Zool. Anz. 233 (1994) 5/6, S. 187—210
Gustav Fischer Verlag Jena

Morphological evidence for a hermit crab ancestry of lithodids (Crustacea, Decapoda, Anomala, Paguroidea)

By Stefan Richter and Gerhard Scholtz

Institut für Zoologie, Freie Universität Berlin

With 7 Figures and 2 Tables (Accepted: May 17, 1994)

Key words: evolution, Dollo's law, homology, phylogenetic systematics, Lithodidae, *Lomis*

Abstract

We analyzed the phylogenetic position of lithodid crabs applying the methods of phylogenetic systematics. It can be shown that lithodids share several apomorphic characters with hermit crabs. It is most likely that they are close relatives of the Paguridae within the asymmetrical hermit crabs. Our morphological results are in good agreement with recent molecular findings. Lithodids are secondarily free living hermit crabs which underwent carcinization in relation to the abandonment of gastropod shells. The process of carcinization led to the appearance of characters which resemble ancestral anomalan characters but are different from hermit crab apomorphies. This reverse evolution is discussed against the background of the homology concept. Most of the reverse characters can be explained by convergent evolution. A corollary of our study are some results on hermit crab relationships. The Paguroidea is monophyletic and its sister group might be the Lomidae. The Pylochelidae represents a paraphyletic assemblage whereas the asymmetrical hermit crabs are a monophyletic taxon.

Introduction

The Lithodidae Samouelle, 1819 belong systematically to the Anomala within the Decapoda (e.g. McLaughlin 1983b; Scholtz & Richter 1994). Due to their widened carapace and the reduced ventrally flexed pleon, their appearance, however, resembles that of brachyuran crabs – a phenomenon called carcinization (Borradaile 1916). Based on adult (Boas 1880a, b, 1924; Bouvier 1895) and larval characters (MacDonald et al. 1957), lithodids have been placed within the hermit crabs. This view has since been adopted by many carcinologists (e.g. Bliss 1982; McLaughlin 1983b; Gruner 1993) and it has recently been supported by molecular data (Cunnigham et al. 1992). Lithodids are generally considered as being secondarily free living hermit crabs which underwent carcinization in correlation to the abandonment of the gastropod shell (see Gould 1992). The problem of this hypothesis is that the existence of several characters which the lithodids share with other decapods but not with hermit crabs must be due to either convergent evolution or the reappearance of ancestral features. MARTIN & ABELE (1986) undertook a cladistic analysis of the Thalassinida and Anomala and suggested, in contrast to the traditional view, that the Lithodidae together with the Lomidae should be placed as the sister group of the monophyletic hermit crabs. All similarities between lithodids and other decapods outside the hermit crabs are interpreted as plesiomorphic characters and lithodids are supposed not to stem from shell-dwelling hermit crab-like ancestors. The conflicts with this view arise from the characters shared by lithodids and asymmetrical hermit crabs which would then be the result of convergent evolution.

The contradictions between the two interpretations of lithodid phylogeny and evolution are due to the different interpretations of the homology and polarity of the problematical lithodid characters. Without a phylogenetic analysis it is impossible to decide whether the evolution from a "hermit" to a "king" or from a "king" to a "hermit" is more likely. The question of polarity of evolutionary change can only be solved on the basis of a phylogenetic analysis using additional characters and with a careful and detailed comparison of the characters examined in order to make homology plausible. To address these problems, we examined representatives of the Lithodidae, the Lomidae, and of the hermit crab families Pylochelidae, Diogenidae, Coenobitidae, Parapaguridae, and Paguridae. It was not our goal to reconstruct the phylogenetic systematics of hermit crabs or to undertake a phylogenetically based revision of the entire group. This would be an impossible task on the basis ot the present state of hermit crab taxonomy where some basic problems are seen quite differently (for a review of the history and present state of hermit crab classification see MCLAUGHLIN 1983b). For instance, even the monophyletic origin of the hermit crabs has been doubted (e.g. MACDONALD et al. 1957; BOWMAN & ABELE 1982; FOREST 1987) whereas MCLAUGHLIN (1983b) provided several arguments in favour of hermit crab monophyly. There are detailed taxonomic revisions of some hermit crab taxa (e.g. MCLAUGHLIN 1974; FOREST 1987; MACPHERSON 1988; LEMAITRE 1989) but phylogenetic analyses of the six hermit crab families are still missing. On these grounds it is only possible to present a framework of hermit crab systematics for further discussions. Some well founded conclusions, however, can be drawn about systematic relationships within the hermit crabs. Our analysis suggests that the hermit crabs (Paguroidea sensu MCLAUGHLIN 1983b) are monophyletic and the Lomidae might be their sister group. The pylochelids are paraphyletic, whereas the asymmetrical hermit crabs represent a monophylum. Lithodids are part of the asymmetrical hermit crabs and are closely related to the probably paraphyletic Paguridae. Therefore, our data support the hypothesis of lithodids as being secondarily free living asymmetrical hermit crabs. A close examination of the characters shared by lithodids and the hypothetisized anomalan stem species reveals that these are not homologous. Some possible explanations for their convergence are provided.

Material and Methods

For the character analysis we investigated 3 species of the Lithodidae:

Lithodinae
Lithodes maja (Linnaeus, 1758)
Paralomis granulosa (Jacquinot, 1847)

Hapalogastrinae
  Hapalogaster dentata (de Haan, 1850)
and 19 species belonging to the 5 other families of the Paguroidea:
Pylochelidae
  Pylocheles miersi Alcock & Anderson, 1898
  Pylocheles mortensii Boas, 1926
  Cheiroplatea laticauda Boas, 1926
  Pomatocheles jeffreysii Miers, 1879
  Parapylocheles scorpio (Alcock, 1884)
  Trizocheles spinosus spinosus (Henderson, 1888)
  Trizocheles brevicaulis (Boas, 1926)
Parapaguridae
  Sympagurus dimorphus (Studer, 1883)
Diogenidae
  Dardanus arrosor (Herbst, 1794)
  Diogenes pugilator (Roux, 1829)
  Clibanarius erythropus (Risso, 1815)
  Calcinus elegans (H. Milne Edwards, 1837)
  Paguristes barbatus Ortmann, 1892
  Paguropsis typica Henderson, 1888
Paguridae
  Nematopagurus squamichelis Alcock, 1905
  Spiropagurus spiriger (de Haan, 1850)
  Pagurus bernhardus (Linnaeus, 1758)
Coenobitidae
  Coenobita sp.
  Birgus latro (Linnaeus, 1767)

and, in addition, the lomid *Lomis hirta* (Lamarck, 1818). Characters from the literature were also used. The material was provided by the Zoologisches Museum, Berlin, the Zoologisk Museum, Copenhagen, and the Zoologische Staatssammlung, Munich. The animals were examined and prepared under dissecting microscopes (WILD and Row). For SEM investigations, the objects were critical point dried and sputter-coated with gold.

We reconstructed the "frame" of a phylogenetic system of hermit crabs according to the methods developed by HENNIG (1950, 1966). For character polarization we applied the outgroup comparison method (WATROUS & WHEELER 1981) using information on Galatheoidea, Hippoidea, Lomoidea and Decapoda Reptantia outside the Anomala (see SCHOLTZ & RICHTER 1994). According to a method proposed by MADDISON et al. (1984) for reconstructing hypothetical ancestors we reconstructed the character states of the stem species of the Anomala with the character states found in other Anomala and Reptantia.

Results

The Lithodidae are clearly real hermit crabs closely related to the probably paraphyletic Paguridae. They are part of a monophyletic taxon of "asymmetrical" hermit crabs (in addition to the Lithodidae: the Parapaguridae, Diogenidae, Coenobitidae, and the Paguridae) which itself is part of the monophyletic Paguroidea (sensu MCLAUGHLIN 1983b). Although lithodids possess only few apomorphies of the Paguroidea and asymmetrical hermit crabs, the character pattern of lithodids can be most parsimoniously and most plausibly explained by a position within the hermit crabs (Table 1).

In the following we discuss the framework of hermit crab phylogeny (Fig. 1) in more detail.

