Abdominal tergite and pleopod changes in *Lithodes aequispinus* Benedict, 1895 (Crustacea: Decapoda: Anomura: Lithodidae) from megalopa to juvenile

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Abstract.—Abdominal tergite development is described and illustrated for the megalopal and first seven crab stages of the golden king crab, *Lithodes aequispinus* Benedict, supplemented by additional information from stage 12. The results of this study, the first to encompass more than the first five juvenile stages in any lithodid species, have shown conclusively that at least in the genus *Lithodes,* the marginal plates of the adult second tergite are not homologous with the so-called marginal plates of the third through fifth tergites; and that tergite development is not particularly stage related. Additionally, the paired abdominal pleopods of the megalopa that are lost in both sexes with the molt to the second crab stage, reappear on the left side of the abdomen in females at the fifth or sixth crab stage.

Since McLaughlin & Lemaitre's (1997) proposition that hermit crabs were not the evolutionary ancestors of king crabs, considerable emphasis has been focused on the megalopal and early juvenile development in the latter group (Crain & McLaughlin 2000a, 2000b; McLaughlin & Lemaitre 2001, McLaughlin et al. 2001, 2002). Although these studies have greatly enhanced our understanding of tergite development and pleopod loss during the very early juvenile stages, none have provided detailed information beyond crab stage 3. For the first time, it is possible to trace these changes from the megalopa through juvenile crabs of approximately three years of age. These new data provide not only further information on tergite development and early juvenile pleopod loss, but also the reappearance of pleopods and sexually associated changes allied with female tergite asymmetry.

The data base of this study includes an uninterrupted series of specimens from the megalopal stage and crab stages 1–7, supplemented by an intermittent series through nearly three years of rearing. Larvae were hatched in the Seward Marine Center laboratory from adult female golden king crabs captured with crab pots at depths of 108 to 152 m on the western side of Prince William Sound, Alaska (Paul & Paul 2001). Zoeae and megalopae were reared in groups of ten in 4 l glass containers held in a water bath at ambient incoming seawater temperature (Adams & Paul 1999, Paul & Paul 1999). Being lecithotrophic (Shirley & Zhou 1997), these larvae were not fed. Beginning with crab stage 1, and continuing though all juvenile stages, the crabs were fed shrimp, live mussel and squid alternating every other day, with excess food removed on the following day. Each day the containers were examined for exuviae and mortalities, which were removed and noted. Each 4 l glass container had 500 ml of raw seawater replaced every other day. When the crabs reached carapace lengths greater than 5 mm, they were placed in 12 l aquaria with running seawater for a study on inter-

molt duration and supplemental morphological study.

The specimens, including exuviae, were preserved in isopropyl alcohol and at the time of examination, transferred to 70% ethyl alcohol for permanent storage. Megalopal and early crab stage specimens were stained with Chlorazole Black E prior to study. Examinations were conducted using a Wild M-5 dissecting microscope provided with 15× oculars. Illustrations were made with the aid of a camera lucida mounted on that microscope. The abbreviation cl (carapace length, as measured from the tip of the anterior rostral process in early stages, or from the fork of the dorsal rostral processes in later stages, to the midpoint of the posterior carapace) provides an indication of specimen size. Measurements, to the nearest 0.1 mm, were made with an ocular micrometer through crab stage 3, and with a pair of Mitutoyo calipers in subsequent stages.

Results

Megalopa (cl = 2.1–2.4 mm; n = 4): The integument of the megalopal abdomen is entirely chitinous; the six somites (Fig. 1A, B) are distinct. The tergite of somite 1 is armed with pair of very prominent spines in the dorsoproximal midline. Tergites 2–6 each have an anterodorsal pair of spines in midline, largest on somite 3; tergites 2–4 also have a row of four posterodorsal, and two pairs of lateral, simple or bifid spines. Tergites 5 and 6 each has pair of small, anterodorsal and a pair of posterodorsal spines in midline, and tergite 5 also has pair of anterolateral spines. Paired biramous pleopods are present on somites 2–5; the exopods each with 11–13 long plumose setae, the endopods each with an appendix masculina consisting of three small hooks. Somite 6 has a pair of uniramous uropods, each with one subterminal and two terminal long setae.

