A NEW HYPOTHESIS OF DECAPOD PHYLOGENY

BY

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ABSTRACT

A cladistic analysis based on external morphology was carried out on 60 taxa of decapod crustaceans. An analysis with unordered characters and one with ordered characters were both in agreement regarding the major relationships. The ordered analysis gave better resolution of more advanced clades, while the unordered analysis gave better resolution of more basal clades. None of the traditional groups Palinura, Anomura, and Macrura is monophyletic. A new classification of decapod crustaceans is proposed. Homarida and Astacida are closely related, as shown by the unique process on the ischium of their first pereiopods. Glypheoidea forms the sister group to Astacura, within an enlarged Astacidea. Achelata is the sister group to Meiura (Anomala + Brachyura) in a new clade, Eurysternalia, characterized by a unique antennular morphology and by the eponymous wide sternum of its members. Thalassinida emerge as the sister group to Eurysternalia, in a new clade, Sterropoda, characterized by fusion of the first segments of the thoracic limbs. The fractostern is interpreted to be a eureptant feature, and a possible burrowing habitus is posited for the ancestral Eureptantia.

RÉSUMÉ

Une analyse cladistique fondée sur la morphologie externe a été menée sur 60 taxons de Crustacés Décapodes. Les deux analyses, l'une utilisant les caractères non ordonnés, l'autre les caractères ordonnés étaient toutes les deux en accord sur les principales relations. L'analyse ordonnée a présenté une meilleure résolution des clades les plus avancés, tandis que l'analyse non ordonnée a donné une meilleure résolution des clades plus basaux. Aucun des groupes traditionnels Palinura, Anomura et Macrura n'est monophylétique. Une nouvelle classification des Crustacés Décapodes est proposée. Les Homarida et les Astacida sont étroitement apparentés, comme déjà montré par le processus unique sur l'ischium de leurs premiers péréiopodes. Les Glypheoidea constituent le groupe-frère des Astacura, à l'intérieur du groupe élargi des Astacidea. Les Achelata sont le groupe-frère des Meiura (Anomala + Brachyura) dans un nouveau clade, Eurysternalia, caractérisé par une morphologie unique de l'antennule et par le large sternum éponyme de ses membres. Les Thalassinida émergent comme le groupe-frère des Eurysternalia, au sein d'un nouveau clade, les Sterropoda, caractérisé par

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la fusion des premiers segments des appendices thoraciques. Le fractosterne est interprété comme un caractère de vrai rampant, et un habitus fouisseur possible est supposé pour l'Eureptantia ancestral.

INTRODUCTION

The order Decapoda is a remarkably diverse group of malacostracans, both morphologically and ecologically, and is a group of great economic and environmental importance. Gruner et al. (1993) estimate 10,000 species in the group, but actual numbers may be at least half again as large. The relationships within the order have been the subject of debate for decades; opinions differed in the early years as to which character(s) should be used to classify decapods, be it tail length (from Linnaeus until Boas, 1880), gill type (Huxley, 1878), number of chelae (Beurlen & Glaessner, 1930), or mode of locomotion (Boas, 1880). These sometimes simplistic approaches have now been replaced by more holistic methods using a wider variety of characters. De Saint Laurent (1979) believed that "les seuls critères de la morphologie externe . . . ne permettront pas de résoudre [les] relations phylétiques entre les différentes lignées de Décapodes", but we would argue that whilst larval, spermatozoal, and other characters are useful, external morphology can be enough to work out such relationships. We will nonetheless make reference to other characters and their agreement or disagreement with the scheme we propose based on external morphology.

Boas in his seminal work of 1880 divided Decapoda into Natantia for the swimming forms, and Reptantia for the walking forms. Although Reptantia is a monophyletic group, Natantia appears to be less valid and as long ago as 1907, Borradaile suggested that Natantia was actually paraphyletic. Burkenroad (1963) finally deconstructed Natantia, recognizing that the three groups of natant decapods are not closely related. Among Reptantia, Boas recognized six groups: Homaridae, Loricata, Eryonidae, Thalassinidae, Anomala, and Brachyura. Although some names have changed, all these groups are generally conceded to be monophyletic (cf. Martin & Davis, 2001). That belief will also be tested by this study.

It is perhaps a shame that at the turn of the twentieth century, authors reverted to the older system of H. Milne Edwards (1834), dividing Reptantia into Palinura, Astacura, Anomura, and Brachyura, which have remained as traditional groups. None of the four has remained unchallenged as a monophyletic taxon. Several authors (Abele, 1991; Forest & De Saint Laurent, 1989) have concluded that Palinura was untenable as a group, and others have considered the differences between Thalassinida and Anomala (which collectively make up Anomura) to be insurmountable (De Saint Laurent, 1979; Martin & Abele, 1986; Tudge, 1997). Scholtz & Richter (1995) separated the two parts of the Astacura, and there has been debate as to whether the Dromiacea, usually considered the most basal part of the Brachyura, may actually belong in the Anomala (Gurney, 1942; Spears et al., 1992). Again, this study will help to test these hypotheses.

The first cladistic study into the relationships of the Reptantia was carried out by Scholtz & Richter (1995) without the aid of computers. Characters that were ambiguous or contradicted the tree were sometimes omitted, biasing the results. They considered the fractured sternum, or fractostern, to be important and so separated true lobsters (Homarida, lacking the fractostern) from freshwater crayfish (Astacida, possessing the fractostern). Another conclusion they drew was that Achelata (spiny lobsters and their allies) was a near basal group among Reptantia. Schram's (2001) study was computerized but for the most part based on the data chosen by Scholtz & Richter (1995) and so, despite correcting some scorings, came to similar conclusions.

