite 14–18 marginal and two or three submarginal plumose or plumodenticulate setae; basial endite with double row of spiniform, cuspidate setae and 9–12 marginal and submarginal, simple and plumose setae; endopod with one terminal and one proximal seta.

Maxilla (figure 3G). Proximal lobe of coxal endite with marginal row of 9–18 plumose and plumodenticulate setae, and submarginal row of 12–14 simple or

plumose setae; distal lobe with one to four submarginal and five to seven marginal plumose or plumodenticulate setae; basial endite with 3–12 marginal plumose setae on proximal lobe, 1–14 marginal and no to three submarginal plumose setae on distal lobe; endopod with one subterminal seta; scaphognathite with 55–63 marginal plumose setae.

First maxilliped (figure 5B). Coxal endite with 7–10 marginal or submarginal plumose setae; basial endite 14–18 marginal plumose and plumodenticulate setae and 8–10 submarginal plumose setae; endopod unsegmented, with three or four setae; exopod two-segmented, with six marginal and four or five surface, simple or plumose setae on proximal segment, six apical, plumose setae on distal segment.

Second maxilliped (figure 5C). Endopod five-segmented, segments all with some marginal plumose setae, fewest proximally, also plumodenticulate setae on propodus and dactyl; exopod two-segmented, with three or four short setae on inner and one seta on outer margin of proximal segment, distal segment with six to eight apical, plumose setae.

Third maxilliped (figure 5E). Endopod with crista dentata now clearly developing, with seven or eight small teeth, accessory tooth apparent; carpus with few denticulate, simple and plumose setae; propodus with some plumose and numerous serrate and/or denticulate setae; exopod with six to eight plumose, apical setae.

Pereopods (figure 7A–D). Chelipeds subequal, dactyls and fixed fingers with few
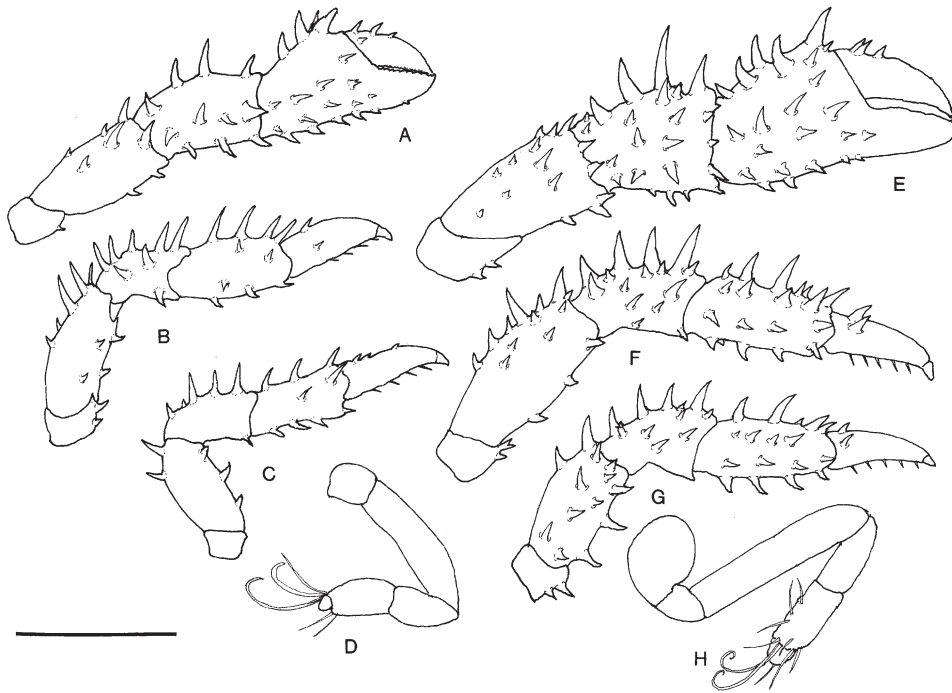
FIG. 7. *Paralomis granulosa* (Jacquinot, 1846). (A–D) Crab stage 1; (E–H) crab stage 2. (A) Right cheliped (dorsal view); (B) right second pereopod (lateral view); (C) right fourth pereopod (lateral view); (D) right fifth pereopod (lateral view); (E) right cheliped (dorsal view); (F) right second pereopod (lateral view); (G) right fourth pereopod (lateral view); (H) right fifth pereopod (lateral view). Scale = 1 mm (A–C, E–G) and 0.5 mm (D, H).

short to moderately long spines; palms, carpi, meri, all with numerous long, slender, usually acute, and often corneous-tipped spines. Ambulatory legs as long or longer than chelipeds, first (second pereopod) longest; dactyls each with row of four or five corneous spines on ventral margin; propodi, carpi and meri all with numerous long, slender, acute spines. Fifth pereopods reduced, carried beneath carapace. Paired biserial arthrobranchs with well-differentiated lamellae on bases of third maxillipeds, chelipeds and pereopods 2–4; equally well-developed pleurobranch on thoracic wall above fourth pereopod.