Crab stage 1 (n = 17 + 27 exuviae; cl = 2.4–2.7 mm): The abdomen is strongly flexed and held closely against the cephalothorax; tergites (Fig. 1D) of somites 1, 2, and 6 remain chitinous or become weakly calcified. Tergite 1 is distinct and undivided. In contrast, tergite 2 now has the two or three-spined marginal plates partially to entirely separated; the broad central plate has only the prominent anterodorsal pair of spines in midline and a row of four smaller posterodorsal spines. The tergite of somite 3 also shows complete or partial separation of weakly calcified marginal plates, as identified by the marginal spines of megalopa. Similar divisions of the marginal plates of the tergites 4 and 5 are indicated by partial to complete sutures. The lateral plates of tergites 3–5 are faintly delineated, and sometimes slightly calcified, but with marked reduction of the posterodorsal spines of megalopa. The median regions remain chitinous or are becoming thinly membranous; megalopal spines are sometimes still present, but more frequently only indicated by setal projections. Somite 6 is now weakly calcified. The paired, biramous pleopods of the megalopa are reduced to uniramous "stumps" (Fig. 1C). The megalopal uropods are vestigial or completely absent.

Crab stage 2 (n = 1 + 27 exuviae; cl = 3.2–3.6 mm): Tergites (Fig. 1E) of somites 1, 2, and 6, as well as the telson are moderately well calcified. The undivided tergite 1 is reduced in size but still armed with a very prominent dorsomedian pair of spines. The central plate of tergite 2 has an additional large spine near each anterodorsal angle, and frequently a small posterodorsal spine near each posterolateral angle; the marginal plates each are well calcified and have three prominent spines. Tergites 3–5 are entirely membranous medially; irregular lateral plates are delineated and weakly to moderately well calcified; well calcified marginal plates are usually separated from the lateral plates, at least on somites 3 and 4. Tergite 6 retains a pair of small spines anteriorly and posteriorly. The telson is unarmed. Pleopods are entirely absent.
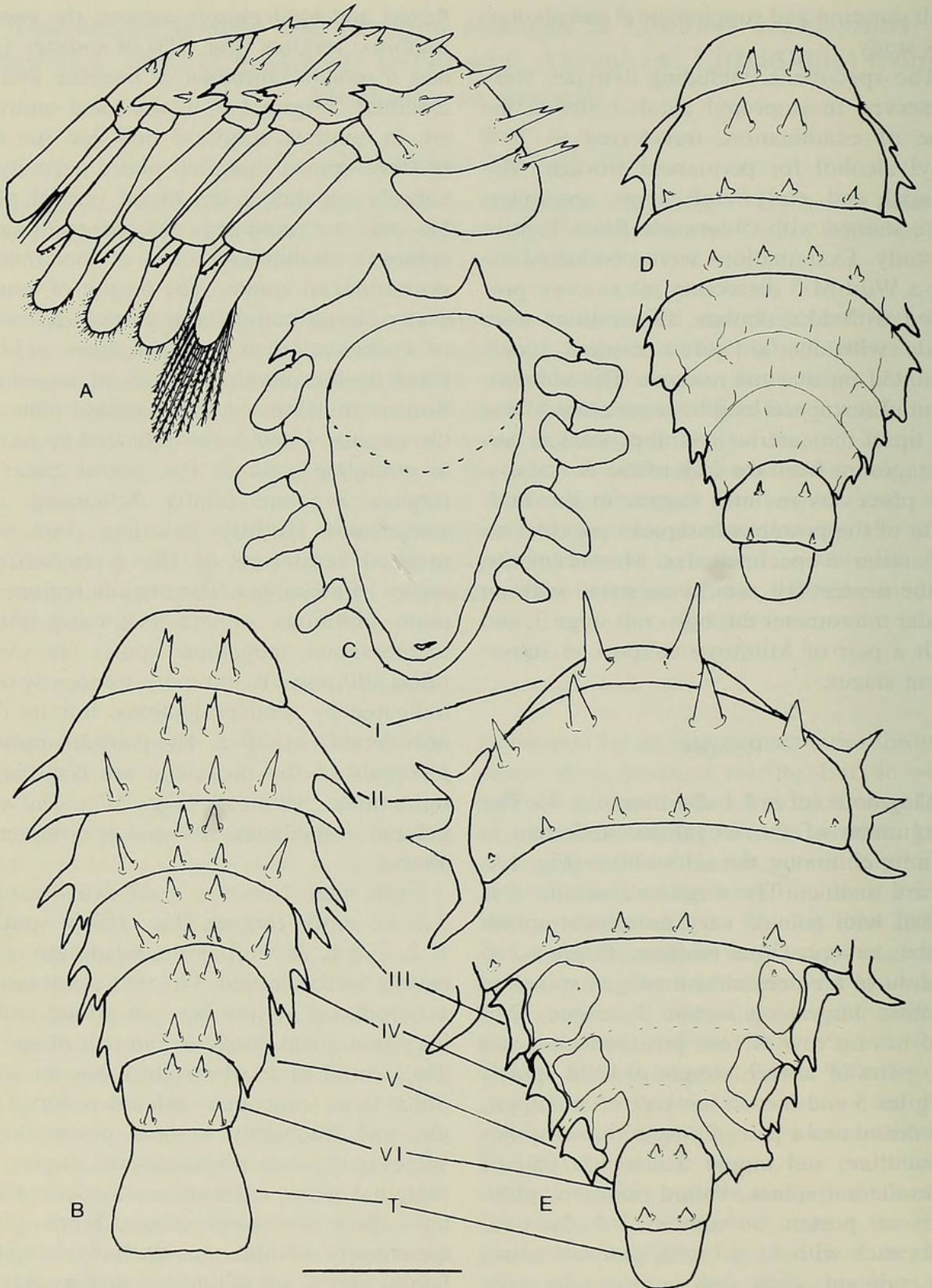
Fig. 1.   Abdominal tergites and telson of *Lithodes aequispinus* Benedict, 1895; A, B, megalopa; C, crab stage 1 (sternal view) 1; D, E, crabs stages with tergites 1 and 2 shown separately from tergites 3–6 and telson because of abdominal flexion. A, lateral view; B, dorsal view; C, crab stage 1 with reduced pleopods; D, crab stage 1; crab stage 2. Roman numerals I–VI indicate abdominal tergites; T indicates telson. Scale equals 0.5 mm.