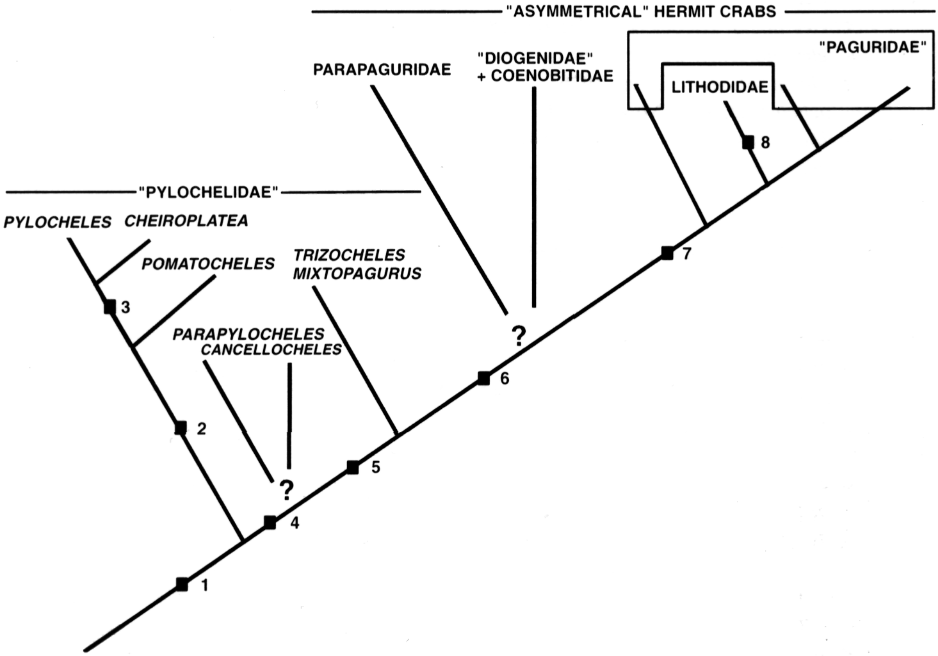


Fig. 1. Proposal of phylogenetic relationships of hermit crabs. **1.** 4th pereiopod smaller than 2nd and 3rd pereiopods and with rasp; 5th pereiopod kept outside the branchial chamber and with rasp; uropods crescent-shaped and with rasp; dorso-posterior part of the carapace weakly calcified and soft. **2.** 1st pereiopods form specialized symmetrical opercula; apart from the basal segment, at least two more segments of the thick flagellum of the 1st antenna without sensory hairs. **3.** The two distal segments of the endopod of the 3rd maxilliped form a chela. **4.** 1st pleon tergite narrow and equipped with a posterior bulge. **5.** Real ocular acicles. **6.** Asymmetrical pleon; tergites 2 to 5 soft; right 3rd to 5th pleopod absent; transverse furrow on the 6th tergite. **7.** 1st pleon sternite fused to the last thoracic sternite; 2nd to 5th pleon tergite divided into two lateral halves; some basal segments of the thick outer flagellum of the 1st antenna fused (perhaps evolved within "Paguridae"); males without left 2nd pleopod; ischium teeth on 3rd maxilliped. **8.** Uropods lacking; males without 3rd to 5th pleopods. Invested commas indicate taxa which are probably paraphyletic. The origin of Lithodidae within the Paguridae is shown semischematically.

Monophyly of the Paguroidea sensu McLaughlin (1983 b)

The families Pylochelidae, Parapaguridae, Diogenidae, Coenobitidae, Paguridae and Lithodidae constitute together the monophyletic taxon Paguroidea (see also McLaughlin 1983 b) characterized by the following synapomorphies:

(1) The 4th pereiopod is significantly smaller than the 2nd and the 3rd pereiopods. The propodus and partially the dactylus of the 4th pereiopods bear rasps. A normally sized 4th pereiopod without rasps occurs in all thalassinids and other ano-

Table 1. Apomorphies of the Paguroidea, the asymmetrical hermit crabs, and a monophyletic taxon comprising Paguridae and Lithodidae (for plesiomorphic character states see text). For comparison the character states of the Lithodidae. The character pattern of lithodids makes a position within hermit crabs plausible.

Apomorphies of the Paguroidea	Apomorphies of the "asymmetrical" hermit crabs	Apomorphies of the Paguridae and Lithodidae	Character state of Lithodidae
4th pereiopod smaller than 2nd and 3rd pereiopod			–
4th pereiopod with rasp			–
5th pereiopod kept outside the branchial chamber			–
5th pereiopod with rasp			+3)
uropods crescent-shaped and with rasps			–4)
dorso-posterior part of the carapace weakly calcified and soft			–
	pleon asymmetrical		+
	soft pleon tergites		–/+5)
	loss of right pleopods		+
	6th pleon tergite with transverse furrow		–
		1st pleon sternite fused to last thoracic sternite	+
		2nd to 5th pleon tergites divided1)	+
		basal segments of the outer flagellum of 1st antenna fused	+
		row of sensory hairs of 1st antenna displaced2)	+
		accessory teeth on the ischium of 3rd maxilliped	+

1) Within the Paguridae only in some taxa; 2) We found this character state in *Pagurus bernhardus*, *Hapalogaster dentata*, and *Lithodes maja*; 3) Vestigal rasps exist in *Lithodes maja*; 4) The lithodids lack uropods; 5) Only the Lithodinae have well calcified tergites.

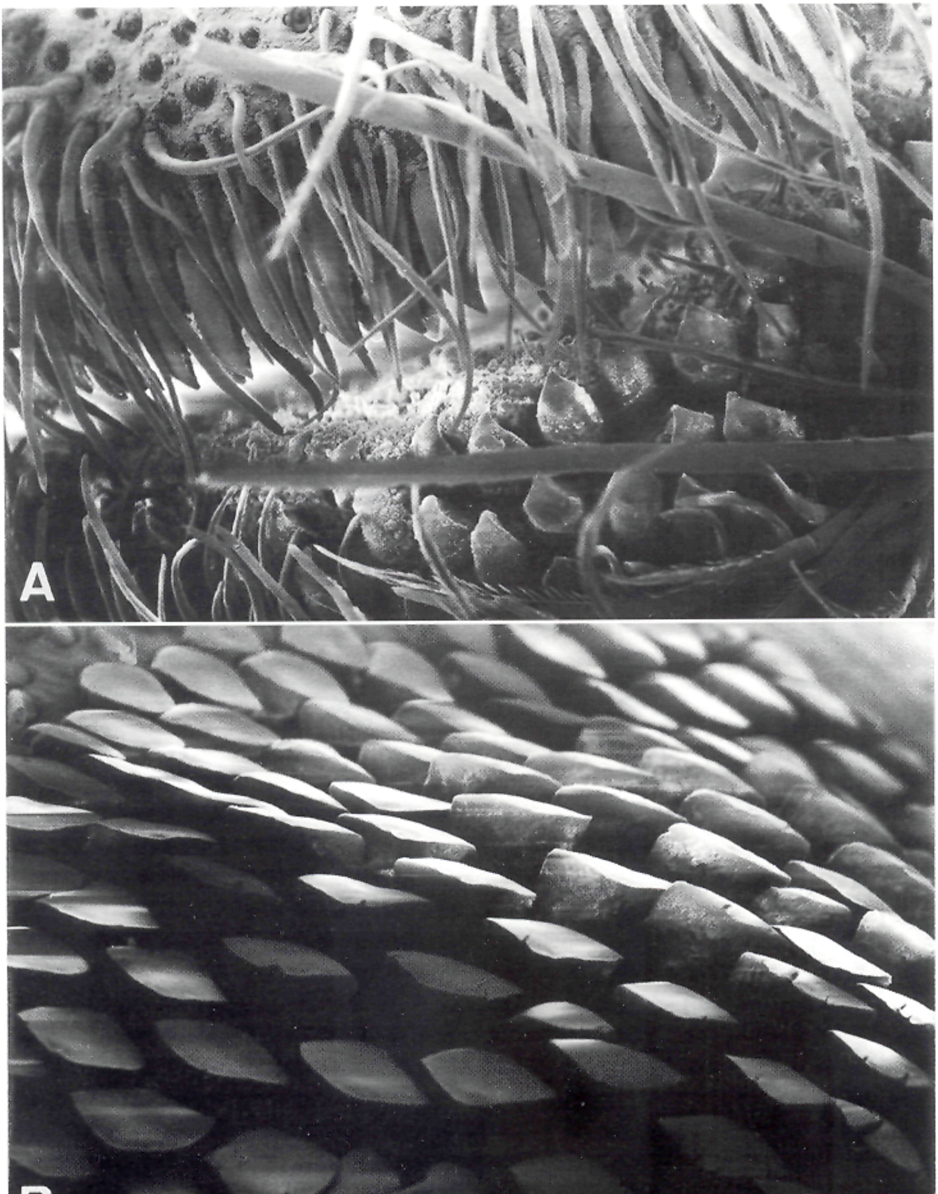


Fig. 2. SEM micrographs of the vestigial rasp of the 5th pereiopod of *Lithodes maja* (A, the dactylus is up) and the rasp of the 5th pereiopod of *Pagurus bernhardus* (B). The plesiomorphic condition found in most Eureptantia is a single row of scale-like teeth (Scholtz & Richter 1994).

malans (plesiomorphic). The Lithodidae do not show any rasp at the 4th pereiopod. In these species the 4th pereiopod is more or less similar in size and appearance to the 2nd and 3rd pereiopods. Within the Diogenidae, Parapaguridae, Paguridae and Coenobitidae, several species (secondarily) lack rasps (e. g. adult *Birgus*, *Paguropsis*, *Ostraconotus*, *Solitariopagurus*, *Tylaspis* and *Probeebei* (BALSS 1924; WOLFF 1961; DE SAINT LAURENT 1972)).

(2) The 5th pereiopod is reduced in size and bears rasps (Fig. 2). It holds the shells and is kept most of the time outside the branchial chamber (e. g. *Dardanus callidus*, *Discorsopagurus schmitti* INNOCENTI et al. 1993 and GHERARDI pers. comm.). The presence of rasps on the 5th pereiopod is restricted to hermit crabs. All Anomala outside the hermit crabs insert the 5th pereiopod beneath the carapace (plesiomorphic). Within the investigated species of hermit crabs only *Hapalogaster dentata* lacks the rasp (few other exceptions exist, e. g. *Probeebei*, WOLFF 1961). It is of interest to note that a vestigial rasp occurs in *Lithodes maja* (Fig. 2) (this is unknown for *Paralomis*). The 5th pereiopods are inserted beneath the carapace in all Lithodidae (MACPHERSON 1988; see also POHLE 1989) and *Birgus*.

