# Aspects of evolution in the anomuran superfamily Paguroidea: one larval prospective

PATSY A. MCLAUGHLIN[1*] and RAFAEL LEMAITRE[2]

[1]*Shannon Point Marine Center, Western Washington University,
1900 Shannon Point Road, Anacortes, WA 98221-9081B, USA
Tel. +1 (360) 293-2188; email: patsy@sos.net*
[2]*Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution,
Washington, DC 20560-0163*

## Summary

McLaughlin and Lemaitre (1997), in their examination of carcinization in the Anomura, rejected the traditional concept of paguroid evolution, which had consistently maintained that the lithodid crab-like body form evolved from a typical shell-dwelling hermit crab. Their hypothesis proposed just the reverse, i.e., the lithodid crab-like body form gave rise to the simple hermit crab body form through calcium loss, habitat change and consequential morphological adaptations. Their original hypothesis was based on characters derived from adult morphology, but they suggested that larval data would support their view. The megalopal and first or first- and second-crab stages of representatives of both subfamilies of the Lithodidae provide the first of such larval information. Ten species in eight genera have been examined specifically for development of abdominal tergites. These data, although preliminary in scope, unequivocally disprove the Bouvierian concept of lithodid abdominal plate development, and in so doing, lend substantial support to McLaughlin and Lemaitre's hypothesis.

*Key words*:   Larval development, carcinization, abdominal evolution, Anomura, Paguroidea, Lithodidae

## Introduction

In the Superfamily Paguroidea, "carcinization" has been used to explain the presumed transition from a simple, shell-dwelling type of hermit crab body form to the crab-like lithodid body form (i.e., Boas, 1880a, 1880b, 1924; Bouvier, 1894, 1895a, 1895b, 1897; Borradaile, 1916; Wolff, 1961; Blackstone, 1989; Cunningham et al., 1992; Richter and Scholtz, 1994). Boas (1880a, 1880b) first proposed pagurid-lithodid consanguinity through the genus *Pagurus*, and Bouvier (1894, 1895a, 1895b, 1897) concurred, using what he perceived to be abdominal tergite development in lithodids as confirming evidence. Because of the presence of paired female first pleopods in genera of the Lithodinae and some pagurid genera, Boas (1924) subsequently revised his hypothesis, concluding that the ancestral pagurid was most probably one exemplifying the characteristics of *Nematopagurus-Pylopagurus*. Thus two theories, differing in the

problematic pagurid stem, but analogous in their conclusion that lithodids arose from a shell-inhabiting hermit ancestor, have received almost universal acceptance.

In a recent review of "carcinization in the Anomura", McLaughlin and Lemaitre (1997) startled the carcinological community with a challenge to these traditional concepts. The McLaughlin–Lemaitre hypothesis suggested the opposite, i.e., that lithodid crabs, through events such as calcium loss, habitat change, and consequential morphological adaptations, gave rise, ultimately, to shell-dwelling hermit crabs. The authors based their proposition on information gleaned from adult morphology, but suggested that larval morphology would provide additional supporting evidence.

In this aspect of our examination of potential evolutionary pathways, we examine Bouvier's (1895a, 1895b, 1897) hypothesis, which called for the gradual transformation of an almost exclusively membranous hermit crab abdomen (Fig. 1a) into a highly complex series of partially to fully calcified tergites. An essential element of his premise was an initial complete loss, in the pagurid ancestor, of all indications of its abdominal tergites with the exception of those of the first and last somites and telson. In Bouvier's evolutionary framework, this resultant, completely membranous integument was then invaded by calcified nodules, producing the structural sequences seen in the abdomens of genera of the Hapalogastrinae (Fig. 1b,c). Subsequently, by the fusion of these nodules, solid plates formed which characterized representatives of the subfamily Lithodinae (Fig. 1d–j). In summary, Bouvier's hypothesis proposed a secondary origin of lithodid tergal plates, and that while tergal plates of somites 3–5 were analogous in their position to those of the pagurid ancestor, they were not homologous with them.

Megalopal and early crab stages of representatives of both subfamilies of the Lithodidae, the Lithodinae and Hapalogastrinae, have furnished the first real evidence of the ontogenetic changes that occur to produce the morphological attributes of the adults. While acknowledging that our data are preliminary in that we do not yet have a complete series for any single lithodid species, the evidence at hand is sufficient to permit us to reexamine Bouvier's proposition. This present study followed Bouvier's (1897) plate terminology as indicated in Fig. 1, although we have substituted "la" for his "l" to indicate lateral plates, added "ac" for the accessory plates, "r" for the thickened rim that separates the tergal integument from

that of the sternites ("st") in the Hapalogastrinae, and used "t" for the telson.

As in the majority of reptant decapods, the pagurid and lithodid zoeal phases of development terminate with the metamorphic molt to the megalop. Megalopal morphology bares considerably more resemblance to the adult body form than to that of the zoea. In considering the McLaughlin–Lemaitre (1997) hypothesis, which at least in part suggests a reversal of Bouvier's abdominal plate theory, we examine and discuss here tergite development in the megalopal, first-, and in two species, second-crab stages of ten lithodid species in eight genera, and compare these with their adult structures.

In recent studies on larval and post-larval development in the Lithodidae, Crain and McLaughlin (2000a, b) documented calcium loss and abdominal tergite formation in one species of Lithodinae, and similar but less dramatic events in a Hapalogastrinae species. Their data have been supplemented here by megalopal and first-, or first- and second-crab, stages of other species from the rearing efforts of several colleagues, to whom we express our sincere gratitude. Information on adults has been gained through examinations of specimens in the collections of the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM).

## Lithodinae

For this study the megalopal and first-, or first- and second-crab, stages of five species in four genera — *Lopholithodes* Brandt, 1848, *Phyllolithodes* Brandt, 1848, *Paralithodes* Brandt, 1848, and *Cryptolithodes* Brandt, 1848 — were examined.

