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Phylogenetic systematics of the reptantian Decapoda (Crustacea, Malacostraca)

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Although the biology of the reptantian Decapoda has been much studied, the last comprehensive review of reptantian systematics was published more than 80 years ago. We have used cladistic methods to reconstruct the phylogenetic system of the reptantian Decapoda. We can show that the Reptantia represent a monophyletic taxon. The classical groups, the 'Palinura', 'Astacura' and 'Anomura' are paraphyletic assemblages. The Polychelida is the sister-group of all other reptantians. The Astacida is not closely related to the Homarida, but is part of a large monophyletic taxon which also includes the Thalassinida, Anomala and Brachyura. The Anomala and Brachyura are sister-groups and the Thalassinida is the sister-group of both of them. Based on our reconstruction of the sister-group relationships within the Reptantia, we discuss alternative hypotheses of reptantian interrelationships, the systematic position of the Reptantia within the decapods, and draw some conclusions concerning the habits and appearance of the reptantian stem species.

ADDITIONAL KEY WORDS:—Palinura – Astacura – Anomura – Brachyura – monophyletic – paraphyletic – cladistics.

CONTENTS

INTRODUCTION

Decapods, and reptantians in particular, are the best known crustaceans in that crabs, crayfishes, and lobsters represent 'typical' crustaceans to many people

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and have significant economic importance. Many reptantian species are common laboratory animals and their physiology, morphology and behaviour have been well investigated. Body form and habits are diverse, from lobsters with a well developed pleon to crabs with a ventrally folded reduced pleon, and from deep sea bottom dwellers to burrowing filter feeders, shell inhabitants and pelagic swimmers. Against this background it is surprising that in the last 85 years so little attention has been paid to the phylogenetic relationships of the reptantian decapods, although several recent systematic studies have been undertaken for 'natant' decapods (Burkenroad, 1963, 1981; Felgenhauer & Abele, 1983; Abele & Felgenhauer, 1986; Christoffersen, 1988a; Kim & Abele, 1990; Abele, 1991). These show that the 'Natantia' of Boas (1880) do not represent a monophyletic taxon. The most recent work on reptantians, however, is limited to some classificatory listings (de Saint Laurent, 1979b; Bowman & Abele, 1982; Abele, 1983; Schram, 1986). The classical investigations of Boas (1880), Ortmann (1896) and Borradaile (1907) are still the main source of reptantian systematics for researchers and textbooks (e.g. Balss, 1957; Kaestner, 1967, 1970; McLaughlin, 1980; Barnes, 1987). However, the systematic position of several taxa has been the subject of controversy since then. Contentious matters concern the inclusion of polychelids in the Palinura (Borradaile, 1907; Burkenroad, 1981; Abele, 1991); the systematic position of the thalassinids, whose monophyletic status has been doubted (Gurney, 1942; de Saint Laurent, 1973) and which have been placed within the 'Anomura' (e.g. Borradaile, 1907; Martin & Abele, 1986) or excluded from them (e.g. Burkenroad, 1963, 1981; Kaestner, 1970); and the question of the relationships of the dromiaceans to the Brachyura (e.g. Gurney, 1942; Guinot, 1978, 1979; de Saint Laurent, 1979b, 1980a; Rice, 1983; Williamson, 1988; Martin, 1991; Jamieson, 1991; Abele, 1991; Spears, Abele & Kim, 1992). The monophyly of the Reptantia has also been questioned (Beurlen & Glaessner, 1930; Felgenhauer & Abele, 1983; Abele, 1991), and others include the Stenopodidea within the reptantians (Gurney, 1942; de Saint Laurent, 1979b). This situation led Schram (1986) to declare that the systematics of the Reptantia was a "morass" and that a phylogenetic analysis of the group as a whole is badly needed.

We present here the phylogenetic systematics of the reptantian Decapoda, reconstructed for the first time according to the methods of Hennig (1950, 1966). Our analysis reveals a monophyletic origin of the Reptantia and that the classical groups 'Palinura', 'Astacura', and 'Anomura' represent paraphyletic assemblages which should be abandoned within a phylogenetic system. The systematic position of the freshwater crayfishes remains uncertain.

MATERIAL AND METHODS

Techniques and animals

We examined specimens from our own collections and from the Museum für Naturkunde, Berlin; Zoologische Staatssammlung, Munich; Zoologisk Museum, Copenhagen; Smithsonian Institution, Washington; and Sammlung des Instituts für Zoologie der Freien Universität, Berlin. The morphological investigations and photography were done with dissecting microscopes (ROW and Wild M5), microscope (Zeiss Axiophot), and a scanning electron microscope (SEM) (Philips). Whole animals were photographed with an Olympus camera (OM2). Some dissected specimens were treated with KOH to remove all soft parts. For SEM studies, specimens or parts of them were dehydrated in an ethanol series, transferred to acetone, and cleaned by sonification. After critical point or air drying, preparations were gold-coated. We also used data from the literature. Where possible, we confirmed existing descriptions by reference to our own material.

We examined the following reptantian species:

Polychelida: *Polycheles typhlops* Heller, 1862

Achelata: *Palinurellus gundlachi* von Martens, 1878, *Palinurus versicolor* (Latreille, 1804), *Scyllarus arctus* (Linnaeus, 1758), *Ibacus peronii* Leach, 1815

Homarida: *Homarus gammarus* (Linnaeus, 1758), *Homarus americanus* H. Milne Edwards, 1837, *Nephrops norvegicus* (Linnaeus, 1758), *Nephropsis stewarti* Wood-Mason, 1872, *Thaumastocheles zaleucus* (Thomson, 1873), *Enoplometopus debelius* Holthuis, 1983

Astacida: *Astacus leptodactylus* Eschscholz, 1823, *Orconectes limosus* (Rafinesque, 1817), *Cherax destructor* Clark, 1936

Thalassinida: *Callianassa australiensis* (Dana, 1852), *Calocaris macandreae* Bell, 1846, *Axius gundlachi* (von Martens, 1872), *Axius stirhynchus* Leach, 1815, *Upogebia pusilla* (Petagna, 1792), *Jaxea nocturna* Nardo, 1847, *Thalassina anomala* (Herbst, 1804)

Anomala: *Galathea intermedia* Lilljeborg, 1851, *Galathea squamifera* Leach, 1814, *Munida rugosa* (Fabricius, 1775), *Pisidia longicornis* (Linnaeus, 1767), *Petrolisthes lamarckii* (Leach, 1820), *Albunea symnista* (Linnaeus, 1766), *Emerita* sp., *Aegla* sp., *Birgus latro* (Linnaeus, 1767), *Lithodes maja* (Linnaeus, 1758), *Pagurus bernhardus* (Linnaeus, 1758), *Pylocheles miersi* Alcock & Anderson, 1898, *Pomatocheles jeffreysii* Miers, 1879, *Lomis hirta* (Lamarck, 1818)

Brachyura: *Homolodromia bouvieri* Doflein, 1904, *Homola barbata* (Fabricius, 1793), *Dromia personata* (Linnaeus, 1759), *Ranina ranina* (Linnaeus, 1758), *Medorippe lanata* (Linnaeus, 1767), *Hyas araneus* (Linnaeus, 1758), *Pilumnus hirtellus* (Linnaeus, 1761), *Xantho poressa* (Olivi, 1792), *Carcinus maenas* (Linnaeus, 1758)

Outgroup comparison

Phylogenetic studies by Burkenroad (1963, 1981), Abele & Felgenhauer (1986), Christoffersen (1988a), and Abele (1991) revealed convincingly that the 'Natantia' of Boas (1880), which comprise Dendrobranchiata, Caridea, and Stenopodidea, do not represent a monophyletic taxon. According to these authors, the Dendrobranchiata is the sister-group of the Pleocyemata which includes the Caridea, Stenopodidea and Reptantia. Apart from several other apomorphies (Christoffersen, 1988a), the pleocyemates are mainly unified by the apomorphic character of egg incubation on the pleopods (Burkenroad, 1963). For outgroup comparison (Watrous & Wheeler, 1981) we examined species of the Dendrobranchiata, Caridea and Stenopodidea, as well as data from the literature concerning these groups. Because of the paraphyly of the 'Natantia', characters that occur in all 'natantian' groups are regarded as plesiomorphic.

The following species were examined:

Dendrobranchiata: *Penaeus* sp., *Euricyonia* sp.
Caridea: *Macrobrachium novaehollandiae* (De Man, 1908), *Crangon crangon* (Linnaeus 1758), *Alpheus sublucanus* (Forsköl, 1775)
Stenopodidea: *Stenopus hispidus* (Olivier, 1811)

Taxon names and classification

As traditional classification causes fruitless debates concerning the ranking of taxa, we followed the lead given by Griffith (1973, 1976) and Ax (1987) and abandoned classificatory ranks in our phylogenetic analysis. To make this principle transparent we have chosen the ending -a for all monophyletic groups in our system. Apart from new names we also changed the endings of traditional names to -a in order to avoid the suggestion of any ranking (compare Burkenroad (1981) who changed the name Thalassinidae of Boas (1880) to Thalassinida).

RESULTS

The phylogenetic system of the reptantian Decapoda

The phylogenetic analysis presented results in the following system. The corresponding phylogenetic tree is depicted in Figure 1.

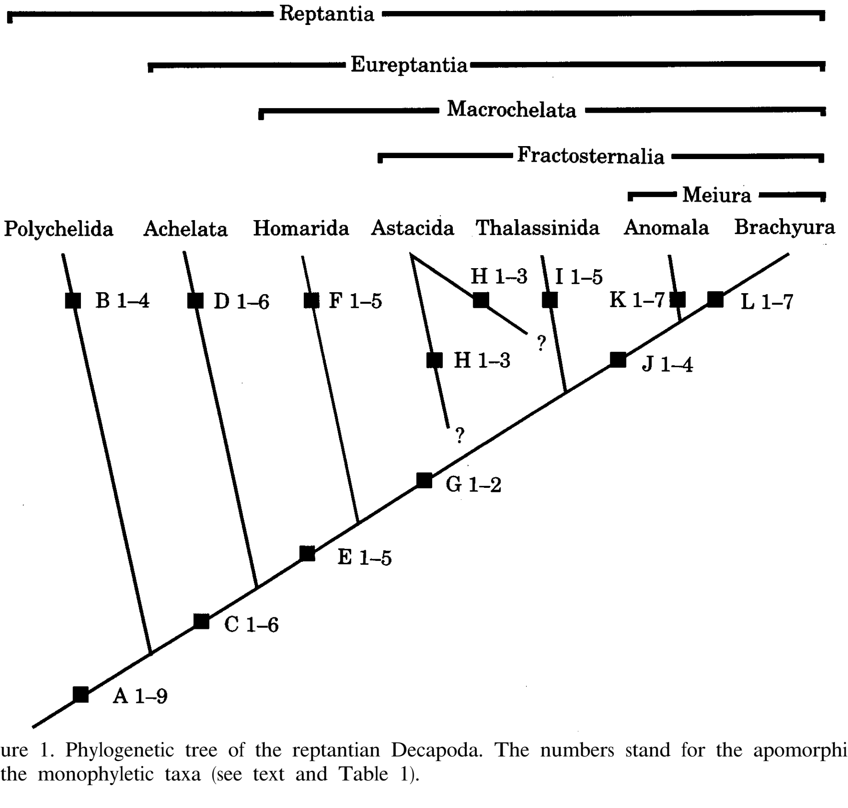

Figure 1. Phylogenetic tree of the reptantian Decapoda. The numbers stand for the apomorphies of the monophyletic taxa (see text and Table 1).

- Reptantia
  - Polychelida
  - Eureptantia *nov.*
    - Achelata *nov.*
    - Macrochelata *nov.*
      - Homarida
      - Fractosternalia *nov.*
        - Astacida *inc. sed.*
        - Thalassinida
        - Meiura *nov.*
          - Anomala
          - Brachyura

This phylogenetic system is based on the characters listed and discussed in the following paragraphs. A summary is given in Table 1.

Characters and taxa

Reptantia

The taxon Reptantia introduced by Boas (1880) is clearly monophyletic. Reptantians share a number of undoubtedly apomorphic characters (A1–9).

(1) The body, and the pleon in particular, is dorsoventrally flattened (depressed) (Fig. 2A). The laterally compressed body (pleon) of dendrobranchiates and carideans (Fig. 2A) is plesiomorphic.

(2) The exoskeleton is heavy and strongly calcified. Except for some thalassinids and the asymmetrical hermit crabs with soft cuticles, this is true for most reptantians. The original condition is a relatively soft cuticle like that of 'natant' decapods.

(3) The anterior articulation of the mandibles is formed by an elongated process of the molar region extending dorsally from the palp (Fig. 9). We found this process in polychelids and most Eureptantia (the thalassinid *Upogebia* is an exception (Fig. 9E)), but not in stenopodids (see also Bruce & Baba, 1973; Manning & Chace, 1990), dendrobranchiates (Fig. 9A), or carideans (see also Balss, 1940; Schram, 1986; Felgenhauer & Abele, 1989).

(4) The coxo-sternal joints of the pereiopods are articulated so that the legs move anteroposteriorly. This is true for all investigated species and is correlated with walking in the benthic reptantians. In dendrobranchiates, carideans and stenopodids the legs move in a more mediolateral direction, a motion that could be related to the plesiomorphic swimming habits of these forms.

(5) The fifth pereiopod is a specialized chelate or subchelate grooming appendage (Fig. 3). Restricted to females in polychelids, achelates and enoplometopodids (see also Holthuis, 1983), in the other taxa this character is shared by both sexes. Secondary reduction occurs in the Brachyura and freshwater crayfishes (Fig. 3) (see below). A chelate grooming appendage (5th pereiopod) was not found in any of the non-reptantian decapods (see also Bauer, 1981; 1989); we regard this lack of chelae as plesiomorphic.

