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THE LARVAL STAGES OF *LITHOTRYA DORSALIS* (ELLIS & SOLANDER, 1786): A BURROWING THORACICAN BARNACLE

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ABSTRACT

Lithotrya dorsalis is a member of the only genus of thoracican barnacles known to burrow and is widely distributed throughout the tropical western Atlantic. It occurs primarily in high energy intertidal environments. *L. dorsalis* undergoes the typical thoracican larval sequence. Six naupliar stages are followed by the cyprid stage. These larvae were reared in the laboratory and their stages are described for the first time. Newly hatched stage I nauplii are typically 360 μm in total length; larval size increases to 1100 μm by the 6th instar. The most distinguishing characteristic of *Lihtotrya dorsalis* nauplii is the presence of unusually long, spinulated posterior shield spines in stages IV through VI. Complete larval development (stage I nauplius to cyprid) averaged 18 days and ranged from 12 to 23 days. Scanning electron micrograph descriptions of the cyprid cuticle of this animal, showing a unique striated appearance, are also included.

INTRODUCTION

First described by Sowerby (1822), the genus *Lithotrya* (family Scalpellidae, subfamily Lithotryinae) is further treated by Darwin (1851), Sewell (1926), Otter (1929), and Cannon (1947). *L. dorsalis* is considered to be the only species occurring in the western Atlantic (Zevina, 1981). Found exclusively in carbonate substrata, this species is an abundant and ubiquitous constituent of exposed tropical coastlines (Ginsburg, 1953; Newell *et al.*, 1959; Ahr and Stanton, 1973; Southward, 1975; Focke, 1977; Spivey, 1981). Settling gregariously, *L. dorsalis* is capable of substantial bioerosion. Bore holes up to 7 cm in length, with a typical oval aperture as large as 5 × 8 mm have been reported (Ahr and Stanton, 1973). These authors described average boring densities in limestone beach rock off Puerto Rico to be one tube per cm^2 of rock with up to 30% of rock excavated in some samples. It has been found subtidally (75–80 ft) (Pequegnat and Ray, 1974) and in fringing reef environments (MacGeachy and Stearn, 1976). However, its larval history has remained virtually unknown.

Complete larval descriptions of pedunculate barnacles are listed by Lang (1976). Dalley (1984) has since successfully reared the naupliar stages of *Conchoderma auritum* (L.). Of these pedunculate barnacles, only four are scalpellids (Thoracica: Scalpellidae): *Capitullum mitella* L. (= *Mitella mitella* = *Pollicipes mitella*) (Yasugi, 1937); *Calantica spinosa* Quoy and Gaimard (= *Pollicipes spinosus*) (Batham, 1946); *Scalpellum scalpellum* L. (Kaufmann, 1965); and *Pollicipes polymerus* Sowerby (Lewis, 1975). The burrowing habit of *Lithotrya* makes it unique not only among the scalpellids but among the thoracican cirripeds in general.

Description of the larval stages of *L. dorsalis* make it possible to identify and stage specimens from tropical plankton tows, thereby enhancing future ecological studies.

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Furthermore, documentation of the plate ontogeny and maturation of the post-cyprid, a direct consequence of this study, may have implications for the geological age of the Lithotryinae and the burrowing rate of newly settled cyprids, respectively.

Cyprid appearance is often cited in the literature as being unhelpful in differentiating species because of its interspecific similarity and intraspecific variability in size. Standing (1980) compared seven species of barnacle cyprids at the light microscopy level and concluded that shape (side view) is a more reliable indicator of species than size and further concluded that carapace sculpturing may prove to be a useful tool for differentiating species at the cyprid level. Carapace sculpturing, along with size, was previously used to differentiate cyprids of *Balanus glandula* from *Balanus cariosus*, respectively (Strathman and Branscomb, 1979). Both Lang (1979) and Standing (1980) alluded to the fact that the use of the scanning electron microscope (SEM) may be a valuable tool in extending our knowledge of the external morphological features of the cyprid larva and thereby rendering these features of some diagnostic value at the interspecific level.

SEM descriptions of the external cuticle of the cyprid larva of *L. dorsalis* are included here in an attempt to encourage similar descriptions of this significant stage in future larval studies.

Complete sets of larvae are deposited with the American Museum of Natural History, New York, New York; and the National Museum of Natural History, Washington, DC.

Materials and Methods

Sampling took place in September and October, 1983, and again, at the same time of year, in 1984. Using a hammer and chisel, pieces of limestone reef rock containing adult barnacles were removed from the intertidal zone of Indian Key, Florida, and placed in buckets containing ambient seawater. This rock was returned to the laboratory the same day and vigorously aerated. Over the next several days, the rock was further chiseled into smaller pieces. Gravid individuals, easily recognized by the bright orange pigmentation of the ovigerous lamellae (paired egg bearing structures) seen through the peduncular cuticle, were removed intact and placed individually into small culture bowls. The capitulum was subsequently disjoined and the lamellae were coaxed from the peduncle by applying gentle pressure.

Culturing techniques

The basic rearing techniques of Freiberger and Cologer (1966) were followed. Depending on the degree of maturation, stage I nauplii would either hatch immediately or after incubation of the lamellae for up to 10 days. Maturation in incubated cultures was gauged by the increasing darkness of the naupliar eyespot. Incubating lamellae were placed in 0.45 μm millipore filtered seawater (MFSW), 30 ppt salinity at 30°C, in the dark. Cultures were observed and seawater was changed daily. Stage I nauplii were transferred at varying densities (2–8 nauplii per ml medium) to stendor dishes containing MFSW reduced to 28 ppt salinity. Cultures were placed in a temperature—controlled chamber at 30°C on a shake table at gentle speed. Either a 12:12 or 18:6 light:dark schedule was used. Various algal diets were tried but the complete larval sequence was only obtained using the mixed algal diets of *Thalassiosira fluviatilus/Tetraselmis suecica* or *Chaetoceros gracilis/Isochrysis* sp. Algae used as food were grown in f/2 medium in batch culture, centrifuged, resuspended in MFSW, and dispensed at initial densities of 2×10^5 cells/ml. The antibiotics Streptomycin sulfate, Polymixin B sulfate (both at 12 μg/ml) and Penicillin G (25 μg/ml) (Sigma) were