In 1975, a first specimen of *Neoglyphea inopinata* Forest & De Saint Laurent, 1975 was reported, representing an unexpectedly extant lineage of Glypheoidea, a group otherwise extinct since the Mesozoic. This discovery and the detailed description of the animal (Forest & De Saint Laurent, 1981) allowed the placement of Glypheoidea to be better ascertained relative to the other extant groups. Interest in reptant phylogeny was reinvigorated, and in a later paper, Forest & De Saint Laurent (1989) suggested that *Neoglyphea* and its relatives may belong as a sister group to Astacura (Astacida + Homarida) and that, therefore, Palinura is not monophyletic. That view was also supported by De Saint Laurent (1979), Scholtz & Richter (1995), and Schram & Ahyong (2002).

The emphasis of this study is to determine the monophyly of, and relationships between, the major groups of extant Decapoda. We have included representatives of every major group and as many sub-groups as possible within those groups. No effort was made to include fossil taxa, and we only include characters of external morphology visible with the naked eye or a dissecting microscope, so that museum specimens can be studied non-destructively. One exception to this principle is the inclusion of the gill form, which occasionally requires one to damage the specimen but is known for most, if not all, taxa.

METHODS

General

Taxa. — The taxa in this study represent twelve apparently monophyletic groups: Euphausiacea (out-group), Dendrobranchiata, Caridea, Stenopodidea, Polychelida, Homarida, Astacida, Glypheoidea, Thalassinida, Achelata, Anomala, and Brachyura (see Appendix I). No Linnaean rank is ascribed to these groups herein, in order to avoid fruitless debates over rank. While the focus of this study remains the relationships between the groups, some characters are only informative within certain groups, and some conclusions may be tentatively drawn.

Wherever possible, data are taken from personal observations. In a few cases, mostly due to incomplete specimens, data have been taken then from the literature. The most important example of this is *Neoglyphea inopinata*, where the published description (Forest & De Saint Laurent 1981, 1989) is so detailed as to make personal observation unnecessary for all but a few characters.

The only higher taxon within Eucarida omitted from this analysis is Amphionidacea. Whilst the identity of the sister group to Decapoda is still uncertain, being either Euphausiacea or Amphionidacea, these latter animals have a highly reduced and derived form, and their anatomy is not well known. For these reasons, and a lack of material, we excluded Amphionidacea from this study leaving Euphausiacea as the sole out-group.

Illustrations. — Specimens were dehydrated in an ethanol series and cleaned by sonication in preparation for scanning electron microscopy (SEM). They were then dried with an Emitech K850 critical-point drier, and coated with gold in a Jeol JFC-1100E Ion Sputtering Device. A Jeol JSM-35C scanning electron microscope was used and images were captured via SemAfore software. Photographs were taken with a Nikon Coolpix 995 digital camera.

Cladistic analysis. — Two analyses were performed, one with all the characters unordered and one with characters ordered. The unordered analysis makes fewer assumptions about the direction and manner of evolution, whereas the ordered analysis may allow better resolution. In the ordered analysis, characters 5, 6, 9-12, 16, 18, 19, 22, 23, 31, 32, 35, 36, 38, 41, 42, 54-58, 60, 61, 66, 69, and 70 were ordered, and step-matrices were constructed for characters 1, 2, 7, 14, 20, 21, 26, 34, 40, 45, 47, 48, 50, 65, and 67. This leaves eighteen characters with two states each, and only nine characters that could not be ordered because all the character state transitions seemed equally possible.

Analyses were carried out in PAUP* 4.0b10 (Swofford, 2002) by a heuristic search with ten replicates using random addition. All characters were un-weighted. Characters were optimized and trees examined with MacClade 4.03 PPC (Maddison & Maddison, 2001). Commands for calculating Bremer Support were produced using the "Decay Index PAUP File..." command of MacClade, which automates the method of Bremer (1994), and they were run in PAUP*. Constraint trees for the comparison of alternative topologies were constructed manually.

Character coding

The literature was studied for characters that could be used in this analysis. The characters are divided into body regions and are arranged in a broadly anterior-posterior order. An asterisk (*) marks each character that was ordered in the ordered analysis, and an obelisk (†) marks each character that had a step-matrix in the ordered analysis. The step matrices are summarized above the character states, and all unlisted changes have a value of one. Wherever appropriate, characters were combined into multistate characters to prevent dependence between characters. It should not be assumed that states numbered [0] are necessarily plesiomorphic states, or that other states are necessarily advanced. Typically, states of absence are coded as [0], even if this is not the plesiomorphic condition. If an alternative numbering of states logically allowed a character to be ordered in the ordered analysis, that numbering was adopted. It should be noted that where a character seems to represent two or more unrelated characters, e.g., char. 7, the scoring is usually such that this effect is lost in the ordered analysis, but the unordered analysis does not make the assumption a priori that there is no dependence between them.

$1^\dagger$ — Orbito-antennularis fossa. $[0] \leftrightarrow [1] = 2$, $[1] \leftrightarrow [4] = 2$.

[0] — absent: eyestalk not surrounded; [1] — formed by carapace and both antennae; [2] — formed by carapace and second antenna only; [3] — formed by carapace and first antenna only; [4] — formed by carapace only.