### *Lopholithodes*

Data on *L. mandtii* Brandt, 1848 are taken from Crain and McLaughlin (2000a) and Nyblade (unpublished). The megalop of *L. mandtii* (Fig. 2a) has the six abdominal tergites all represented by individually distinct, moderately well calcified plates, each with several identifying spines. With the molt to the first-crab stage (Fig. 2b), the first and second tergites are still entire, the first with four large spines, the second with a pair of median spines on a raised prominence, six smaller spines on the dorsodistal margin, and three small spines on each lateral margin (including the spine at each posterolateral angle). The third through the fifth tergites now show incomplete or complete lateral sutures, dividing each tergite into
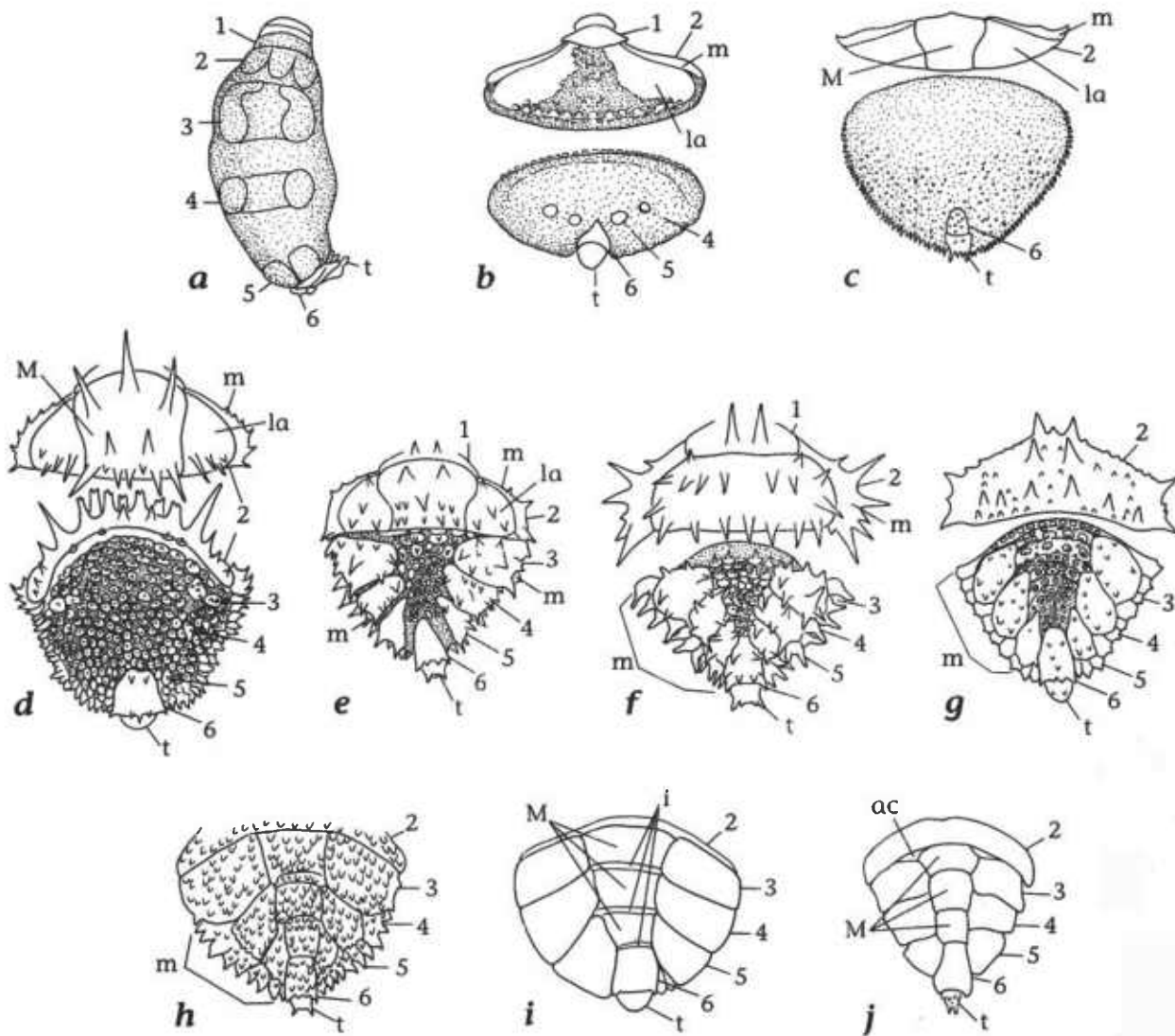
Fig. 1. Stages in the hypothetical transformation of the abdomen from a pagurid ancestor to a lithodid as proposed by Bouvier (1895a, 1895b, 1897). a, typical pagurid, dorsal view; b, *Hapalogaster* Brandt, 1850, dorsal (top) and ventral (bottom) views; c, *Acantholithodes* Holmes, 1895, posterior (top) and ventral (bottom) views; d, *Neolithodes* A. Milne-Edwards and Bouvier, 1894, posterior (top) and ventral (bottom) views; e, *Paralithodes* Brandt, 1848, ventral view; f, *Lithodes* Latreille, 1806, posterior (top) and ventral (bottom) views; g, *Lopholithodes* Brandt, 1848, posterior (top) and ventral (bottom) views; h, *Paralomis* White, 1856, ventral view; i, *Rhinolithodes* Brandt, 1848, ventral view; j, Cryptolithodes Brandt, 1848, ventral view. ac, accessory plates; i, intercalary plates; la, lateral plates; m, marginal plates; M, unpaired median plates; t, telson. Numbers indicate abdominal somites 1–6. Stippling indicates membranous areas. (Redrawn and modified from Bouvier, 1897).

