# Evolutionary trends and ecology of Mesozoic decapod crustaceans

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ABSTRACT: The fossil record of unquestionable decapod remains dates back to Permo-Triassic times. Evaluation of all available data from the fossil record, trace fossils and facies reveals various trends within the evolution of Mesozoic decapods, and its relation to their ecology. One of these trends is the protection of the long vulnerable abdomen. The most successful method, gradual reduction and inflection of the abdomen against the ventral cephalothorax, led to the Brachyura. Brachyurans exhibit the broadest spectrum of habitat adaptions.

KEY WORDS: Anomura, Astacidea, Brachyura, burrows, coprolites, Decapoda, Dromioidea, ecology, evolution, fossil record, Homolodromioidea, Mesozoic, Palinura, Penaeoidea, taphonomy.
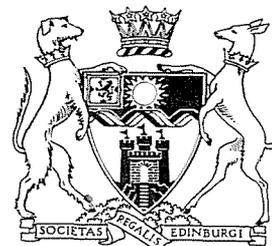
Fossil decapod crustaceans play a minor role in the geosciences. They are of little practical use in stratigraphy but provide valuable information for palaeoecological studies.

1. Taphonomy

Remains of decapods are infrequently represented in the fossil record, because several processes decreased their preservational potential. Crustacean cuticles—even in strongly calcified parts of the skeleton such as the chelae—contain a significant amount of organic material. If not eaten by other predators, skeletons rapidly decompose after death. Furthermore the integument disintegrates by microbiological processes. In tropical climates even strongly calcified shells become friable within a few days and are destroyed by wave action if they are not buried quickly.

Weakly calcified forms, such as most swimming shrimps (Penaeoidea, Caridea), are even less likely to be preserved. Thus natantian decapods are rather rare. Most of them occur in unusual deposits only: well bedded aphanitic black shales, rich in organic matter, or in sublithographic limestones like those at Holzmaden, Solnhofen, Lebanon or Bolca.

In these deposits the specimens are often unusually well preserved, even nearly complete, but strongly compressed. The completeness may be due to the absence of scavengers and bottom-dwelling organisms, to anaerobic conditions at the bottom, and to quiet sedimentation in a low-energy environment. Taphonomic analyses of such fossil assemblages show that they are death assemblages (thanatocoenoses). Swimming forms usually predominate. Reptant bottom-dwellers are absent or under-represented.

Similarly, among reptants, those species are favoured in the fossil record that lived in areas of quiet sedimentation in low-energy environments. Most remains occur in fine-grained, off-shore sediments, often in calcareous or phosphatic nodules as nearly complete, undeformed and well preserved individuals. Inhabitants of the littoral and sublittoral zones, of rock shelters or reefs—the favoured environments in which most of the decapods live today and

probably have lived in the past—are much scarcer. Some are completely absent from the fossil record, like the anomuran Hippoidea. In such high-energy environments, where sediments are frequently reworked, only the most resistant parts, such as claws or tips of fingers survive microbiotic processes, transport and reworking. In many cases, however, the fossil evidence of decapods is indirectly indicated by their life activities.

The most common trace fossils are burrows. They can be definitely identified when they contain remains of the burrower. Such burrows are combinations of horizontal, inclined and vertical tubes with Y-shaped branchings (Fig. 1). They are regarded as one of the most reliable environmental indicators among trace fossils. Taxonomic criteria are based upon a variety of features including burrow configuration or modes of wall construction. The known modern analogues which include not only various species of *Callianassa*, but also certain species of *Upogebia* and possibly of *Axius*, show that each producer has its own peculiar range of habits and habitats. Each occurrence must be evaluated independently to be a valuable aid in environmental and phyletic interpretion.

The same applies to all other types of burrows produced by various species of shrimps, lobsters or crabs (Frey *et al.* 1984), or to coprolites, another common trace fossil attributed to decapods. Based on the arrangement, outline, and number of longitudinal canals which pierce fecal pellets of modern analogues (Fig. 1), they have been assigned to anomuran shrimps (Brönnimann 1972). New finds of producer-pellet-associations (Förster & Hillebrandt 1984) show however, that the Glypheoidea must be included in the group of potential producers.