Abdomen (figure 6B, C). Strongly flexed against cephalothorax; first and second somites with tergal plates entire, distinct or partially to almost entirely fused; four large spines of first still very prominent, or with lateral pair markedly reduced; second still with both anterodorsal and posterodorsal row of four spines, additional one or two pairs of spines on each lateral margin; third to fifth somites each with incomplete or complete lateral sutures dividing tergites into median and lateral plates, median plates each still with pair of anterodorsal spines and row of four posterodorsal smaller spines; lateral plates each sometimes with additional one to three marginal or submarginal spines, largest at posterolateral angle; sixth somite with tergite entire, armed with pair of spines on posterodorsal margin.

Pleopods (figure 6C). Varying from still present, but rudimentary, with left slightly larger than right, to entirely absent on both sides.

Telson. Subcircular to laterally subovate, unarmed.

Second crab stage (cl=2.60–3.26 mm; N=9)

Carapace (figure 1D). Roundly subtriangular; dorsal spines of rostrum somewhat smaller but still prominent, and sometimes with one or two accessory spinules, terminally simple or weakly bifid; external orbital and antero-external spines reduced; gastric region sometimes with pair of somewhat larger median spines and two additional pairs of moderately large spines distinguishable, sometimes only with numerous small spines; cardiac region also with numerous small spines, frequently two slightly larger median pairs; branchial regions with numerous smaller spines and often one larger pair posteriorly. Ocular peduncles with second segment somewhat larger than in previous stage; distal segment usually with one or two additional spines.

Antennule. Two to four additional aesthetascs and two or three additional setae on upper ramus; lower ramus usually incompletely three-segmented.

Antenna. Scaphocerite more prominently produced, margins occasionally microscopically serrate; flagellum with seven or eight articles.

Mandible (figure 2I). Medial margin smooth or with few minute denticles, inner surface with broad thick shelf in lower half; palp still with 10–12 short marginal setae.

Maxillule. Little changed from previous stage.

Maxilla. Proximal lobe of coxal endite with marginal row of 12–16 plumose and/or plumodenticulate setae, and submarginal row of 10 or 11 weakly plumose setae; distal lobe with five to seven submarginal and four to six marginal plumose or plumodenticulate setae; basial endite usually with one submarginal and five to seven marginal plumose setae on proximal lobe, one submarginal and 12–14 marginal plumose setae on distal lobe; endopod still with one subterminal seta; scaphognathite with 56–62 marginal plumose setae.

First maxilliped. Coxal endite with 7–10 marginal or submarginal plumose setae; basial endite with 15–18 marginal plumose and plumodenticulate setae and seven

to nine submarginal plumose setae; endopod with one or two subterminal and four to seven surface plumose or simple setae; exopod with six simple, marginal and four simple or plumose, surface setae on proximal segment, six apical setae on distal segment. Second and third maxillipeds with endopod setation slightly increased.

Pereopods. Chelipeds and ambulatory legs all with increased length and spination.

Abdomen (figure 6D). Symmetrically subtriangular; tergite of somite 1 usually partially to completely fused with tergite of somite 2; lateral plates of tergites 3–5 entirely separated from median plates.

Pleopods. Completely absent.

Telson. Roundly subquadrate; pair of small terminal spines developing.

Third crab stage (cl=3.26–3.92 mm; N=9)

Carapace (figure 1E). Still roundly subtriangular; dorsal spines of rostrum still prominent, with simple or weakly bifid tips; external orbital and antero-external spines as in previous stage; gastric region with numerous moderate to small spines; cardiac and branchial regions also with increased number of small spines. Ocular peduncles (figure 2B) with slight increase in spination on distal segments, second segments each with area of calcification dorsally, medial plate still membranous.

Antennule. Upper ramus still with five, sometimes now with six articles, one or two additional pairs of aesthetascs; lower ramus usually completely three-segmented.