(6) The 1st pleomere is shorter than the rest (Fig. 2A) and forms anterior lobes which overlap the posterior lateral margin of the carapace (Fig. 2A, B). In this way a stable connection between carapace and pleon is achieved with

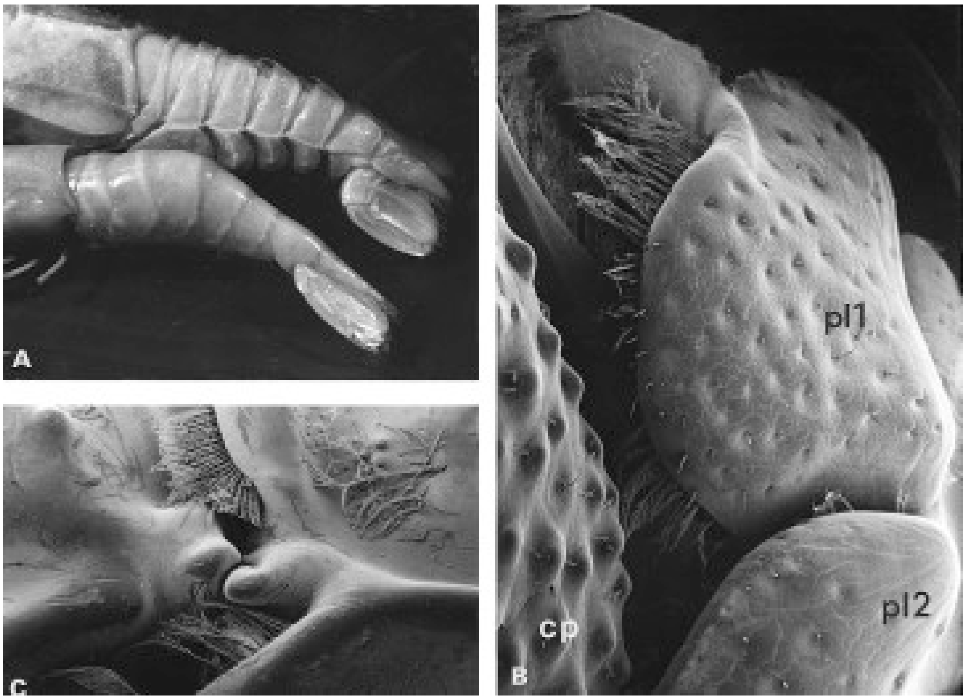

Figure 2. Reptantian characters. (A) Posterior part of the bodies of the caridean shrimp *Macrobrachium novaehollandiae* (below) and the reptantian *Polycheles typhlops* (above), showing the apomorphic flattened body, stronger cuticle and short 1st pleon segment with the lateral lobes of the Reptantia. Note that in both animals the 2nd pleonic pleuron is extended anteriorly and that both telsons are narrow and triangular. (B) Articulation between the posterior carapace margin (cp) and the overlapping lateral lobe of the 1st pleon segment (pl 1) of *Orconectes limosus* (anterior is left, dorsal is up). The pleuron of the 2nd pleomere (pl 2) is extended anteriorly. (SEM). (C) Mid-lateral hinge between 1st and 2nd pleon segment of *Polycheles* (anterior is left, dorsal is up). This type of articulation is plesiomorphic within decapods and corresponding hinges can be seen in the Dendrobranchiata. (SEM) (compare Fig. 13).

the lobes forming lateral joints. This device can be found on the 1st pleomere in most reptantians. The lateral overlapping lobes are somewhat reduced in several thalassinids (e.g. *Callianassa*) and lacking in some anomalans (hermit crabs, hippoids) and most Brachyura (vestiges of overlapping lobes were found in *Homola barbata*). These alterations can be related to the reduction of the pleon in these taxa and are obviously secondary, as can be concluded from the relationships within the Reptantia. The plesiomorphic condition is found in Dendrobranchiata and Caridea and is characterized by a relatively large 1st pleomere (Fig. 2A). Although in some groups the large pleura of the 1st pleomere do overlap the carapace (e.g. Crangonidae; see also Chase & Kensley, 1992), in no case is an articulation formed like that of reptantians. The 1st pleomere of some stenopodids (e.g. *Stenopus hispidus*) is somewhat reduced in size, but the pleura do not overlap the posterior carapace margin.

(7) The brain of reptantians is wider than long. This is due to the lateral orientation of the neuropil of the second antenna (Sandeman, Scholtz & Sandeman, 1993). Originally, the decapod brain is elongate, as in dendrobranchiates, carideans and stenopodids (Sandeman *et al.*, 1993).

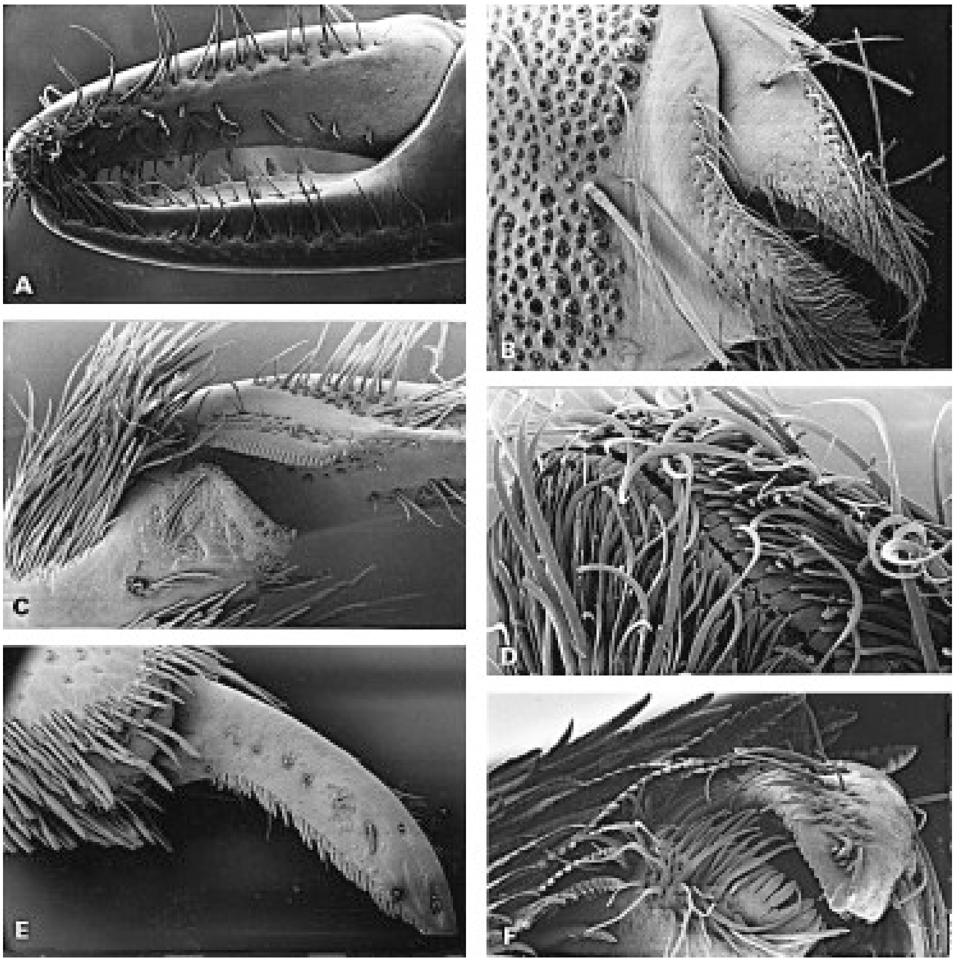

Figure 3. Propodus and dactylus of the 5th pereiopod of various reptantian species (SEM). (A) Polychelida, *Polycheles typhlops*. (B) Thalassinida, *Callianassa australiensis* (most setae have been removed). (C) Homarida, *Nephrops norvegicus*. (D) Anomala, *Munida rugosa*. (E) Astacida, *Cherax destructor*. (F) Thalassinida, *Axius gundlachi*.

(8) During copulation both partners lie oriented head-to-head with their ventral surfaces opposed, the male usually in the uppermost position (e.g. Herrick, 1895; Zehnder, 1934; Bott, 1940; Berry, 1970; Donaldson & Adams, 1989). In dendrobranchiates (e.g. de Saint-Brisson, 1985; Bauer, 1992), the carideans (e.g. Bauer, 1976; Boddeke, Bosschieter & Goudswaard, 1991) and stenopodids (Debelius, 1983), the partners are oriented perpendicularly to each other during copulation with the female usually uppermost. Nothing is known about the mating behaviour of polychelids, except that the shape of the spermatophore attached to the females of several species suggests a parallel mating position (own observations; Andrews, 1911).

(9) Reptantian spermatozoa bear characteristic nuclear arms not found in other decapods (for review see Jamieson, 1991; Felgenhauer & Abele, 1991). From a brief description by Andrews (1911), polychelid spermatozoa appear to be similar to those of other reptantians. We suggest that having spermatozoa

with three nuclear arms is the original condition in reptantian or at least eureptantian decapods, because this feature is found among achelates, homarids, astacids, thalassinids, anomalans and brachyurans (Koltzoff, 1906; Jamieson, 1991; Felgenhauer & Abele, 1991). Higher numbers seen in astacids, thalassinids and achelates (Jamieson, 1991) are apparently derived characters. One large acrosomal spike has been reported for dendrobranchiate and caridean sperms, whereas stenopodid sperms are devoid of spikes or arms (Burkenroad, 1981; Jamieson, 1991; Felgenhauer & Abele, 1991).

Polychelida

This name is derived from the term Polychelidae introduced in 1874 by Wood-Mason. All extant polychelids inhabit the deep sea. Their morphology and shape is similar (De Man, 1916; Boas, 1939; Barnard, 1950; Bernard, 1953) and they share the following derived characters (B1–4).

(1) Basis, ischium and merus of the 2nd to 5th pereiopods are fused. Whereas the fusion of basis and ischium seems to have been evolved independently several times within carideans and reptantians (Burkenroad, 1981; present investigation), the addition of the merus to the basis and ischium is an apomorphic character of polychelids.

(2) The 4th pereiopod bears true chelae in addition to the first three pereiopods. This is not found in any other decapod group, but in some hermit crabs a subchelate 4th pereiopod has been independently evolved.

(3) A pair of knob-like structures connects the first pleon segment and the carapace (Fig. 6A). The knobs are situated in the pleural area of the 1st pleomere on either side of the animal and fit into a socket on the inner side of the posterior margin of the carapace. There is no corresponding structure in any other decapod group, but achelates have a similar but apparently convergent character on the last thoracic segment (Fig. 6B) (see below).

(4) Additional evidence for the monophyly of the Polychelida is given by the characteristic eryoneicus larva with a spiny and inflated carapace (Bernard, 1953).

Eureptantia (new taxon)

The name Reptantia of Boas (1880) is combined with the Greek prefix *eu-*, meaning typical. This taxon is the sister-group of the Polychelida and comprises all other reptantian taxa. The Eureptantia is characterized by the following shared apomorphic characters (C1–6).

(1) The ischium of the 3rd maxilliped bears a comb-like row of strong teeth, the so-called crista dentata (Fig. 4). All 'natant' decapods and the polychelids (Fig. 4A) lack this character. We found the crista dentata in representatives of all eureptantian groups. Its absence in some achelates (e.g. *Scyllarus arctus*), thalassinids (e.g. *Callianassa australiensis*), anomalans and brachyurans (e.g. *Medorippe lanata*) must be considered as secondary, since most representatives of these taxa (even in the genus *Callianassa* (Lutze, 1938)) possess a crista dentata.

(2) The blunt-tipped dactylus of the 3rd maxilliped differs from those of the pereiopods (Fig. 21C). The plesiomorphic character found in all other decapod groups, including the polychelids, is a sharp-tipped dactylus which resembles the dactylus of the pereiopods.

(3) A distinct two-hinged articulation exists between propodus and carpus in the 1st pereiopod (cheliped). This second articulation is found not only in

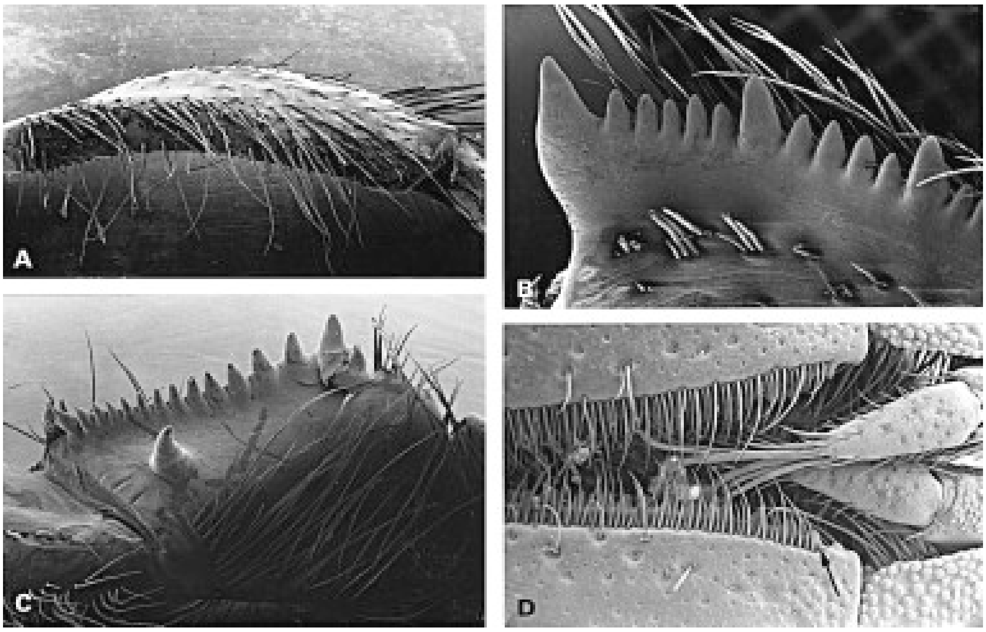

Figure 4. Ischium of the 3rd maxilliped of several reptantians. (SEM). (A) The plesiomorphic condition lacking a crista dentata (*Polycheles typhlops*). (B–D) Eureptantian representatives with an ischium of the 3rd maxilliped bearing the comb-like crista dentata. (B) Astacida, *Orconectes limosus*. (C) Anomala, *Pagurus bernhardus*. (D) Brachyura, *Xantho poressa* (arrow points to teeth of the crista dentata).

animals with large chelae, but also in the Achelata (e.g. *Palinurellus gundlachi*) and other species with a reduced chela (e.g. *Thalassina anomala* (Fig. 13E), *Neoglyphea inopinata* Forest & Saint Laurent, 1975 (Forest & de Saint Laurent, 1981)). There is only one propodus/carpus hinge in the polychelids, carideans, stenopodids and dendrobranchiates. The anterior segments of the 1st pereiopod are mobile in many directions (see also Burkenroad, 1981).

(4) The chelae or subchelae of the 5th pereiopod bear characteristic scale-like teeth (Fig. 3). This character is restricted to and found in almost all eureptantian groups (see also Bauer, 1989). In achelates and homarids, the tip of the dactylus is expanded and similar to those of the 4th leg (Fig. 3C) (see also Forest & de Saint Laurent (1981) for *Neoglyphea inopinata*). The tip of the dactylus has been reduced convergently within thalassinids and anomalans (Fig. 3B, D). Whereas in thalassinids only one side of the dactylus bears the scale-like teeth (this is plesiomorphic, compare Fig. 3A, C), in anomalans both sides of the dactylus are equipped with teeth. In the axiids we found species with an elongated tip (*Axius stirynchus*) and with a reduced tip (*Axius gundlachi* (Fig. 3F)). These teeth have been lost in brachyurans with the loss of the grooming function of the 5th pereiopod.