An orbito-antennularis fossa is considered to be present when the base of the eyestalk is surrounded by a ridge of the carapace and/or the basal articles of the antennae. *Pisidia* is considered not to possess an orbito-antennularis fossa, since there is not a complete ring around the eye [0]. A differentiation is made between orbits made from different body parts: whilst some use the carapace and the second antenna for the orbit [2], others use the carapace and both antennae [1]. *Latreilla*, despite having eyes on long stalks, does have an orbito-antennularis fossa, because the bases of the eyestalks are surrounded by projections of the carapace and the first antenna [3], albeit small ones. The orbits of *Thenus* involve neither set of antennae [4]. This character was scored as inapplicable [-] for *Thaumastocheles* and *Polycheles*, in which the eyes are absent.

$2^\dagger$ — Eyestalks. $[1] \leftrightarrow [2] = 2$, $[1] \leftrightarrow [3] = 2$.

[0] — cylindrical, without acicles; [1] — cylindrical, with acicles; [2] — flattened, without acicles, dorsal pigment; [3] — flattened, without acicles, terminal pigment.

Like Martin & Abele (1986), we were unable to differentiate between "true ocular acicles" and "pieces of the ocular plate", and have therefore scored any structure that resembles an ocular acicle as being one [1]. The flattened eyestalks of some callianassids [2] are very distinctive, with the pigmented area on the dorsal surface of the eyestalk. *Jaxea* also has flattened eyestalks but with the pigmented area at the end of the stalk [3]. The majority of taxa have eyestalks that are cylindrical, rather than flattened, and that lack acicles [0]. Despite the reported presence of ocular acicles (McLaughlin, 1983a, b) in some members of Lithodidae, they were absent in the specimen we studied (see also Richter & Scholtz, 1994). Some taxa, without evident eyestalks, were scored as inapplicable [-].

3 — Ocular ornamentation.

[0] — absent; [1] — setae; [2] — spines.

The pigmented areas of the eyes of decapods typically have a round shape but with an indentation on the median side. Some taxa, notably Achelata, have a row of setae along the edge of this indentation [1], and *Stenopus* has a row of spines in an identical location [2], in contrast to the usual condition, which lacks both spines and setae [0]. Whether the ocular hairs of crabs such as *Homola* are homologous is uncertain, since these animals are covered in setae across their entire bodies. *Maja* was scored as [0], since although the eyestalks are setose, the edge of the eye itself is not further augmented with setae. This character could not be scored for *Alpheus* where the eyestalks are concealed beneath the carapace.

4 — First antenna (antennule, A1) concealing chamber.

[0] — absent; [1] — present.

In many crabs, the antennule can be folded into a chamber [1] ("fossette" of Dana, 1856), concealing the flagella from the environment. In other taxa, the antennules cannot be hidden [0].

5* — A1 flagellar shape.

[0] — straight, sensilla not one-sided; [1] — straight, sensilla one-sided; [2] — strongly curved, sensilla one-sided.

This feature must be observed with the specimen immersed under liquid in order to make the sensilla float away from the flagellum and become visible. It can then be seen if the sensilla are scattered across the flagellum [0], or present only in a small area, on one side of the flagellum, and only towards the distal extremity [1 & 2] (fig. 1A, B, C). In many specimens, the larger flagellum is strongly curved, though its partner may remain straight [2] (fig. 1B, C), rather than their both being straight [1] (fig. 1A).

6* — A1 flagellar proportions.

[0] — annuli roughly 1 : 1, flagella longer than 2nd peduncle segment; [1] — annuli wider than long, flagella similar in length to 2nd peduncle segment; [2] — annuli roughly 1 : 1, flagella similar in length to 2nd peduncle segment.

Whilst in most groups, the flagella are long with annuli roughly as long as they are wide [0] (fig. 1A), some decapods have markedly shortened annuli, corresponding with a shortening of the whole flagellum to something like the length of the second peduncular segment (counting from the flagellum inwards; the other segments tend to be more variable in length) [1] (fig. 1B, C). In a few cases, e.g., *Pisidia*, the many short annuli have fused together or by some other means been replaced by a few segments, again with the annuli about as wide as long [2], but the shortness of the flagella, and the character state in close relatives in these cases, show that they are not homologous with state [0].

7† — A1 peduncle. [0] ↔ [3] = 2, [1] ↔ [2] = 2.

[0] — straight, with stylocerite; [1] — straight without stylocerite; [2] — Z-shaped with stylocerite; [3] — Z-shaped without stylocerite.

In some taxa, the peduncle is augmented by a spike, known as the stylocerite [0 & 2] (fig. 1B), whereas in others it is absent [1 & 3]. The shape of the peduncle also varies, with some being straight [0 & 1] and some being bent twice, resulting in a Z-shape [2 & 3] (fig. 1B).