median and lateral plates. The median plates each are provided with a pair of central spines and four slightly smaller spines on the dorsodistal margin, corresponding to the same spines seen in the megalopal stage. The lateral plates are armed with those same lateral spines of the megalop. Now, with the molt to the second-crab stage (Fig. 2c), the first and second tergites fuse, either partially or completely; the third

tergite is now divided into one median, two small accessory plates and two lateral plates, all separated by membranous areas. The fourth tergite is now represented by a median and two lateral plates, as is the fifth, although the membranous areas of separations are more apparent in the fourth. It is possible to find these very same plates in the adult abdomen (Fig. 2d, e), by comparing the patterns of spines. For example, while
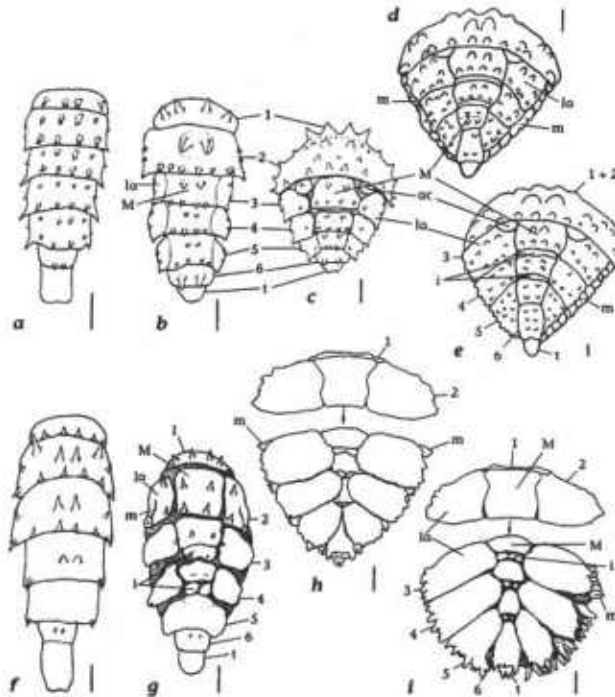
Fig. 2. Abdominal development in representatives of the Lithodinae. a–e, *Lopholithodes mandtii* Brandt, 1848; f–i, *Phyllolithodes papillosus* Brandt, 1848. a, f, megalop (dorsal view); b, g, crab stage 1 (dorsal view); c, crab stage 2 (dorsal view); d, h, male [d, ventral view; h (top), posterior view of somites 1 and 2; h (bottom), ventral view of somites 3–5 and telson]; e, i, female [e, ventral view; i (top), posterior view of somites 1 and 2; i (bottom), ventral view of somites 3–5 and telson, tuberculation on the dorsal surface of plates not shown]. Abbreviations as in Fig. 1. Stippling indicates membranous areas. Scales equal 0.5 mm (a–c), 5 mm (d, e, h, i), and 0.25 mm (f, g), (d, male USNM 3120; e, female, USNM 2103; h, male, USNM 18596; i, female ovig., USNM 2082).

there is no evidence in the adult that the second tergite represents a fusion of both the first and the second, the remnants of the spines show clearly the fusion that began at crab stage 2. Equally as clear are the two initial supplemental plates formed between the median and lateral plates of the third tergite at that stage. Similarly, the median plates of tergites four and five are still clearly distinguished as those of the early crab stages. The lateral plates of the adult are somewhat more tuberculate, but nonetheless are homologous with the plates of the second-crab stage. Marginal plates are present in the adult that have not appeared by the second crab stage. Although we do not have direct information on marginal plate development from *Lopholithodes*, it can be seen to a certain extent in *Phyllolithodes* and very clearly in *Acantholithodes* that

marginal plates similarly arise from division of the existing lateral plates. In adult males of *L. mandtii* (Fig. 2d), this lateral plate division occurs in the third through fifth tergites on both sides, with the resulting marginal plates in turn fragmented into smaller pieces. However, in the female (Fig. 2e), only the lateral plates of the right side separate into marginal plates; the left lateral plates remain entire. Crain and McLaughlin (2000a, b) found that the tergal changes in the early crab stages progressed at varying rates among individuals, and were not entirely molt dependent.

### Phyllolithodes

We have only the megalopal and first-crab stages of *P. papillosus* Brandt, 1848 (courtesy of G. Jensen). The six tergites of the megalop (Fig. 2f) are well formed, somewhat calcified, and all are provided with two or more spines. With the molt to the first-crab stage (Fig. 2g), considerable decalcification and sundering have begun. The median and lateral plates of the second tergite are well separated, and evidence of the presumed upcoming separation of marginal plates is indicated. The fifth tergite is entire, although a weak indication of the presumed separation of a median plate can be observed. When the adult abdomen is examined (Fig. 2h, i) the spines on the tergites of the megalopal and first-crab stages are no longer visible; instead the tergites are densely tuberculate except for the first tergite which is now smooth, unarmed, reduced in size and completely covered by the carapace. The same pattern of tergal plates seen in crab stage 1 is clearly visible in adults, although considerable more division has occurred. In both male and female the first tergite is clearly delineated by a suture; the second tergite still shows median and lateral plates, although no marginal plates are evident. The third to fifth tergites have now undergone more sundering than seen from megalopal to first-crab stages, and are all now divided into median, intercalary, lateral, and marginal plates. In the male (Fig. 2h), marginal plates develop on both sides as small, spine-like plates located on the indentations that separate the third to fifth tergites; in the female (Fig. 2i), marginal, spine-like plates develop only on the right side. The sixth tergite and telson remain undivided.