(5) The telson is wide with a more or less square shape and posteriorly rounded (Fig. 5). The original decapod telson is triangular and pointed posteriorly like that of the dendrobranchiates, carideans, stenopodids, and polychelids (Fig. 5A). A triangular telson also occurs within the Brachyura. However, this is usually relatively wide, and some taxa with many plesiomorphic

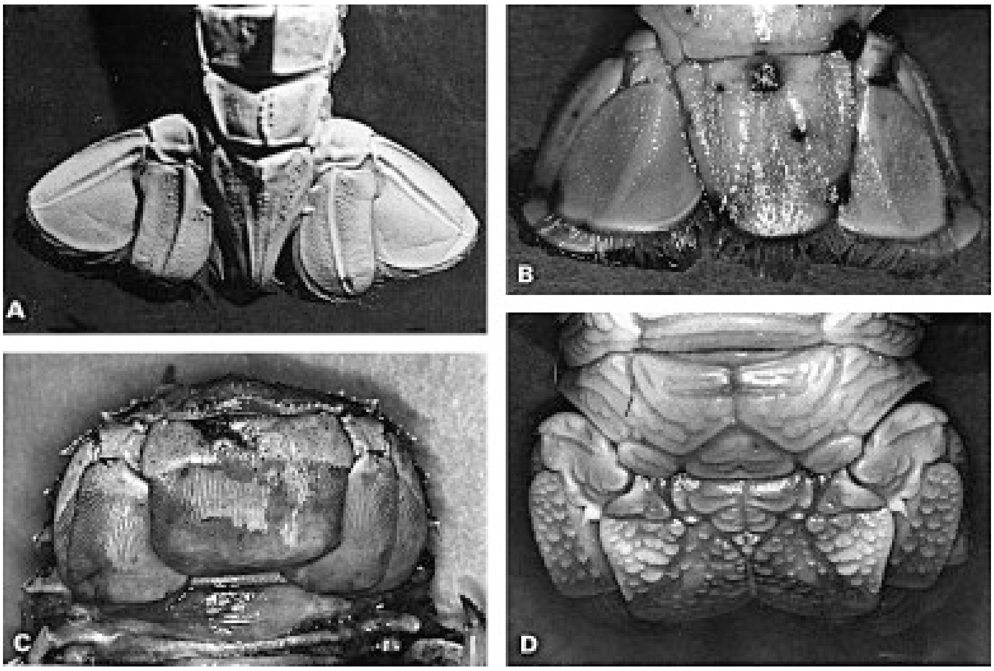

Figure 5. Tail fans of various reptantians. (A) The polychelid *Polycheles typhlops* with the plesiomorphic triangular telson (compare Fig. 1A). (B–D) The apomorphic rounded telson of the Eureptantia. (B) Homarida, *Nephrops norvegicus*. The telson bears a pair of post-lateral spines. (C) Achelata, *Ibacus peronii*. The posterior part of the tail fan is soft and uncalcified. (D) Anomala, *Munida rugosa*. Note the vertical and horizontal (cross-like) sutures on the telson. In (A, B, D) anterior is up, in (C) anterior is down.

characters possess a rounded (*Dromia personata*) or squared telson (*Homolodromia bouvieri*) (see also McLay, 1993). Thus, we conclude that the triangular telson in crabs is a secondary alteration perhaps related to the reduction of the pleon and the loss of the tail fan.

(6) An additional neuropil area, the accessory lobe, occurs in the deutocerebrum (Sandeman *et al.*, 1993). This characteristically structured neuropil has not been found in any other crustacean group.

Further evidence for eureptantian monophyly is provided by the thoracic endoskeleton. Polychelids resemble the 'natant' forms in this respect, whereas eureptantians are derived (Drach, 1950).

Achelata (new taxon)

Achelata = bearing no chelae. From the Greek *hae chaela* = chela and the prefix alpha in the sense of a negation (alpha privativum).

We abandoned the synonyms Loricata (Boas, 1880) and Scyllaridea (Borradaile, 1907), because these sometimes include the glypheids and some fossil species of uncertain affinities (Ortmann, 1896). Furthermore, the name Loricata is well established for a higher taxon within the molluscs (Götting, 1985). We believe the name Achelata clearly characterizes the group because all members lack true chelae in the first four pereiopods.

The Achelata represents a well defined group of undoubtedly monophyletic

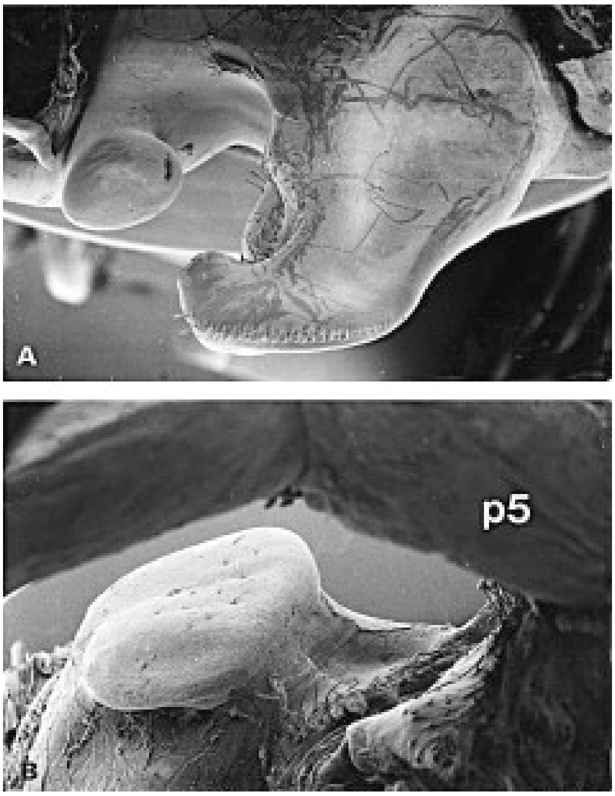

Figure 6. The knob-like structures which connect body and carapace in Polychelida and Achelata. (SEM). (A) The first pleon segment of *Polycheles typhlops* (dorso-lateral view, anterior is left). The knob is part of 1st pleon segment and lies anterior to the lateral lobe. (B) The lateral part of the 8th thoracic segment of *Scyllarus arctus* (dorsal is left, anterior is down). The knob is part of the 8th thoracic segment and lies dorsal to the coxa of the 5th pereiopod (p5).

origin. It consists of the clearly monophyletic Scyllaridae (slipper lobsters) with many apomorphic characters and the Palinuridae (rock lobsters, spiny lobsters and hairy lobsters) of uncertain phylogenetic relationships (George & Main, 1967); they are probably paraphyletic. The position of the 'Synaxidae', in particular, seems insecure (Davie, 1990) (D1–6).

(1) The first antenna has relatively short and asymmetrical flagella and an elongated peduncle (Fig. 7). The flagella are twisted around each other. The aesthetasc sensilla on the thick outer flagellum are concentrated mainly on one side in a brush-like manner. This type of first antenna can be found in most achelate species. Only in the genus *Panulirus* do first antennae occur which bear long symmetrical flagella (Holthuis, 1991), which superficially resemble the plesiomorphic condition in 'natant decapods', and in polychelids, homarids, astacids, and thalassinids (see Fig. 15A). However, in contrast to the original decapod pattern, the aesthetascs are still concentrated in a brush-like arrangement on the tip of the thick branch (Laverack & Ardill, 1965). Thus we consider the first antenna of *Panulirus* as derived from the original achelate pattern.

(2) The first articles of the left and right second antennae are fused with each other medially and with the epistome, and laterally with the carapace

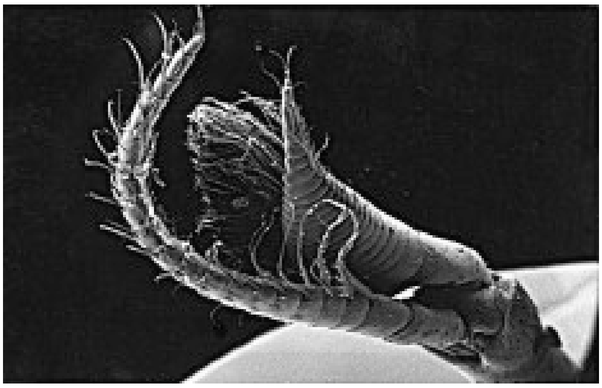

Figure 7. The flagella of the first antenna of the achelate *Scyllarus arctus*. (SEM). The two flagella are twisted around each other. The thicker outer flagellum bears a brush of aesthetascs on one side and a few setae on the other side. Compare Fig. 15.

(Fig. 8). This feature is combined with the posterior location of the pores of the antennal glands. This complex character was seen in all scyllarid and palinurid species under investigation. It is also reported from several other species and there seem to be no exceptions (e.g. Snodgrass, 1951; Davie, 1990; Holthuis, 1991). In the plesiomorphic condition found in most other decapods, the coxae of the second antennae are separated and there is no fusion of the epistome with the carapace margin. The fusion of epistome and carapace in the Brachyura exhibits a different pattern (see below).

(3) All pereiopods lack chelae except for the small grooming chela of the fifth pereiopod in females. Only the males of the genus *Justitia* have enlarged subchelate first pereiopods (Gordon, 1960; Holthuis, 1991). Since this phenomenon is restricted to this genus, it seems likely to represent an apomorphy within the palinurids. Because dendrobranchiates, stenopodids and some reptantians possess three pairs of chelae (pereiopods 1 to 3), we propose this to be the plesiomorphic condition. The loss of chelae in other reptantian taxa (e.g. *Neoglyphea* (Forest & de Saint Laurent, 1981), Thalassinida, Meiura) is apparently convergent with the achelate condition of scyllarids and palinurids.

(4) A knob-like structure, positioned above the coxa of the fifth pereiopod, connects the eighth thoracic segment with the posterior margin of the carapace (Fig. 6B). A similar knob occurs only in the polychelids (Fig. 6A), where it is part of the first pleon segment (see above) and therefore considered to be convergent. We regard the lack of this knob to be plesiomorphic.

(5) The distal portion of the tail fan is soft and uncalcified (Fig. 5C). We found this in all species examined, and corresponding conditions are reported for many members of this group (see Holthuis, 1991). A similar character is to be seen in parastacid crayfishes. This is clearly convergent because the parastacids belong to the monophyletic Astacida (see below; Scholtz, 1995). In all other decapods the whole tail fan is hard and calcified. This character is plesiomorphic.

(6) For many palinurids and scyllarids a characteristic larva, the phyllosoma larva, has been reported (e.g. Gurney, 1942; Sims, 1966; Lesser, 1974). This

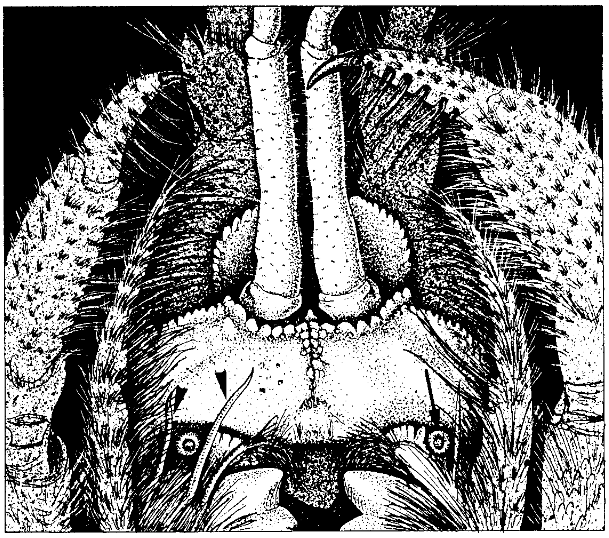

Figure 8. Anterior region of the achelate *Palinurellus gundlachi* (ventral aspect). The basal articles of the 2nd antennae are medially fused and surround the 1st articles of the 1st antennae. The nephropores (arrow) are located posteriorly. The epistome is fused to the basal antennal articles. The 1st and 2nd pereiopods bear no chelae. Note the straight flagella of the exopods of the maxillipeds (arrowheads) (compare with Fig. 16).

type of larva is mainly characterized by a flattened and leaf-like carapace and does not occur outside the achelates.

Macrochelata (new taxon)

Macrochelata = bearing large chelae. The name comes from the Greek words *makros* = large and *hae chaela* = chela. The Macrochelata is the sister-group of the Achelata and contains all the remaining taxa. Its apomorphies are as follows (E1–5).

(1) The molar process of the mandible has a trapezoid shape, is relatively strong and lies opposite the palp (Fig. 9). Achelates and polychelids have a smaller molar process with a different shape (Fig. 9B) (see also Boas, 1939). The molar process of *Stenopus hispidus* and of other stenopodids (e.g. Bruce & Baba, 1973; Manning & Chace, 1990) is also weaker. On the other hand *Penaeus* possesses a very large molar process, but of different round shape (Fig. 9A). Examined carideans were highly variable in this respect (see also Felgenhauer & Abele, 1989). Against this background we conclude that Reptantia originally possessed a relatively weak molar process, which has been retained by polychelids and achelates.

(2) The 1st pereiopod and its chelae are hypertrophied in size compared with the subsequent pereiopods. The 1st pereiopods of most Achelata are not much larger than the others (see above) and the 1st pereiopods of polychelids are barely longer than pereiopods two to five. In dendrobranchiates all pereiopods are more or less the same size. The 3rd pereiopods in stenopodids are enlarged and the condition is highly variable in carideans (e.g. a convergent enlargement of the chelae of the 1st pereiopods occurs in alpheids). We suggest that a very large 1st pereiopod is a derived character.