TABLE I

Lithotrya dorsalis: *Measurements of larvae**

	Total length (μm)			Shield length (μm)			Width (μm)		
Stage	$\bar{x}$	SD	Range	$\bar{x}$	SD	Range	$\bar{x}$	SD	Range
I	362	25	333–421				186	15	170–219
II	546	10	540–564	202	9	190–220	238	14	220–263
III	749	35	681–795	243	13	220–257	258	10	237–267
IV	899	44	799–952	345	17	303–360	323	17	284–335
V	1035	40	936–1070	446	13	435–472	409	19	366–438
VI	1141	37	1070–1171	510	15	484–536	464	22	424–493
cyprid	518	15	496–542				240	8	233–252

* n = 10 in stages I–V and cyprid, n = 8 in stage VI.
$\bar{x}$ = mean; SD = standard deviation.

used (Landau and D'Agostano, 1977). Glassware was autoclaved daily. Cultures were transferred by pipet every 24 h. Several individuals from each culture were removed daily and preserved in either 70% ethanol or 5% buffered formalin in seawater. An ocular micrometer was used to approximate the stage of these individuals. Representatives from each stage were later stained with chlorazol black in a 10% solution of glycerin in 70% ethanol. The alcohol was allowed to slowly evaporate. Larvae, now more manipulable, were then either mounted whole or dissected with fine tungsten needles. Stages were verified and drawings were made using camera lucida on a Wild M20 compound microscope.

Specimen preparation—SEM

Cyprids prepared for scanning electron microscopy were initially fixed in buffered glutaraldehyde and dehydrated through a graded series of ethanols. Then the cyprids were either placed in trichlorotriflouroethane (Nott, 1969) which was allowed to slowly evaporate under a bell jar through which nitrogen gas was gently bubbled, or were transferred to acetone and then critical point dried (Samdri pvt.3, Tousimis). Using a method similar to Waller (1981), these larvae were individually glued with polyvinyl acetate to one end of a small platinum wire. The other end of this wire was twisted into a loop which was then attached to a glass cover slip using silver paint. The cover slip was then affixed to a mounting stub using double sided tape. The animals were then sputter coated with gold/palladium under vacuum (Hummer 5, Technics). This method allows manipulation of the specimen by bending the wire with fine forceps. Larvae treated this way were examined with either a JSM-U3, JEOL or a 1000A, AMRay scanning electron microscope at a gun potential of 15 to 20 kV.

RESULTS

Larval cultures

Lithotrya dorsalis exhibited the typical thoracican larval sequence. Six naupliar stages were followed by the cyprid stage. Average survival from naupliar stage I to cyprid in 29 larval cultures was 12.5% (range = .54–46.1%). Cultures with initially lower densities (1–2 nauplii/ml medium) yielded higher percent survival. Complete larval development (stage N I to cyprid) averaged 18 days and ranged from 12 to 23 days. Several cultures molted in synchrony, the majority did not. Sizes of larval stages are given in Table I. Shield lengths were approximated for naupliar stages II and III because of the lack of a distinct posterior margin in these stages.

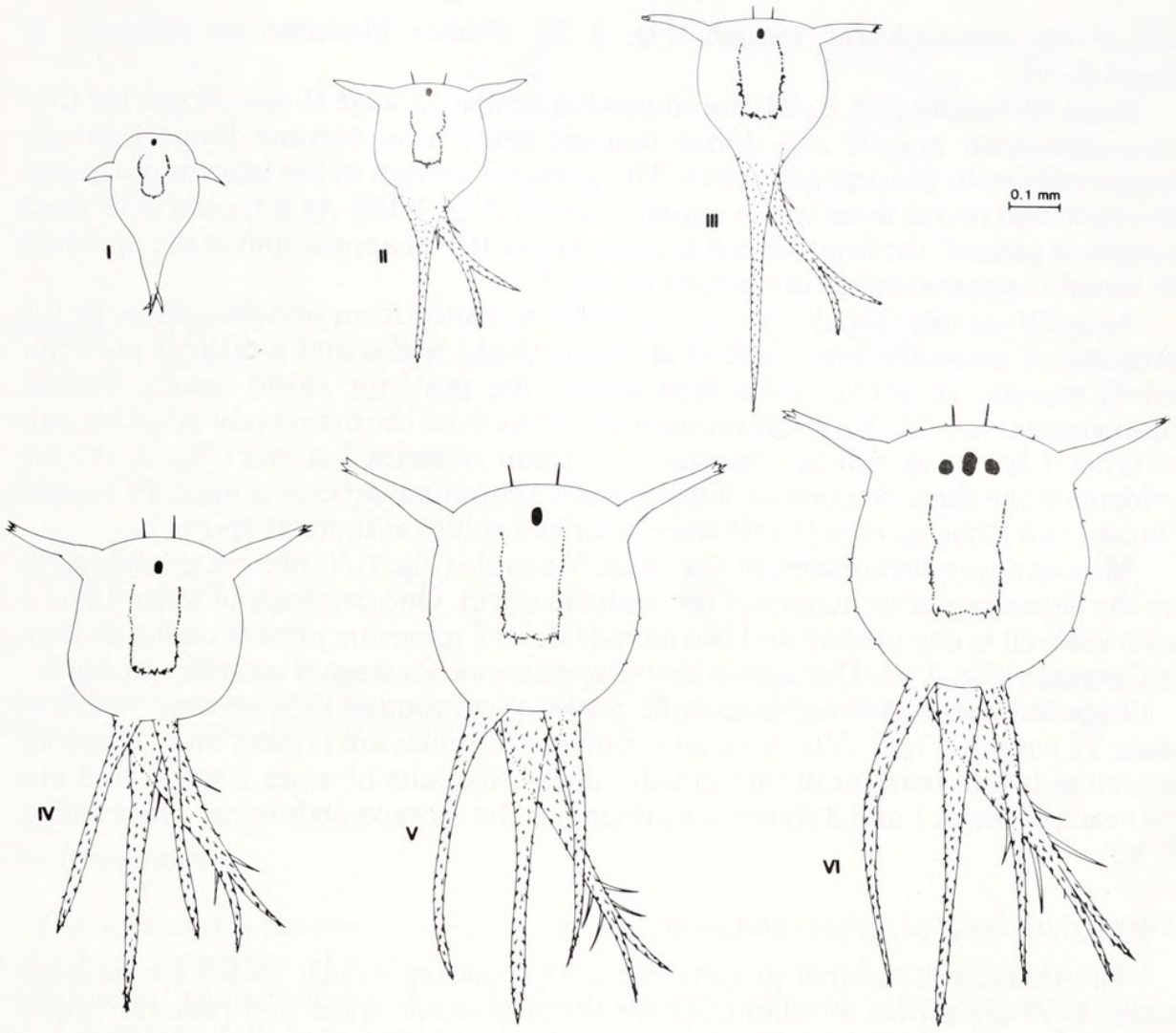

FIGURE 1. *Lithotrya dorsalis*. Dorsal view of shield outlines of naupliar stages I–VI.