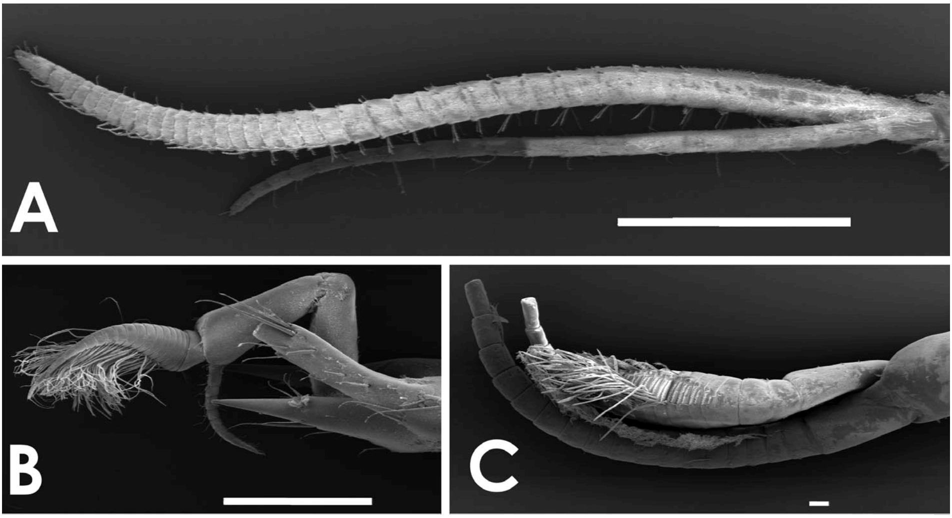

Fig. 1. A, SEM, lateral view of flagella of A1 of *Thalassina anomala* (Herbst, 1804) (anterior is left), showing straight flagella (char. 5), one-sided sensilla (char. 5, note concentration of sensilla at one end), and annuli as wide as long (char. 6) (scale bar represents 1 mm); B, SEM, lateral view of A1 of *Galathea squamifera* Leach, 1814 (anterior is left), showing Z-shaped peduncle (char. 7), strongly curved flagella (char. 5), one-sided sensilla (char. 5), short wide annuli (char. 6), flagella similar to second peduncle segment (char. 6) and stylocerite (char. 7) (scale-bar represents 1 mm); C, SEM, lateral view of flagella of the A1 of *Thenus orientalis* (Lund, 1793), showing strongly curved flagella (char. 5), one-sided sensilla (many sensilla missing) (char. 5), short, wide annuli (char. 6) (scale bar represents 100 μm).

8 — Scaphocerite.

[0] — present, articulating; [1] — absent or present, but fixed.

The scaphocerite is a mobile scale arising from the basal articles of the second antenna [0], which may be lost in some taxa [1]. The test of its presence is the existence of an articulation, rather than the mere presence of a spike. Animals such as *Eiconaxius*, in which there are two outwardly similar spikes, one fixed and one articulating, confirm that a simple spike is not homologous with an articulating scaphocerite.

9* — Second antenna (A2) size.

[0] — thin, circular cross-section; [1] — much enlarged, circular cross-section; [2] — much enlarged, flattened, flagellum reduced to a single segment.

In most decapods, the flagella of the second antenna are long, slender, whip-like structures comprising a large number of annuli [0]. In Palinuridae and Synaxidae, the flagellum is significantly thicker [1], and in Scyllaridae, the flagellum is reduced to a single spatulate segment [2].

10* — A2 basal articles.

[0] — in carapace notch; [1] — separate from carapace; [2] — fused with carapace.

Whilst in most taxa there is no connection between the second antenna and the carapace [1], a few taxa have the two fused together [2], and members of Anomala have a distinctive notch in the lateral side of the carapace into which the basal articles of the second antenna fit [0].

11* — Antennal gland opening.

[0] — lateral; [1] — ventral; [2] — dorsal.

In some thalassinidans, the opening of the antennal gland is directed outwards [0], away from the mouthparts, and in Polychelida, the renal process of the antenna directs the opening dorsally [2], where it can be blocked off by the antennule. All other decapods have the opening of the antennal gland in a ventral position [1].

12* — Epistome.

[0] — point contact or no contact with carapace; [1] — line contact with carapace; [2] — fused with carapace.

Schram & Ahyong (2001) flagged the possible phylogenetic utility of the articulation between carapace and epistome. Lobsters, for instance, have a point articulation [0], whereas *Thaumastocheles*, crayfish, and *Neoglyphea* have a longer contact [1]. In achelates and some crabs, the basal articles of the second antenna are fused with the carapace (char. 10, state [2]), making it impossible to tell what contact the epistome makes with the carapace, and so they are scored as inapplicable [-] for this character. In *Palinurus vulgaris* Latreille, 1804, the boundaries of the basal articles are still clear, despite the fusion, and the fusion of the epistome to the carapace can be clearly seen [2]. Since we could see no fusion of the carapace to the epistome in anomalans, we have scored them as lacking such contact [0], although it is reported that this fusion does occur, but is hidden (Burkenroad, 1981; Števčić, 1995).

13 — Anterior mandible articulation.

[0] — short; [1] — long.

A long articulation, limiting the mandible to movement around a single axis [1], was found in most members of Reptantia and a short, more flexible articulation [0] was found in all other taxa.

14† — Mandibular form. [0] ↔ [3] = 2, [1] ↔ [3] = 2.

[0] — no palp, weak or no molar process; [1] — straight palp, weak or no molar process; [2] — curved palp, weak or no molar process; [3] — curved palp, strong molar process.

The mandible has a long, often serrate, cutting edge, and may be augmented by a molar process of various shapes, closer to the mouth. We do not believe that the form of the molar process is important at this level. The mandibular palp of natant forms is typically straight, and directed forwards [1], whereas in other animals, the palp is curved around the mandible [2 & 3]. Some animals lack the palp altogether [0]. The palp of *Palinurus vulgaris* is predominantly straight, but does follow the line of the mandible and curve towards the tip, and is therefore scored as [3].

15 — Third maxilliped (mxp3) dactylus tip.

[0] — sharp; [1] — blunt.

16* — Mxp3 overall form.

[0] — pediform, as long as pereiopods; [1] — pediform, short, straight; [2] — pediform, short, bent; [3] — operculiform, bent.

Primitively, mxp3 is undifferentiated from other thoracopods and is of a similar length to them [0], but others have mxp3 considerably shorter than P1-5. Of these, some are basically straight (so that it cannot bend to lie flat against itself) [1] and some are bent so that distal segments can lie flat against the proximal segments [2]. The operculiform condition, where third maxillipedes are flattened and form a plate together over the other mouthparts [3], is a special case of this.