2. Ecology and evolution

Evaluation of all data—fossil record, trace fossils, and facies—reveals some interesting trends within the evolution of Mesozoic decapods, their ecology and some relations between ecology and evolution.

The fossil record of unquestionable decapods dates back to the Permo-Triassic, probably to the Early Triassic (Birshtein 1958; Besairie & Collignon 1960). This may be an accidental coincidence with the so-called Permo-Triassic marine faunal crisis (Schopf 1974; Hüssner 1983). Indeed, the rate of origination during the Early Triassic is extraordinarily high in the decapods, comparable to that of many other new taxa of invertebrates during this time. On the other hand the Palaeozoic record of possible decapods is rather sparse. These few records from the Upper Permian Zechstein (Bachmayer & Malzahn 1983), from the Upper Mississippian (Schram & Mapes 1984) and from the Late Devonian (Schram et al. 1978) remain ambiguous until their suggested decapod affinities can be verified and possible adaptive convergences can be excluded on the basis of more and better preserved material.

According to the palaeoenvironment of the better known Triassic decapod communities, nearshore or perhaps even brackish or deltaic fresh water environments seem to have been the primordial biotope. Moreover, the two oldest known specimens, from western Siberia and northern Madagascar, give evidence that the two suborders of the Decapoda, the swimming dendobranchiate 'Natantia', and the bottom-dwelling pleocyemate 'Reptantia' were separate at this time. The swimming Penaeoidea are regarded as the most conservative decapods (Kaestner 1967). They show no significant morphological changes since their first fossil record, whereas, in the Reptantia, an abundance of forms evolved, living in various habits and habitats from the deep sea to the supralittoral. Some are even adapted for terrestrial life.

Within the reptantian decapods the record of two of the four living infraorders dates from the Triassic: the Astacidea and the Palinura (lobsters and spiny lobsters; Förster & Crane 1984). A Triassic origin can be assumed for the third infraorder Anomura by an indirect ichnological record. Only the short-tailed Brachyura, the most successful infraorder with more than 640 living genera, dates back to Early Jurassic times. Their adaptive radiation which led to an extensive exploitation of various habitats undoubtedly lies in the compact morphology of their carapaces after a progressive reduction of the abdomen (Fig. 2).

All natantians as well as all ancestral reptantian tribes, which means all Triassic decapods (Förster 1967), have, among other ancestral features, a long abdomen. On this account they were formerly included in the Macrura. In all macruran natantians the appendages of the abdomen, the
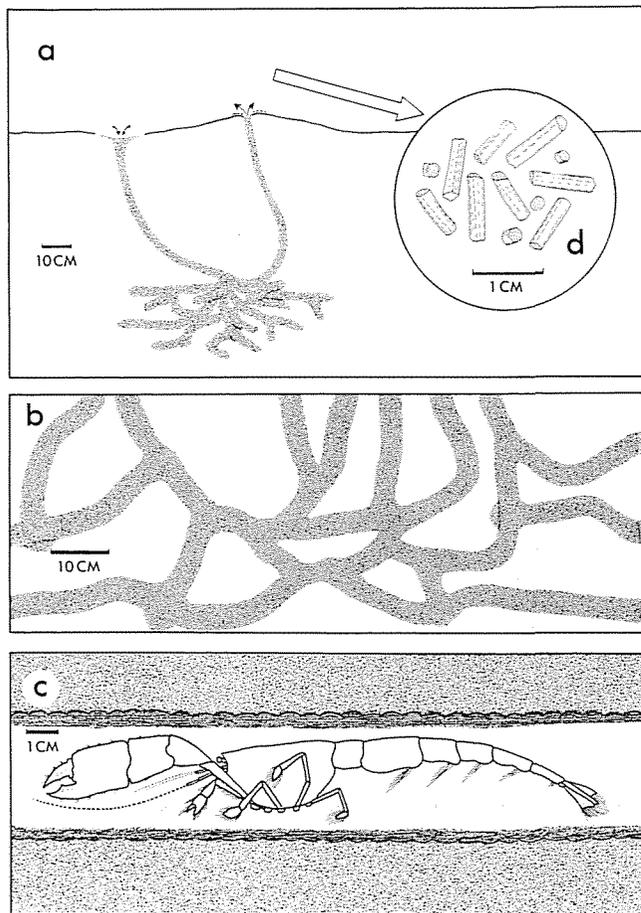

