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ORIGINAL PAPER

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A description of larval and early juvenile development in *Paralomis spinosissima* (Decapoda: Anomura: Paguroidea: Lithodidae) from South Georgia waters (Southern Ocean)

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Abstract The early ontogenetic stages of *Paralomis spinosissima* Birstein and Vinogradow, 1972, are described in detail and illustrated, with notes on morphological variability observed. Larval and early juvenile development was described to the crab I instar reared under controlled conditions of temperature and food supply. The abbreviated larval development invariably passed through two zoeal stages and the benthic megalopa stage. The larval development was completed without food supply, and food *Artemia* nauplii were first given after moult to the crab-I stage. Simplification and retarded development of the mouthparts are discussed as a function of lecithotrophy of these larvae and based on morphology no facultative feeding mode is suggested. Lecithotrophy in the Southern Ocean Lithodidae is discussed to be an adaptation allowing independence from seasonal food availability at high latitudes.

Introduction

The Antarctic decapod fauna is highly impoverished and most species belong to the natant shrimps (Gorny 1999). Crabs are only represented by about a dozen species of the anomuran family Lithodidae found in the deeper waters of the Southern Ocean, which remain completely absent from the high Antarctic continental shelf (Macpherson 1988; for review see Thatje and Arntz 2004; Spiridonov et al. 2006). Lithodids, commonly known as 'king crabs' or 'stone crabs', are slow maturing crabs (Lovrich 1997), found in deep or cold seas outside the tropics (Dawson 1989; Zaklan 2002). Subantarctic and Antarctic lithodids appear to tolerate cold water better than other crabs. This is believed to be in part due to prolonged embryonic development and brooding periods, producing large yolky eggs and embryos, which in turn allows for abbreviated, food-independent, and lecithotrophic larval development (Kattner et al. 2003; Lovrich et al. 2003; Calgcagno et al. 2004). These adaptations are thought to allow a degree of independence from seasonal food supplies (Thatje and Arntz 2004; Thatje et al. 2004, 2005) and help explain the survival of lithodids alone amongst reptant decapods in Antarctic regions (Anger et al. 2003). The slow metabolism and low activity levels of lithodids support a long, slow egg development, and are probably made necessary by reptant decapods' poor tolerance to and poor regulation capability of magnesium in their haemolymph. High magnesium contents in the haemolymph of decapods in combination with low temperatures typical of polar seas are thought to act as an anaesthetic or paralysing agent affecting any kind of behaviour (Frederich et al. 2001), which has been used to explain the absence of lithodid crabs from the high Antarctic continental shelf, where temperatures drop below critical thresholds to maintain activity levels (Thatje et al. 2005).

South Georgia supports large populations of *Paralomis spinosissima* and *P. formosa* (Collins et al. 2002), which has attracted the interest of commercial fishermen, although no fishery currently exists at South Georgia. At South Georgia, *P. spinosissima* is found from about 50 to 950 m water depth (Thatje et al. 2005) and can be found in dense aggregations (Purves et al. 2003). Preliminary biological investigations have been driven by the need to obtain information for management and have focussed on determining size at sexual maturity for these species (Watters and Hobday 1998; Otto and MacIntosh 1996; Purves et al. 2003), although

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growth rate and larval and juvenile development have not yet been studied or described. Basson and Hoggarth (1999) discuss management and assessment of the stocks, including the need for further work on the reproductive and developmental biology of these crabs.

The purpose of the current work is to describe larval development for *P. spinosissima* and the study of its feeding mode inferred from morphology. Results are compared and discussed with scarce data available from the family, mainly with the congener *P. granulosa* from southernmost South America.

Materials and methods

Gravid female, *P. spinosissima* were obtained by scientific observers working on longliners in the commercial Toothfish (*Dissostichus eleginoides*) fishery around South Georgia from 2001 to 2005 where they are regularly caught as bycatch (Purves et al. 2003). They were held in live tanks in the controlled temperature facility at the King Edward Point applied fisheries research station (British Antarctic Survey). The crabs were kept at 1.8–3.0°C and a salinity of 33–35ppt, with a light/dark cycle run by an outside photocell to match seasonal day length. Newly hatched larvae were removed to individual 100 ml beakers, and kept in darkness at 2–3°C. Several zoea I larvae were removed and maintained at an increased temperature of 5–6°C, to accelerate further development and due to local infrastructure restrictions. Following metamorphosis, the benthic megalopa was provided a mesh for settlement.

The larvae and megalopa stage were not fed, as earlier rearing experiments had shown no apparent difference in survival between crabs fed on *Artemia* nauplii and unfed crabs. These observations, coupled with those from other studies (e.g. Calcagno et al. 2004; British Antarctic Survey, unpublished data), strongly suggests that the zoeal and megalopal stages were lecithotrophic. Following moult to the crab-I stage, crab-I juvenile crabs were fed with freshly hatched *Artemia* nauplii once a week. Water was changed every second day.

Thirty individuals from the zoea-I stage, seven from the zoea-II stage, four from the megalopa stage and one from the crab-I stage were examined. For the zoea-I stage, earlier work carried out at the King Edward Point Research station (J. Dickson, unpublished data), sketches and descriptions were available for comparison. Fresh specimens (newly released larvae) as well as preserved specimens were examined for zoea I. For the other stages the crabs examined were preserved in 70% ethanol. Specimens were dissected under a Meiji dissecting microscope, and then examined using a Meiji compound microscope. Terminology for the morphological descriptions follows previous work (Campodonico and Guzman 1981; MacLaughlin et al. 2001, 2003). Carapace length (CL) was measured from the posteriolateral margin of the carapace to the tip of the rostral spine, and a graticule was used to scale the appendages. Setae appeared simple under light microscopy, except where otherwise indicated in the text, and secondary setation is not illustrated.