17 — Mxp3 exopod.

[0] — absent; [1] — present, no flagellum; [2] — present with straight flagellum; [3] — present with double-bent flagellum.

The third maxilliped comprises an endopod and an exopod, except in the Hippoidea, where the exopod is lacking [0]. The exopod, when present, may be unadorned [1], or may possess a flagellum, which in turn may be straight (in line with the exopod) [2], or may be double-bent [3] (see Scholtz & Richter, 1995).

18* — Crista dentata.

[0] — absent; [1] — present; [2] — present with accessory tooth or teeth.

The crista dentata is only scored as absent [0] when no trace of it can be found. In many crabs, the crista dentata is strongly reduced, but can still be seen, and is therefore scored as [1]. Accessory teeth are found [2] in many paguroids. McLaughlin & Lemaître (1997) report that *Neoglyphea inopinata* has several accessory teeth, but this is incorrect. Several pointed projections are present in the diagrams of Forest & De Saint Laurent (1981), but these are described as "parasites encore indéterminés", and are not accessory teeth. All specimens of *N. inopinata* examined by us lack accessory teeth.

19* — Thoracic sternite widths.

[0] — 3rd and following thoracic somites narrow; [1] — 3rd thoracic somites narrow, following thoracic somites wide; [2] — 3rd and following thoracic somites wide.

A sternite was scored as 'wide' when the coxae of the associated appendage were unable to touch; a sternite was scored as 'narrow' when the coxae of the associated appendage were able to touch or nearly so. To code the width of every thoracic sternite separately would be to over-weight this character complex; the widths of the fourth to eighth thoracic somites are linked. See fig. 2 for examples.

20† — Pereiopods 1-3. $[1] \leftrightarrow [2] = 2, [1] \leftrightarrow [3] = 2, [2] \leftrightarrow [3] = 2.$

[0] — all similar size; [1] — first pereiopod (P1) enlarged; [2] — second pereiopod (P2) enlarged; [3] — third pereiopod (P3) enlarged.

Among decapods, at most one pair of pereiopods is greatly enlarged relative to the other pairs. This is typically the first pereiopod [1], but can also be the second (as in some Caridea) [2] or the third (as in stenopodids) [3]. Despite its right P1 being slightly enlarged, *Lithodes* is scored as having no pair of pereiopods greatly enlarged [0].

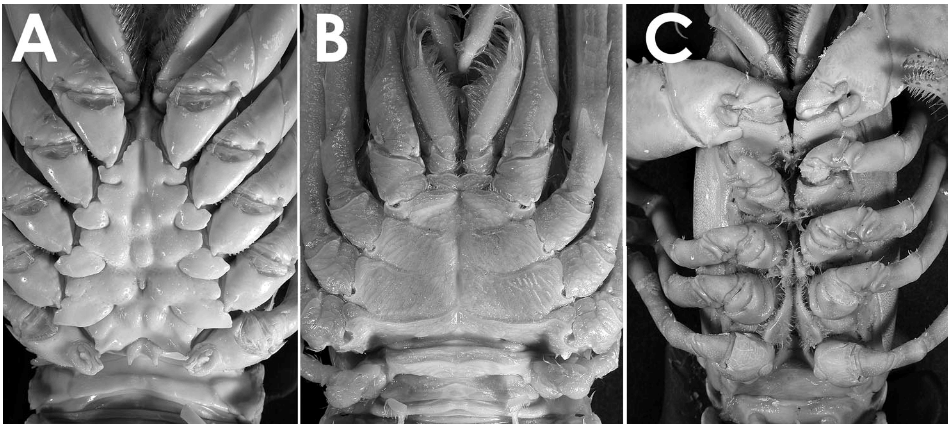

Fig. 2. Character 19: reptant sterna (anterior is up in each case). A, wide sternum with narrow mxp3 sternite [1] of *Panulirus vulgaris* Latreille, 1804; B, wide sternum with wide mxp3 sternite [2] of *Agononida incerta* (Henderson, 1888) (Note also the separation between last two thoracic sternites (fractostern)); C, narrow sternum [0] of *Homarus gammarus* (Linnaeus, 1758).

21† — Chelae. [0] ↔ [1] = 3, [0] ↔ [2] = 2, [1] ↔ [3] = 2, [1] ↔ [4] = 2, [3] ↔ [4] = 2.

[0] — achelate; [1] — P1, P2, and P3 chelate; [2] — P1 and P2 chelate, P3 achelate; [3] — P1 chelate, P2 and P3 achelate; [4] — P2 chelate, P1 and P3 achelate.

Many studies (Martin & Abele, 1986; Poore, 1994; Tudge et al., 2000) have coded the chelae of each pereiopod separately, effectively over-weighting this character. A complete loss of chelae (with the exception of the 'grooming chela' of the fifth pereiopod) has occurred independently in several lineages (*Procaris*, *Neoglyphea*, Achelata, and Hippoidea) and must be considered a single evolutionary step. The chelae on the fourth and fifth pereiopods seem to be independent of the first three chelae, and are dealt with elsewhere (characters 35 and 36). For the purposes of this character, semi-chelate pereiopods are scored as chelate, but sub-chelate (dactylus folding back against unmodified propodus) pereiopods are scored as achelate.

22* — Sternite-coxa articulation.

[0] — anterior-posterior movement; [1] — medio-lateral movement, joints not 'reversed'; [2] — medio-lateral movement, joints 'reversed'.