Figure 1 Burrow complex of *Callianassa* (compiled from Weimer & Hoyt 1964, Frey et al. 1978);
(a) Burrow complex showing burrow openings for water circulation; exit surrounded by fecal pellets.
(b) Burrow complex with Y-shaped branchings of tubes from the Santonian of northwestern Germany.
(c) Cross-section of tunnel with *Callianassa* showing concentrically laminated, cemented walls to prevent burrow from caving. Interior of the burrow smooth, exterior of wall irregular, diffuse or with a knobby surface because of a layer of cemented mud pellets.
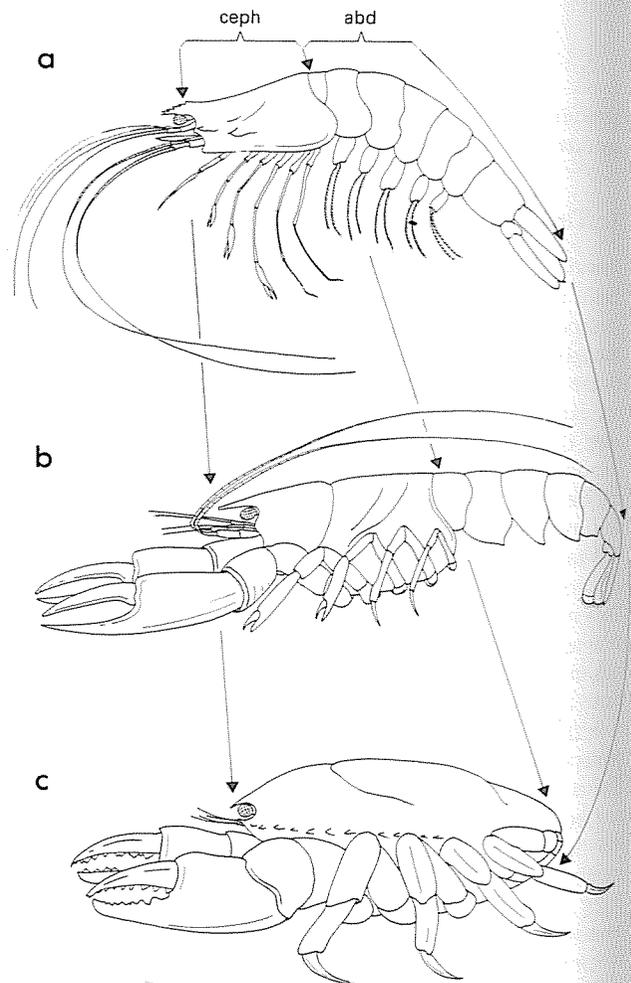(d) Fecal pellets with longitudinal canals.

Figure 2 Reduction of the abdomen in Decapoda (drawing modified from Glaessner 1969).
(a) Swimming natantian penaeoid; locomotion by abdominal appendages (pleopods) (*Penaeus*).
(b) Bottom-dwelling reptantian astacid with thoracopod walking legs (*Eryma*).
(c) Short-tailed crab, abdomen inflexed against sternum (*Carcinus*); ceph cephalothorax, abd abdomen.
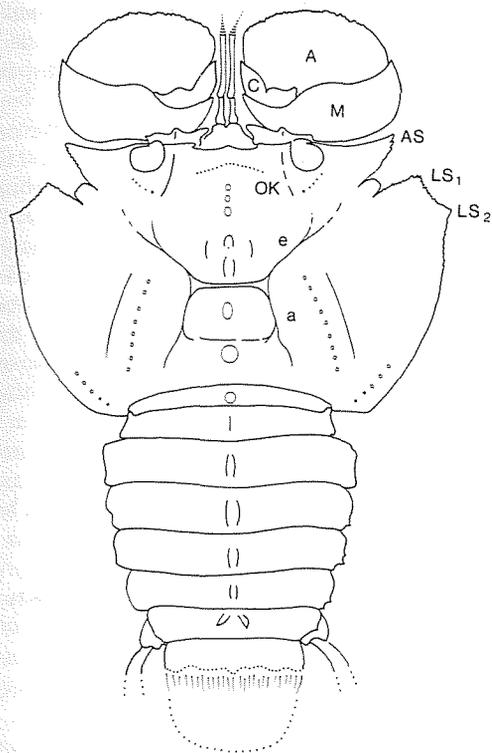
Figure 3 Depressiform Scyllaridae; carapace dorsoventrally compressed, wider than long. Antennae modified for burrowing with enlarged and shovel-like flattened segments. *Palibacus praecursor* (Dames) from the Cenomanian of Lebanon (Förster 1984); A antennal plate, modified flagellum, C & M carpocerite and merocerite of antennae, OK orbital ridge, AS anterolateral spine, LS₁ and LS₂ anterior and posterior lateral spines, e cervical groove, a branchiocardiac groove.