### Paralithodes

It was from the purported relationship between a species of *Paralithodes* and *Pagurus* that the phrase "from Hermit to King" was coined (Cunningham et al.,
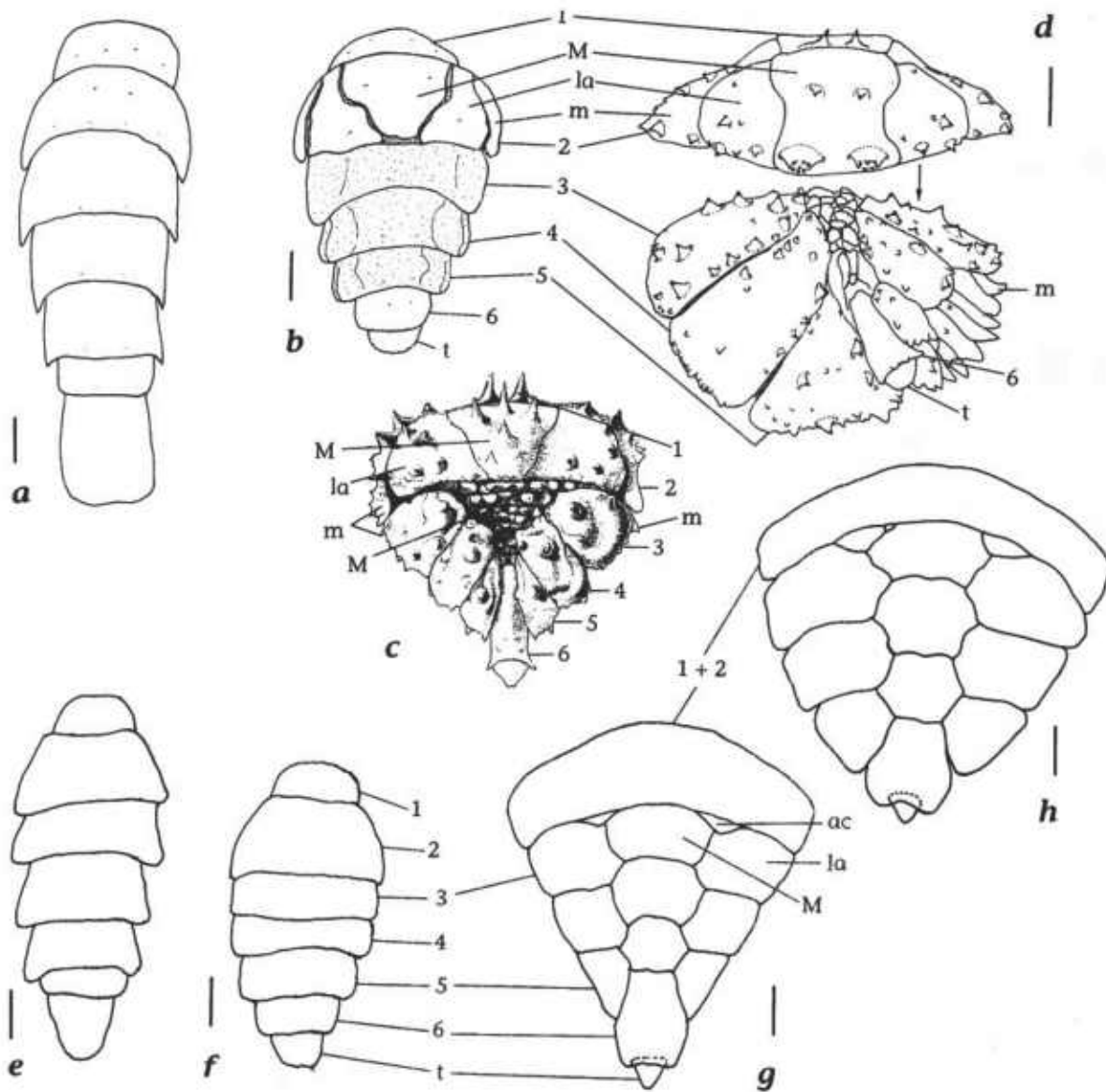
Fig. 3. Abdominal development in representatives of the Lithodinae. a–d, *Paralithodes brevipes* H. Milne-Edwards and Lucas, 1841; e–h, *Cryptolithodes sitchensis* Brandt, 1853. a, e, megalop (dorsal view); b, f, crabs stage 1 (dorsal view); c, male (ventral view showing portion of carapace; after H. Milne-Edwards and Lucas, 1841: pl. 27, Fig. 2); g, male (ventral view); d, h, female [d (top), posterior view of somites 1 and 2; d (bottom), ventral view of somites 3–5 and telson; h, ventral view]. Abbreviations as in Fig. 1. Stippling indicates membranous areas. Scales equal 0.25 mm (a, b, e, f), 20 mm (d), and 2 mm (g, h). (d, female ovig., USNM 18580; g, male, USNM 22591; h, female, USNM 22886).

1992). Kurata (1956: Fig. 3I) illustrated a plate division in the first-crab stage of *P. brevipes* (H. Milne-Edwards and Lucas, 1841) similar to that seen in *Phyllolithodes*; however, he did not discuss the abdominal structure at all. We have now been able to examine the megalopal and first-crab stages of *P. brevipes* personally [courtesy of A. Nishiki and S. Ashidate, Akkeshi Station of the Japan Sea-Farming Association (JASFA), via K. Konishi]. The six abdominal somites of the megalop (Fig. 3a) are entire, and the integument is chitinous. No true spines are developed, but possibly incipient spines are indicated on the first and second tergites by slight protuberances and setae. With the molt to crab stage 1, the entire

carapace, thoracic appendages, first, second, and sixth abdominal tergites and telson begin to exhibit integumental calcification. Among our 12 specimens, calcification of the first and sixth tergites is complete, whereas calcification of the second is partial to complete. The second tergite also has now partially to completely divided into median, lateral, and marginal plates (Fig. 3b). Tergites of somites 3–5 remain chitinous; however, indications of lateral and marginal plate divisions are already apparent. Similar tergite division was illustrated by Kurata (1964) for the first-crab stage of *P. camtschaticus* Tilesius, 1815. In the adult condition of *P. brevipes* (Fig. 3c, d), all tergal plates are well calcified. The first tergite is reduced and covered by the carapace except for the posterior portion which bears two strong spines. The division of the second tergite is now complete, with a median, paired lateral, and paired marginal plates. In the male (Fig. 3c), the third through fifth tergites are each divided into a pair of lateral plates, and transverse rows of tightly packed nodules medially representing median and intercalary plates; the marginal plates are very small. In the female (Fig. 3d), the third through fifth tergites are similarly divided except that the lateral plates on the left side are considerably larger than those on the right, and there are marginal, spine-like plates on the right side. The sixth tergite and telson remain entire.

### *Cryptolithodes*

We have studied specimens of *C. sitchensis* Brandt, 1853 and *C. typicus* Brandt, 1849. The megalop of *C. sitchensis* (Fig. 3e) (courtesy of G. Jensen) has six distinct unarmed chitinous tergites. Although some flexion in the abdomen was apparent in the first-crab stage (Fig. 3f), no marked changes in tergite development were observed, except for very faint lateral depressions; however, the increase in overall size and reduction in the pleopods, clearly marked this stage. For *C. typicus*, we reexamined Hart's (1965) specimens (courtesy of the Royal British Columbia Museum) as well as material reared by C. Nyblade (unpublished). As in *C. sitchensis*, six chitinous tergites are present in the megalopal stage. Hart reportedly had four specimens of crab stage I, but none were specifically so indicated. We did find one specimen in which the sixth abdominal tergite and telson agreed with her illustration of these structures; thus we presume that this specimen represented crab stage I. The abdomen was strongly flexed against the cephalo-thorax, but there was very little reduction in

pleopod structure. The tergites were still six in number, completely chitinous, and with no indications of division into median and lateral plates. However, in Nyblade's first-crab stage specimen, pleopod reduction had clearly begun; there was a slight shortening of the abdomen, and tergites 2–5 showed slight lateral indentations. In adults of *C. sitchensis* (Fig. 3g, h) and *C. typicus*, the first abdominal somite has fused with the second. Tergite arrangement in adults of both species shows that the second tergite remains undivided, whereas tergites 3–5 have divided into median and lateral plates, with tergite 3 additionally showing small accessory plates (usually one or two, or occasionally three on each side). The sixth tergite and telson are entire. The male and female abdomen in both species is symmetrical, although often the third tergite in females shows more accessory plates on the left side than on the right.