One key advance related to the reptant lifestyle is the change of orientation of the pereiopods: reptants walk with legs that move to the side of the body [1 & 2], whereas natants swim with legs that move forwards and backwards along the midline of the animal [0]. Scholtz & Richter (1995) pointed out a further change in Anomala where the joints between the coxae and sternites of the pereiopods are 'reversed', so that a protrusion from the sternite fits into a cavity in the coxa [2], rather than a protrusion from the coxa fitting into a cavity in the sternite [1].

23* — Dactyli.

[0] — dactylus and propodus flattened laterally; [1] — sharp, claw-like; [2] — spatulate, dactylus moves across propodus.

Some thalassinidans have their dactyli and propodi flattened laterally as an adaptation to burrowing [0]. Hippoids and raninoids also have flattened dactyli for burrowing, but these are flattened in a different manner, with the dactylus sliding across the face of the propodus [2]. The similarity of hippoid and raninoid dactyli must be an example of convergence since the two cannot be closely related. Most taxa retain sharp, pointed chelae [1].

24 — Male pereiopods.

[0] — without hooks; [1] — with hooks.

The presence in males of hooks on the third and/or fourth pereiopods [1] is an autapomorphy of crayfishes of the family Cambaridae (Hobbs, 1974; Scholtz, 2002); all other decapods lack such hooks [0].

25 — P1 twist.

[0] — horizontal (internal) dactylus; [1] — vertical dactylus; [2] — horizontal (external) dactylus.

In order to ascertain the amount of twist along the length of P1, the limb must be held in the same position in all taxa, but this is not always possible. For instance, many crabs cannot extend their P1 directly forwards. Three positions were therefore studied: the first is with P1 directly forward, the second is with P1 out sideways, and the third is with the P1 folded in and the dactylus close in front of the head of the animal. It was noticed that those animals in which the dactylus was vertical when forwards and sideways, held P1 with the dactylus at 45° between upwards and forwards [1], but those whose dactylus was horizontal when forwards and sideways, hold P1 with the dactylus at 45° between upwards and backwards [0]. It is possible to score this character for taxa which cannot adopt any one of the above positions by reference to different positions.

The shrimp *Macrobrachium* has a horizontal dactylus, but with the mobile finger on the external side [2]. It is unclear whether this is due to a twist in the P1 or because the condition is not homologous. This character was scored as inapplicable [-] for those taxa in which the propodus-dactylus articulation is not a double-hinge (char. 26, states [0] and [2]).

26† — P1 articulations. [0] ↔ [3] = 2, [1] ↔ [2] = 2.

[0] — carpus-propodus and propodus-dactylus single-jointed (pivot point); [1] — carpus-propodus single-jointed, propodus-dactylus double-hinged; [2] — carpus-propodus double-hinged, propodus-dactylus single-jointed; [3] — carpus-propodus and propodus-dactylus double-hinged.

27 — P1 ischium process.

[0] — no process; [1] — long process; [2] — short process.

The joint between the coxa of the first pereiopod and its associated basis and ischium may be augmented by an expansion of the ischium. In some taxa, the process is a bulge on the medial edge of the ischium and is therefore of a rounded curving shape [2]; whereas in others, the process is longer than wide, with straight parallel edges, and a rounded tip [1] (fig. 3). As the joint moves, this process slides across the face of the coxa, giving the joint extra stability.

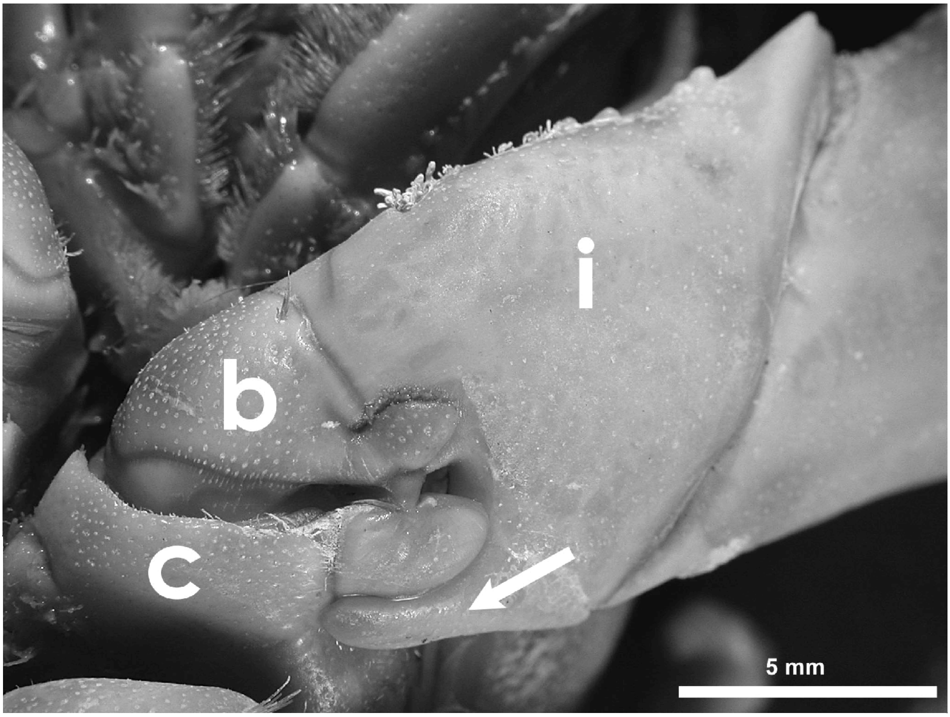

Fig. 3. First pereiopod (P1) of *Homarus gammarus* (Linnaeus, 1758) showing the process from the ischium strengthening the basis-coxa joint (char. 27 [1], arrow), with: c, the coxa; b, the basis; and, i, the ischium. See fig. 2a for the plesiomorphic state, without this process.