Crab stage 3 ($n = 8 + 19$ exuviae, cl = 3.8–4.7 mm): Tergites (Fig. 2A) 1, 2, 6, and the telson are better calcified. The median pair of spines on tergite 1 is still very prominent. The four anterodorsal spines of tergite 2 are reduced in size, an additional pair is present medially, and frequently a very small spine as been added above each posterolateral angle. The lateral and marginal plates of tergites 3–5 may be undivided, completely and widely separated, separated but contiguous, or partially rejoined. The median area of tergite 3 frequently will have two or sometimes and entire row of small calcified nodules anteriorly, whereas these regions of tergites 4 and 5 remain completely membranous or show only one or two pairs of minute, slightly calcified granules. However, two or three accessory, and usually spinose, calcified nodules often can be detected developing in the marginal integument on one or both sides. Tergite 6 is larger than in the previous stage, but otherwise unchanged, whereas the telson now is armed with a pair of small spines.

Crab stage 4 ($n = 13$, all exuviae, cl = 5.6–7.2 mm): Tergite 1 remains unchanged. Tergite 2 (Fig. 2B) usually has another anterolateral spine on each side; the posteromedial spine is larger and an additional tiny pair of median spines is often present anteriorly. The lateral and marginal plates of tergites 3–5 show considerable variation, but usually are partially to completely rejoined. The median area of each tergite most frequently has a few calcified nodules, most numerous and largest on tergite 3. Much more prominent and usually spiniform accessory nodules are now present on both, or only on the right side of the marginal integument. Tergite 6 and the telson show increases in size, but otherwise remain unchanged.