Results

Description of early developmental stages of *P. spinosissima*

First zoeal stage (Fig. 1; n = 30)

Carapace (Fig. 1a, b, CL = 3.8–4.2 mm, including rostrum) with long rostral spine, and a spine on each posteriolateral edge. The carapace is longer than it is wide in live specimens. In dead individuals, at the onset of moult or when preserved in alcohol or formalin, the carapace swells laterally, to become as wide as it is long. A slight medial crest runs from the rostral spine onto the anterior portion of the carapace. The eyes are sessile, but clearly demarcated from the rest of the carapace. The anterior two-thirds of the carapace are filled with a mass of yolk globules. In preserved specimens large oil droplets are visible through the carapace.

The abdomen (Fig. 1c) consists of five segments plus the telson. The sixth abdominal somite is fused to the telson. In some individuals there is a crease between the two, in others the sixth abdominal somite and the telson are smoothly continuous. The posterior margins of the abdominal segments each bear six spines, which are low and indistinct on segments close to the base of the abdomen. These abdominal spines become progressively longer laterally, and toward the posterior segments. Segments 3–5 have an additional pair of small spines lateral to the medial pair. Segments 3 and 4 each have a pair of dorsal setae in some individuals. The posterior margin of the telson has a median notch, and bears nine finely setose spines on each side, and a small seta on each side between the two outermost spines. The third spine is longer than the others, and the ninth (innermost) spine is tiny and inconspicuous in some specimens.

The antennule (Fig. 1d) consists of a basal peduncle, an exopodite and an endopodite, all unsegmented. The exopodite bears 8–10 aesthetascs and two terminal setae. The endopodite is approximately half as long as the exopodite, and has a spine at or immediately behind its distal end. In some specimens this spine is small.

The antenna (Fig. 1e) has a basal segment bearing two ventral spines, the medial being more developed, and conspicuously setose or denticulate along its medial margin. There is no antennal gland protrusion apparent. The antennal scale has eight setose setae on the inner margin, and terminates in a spinous projection. The endopodite is slightly shorter than the antennal scale, including spine and unsegmented.

The mandible (Fig. 1f) has a blunt, rounded, unsegmented palp, a single distinct distal tooth and 2–5 low and indistinct teeth.