(3) The uropods of hermit crabs are crescent like and equipped with rasps (see Fig. 4). Crescent-shaped uropods and rasps do not occur in other reptant groups (plesiomorphic). Within the asymmetrical hermit crabs, *Probeebei* lacks rasps on the uropods (WOLFF 1961). The adult Lithodidae lack uropods.

(4) The dorso-posterior portion of the carapace is weakly calcified and soft. The carapace of most Reptantia is hard and calcified. Galatheoids (including hippids) and lomids possess a carapace with soft lateral parts but not a soft dorsum (plesiomorphic). Within pagurids, parapagurids, diogenids and coenobitids some exceptions from the apomorphic state in hermit crabs exist (e. g. *Birgus*, *Probeebei*, *Porcellanopagurus*, *Ostraconotus*, *Labidochirus* possess a secondarily well calcified carapace; (BALSS 1924; HARMS 1932; WOLFF 1961; MCLAUGHLIN 1974)). The dorsolateral parts of the carapace of the Lithoidae are completely calcified and hard except for the linea anomalica. The carapace of *Lithodes maja* like that of the other lithodids (MACPHERSON 1988) is characterized by its protruded dorso-lateral portions.

Paraphyly of Pylochelidae

The primarily symmetrical hermit crabs, the Pylochelidae (FOREST 1987), are most likely paraphyletic. The genera *Trizocheles* and *Mixtopagurus* together with all asymmetrical hermit crabs represent a monophylum. *Parapylocheles* and/or *Cancellocheles* are the sister group. The genera *Pomatocheles*, *Pylocheles* and *Cheiroplatea* together constitute a monophyletic taxon, the sister group of all other hermit crabs.

Trizocheles and *Mixtopagurus* share with the asymmetrical hermit crabs the possession of real ocular acicles. All other pylochelids lack real ocular acicles (Fig. 3 A, B). Here we found only a "piece basilaire" (FOREST 1987) (Fig. 3 A). We found no ocular acicles in the examined representatives of Lithodidae, but MCLAUGHLIN (1983 b) has reported the existence of ocular acicles in some lithodid species. Within the parapagurids, *Tylaspis* lacks ocular acicles (DE SAINT LAURENT 1972). The so-called ocular acicles of *Albunea* (Hippidae) "are not ocular acicles, but calcified portions of the hippoid ocular plate" (MCLAUGHLIN 1983 b). Thus, the ocular acicles found in hermit crabs do not occur in any other reptant group.

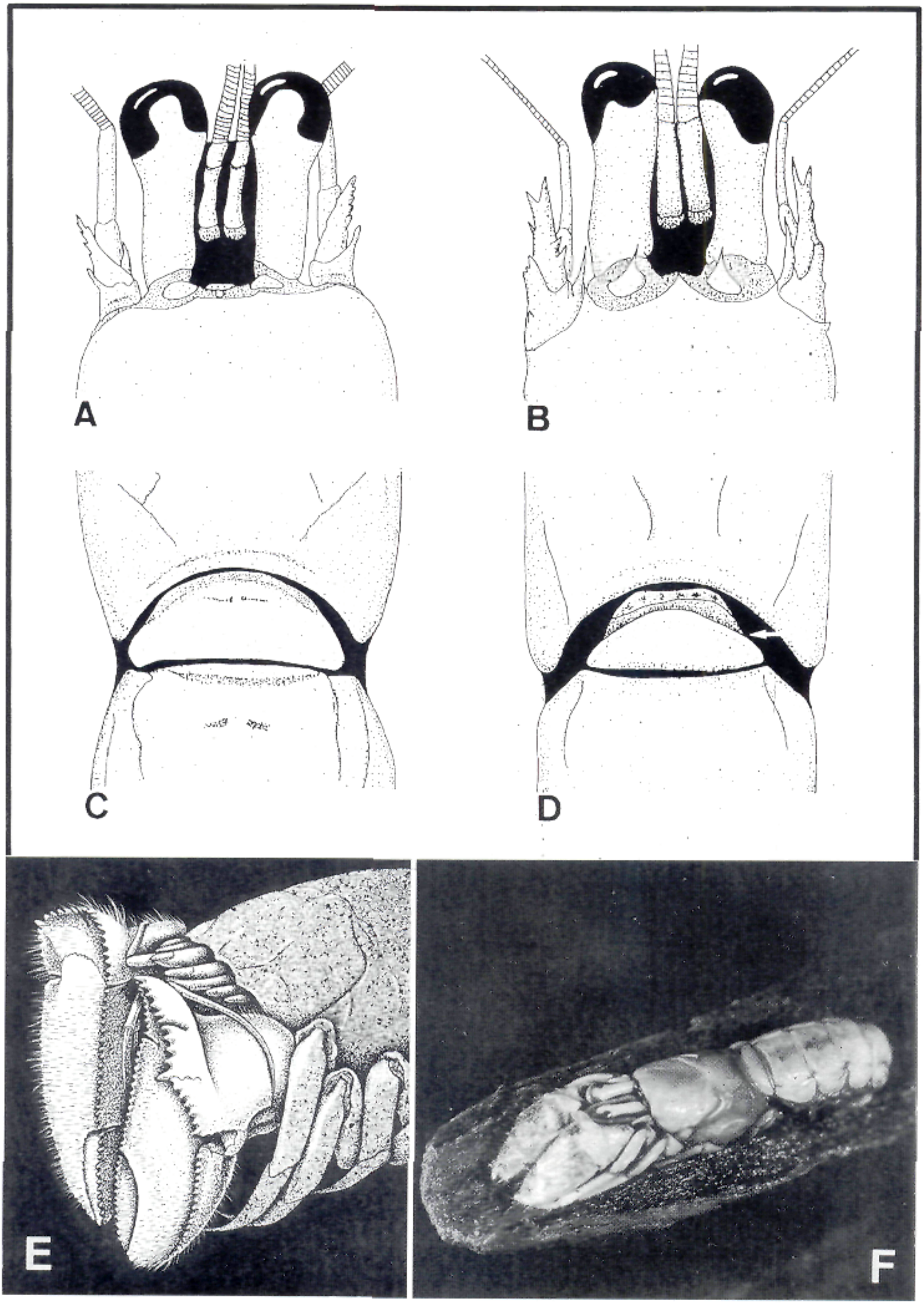


Fig. 3

The 1st pleon tergite of the symmetrical hermit crab genera *Parapylocheles*, *Cancellocheles*, *Trizocheles*, and *Mixtopagurus* as well as that of the asymmetrical hermit crabs including the Lithodidae is narrow and equipped with a posterior bulge (see also Forest 1987) (Fig. 3 D). However, in many Paguridae the 1st pleon tergite is not discernable and no posterior bulge can be recognized. The bulge is lacking and the 1st pleon tergite is relatively wide in the pylochelid genera *Cheiroplatea*, *Pylocheles* and *Pomatocheles* (see also Forest 1987) (Fig. 3 C). The 1st pleon tergite of most of the other Anomala is wide. *Lomis hirta* possesses a narrow 1st pleon tergite without a bulge. The pairs of 1st pereiopods of *Pylocheles*, *Cheiroplatea*, and *Pomatocheles* form specialized symmetrical opercula (Fig. 3 E, F) (for figures see also Boas 1926a; Forest 1987). In *Cancellocheles*, we found another kind of operculum. Here the 2nd pereiopods contribute to the operculum (like *Cancellus*, Forest 1987). Some asymmetrical hermit crabs have also opercula formed by one or sometimes two chelae (see detailed discussion in Balss 1924). These opercula are obviously convergent with those of the symmetrical forms. A second character confirms the monophyly of a group comprising *Pylocheles*, *Cheiroplatea* and *Pomatocheles*. In the Paguroidea the two flagella of the 1st antennae differ remarkably. The originally outer flagellum is shifted to a dorsal position, it is thick and it has numerous aesthetasc sensilla except for the hairless basal segments. The inner, now ventrally positioned, flagellum is relatively thin and bears only few sensoric hairs. This characteristic type of 1st antenna is part of the ground pattern of the Meiura (Anomala and Brachyura, Scholtz & Richter 1994). In *Pylocheles miersi*, *Cheiroplatea laticauda*, and *Pomatocheles jeffreysii* apart from the basal segment, at least 2 more segments of the thick flagellum lack the sensory hairs. Outside these genera all segments of the thick flagellum of the 1st antenna except the basal segment bear sensory hairs. Within the monophyletic taxon comprising *Pomatocheles*, *Pylocheles* and *Cheiroplatea* the last two genera are sister groups. In these genera the two distal segments of the endopod of the 3rd maxilliped form a chela. This has been reported for all species of these genera (Forest 1987) and cannot be found in any other reptant group.