### Hapalogastrinae

For this subfamily we also have data for species of four genera: *Acantholithodes* Holmes, 1895, *Hapalogaster* Brandt, 1850, *Placetron* Schalfeew, 1892, and *Oedignathus* Benedict, 1895.

### *Acantholithodes*

It should be noted first that Dawson and Yaldwyn (1985) were incorrect when they reported the second abdominal tergite in *Acantholithodes* ("all species") consisted of an unpaired median plate. Our data for the monotypic *A. hispidus* (Stimpson, 1860) (courtesy G. Jensen, in prep.) consist of megalopal and first-crab stages. The megalop of *A. hispidus* (Fig. 4a) has six well developed, lightly calcified tergal plates each provided with prominent spines. In our representative of the first-crab stage (Fig. 4b), the second tergite has already divided into a single median, and paired lateral and marginal plates. The marginal and lateral plates each have two to four additional spines; however, most of the megalopal spines still can be recognized in this stage. For example, on the second tergite, two of the posterior spines of the megalop are present on the first-crab median plate, while three are represented on each of the lateral plates. Marginally, tergites 3 and 4 are still delineated; however, decalcification is well underway centrally, with only a few chitinous patches and still calcified spines of the third still visible. The fifth tergite is also still calcified marginally, but centrally the tergite is now chitinous and subdivided. In adults of both sexes, the first and second tergites
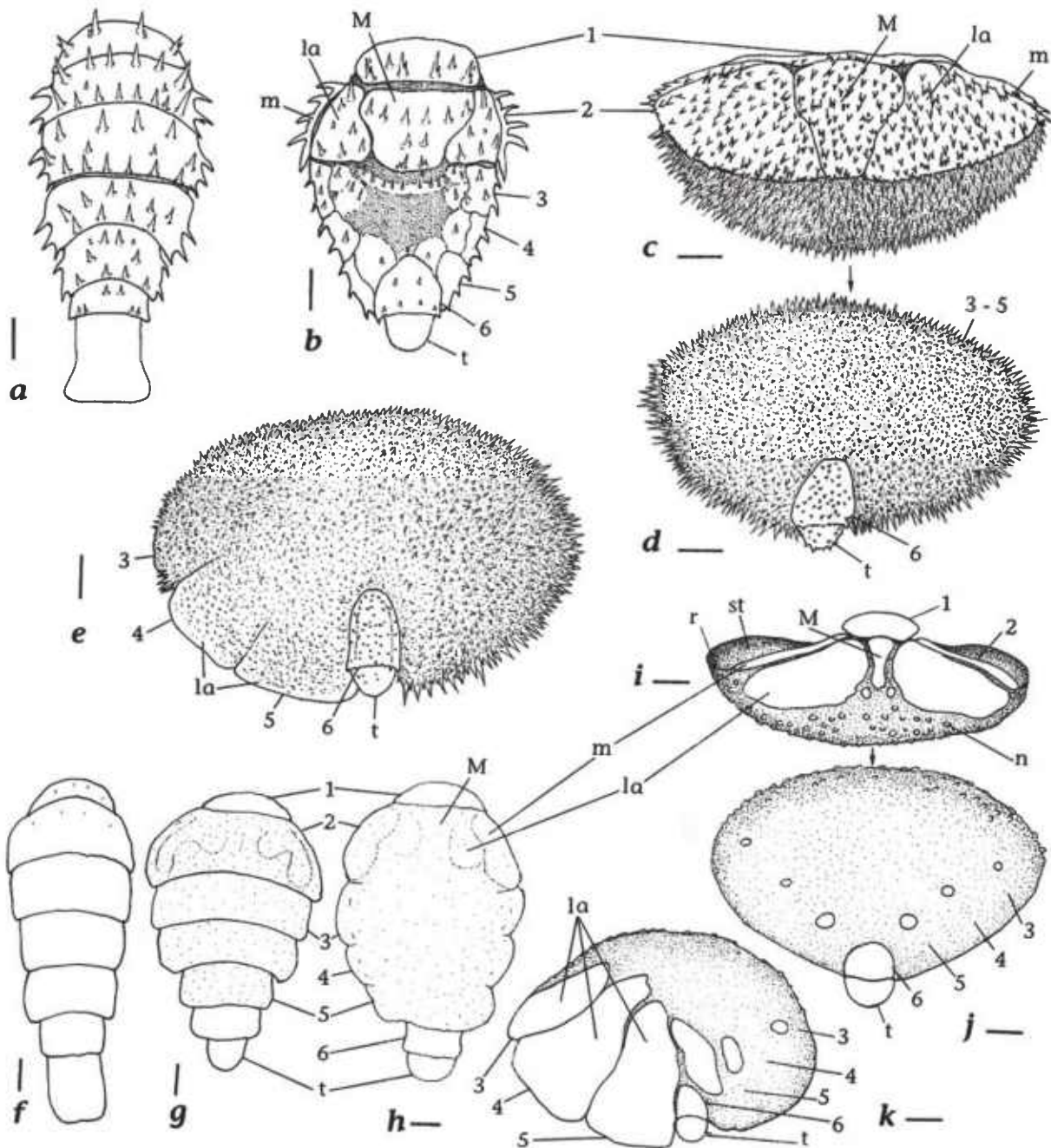
Fig. 4. Abdominal development in representatives of the Hapalogastrinae. a–e, *Acantholithodes hispidus* (Stimpson, 1860); f–k, *Hapalogaster mertensii* Brandt, 1848. a, f, megalop (dorsal view); b, g, crab stage 1 (dorsal view); h, crab stage 2; c, d, i, j male [c, posterior view; d, j, ventral view; i, dorsal view]; e, k, female (ventral view). Abbreviations as in Fig. 1, except: c, crease; r, rim; st, sternite. Stippling indicates membranous areas. Scales equal 0.25 mm (a, b, f– h), 2 mm (i–k), and 5 mm (c–e). (c, d, male, USNM 77420; e, female, USNM 77420; i, j male USNM 267742; k, female, USNM 267742).