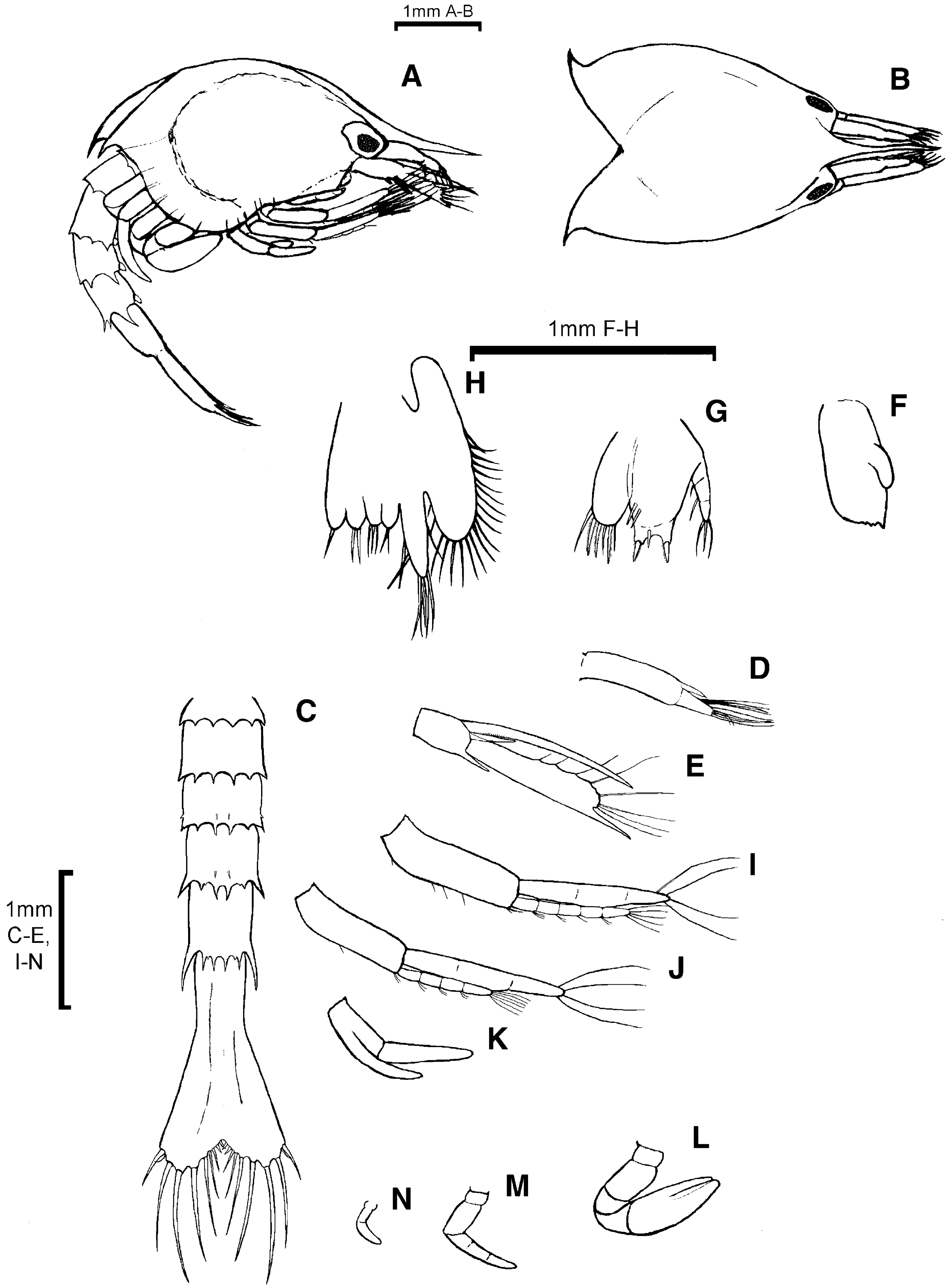

Fig. 1 *Paralomis spinosissima* Birstein and Vinogradov; First Zoea. **a** lateral view, **b** dorsal view of carapace, **c** dorsal view of abdomen, **d** antennule, **e** antenna, **f** mandible, **g** maxillule, **h** maxilla, **i** first maxilliped, **j** second maxilliped, **k** third maxilliped, **l** first pereopod, **m** third pereopod, **n** fifth pereopod

The maxillule (Fig. 1g) has a three-segmented endopodite, with 2–3 setae on the terminal end. The basipodite has two strong, denticulate spines, and 2–3 setae. The coxopodite has six setose setae.

The scaphognathite of the maxilla (Fig. 1h) bears 16–18 setose setae and terminates in a lobe, the endopodite has 4–5 terminal, 2–4 subterminal and 0 or 1 basal setae. The basipodite and coxopodite of the maxilla are bilobate and have 2 to 3 + 3 to 4 and 2 to 3 + 1 to 3 setae, respectively.

The protopodite of the first maxilliped (Fig. 1i) has one proximal, 1–3 median and 2–3 simple, distal setae, although the proximal and median setae were missing in most preserved specimens. J. Dickson (unpublished data, 2001–2002) found five median setae. The five-segmented endopodite bears 3–2–1–2–5 setose setae and the exopodite bears four setose terminal setae.

The protopodite of the second maxilliped (Fig. 1j) has one median and two distal, simple setae. The four-segmented endopodite bears 2-2-2-6 setae, and the exopodite bears four terminal setae.

The third maxilliped (Fig. 1k) is less developed than the others, only partly segmented and bears no setae.

The pereopods (Fig. 1l–n) are present; first pereopod with rudimentary chela, the first four pereopods are segmented, the fifth is rudimentary and only partially segmented (Fig. 1n). Simple, bilobed branchial buds (not illustrated) are present at the bases of the pereopods.

There are pairs of short pleopod buds on abdominal segments 2–5 (Fig. 1a), each consisting of a short, blunt, spine-like endopod.

Second zoeal stage (Fig. 2; n = 7)

Carapace (Fig. 2a, b, CL = 3.8–4.2 mm, including rostrum) very similar to previous stage. The carapace in specimens preserved in formalin is as wide or nearly as wide as it is long. The eyes are now stalked and free from the rest of the carapace. The anterior half of the carapace is filled with a mass of yolk globules, noticeably less than in the zoea-I stage.

The abdomen (Fig. 2c) consists of five segments plus the telson. It is more robust proximally than in zoea I, and the lateral spines are slightly longer. The sixth abdominal somite is fused to the telson, as in zoea I. The posterior margins of abdominal segments 3–5 each bear six spines, some of which are low and very indistinct on segments close to the base of the abdomen. These abdominal spines become progressively longer laterally, and toward the posterior segments. The posterior margin of the telson is slightly concave, but has less of a median notch than in zoea I. The telson bears 7–10 finely setose spines on each side, and a in some specimens a small seta on each side between the two outermost spines. The third spine is longer than the others, and the ninth (innermost) spine is tiny and inconspicuous in some specimens. The telson spines are shorter than in zoea I, and several specimens have bluntly rounded or missing spines.

The antennule (Fig. 2d) consists of a basal peduncle, an exopodite and an endopodite, all unsegmented. The exopodite bears 9–10 aesthetes. The endopodite is approximately two thirds as long as the exopodite, and has no spine.

The antenna (Fig. 2e) has a basal segment bearing two ventral spines, the medial being more developed, and conspicuously setose or denticulate along its medial margin. The antennal gland protrusion is apparent on the ventromedial side. The peduncle, spines and endopodite are more robust than in zoea I. The antennal scale has 8–10 setose setae on the inner margin, and terminates in a blunt projection. The endopodite is now slightly longer than the antennal scale, including spine and unsegmented.

The palp of the mandible (Fig. 2f) is more developed than in zoea I, but is still unsegmented. The mandible has a single distinct distal tooth and 11–14 low, indistinct teeth.

The endopodite of the maxillule (Fig. 2g) now of two segments only, with one seta on the proximal segment and three setae on the terminal end. The basipodite has four large and three shorter spines. The coxopodite has five setose setae.

The scaphognathite of the maxilla (Fig. 2h) bears 16–18 setose setae and terminates in a lobe, which is slightly longer than in zoea I. The endopodite has 3–4 terminal, 2–3 subterminal and one basal seta. The basipodite and coxopodite of the maxilla are bilobate and have 3–4 + 4–5 and 3–4 + 5–6 setose setae, respectively. Many small sub-epidermal setae are visible forming at the distal end of the scaphognathite.