28 — P1 ischium-merus articulation.

[0] — oblique; [1] — perpendicular; [2] — curved.

The perpendicular nature of this articulation [1] is a synapomorphy for Astacida in contrast to the oblique articulation of Homarida and other taxa [0], but other states exist among Decapoda. Most thalassinidans possess a curving articulation [2], which cannot be considered either oblique or perpendicular.

29 — P1 basis and ischium.

[0] — articulating; [1] — fused.

30 — P2 setal row.

[0] — absent; [1] — present.

Whilst the presence of a setal row on the merus of P2 is a synapomorphy of the Thalassinida, a few other taxa also possess such a feature, chiefly burrowing forms such as *Emerita* and *Raninoides*. Interestingly, *Neoglyphea inopinata* also bears a similar row of setae, suggesting the possibility of a burrowing habitus.

31* — Fusion P3-5.

[0] — basis, ischium, and merus free; [1] — basis-ischium fused, merus free; [2] — basis-ischium-merus fused.

32* — Gonopores.

[0] — coxal in both sexes; [1] — male coxal, female sternal; [2] — sternal in both sexes.

33 — Seventh thoracic sternite.

[0] — not enlarged and lobate; [1] — enlarged and lobate.

As outlined in Scholtz & Richter (1995), the 7th thoracic sternite of thalassinidans has a distinctive shape [1], compared with that of other taxa [0].

34† — Fourth and fifth pereiopods (P4 and P5). [0] ↔ [1] = 2, [0] ↔ [2] = 3, [0] ↔ [3] = 3, [0] ↔ [4] = 2, [1] ↔ [4] = 2, [2] ↔ [3] = 2, [2] ↔ [4] = 3, [2] ↔ [5] = 2, [3] ↔ [5] = 2, [4] ↔ [5] = 3.

[0] — both normal size and position; [1] — P4 normal, P5 reduced, dorsal; [2] — P4 normal, P5 reduced, internal; [3] — both reduced, P5 dorsal; [4] — both reduced, P5 normal position; [5] — both normal size, P5 dorsal.

The size and position of the two most posterior pereiopods seem to be functionally linked. Outside Meiura, they are of similar size and position among all taxa [0], but in Meiura, various positions and degrees of reduction are seen. State [2] covers specimens where P5 is held within the branchial chamber as well as those where P5 is held on the dorsal surface of the carapace, but is capable of being held within the branchial chamber. Although the resting position is the dorsal position (Fleischer et al., 1992), specimens are often found with P5 held internally, presumably in an attempt to clean their gills of the chemical used to kill them.

35* — P4.

[0] — achelate; [1] — semi-chelate; [2] — chelate.

36* — P5.

[0] — achelate; [1] — female chelate or semi-chelate, male achelate; [2] — male and female chelate or semi-chelate.

Whilst Scholtz & Richter (1995) found a ‘grooming chela’ ([1] or [2]) on most reptants, we were unable to find such a chela in Homarida, or in most crabs. It is clear from their figures (such as their fig. 3c) that they used an unusual definition of ‘chela’, and may well be referring to a function rather than a structure. A pair of toothed ridges is visible on the diagram, but this is not a chela, in our opinion. The chela of *Lauridromia* is explicable by the sponge-carrying behaviour of this group, rather than a grooming function.

37 — P5 rasp.

[0] — absent; [1] — present.

38* — Seventh and eighth thoracic, and 1st pleonic somites (TS7, TS8, and AS1).
[0] — TS7 fused to TS8, AS1 free; [1] — no fusion; [2] — TS7 free, TS8 fused to AS1.

The fractostern of Scholtz & Richter (1995) is represented here by states [1] and [2]. Animals that lack the fractostern are scored as [0]. Further distinction is made between those fractosternalians wherein the freely mobile eighth thoracic somite is fused with the first pleonic somite (hippoids and most paguroids) [2], and those wherein this fusion has not occurred [1].

39 — Rostrum.
[0] — absent or small; [1] — present, long.

We take the opinion that a small rostrum is closer to no rostrum at all [0] than it is to a long, serrate rostrum, such as that found in some carideans [1], and so we have scored many taxa as [0] which have traditionally been scored as possessing a rostrum. This also avoids arguments about whether a peculiar structure such as the bifid rostrum found in polychelids [0] is really homologous with another, such as the rostrum in homarids [1].

40† — Carapace calcification. $[0] \leftrightarrow [2] = 2$, $[0] \leftrightarrow [3] = 2$.
[0] — soft; [1] — uniformly calcified; [2] — branchiostegites soft, otherwise calcified; [3] — posterior carapace and branchiostegites soft.

In natant decapods, the carapace is typically quite flexible, or soft [0], whereas a typical reptant has a hard, calcified carapace [1]. Some reptants, however, have a carapace that is basically hard, but with soft patches over the gills [2], or soft both over the gills and in the posterior part of the carapace [3].

41* — Carapace shape.
[0] — elongate, subcylindrical; [1] — elongate, depressed; [2] — as wide as long, depressed.

42* — Carapace transverse groove.
[0] — absent; [1] — shallow; [2] — deep.

43 — Carapace postero-dorsal margin.
[0] — two corners or curved inwards; [1] — V-shaped towards anterior; [2] — W-shaped; [3] — straight or curving outwards.