pleopods, are well-developed swimming paddles for locomotion. The remaining bottom-dwelling reptantians developed thoracopod walking legs, though most of them were able to swim backwards over short distances as an escape reaction. This was effected by a sudden flexure of the abdomen against the ventral surface of the cephalothorax.

For the more strongly calcified, slow-moving bottom-dwellers, the long abdomen was merely a disadvantage for all faster locomotion. In the Palinura, which are dominant in the Early Mesozoic record, various evolutionary trends can be recognised to protect this most vulnerable part of the body, always in close relationship to the mode of life under different environmental conditions.

One of the first steps in this direction was a change in life habit to soft muddy bottoms in quiet water areas below wave base. Primarily to seek shelter, burial in loose sediments would have been advantageous, particularly for the vulnerable soft-shelled phase after moulting. The gradual change to living in semi-permanent burrows and finally in permanent dwelling structures may have permitted a gradual reduction of the calcification of the integument, for example in the Mecochiridae. Additionally, the abdominal pleura were gradually lost, as in the Thalassinoidea.

Another most successful trend, in which the abdomen became concealed in gastropod shells, led to the Paguroidea—the hermit crabs with more than 65 living genera. Pagurids exhibit a broad spectrum of habitat adaptations. They live in marine, brackish and fresh waters, as well as in terrestrial environments (Coenobitidae; *Birgus*, the palm crab). In Paguroidea and in Thalassinoidea only the more calcified parts, usually the chelae, have been preserved. Such claws are known since the Early Liassic. A much older (at least Middle Triassic) age of origin can be assumed for the Thalassinoidea on the grounds of their life activities.
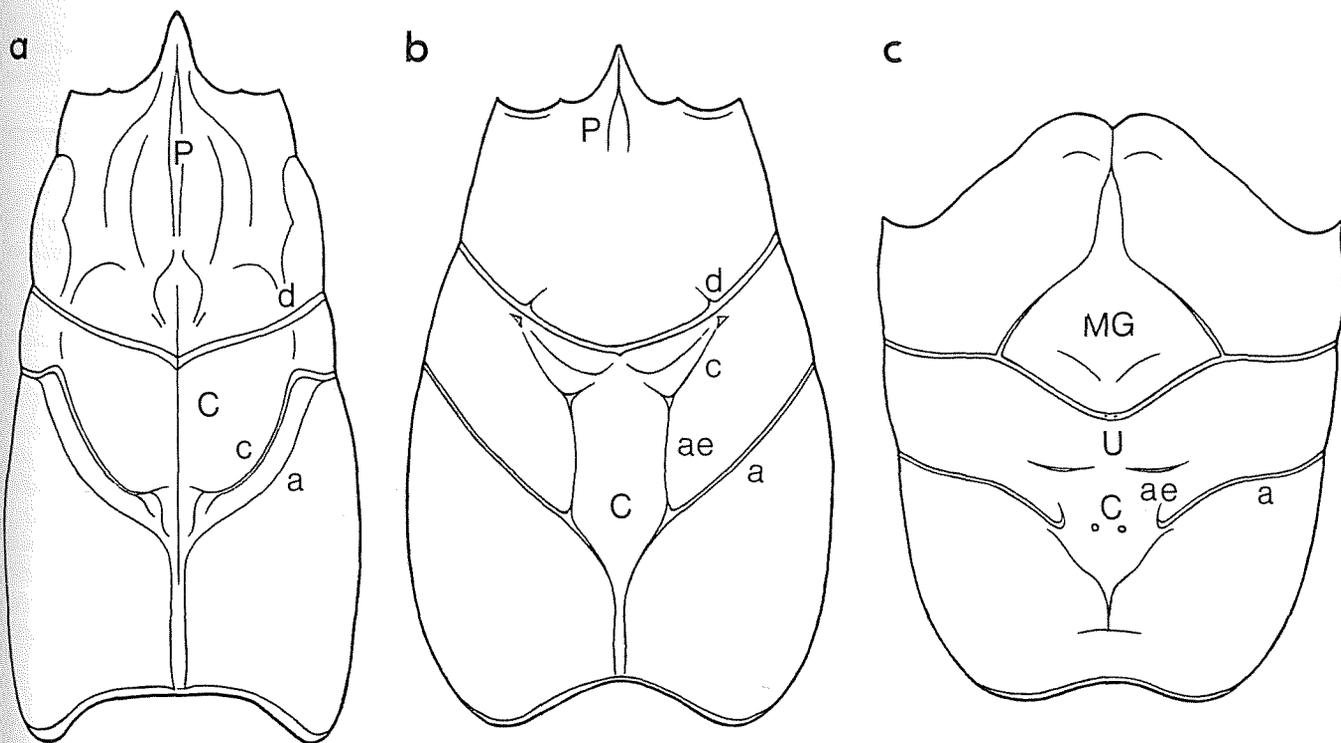