The protopodite of the first maxilliped (Fig. 2i) has one proximal, 2–5 median and three simple, distal setae. The five-segmented endopodite bears 3–3–1–2–4 setose setae and the exopodite, which now has two segments, bears eight setose terminal setae.

The protopodite of the second maxilliped (Fig. 2j) has one median and two distal, simple setae. The four segmented endopodite bears 2–3–2–4 to 5 setae, and the two segmented exopodite bears eight setose terminal setae, The third maxilliped (Fig. 2k) is still less well developed than the others, although more developed than in zoea I. The endopodite has four or five partial segments; the exopodite two or three partial segments, and bears 7–8 setose terminal setae.

The pereopods (Fig. 2l–n) are more developed than in zoea I; pereopod one with developed chela; all five pereopods are now segmented, the fifth smaller and held under the base of the tail (Fig. 2n). The branchial buds (not illustrated) at the base of the pereopods are more developed than in zoea I.

There are pairs of pleopods (Fig. 2o) on abdominal segments 2–5 (Fig. 2a). These are more developed than in zoea I, each consisting of a protopod, with a short, bluntly pointed endopod and a short, bluntly pointed exopod.

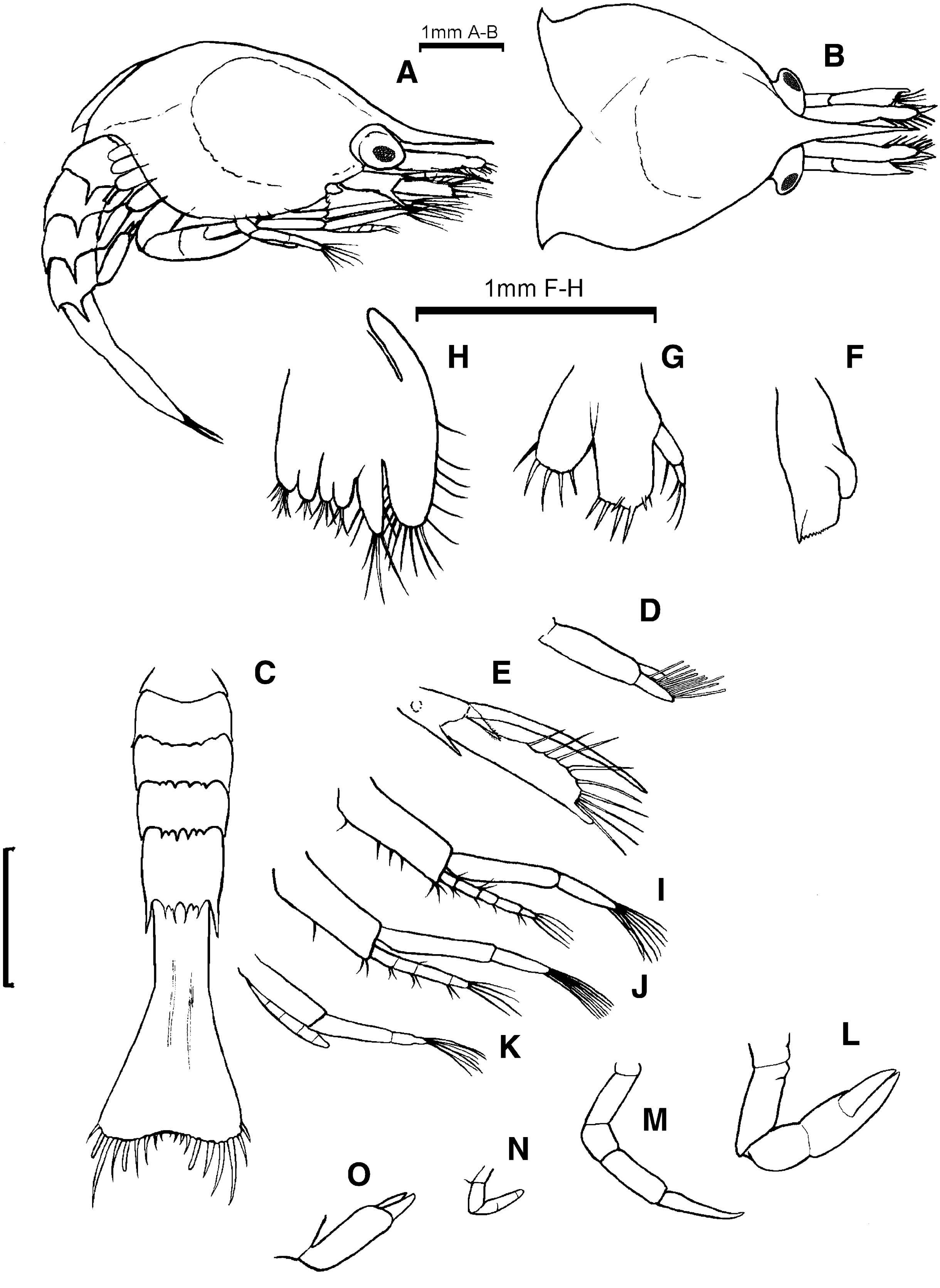

Fig. 2 *Paralomis spinosissima* Birstein and Vinogradov; Second Zoea. **a** lateral view, **b** dorsal view of carapace, **c** dorsal view of abdomen, **d** antennule, **e** antenna, **f** mandible, **g** maxillule, **h** maxilla, **i** first maxilliped, **j** second maxilliped, **k** third maxilliped, **l** first pereopod, **m** third pereopod, **n** fifth pereopod, **o** third pleopod

Megalopa stage (Fig. 3; n = 4)