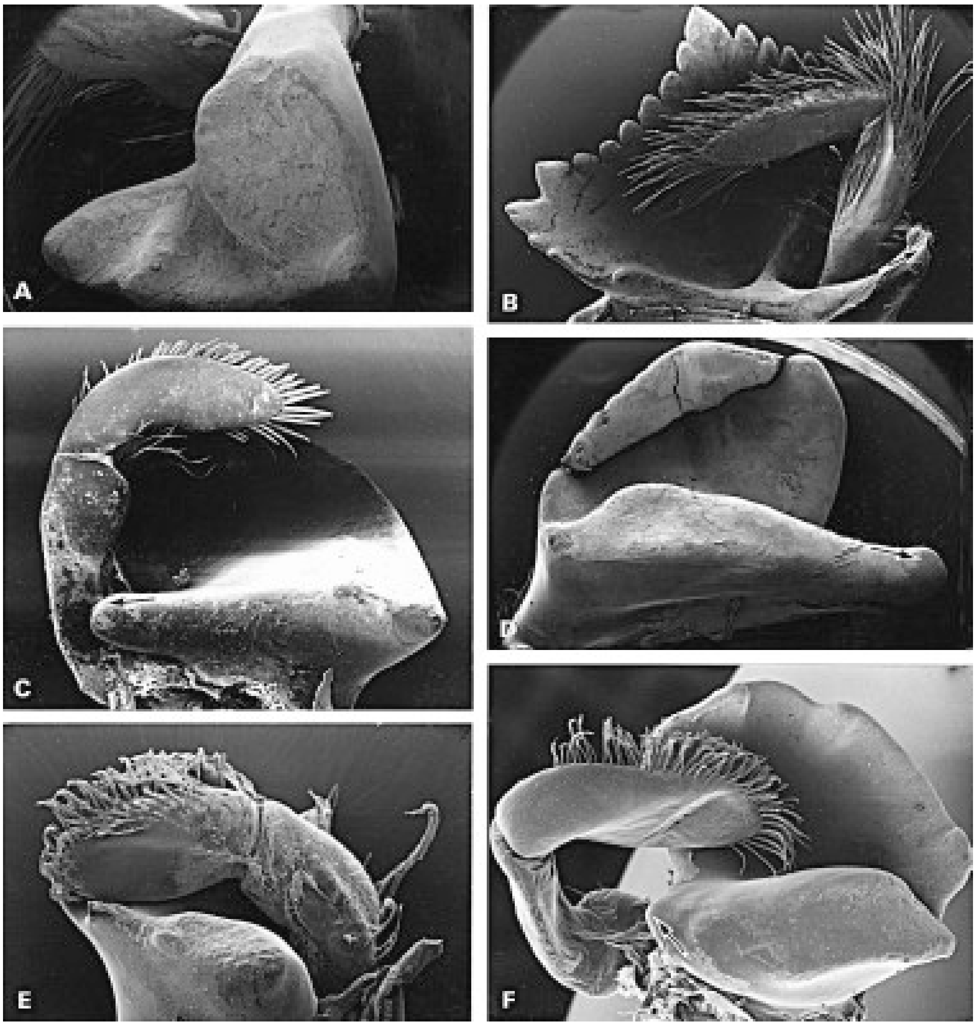

Figure 9. Mandibles of various decapods. (SEM). (A) Dendrobranchiata, *Penaeus sp.* Note the large molar process and the leaf-like mandibular palp. (B–F) Reptant mandibles. All possess the curved palp which is apomorphic for the Pleocyemata (it has been removed in D). The anterior articulation is formed by an elongated process (arrows). (C–F) The mandibles of the Macrochelata. (B) Polychelida, *Polycheles typhlops.* (C) Brachyura, *Pilumnus hirtellus.* (D) Homarida, *Nephrops norvegicus.* (E) Thalassinida, *Upogebia pulsilla.* In contrast to the situation in *Upogebia*, the process of the anterior articulation is long in axiids. (F) Anomala, *Pagurus bernhardus.* The process of the anterior articulation is somewhat reduced. It was longer in the examined galatheoids.

(3) The eureptantian type of grooming appendage (5th pereiopod) occurs in both sexes (with the exception of the enoplometopodids (see above)). The plesiomorphic condition, with only females bearing chelate 5th pereiopods, is found in Polychelida and Achelata.

(4) The mid-lateral pleonic hinges are flat, loose joints with a relatively high mobility (Fig. 13D, E). Originally, the hinge points are exposed and strong with a well defined articulation and plane of movement, as seen in polychelids and achelates (Fig. 2C).

(5) The proto-, deuto- and tritocerebrum lie in one plane; in other decapods,

and in other malacostracans, the brain is folded with the protocerebrum in an elevated position (Helm, 1928; Sandeman *et al.*, 1993).

Homarida

This name is derived from the family name Homaridae introduced in 1888 by Bate. In addition to the Nephropoidea (see Holthuis, 1974, 1991), the true lobsters, this taxon probably contains the Enoplometopodidae (see also de Saint Laurent, 1988). We found only a few and weak apomorphies, which could not be seen in all examined representatives and which are mostly restricted to the Nephropoidea, so the monophyly of the Homarida cannot be very well established (F1–5).

(1) The cervical groove and the hepatic (antennal) groove of the lateral carapace form a characteristic ‘W’. We found this groove pattern in *Homarus, Nephrops, Nephropsis* and *Thaumastocheles* (for other homarid genera see Holthuis, 1974, 1991). The carapace of *Enoplometopus* does not bear significant grooves. The carapace grooves of the other reptantians show another arrangement and lack the ‘W’ (see also Boas, 1880).

(2) The telson bears a pair of strong postlateral spines (Fig. 5B). This character is shared by all examined species, except *Thaumastocheles zaleucus*, and is restricted to homarids (see Holthuis, 1991). However, telson-spines can also be found in other reptant taxa such as astacids and achelates (Fig. 5C). These spines are located more anteriorly (i.e. about half-way down the telson) and are somewhat smaller than those in homarids.

(3) The telson of the first larval stages forms a crescent with a large median and a pair of lateral spines. This is so in *Homarus americanus* (Helluy & Beltz, 1991), *Nephrops norvegicus* (Jorgensen, 1925) and *Metanephrops challengeri* (Balss, 1914) (Wear, 1976). Large median spines are present in other decapod larvae (e.g. some thalassinids (axiids) (Gurney, 1942; Thiriot, 1974)), but the combination of large median spines and crescent-shaped telson can only be seen in Homarida. Little is known about the larvae of enoplometopodids. The affinities of the ‘enoplometopodid’ larva described by Gurney (1938) are uncertain. Nothing is known about the larvae of thaumastochelids.

(4) Juveniles hatch with all pereiopods but no pleopods or uropods (late zoea or mysis stage). This is so in species of *Nephrops* and *Homarus* (Jorgensen, 1925; Gurney, 1942; Helluy & Beltz, 1991). A more advanced hatchling stage with pleopods has been reported for *Metanephrops* (Wear, 1976). It is not clear whether this is a derived feature within the homarids, and no data exist for most other homarid genera. Larvae of dendrobranchiates hatch as nauplii (e.g. Kishinouye, 1900; Gurney, 1942); this is plesiomorphic. Pleocyemates usually hatch at an earlier zoea stage than homarids (Gurney, 1942; Rabalais & Gore, 1985). The early hatchling stage therefore represents the original character within pleocyemates.

(5) The acrosome of the spermatozoa is elongated. This is true for the Nephropoidea but again not for *Enoplometopus,* which shows the plesiomorphic spherical acrosome (Jamieson, 1991).

Fractosternalia (new taxon)

The name Fractosternalia is the combination of the Latin *frangere* = to break and the Greek *ho sternon* = breastbone. It indicates that members of this group

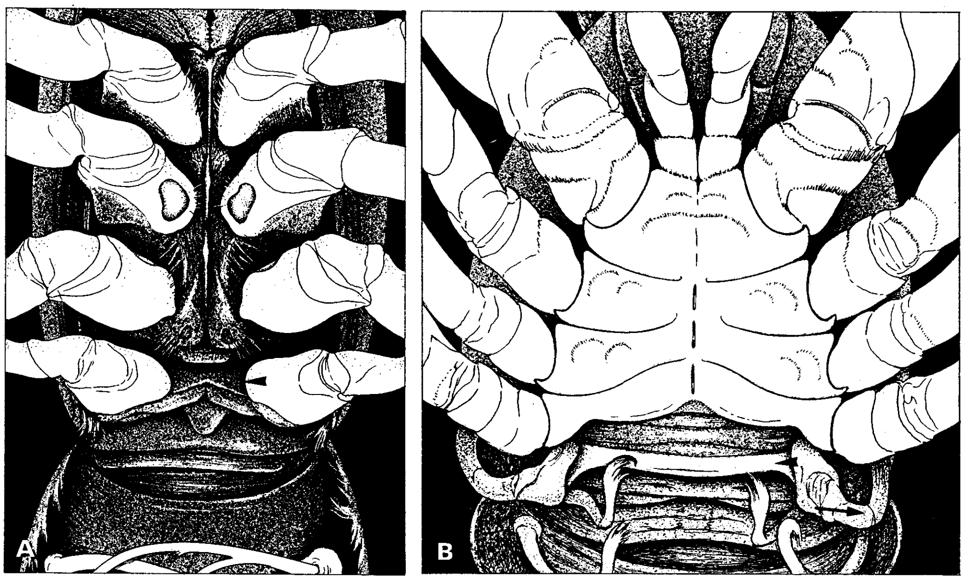

Figure 10. Thoracic sternum of the Fractosternalia represented by the crayfish *Cherax destructor* (A) and the anomalan *Galathea squamifera* (B). The animal's ventral side is shown, anterior is up. Arrowheads point to the movable last thoracic sternites (see also Fig. 13). Note the reduced 5th pereiopods in the anomalan *Galathea* (B) (arrow).

have a divided sternum. The Fractosternalia is the sister-group of the Homarida (if homarids are monophyletic) and includes the Astacida, the Thalassinida and the Meiura. The detailed descriptions given by Forest & de Saint Laurent (1981, 1989) lead us to suggest that *Neoglyphea inopinata* also belongs to the Fractosternalia. Although the exact phylogenetic position of *Neoglyphea* is unclear, we assume it to have branched off early in the fractosternalian lineage since, as in astacids (but in contrast to all other fractosternalian groups), the basis and ischium of the 2nd to 5th pereiopods are not fused.

The taxa named below share some characteristic features not present in any other decapod group. These characters are suggested to be apomorphies that unite the monophyletic Fractosternalia (G1–2).

(1) The last thoracic sternite (8th) is movable anteroposteriorly and laterally and is separated from the next anterior sternite (Figs 10, 13), in contrast to homarids, achelates, polychelids, and stenopodids, where all thoracic sternites (or at least the last two) are fused or show restricted mobility. The fused sternum (at least the fusion of the last two sternites, 7 and 8) represents a plesiomorphic character, because we observed a fusion of posterior sternites in the dendrobranchiates *Penaeus* and *Ericyonia* (see also Andrews, 1911) and the caridean shrimp *Crangon*. Some alterations of the apomorphic sternal pattern occur within the Fractosternalia. Most species within the paguroids have additionally unfused the sternite of the fourth pereiopod. In brachyurans the last thoracic sternite is fused to the other sternites (Fig. 21E). That this has to be regarded as a secondary feature evolved in the ancestral lineage of Brachyura can be seen from the incomplete lateral fusion in some 'dromiacean' species (e.g. *Homola barbata*, Fig. 21E) (see also Ihle, 1913).

(2) The thoraco-pleonic articulation (the secula of Pilgrim & Wiersma, 1963)

is complex (Fig. 11). This articulation in polychelids, achelates (see also Pilgrim & Wiersma, 1963) and homarids consists of two weakly calcified elements (uncus and solea (Pilgrim & Wiersma, 1963)) in the pleural region of the last thoracic segment (Fig. 11C). We found a similar condition or no recognizable sclerites at all in the 'natant' decapods (see also Coutière (1899), cited by Chace & Kensley (1992)). In the Fractosternalia a third sclerotized element occurs, the manubrium (Pilgrim & Wiersma, 1963) (Fig. 11A, B). All parts of the secula are more strongly calcified than in the other decapods. We found this type of secula in Astacida, Thalassinida and Anomala. Thereby the solea is not as distinct in paguroids as in other fractosternalians (Pilgrim, 1973). A secula cannot be recognized in Brachyura because the pleon is reduced and ventrally folded. This is clearly a derived character.

Astacida

We derived this term from the classical Astacidae (Latreille, 1803). This taxon includes all freshwater crayfishes, the Astacoidea and the Parastacoidea. The systematics of the crayfishes has been studied extensively (e.g. Riek, 1972; Hobbs, 1974; Albrecht, 1980), but the monophyly of astacids has been disputed (Albrecht, 1980). Astacid monophyly is based on the following apomorphies (H1–3).

(1) The 5th pereiopods bear a comb-like dactylus in both sexes instead of the eureptantian grooming chelae (Fig. 3E, F). We found this in *Orconectes limosus, Astacus leptodactylus* and *Cherax destructor* and suggest that it is part of the astacid ground pattern. A convergent character occurs in the thalassinid genus *Naushonia* (Berggren, 1992) and in the caridean atyid shrimps (Bauer, 1989).

(2) The embryonic growth zone consists of about 40 ectoteloblasts (Fig. 12B) arranged in a complete circle. This has been confirmed for several astacoids and parastacoids (Scholtz, 1992, 1993). The plesiomorphic condition, reported for all other decapod and most malacostracan groups (Dohle, 1972; Scholtz, 1984, 1993), is a ring of 19 ectoteloblasts (Fig. 12A).

(3) Astacida undergo direct development, with hatchlings which possess all appendages except uropods and first pleopods. The general appearance of the hatchlings is adult-like without zoeal traits such as exopods bearing pereiopods or a larval telson (Zehnder, 1934; Sandeman & Sandeman, 1991). In other decapods with direct development, at least some larval characters such as setose exopods and a larval telson are maintained (Gurney, 1942; Rabalais & Gore, 1985).

In addition, all freshwater crayfishes have in common an ischium of the first pereiopod of a more or less squared shape with a straight anterior margin (Fig. 14B). Originally, the anterior margin was oblique and the ischium trapezoidal (Fig. 14A). The plesiomorphic ischium shape is found in all reptantian groups except for the thalassinids (Fig. 14C) and some brachyurans.