The nauplii[1]

The naupliar stages as seen from above are illustrated in Figure 1. First stage nauplii (Fig. 1, I) are characterized by frontolateral horns directed posteriorly with the posterior region of the cephalic shield tapering distinctly into a rudimentary thoracic spine dorsal to a small, forked thoraco-abdominal process. A median naupliar eye is evident and remains throughout naupliar development. A unilobed labrum with one median tooth is present. Stage I nauplii have the full complement of naupliar appendages, the uniramous antennules, biramous antennae, and mandibles, provided with simple setae. It is a nonfeeding stage and molts to stage II within one or two hours post hatching.

The thoraco-abdominal process and dorsal thoracic spine become elongated and spinulated at stage II (Fig. 1, II) and remain this way throughout naupliar development. The thoraco-abdominal process is distinctly and deeply forked and contains one pair of series 1 spines (Fig, 2, II). A row of fine, slightly arched hairs appear on each side of the proximal portion of the labrum. An additional tooth appears at either

[1] Descriptive terminology after Lang (1979) with the exception of the term "thoraco-abdominal" process suggested by W. A. Newman.

end of the posteriolateral margin (Fig. 3, II). Frontal filaments are apparent at stages II–VI.

Stage III nauplii (Fig. 1, III) are somewhat similar to stage II nauplii but the thoraco-abdominal process and dorsal thoracic spine have become proportionately longer relative to the cephalic shield. The posterior margin of the labrum now bears five teeth and two to three spines appear laterally (Fig. 3, III). As is typical of cirriped nauplii in general, the frontolateral horns at stages III–VI appear split at the tip. Stage III nauplii appeared in culture as early as day 3.

Stage IV nauplii (Fig. 1, IV) are easily distinguished from previous stages by the presence of unusually long, barbed posterior shield spines and a distinct posterior shield margin. In active, swimming larvae, the posterior shield spines, present throughout stages IV–VI, curve prominently away from the main body axis. One pair of series 1 spines as well as 1 median and 1 pair of series 2 spines (Fig. 2, IV) are evident on the thoracic portion of the thoraco-abdominal process of stage IV nauplii [Brown and Roughgarden (1985) refer to series 2 spines as thoracic spines.]

Increasing proportionately in size, stage V nauplii (Fig. 1, V) possess several spines on the lateral posterior margin of the cephalic shield. One pair each of series 1 and 3 spines as well as one median and two pairs of series 2 spines are present on the abdominal process (Fig. 2 V). The earliest day of appearance for stage V nauplii was day 7.

Approximately 24 hours post-molt, a pair of compound eyes become visible in stage VI nauplii (Fig. 1, VI). A variable number of spines are present on the anterior as well as lateral margins of the cephalic shield. Six pairs of series 2 spines and one pair each of series 1 and 3 spines are present on the thoraco-abdominal process (Fig. 2, VI).

Thoraco-abdominal process and caudal spines

The thoraco-abdominal process and corresponding caudal spines for naupliar stages I–VI are shown in relation to the dorsal thoracic spine and posterior shield spines in Figure 2. The thoraco-abdominal process in all stages is shorter than the dorsal thoracic spine. The distal end of the thoraco-abdominal process is deeply forked in naupliar stages II–VI. The appearance of caudal spine series 1, 2, and 3 on this process closely follows the sequence established for other cirripeds (Moyse, 1961; Lang, 1979). However, examination of several stage V nauplii revealed 3 pairs of series 2 spines instead of the usual 2 as drawn. The thoraco-abdominal process along with the dorsal thoracic spine (stages II–VI) and the posterior shield spines (stage IV–VI) are heavily spinulated. There appears to be no pattern to this secondary ornamentation.

Labrum

The unilobed labrum (Fig. 3), characteristic of all lepadomorph nauplii, is distinctly indented at approximately midlength in naupliar stages I and II of *Lithotrya dorsalis* (Fig. 3, I & II). The proximal half of the stage I labrum is noticeably wider than the distal portion. By naupliar stage III, the median tooth now appears clearly associated with the labral gland (Fig. 3, III). Two to three spines are now present on the lateral edges. On the dorsal (inside) surface a row of very fine hair-like processes appear along either side of the labral gland duct. At stages IV–VI (Fig. 3, IV, V, & VI), very thick, hair-like projections appear to surround all but the median tooth on the posterior margin. By stage V, the median tooth becomes less prominent while the remaining teeth become more pronounced. By stage VI, the median tooth is reduced to an inconspicuous knob and appears disassociated from the now indistinct labral gland.