Carapace (Fig. 3a, b, CL = 3.0–3.1 mm, including rostrum) shorter than in zoea II, mainly due to the shorter rostrum and more compact rear margin. Yolk globules are visible in the gastric area. The carapace has numerous spines, and has started to take on the shape of the adult crab carapace, although cardiac, gastric and branchial regions are not differentiated. The carapace is narrower than long. There is some variation in spination, two individuals with predominantly simple spines, two with predominantly bifid spines. In two specimens several of the spines were low and inconspicuous. Many carapace spines bear a basal seta. The rostrum is slightly longer than the robust paired trifid dorsal rostral spines. There is a prominent dorsal gastric spine, 1–2 pairs of gastric spines, 2–5 pairs of branchial spines and 1–2 pairs of cardiac spines, and a variable number of marginal spines. The eyes each bear 1–3 spines on the dorsal surface.

The abdomen (Fig. 3c) consists of five segments plus a sixth partially fused with the telson. The abdomen is shorter and more robust proximally than in the zoeal stages. The first segment bears a pair of dorsal spines, the second segment a row of four spines, the third and fourth segments; two pairs of spines, and the fourth to sixth segments; a single pair of spines. Additionally, segments 2–4 each bear two pairs of lateral spines, and the fifth segment bears 1 or 2 dorsal setae. Abdominal spines in most cases bear a basal seta. Small additional marginal spines, some of which are low and very indistinct, were variably seen on segments 3–5. The telson is rounded, and is less developed than in the zoeal stages. One specimen bore a pair of setae on the distal edge of the telson, and another bore three setae.

The antennule (Fig. 3d) consists of a three-segmented basal peduncle, an exopodite and an endopodite. The endopodite has two segments, bearing 3–3 setae and the exopodite has two segments, bearing 5 or 6 aestheascs and six setae, respectively. The proximal segment of the antennule exopodite is itself incompletely divided into three segments.

The basal peduncle of the antenna (Fig. 3e) bears a long spine. The endopodite of the antenna has nine segments with 0–1–0–1 to 2–1 to 2–3 to 4–2–3 to 5–2 to 4–3 to 7 setae. The antennal scale is reduced to a naked, finger-like projection ending in a protrusion.

The palp of the mandible (Fig. 3f) is more developed than in the zoeal stages, and bears seven low spines distally, but is still unsegmented. Mandible without distinct teeth or spines observed.

The endopodite of the maxillule (Fig. 3g) now only has three segments, with a short spine on the terminal end. The basipodite has ten spines, two of them longer in two of the specimens examined, and a single setose seta. The coxopodite has two setose setae.

The scaphognathite of the maxilla (Fig. 3h) bears 60–67 setose setae and terminates in a lobe, which is slightly longer than in the zoeal stages. The endopodite is sharply pointed and naked. The basipodite and coxopodite of the maxilla are bilobate and have 7 to 13 + 7 to 13 and 2 to 5 + 2 to 3 setose setae, respectively.

The basipodite of the first maxilliped (Fig. 3i) bears a single seta; the protopodite of the first maxilliped has eight simple, distal setae. The unsegmented endopodite bears two small setose setae and the exopodite, which is incompletely segmented, bears 2–3 short terminal setose setae.

The protopodite of the second maxilliped (Fig. 3j) is naked. The endopodite has four incompletely divided segments, and bears 1 or 2-0-0-2 to 3 setae, and several small spines. The two-segmented exopodite bears 3–6 setose terminal setae, and a few small, indistinct spines.

The third maxilliped (Fig. 3k) is now more developed than the others. The endopodite has four segments, bearing 2 to 5–2 to 4–16 and 8–11 setose setae. A spine is also present at the base of the endopodite and on segments 1 and 2. The exopodite has two segments, and bears four setose terminal setae.

The pereopods (Fig. 3l–n) are more developed than in the zoeal stages; the chelae are symmetrical, and three pairs of walking legs are fully articulated and bear numerous spines, each spine bearing a basal seta. The distal chela segment is variable, heavily spined in two specimens, without spines in two specimens. In both cases the chelae bear many setae. The fifth pair of pereopods is smaller and is held under the base of the tail (Fig. 3n). The coxopodite bears two setae, the carpus a single seta, the propodus four setae and the dactyl bears seven short and 1–3 long, curved setae. The branchial buds (not illustrated) at the base of the pereopods are larger and more developed than in the zoeal stages.

There are pairs of well-developed pleopods (Fig. 3o) on abdominal segments 2–5 (Fig. 3a). Each consists of a protopod, with a short, bluntly pointed endopod with a small terminal spine and a short, bluntly pointed exopod, which bears 11–14 setose setae on the pleopods of segments 2–4, and 9–11 setose setae on the pleopods of segment 5, which is slightly smaller than the other pleopods. A pair of single segmented, rounded uropods is present on two specimens (Fig. 3a), but is absent from the other two.