Crab stage 5 ($n = 5$, 2 ♂, 3 ♀ + 15 exuviae, 4 ♂, 6 ♀ clearly identifiable); cl = 6.5–8.4 mm): Sexual dimorphism, as indicated by tergite development (Fig. 2C, E) is now clearly apparent. Tergite 1 remains

unchanged in both sexes, whereas the number of spines present on the median plate of tergite 2 has frequently, but not uniformly, increased. In one specimen a small fourth spine is present anteriorly on the right marginal plate of this tergite.

Fusion of the marginal and lateral plate elements of tergites 3–5 in males may or may not be complete, and while their shapes are irregular, the pairs are generally symmetrical in size. Spiniform nodules can be observed developing in the marginal integument on both sides of the abdomen. The median areas remain membranous but with a slight increase in the number of calcified nodules.

At this stage in females, the usually, now entirely fused lateral and marginal plates of tergites 3–5 are somewhat to appreciably larger on the left side of the abdomen than on the right; however on the right side several accessory spiniform nodules have developed in the integumental margin. Similar nodular development is completely lacking on the left side. As in males, the median areas of these tergites, while still membranous, show slight increases in the number of calcified nodules present, some of which are minutely spinulose. With one exception, there is no indication of pleopods on any of the somites; however, incipient gonopores occasionally can be observed on the coxae of the third pereopods. The exceptional female (cl = 6.5 mm) has minute, uniramous buds on somites 2–5 (Fig. 2D).