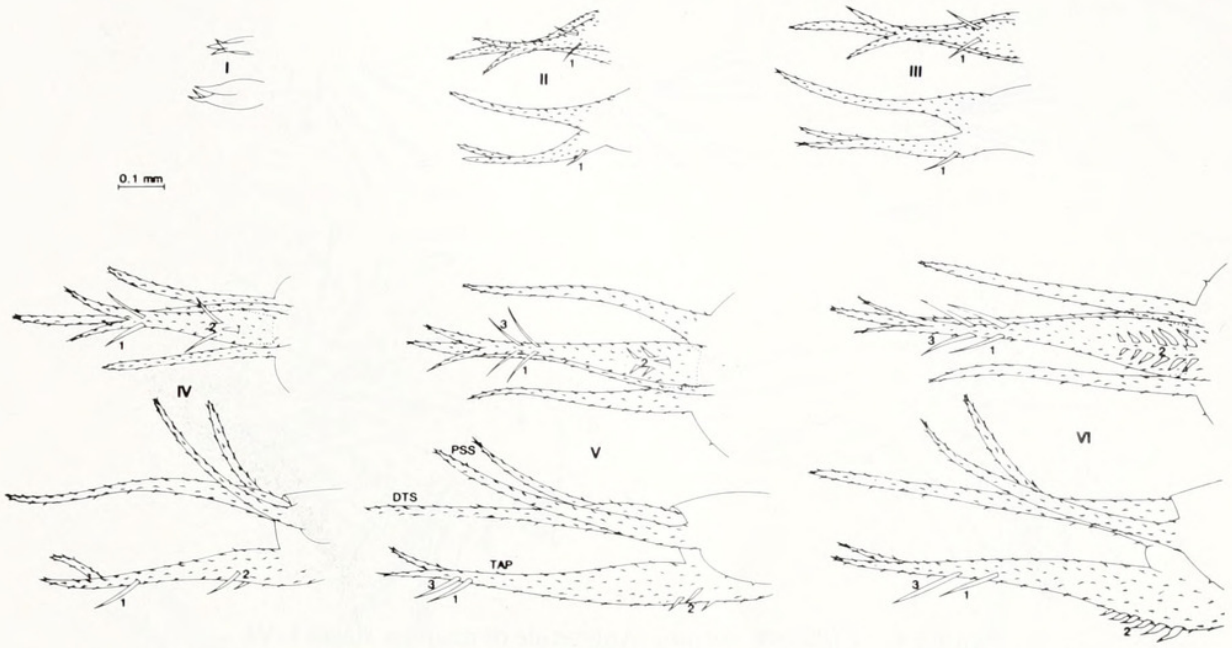

FIGURE 2. *Lithotrya dorsalis.* Ventral and lateral views of the dorsal thoracic spine (DTS) and thoraco-abdominal process (TAP) relative to the posterior shield spines (PSS) in naupliar stages I–VI. Caudal spine series are designated by Arabic Numbers (1, 2, and 3).

The appendages

The uniramous antennules (Fig. 4), biramous antennae (Fig. 5), and mandibles (Fig. 6) are shown for all 6 naupliar stages. The entire setae are not drawn, in most cases, due to their extremely long and delicate nature. Using the basic setation formulae of Newman (1965) as modified by Lang (1979), these appendages are further described in Table II.

The number of setae appearing within a particular stage was relatively constant, reinforcing the idea that setation of an appendage (barring the consequences of dissection) is an accurate indication of naupliar stage (Lang, 1979; Dalley, 1984). The transition from simple to plumose setae appeared to be somewhat variable, particularly on the antennal and mandibular endopodites of stages IV–VI.

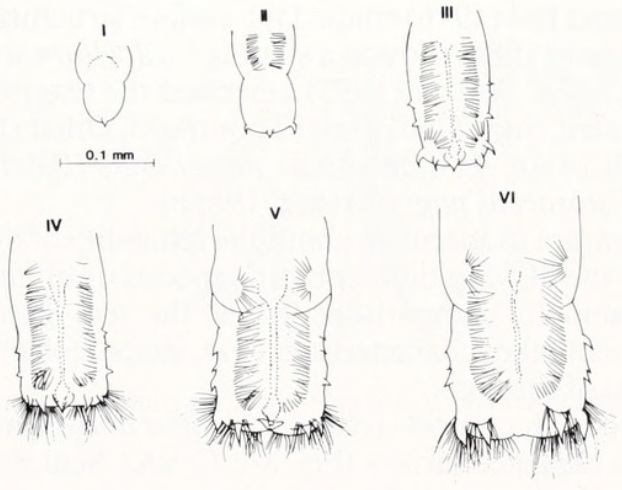

FIGURE 3. *Lithotrya dorsalis.* Labrum of naupliar stages I–VI.

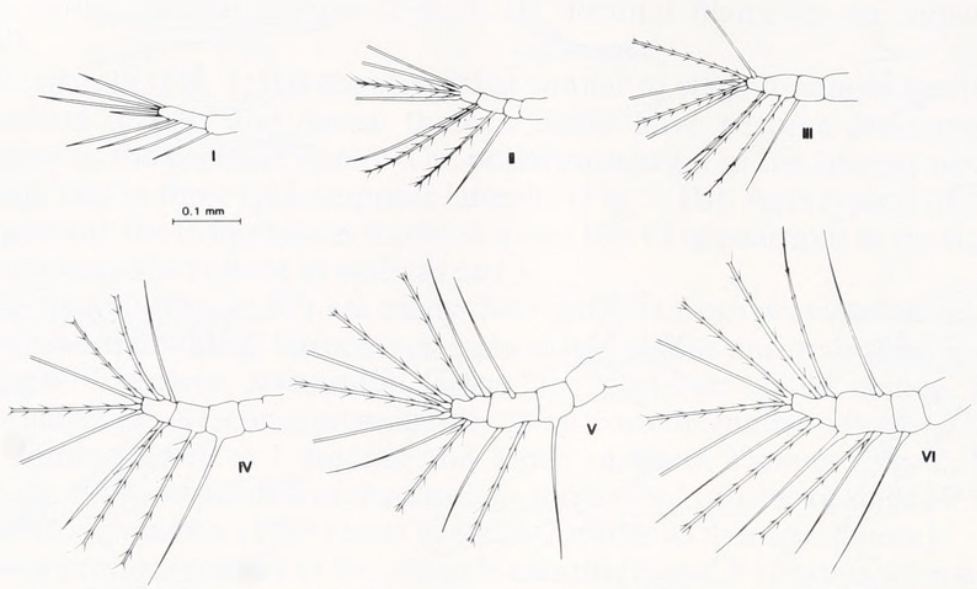

FIGURE 4. *Lithotrya dorsalis.* Antennule of naupliar stages I–VI.

The cyprid

The cyprid (Fig. 7A) is relatively small (averaging 518 μm total length) and similar in overall appearance to other previously described cyprid larvae at the level of light microscopy. A bivalved carapace, compound and median eyes, six pairs of biramous natatory appendages (Fig. 7B), caudal furca (Fig. 7C), and a pair of antennules (Fig. 7D) modified to act as exploratory and attachment organs are present. The anterior margin of the cyprid is evenly rounded. The posterior ventral margin tapers more sharply than the dorsal margin. As a consequence, the posterior end appears more ovoid (Fig. 7A). The living cyprid is somewhat translucent in both the anterior and posterior extremities. The bulk of the body is filled with golden-colored oil cells. There is an irregularly shaped, orange pigment area in the mid to posterior region. The compound eyes have a distinct dark red coloration. The setation of the cyprid appendages (Fig. 7B, C, D) is remarkably consistent with that described for other species (Batham, 1946; Walker and Lee, 1976).