First crab stage (Fig. 4; n = 1)

Carapace (Fig. 4a, b, CL = 3.5 mm, including rostrum) showing starting separation of cardiac, branchial and gastric regions; carapace more robust and heavily spined than in the megalopa stage. The carapace is longer than it is wide. The eyes are stalked, and bear two spines (three on the left eye). There is an oily mass inside the carapace, denser and more viscous than the yolk seen in earlier stages. The abdomen (Fig. 4c) is triangular, and consists of six partially separated segments plus the telson. The lateral margins have two or three pairs of spines on each segment, apart from the sixth, which has two pairs of lateral setae. One dorsal spine was seen on the left outer dorsal surface of the

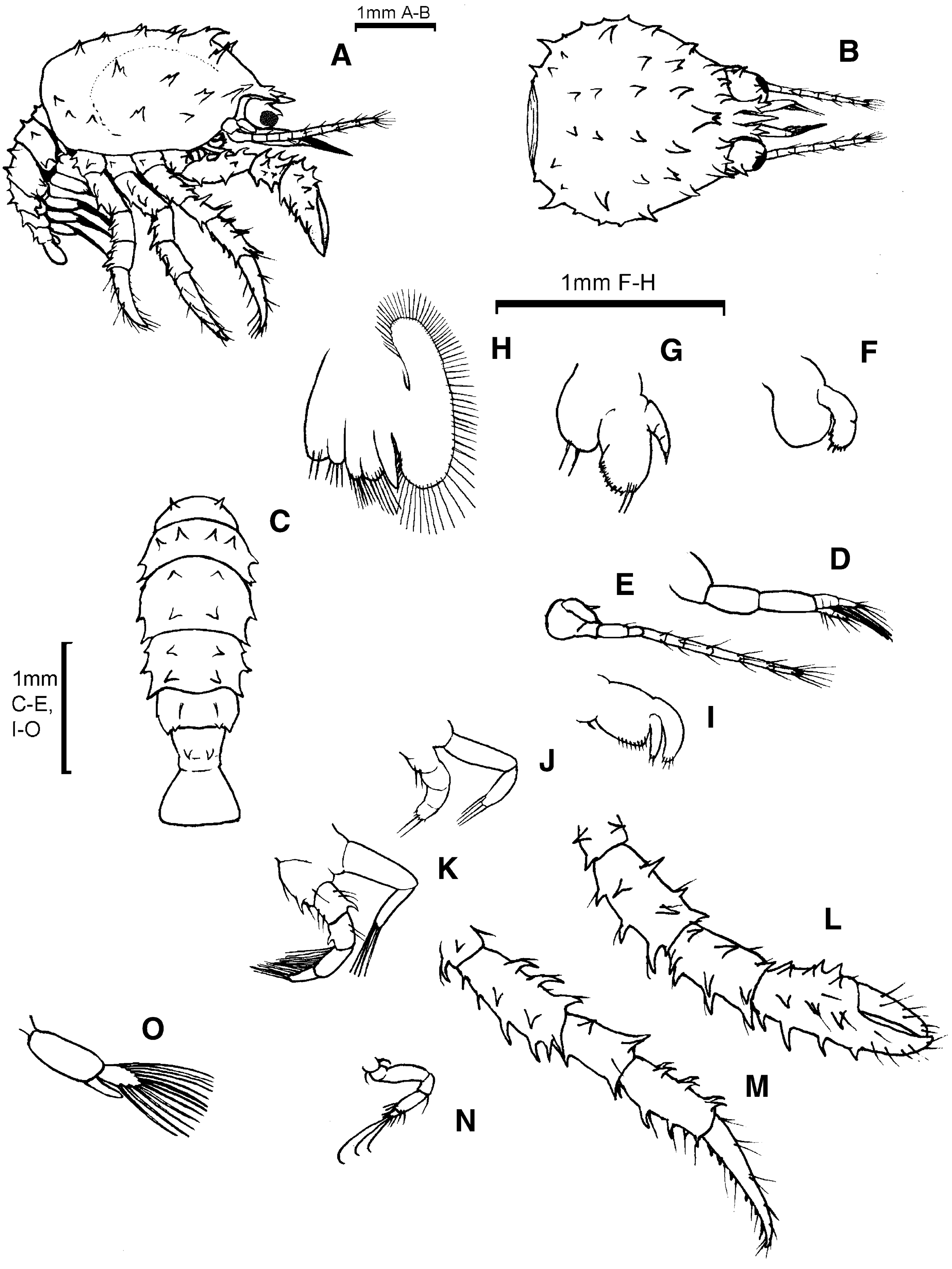

Fig. 3 *Paralomis spinosissima* Birstein and Vinogradov; Megalopa. **a** lateral view, **b** dorsal view of carapace, **c** dorsal view of abdomen, **d** antennule, **e** antenna, **f** mandible, **g** maxillule, **h** maxilla, **i** first maxilliped, **j** second maxilliped, **k** third maxilliped, **l** first pereopod, **m** third pereopod, **n** fifth pereopod, **o** third pleopod

second segment, a pair of dorsal spines on the third segment, and spine-like setae on the lateral dorsal surfaces and distal margins of segments 3–5. Segment 6 additionally bears a pair of distal margin spines. The abdomen is more robust proximally than in earlier stages, and held tight against the underside of the body. No pleopods or uropods.

The antennule (Fig. 4d) consists of a three-segmented basal peduncle, which bears 2–0–3 setae, an exopodite and an endopodite. The endopodite has three segments, bearing 2–0–5 setae, and the exopodite has three segments, bearing 12–0–0 aesthetes and 2–0–5 setae. The proximal segment of the antennule exopodite is incompletely divided into two segments.

The basal peduncle of the antenna (Fig. 4e) bears a long spine. The endopodite of the antenna has nine segments with 1–0–0–2–5 to 6–1 to 2–6–3 to 4–2 to 4–7 to 8 setae. The antennal scale is short, bears three setae and terminates in a spine.

The palp of the mandible (Fig. 4f) is more developed than in the earlier stages, has three segments and bears 12 low spines distally. The mandible has two large teeth and a shorter spine distally.