Antenna. First peduncular segment with prominent spine on lateral surface; scaphocerite larger and more acutely triangular, with prominent lateral spine; flagella each with eight or nine articles, setation as in previous stages.

Mandible (figure 2J). Medial margin smooth and sometimes slightly sinuous but also noticeably thickened, inner surface still with broad thick shelf in lower half; palp with 15–17 short marginal setae.

Maxillule. Coxal endite with additional simple and plumodenticulate setae; basial endite with additional spiniform, cuspidate setae marginally and plumose setae in submarginal row.

Maxilla. Lobes of coxal and basial endites all with additional setae; endopod unchanged; scaphognathite with 76–82 marginal plumose setae.

First maxilliped. Coxal and basial endites with increased setation; exopod now with 8–10 apical setae on distal segment. Second and third maxillipeds with endopod setation increased, exopods each with 10–12 apical setae.

Pereopods. Chelipeds distinctly asymmetrical, segments all with few additional spines; dactyls of ambulatory legs each still with five corneous spines on ventral margin and two calcareous spines on dorsal surface proximally; propodi, carpi and meri all with increased length and spination.

Abdomen (figure 6E, F). Symmetrically subtriangular; tergite of somite 1 completely fused with tergite of somite 2 (figure 6E), spines of second appreciably increased in number but not in size; tergites 3–5 (figure 6F) strongly flexed against thorax, lateral plates entirely separated from median plates, both with increased spination, marginal spines somewhat reduced in size.

Pleopods. Completely absent, sex indeterminate.

Telson. Subsemicircular, pair of small spines no longer terminal in position.

Abdominal plate development in supplemental stages (fourth crab stage cl= 3.6–4.2 mm, N=8; fifth crab stage cl=4.5–5.6 mm, N=5).

As previously indicated, five specimens that moulted to the fourth stage and exuviae of three individuals that successfully reached the fifth stage have been

examined, together with five fifth crab stage individuals that either died or were killed at the termination of the nutritional study. No changes were observed in fused tergites 1 and 2 in these subsequent stages other than increases in size and some additional surface spines. The very preliminary development of accessory nodules in the marginal integument of tergites 3 and/or 4 such as that observed in the third stage in *Lithodes santolla* (Molina, 1782) (cf. McLaughlin *et al.*, 2001) and *L. aequispinus* (Benedict, 1895) (cf. McLaughlin and Paul, 2002), was apparent at least on the right side of the abdomen in all but one of the fourth-stage specimens and exuviae. However, of those individuals where nodular development was limited to the right side, no asymmetry in the lateral plates could be detected. By the fifth crab stage (figure 8A, B), sexual dimorphism was clearly apparent, with quite small, but well-defined accessory marginal plates present on the right side in the three females and on both sides in the two males. Despite the absence of observable gonopores, the onset of female lateral plate asymmetry was unmistakable, particularly in tergite 5. There was no indication of pleopod development in these females.

Results

Although the initial zoeal stage in *Paralomis* is technically Zoea I (ZI), as reported by Konishi and Taishaku (1994), it is an atypical ZI. While the setation of the first and second maxillipeds corresponds to characteristic ZI setation, and the basial endite of the maxillule has two teeth, in all other respects, the first zoeal stage to hatch in this genus exhibits much more precocious morphology than typical Zoea I paguroid larvae. For example, the antennular endopod is already separated from the protopod, and the mandibular palp bud is already apparent. Additionally, the third maxilliped has both rami differentiated, and incipient or small pleopod buds are apparent on abdominal somites 2–5. Not only are all five pairs of pereopods present, with segments at last partially indicated, arthrobranchial gill buds also are moderately well developed at the bases of the chelipeds and ambulatory legs. Furthermore, but in contrast to the condition reported by earlier investigators, the eyes in our *Paralomis* first stage are stalked, not sessile.