Crab stage 6 ($n = 2$ ♀ + 16 exuviae, 7 ♂, 5 ♀ clearly identifiable; cl = 8.1–10.9 mm): The marginal plates of tergite 2 (Fig. 3A) each now usually has a small spine present at the inner posterodorsal angle, and occasionally one or two additional spines are present on the dorsal surface of the median plate. The median areas of tergites 3–5 in both sexes show an increase in the number and size of calcareous nodules. In males the size and number of accessory spiniform nodules increases in the marginal integument on both sides, whereas development of these nodules is still restricted to
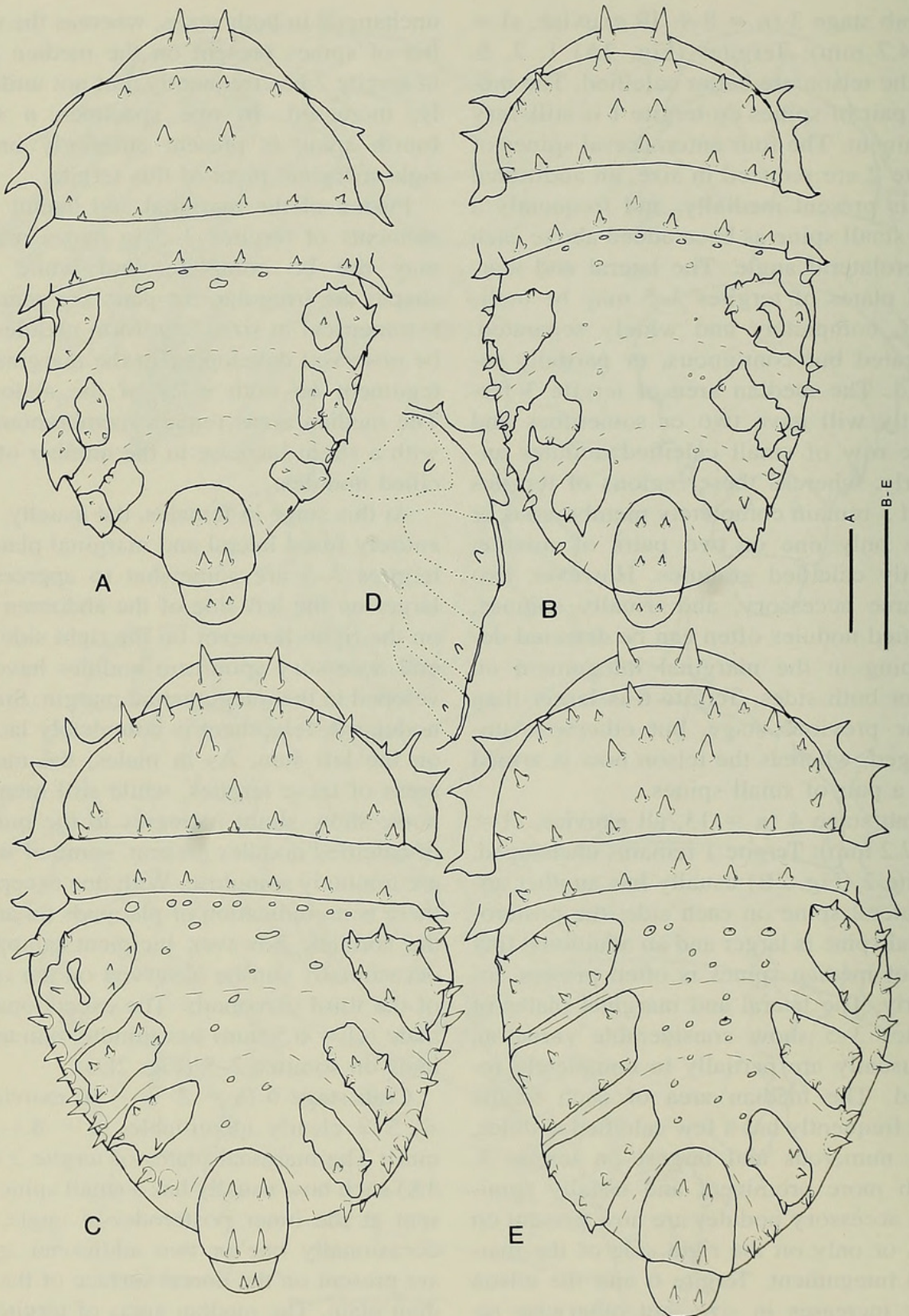
Fig. 2.   Abdominal tergites and telson of *Lithodes aequispinus* Benedict, 1895; tergites 1 and 2 shown separately from tergites 3–6 and telson because of abdominal flexion. A, crab stage 3; B, crab stage 4; C, male crab stage 5 (tergal view); D, left side of somites 3–5 of female crab stage 5 (sternal view showing developing pleopods); E, female crab stage 5 (tergal view). Scales 0.5 mm (A) and 1.0 mm (B–E).
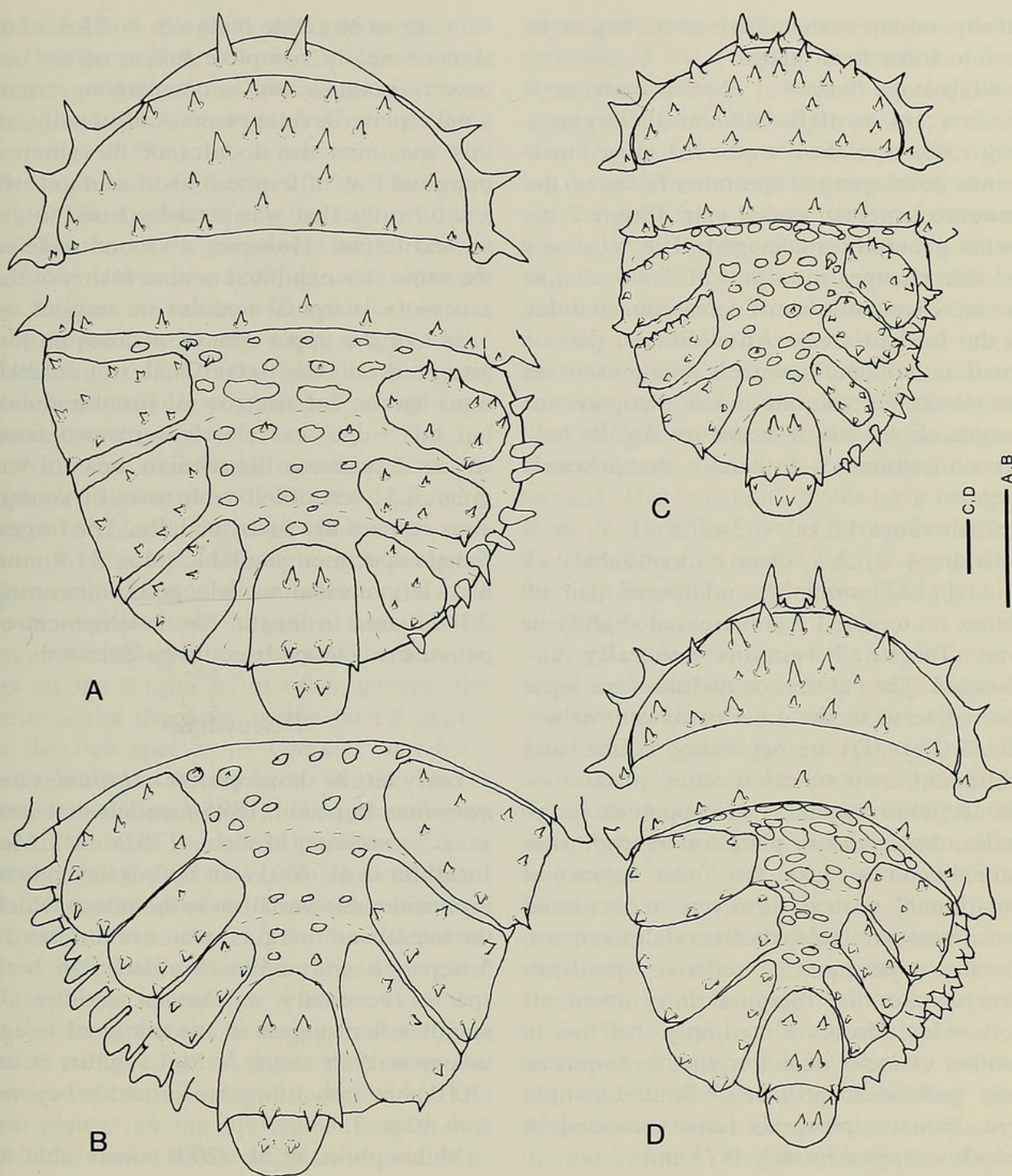
Fig. 3. Abdominal tergites and telson of *Lithodes aequispinus* Benedict, 1895; A, C, D, tergites 1 and 2 shown separately from tergites 3–6 and telson because of abdominal flexion. A, normal sixth female crab stage; B, abnormal sixth female crab stage; crab stage 7; crab stage 12. Scales equal 1 mm.