Thalassinida

We adopt the name Thalassinida from Burkenroad (1981). This group is relatively uniform in habits and morphology. All thalassinids are burrowers (e.g. Lutze, 1938; Atkinson & Taylor, 1988; Griffis & Suchanek, 1991). Relationships within the group are not finally settled (Borradaile, 1903; de Saint Laurent, 1973, 1979a; Poore, 1992) and even their monophyly has been doubted by

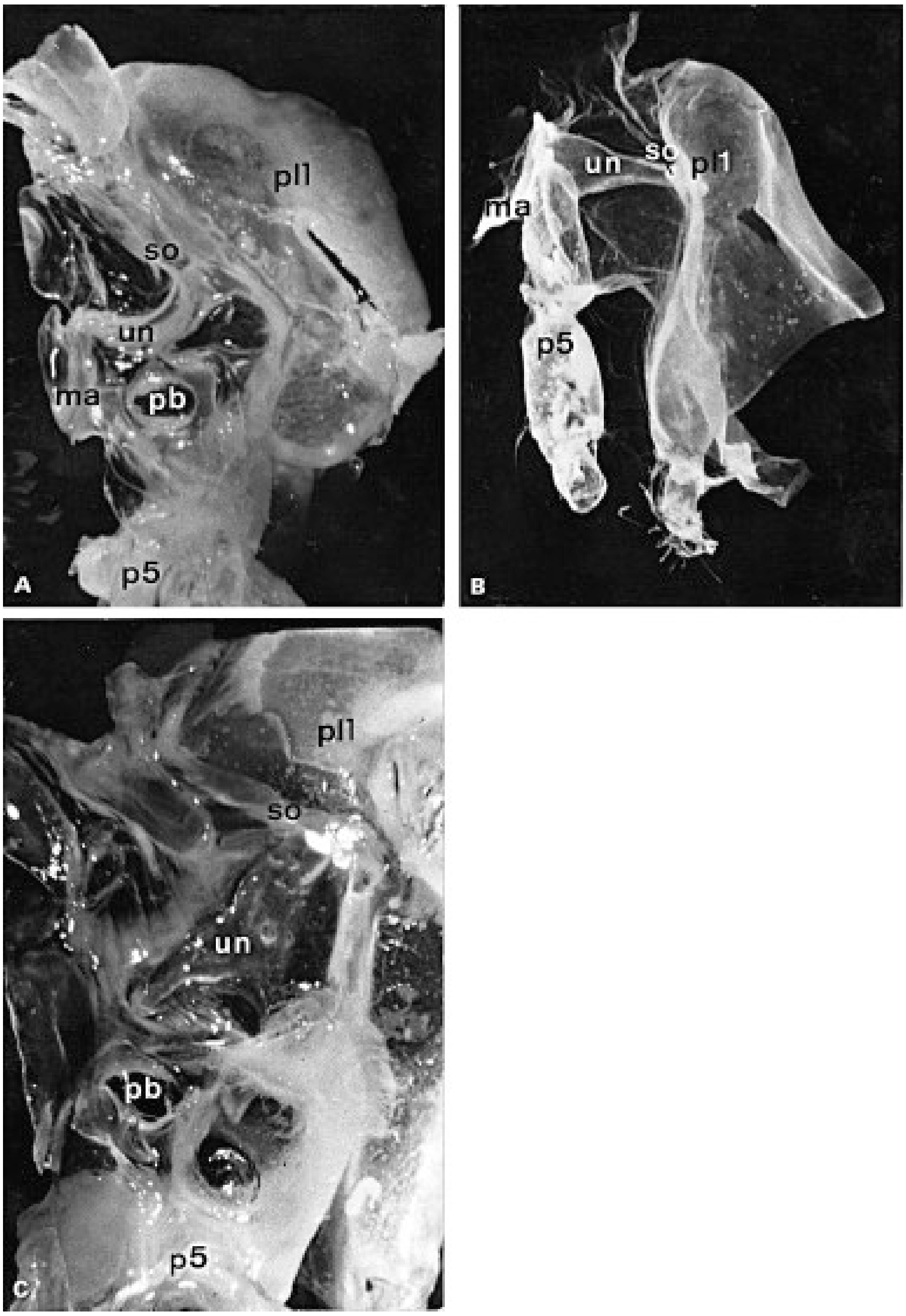

Figure 11. The thoraco-pleonic articulation (secula). The tissues were treated with KOH, anterior is left, dorsal is up. The secula was first detected by Huxley (1884). For the description of its function see Pilgrim & Wiersma (1963), Rayner (1965) and Pilgrim (1973). In the crayfish *Astacus leptodactylus* (A) three distinct sclerotized parts can be recognized, the manubrium (ma), the uncus (un) and the solea (so). The situation in the thalassinid *Callianassa australiensis* is similar except that the solea is less distinct (B). The plesiomorphic feature is represented in the homarid lobster *Nephrops norvegicus* (C). Here, the manubrium is missing and the T-shaped uncus and the solea are less calcified than in the crayfish. p5 5th pereiopod (coxa), pl1 1st pleomere, pb attachment point of the pleurobranchia.

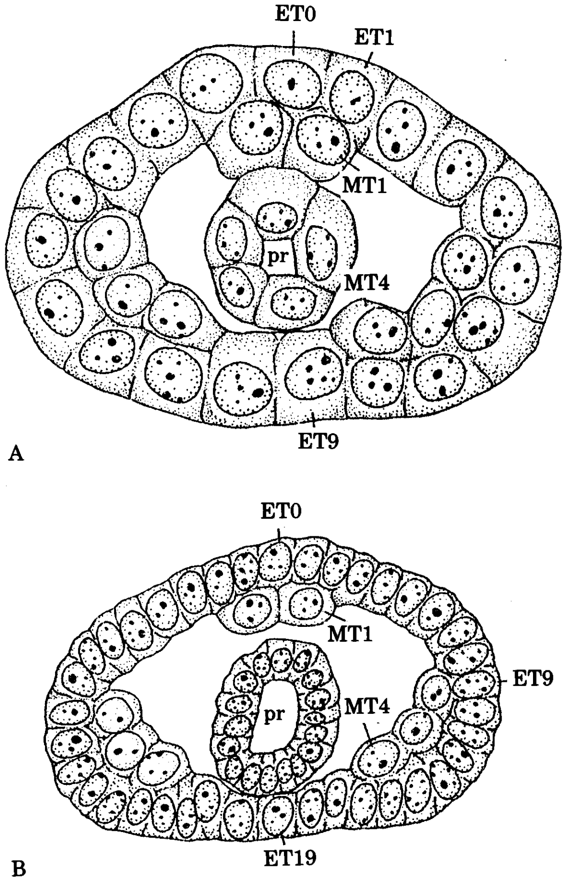

Figure 12. Teloblasts in decapod embryos. Transverse section through the growth zone of an early embryo of *Homarus americanus* (A) and *Cherax destructor* (B). (A) Displays the plesiomorphic character of a ring of 19 ectoteloblasts (ET) (nine paired (ET1–ET9) and one median ectoteloblast (ET0)). (B) The apomorphic number of about 40 ectoteloblasts of the freshwater crayfishes. Eight mesoteloblasts occur in all cases (four paired mesoteloblasts (MT1–MT4)). pr proctodaeum.

some authors (Gurney, 1942; de Saint Laurent, 1973). We regard the Thalassinida as monophyletic, because of the following derived characters (I1–5).

(1) The cheliped (1st pereiopod) is flattened and the joint between propodus and carpus is oriented in such a way that the plane of movement is at right angles to that of the dactylus (Fig. 13E). The dactylus originates in an upper position. These characters are also recognizable in taxa with a subchelate cheliped (*Upogebia, Thalassina, Naushonia* (Berggren, 1992)). The merus is vertically oriented and adapted to move closely along the side of the carapace (Fig. 13E). Similar chelipeds occur in most thalassinids (e.g. Sakai, 1962; de Saint Laurent, 1972; Gore, 1987; Manning & Chace, 1990). The ancestral character state can be seen in homarids, astacids, and galatheoids. In all these the angle of the propodus-carpus joint is inclined towards the axis of symmetry of the animals and the dactylus has an internal position.

(2) The sternite of the 7th thoracic segment is relatively large and characteristically shaped (Fig. 13A, B). It bears a transverse anterior edge, the

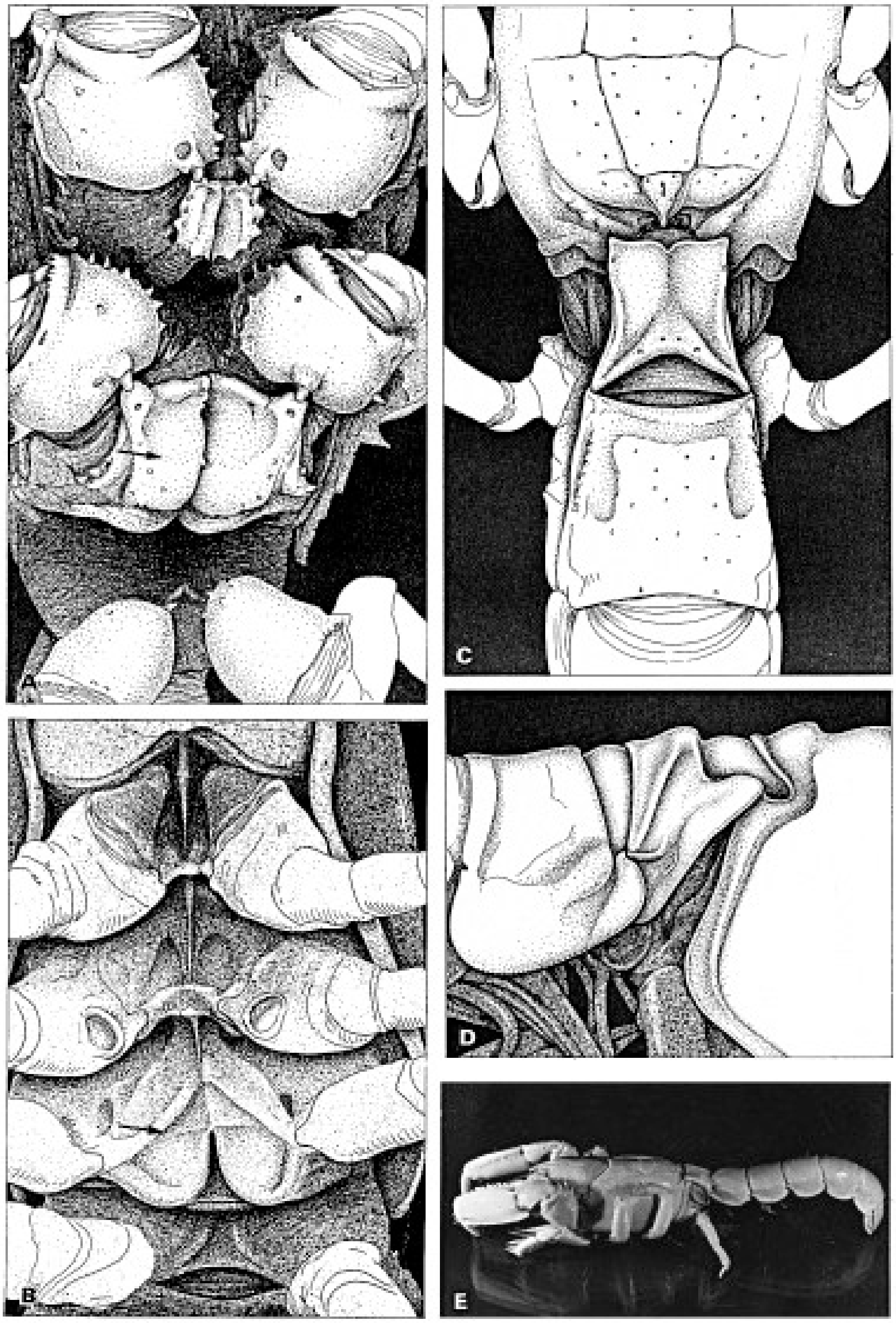

Figure 13. Thalassinidan characters. In (A) (*Thalassina anomala*) and (B) (*Calocaris macandrae*) the characteristically shaped and enlarged sternite of the 7th thoracic segment is shown (arrow) (ventral aspect, anterior is up). Note the movable last (8th) sternite (see Fig. 10). (C) Dorsal view of

joints of the 4th pereiopods are located anteriorly, and the posterior portion of the sternite forms two crescents. We found corresponding conditions, in all species examined independent of sex (for laomediids see also Sakai, 1962). A plesiomorphic 7th thoracic sternite (e.g. in crayfish) is shown for comparison in Figure 10A. It has neither the characteristic size nor the shape of the 7th thoracic sternite of the thalassinids and the coxae are hinged more posteriorly.

(3) The carapace has a pair of lateral protrusions and a median dorsal protrusion along its posterior margin resulting in a characteristic lateral notch on either side ('cardiac notch': see Chace & Kensley, 1992) (Fig. 13C, D, E). The lateral protrusions connect the carapace and the first pleomer. We found this character complex in *Axius, Calocaris* and *Thalassina.* It is also reported for other axiids, laomediids (Sakai, 1962) and *Callianidea vandoverae* (Gore, 1987). The cardiac notch does not occur in *Callianassa, Jaxea* or *Upogebia.* However, from its distribution within the thalassinids we conclude that this seems to represent a secondary loss. For descriptions of similar but apparently convergent structures in other decapods (alpheid shrimps) see Chace & Kensley (1992).

(4) All Thalassinida share a narrow waist in the region of the first pleomer (Fig. 13C, E). A characteristic feature of the first pleomer is that the lateral lobes connecting the pleon to the carapace are elevated in comparison with the lateral hinges of the pleura of the pleon (Fig. 13D, E). Originally the connection between carapace and pleon lay in the same plane as the mid-lateral hinges of the pleon segments (Fig. 2A).

(5) Further evidence of monophyly is provided by the habit of thalassinids of constructing complex vertical burrows (Atkinson & Taylor, 1988; Griffis & Suchanek, 1991).

Meiura (new taxon)

Meiura = reduced tail. This name is from the Greek *meioo* = I reduce and *hae oura* = tail. A name for similar groupings is Heterura, but this either excludes the paguroids (Beurlen & Glaessner, 1930) or includes the thalassinids (Hennig, 1986). The Meiura is the sister-group of the Thalassinida (or of both Thalassinida and Astacida—see below) and comprises the monophyletic taxa Anomala and Brachyura. The sister-group relationship between these two is well established by the following synapomorphies (J1–4).

(1) The 1st antennae bear short asymmetrical flagella (a thick outer flagellum and a thin and shorter inner flagellum) with the aesthetasc hairs concentrated on one side of the thick branch (Fig. 15). The 1st article is relatively wide and large and the peduncle is bent twice (Fig. 21). This type of 1st antenna is very similar throughout the Anomala and Brachyura. Exceptions are found in filter-feeding hippoids and the terrestrial hermit crabs and are clearly related to the habits of these animals. The plesiomorphic 1st antennae of reptants possess a short and straight peduncle without a significantly enlarged first article

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posterior thoracic and anterior pleonic regions of *Thalassina.* The 1st pleomer is narrow and the posterior carapace margin exhibits the characteristic dorso-lateral notches. (D) Lateral view of the thoracic-pleonic connection of *Calocaris* (anterior is right). Note the elevated overlapping lobe of the 1st pleon segment (see Fig. 2) and the notch in the posterior carapace margin (compare with C and E). Note also the reduced midlateral hinges between the pleon segments (compare with Fig. 2). (E) *Thalassina anomala*, showing the orientation of the 1st pereiopod (cheliped) (compare Fig 14A for the plesiomorphic condition).