The use of the scanning electron microscope in describing barnacle cyprids has been limited. The cyprid antennule of *Semibalanus balanoides* L. was described by Nott (1969). Walker and Lee (1976) studied the surface structure of the *S. balanoides* cyprid using SEM. Svane (1986) showed a settling *Scalpellum scalpellum* cyprid (low magnification) using SEM. Walker (1985) described the external features of the cyprid of the rhizocephalan, *Sacculina carcini* Thompson. Other rhizocephalan cyprids described with the SEM are *Lernaeodiscus porcellanae* (Ritchie and Høeg, 1981; Høeg, 1985a) and *Clistosaccus paguri* (Høeg, 1985b).

It is perhaps premature to speculate about the reliability of cyprid carapace sculpturing as revealed by the SEM in differentiating species until more such descriptions are available for meaningful comparisons. But at the very least, such SEM descriptions should supplement other characteristics (size, shape, color) currently being used with varying amounts of success.

SEM investigation of the cyprid larva of *Lithotrya dorsalis* reveals distinct sculpturing over the entire carapace surface (Fig. 8A, C; 9A). Sculpturing consists of carinae arranged in a somewhat parallel configuration and interspersed with numerous cuticular setae (Fig. 9B), pores (Fig. 9C) and small papillae (Fig. 9D). The parallel

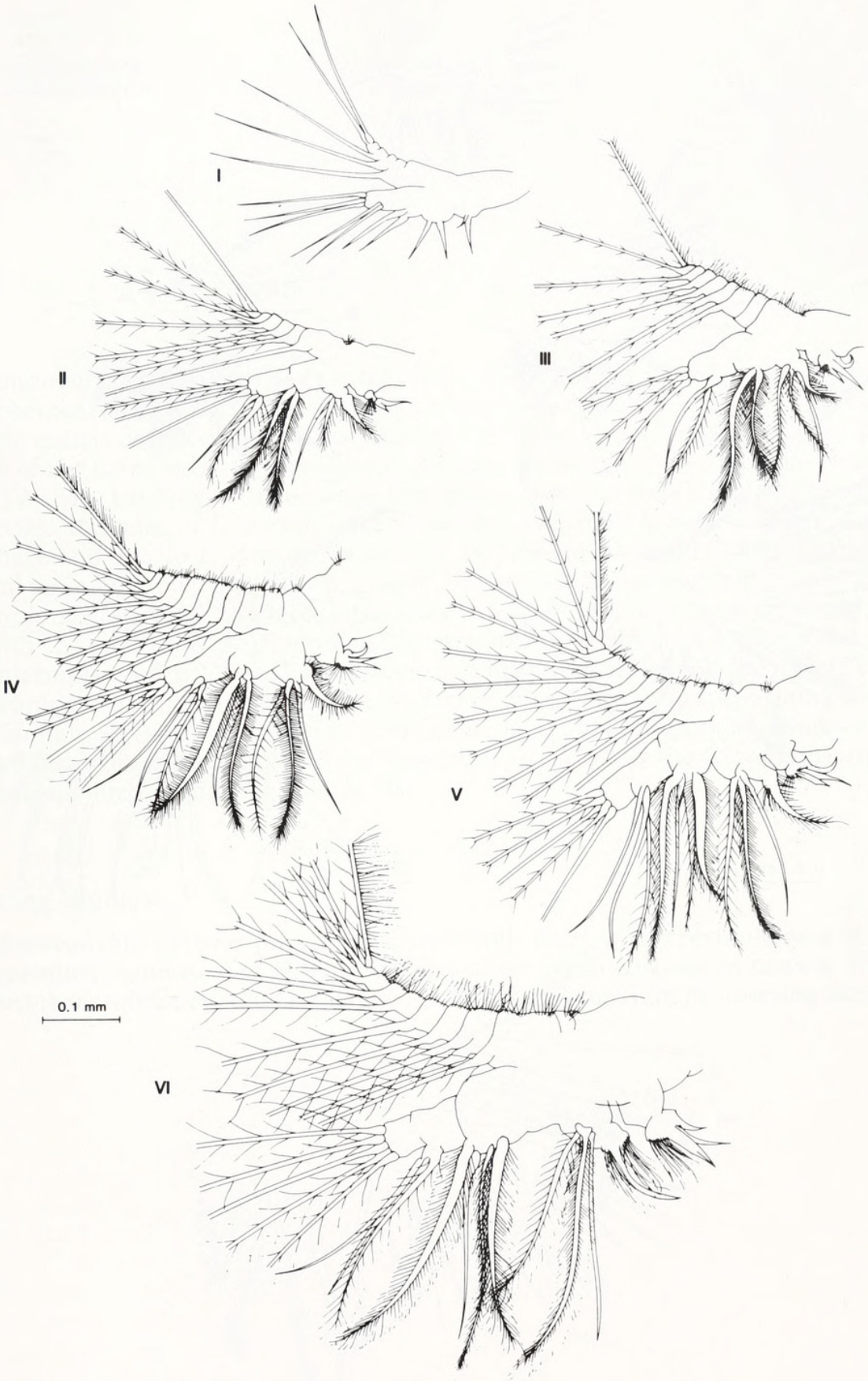

FIGURE 5. *Lithotrya dorsalis*. Antenna of naupliar stages I–VI.