Monophyly of the "asymmetrical" hermit crabs

The parapagurids, diogenids, coenobitids, pagurids and lithodids constitute together the monophyletic taxon of the "asymmetrical" hermit crabs characterized by the following synapomorphies:

(1) The pleon of the Parapaguridae, Paguridae, Diogenidae, Coenobitidae, and Lithodidae (females) (see Fig. 7 B) is asymmetrical, i. e. the telson lies beside the

◀ Fig. 3. Characters of symmetrical hermit crabs (pylochelids). Eye region of the symmetrical hermit crabs *Pylocheles miersi* (A) without true ocular acicles and *Trizocheles brevicaulis* (B) with ocular acicles. (C) The wide 1st pleon tergite of *Pylocheles miersi* lacking a bulge. (D) The narrow 1st pleon tergite of *Trizocheles brevicaulis* with a characteristical bulge (arrow). In all pictures anterior is up. (E) Anterior part of *Cheroiplatea laticauda* showing the operculate 1st pereiopods with serrate margins and typical vertical orientation. (F) *Pylocheles miersi* in its house, a hollow piece of wood (the top has been removed), to demonstrate the function of the operculate chelae.

symmetry axis of the animal. The pleon of the pylochelids and all other Reptantia is symmetrical (plesiomorphic). Within the asymmetrical hermit crabs, some exceptions with a secondarily symmetrical pleon exist, e. g. *Paguropsis*, *Cancellus* (Balss 1924, Boas 1926b, for more examples see Wolff 1961) and male lithodids.

(2) The tergites 2 to 5 of the pleon are soft. The tergites of the pleon are hard and calcified in the pylochelids and all other reptants (plesiomorphic). However, within the asymmetrical hermit crabs some Lithodidae (see Fig. 7 B) (Makarov 1962; MacPherson 1988) and a few other species possess hard pleon tergites (e. g. *Birgus* and *Probeebei* (Harms 1932; Wolff 1961)).

(3) In correlation to the asymmetrical pleon some pleopods have been lost. The females and males of the asymmetrical hermit crabs including the Lithodidae possess only the 3rd to 5th pleopods on the left side (e. g. Boas 1924; Melin 1939; Makarov 1962; McLaughlin 1974, Lemaitre 1989). An exception is the genus *Paguropsis*, where they occur on the right side in some individuals (see also Boas 1926b). Sometimes the pleopod number is more reduced. The males of *Coenobitidae* and *Lithodidae* lack the pleopods completely. (This is also true for other genera, e. g. *Paguridium* and *Paguritta*, Melin 1939). All Pylochelidae and the other Anomala possess paired 3rd to 5th pleopods (plesiomorphic).

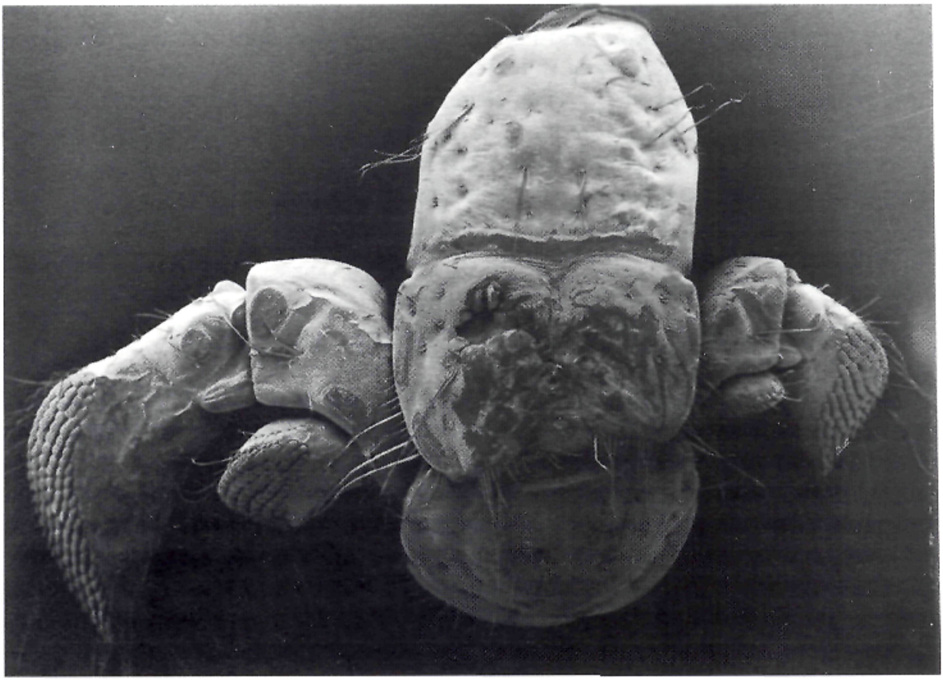


Fig. 4. SEM micrograph of the 6th pleon segment and telson of *Clibanarius erythropus* (dorsal view). The tergite of the 6th pleon segment is divided by a transverse furrow. Note the rasps bearing uropods and that the exopod is much longer than the endopod and that the exopod cannot be folded under the endopod.

The situation regarding the 1st and 2nd pleopods is more complex. Males of *Paguropsis typica*, *Paguristes barbatus* and *Sympagurus dimorphus*, for example, possess two pairs of pleopods (for other species see McLaughlin 1974; Lemaitre 1989; Wolff 1961). Therefore, this plesiomorphic condition is considered to be the character state in the stem species of asymmetrical hermit crabs. In females of most asymmetrical hermit crabs, at least the right 2nd pleopod is missing. However, a vestigial right 2nd pleopod exists in some parapagurids (Lemaitre 1989, 1990). Based on the existence of 1st pleopods in females of some asymmetrical hermit crabs (e.g. *Nematopagurus squamicheles*, *Paguropsis typica*), it can be inferred that the stem species of asymmetrical hermit crabs had most likely paired 1st and 2nd pleopods. Perhaps, the stem species of asymmetrical hermit crabs already possessed a vestigial right 2nd pleopod.

(4) A further argument for the monophyly of asymmetrical hermit crabs is the existence of a transverse furrow on the 6th tergite of the pleon (Fig. 4). The 6th tergite of pylochelids bears only a pair of lateral notches (see also Forest 1987). However, neither furrows nor notches can be found in the corresponding tergites of Lithodidae (MacPherson 1988) and *Birgus*. Notches in the 6th pleon tergite also occur in other anomalans and brachyurans. A furrow does not occur outside the hermit crabs.

Within the asymmetrical hermit crabs, the phylogenetic relationships are unresolved and seem to be very complex. Even the monophyletic status of most of the five families, Parapaguridae, Diogenidae, Coenobitidae, Paguridae, and Lithodidae is uncertain. The Coenobitidae clearly represent a monophyletic taxon because *Coenobita* and *Birgus* share an apomorphic type of 1st antenna with specialised flagella and sensory hairs (see also McLaughlin 1983b; Martin & Abele 1986). The Lithodidae can also be shown to be monophyletic (see below). Some arguments exist for the monophyly of the Parapaguridae (see McLaughlin 1983b; Martin & Abele 1986; Lemaitre 1989). The Paguridae and Diogenidae are most likely paraphyletic (see Fig. 1) (for a discussion of polyphyly of the Paguridae see Gore & Scotto 1983). Arguments for a closer relationship between diogenids and coenobitids are given by McLaughlin (1983b) and Tudge (1991, 1992).

Paguridae and Lithodidae seem to be closely related

Several arguments can be found supporting the assumption that Paguridae and Lithodidae together constitute a monophyletic taxon.

(1) In both taxa the 1st pleon sternite is fused to the last thoracic sternite. In the Diogenidae, Coenobitidae, and Pylochelidae and all other Reptantia the 1st pleon sternite is separated from the last thoracic sternite. McLaughlin (1983b) has suggested that the last thoracic and the 1st pleon somites are also fused in the Parapaguridae. However, our own observations have led us to a different view. The 1st pleon sternite is clearly separated from the last thoracic sternite in the parapagurid *Sympagurus dimorphus* and the sclerites of the 1st pleon sternite show a different pattern compared with the above mentioned species with a clear fusion. These findings are in agreement with what Wolff (1961) has described for *Probeebei* and with the interpretation of Boas (1924) who was the first to mention the sternite fusion.

(2) The 2nd to 5th pleon tergites of most Paguridae are divided into two lateral plates. This means that the calcification is lost in the median line and the tergites are only represented by lateral thickenings or weak calcification. However, in some Paguridae, the tergites 2 to 5 are not discernable. Divided pleon tergites also occur in the Lithodidae. In *Lithodes maja*, the lateral plates of the tergites are secondarily connected by calcified nodules (see Fig. 7B). And in *Paralomis granulosa*, median plates connect the lateral pleon tergites. The 2nd tergite of *Hapalogaster* is divided into two lateral plates which are connected by two small median plates. MAKAROV (1962) described for the females of *Hapalogaster* that on the left side, the 3rd to 5th pleon segments are only calcified in the marginal part. On the right side, the segments 3 and 4 show only a small unsegmented round plate and the plate of the 5th segment corresponds to that on the left side. We found divided tergites also in the diogenid *Paguristes barbatus* (convergent?). The other hermit crab species examined as well as all other decapods show undivided pleon tergites. A detailled discussion of this character is given by BOAS (1924).

(3) Some basal segments of the thick, outer flagellum of the 1st antenna fuse in a characteristic manner in the Paguridae and Lithodidae examined (Fig. 5 A – D). We found 4 to 7 segments fused in *Nematopagurus squamicheles*, *Pagurus bernhardus* (see also SNOW (1974) for *P. ochotensis*), *Spiropagurus spiriger*, *Lithodes maja*, *Paralomis granulosa*, and *Hapalogaster dentata*. However, we found a similar fusion of fewer segments (up to 4) in the diogenids *Paguristes barbatus* and *Dardanus arrosor*. A corresponding fusion is not known from any other representative ot the Paguroidea or the Anomala.