Figure 4 Dorsal views of carapaces: a Triassic *Pseudopemphix*, b Liassic *Eocarcinus*, c Upper Jurassic *Pithonoton*. Note reduction of ridges of the anterior part, reduction of postcervical groove c, the development of a distinct lateral gastrocardiac marking ae, and of a distinct urogastric region U. C cardiac region, Mg mesogastric region, P spindle-shaped median plate, a branchiocardiac groove, d gastroorbital groove (Förster 1979).
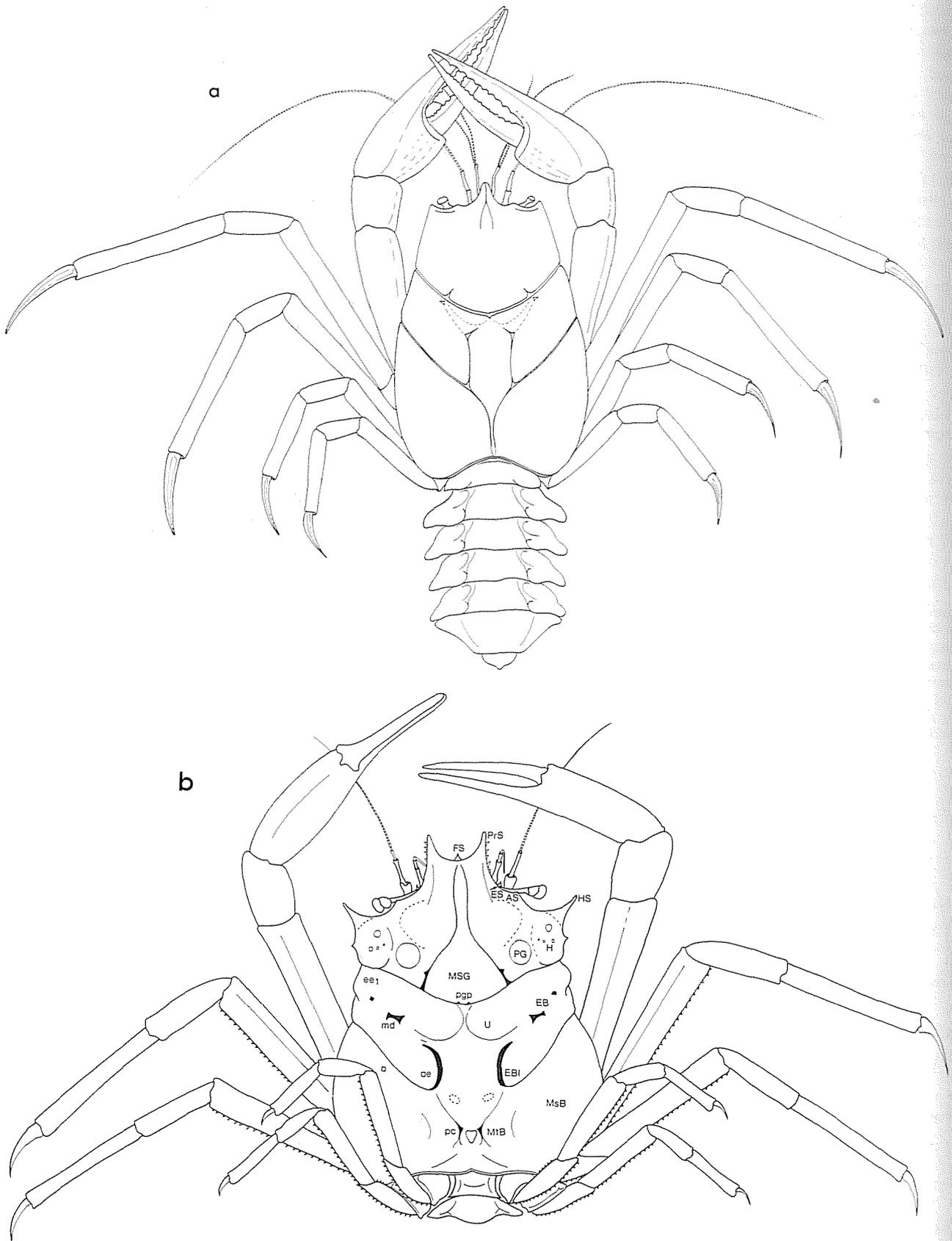
Figure 5 Reconstruction of (a) *Eocarcinus praecursor* Withers and the homolodromiid crab (b) *Antarctidromia inflata* Förster, showing the progressive reduction of the abdomen and its inflexion against the sternum. As a consequence of the inflexion there was a lack of space around the last two thoracic somites in the early stages of the evolution of the Brachyura. For this reason, the last two thoracopods were shifted dorsally and reduced in size (Förster *et al.* 1985). A branchiocardiac groove, ae lateral gastrocardiac marking, AS antennal spine, ee₁ cervical groove, EB epibranchial region, EBl epibranchial lobe, ES exorbital tooth, FS frontal spine, H hepatic lobe, HS hepatic spine, md median dorsoventral muscle marking. MsG mesogastric lobe. MsB mesobranchial region, MtB metabranchial region, pc posterior cardiac marking, PG protogastric lobe, pgp posterior gastric pits, PrS preorbital spine, U urogastric region.