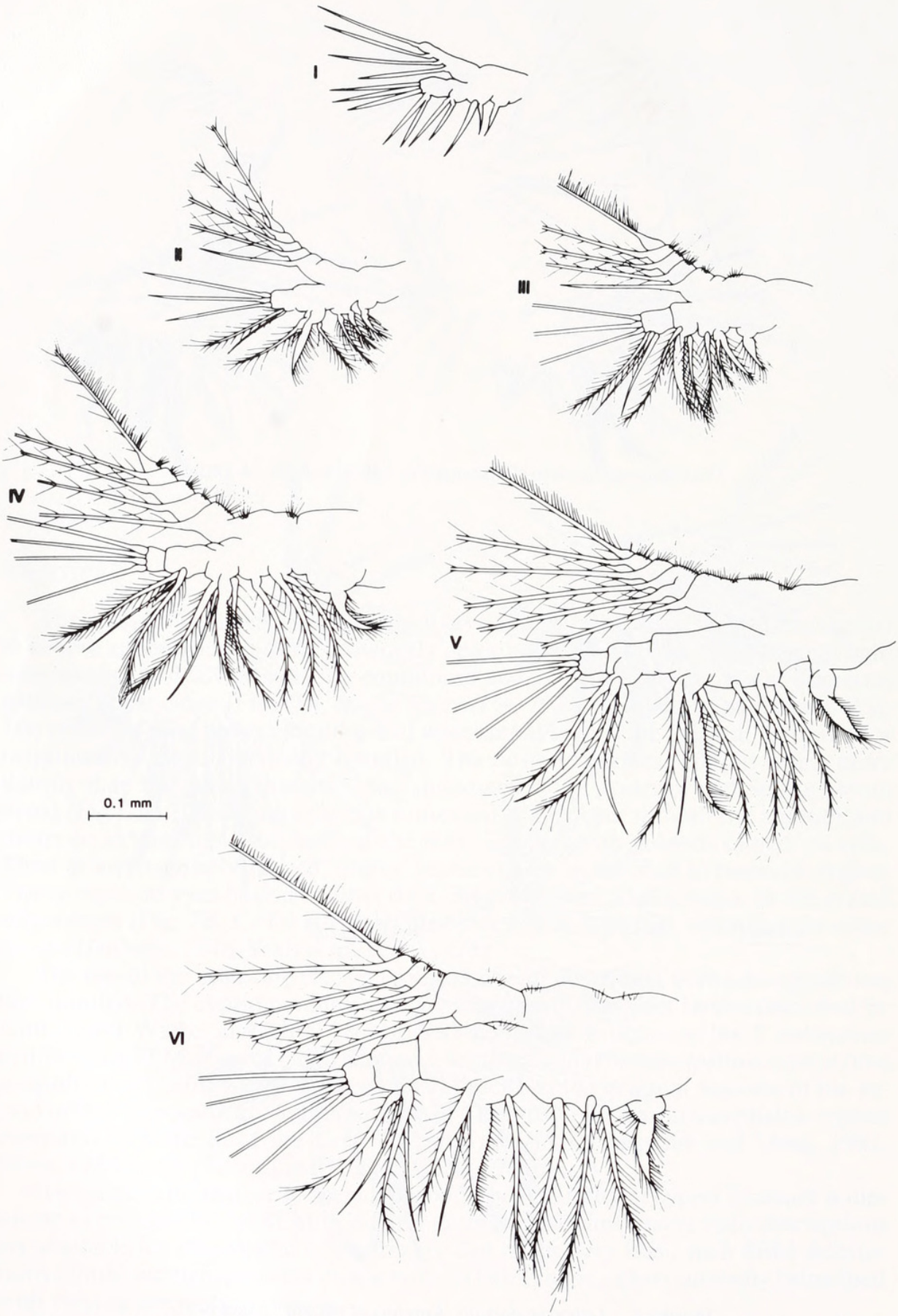

FIGURE 6. *Lithotrya dorsalis.* Mandible of naupliar stages I–VI.

TABLE II

Setation formulae for nauplii of Lithotrya dorsalis

Stage	Antennule	Antenna	Mandible
VI	S P P PSPS SP S PS S	4P 8P PPSPP SSP FSFF PFSC G	P 5P 5S PSPS PSCP PPP G
V	S S P PSPS SP S P S	3P 7PS PPSPS SSP FSPF PFSC G	P 5P 5S PSPS PSCP PPP G
IV	S P PSPS SP P S	2P 7P PPSPS SSP F SF PFSC G	P 4P 4S PSP PSCP PPP G
III	S PSPS SP P S	2P 5P PP P S P F F PPSC G	P 3PS 3S PSS P CP PPP G
II	SSPS SP P S	SP 4PS PS S S P F F SP C G	P 3PS 3S P S P CP PP G
I	SSSS SS S S	S 4S SS S S S S S SS G	S 3S 3S S S S S SS G

arrangement of these carinae or ridges give the *L. dorsalis* cyprid cuticle a striated appearance quite distinct from the pitted appearance of the *Semibalanus balanoides* cyprid cuticle described by Walker and Lee (1976) and the somewhat hairy appearance of the *Lernaeodiscus porcellanae* (Ritchie and Høeg, 1981) and *Sacculina carcini* (Walker, 1985) cyprids due to the long setae present on their cuticles. The cuticular pores and setae of *L. dorsalis* and *S. balanoides* cyprids however, appear similar in shape and size. In *L. dorsalis,* pores (Fig. 9C) are round, small (approximately 5–8 μm) and numerous. Cuticular setae (Fig. 9B) are also numerous, particularly in the posterior region of the carapace. These setae extend from a pore-like process and vary slightly in length (5–8 μm). Dorsal and ventral marginal carinae sometimes continue uninterrupted for the entire length of the cyprid. Towards the mid-lateral section of the carapace (Fig. 9A) the carinae become shorter and appear to follow more closely the contour of the animal causing some degradation of their parallel arrangement. The distinct dorsal junction of the carapace valves including the dorsal hinge region is shown in high magnification (Fig. 8B).

DISCUSSION

Rearing techniques

Survivorship to the cyprid stage was relatively poor. Many permutations of diet, temperature, salinity, and light were tried with varying degrees of success. It was hoped that antibiotics could be avoided in the culture medium by lowering the tem-

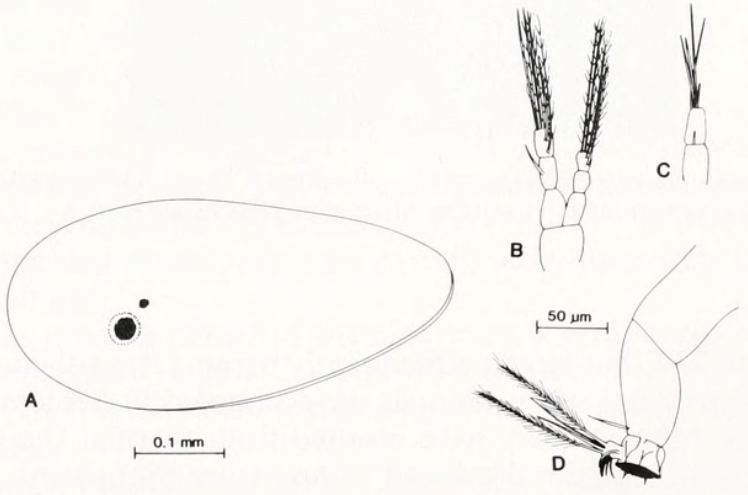

FIGURE 7. *Lithotrya dorsalis.* Carapace shield outline of cyprid (A); natatory appendage (B); caudal furca (C); and antennule (D).