the right side in females. Tergite 6 in both sexes usually has a small spine developing on each posterodorsal angle. Very small (0.5–0.6 mm length) pleopod buds are now apparent ventrally on somites 2–4 of the two preserved females; gonopores are detectable on the female exuviae. One of the preserved females (cl = 10.2 mm) exhibits reversal in tergite and pleopod asymmetry. The stage 6 abnormal female has larger fused lateral/marginal plates on tergites 3–5 (Fig. 3B) than is seen in the normal female (cl = 9.7 mm), as well as much more advanced development of the accessory spi-

niform nodules, that have even begun to fuse to form weak plates.

Crab stage 7 (n = 1 ♀ + 6 exuviae, 4 ♂, 2 ♀; cl = 10.0–12.6 mm): Tergite 1 (Fig. 3C) now has a pair of very small spines developing at the inner bases of the prominent median dorsal pair. Tergite 2 remains generally unchanged. The most noticeable changes in tergites 3–5 are seen in the increased number of calcareous nodules in the median areas. An additional pair of small anterolateral spines is now present on the telson. Female uniramous pleopods are present on somites 2–5 and are slightly longer on somites 2–4 than in the previous stage.

Crab stage 12 (n = 3, 2 ♂, 1 ♀, + 8 exuviae, 4 ♂, 2 ♀ clearly identifiable); cl = 11.1–14.8 mm): The additional pair of spines on tergite 1 has increased slightly in size. Tergite 2 remains generally unchanged. The calcareous nodules forming a row adjacent to the anterior margin of tergite 3 (Fig. 3D) are beginning to fuse, and additional areas of calcification in the median regions frequently are apparent. In females, the accessory plates on the right side have begun to fuse and form segmental "marginal" plates; however, in the male specimens available, these nodules remain, for the most part, as separate spiniform structures in the marginal integument on both sides. However, to imply that this is another example of dimorphic development may well be an artifact of limited sample size. Females pleopods have increased in length to approximately 0.75 mm.