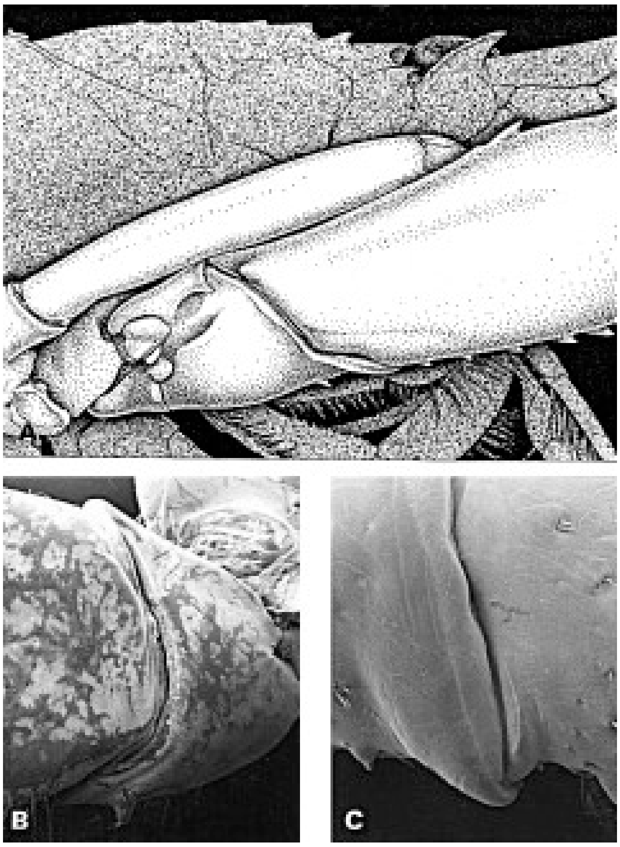

Figure 14. The anterior margin of the ischium of the 1st pereiopod. (A) The plesiomorphic character of an oblique anterior margin of the ischium in *Nephrops norvegicus* (anterior is right). The derived feature occurs in the thalassinid *Upogebia pulsilla* (B) (anterior is left) and the crayfish *Orconectes limosus* (C) (anterior is right), where the anterior margin of the ischium is vertical.

and long flagella with only slight asymmetry. The aesthetascs are not concentrated in a brush-like manner (Fig. 15A). The 1st antenna of the Meiura superficially resembles that of the Achelata to a certain extent (see Fig. 7), but this seems to be convergent.

(2) The exopods of all three maxillipeds are bent twice to result in a Z-shape (Fig. 16). Originally they are more or less straight, as in crayfishes or lobsters (Fig. 8). A similar character is present in some thalassinids (e.g. *Thalassina anomala* and *Laomedia* (Sakai, 1962)) and crangonids (see also Christoffersen, 1988b). This must be convergent since thalassinids are monophyletic and the crangonids are carideans and only distantly related.

(3) Only the 1st pereiopods have chelae. This is correlated with feeding behaviour. Whereas astacids pick up most of their food with the chelate second pereiopods, anomalans and brachyurans use their large chelipeds. The entire character complex occurs in all anomalans and brachyurans. A convergent loss of the chelae of the 2nd and 3rd pereiopods has occurred within thalassinids (e.g. *Upogebia, Laomedia* (Sakai, 1962)). In this case reduction of chelae might be related to the burrowing life style and filter and deposit feeding.

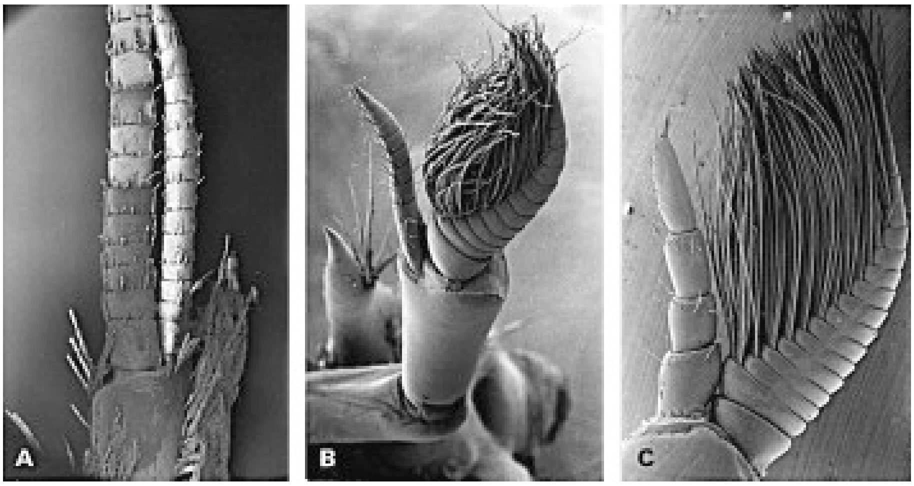

Figure 15. The 1st antenna of the astacid *Orconectes limosus* (A) and of two representatives of the Meiura, showing the apomorphic characters, the anomalan *Galathea squamifera* (B) and the brachyuran *Medorippe lanata* (C). (see also Fig. 21.)

(4) The ganglion of the 1st pleomere is fused with the last thoracic ganglion (Fig. 17). This is so in several anomalans and seems to be a general character of the group (e.g. Pike, 1947; Sayed, 1963). Most brachyurans, on the other hand, have all ganglia of the pleon fused with the thoracic ganglion mass (e.g. Bouvier, 1889; Balss, 1941). The original condition for Brachyura can be seen in dromiids. Here the ganglia of the pleon are still separated but the first ganglion is fused with the thoracic mass (Bouvier, 1897, cited after Balss, 1941) (Fig. 17C). In thalassinids, as in other decapods, the first pleonic ganglion is not fused with that of the last thoracic segment (Fig. 17A). A more anterior position of the first pleonic ganglion has also been reported for the thalassinid *Upogebia* (Bouvier, 1889; Schram, 1986), but no fusion with the last thoracic ganglion occurs.

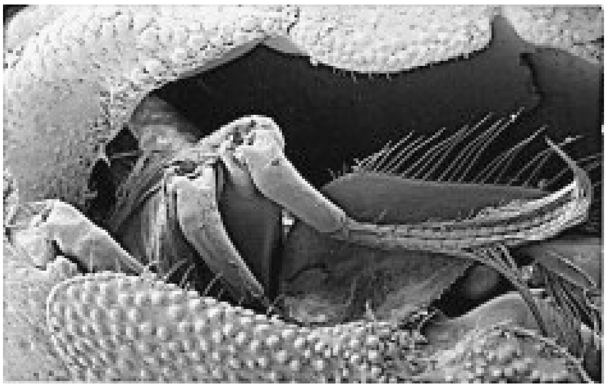

Figure 16. The Z-shaped flagella of the maxillipeds of the brachyuran crab *Xantho poressa* (ventral aspect, anterior is up). (SEM). See Fig. 8 for the plesiomorphic condition.

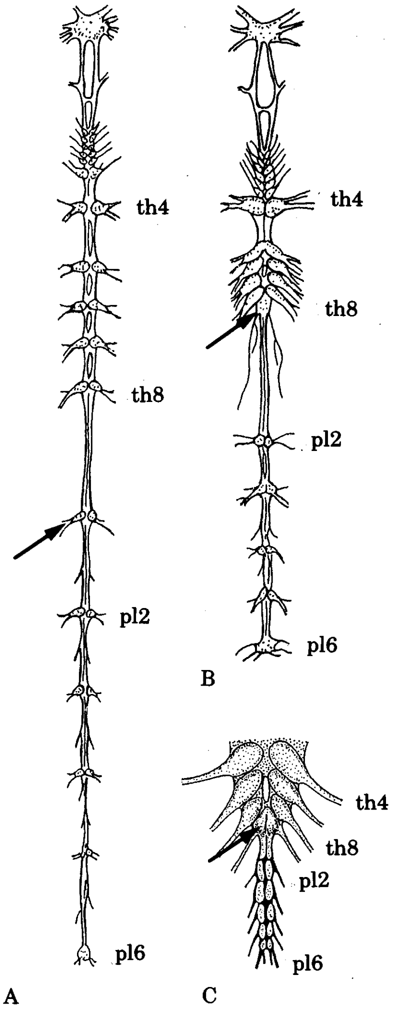

Figure 17. The central nervous system of certain reptantians (redrawn after Bouvier, 1889; Balss, 1941) (anterior is up). (A) Plesiomorphic condition: the 1st pleonic ganglion is situated within the corresponding 1st pleon segment (*Axius stirynchus*). (B, C) Apomorphic condition of the Meiura: the 1st pleonic ganglion is fused to the last thoracic ganglion. (B) *Galathea strigosa* (Anomala). (C) *Dromia personata* (Brachyura). The position of the 1st pleonic ganglion is indicated by an arrow. th4–th8 ganglia of the pereion, pl1–pl6 pleonic ganglia.

Anomala

This is the Anomala of Boas (1880). We do not use Anomura in the sense of Borradaile (1907) because it includes the thalassinids. We prefer the term Anomala, despite the suggestions of McLaughlin & Holthuis (1985), because it does not obscure the well established sister-group relationship between the Anomala and Brachyura.

The Anomala is a very heterogenous group in habits and morphology. Analyses of anomalan phylogenetic relationships have been undertaken by McLaughlin (1983) and Martin & Abele (1986) but led to some contradictory results. We discern two higher monophyletic taxa within the Anomala. One group comprises galatheoids and hippoids. They share the apomorphic character of a telson stretch receptor, which is not found in any other malacostracan group (Paul, 1989). The other group is represented by *Lomis* and the hermit crabs including coenobitids and lithodids, which share some apomorphic characters (Richter & Scholtz, 1994). The Anomala as a whole can be united by the following apomorphies (K1–7).

(1) The carapace has a weakly calcified lateral line (linea anomalica = anomurica) that ends in a soft field at the posterior carapace margin (Fig. 18). This character was found in all investigated species but the size of the soft field varies in extent; in galatheoids it is small, whereas in hippoids and hermit crabs it extends over a large area of the carapace. Lineae are also found in some thalassinids and brachyurans, but these never end in a wide uncalcified field at the posterior carapace margin and homology seems unlikely (see below).

(2) The basis of the 2nd antenna is located laterally in a triangular notch in the anterior margin of the carapace (Fig. 18). This was found in all representatives of the Anomala and is restricted to them.

(3) The coxa-sternite joints of the thoracopods are inverted when compared with those of other reptantians (Figs 10, 19), with the result that the sternites form a protrusion that fits into a cavity in the coxae. The reverse represents the original condition. The inversion of this joint occurs in most anomalan species but is not as evident in some hermit crabs and in the posterior pereiopods of several galatheoids.

(4) The 5th pereiopod is reduced in size and kept in the branchial chamber as a cleaner leg (Fig. 10B). This is so in all anomalan members except shell-dwelling hermit crabs, which use the 5th pereiopod to hold onto their shell. Interestingly, secondarily free-living hermit crabs such as *Birgus latro* and lithodids possess a cleaner leg (Richter & Scholtz, 1994).

(5) The telson bears a vertical and a horizontal suture which together form a cross (Fig. 5D). We found this cross in galatheoids and some symmetrical hermit crabs. The distribution of this type of telson within the Anomala suggests an apomorphic state.

(6) The 5th pereiopod in the late zoea stages is reduced in size, slender, and inserted medially between the coxae of the third and fourth pereiopods (Fig. 20). This character is reported for larvae of all anomalan taxa (e.g. Gurney, 1942; Dechancé, 1961; Knight, 1966, 1970). In the larvae of all other reptants, the pereiopods lie in a row and the 5th pereiopod is not significantly smaller than the rest (Gurney, 1942).

(7) Further evidence for anomalan monophyly is provided by the stalked structure of the spermatophores (e.g. Subramoniam, 1984; Hinsch, 1991; Tudge, 1991).

Brachyura

We use this name following Borradaile (1907), who includes the 'Dromiacea'. The monophyletic Brachyura is the sister-group of the Anomala and includes forms with many plesiomorphic characters assembled as the apparently paraphyletic 'Dromiacea' (see below). Brachyuran systematics is still under debate (e.g. Guinot, 1978, 1979; de Saint Laurent, 1980a, b). Brachyuran apomorphies are as follows (L1–7).

(1) The anterior carapace forms a fossa orbito-antennularis, which surrounds

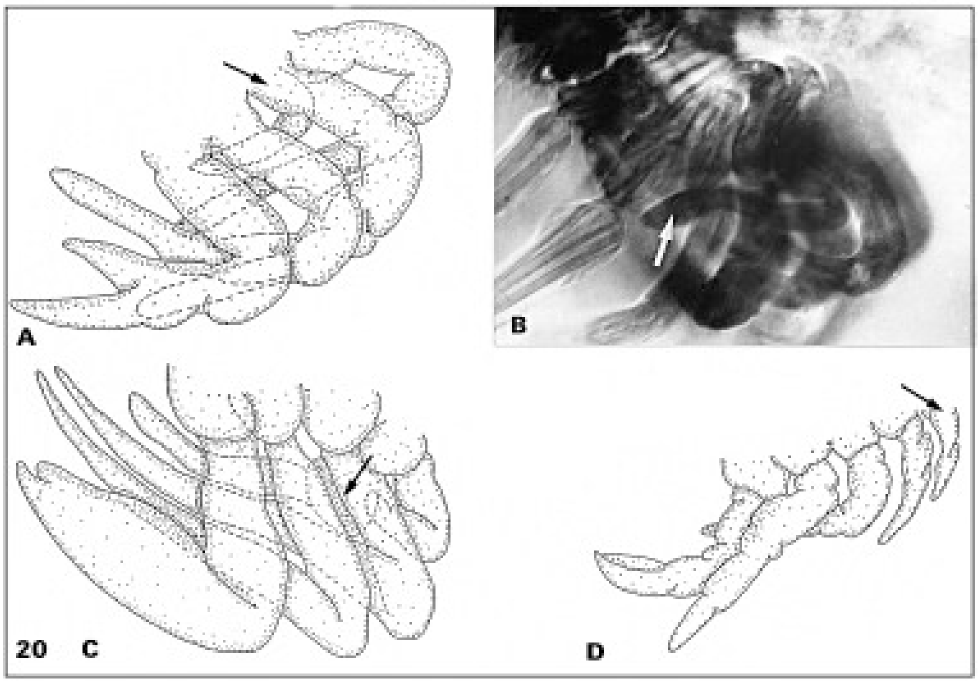

Figure 18. Lateral view of the carapace of *Galathea intermedia* (Anomala) (SEM, anterior is right, dorsal is up). The 'linea anomalica' and the characteristic location of the 2nd antenna basal article in a notch in the carapace are shown.

Figure 19. The anterior thoracic sternites of *Lomis hirta*, (Anomala) showing the inverted articulation between sternites and coxae (compare Fig. 10B). The original type of articulation is shown in Fig. 13A.

Figure 20. The pereiopods of various zoea larvae (anterior is left). The apomorphic character of an anterio-medial position of the larval 5th pereiopod in Anomalans is depicted in (A–C). (A) The hippoid *Lepidopa myops* (redrawn after Knight, 1970). (B) The galatheoid *Porcellana sp.* (Nomarski optics). (C) The brachyuran *Petalomera wilsoni*, showing the plesiomorphic arrangement of the 5th zoeal pereiopod (redrawn after Wear, 1970). (D) The hermit crab *Catapaguroides timidus* (redrawn after Dechancé, 1961). Arrows point to the 5th pereiopods.

the eyestalks and the 1st antenna (Fig. 21B). We found this character in all brachyurans examined. We agree with Ihle (1913) and Báez & Martin (1989), who describe a corresponding character in homolodromiids. Within the brachyurans the fossa becomes divided and the orbits separated by fusion of the 2nd segment of the 2nd antenna with the dorsal margin of the anterior carapace (Fig. 21B). This happened several times convergently (Balss, 1940).