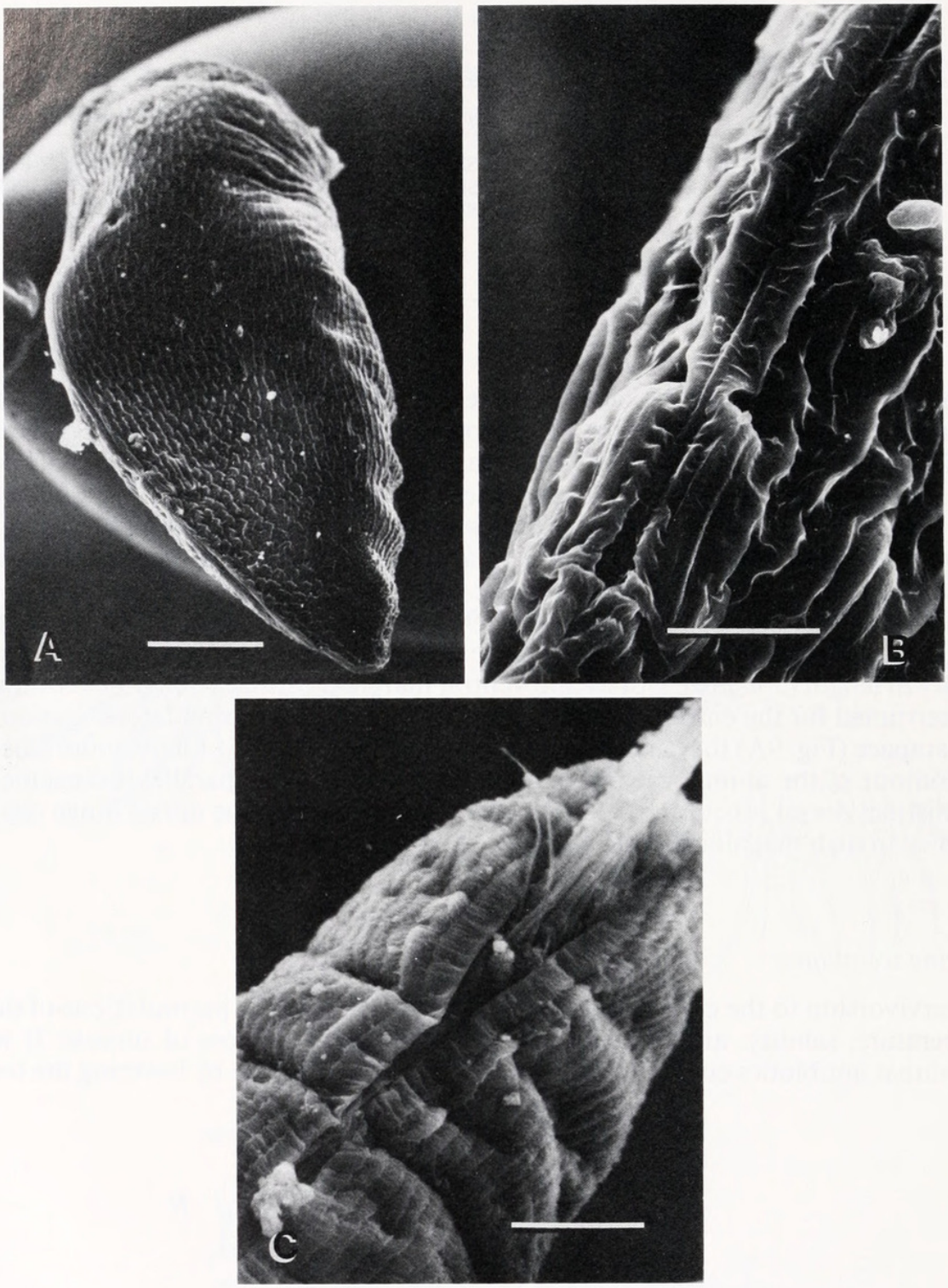

FIGURE 8. *Lithotrya dorsalis*. SEM Dorsal (A) and ventral (C) view of bivalved cyprid carapace; high magnification view of carapace junction including hinge region (B). (Scale bars: A = 50 μm; B = 10 μm; C = 100 μm).

perature from 30 to 22°C but larvae subsequently became sluggish and died off. Ambient seawater temperature when animals were sampled in September, 1983, was 32°C. This sluggish behavior may have resulted from thermal shock or perhaps a lower feeding efficiency at the decreased temperature (Scheltema and Williams, 1982). By lowering the salinity to 28 ppt in combination with antibiotics, entanglement of nauplii, particularly in mature cultures when appendage setation became