Later stages: Only a few specimens of various subsequent stages are available, but from these, it is apparent that rate of development of the median nodular areas of tergites 3–5 is extremely variable. Similarly, although the accessory nodular fusion and accompanying plate formation was first observed in a stage 12 female (cl = 14.7 mm), a much larger and considerably older female (cl = 26.3 mm, pleopod length of 1.8 mm) had large, but distinct accessory spiniform nodules exhibiting no sign of fu-

sion. In contrast, a male (cl = 23.5 mm) showed nearly complete fusion of the accessory nodules with accompanying "marginal" plate development. Additionally, in this specimen the nodules of the anterior marginal row of tergite 3 had fused to form a solid ridge that was partially fused to the second tergite. However, a second male of the same size exhibited neither fusion of the accessory marginal nodules on tergites 3–5, nor of the upper row of nodules on tergite 3. A slightly larger male (cl = 29.0 mm) had an anterior row of fused nodules, but this ridge was clearly separated from tergite 2, whereas the median areas of tergites 3–5 were filled with rows of contiguous or partially fused nodules. The largest female specimen available (cl = 31.8 mm) had left uniramous pleopods measuring 2.1–2.3 mm in length. No development of paired first pleopods could be detected.

Discussion

Early tergite development in *Lithodes aequispinus* Benedict, 1895 parallels that seen in *L. santolla* (Molina, 1782) (cf. McLaughlin et al. 2001). In both species there is considerable variation in the rate at which the lateral and marginal plates of tergites 3–5 separate and rejoin. Similarly, in both species accessory calcareous nodules or spinules first appear in the marginal integument at crab stage 3. McLaughlin et al. (2001) had only limited information beyond crab stage 3.

McLaughlin, et al. (2001) were able to confirm that the calcareous nodules observed in the integumental margins of tergites 3–5 in *L. santolla* began to fuse to form the so-called "marginal plates" of the adult. These authors pointed out that the marginal plates of tergite 2 were analogous with, but not homologous with those of tergites 3–5. As we have seen in the very early juvenile stages of *L. aequispinus*, there is initial division of the tergites, first with separation of marginal plates of the tergite 2, and subsequently delineation and separation

of lateral and marginal plates of tergites 3–5. However, plate division in these latter tergites of *Lithodes* is not as decisive as is seen in *Lopholithodes* (cf. Crain & McLaughlin 2000a) or *Acantholithodes* (cf. McLaughlin & Lemaitre 2001). This may, in part, be attributable to the lack of initial calcification of the megalopal integument in *Lithodes*. However, in *Paralomis,* although the tergites all were well calcified in the megalopal and early crab stages, McLaughlin, et al. (2002) found no marginal plate separation in tergites 3–5 at any stage through crab stage 5.

With the megalopal metamorphosis in *Lithodes,* the tergites of somites 1, 2 and 6 begin to calcify, but those of tergites 3–5 remain chitinous. Although each marginal plate delineation in these latter tergites appears initially with a suture forming between the marginal region and the remainder of the tergite as in other genera, the same is not the case for the lateral plates. In the two species of *Lithodes* that have been studied, demarcation of the lateral plates occurs principally through increased calcification of the lateral portions of each tergite, and the accompanying loss of chitin in the median portion. However, once separated, at crab stage 3 in the most precocious individuals, these lateral and marginal plates begin to undergo refusion. It is also at this stage that the first appearance of calcified nodules can be detected. Neither the process of the rejoining of marginal and lateral plates, nor the subsequent growth and ultimate fusion of the accessory nodules in the marginal integument to form plates is stage related. Both proceed at highly variable individual rates. Nevertheless, when the mature crab is examined, as descriptions of adult *Lithodes* abdomens reflect (e.g., Dawson & Yaldwyn 1985, Macpherson 1988), the observer sees an abdomen with a small, entire tergal plate 1, a three-sectioned tergite 2, heretofore thought to have been formed by the fusion of lateral and median plates, and tergites 3–5 formed by nodular marginal plates, weakly spinose or tuberculate lateral plates, and median plates represented by a series of fused nodules. From the evidence presented herein, these observations and descriptions are erroneous. Tergite 1 is correctly interpreted as being entire. The three-plated condition of tergite 2 results from the sundering of the marginal plates. Tergites 3–5 do reflect a three-plated condition, but not as interpreted by previous authors. The "marginal" plates actually are formed in the marginal integument by the development and fusion of accessory, spiniform nodules, whereas the "lateral" plates represent the fused marginal and lateral plates of the early juvenile tergites. The "median" plates have resulted from calcification, in the form of nodules, that has occurred in the central portion of the membranous integument of the juvenile tergites.