(Fig. 4c) remain calcified and spinose; the first is broad, but quite narrow, the second shows the same division of paired marginal and lateral plates, and single median plate that were delineated in the first-crab stage. In the adult male (Fig. 4c, d), tergites 3–5 have completely lost all calcification and segmental identity, although numerous integumental small spines cover the surface. In the adult female (Fig. 4e), tergites 3–5 on the right side have been rendered indistinguishable by complete calcium loss, although their

surfaces have numerous small spines, and the margins are strongly spinose; on the left side, tergites 3–5 are partially delineated, marginally chitinous or weakly calcified, and with scattered surface spines; the margins of tergites 4 and 5 lack spines. The sixth tergite and telson are well calcified.

### Hapalogaster

For this genus we have examined the megalopal and first-crab stages of H. dentata de Haan, 1844 (specimens of Konishi, 1986; courtesy of Hokkaido University), and megalopal, first- and second-crab stages of H. mertensii Brandt, 1850 (courtesy of B. Stevens; C. Nyblade). In both species, six distinct, chitinous tergites are present in both the megalopal (Fig. 4f) and the first-crab stages (Fig. 4g). In the first-crab stage of H. mertensii, the surface is provided with scattered short setae, but granules are not apparent, and just slight lateral thickenings can be observed in the second tergite. Only the first and sixth tergites and telson are clearly delineated in the second-crab stage (Fig. 4h). Segmentation of the second through fifth tergites is apparent only laterally. Very faint indications of incipient lateral and possibly marginal plates can be detected on the second tergite, and very slight lateral thickenings mark the third and fourth tergites. The abdomen of adult H. mertensii in both sexes (Fig. 4i–k) has first and second tergites well calcified. Division of the second tergite into a subtriangular median plate and partial pairs of lateral and marginal plates are readily recognizable, with a series of calcified nodules centrally below the now reduced median plate. Tergites 3–5 of males (Fig. 4j) are membranous except for small, subovate or subcircular calcified remnants. In females (Fig. 4k), well developed lateral plates of tergites 3–5 are present on the left side, while only moderately small, calcified patches are present on the right 3–5. The sixth tergite and telson are calcified and readily identified. Following the molt to crab stage 1 in H. dentata, the second tergite becomes slightly more bulbous, while the succeeding tergites become generally broadened laterally; however, segmentation is still distinct in both species. The integumental surface of the first-crab stage is provided with scattered minute granules or setae, except for a somewhat roughened area medially near the posterior margin and two smooth patches laterally on the second tergite. These appear to be the incipient median and lateral plates of the second tergite of the adult. The abdomens of adult H. dentata both sexes are very similar to those of H. mertensii, except that a semi-circular crease may

be seen medially that possibly represents the division between the fourth and fifth tergites. The tergites on the right side in females of H. dentata are smaller and subcircular.

### Placetron

In this monotypic genus, represented by P. wosnessenskii Schalfeew, 1892, changes in the abdominal tergites appear to proceed more slowly than in other genera for which we have information, except Cryptolithodes. In both the megalopal and first-crab stage of P. wosnessenskii (courtesy of J. Crain), the six abdominal tergites are distinct and are neither calcified nor armed (Fig. 5a, b). In the first-crab stage changes from the megalopal abdomen are seen first with tergites 3–5 becoming centrally narrower, with late crab stage 1 specimens showing indications of lateral plate delineation. Adults of both sexes (Fig. 5c, d) have all tergites covered with generally transverse ridges and furrows; the abdomen is tucked almost completely under the thorax leaving only a small portion of the second somite visible in dorsal view; the first tergite is very narrow and partially covered by the carapace. In contrast to the other lithodids we have examined, the well calcified second tergite has divided almost centrally, with a resulting pair of broad lateral plates, and narrower pair of marginal plates. The typical median plate is virtually nonexistent, with only a very narrow membranous area separating the lateral plates. The sixth tergite is a well calcified, triangular plate, whereas the telson is small, membranous, hidden from dorsal view, bent under the sixth tergite and forming a flap covering the anus. The membranous third through fifth tergites of adult males (Fig. 5c) are each represented by a pair of small, calcified remnants. The adult female (Fig. 5d) has well developed, calcified left lateral plates on tergites 3–5, with possibly a slight hint of marginal plate differentiation on the third. These tergites on the right side are represented by calcified remnants as in males.