The endopodite of the maxillule (Fig. 4g) is now unsegmented, with a seta at the terminal end. The basipodite has 25 spine-like setae distally, and a row of five proximal to this. The coxopodite has two anterior setae and 13 posterior/distal setae.

The scaphognathite of the maxilla (Fig. 4h) bears 61 setose setae and terminates in a lobe, and is slightly larger than in the earlier stages. The endopodite is sharply pointed and bears two setae. The basipodite and coxopodite of the maxilla are bilobate and have 14 + 10 and 6 + 20 setose setae, respectively.

The basipodite of the first maxilliped (Fig. 4i) bears 10 setae, the protopodite has eight subterminal and 26 setose terminal setae. The unsegmented endopodite is naked and the exopodite, which is incompletely trisegmented, bears 7–2 or 3–6 setae.

The protopodite of the second maxilliped (Fig. 4j) bears five setae. The endopodite has five segments, and bears 2–1–0–4–8 setae. The two-segmented exopodite bears 2–7 setae, and is incompletely bisegmented.

The third maxilliped (Fig. 4k) has an endopodite with five segments, bearing 2–4–7–12–9 setae. A spine is also present on segment 2. The exopodite has two segments, and bears 4–7 setae, the seven distal setae being setose.

The pereopods (Fig. 4l–n) are more developed than in the megalopa stage, and the crab has taken on the basic adult stance and form; the chelae are basically symmetrical, although in the single specimen examined the left chela was slightly larger. The three pairs of walking legs are fully articulated and bear numerous spines, each spine bearing a basal seta. The distal chela segments are heavily spined and setose. The fifth pair of pereopods is smaller and is held under the base of the tail (Fig. 4n). The coxopodite bears two setae, the carpus 1 or 2 setae, the propodus 2 setae and the dactyl bears 13 to 15 short and 2–3 long, curved setae.

Discussion

P. spinosissima shows an abbreviated larval development with two zoeal stages and one benthic megalopa stage only, which coincides very well with the larval development of the subantarctic congener *P. granulosa* (Campodonico and Guzmán 1981; McLaughlin et al. 2003) found in southern Chilean and Argentinean waters (Gorny 1999), and confirms the proposed pattern of abbreviated larval developments in southern hemisphere Lithodidae (Thatje et al. 2003, 2005). An endotrophic larval development in *P. spinosissima* is indicated by the successful completion of the larval cycle under absence of food, including the benthic megalopa stage. This is an essential adaptation to uncouple from short periods of food availability in short summers in the Southern Ocean or in food scarcity in deep-sea environments (Clarke 1983). Biochemical and physiological studies on subantarctic lithodids, including the closely related congener *P. granulosa*, demonstrated that larval stages and the megalopa do rely upon lipid storage of maternal origin, which allow for a food independent larval developmental cycle (Anger et al. 2003; Kattner et al. 2003). Primitive morphology of the mouthparts and in particular in the mandible throughout larval development including the megalopa stage, already suggested that there is no facultative feeding mode in the lithodid species *P. granulosa* and *Lithodes santolla* (McLaughlin et al. 2001, 2003). In *L. santolla*, such evidence derived from morphology studies is supported by the lack of the endopeptidases trypsin and chymotrypsin throughout the larval development, indicating that the early ontogenetic stages in this species are not adapted to digest food until reaching the crab I instar (Saborowski et al. 2006). Probably the same situation can be expected in *P. spinosissima*, although energetic and enzymatic evidence is still lacking. However, the primitive morphology of the mandibles is strikingly similar to that of the congener *P. granulosa* (Campodonico and Guzman 1981; McLaughlin et al. 2003) and one slightly more developed than in *L. santolla* (McLaughlin et al. 2001). With a fully segmented palp and most important cutting edges missing up to the crab-I stage (cf. Fig. 4) an active and facultative feeding mode is far from being likely. We suggest that the present study gives evidence for a family-specific pattern in closely related species of Lithodidae, which might be a result of the evolutionary history of the southern hemisphere representatives (for discussion see Zaklan 2002; Thatje et al. 2005 and references therein).

A recent study (Morley et al. 2006) has shown that egg size in South Georgia lithodid crab species increases with water depth and it has been suggested that this is a result of an increased energy investment into the single offspring at a reduced fecundity with increasing water depth. Considering that the non-feeding larval developmental mode in *P. spinosissima* from shallower waters is based on the smallest eggs found in South Georgia lithodid populations, implies that the other lithodid