There is no division of abdominal tergite 2 in *Paralomis granulosa* (figure 6B, D) early crab stages; there is only fusion of tergites 1 and 2. Nonetheless, the types of segmental changes in tergites 3–5 between the megalopal and early crab stages in
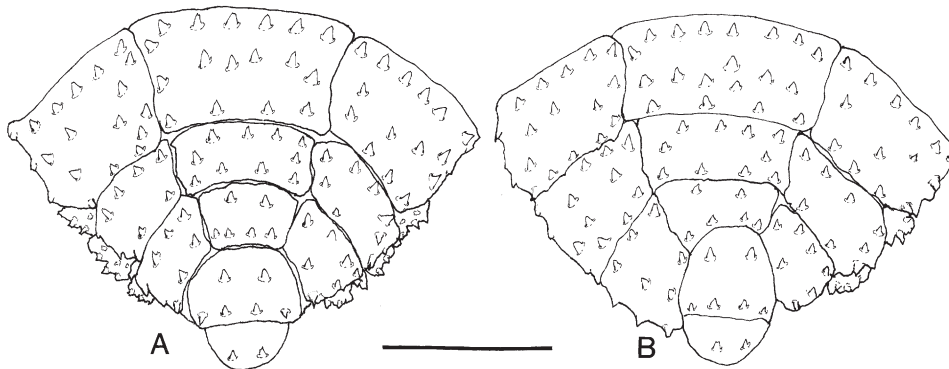

FIG. 8. *Paralomis granulosa* (Jacquinot, 1846). (A, B) Abdominal tergites 3–6 and telson (dorsal view). (A) Fifth crab stage male; (B) fifth crab stage female. Scale = 1.0 mm.

this species, i.e. division of megalopal tergites into median and lateral plates
(figure 6B, D, F), are consistent with the findings of Crain and McLaughlin (2000a,
2000b) and McLaughlin and Lemaitre (2001) for other lithodids. However, com-
ments by these authors regarding marginal plate development in tergites 3–5 were
based on the assumption that similar sundering of the lateral plates, as suggested
by marginal sutures in the first crab stages of *Phyllolithodes* and *Acantholithodes*
(McLaughlin and Lemaitre, 2000: figures 2g, 4b), was equivalent to that observed
in tergite 2 in these genera. McLaughlin *et al.* (2001) and McLaughlin and Paul
(2002) have shown that not to be the case; marginal plate development, when it
occurs in tergite 2, is not homologous with 'marginal' plate development in tergites
3–5. These latter authors have demonstrated that although there is initial, complete
or partial sundering of the lateral plates of tergites 3–5 in species of *Lithodes*, by
the fourth stage, total refusion has occurred. The 'marginal' plates that develop do
not represent a division of the lateral plates into lateral and marginal elements as
they do in tergite 2 in some genera. Rather, the so-called 'marginal' plates of tergites
3–5 result from accessory nodular calcification in the marginal integument beginning
at the third crab stage in the two species studies. During the first three crab stages
of *P. granulosa* there is no indication of sundering of the lateral plates, nor of any
accessory nodular calcification. The first evidence of accessory marginal plate devel-
opment occurs at the fourth crab stage in *Paralomis granulosa*, and appears to
proceed rather rapidly in stage 5 (figure 8A, B).

Discussion

In a recent review of the Lithodidae from the Atlantic Ocean, Macpherson
(1988) defined the genus *Paralomis* as having the second abdominal segment formed
by a single plate. The third to fifth segments (tergites) were said to exhibit clearly
differentiated, well-calcified plates without nodules or membranous areas. A median
plate, a pair of lateral plates and a pair of marginal plates were present on each of
these segments, with the marginal and lateral plates of the third segment, and rarely
also the fourth, sometimes fused. Marginal plates on any segment might also be
subdivided. Macpherson did not mention the first segment, but it is clear from
development in *P. granulosa* juveniles of stages 3–5 that the tergites of the first and
second somites fuse to present a single 'second' segment.

Macpherson's (1988) reference to 'well calcified plates without nodules or mem-
branous areas' reflects the acceptance, at that time, of Bouvier's (1894a, 1894b,
1895, 1897) hypothesis, which called for the gradual transformation of an almost
exclusively membranous hermit crab abdomen into a highly complex series of
partially to fully calcified tergites in the lithodids. In Bouvier's evolutionary frame-
work, this almost completely membranous integument was first invaded by calcified
nodules, and ultimately, through the fusion of these nodules, solid plates were
formed such as those seen in *Paralomis*. However, Crain and McLaughlin (2000a)
demonstrated that in the first and second crab stages of *Lopholithodes mandtii* the
initially, completely calcified tergites of the megalopa developed sutures that divided
the third to the fifth tergites into separate median and lateral plates. As the divi-
sionary process proceeded, a certain amount of decalcification occurred, resulting
in the separation of the median and lateral plates by membranous areas. Similar,
albeit less dramatic, results were shown by these authors to occur in a second
lithodid genus (Crain and McLaughlin, 2000b). McLaughlin and Lemaitre (2001)
subsequently examined megalopal and first crab stages from six additional lithodid