(4) In addition to the crista dentata, the ischium of the 3rd maxilliped bears one or more accessory teeth in Paguridae and Lithodidae (Fig. 6) (e.g. MCLAUGHLIN 1974; MACPHERSON 1988). Accessory teeth also exist in some Pylochelidae (FOREST 1987). None of the other pagurids possess these teeth. BOAS (1924) mentioned the single ischium tooth of *Pagurus* and *Lithodes* and he considered it to be a character of high systematic importance, but he was unaware of its existence in symmetrical hermit crabs. Outside the hermit crabs, an ischium tooth also occurs in *Aegla*. We do not know whether the existence of one or more teeth on the ischium of the 3rd maxilliped for the Paguridae and the Lithodidae is a plesiomorphic character state or an apomorphy convergent to some Pylochelidae and *Aegla*. Only in the latter case, would it be an argument for the monophyly of both taxa.

Further arguments exist for a monophyletic taxon comprising at least some Paguridae and the Lithodidae.

(5) The males of some Paguridae and the Lithodidae have lost the left 2nd pleopod (this means 1st and 2nd pleopods are completely absent). At least the left

Fig. 5. SEM micrographs of the 1st antennae of various hermit crabs. The basal segments of the thick flagellum are fused in the 1st antennae of *Pagurus bernhardus* (A), *Lithodes maja* (B), and *Hapalogaster dentata* (C). The plesiomorphic condition with all segments separated can be seen in *Sympagurus dimorphus* (D). The two rows of sensory hairs per segment are aligned in *Paguristes barbatus* (E), the one row is displaced in *Lithodes maja* (F) and *Pagurus bernhardus* (G). ▶

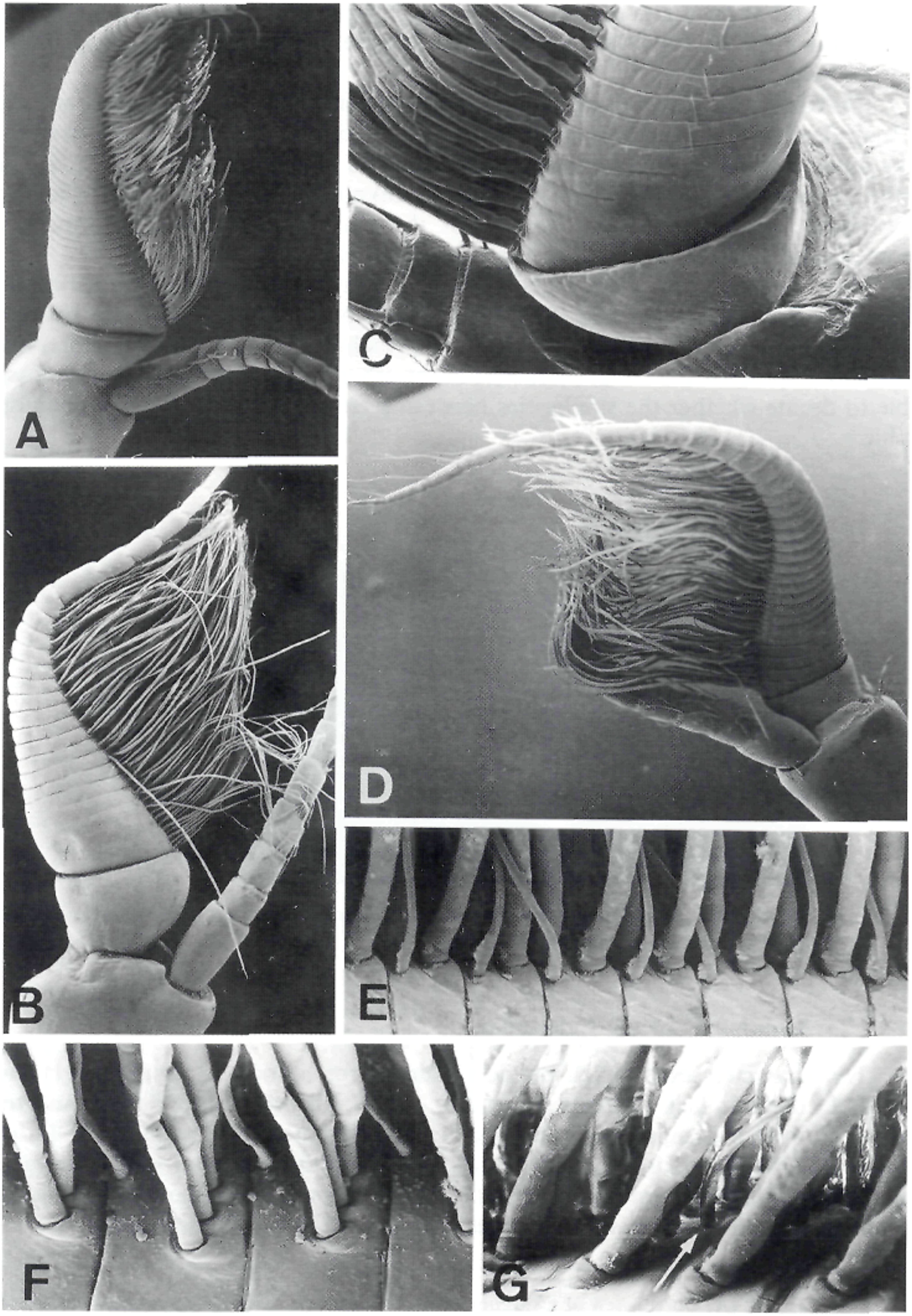


Fig. 5

2nd pleopod of the males exist in Diogenidae, Parapaguridae and Pylochelidae (e.g. Lemaitre 1989, Forest 1987). In the Coenobitidae, however, the 2nd pleopods are also absent.

(6) Within the proposed monophyletic taxon comprising Lithodidae and Paguridae, we found a correspondence in the structure of the thick flagellum of the 1st antenna between *Pagurus bernhardus*, *Lithodes maja* and *Hapalogaster dentata* (the character state in *Paralomis granulosa* is unknown). In contrast to all other investigated hermit crab taxa, one row of the sensory hairs of each segment is somewhat displaced compared to the second row (Fig. 5E–G).

MacDonald et al. (1957) describe some similarities between the larvae of pagurids (i.e. Paguridae) and lithodids and propose a close relationship between these two taxa. Unfortunately, no larvae of pylochelids are known. Therefore, it is difficult to polarize the larval characters of the other hermit crabs and it is not possible to decide whether the similarities between pagurids and lithodids are apomorphic.

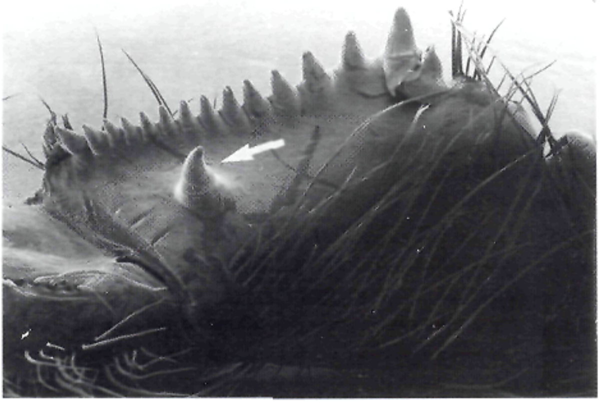
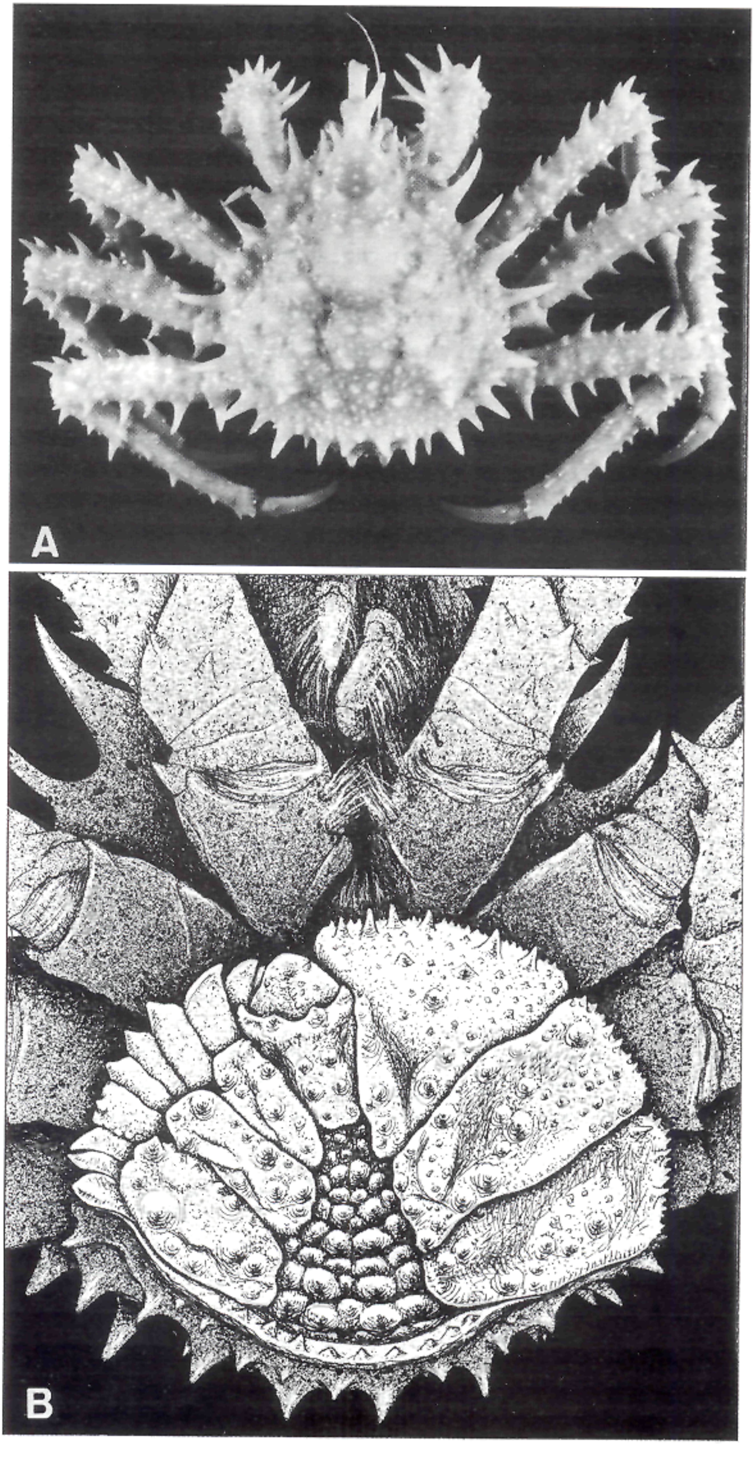


Fig. 6. Ischium of the 3rd maxilliped of *Pagurus bernhardus*. The characteristic accessory tooth is indicated by an arrow.