### Oedignathus

This is another monotypic Hapalogastrinae genus. Like Placetron, the six abdominal tergites of megalops of O. inermis (Stimpson, 1860) (courtesy of C. Nyblade) are simply chitinous (Fig. 5e). However, in the first-crab stage (Fig. 5f), while the first and second tergites are quite distinct, tergites 3–5 are only clearly distinguishable laterally. The first tergite is still chitinous; the second has the marginal regions noticeably thickened, and the lateral areas are faintly
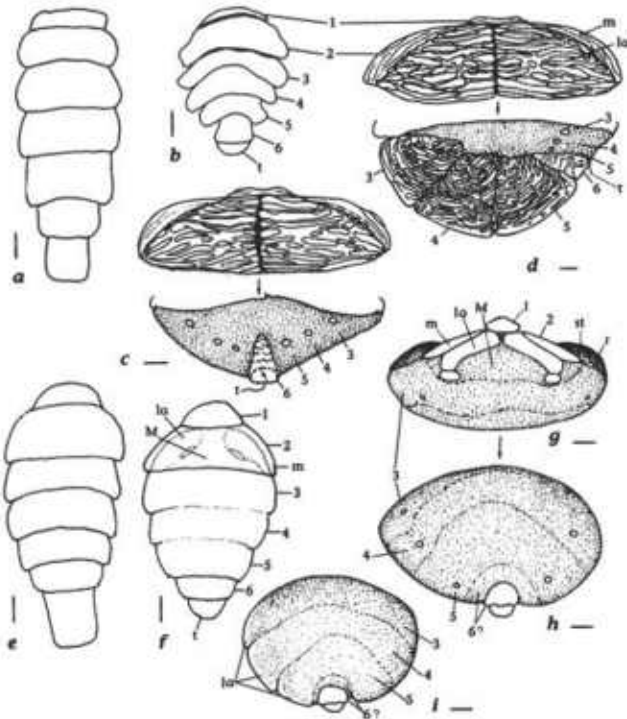
Fig. 5. Abdominal development in representatives of the Hapalogastrinae. a–d, *Placetron wosnessenskii* Schalfeew, 1892; e–i, *Oedignathus inermis* (Stimpson, 1860). a,e, megalop (dorsal view); b, f, crab stage 1 (dorsal view); c, g, h, male [c (top), posterior view of somites 1 and 2; c (bottom), ventral view of somites 3–6; g, dorsal view; h, ventral view]; d, i, female [d (top), posterior view of somites 1 and 2; d (bottom), ventral view of somites 3–6 and telson; i, ventral view]. Abbreviations as in Fig. 1, except: r, rim; st, sternite. Stippling indicates membranous areas. Scales equal 0.25 mm (a, b, e, f), 5 mm (c, d), and 2 mm (g–i). (c, male, USNM 276166; d, female, USNM 259214; g, h, male, USNM 90680; i, female, USNM 267725).

indicated. The tergites of the third through fifth somites have become completely membranous, although each is still faintly delineated. The dorsal abdominal surface is covered with scattered tiny short bristles and occasional minute spinules. The first tergite of the adults (Fig. 5g) is calcified and clearly visible adjacent to the posterior margin of the carapace. The second consists of an almost entirely membranous, poorly delineated median plate, a pair of weakly calcified lateral plates, and a pair of calcified rod-like marginal plates. With the exception of small, weakly calcified, subcircular patches, the third–fifth tergites of males (Fig. 5g, h) are entirely membranous and only very faint indications of segmentation remain; however, they are separated from the sternal membranes of their respective somites by a very fine marginal rim. In

females (Fig. 5i), the lateral margins of these tergites on the left side are thickened, weakly calcified, and partial segmentation can be detected. In both sexes definition of the sixth tergite and telson is puzzling. By following the very faint delineation of the posterior margin of the fifth tergite on the left side in females (clearly identified by the presence of the fifth pleopod), it would appear that another membranous tergite is present, forming an arc around the weakly calcified structure commonly considered to represent the sixth tergite. Two interpretations are possible, but which might be correct cannot be determined until additional juveniles stages can be examined. The first would be to suggest that this area represents an unusually large and membranous portion of the sixth tergite. Alternatively, it could be that in *Oedignathus*, the sixth tergite looses all traces of calcification, and the calcified structure represents just the telson, divided by a transverse suture into anterior and posterior lobes, as is seen in many pagurids.

## Discussion

In their discussion of hermit crab-lithodid relations Richter and Scholtz (1994) reported that "divided pleon tergites" similar to those of most Paguridae occurred in the Lithodidae, and that in *Lithodes maja* (Linnaeus, 1758) these were secondarily connected by calcified nodules, or in *Paralomis granulosa* (Jacquinot, 1847) by median plates. In terms of evolution, these authors concluded that the secondary evolution of hard and calcified tergites produced a pattern different to the original, which therefore suggested convergence. However, from the evidence presented in the present study, there can be no doubt that the megalopal and adult abdominal plate structures within the Lithodidae are homologous, and are formed by decalcification and/or sundering of the megalopal tergites to varying degrees, not by the secondary formation and subsequent fusion of calcified nodules. Even among genera and species with the most well calcified adult tergal plates, the onset of calcification, both cephalothoracic and abdominal, may accompany the megalopal molt, or may begin only after the first-crab stage, and may progress at varying rates among genera and among species within genera. These data decisively refute both Bouvier's (1894, 1895a, 1895b) theory and the evolutionary scenario proposed by Richter and Scholtz (1994), thus lending significant support to McLaughlin and Lemaitre's (1997) hypothesis that hermit crabs did not give rise to king crabs.

## Acknowledgements

## References

Benedict, J.E., Scientific results of explorations by the U.S. Fish Commission Steamer Albatross. 31. Descriptions of new genera and species of crabs of the family Lithodidae, with notes on the young of *Lithodes camtschaticus* and *Lithodes brevipes*. Proc. U.S. Natl. Mus., 17 (1895) 479–488 [1894].

Blackstone, N.W., Size, shell-living and carcinization in geographic populations of a hermit crab, *Pagurus hirsutiusculus*. J. Zool., Lond., 217 (1989) 477–490.

Boas, J.E.V., II. Wissenschaftliche Mittheilungen. 1. *Lithodes* und *Pagurus*. Zool. Anz., 3 (1880a) 349–352.

Boas, J.E.V., Studier over decapodernes Slægtskabsforhold. K. Danske Vidensk. Selsk. Skr., (5) 6 (1880b) 25–210.

Boas, J.E.V., Die verwandtschaftliche Stellung der Gattung *Lithodes*. K. Danske Vidensk. Selsk. Skr., 4(4) (1924) 1–34.

Borradaile, L.A., Crustacea. Part 11. *Porcellanopagurus*: An instance of carcinization. In: British Antarctic ("Terra Nova") Expedition, 1910. Natural History Report. Zoology, 3(3) (1916) 111–126.

Bouvier, E.L., Sur la transformation des Paguriens en crabes anomoures de la sous-famille des Lithodinés. C.R. Acad. Sci., 119 (1894) 350–352.

Bouvier, E.L., Sur les Lithodinés hapalogastriques *Hapalogaster* et *Dermaturus*. C.R. Soc. Philom., 18 (1895a) 56.

Bouvier, E.L., Recherches sur les affinités des *Lithodes* et des *Lomis* avec les Pagurides. Ann. Sci. Nat. Zool. Paléont., (7) 18 (1895b) 157–213.