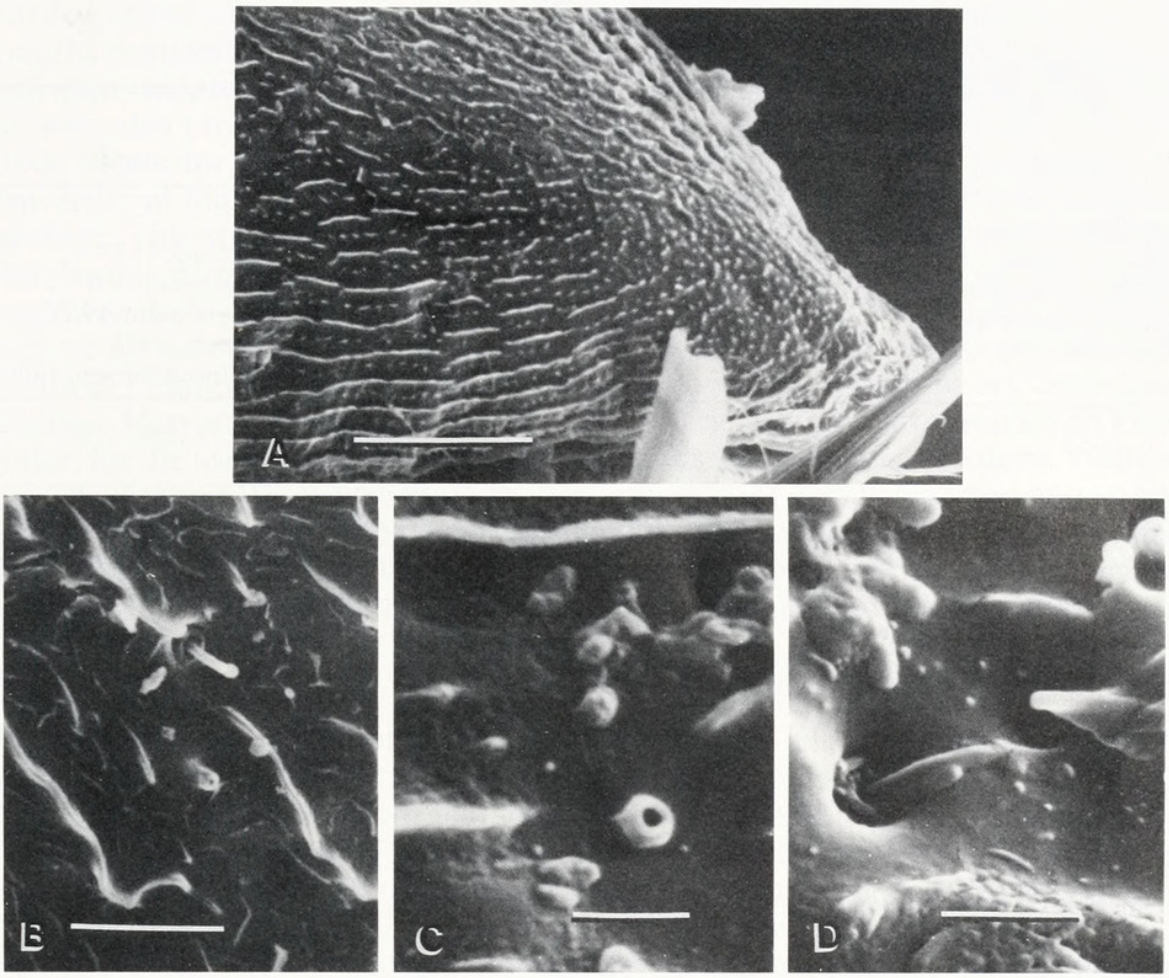

FIGURE 9. *Lithotrya dorsalis*. SEM Posterior lateral view of cyprid carapace (A) and cuticular structures: Seta (B), pore (C) and papillae (D). (Scale bars: A = 50 μm; B = 10 μm; C and D = 1.0 μm).

more elaborate, was avoided. In an attempt to increase the cyprid yield, while keeping the logistics of culture maintenance at a minimum, initial densities were increased from 1 or 2 to 6 or 8 nauplii per ml culture medium. Some of these high density cultures reached stage IV nauplius with no apparent deleterious effects. At this time, however, the algae being used as food (*Thalassiosira fluviatilus/Tetraselmis suecica*) became contaminated. By the time a new diet was selected (*Chaetoceros gracilis/Isochrysis* sp.), most cultures had been without food for 36 h. This apparent starvation resulted in substantial mortality, especially in older cultures. Younger cultures survived somewhat better, perhaps due to yolky material still present in these early naupliar stages. Because of the unexpected mortality, it was impossible to compare survivorship between low and high density cultures statistically. However, even though percent survival to the cyprid stage was lower in the "higher density" cultures, it was encouraging that actual cyprid yields in these cultures were higher than in the "low density" cultures.

Suspecting the possible release of chemical cues, several unsuccessful attempts to initiate metamorphosis of stage VI nauplius to the cyprid stage were made by placing stage VI nauplii in "conditioned" culture medium where metamorphosis had previously taken place.

The size of gravid individuals at the time of sampling (September and October) was small; their carinal-rostral axes averaged 3.4 mm. The larger individuals sampled at this time (carinal-rostral axes as large as 7.8 mm) were not gravid. This may have

TABLE III

Measurements of scalpellid cyprid larvae

Species	Length (μm)	Width (μm)	Author
Capitullum mitella	1050	400	
Calantica spinosa	850	385	Yasugi, 1937
Scalpellum scalpellum	686	329	Batham, 1946
Pollicipes polymerus	425	232	Kaufmann, 1965
Lithotrya dorsalis	518	240	Lewis, 1975
			Dineen (present study)

been a consequence of sampling at the end of the breeding season. Reproductive patterns in *Lithotrya dorsalis* have not been documented. Attempts to induce reproduction in the laboratory by increasing food availability and temperature failed.

Comparison of scalpellid larvae

Adaptive radiation in the scalpelloids has given rise to the more advanced sessile barnacles [Suborders: Brachylepadomorpha (now extinct), Verrucomorpha, and Balanomorpha (Newman, 1982)]. It is noteworthy that the basic sequential pattern of larval development of this relatively primitive scalpellid barnacle is remarkably similar to that of other more advanced cirripeds described to date.

When comparing the larval stages of *Lithotrya dorsalis* with the four other described scalpellid species, the most striking similarity occurs between the cephalic shield outlines of *L. dorsalis* and *Capitullum mitella* (Yasugi, 1937). Although the length of *L. dorsalis* nauplii is greater at all stages, the same basic shield shape, along with the elongated and spinulated thoraco-abdominal process and dorsal thoracic spine and in particular, the elongated posterior shield spines in larval stages IV–VI, are present in both species. Rudimentary posterior shield spines appear in *C. mitella* naupliar stages II and III. Nauplii of the three other scalpelloids described, *Calantica spinosa* (Batham, 1946), *Scalpellum scalpellum* (Kaufman, 1965), and *Pollicipes polymerus* (Lewis, 1975) have relatively abbreviated thoraco-abdominal processes and dorsal thoracic spines and appear to lack posterior shield spines entirely. The unilobate labra of *L. dorsalis, P. polymerus,* and *C. mitella* are similar in outline, having a blunt posterior margin with numerous teeth, particularly in later stages. This same region in the naupliar labrum of stage VI *C. spinosa* appears narrowly rounded, with a single middle tooth. Labra of stage I nauplii of both *L. dorsalis* and *C. mitella* widen in the proximal region. Unfortunately, setation formulae for *C. mitella* are not given.

Cyprid sizes of these five scalpellids are compared in Table III.

The similarity between *Lithotrya dorsalis* and *Capitullum mitella* nauplii stimulate two questions. (1) Are these two species more closely aligned than presently thought? [Zevina (1981) places them in separate subfamilies: *Lithotryinae* and *Pollicipinae,* respectively). (2) More fundamentally, how reliable are naupliar characteristics as indicators of phylogenetic affinities among the Cirripedia?

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