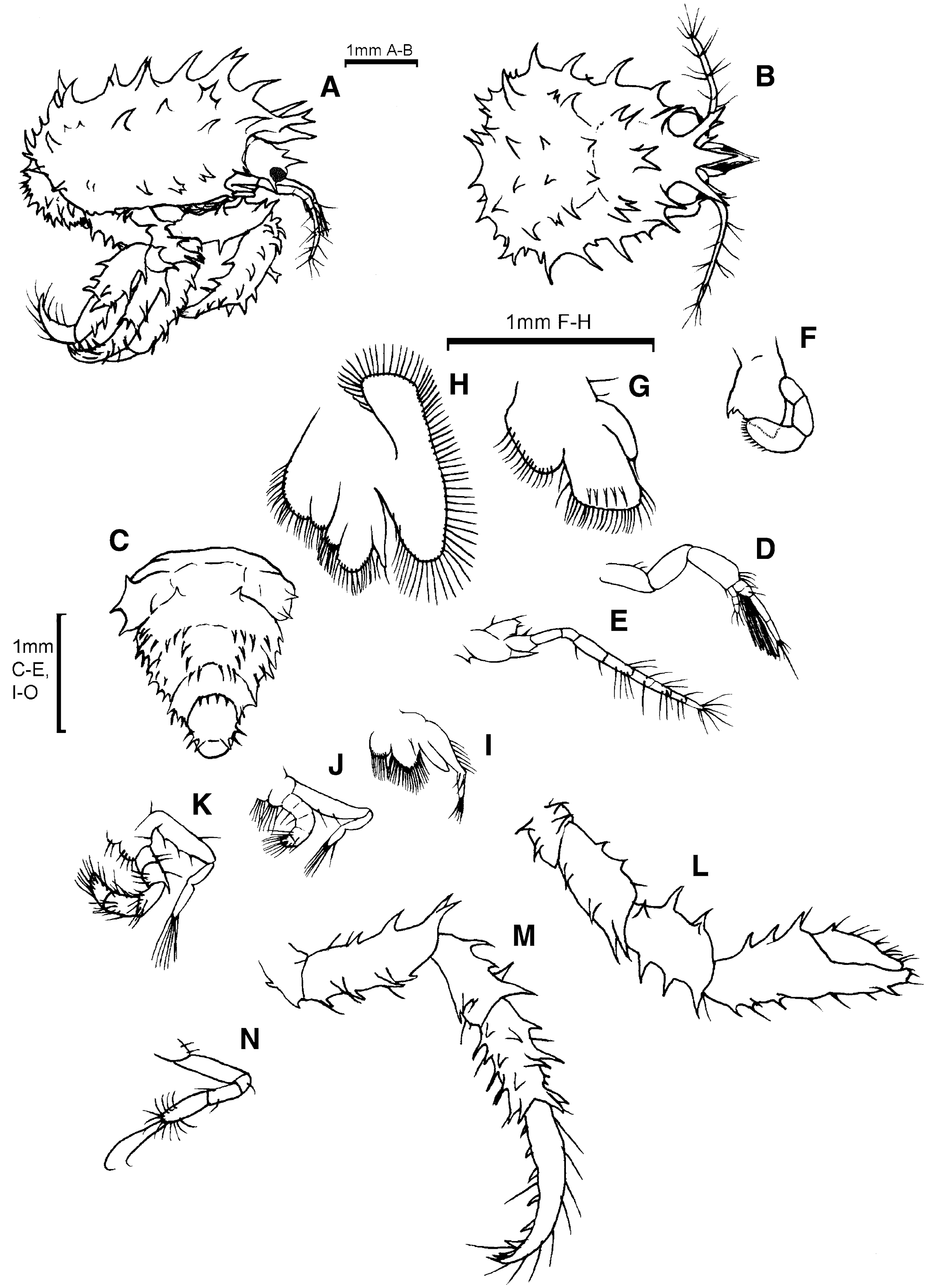

Fig. 4 *Paralomis spinosissima* Birstein and Vinogradov; First Crab. **a** lateral view, **b** dorsal view of carapace, **c** dorsal view of abdomen, **d** antennule, **e** antenna, **f** mandible, **g** maxillule, **h** maxilla, **i** first maxilliped, **j** second maxilliped, **k** third maxilliped, **l** first pereopod, third pereopod, **n** fifth pereopod

species from deeper waters do all possess a lecithotrophic larval developmental mode (for discussion see Thatje et al. 2005; Morley et al. 2006). This, however, needs to be confirmed in future investigation.

McLaughlin et al. (2001) discusses the high variability in lithodid development from literature, and the present study has shown some variation in form within the megalopa stage, although morphology of the zoea stages and a single megalopa stage appears consistent in our study. The low number of specimens examined makes it difficult to draw any conclusions about the appearance of uropod buds in the two megalopae studied, and the absence of pleopods from the single crab I specimen examined. Similarly, the incomplete separation of plates and spination of the abdomen on the single crab I stage examined makes it difficult to comment further on this stage. However, our observations support the idea of a family-specific pleopod loss in juvenile Lithodidae (Sandberg and McLaughlin 1998). At some stage, however, left side pleopods do reappear in female lithodids for egg carrying purposes, but it does still remain unknown when this process is taking place (McLaughlin et al. 2003).

The Scotia Sea and South Georgia region support dense lithodid populations, provoking interest in potential fisheries for *P. spinosissima* and *P. formosa* (Agnew 2004). *Paralomis* crabs were taken in experimental hauls from around the shelf break (López Abellan and Baguerias 2004). An experimental fishery in 1992 yielded large catches, mostly *P. spinosissima* (Otto and Macintosh 1992), and the authors tentatively suggested an annual potential catch of 6000 tonnes for area 48. Further experimental fishing in 1995 (Watters 1997) also yielded high catches, and showed the highest CPUEs between 200 and 300 m, to the north of the island. The small size of individuals, and the low proportion above minimum landed size resulted in large bycatches of small crabs of the target species. This has limited the interest in a dedicated fishery to date. Assessments of numbers have been carried out via baited camera systems (Collins et al. 2002). The results showed high numbers of *P. spinosissima* and *P. formosa*, although the authors noted that stock estimates are difficult to assess. Declining stocks due to intensive exploitation of the South American species *P. granulosa* and *L. santolla* give rise for comprehensive life history studies previous to industrial exploitation (Lovrich 1997).

Studies of the early life history of king crabs can serve important clues to evaluate the resilience potential and vulnerability of stocks to exploitation, especially in cold waters. The study of morphological changes in early juveniles can help assessing age and growth of field-collected specimens, thus identifying recruitment areas, and could potentially aid to support restocking programmes, although this might not be economically feasible in cold water species (Calcagno et al. 2004).

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