genera. These authors expressed the belief that their evidence showed conclusively that adult abdominal plate structures were formed by decalcification and/or sundering of the megalopal tergites to varying degrees, not by the formation and subsequent fusion of calcified nodules. Our findings of plate development in *Paralomis* support their conclusion as far as median and lateral plate formation is concerned. Similarly, our observations on tergite development in *P. granulosa* and *Lithodes santolla* (McLaughlin *et al.*, 2001) negate the hypothesis of secondary abdominal plate calcification in these particular genera as proposed by Richter and Scholtz (1994). Macpherson (1988) observed the absence of the marginal plates of the third tergite sometimes, and also the fourth rarely, and suggested that in some instances the marginal and lateral plates fused in *Paralomis granulosa*. As is evidenced by the development of accessory marginal plates by the fifth crab stage in our specimens, a more accurate interpretation would be that accessory marginal plates occasionally may not always develop on tergite 3, and less frequently, also on tergite 4.

Crain and McLaughlin (2000b) discussed the developmental variability in morphological characters displayed among genera of the Lithodidae. This variability is particularly true of pleopod development and loss. Contrary to the statement by these authors that pleopods develop on the second to fifth abdominal somites only in the megalopal stage in species of *Paralomis*, biramous pleopod buds were developed in first-stage zoeas reared by Campodonico and Guzmán (1981), but only uniramous buds were present both in our first-stage specimens and in those of *Paralomis hystrix* reared by Konishi and Taishaku (1994). McLaughlin *et al.* (2001) discussed the apparent errors in zoeal stage identification by MacDonald *et al.* (1957) and Haynes (1982) for *Lithodes* species, which led to inaccurate pleopod staging by these authors. Thus it would appear that these four pairs of pleopods first develop in second-stage zoeas in *Lithodes* (Campodonico, 1971; Anger, 1996, McLaughlin *et al.*, 2001), *Cryptolithodes* (Hart, 1965; Kim and Hong, 2000) and *Dermaturus* (Kurata, 1956), in the second- to fourth-stage zoeas in *Paralithodes* (e.g. Kurata, 1960; Makarov, 1966; Hoffman, 1968), in the third stage in *Lopholithodes* (Crain and McLaughlin, 2000a) and *Placetron* (Crain and McLaughlin, 2000b), and in the third or fourth stage in *Hapalogaster* (Miller and Coffin, 1961; Konishi, 1986). No pleopods develop on the first abdominal somite in any lithodid species during larval and early juveniles stages.

Pleopod loss has only recently been addressed. Sandberg and McLaughlin (1998) reported that pleopods were entirely absent in juvenile specimens of *Lithodes maja* (Linnaeus, 1758) with carapace lengths of less than 6.0 mm. Crain and McLaughlin (2000a) noted reduction of pleopods in the first crab stage of *Lopholithodes mandtii*, with complete loss almost universal in their second-stage specimens. Pleopods were completely absent in four of the five first crab stage specimens of *Paralomis granulosa* that we examined. The pleopods of the fifth specimen were markedly reduced (figure 6C). No evidence of pleopods was found in any of our second to fifth crab stage specimens of *P. granulosa*. In contrast, paired, but reduced pleopods in first crab stage specimens of *Paralithodes brevipes* (H. Milne Edwards and Lucas, 1841) were reported by Kurata (1956), and by Hart (1965) for *Cryptolithodes typicus* Brandt, 1848. Crain and McLaughlin (2000b) found reduction in the pleopods of *Placetron wosnessenskii* Schalfeew, 1892, during the first crab stage, as did Miller and Coffin (1961) for *Hapalogaster mertensii* Brandt, 1850. No subsequent stages of these species were available to the investigators. McLaughlin *et al.* (2001) found

pleopods present, but reduced during the first crab stage of *Lithodes santolla* and vestigial or absent by the second stage, while McLaughlin and Paul (2002) found pleopod loss occurring almost uniformly during the first crab stage of *L. aequispinus*. Given these findings, it is highly probable that complete pleopod loss occurs in both sexes during the early juveniles stages, but varies within and among species. It clearly is not an exclusively moult or stage-controlled phenomenon. Pleopods remain completely absent in male lithodids but, as reported by Sandberg and McLaughlin (1998) and McLaughlin and Paul (2002), redevelop on the left side in females, presumably for egg-carrying purposes.

Acknowledgements

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