Monophyly of the Lithodidae

Two characters exist which provide evidence for lithodid monophyly: (1) The adult Lithodidae lack uropods (Makarov 1962). All other hermit crabs and the other anomalan groups possess uropods (plesiomorphic). (2) The males of Lithodidae lack the pleopods 3 to 5 completely. We found this character state convergent in Coenobitidae and some other hermit crabs (see above). The males of most hermit crabs possess the pleopods 3 to 5 at least on the left side (plesiomorphic).

Fig. 7. (A) Dorsal view of a specimen of *Lithodes maja*. The 5th pereiopod is hidden in the branchial chamber. Note the similar arrangement of spines on pereiopods 2 to 4 and that pereiopod 4 is of the same size as the anterior pereiopods. (B) Ventral view of the pleon of a female of *Lithodes maja*. The pleon is asymmetrical and the tergites are divided. The space between the tergites is filled with calcified nodules. ▶


A
B

Many characters of the Lithodidae (Lithodinae and Hapalogastrinae) are reverse characters in comparison to the apomorphies of Paguroidea and their apomorphic state can be concluded on the basis of the character distribution within the hermit crabs: 4th pereiopod equal to 2nd and 3rd (Fig. 7 A), 4th pereiopod without rasp, dorso-posterior part of the carapace calcified and hard (Fig. 7 A), 5th pereiopod kept inside the branchial chamber (Fig. 7 A).

Systematic position of the Paguroidea within the Decapoda Reptantia

The Paguroidea together with the Galatheoidea, the Lomoidea and the Hippoidea constitute the taxon Anomala (sensu McLAUGHLIN 1983 b). This taxon has been established as a monophylum by several apomorphies (SCHOLTZ & RICHTER 1994).

The most probable sister group of the Paguroidea is the monotypic Lomidae. In the uropods of both *Lomis hirta* females (the males lack uropods) and the Paguroidea, the exopods are significantly longer than the endopods (Fig. 4) and cannot be folded under the latter. The uropods of Lomis females are rod like and relatively long. The uropods of hermit crabs are mostly crescent like. The exopods and endopods of most Reptantia, and in particular of the Galatheoidea, are of similar size and can be folded under each other.

Discussion

Phylogenetic considerations

In contrast to the suggestion of MACDONALD et al. (1957) and the classification given by BOWMAN & ABELE (1982), the Paguroidea sensu McLAUGHLIN (1983 b) are clearly a monophyletic taxon. Based on the characteristic uropods, it is suggested that *Lomis hirta* is the sister group of the Paguroidea supporting the view of PILGRIM (1965) (see McLAUGHLIN 1983 a for different conclusions). The inclusion of *Lomis hirta* in the Paguroidea is not possible with our data because *Lomis* lacks all hermit crab characters (for further discussion see McLAUGHLIN 1983 b). Some of our apomorphies for the Paguroidea have also been discussed by McLAUGHLIN (1983 b) and MARTIN & ABELE (1986). However, real ocular acicles suggested in these papers to be an apomorphy of the Paguroidea have apparently been evolved within the hermit crabs. In contrast to the suggestions of MARTIN & ABELE (1986) and the traditional view, the pylochelids are a paraphyletic assemblage. The gonopods which are considered by MARTIN & ABELE (1986) to be an apomorphy of the pylochelids are clearly plesiomorphic since homologous gonopods occur in galatheoids. Furthermore, a divided telson which appears in *Aegla* in a similar manner as in pylochelids (MARTIN & ABELE 1986) cannot be used as an apomorphy for the pylochelids – this character seems also to be plesiomorphic within the Anomala (SCHOLTZ & RICHTER 1994).

The monophyly of the asymmetrical hermit crabs is based on a number of apomorphic characters which partly correspond to the characters mentioned by McLAUGHLIN (1983 b) and MARTIN & ABELE (1986).

Our analysis provides new evidence for the lithodids being part of the hermit crabs and for a close Lithodidae-Paguridae relationship. We found several apomorphies shared by lithodids and asymmetrical hermit crabs and some characters unifying Lithodidae and Paguridae. This supports the suggestions of BOAS (1880a, b, 1924) and BOUVIER (1895) and more recently of MCLAUGHLIN (1983b) and CUNNINGHAM et al. (1992). The position of the lithodids outside the hermit crabs by MARTIN & ABELE (1986) seems to be based on convergent characters and an erroneous interpretation of character polarity (see next paragraph). Using molecular data, CUNNINGHAM et al. (1992) suggest that the genus *Pagurus* is paraphyletic and that only a part of it, including *Labidochirus* and *Ellasochirus*, might be the closest relatives of the lithodids. The similarities of the 1st antennae of *Pagurus bernhardus* and the investigated Lithodidae suggest a similar view. In contrast, BOAS (1924) suggested a close relationship between *Nematopagurus* and the Lithodidae. This opinion is based on the occurrence of the 1st pleopods in the females of *Nematopagurus*. However, the 1st pleopods of *Nematopagurus* and other Paguridae might be plesiomorphic.

The evolution of Lithodidae

As mentioned above, some of the lithodid characters are not hermit crab-like but resemble ancestral characters which we would expect to have occurred in the stem species ot the Anomala (Table 2). How can these similarities be explained? Do lithodids provide an example for an exception from "Dollo's law" which claims that characters once lost cannot be regained in the course of evolution (see FERRARI 1988; STIASSNY 1992)? Or are all similarities simply convergent features? To answer these questions we analyze some of the problematical lithodid characters applying the homology concept. We discuss whether the similarities are complex enough to claim their homology (REMANE 1952; RIEDL 1975; DOHLE 1989) and whether there are criteria based on functional constraints or similar adaptive values that make convergence plausible (RIEGER & TYLER 1985).

1) The calcified pleon tergites (Fig. 7B): A closer examination of the pleon tergites in *Lithodes maja* reveals that tergites 2 to 5 are divided and that only the lateral parts are completely calcified. The median portions consist of small calcified plates. The Lithodidae retained the divided tergites from its hermit crab-like ancestors and within the lithodids the gap between those tergites was filled by secondary calcification (either calcified nodules as in *Lithodes maja* or segmental plates as in *Paralomis granulosa*). The similarity between lithodids and the anomalan stem species is therefore only superficial. The secondary evolution of hard and calcified tergites has produced a pattern different to the original, which is therefore suggested to be convergent.

2) Calcified carapace (Fig. 7A): At first sight the description "completely calcified" assumes homology between this character in lithodids and the anomalan stem species. A closer view shows some similarities between hermit crab carapaces and those of some lithodids. The dorso-lateral parts ot the lithodid carapace appear inflated and are separated from the dorsal shield. This could be explained as a derivative of the soft lateral sides of the hermit crab-like ancestors of the lithodids.

Table 2. Comparison of the states of selected characters between the anomalan stem species, a representative of the hermit crabs (*Pagurus bernhardus*), and two lithodid species (*Lithodes maja, Hapologaster dentata*) to show the similarities between lithodid apomorphies and ancestral characters. In most cases the similarities are convergences.

	character states of anomalan stem species	character states in *Pagurus bernhardus*	character states in *Lithodes maja*	character states in *Hapalogaster dentata*
calcified pleon tergites	+	–	+	–
dorsally calcified carapace	+	–	+	+
large locomotory 4th pereiopod without rasps	+	–	+	+
5th pereiopod kept in branchial chamber	+	–	+	+
6th pleon tergite with transverse furrow	–	+	–	–
females with 1st pleopods	+	–	+	+

Like the calcified pleon tergites, the calcified carapace of lithodids is a convergent character when compared to that of the anomalan stem species.