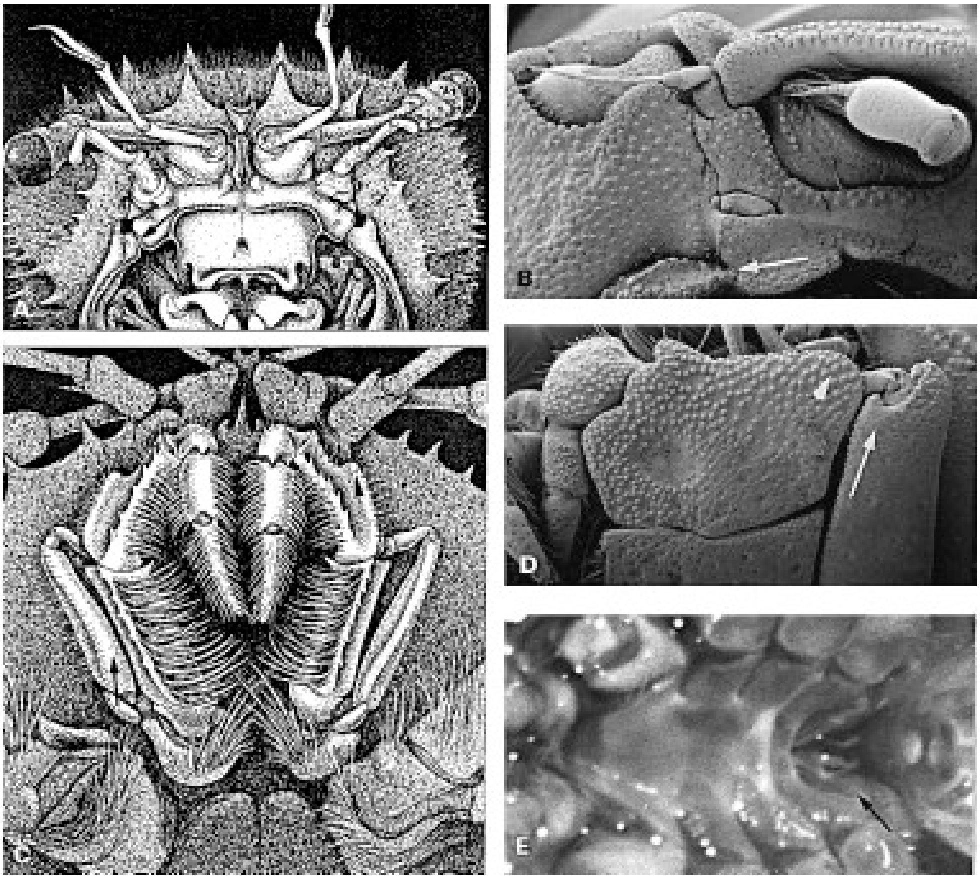

Figure 21. Some brachyuran apomorphies. (A) Head and mouth region of *Homola barbata* (ventral). The characteristic fusion of epistome and carapace can be seen (see text) (compare B). Note the bent peduncle, large basal article of the 1st antenna and long eye stalks. (B) Anterior region of *Xantho poressa* (SEM). The fossa orbito-antennularis is divided by the fusion of the 2nd article of the 2nd antenna and the dorsal carapace. The characteristic fissure or notch between carapace and epistome is indicated by an arrow in (A) and (B). The flattened 3rd maxilliped in *Homola* (C) and *Xantho* (SEM) (D). Endopod and exopod (arrows) lie in one plane. Note the expanded outer margin of the merus (arrowheads) and the inner position of the three distal segments, the short carpus, propodus and dactylus. (E) The thoracic sternum of *Homola barbata*. All sternites of the pereion and of the 3rd maxilliped are fused and lie in one plane. Note that the 8th thoracic sternite is fused but the fusion plane is deeply cleft (arrow).

The orbito-antennular fossa of the homolids is shallow, correlated with their long, slender eyestalks (Fig. 21A). This is considered to be a secondary alteration. Outside the Brachyura, orbits occur in the achelate scyllarids. These are clearly convergent, because they are differently formed and palinurids do not possess orbits (plesiomorphic condition).

(2) The epistome bears a transverse ridge which is fused laterally with the bent margin of the carapace to form a characteristic notch (Fig. 21A, B). We found this character in all species examined, including *Homolodromia bouvieri, Homola barbata* and *Dromia personata* (see also Snodgrass, 1951). According to Milne Edwards & Bouvier (1902), Doflein (1904) and Ihle (1913), a corresponding character occurs also in other representatives of the homolodromiids. The fusion

of the epistome and the carapace in the Achelata (see above) (Fig. 8) shows a different arrangement and we therefore suggest convergent evolution. Transverse ridges are also found on the epistomes of *Nephropsis* and some galatheoid species. These are never combined with a fusion of the carapace with the epistome.

(3) The distal segments (dactylus, propodus, carpus) of the 3rd maxilliped are bent posteriorly and oriented medially (Fig. 21C, D). The carpus is relatively short. The proximal segments (basis, ischium, merus) have expanded margins, are flattened and form one broad plane, with the exopod lying beside the ischium (Fig. 21C, D). The proximal segments are flattened and broadened to different extents within the brachyurans. The third maxilliped of homolids and homolodromiids is still by and large leg-like (Fig. 21C), but is very flat in dromiids and the other crabs and forms a so-called operculum that covers the mouth (Fig. 21D). Flattened 3rd maxillipeds also occur in some thalassinids (*Callianassa*), scyllarids, and hippoids, but all these examples bear only a superficial similarity to the flattening found in brachyurans (e.g. the operculiform appearance of the 3rd maxillipeds in *Callianassa* is due to an expansion of the *inner* margins of ischium and merus) and are therefore suggested as being convergent.

(4) The chelae of the 1st pereiopod are oriented so that the inner side of the palm faces the anterior side of the carapace. This results in the external location of the movable finger (dactylus) of the chelae. This phenomenon can also be recognized in homolids and homolodromiids (e.g. Doflein, 1904; Ihle, 1913; Báez & Martin, 1989). The plesiomorphic condition can be seen in homarids, astacids and galatheoids, where the upper edge of the chelae and dactyli are oriented towards the anterior side of the carapace.

(5) All thoracic sternites are fused and form a wide sternum with a median groove (Fig. 21E). This fused brachyuran sternum is apparently derived from the divided sternum of the Fractosternalia, indicated by the incomplete fusion of the lateral parts of the last sternites in homolids and homolodromiids (Fig. 21E) (see also Ihle, 1913). The coxae of the 1st pereiopods of homolodromiids lie close together, whereas those of the other crabs are separated and the sternite of the 3rd maxilliped lies in the same plane as those of the pereiopods.

(6) The pleon is flattened and ventrally flexed and the uropods reduced to small intercalary plates. These vestigial uropods are convergently lost in several lines within the Brachyura (e.g. McLay, 1993). The reduced pleon in anomalan crabs is apparently convergent.

(7) The sexes differ strongly in pleon size, being smaller and narrower in males than in females. This is also true for homolodromiids (see table 1, pp. 496/7 in Báez & Martin 1989)). Sexual dimorphism of the pleon can also be seen in crayfishes, *Lomis hirta,* and the Lithodidae. This, however, does not show the degree found in brachyurans.

Evidence for brachyuran monophyly also comes from comparative studies of the thoracic endoskeleton and musculature patterns (Abrahamczik-Scanzoni, 1942).

CONCLUSIONS

'Palinura' is not a monophyletic taxon

Boas (1880, 1939) and Borradaile (1907) suggested a close relationship between polychelids and achelates, and Borradaile (1907) erected the taxon 'Palinura' to indicate the common origin of these groups. He based this conclusion mainly on characters like the reduction of the inner lobes of the 2nd maxillae and 1st maxillipeds. This view and the term 'Palinura' have been adopted by most carcinologists (e.g. Balss, 1957; McLaughlin, 1980; Bowman & Abele, 1982; Schram, 1986). Burkenroad (1981) has questioned the monophyly of the 'Palinura', stressing a number of differences between polychelids and achelates. On the other hand, he mentioned the possession of a button fastening the carapace to the last thoracic segment and he considered this character as a possible synapomorphy indicating a sister-group relationship of polychelids and achelates.

The present investigation shows that the 'Palinura' represent a paraphyletic assemblage and therefore the name should be abandoned in phylogenetic systematics. In our analysis the Polychelida is the sister group of all other reptantians, which we call Eureptantia. The remaining groups of the 'Palinura', the scyllarids and palinurids, form the monophyletic taxon Achelata. The Achelata is part of the Eureptantia, because it shares a number of derived characters with the other members of this group. The knobs of polychelids and achelates originate from different segments and presumably evolved independently. If the polychelids were the sister group of the achelates, either all eureptantian features of the latter would be convergent, or the polychelids would have lost all eureptantian apomorphies. The reduction of the inner lobes of the 2nd maxillae and 1st maxillipeds by convergent evolution is the more parsimonious explanation which is supported by the different degrees of their reduction (see Boas (1939), Fig. 4, p. 11).

'Astacura' and the unresolved relationships of the Astacida

The Astacura (Borradaile, 1907) (=Homaridea, Astacidea), including Homarida and Astacida, has always been considered to be a monophyletic taxon. Only the thaumastochelids and enoplometopodids are placed with the thalassinids by some carcinologists (Ortmann, 1896; Gurney, 1938), and Kaestner (1970) included the thalassinids in the Astacura. Our own phylogenetic analysis reveals that 'Astacura' represents a paraphyletic assemblage. Homarids and astacids share the same general appearance, but this is based on plesiomorphic characters and we found no synapomorphy which could unite these taxa, whereas the Astacida share apomorphic characters with the other Fractosternalia, namely the movable last thoracic sternite and the pattern of calcified pleural parts connecting thorax and pleon. We suggest the term 'Astacura' and its synonyms be abandoned.

Although we found only a few apomorphies for them, we regard the Homarida as monophyletic. Additional studies are needed for a broader base of comparison. It seems likely that thaumastochelids belong to the Homarida because they share the apomorphic carapace groove arrangement with other homarids and lack all fractosternalian or thalassinid apomorphies. We agree with de Saint Laurent (1988) that enoplometopodids do not belong to the thalassinids, because they lack the apomorphic characters of the Fractosternalia and the Thalassinida such as the movable last thoracic sternite or the narrow first pleomer. The possession of the post-lateral telson spines suggests a homarid relationship for enoplometopodids. On the other hand, the lack of most homarid

TABLE 1. List of apomorphic and corresponding plesiomorphic characters of the reptantian monophyla. Numbers refer to text and Fig. 1. a1, a2 1st and 2nd antennae, mxp maxilliped, p1–p5 pereiopods.

	Apomorphic	Plesiomorphic
A1	dorsoventrally flattened pleon	laterally compressed pleon
A2	strong exoskeleton	weakly calcified exoskeleton
A3	long anterior mandible articulation	short mandible articulation
A4	sternite-coxa articulation with anterior-posterior leg movement	medio-lateral leg movement
A5	p5 with grooming chela	p5 without chela
A6	1st pleomere with overlapping lobes	no overlapping lobes
A7	brain wider than long	brain longer than wide
A8	parallel mating position	perpendicular mating position
A9	spermatozoa with three nuclear arms	spermatozoa without nuclear arms
B1	basis, ischium, mersus fused in p2 to p5	all three unfused
B2	p4 chelate	p4 not chelate
B3	knob between 1st pleomere and carapace	knob absent
B4	eryoneicus larva	zoea larva
C1	mxp3 with crista dentata	crista dentata absent
C2	mxp3 with blunt dactylus	mxp3 with sharp dactylus
C3	propodus and dactylus of p1 with double-hinge	articulation simple
C4	5th pereiopod with many scale like teeth	with few triangular teeth
C5	wide and rounded telson	narrow triangular telson
C6	brain with accessory lobes	accessory lobes absent
D1	a1 with asymmetrical and twisted flagella	a1 with straight flagella
D2	basal articles of a2 fused medially with carapace and epistome	a2 unfused with carapace
D3	pereiopods without chelae	p1 to p3 chelate
D4	knob between 8th thoracic segment and carapace	knob absent
D5	soft tail fan	hard tail fan
D6	phyllosoma larva	zoea larva
E1	mandible with strong trapezoid molar process	weaker molar process
E2	hypertrophied 1st cheliped	1st cheliped similar to other pereiopods
E3	grooming appendage (p5) in both sexes	in females only
E4	flat mid-lateral pleonic hinges	prominent lateral hinges
E5	proto-, deuto- and tritocerebrum in one plain	with raised protocerebrum
F1	carapace grooves form a W	grooves form no W
F2	telson with post-lateral spines	spines absent or more anterior
F3	crescent larval telson with three large spines	this combination of shape and spines absent
F4	young hatch at mysis stage	young hatch as early zoea
F5	spermatozoa with elongated acrosome	sperm with spherical acrosome
G1	movable 8th thoracic sternite	8th thoracic sternite fused with anterior sternites
G2	secula with three sclerites	secula with two or less sclerites
H1	dactylus of p5 with comb-like spines	p5 chelate with scale-like teeth
H2	embryonic growth zone with 40 ectoteloblasts	growth zone with 19 ectoteloblasts
H3	hatchlings lacking zoeal characters	hatchlings with zoeal characters
I1	flattened and upright 1st cheliped	1st cheliped not flat and inclined
I2	large 7th thoracic sternite with anterior edge and posterior lobes	this character combination absent
I3	posterior carapace margin with cardiac notches	cardiac notches absent
I4	narrow waist in the area of 1st pleomer	1st pleomer wide
I5	complex vertical burrows	simple horizontal burrows
J1	a1 double bent, flagella short and highly asymmetrical	a1 straight, flagella long and slightly asymmetrical
J2	exopods of maxillipeds with double bent flagella	with straight flagella
J3	p2 and p3 without chelae	p1 to p3 chelate
J4	ganglia of 1st pleon and last thoracic segments fused	these ganglia unfused
K1	carapace with linea anomalica	carapace without linea
K2	1st article of a2 in carapace notch	a2 not in notch
K3	inverted joints between coxae and sternites in the thoracic region	regular joints

(continued)

TABLE 1. *(continued).*

	Apomorphic	Plesiomorphic
K4	p5 reduced and in branchial chamber	p5 large and outside branchial chamber
K5	telson with cross-like sutures	cross-like sutures absent
K6	p5 of late zoea reduced and in antero-medial position	p5 aligned with other pereiopods and not reduced
K7	stalked spermatophores	spermatophores unstalked
L1	fossa orbito-antennularis	fossa absent
L2	fusion of epistomial ridge and carapace margin	epistome and carapace unfused
L3	mxp3 with expansions of merus and ischium	mxp3 leg like without expansions
L4	movable finger of cheliped external	movable finger internal
L5	fused thoracic sternum	last thoracic sternite movable
L6	ventrally flexed pleon with vestigial uropods	straight pleon with uropods
L7	strong sexual dimorphism of pleon	slight sexual dimorphism

apomorphies, the lack of grooming chelae in the 5th pereiopods of the males, and the gill formula which is more complete than in homarids (Gurney, 1938) might indicate a possible sister-group relationship between enoplometopodids and all other macrochelates.