The first indications of sexual differentiation are sometimes seen as early as stage 4 where development of the accessory marginal spines becomes more apparent, and in some individuals is observed only on the right side. Nonetheless, since individual development is so highly variable, this cannot be viewed with assurance as an accurate indicator of sex. Similarly, the lateral and marginal plates still may be completely distinct, or partially to completely rejoined. However, by crab stage 5, in some specimens, the fused lateral-marginal plates of tergites 3–5 have enlarged slightly on the left side of the abdomen indicating that these individuals are females; accessory marginal spines or nodules have developed only on the right. In contrast, in males the marginal and lateral plates remain approximately the same size on both the right and left sides, while accessory spines or spinulose nodules are clearly apparent in the marginal integument on both sides. Despite the change in plate size from left to right in females, there is yet no skewing of the abdomen, as reflected by the deflection of tergite 6 and the telson to the right in mature females.

Female pleopod development in *Lithodes*

appears not to be entirely stage dependent. In *L. aequispinus*, the first indication of developing pleopods occurred at stage 5 or 6. In one preserved female of crab stage 5, minute buds were present on somites 2–5, whereas in the other two, no buds were observed at this stage. The two preserved females of crab stage 6 both had small uniramous buds only on somites 2–4; the pleopod of somite 5 was present in the single preserved stage 7 female. McLaughlin et al. (2001) found no pleopod development in their two females of stage 5 *L. santolla*. Sandberg & McLaughlin (1998) reported that no female pleopod development accompanied the first indications of plate asymmetry in juvenile specimens of *L. maja* (Linnaeus, 1758) with carapace lengths of less than 6.0 mm from museum collections, but they were not able to stage their specimens. In females with carapace lengths between 6.6 and 10.5 mm, rudimentary pleopods were observed on somites 2–4, but in only one instance was a pleopod bud also present on somite 5. It was only in females of carapace lengths of 13.6 mm and larger that all four pleopods routinely were present.

In our very small sample of identifiable females (<30), two exhibited reversed abdominal asymmetry. Zaklan (2000), in a note on reversed asymmetry in *Lithodes maja*, commented that although the frequency of reversed abdominal asymmetry was unknown, it was thought to be low for *Lithodes* and other king crabs. However, she quoted Campodonico (1978) as having estimated that 2.5% of the population of *Paralomis granulosa* (Jacquinot in Hombron and Jacquinot, 1846) in Porta Zenteno, southern Chile, exhibited this abdominal reversal. A review of Campodonico's (1978) report suggests that he was referring to the tendency in 2.5% of the females for the left chela to be larger than the right. He had only a single female specimen that exhibited abdominal reversal, although he indicated in an addendum that there were other unpublished records of this phenomenon.

Zaklan (2000) went on to suggest that her's was the first report of accompanying cheliped reversal, although Sandberg & McLaughlin (1998) had observed similar reversals in both chelipeds and abdomen in a Scandinavian specimen of *L. maja*. Only one of our two females that exhibited reversed abdominal asymmetry still had its chelipeds attached; however in that specimen cheliped reversal also occurred. Since only females show abdominal plate asymmetry, and females are usually selectively avoided in fisheries catches, it is quite possible that reversed asymmetry is more frequent than heretofore thought, just simply not readily observed.

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