3) Large locomotory 4th pereiopod (Fig. 7 A): The 4th pereiopods of *Lithodes maja*, *Paralomis granulosa*, and *Hapalogaster dentata* not only resemble the 3rd and 2nd pereiopods in size but also in the arrangement of spines (this is true for all Lithodidae (MAKAROV 1962; MACPHERSON 1988)). In addition, the 4th pereiopods of lithodids bear no rasps. All this occurs already in the lithodid megalopa (MACDONALD et al. 1957). According to the suggested relationships of lithodids, this 4th pereiopod must have evolved from a small, rasp bearing pereiopod typical for hermit crabs. The identical arrangement of spines on pereiopods 2, 3, and 4 suggests that the genetical information for size and the spine pattern of the anterior pereiopods might be shifted posteriorly and might also be expressed in the 4th pereiopods. There is evidence that this is not a mere speculation and might be the subject for future experimental tests. In *Drosophila melanogaster*, segment identity is specified by homeotic genes (AKAM 1987). In the *Drosophila* homeotic mutant *bithorax*, for instance, the 3rd thoracic segment repeats several characteristics of the 2nd thoracic segment including the occurrence of wings and the appearance of legs (LEWIS 1964). AVEROF & AKAM (1993) have recently shown that the class of homeotic genes also occurs in Crustacea and that there are several homologs to genes found in *Drosophila*.

4) The 5th pereiopods are kept in the branchial chamber (Fig. 7 A): The 5th pereiopod is reduced, functions as a gill cleaner leg, and is kept in the branchial chamber. This complex set of characters resembles to a high degree the conditions found in galatheoids and in the anomalan stem species (SCHOLTZ & RICHTER 1994). Gastropod shell dwelling hermit crabs not only hold their shells with the rasp bearing 5th pereiopods (apomorphic) but they also put them into the branchial chamber to clean their gills (e. g. INNOCENTI et al. 1993; GHERARDI pers comm.) (plesiomorphic) and this has become the main function with the loss of shell dwelling habits in lithodids. If the 5th pereiopods of lithodids are experimentally removed, the animals die due to a pollution and infection of the gills (POHLE 1989). Interestingly enough, vestiges of a rasp exist on the 5th pereiopod of *Lithodes maja* (but not in *Hapalogaster dentata*).

5) The 1st pleopods in females: The occurrence of 1st pleopods in the females of lithodids (see MAKAROV 1962; MACPHERSON 1988) is difficult to interpret. BOAS (1880b) suggested that it could be an "atavistic" character but he changed his opinion after the examination of *Nematopagurus* (BOAS 1924). Our data point to a close relationship between *Pagurus* or at least some species of that genus and the Lithodidae (see also CUNNINGHAM et al. 1992). Because all *Pagurus*-species lack 1st pleopods (MCLAUGHLIN 1974), the assumption of a secondary appearance (atavism) of the 1st pleopods in *Lithodes*-females would be more parsimonious than the independent loss in several lines. Interestingly, the first pleopods are also absent in the larvae of all investigated *Pagurus*-species (e. g. GORE & SCOTTO 1983; review in MCLAUGHLIN & GORE 1988). In other species which as adults possess 1st pleopods these appear after the larval period (LEMAITRE & MCLAUGHLIN 1992). Based on the late appearance of the 1st pleopods, PROVENZANO & RICE (1966) suggested that they are new structures in hermit crabs which are not derived from pre-existing pleopods. This is no argument against homology because homologous structures can arise via

different developmental pathways (e.g. Scholtz 1993). Furthermore, buds of 1st pleopods occur in earlier stages of anomalan and hermit crab development (unpub. observation) which indicates that the genetic information for limb formation is still there and could have been heterochroneously shifted to adult stages. This is a special case of "cryptotype" (Osche 1966). Genetic information is not entirely suppressed in the phenotype but restricted to early ontogenetic stages. Thus the 1st pleopods of lithodid females may represent an example for the reappearance of an ancestral character. The lithodid apomorphy would be identical to a plesiomorphic character of hermit crabs.

In summary, a detailed analysis of the derived lithodid characters which resemble ancestral anomalan characters shows that most similarities can be explained by convergent evolution. Only the 1st pleopods of lithodid females might represent a reappearance of an ancestral character (a "taxic atavism" of Stiassny (1992)). If this suggestion holds true (and more data are certainly needed) it represents a general problem for the method of phylogenetic systematics. When true apomorphic character states of a given group are not different from the corresponding plesiomorphic character states, character state polarity is obscured and paraphyletic groups are considered as being monophyletic. The example given shows that only if there is sufficient evidence from other clear apomorphies the claim for the reappearance of ancestral characters can be made.

The considered characters of lithodids can be seen in the light of the secondary change toward a free living habit. A strong calcification of the carapace and of the pleon tergites substitutes the protection previously offered by a shell. The pereiopods 4 and 5 lose their function of holding the shell. The 4th pereiopod regains its function as a walking leg and the 5th pereiopod is again kept in the branchial chamber and cleans the gills. The vestigial rasp on the 5th pereiopod of *Lithodes maja* has an unknown function but it reminds of the ancestral function holding the shell. The asymmetrical pleon with unpaired pleopods of lithodid females can be explained as an ancestral hermit crab character maintained due to the necessity to carry the eggs. The symmetrical pleon of the males is a secondary feature correlated with the entire loss of pleopods (the same character distribution is true for *Probeebei* (Wolff 1961)).

The Lithodidae is not the only group within the hermit crabs which has changed its habits from gastropod shell-dwelling to free-living. Further examples are *Probeebei* (Wolff 1961), and *Birgus* (Harms 1932). The latter species, in particular, shows remarkably convergent similarities with the lithodids. As in lithodids, the carapace and the pleon tergites are fully calcified (the latter undivided), the 4th pereiopod is large, lacks rasps, and functions as a walking leg, the 5th pereiopod is a gill cleaner and is carried under the carapace. Interestingly, *Birgus* undergoes the transformation from a shell-dwelling hermit crab with all its characteristic features to the free-living habits during ontogenesis (Harms 1932; Reese 1968). Even shell-dwelling hermit crab species develop a more symmetrical and more calcified pleon in subsequent moults when deprived of gastropod shells (Przibam 1907).

The listed convergent features lead to the question of the selection pressure that might be responsible for the loss of the gastropod shell-dwelling habits. Harms (1932) suggested for *Birgus* that an easier achievement of the terrestrial food resources and the subsequent specialization might have led to gigantism which made the use of shells impossible. Blackstone (1989) and Cunningham et al. (1992) come to similar conclusions concerning lithodids. An increase in size in the ancestral lineage of Lithodidae led to limited resources of suitable gastropod shells and eventually the lithodids were of such a size that there were no fitting shells at all. These suggestions are only plausible if the larger specimens have a real selective advantage compared with the smaller specimens within the same population which had a size that allowed them to find a protecting shell. Furthermore, it is striking that many lithodid species are not very large. This is in particular true for the Hapalogastrinae which is believed to represent the lithodid group with many primitive characters that resembles the lithodid stem species. It has been suggested that the number of gastropod shells is a limiting resource for hermit crab populations (Hazlett 1981). Therefore, it is more likely that the lack of suitable shells in certain habitats represents the starting point for lithodid evolution. Subsequently, all the characters which compensate the protection mechanisms of the shells have evolved and it seems plausible that in some lithodid lines, size was one of these characters.

Acknowledgements

We thank H.-E. Gruner (Berlin), L. Tiefenbacher (Munich) and T. Wolff (Copenhagen) for the loan of material, K. Kiontke and P. Lederer for technical assistance, and P. Adam for drawing figures 3E and 7B. H.-E. Gruner also provided some literature. We are grateful to W. Dohle, P. Greenaway, and R. Lemaitre for critical comments on various versions of the manuscript, H. Cooper-Kovács for correcting the English, and the participants of the workshop "Gesprächskreis Phylogenetische Systematik" in Berlin (1992) for helpful discussions. S. Richter was supported by the "Studienstiftung des Deutschen Volkes".

References

Akam, M.: The molecular basis for metameric pattern in the *Drosophila* embryo. Development **101** (1987) 1–22.

Averof, M. and M. Akam: *HOM/Hox* genes of *Artemia*: implications for the origin of insect and crustacean body plans. – Curr. Biol. **3** (1993) 73–78.

Balss, H.: Über Anpassungen und Symbiose der Paguriden – eine zusammenfassende Übersicht: – Z. Morphol. Ökol. Tiere **1** (1924) 752–792.

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

Bliss, D. E.: Shrimps, lobsters and crabs. Columbia University Press, New York 1982.

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

–: Studier over Decapodernes Slaegtskabsforhold. – Vidensk. Selsk. Skr. Raekke nat.-math.-Afd. **I.2** (1880b) 25–210.

–: Die verwandtschaftliche Stellung der Gattung *Lithodes*. – Kgl. Dan. Vid. Selsk. Biol. Med. **4** (1924) 1–34.

–: Zur Kenntnis symmetrischer Paguriden. – Kgl. Dan. Vid. Selsk. Biol. Med. **5(6)** (1926a) 1–52.

–: Zur Kenntnis des Einsiedlerkrebses *Paguropsis* und seiner eigenartigen Behausung. – Kgl. Dan. Vid. Selsk. Biol. Med. **5(7)** (1926b) 1–23.

Borradaile, L. A.: Crustacea I. Decapoda II. *Porcellanopagurus*; an instance of carcinization. – Brit. Antarct. ("Terra Nova") Exp. 1910. Nat. Hist. Rep. Zool. **3** (1916) 75–126.

BOUVIER, M. E. L.: Recherches sur les Affinités des *Lithodes* & des *Lomis* avec les Pagurides. – Ann. Sci. nat., Zool. Palaeont., 7. Ser. **18** (1895) 157–213.