One of the unsolved problems of our phylogenetic analysis is the systematic position of the freshwater crayfishes (Astacida). We can show that the Astacida most probably represents a monophyletic group (see also Scholtz, 1993), although its sister-group remains obscure. Our investigation clearly suggests that the traditional view of a close relationship between homarids and astacids cannot be maintained. Whether the Astacida is the sister-group of both the Thalassinida and the Meiura or exclusively of the Thalassinida remains an open question. The shape of the ischium of the first pereiopod of astacids resembles that of thalassinids (see above), but this apomorphy is not very convincing and is probably a convergence, because a similar character can be seen in some brachyurans (e.g. *Carcinus maenas*). On the other hand, thalassinids share a number of characters with the meiurans, namely the lack of chelae in the third pereiopods, the reduction of some giant neurons in the nerve cord (Paul, 1991), and the fusion of basis and ischium in all pereiopods (a character which occurs convergently in polychelids, achelates and some carideans (Burkenroad, 1981)). These common characters might indicate a possible sister-group relationship between Thalassinida and Meirua.

'Anomura' and the phylogenetic position of the Thalassinida

The 'Anomura' has always been a group under dispute. There has been little doubt that galatheoids, lomids, hippoids and paguroids form a monophyletic taxon, the Anomala (Anomura *sensu stricto*) (e.g. Boas, 1880; Burkenroad, 1963; McLaughlin, 1983; Martin & Abele, 1986). We agree with McLaughlin's (1983) phylogenetic diagnosis of anomalan monophyly, although some of the characters which she suggested to be apomorphies for this taxon are actually plesiomorphies. The movable last thoracic sternite, for instance, is an apomorphy of the Fractosternalia, and the fusion of the last thoracic and the 1st pleonic ganglia an apomorphy of the Meiura.

In contrast to the situation in the Anomala, the interrelationships of the

Thalassinida and their monophyly are controversial. Borradaile (1903, 1907) was the first to stress similarities between the thalassinids and anomalans of Boas (1880), and he combined these groups in the 'Anomura', a view adopted by several authors (e.g. Balss, 1957; McLaughlin, 1980). In their cladistic analysis Martin & Abele (1986) came to a similar conclusion. According to them, the thalassinids are the sister-group of the Anomala (their anomurans *sensu stricto*). The above close affinities between thalassinids and Anomala have nevertheless been doubted by authors such as Bouvier (1940), Kaestner (1970), de Saint Laurent (1979a) and Burkenroad (1963, 1981).

Our cladistic analysis reveals a sister-group relationship between the Anomala (excluding the thalassinids!) and the Brachyura, both forming the monophylum Meiura. The Thalassinida (or Thalassinida and Astacida) is the sister group of the Meiura, and the 'Anomura' of Borradaile (1907) represents a paraphyletic assemblage. Similarities between thalassinids and anomalans are only superficial and concern their general appearance, such as a soft cuticle, a narrow waist, and the occurrence of a 'linea' on the lateral sides of the carapace. These characters are clearly convergent. The soft cuticle and narrow waist of some hermit crabs have been evolved within the paguroids and are not part of the anomalan ground pattern (Richter & Scholtz, 1994). The 'linea anomalica' is not homologous to the 'linea thalassinica' since the latter seems to have evolved within the thalassinids and several thalassinidan groups lack a linea (see also Poore, 1992). Furthermore, in contrast to the 'linea thalassinica' the 'linea anomurica' always ends in a wide field of uncalcified cuticle and in a lower position on the posterior carapace margin.

The characters mentioned by Martin & Abele (1986), which would indicate a sister-group relationship between Thalassinida and Anomala, are all either plesiomorphic (e.g. unfused last thoracic sternite, crista dentata, achelate 3rd pereiopod) or convergent (e.g. linea thalassinica, linea anomalica). This erroneous interpretation of characters is due to the choice of a too distantly related outgroup (*Panaeus*) and the omission of a possible sister group (Brachyura). This results in the entire evolution of characters within the reptantians being neglected and the data used by Martin & Abele necessarily culminating in a false thalassinid anomalan sister-group relationship.

The monophyletic origin of Thalassinida has been doubted by some authors. Gurney (1924, 1938, 1942) and de Saint Laurent (1973) stress the similarity of the zoeal 3rd maxilliped of the thalassinidan subgroups Laomediidae and Upogebiidae with that of the anomalans. The main feature in this comparison is that the zoeal endopod originates near the proximal end of the basis and not at the distal end, as in other decapods. On these grounds Gurney (1924, 1938, 1942) and de Saint Laurent (1973) suggest a closer relationship between laomediids, upogebiids and the Anomala. This would mean the thalassinids are paraphyletic. However, Gurney (1924) has described a larval 3rd maxilliped in stenopodids which also resembles that of anomalan larvae. This character is apparently not homologous and thus it is also highly likely to have been evolved convergently in thalassinids and anomalans.

In contrast to the suggestions of Gurney (1924, 1938, 1942) and de Saint Laurent (1973), our results indicate thalassinidan monophyly (see also Poore, 1992). Otherwise, all apomorphic characters shared by the thalassinid species would be convergent, which is unlikely.

The monophyly of the Brachyura and the phylogeny of the 'Dromiacea'

The monophyletic origin of the Brachyura, and the phylogenetic position of the 'Dromiacea' in particular, have been debated for more than a century. Based on similarities in adult morphology, some authors have included the 'Dromiacea' in the Brachyura (e.g. Boas, 1880; Borradaile, 1907; Beurlen & Glaessner, 1930; Bouvier, 1940; Abrahamczik-Scanzoni, 1942; Balss, 1957; Glaessner, 1969; Warner, 1977; de Saint Laurent, 1980a). On the other hand, because dromiaceans lack several features of other brachyurans, there has been considerable doubt about whether they are 'true' brachyuran crabs at all and whether they should not be separated from the Brachyura (e.g. Ortmann, 1892, 1896; Gordon, 1963; Guinot, 1978, 1979; de Saint Laurent, 1979b).

The main arguments for the exclusion of dromiaceans or at least dromiids are based on investigations on sperm ultrastructure, larval development and RNA sequences (see Spears *et al.*, 1992).

Based on investigations of sperm ultrastructure, Jamieson (1990, 1991) has discussed the possible relationships between dromiids and true Brachyura. In general, dromiid spermatozoa differ from brachyuran spermatozoa in some characters which might be plesiomorphic, such as the relatively simple acrosome which is not embedded in the nucleus as in the true brachyuran sperm, and in some characters that represent dromiid apomorphies, such as the capitate form of the perforatorium. On the other hand, the tubular elements in the perforatorium of dromiids could be viewed as an apomorphy of dromiids and other brachyurans (Jamieson, 1990). The brevity of nuclear arms found in dromiids seems to be an apomorphic loss, since three nuclear arms are most likely part of the ground pattern of the Reptantia (see above). In summary, sperm ultrastructure provides no evidence for the exclusion of dromiids from the Brachyura but at least one character which might indicate close relationship.

Anomalan and thalassinid affinities of dromiaceans have been suggested by students of larval development, because the appearance of dromiacean zoea larvae differs from that of other brachyuran zoeae but resembles to a certain extent that of anomalans and thalassinids (e.g. Gurney, 1942; Williamson, 1974, 1988; Rice, 1980, 1983; Martin, 1991). The second telson process is regarded as having particular significance, as it is hair-like in zoea larvae of dromiids, thalassinids, anomalans and stenopodids, but is either a spine or absent in all other decapods (Rice, 1980, 1983). The phylogenetic study of Spears *et al.* (1992), based on 18S rRNA, also places the dromiids within the Anomala. We regard this as unlikely because the consequence of all these suggestions of either anomalan or thalassinid relationships would be that all brachyuran-like characters—some of them of high complexity—of dromiaceans were the result of convergent evolution.

Our own phylogenetic analysis suggests a monophyletic origin of all Brachyura including dromiaceans, because dromiaceans share a number of derived and apparently homologous characters (apomorphies) with 'true' crabs, and lack all anomalan apomorphies. We can show that the Brachyura is the sister-group of the Anomala. The larval characters of dromiaceans which resemble those of anomalans and thalassinids are plesiomorphic (e.g. the hair-like second telson process, see also Burkenroad (1981)) and inherited from the last common ancestor of Meiura (Brachyura and Anomala) or of Thalassinida and Meiura respectively. In other words, larval development in dromiaceans shows some plesiomorphic characteristics which are combined with brachyuran apomorphies in the adult animals. No venturesome hypotheses, such as transspecific gene-flow from interbreeding between a true anomalan with a true brachyuran (Williamson, 1988), are required to explain this blend. All organisms represent mosaics of plesiomorphic and apomorphic characters, and a faster evolution of adult than of larval characters has apparently taken place in the ancestral lineage (*sensu* Meier & Richter, 1992) of brachyurans.

It is beyond the scope of this paper to reconstruct phylogenetic relationships within the Brachyura, although some aspects can be discussed concerning the affinities and phylogeny of the 'Dromiacea'. In the classical works of Boas (1880), Ortmann (1892, 1896) and Borradaile (1907), the homolids are placed within the dromiaceans. This has been questioned by Williamson (1974), Guinot (1978, 1979) and Rice (1980) who propose a closer relationship between homolids and 'higher' brachyurans. A tentative first phylogenetic analysis based on our own investigations and data from the literature also suggests that dromiaceans are not a monophyletic taxon but a paraphyletic assemblage.

The homolodromiids branch off first from the brachyuran lineage and are the sister-group of all other brachyurans. They retained some plesiomorphic characters such as trichobranchiate gills, the relatively narrow sternite of the cheliped segment, and the upper position of the sternite of the segment of the 3rd maxillipeds (Milne Edwards & Bouvier, 1902; Doflein, 1904; Ihle, 1913; Martin, 1992). The next branch is formed by the homolids, which are the sister-group of dromiids and the 'true' Brachyura. Like the remaining crabs, homolids possess phyllobranch gills and the sternite of the segment of the 3rd maxillipeds is on the same level as the sternites of the pereion. The sternite associated with the chelipeds is wide. The dromiids, which branch off next, share with the rest of the Brachyura (their sister-group) the true operculiform 3rd maxillipeds and an elongate epipodite of the 1st maxilliped, which forms the gill cleaning flabellum (Balss, 1940). The epipodite of the 1st maxilliped in homolodromiids and homolids is relatively short and similar to that of astacids (Doflein, 1904; Milne Edwards & Bouvier, 1902), and is regarded as plesiomorphic.

This is a preliminary analysis and more detailed studies are necessary to show whether it holds true and whether homolodromiids, homolids and dromiids themselves are monophyletic.

Reptantian monophyly and a possible sister-group

That the Reptantia represent a monophyletic taxon can be shown by several apomorphies, and the doubts of Felgenhauer & Abele (1983) and Abele (1991) in this regard cannot be substantiated. The group 'Trichelida' of Beurlen & Glaessner (1930), which includes the dendrobranchiates, the stenopodids and some reptantians, is artificial and based on the plesiomorphic character of the first three pairs of pereiopods bearing chelae. It seems likely that three pairs of chelae are part of the decapod ground pattern (Christoffersen, 1988a) and that all other patterns are derived.

The identity of the sister-group of the reptantians is still unclear (see Burkenroad, 1981; Felgenhauer & Abele, 1983; Christofferson, 1988a; Abele, 1991). We agree with Kim & Abele (1990) and Abele (1991) that the stenopodids are the most likely candidates. Stenopodidea and Reptantia share several derived features, such as the reduced 1st pleomer, a similar form of foregut (Felgenhauer & Abele, 1989), and spermatozoa that lack the single acrosomal spike found in dendrobranchiates and carideans (Jamieson, 1991; Felgenhauer & Abele, 1991). The pleura of the 2nd pleon segment are a problem. In several reptantians, such as the polychelids, homarids, astacids, and the thalassinid genus *Naushonia* (Berggren, 1992), these pleura overlap those of the 1st and 3rd pleomer, corresponding to the situation found in carideans (including procarideans) (Burkenroad, 1981; Christofferson, 1988a). This is not the case in stenopodids where the pleura of the 2nd pleon segment overlap only those of the 3rd, as in dendrobranchiates. Large pleura of the 2nd pleon segment, which overlap the 1st and 3rd pleomer in combination with the characteristic hump formed by the 3rd pleomer, are probably part of the pleocyemate ground pattern. These structures could play a role in forming a brood chamber for the developing embryos. Many reptantians and stenopodids could have reduced the anterior expansion of the pleura of the 2nd pleon segment convergently.

The reptantian ground pattern

The morphology and habits of the Ur-reptantian have been the subject of some conjecture. Burkenroad (1963), for instance, speculated that the early reptantians were thalassinid-like animals. We do not think that this is plausible. Thalassinids are specialized burrowers which are derived from the reptant ground pattern in many respects. If Burkenroad's hypothesis was true, all corresponding characters in polychelids, achelates, homarids and astacids would be convergent and the plesiomorphic characters of the polychelids must all be secondary alterations towards a natant type of decapod. Both is very unlikely.

Suggestions concerning the ground pattern of the reptantians should be based on knowledge of the phylogenetic system. We draw the following conclusions about the morphology and habits of the stem species of the reptantians (crown-reptantians *sensu* Jefferies, 1979) from the distribution of characters in the phylogenetic system of the Reptantia.

The reptantian stem-species seems to have been a bottom dweller, since most apomorphies of reptantians can be seen as adaptations to a benthic life style: the dorso-ventrally flattened body, the strongly calcified cuticle, the stable connection between carapace and pleon, and the articulation of the pereiopods. The original reptantian probably had a similar overall appearance to recent homarids but was somewhat smaller. Apart from the reptantian apomorphies, it possessed a cylindrical carapace, three pairs of more or less equally sized chelae, a fused 7th and 8th thoracic sternite, strong mid-lateral hinges between all pleon segments, and an elongated triangular telson. The cuticle was less calcified than that of recent crayfishes but more so than that of the natant decapods. The animal swam by beating its pleopods which were equipped with an appendix interna. The triassic Clytiopsinae (Beurlen & Glaessner, 1930) correspond quite well with our reconstruction and we surmise that from such a form one branch led to recent deep-sea dwelling polychelids and another to the Eureptantia. The additional characters acquired by the eureptantians resulted in the modern reptantians with their great variety of morphology and habits.

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Note added in proof:
In a recent cladistic analysis using mainly spermatozoal data our view of brachyuran monophyly including the 'Dromiacea' has been supported (Jamieson, BGM. (1994) Phil. Trans. R. Soc. London B **345**: 373–393). However, Jamieson's suggestions concerning the relationships within the Brachyura differ considerably from our proposal.