Bouvier, E.L., La transformation des Bernards l'Ermite en *Lithodes*. Naturaliste, (2)19(230) (1897) 41–43.

Brandt, J.F., Die Gattung *Lithodes* Latreille nebst vier neuen ihr verwandten von Wosnessenski entdeckten, als Typen einer besondern Unterabtheilung (Tribus Lithodea) der Edward'shen Anomuren. Bull. Phys. Math Acad. St.-Pétersbourg, 7(11) (1848) 171–176.

Brandt, J.F., Bericht über die für die Reisebeschreibung des Herrn von Middendorff von J.F. Brandt bearbeiteten Krebsthiere aus den Abtheilungen der Brachyuren (Krabben), Anomuren und Makrouren (Krebse). Bull. Phys. Math Acad. St.-Pétersbourg, 8(13) (1850) 234–238.

Brandt, J.F., Ueber eine neue Art der Gattung *Cryptolithodes* (*Cryptolithodes sitchensis*). Bull. Phys. Math Acad. St.-Pétersbourg, 11(15–16) (1853) 653–654.

Crain, J.A. and McLaughlin, P.A., Larval and early juvenile development in the Lithodidae (Decapoda: Anomura: Paguroidea) reared under laboratory conditions. 1. Subfamily Lithodinae: *Lopholithodes mandtii* Brandt, 1848. Invert. Reprod. Develop., 37 (2000) 43–59.

Crain, J.A. and McLaughlin, P.A., Larval and early juvenile development in the Lithodidae (Decapoda: Anomura: Paguroidea) reared under laboratory conditions. 2. Subfamily Hapalogastrinae: *Placetron wosnessenskii* Schalfeew, 1892, with notes on comparative development within the subfamilies of the Lithodidae. Invert. Reprod. Develop., 37 (2000) 113–127.

Cunningham, C.W., Blackstone, N.W, and Buss, L.W., Evolution of king crabs from hermit crab ancestors. Nature, Lond., 355 (1992) 539–542.

Dawson, E.W. and Yaldwyn, J C., King crabs of the world or the world of king crabs: an overview of identity and distribution — with illustrated diagnostic keys to the genera of the Lithodidae and to the species of *Lithodes*. Proc., Intern. King Crab Symp., 1985, pp. 69–106.

Haan, W. de, Crustacea. In: P.F. von Siebold, *Fauna Japonica sive Descriptio Animalium, quae in itinere per Japoniam, jussu et auspiciis superiorum, qui summum in India Batava imperium tenent, suscepto, annis 1823–1830 collegit, notis, observationibus et adumbrationibus illustravit* P.F. de Siebold. *Conjunctis studiis* C.J. Temminck *et* H. Schlegel *pro Vertebratis atque* W. de Haan *pro Invertebratis elaborata Regis aupicus edita.* 1. P. E. v. Siebold. Lugduni–Batavorum, Leiden (1833–1850) i–xxxi, ix–xvi, 1–243.

Hart, J.F.L., Life history and larval development of *Cryptolithodes typicus* Brandt (Decapoda, Anomura) from British Columbia. Crustaceana, 8 (1965) 255–276.

Holmes, S.J., Notes on West American Crustacea. Proc., Calif. Acad. Sci., 4 (1895) 563–588.

Konishi, K., Larval development of the stone crab,

*Hapalogaster dentata* (DeHaan, 1844) (Crustacea: Anomura: Lithodidae) reared in the laboratory. J. Fac. Sci., Hokkaido Univ., (4) Zool., 24 (1986) 155–172.

Kurata, H., The larval stages of *Paralithodes brevipes* (Decapoda, Anomura). Bull. Hokkaido Reg. Fish. Res. Lab., 14 (1956) 25–34.

Kurata, H., Larvae of decapod Crustacea of Hokkaido. 6. Lithodidae (Anomura). Bull. Hokkaido Reg. Fish. Res. Lab., 28 (1964) 49–65.

Latreille, P.A., *Genera Crustaceorum et Insectorum secundum Ordinem naturalem in Familias disposita, Iconibus Exemplisque plurimis explicata. Apud Amand Koenig Bibliopolam, Parisiis et Argentorati., Tomus Primus*, Paris and Strasbourg, 1806. xviii + 1–302.

McLaughlin, P.A. and Lemaitre, R., Carcinization in the Anomura — fact or fiction? 1. Evidence from adult morphology. Contr. Zool., Amsterdam, 67(2) (1997) 79–123.

Milne-Edwards, A. and Bouvier, E.L, Troisième campagne du yacht *l'Hirondelle*, 1887. *Neolithodes*, genre nouveau de la sous-famille des Lithodinés. Bull. Soc. Zool. Fr., 19 (1894) 120–122.

Milne-Edwards, H. and Lucas, H., Description des Crustacés nouveaux ou peu connus conservés dans la collection du Muséum d'Histoire Naturelle. Arch. Mus. natl Hist. Nat. Paris, 2 (1841) 461–483.

Richter, S. and Scholtz, G., Morphological evidence for a hermit crab ancestry of lithodids (Crustacea, Decapoda, Anomala, Paguroidea). Zool. Anz., 223(5/6) (1994) 187–219.

Schalfeew, P., Carcinologische Bemerkungen aus dem Zoologischen Museum der Kaiserlichen Akademie der Wissenschaften. Bull. Acad. Imp. Sci. St.-Petersbourg, 35 (1892) 331–342.

Stimpson, W., Notes on North American Crustacea, in the Museum of the Smithsonian Institution. No. II. Ann. Lyc. Nat. Hist. New York, 7 (1860) 176–246 (preprint of 1862 journal paper).

Tilesius, W.G., De Cancris Camtschaticis, Oniscis, Entomostracis et Cancellis marinis microscopicis noctilucentibus, Cum tabulis 1V: Aenacis et appendice adnexo de acaris et Ricinis Camtschaticis. Auctore Tilesio. Conventui exhibuit die 3 Februarii 1813. Mém. Acad. Imp. Sci. St.-Petersbourg, 5 (1815) 331–405.

Wolff, T., Description of a remarkable deep-sea hermit crab with notes on the evolution of the Paguridae. Galathea Rept, 4 (1961) 11–32.+