BOWMAN, T. E. and L. G. ABELE: Classification of the recent Crustacea. In: The biology of the Crustacea. I. Systematics, the fossil record and biogeography. Ed. by ABELE, L. G. Academic Press, New York 1982, 1–27.

CUNNINGHAM, C. W., N. W. BLACKSTONE, and L. W. BUSS: Evolution of king crabs from hermit crab ancestors. – Nature **355** (1992) 539–542.

DOHLE, W.: Zur Frage der Homologie ontogenetischer Muster. – Zool. Beitr. (N. F.) **32** (1989) 355–389.

FERRARI, F. D.: Evolutionary transformations and DOLLO's Law. – J. Crust Biol. **8** (1988) 618–619.

FOREST, J.: Les Pylochelidae ou "Pagures symétriques" (Crustacea Coenobitoidea). – Mém. Mus. natn. Hist. nat. (Sér. A, Zool.) **137** (1987) 1–249.

GORE, R. H., and L. E. SCOTTO: Studies on decapod crustacea from the indian river region of Florida XXVII. *Phimochirus holthuisi* (Provenzano, 1961) (Anomura: Paguridae): The complete larval development under laboratory conditions, and the systematic relationships of its larvae. – J. Crust. Biol. **3** (1983) 93–116.

GOULD, S. J.: We are all monkeys' uncles. – Natural History (1992) 14–21.

GRUNER, H. E.: Crustacea. In: KAESTNER, Lehrbuch der speziellen Zoologie, Bd. 1: Wirbellose Tiere 4. Teil Arthropoda (ohne Insecta). Ed. by H.-E. GRUNER. Gustav Fischer, Jena. 1993, 448–1030.

HARMS, J. W.: Die Realisation von Genen und die consecutive Adaption. II. *Birgus latro* L. als Landkrebs und seine Beziehungen zu den Coenobiten. – Z. wiss. Zool. **140** (1932) 167-290.

HAZLETT, B. A.: Influence of rearing conditions on initial shell entering behaviour of a hermit crab (Decapoda, Paguridae). – Crustaceana **20** (1981) 167–170.

HENNIG, W.: Grundzüge einer Theorie der phylogenetischen Systematik. Deutscher Zentralverlag, Berlin 1950.

–: Phylogenetic systematics. University of Illinois Press, Urbana 1966.

INNOCENTI, A., F. GHERARDI and M. VANNINI: Use of appendages in hermit crab cleaning activity. – International Senckenberg Symposium Crustacea Decapoda (Abstract) (1993) 32–33.

LEMAITRE, R.: Revision of the genus *Parapagurus* (Anomura: Paguroidea: Parapaguridae), including rediscriptions of the western Atlantic species. – Zool. Verh. **253** (1989) 1–106.

–: A review of eastern Atlantic species of the family Parapaguridae (Decapoda, Anomura, Paguroidea). – J. nat. Hist. **24** (1990) 219–240.

LEMAITRE, R. and P. A. MCLAUGHLIN: Descriptions of megalopa and juveniles of *Sympagurus dimorphus* (Studer, 1883), with an account of the Parapaguridae (Crustacea: Anomura: Paguroidea) from Antarctic and Subantarctic waters. – J. nat. Hist. **26** (1992) 745–768.

LEWIS, E. B.: Genetic control and regulation of developmental pathways. The role of chromosomes in development. Ed. by LOCKE, M., Academic Press. New York. 1964, 231–252.

MACDONALD, J. D., R. B. PIKE, and D. I. WILLIAMSON: Larvae of the British species of *Diogenes*, *Pagurus*, *Anapagurus* and *Lithodes* (Crustacea, Decapoda). – Proc. Zool. Soc. Lond. **128** (1957) 209–257.

MACPHERSON, E.: Revision of the family Lithodidae Samouelle, 1819 (Crustacea, Decapoda, Anomura) in the atlantic ocean. – Monogr. zool. Mar. **2** (1988) 9–153.

MADDISON, W. P., M. J. DONOGHUE, and D. R. MADDISON: Outgroup analysis and parsimony. – Syst. Zool. **33** (1984) 83–103.

MAKAROV, V. V.: Anomura. In: Fauna of U.S.S.R. Crustacea Vol. 10 No. 3. Ed. by SHTAKELBERG, A. A.: (Translation from Russian by F. D. POR). Israel Program for Scientific Translations, Jerusalem, 1962, 1–283.

MARTIN, J. W., and L. G. ABELE: Phylogenetic relationships of the genus *Aegla* (Decapoda: Anomura: Aeglidae), with comments on anomuran phylogeny. – J. Crust. Biol. **6** (1986) 576–616.

MCLAUGHLIN, P. A.: The hermit crabs (Crustacea Decapoda, Paguridea) of northwestern North America. – Zool. Verh. **130** (1974) 1–396.

–: A review of the phylogenetic position of the Lomidae (Crustacea: Decapoda: Anomala). – J. Crust. Biol. **3** (1983 a) 431–437.

–: Hermit crabs – are they really polyphyletic? – J. Crust. Biol. **3** (1983 b) 608–621.

MCLAUGHLIN, P. A., and R. H. GORE: Studies on the *Provenzano* and other pagurid groups: I. The larval stages of *Pagurus mclaughlinae* Garcia-Gomez 1982 (Decapoda: Anomura: Paguridae) reared under laboratory conditions. – J. Crust. Biol. **8** (1988) 262–282.

MELIN, G.: Paguriden und Galatheiden von Prof. Dr. SIXTEN BOCKS, Expedition nach den Bonin-Inseln 1914. – Kungl. Svensk. Vetensk. Handl. **18** (1939) 1–119.

OSCHE, G.: Grundzüge der allgemeinen Phylogenetik. In: Handbuch der Biologie III(2). Ed. by GESSNER, F. Athenaion, Konstanz. 1966, 817–906.

PILGRIM, R. L. C.: Some features in the morphology of *Lomis hirta* (Lamarck) (Crustacea: Decapoda) and a discussion of its systematic position and phylogeny. – Austral. J. Zool. **13** (1965) 545–557.

POHLE, G.: Gill and embryo grooming in lithodid crabs: Comparative functional morphology based on *Lithodes maja.* In: functional morphology of feeding and grooming in crustacea. Ed. by FELGENHAUER, B. E., L. WATLING, and A. B. THISTLE. Balkema, Rotterdam. 1989, 75–94.

PROVENZANO, A. J. Jr. and A. L. RICE: Juvenile morphology and the development of taxonomic characters in *Paguristes sericeus* A. Milne-Edwards (Decapoda, Diogenidae). – Crustaceana **10** (1966) 53–69.

PRZIBAM, H.: Differenzierung des Abdomens enthäuster Einsiedlerkrebse. – Arch. Entw. Mech. **23** (1907) 245–261.

REESE, E. S. Shell use: an adaptation for emigration from the sea by the coconut crab. – Science **161** (1968) 385–386.

REMANE. A.: Die Grundlagen des natürlichen Systems, der vergleichenden Anatomie und der Phylogenetik. Akademische Verlagsgesellschaft Geest & Portig, Leipzig 1952.

RIEDL, R.: Die Ordnung des Lebendigen. Systembedingungen der Evolution. Parey. Hamburg, 1975.

RIEGER, R., and S. TYLER: Das Homologietheorem in der Ultrastrukturforschung. In: Evolution, Ordnung und Erkenntnis. Ed. by OTT, J. A., G. P. WAGNER and F. M. WUKETITS. Parey, Hamburg. 1985, 21–36.

SAINT LAURENT, M. DE: Sur la famille Parapaguridae Smith, 1882. Description de *Typhlopagurus foresti* gen. nov., sp. nov., et de quinze espèces ou sous-espèces nouvelles de *Parapagurus* Smith (Crustacea, Decapoda). – Bijdr. Dierkd. **42** (1972) 97–123.

SCHOLTZ, G.: Teloblasts in decapod embryos: an embryonic character reveals the monophyletic origin of freshwater crayfishes (Crustacea, Decapoda). – Zool. Anz. **230** (1993) 45–54.

SCHOLTZ, G. and S. RICHTER: Phylogenetic systematics of the Decapoda Reptantia (Crustacea, Malacostraca). – Zool. J. Linn. Soc. (1994) (in press.).

SNOW, P. J.: Surface structures of the antennular flagella of the hermit crab *Pagurus alaskensis* (Benedict): a light and scanning electron microscopy study. – J. Morphol. **44** (1974) 195–216.

STIASSNY, M. L. J.: Atavisms, phylogenetic character reversals, and the origin of evolutionary novelties. – Neth. J. Zool. **42** (1992) 260–276.

TUDGE, C. C.: Spermatophore diversity within and among the hermit crab families, Coenobitidae, Diogenidae, and Paguridae (Paguroidea, Anomura, Decapoda). – Biol. Bull. **181** (1991) 238–247.

–: Comparative ultrastructure of hermit crab spermatozoa (Decapoda: Anomura: Paguroidea). – J. Crust. Biol. **12** (1992) 397–409.

WATROUS, L. E., and Q. D. WHEELER: The outgroup comparison method of character analysis. – Syst. Zool. **30** (1981) 1–11.

WOLFF, T.: Description of a remarkable deep-sea hermit crab, with notes on the evolution of the Paguridea. – Galathea Rep. **4** (1961) 11–32.

STEFAN RICHTER and GERHARD SCHOLTZ, Institut für Zoologie, Freie Universität Berlin, Königin-Luise-Str. 1–3, D-14195 Berlin, Germany.