Alternatively, only the appendages became modified for rapid burrowing in loose sediments, or the formerly subcylindrical cephalothorax became depressiform as in the Eryonoidea, the Scyllaridae or in the anomuran Galatheoidea. The abdomen was slightly reduced in length and the tail fan was inflected against the abdominal segments (Scyllaridae, Galatheoidea). In the Scyllaridae, the antennae have been drastically modified. Initially the annulated flaggellum was reduced and widened as in *Cancrinos* from the Solnhofen Limestone. Finally, the antennae consisted of four moveable segments only (Fig. 3), the second and fourth of which are enlarged and flattened as shovels, such as in the Cenomanian *Palibacus* (Förster 1984), and in all Recent Scyllaridae.

The most successful evolutionary trend, however, was a progressive reduction of the long abdomen, which greatly hindered all faster locomotion, and the inflexion of the reduced abdomen against the sternum. This was realised in some crab-like anomurans (Porcellanidae) and in the Brachyura. The earliest fossil record of the Brachyura, *Eocarcinus praecursor* Withers from near-shore deposits of the Lower Liassic, connects the Triassic Palinura with the Late Jurassic Prosopidae (Förster 1979). *Eocarcinus* still has a subcylindrical cephalothorax like Triassic Palinura, but it shows a transitional pattern of grooves (Fig. 4). The abdomen is already reduced in length. The seventh segment is a small triangular plate. A tail fan is missing. The two last walking legs are reduced in size but they are not shifted to a subdorsal position as in the prosopids (Fig. 5). It seems that the long span of the Early and Middle Jurassic, more than 30 million years, was necessary for this new tribe to consolidate its organisation on the level of the Homolodromiinae, the most primitive crabs.

It was not mere coincidence that the explosive adaptive radiation of the new short-tailed crab-like type took place in the Late Jurassic. The worldwide vast expanse of shelf seas with the expansion of redundant bioherms after the Callovian transgression offered various new ecological niches and led to the rapid diversification in the prosopids.

Quite by contrast a new major rapid environmental change, caused by the worldwide Late Jurassic–Early Cretaceous regression, led to increased competition for space and food. Crabs as superior competitors for the available resources easily outcompeted the long-tailed reptantian macrurans. During this process, many macrurans, and even many ancestral prosopids, had to shift their ecologic niches. One such new niche was the fresh water into which members of the Late Jurassic *Pseudastacus* group migrated, the ancestors of the crayfish. Another environment exploited successful by macrurans was the deeper water. Well known examples of such a migration to the deep sea are the Eryonoidea, many Astacidea and Homolodromiinae.

Other groups, such as the ancestral astacid Erymidae or most Glypheoidea, became extinct. The Erymidae show almost no change in their groove pattern from the oldest known reptantian, *Protoclytiopsis antiqua* Birshtein from the Permo-Triassic to the last members of the genus *Eryma* from the Hauterivian, a period of more than 100 million years (Förster 1966). The last fossil record of the other dominating family, the Glypheoidea, was from the Eocene London Clay. The recently discovered *Neoglyphea inopinata* Forest & Saint Laurent (1976) from the South China Sea, at a depth of 200 m, makes it likely that additional members of extinct decapod groups may have survived in the deep sea. *Neoglyphea* is a mud dweller with a weakly calcified integument, comparable to the Mesozoic *Mecochirus*.

The most successful of all decapod groups, not only in terms of numbers of Recent genera but also in terms of numbers of exploited ecologic niches, are the crabs. Their compact and tight carapace, their broad spectrum of habitat adaptions, their ability to walk, run, climb, swim, burrow or incorporate camouflage (Warner 1977) enabled them to colonize niches from the abyssal deep sea to the littoral and supralittoral, from normal marine to brackish and fresh waters. In the Late Tertiary they even became adapted for terrestrial life in tropical regions.

The primitive Homolodromioidea had their maximum diversity in the Late Jurassic. Dromioidea and Homoloidea can be regarded as their successors, until the worldwide Late Cretaceous expansion of widespread bioherms made possible a new adaptive radiation of more advanced brachyurans such as the Xanthidae. In sandy substrates of nearshore environments, the sand-dwelling archaeobrachyuran Raninoidea and the heterotremate Calappoidea appeared in the Early Cretaceous and showed a remarkable diversity.

Thus, the evolution of the Mesozoic macruran decapods can be viewed as a continual search for shelter which was indispensible for survival. The most successful evolutionary trend, with an exploitation of the broadest spectrum of habitat adaptions, led to the short-tailed crabs.

3. References

Bachmayer, F. & Malzahn, E. 1983. Der erste Nachweis eines dekapoden Krebses im niederrheinischen Kupferschiefer. ANN NAT HIST MUS WIEN **85A**, 99–106.

Besairie, H. & Collignon, M. 1960. Madagascar (Supplement). *Lexique Stratigraphique International*, Vol. IV *Afrique*, Fasc. 11. Paris: Congrès Géologique International.

Birshtein, Y. A. 1958. Drevneishii predstavital otryada desyatinogikh rakoobraznikh, *Protoclytiopsis antiqua*, iz Permakikh otlozhenii zapadnoi Sibiri. DOKL AKAD NAUK SSSR **122**, 477–80.

Brönnimann, P. 1972. Remarks on the classification of fossil Anomuran coprolites. PALAEONTOL Z **46**, 99–103.

Förster, R. 1966. Über die Erymiden, eine alte konservative Familie der mesozoischen Dekapoden. PALAEONTOGRAPHICA **125**, 61–175.

Förster, R. 1967. Die reptanten Dekapoden der Trias. NEUES JAHRB GEOL PALAEONTOL ABH **128**, 136–94.

Förster, R. 1979. *Eocarcinus praecursor* Withers (Decapoda, Brachyura) from the Lower Pliensbachian of Yorkshire and the early crabs. NEUES JAHRB PALAEONTOL MONATSH **1979**, 15–27.

Förster, R. 1984. Bärenkrebse (Crustacea, Decapoda) aus dem Cenoman des Libanon und dem Eozän Italiens. MITT BAYERISCHE STAATSSAMML PALAEONTOL HIST GEOL **24**, 57–66.

Förster, R. & Crane, M. D. 1984. A new species of the penaeid shrimp *Aeger* Münster (Crustacea, Decapoda) from the Upper Triassic of Somerset, England. NEUES JAHRB GEOL PALAEONTOL MONATSH **1984**, 455–62.

Förster, R., Gazdzicki, A. & Wrona, R. 1985. First record of homolodromiid crab from a Lower Miocene glacio-marine sequence of West Antarctica. NEUES JAHRB GEOL PALAEONTOL MONATSH **1985**, 340–48.

Förster, R. & Hillebrandt, A. v. 1984. Das Kimmeridge des Profeta-Jura in Nordchile mit einer *Mecochirus–Favreina*–Vergesellschaftung (Crustacea, Decapoda–Ichnogenus). MITT BAYERISCHE STAATSSAMML PALAEONTOL HIST GEOL **24**, 67–87.

Forest, J. & Saint Laurent, M. de 1981. La morphologie externe de *Neoglyphea inopinata*, espèce actuelle de Crustacé Décapode Glyphéide. In *Résultats des Campagnes MUSORSTOM*, I. Philippines, vol. 1, 2. MEM ORSTOM **91**, 51–84.

Frey, R. W., Curran, H. A. & Pemberton, S. G. 1984. Tracemaking activities of crabs and their environmental significance: the ichnogenus *Psilonichnus*. J. PALEONTOL **58**, 333–50.

Frey, R. W., Howard, J. D. & Pryor, W. A. 1978. *Ophiomorpha:* its morphologic, taxonomic, and environmental significance. PALAEOGEOGR PALAEOCLIM PALAEOECOL **23,** 199–229.

Glaessner, M. F. 1969. Decapoda. In *Treatise on Invertebrate Paleontology*, Part R, Arthropoda 4, 399–533. Lawrence, Kansas: Geol. Soc. Am. & Univ. Kansas Press.

Hüssner, H. 1983. Die Faunenwende Perm/Trias. GEOL RUNDSCH **72,** 1–22.

Kaestner, A. 1967. *Lehrbuch der Speziellen Zoologie*, Bd.I.: *Wirbellose* 2. Teil *Crustacea*, 849–1242. Stuttgart: Fischer.

Schopf, T. J. M. 1974. Permo-Triassic extinctions: Relation to sea-floor spreading. J GEOL **82,** 129–43.

Schram, F. R., Feldmann, R. M. & Copeland, M. J. 1978. The Late Devonian Palaeopalaemonidae and the earliest decapod crustaceans. J PALEONTOL **52,** 1375–87.

Schram, F. R. & Mapes, R. H. 1984. *Imocaris tuberculata,* n.gen., n.sp. (Crustacea: Decapoda) from the upper Mississippian Imo Formation, Arkansas. TRANS SAN DIEGO SOC NAT HIST **20,** 165–8.

Warner, G. F. 1977. *The Biology of Crabs*. New York: Van Nostrand-Reinhold.

Weimer, R. J. & Hoyt. J. H. 1964. Burrows of *Callianassa major* Say, geologic indicators of littoral and shallow neritic environments. J PALEONTOL **38,** 761–7.

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