A number of forms are seen in the posterior margin of decapod carapaces. The most common is for a curving, concave line, often with two more strongly curving parts [0]. When accentuated, these curves become "cardiac notches", such as in alpheid shrimp, but there is no qualitative difference between taxa with and without cardiac notches. Polychelids have a strongly concave V-shaped margin [1] and *Thalassina* has a distinctive spike projecting centrally and a notch on either side, resulting in a W-shape [2]. The notches of *Thalassina* are probably not homologous with those in other taxa. In some taxa, the posterior margin loses its anterior curvature and may even curve outwards slightly [3].

44 — Carapace posterior suture or ridge.

[0] — absent; [1] — present.

Whilst most decapods lack any ridge or suture on the posterior portion of the carapace [0], some groups have a clear suture or ridge running longitudinally along the mid-line [1]. This is one of the characters used by Hobbs (1974) to distinguish Nephropoidea (= Homarida) from Astacoidea (= Astacida).

45† — Carapace holding device. [1] ↔ [2] = 2, [1] ↔ [3] = 2, [2] ↔ [3] = 2.

[0] — not held down; [1] — knob of TS8; [2] — knob of AS1; [3] – fusion with sternum.

Scholtz & Richter (1995) noted the difference between the device holding the carapace down in Polychelida [2] and its analogue in Achelata [1], as to which somite is the source of the knob. Some crabs also have their carapaces held down, but in this case by fusion of the carapace to the sternum around the bases of the pereiopods [3]. In other decapods, the carapace is not held down and can be lifted away from the body at the posterior end [0].

46 — Lineae.

[0] — absent; [1] — present.

We could see no compelling reasons to differentiate the various types of lineae reported among Decapoda ('linea thalassinica', 'linea anomurica', 'linea homolica', and 'linea aeglica'), and so have simply chosen to score the lineae as present [1] or absent [0], disregarding other aspects. Similarly, Poore (1994) concluded that the lineae anomalica and thalassinica are probably homologous. Scholtz & Richter (1995), however, considered at least the linea thalassinica and the linea anomurica to be different.

47† — Gill type. [0] ↔ [3] = 2.

[0] — dendrobranch; [1] — trichobranch; [2] — phyllobranch; [3] — thalassinobranch; [4] — 'match-stick'.

Following the suggestion of Martin & Abele (1986), a separate state of 'thalassinobranch' is used to distinguish those gills that appear trichobranch near the base but have flattened plates arranged longitudinally nearer the tip [3], found exclusively in *Thalassina anomala* (Herbst, 1864). Also, a distinction was made between two types of trichobranch gill; in a few taxa, the gill filaments have bulbous tips, so resembling match-sticks [4] (fig. 4B), whereas others have simpler, tapering ends [1] (fig. 4A). The difference is subtle but, we believe, useful.

Dendrobranch [0] gills are tree-like structures found in prawns, and phyllobranch [2] gills comprise flattened lamellae. The term "phyllobranch" in fact covers two distinct morphologies, one found in caridean shrimp, and one in higher taxa, such as brachyuran crabs. The palaemonid phyllobranch has two efferent vessels in cross-section and the lamellae are relatively long, whereas the brachyuran phyllobranch has a single efferent vessel and shorter, rounded lamellae (Taylor & Taylor, 1992). The distinction between these two types is difficult to see under a dissecting microscope, and is not maintained here, although they are clearly not homologous. Felgenhauer & Abele (1983) considered there to be no real difference between phyllobranchiate and trichobranchiate gills, in light of intermediates between the two.

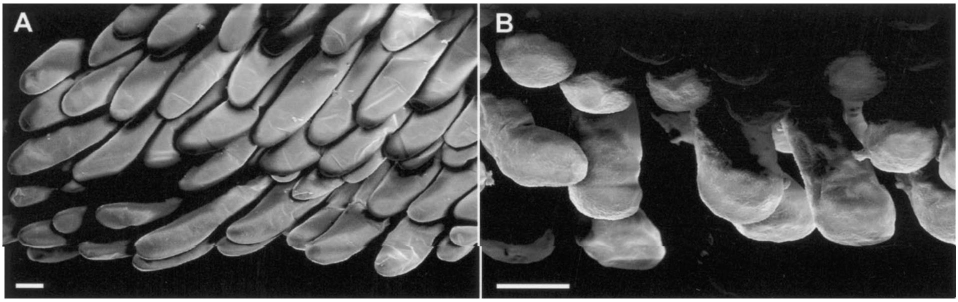

Fig. 4. A, SEM of trichobranchiate gill of *Palinurellus gundlachi* Von Martens, 1878; scale bar is 100 μm; B, SEM of "match-stick" gill of *Panulirus regius* De Brito Capello, 1864; scale bar = 10 μm. Some deformation has occurred during preparation.

48[†] — 'Waist': first pleonic somite. [0] ↔ [3] = 2, [1] ↔ [2] = 2.

[0] — long, wide; [1] — short, wide; [2] — long, narrow; [3] — short, narrow.

Whilst a narrow 'waist' has been seen as a distinguishing feature of the Thalassinida, the true situation is more complicated than that. The first pleonic somite is also markedly narrower than the following somites in most of the Meiura [2 & 3]. The shortening of the first pleonic somite [1 & 3] in pleocyemates was noted by Burkenroad (1981).

49 — Lobes overlapping carapace.

[0] — absent; [1] — from first pleonic somite; [2] — from second pleonic somite.

The presence of a lobe from the 1st pleonic somite overlapping the carapace [1] is widespread among Decapoda, but is not found in *Euphausia* [0]. Some thalassinidans, together with all meiurans lack this lobe [0], and hippoids have a similar lobe, but emanating instead from the 2nd pleonic somite [2]. There may be some dependence between this character and char. 45, since the knob present in polychelids derives from the overlapping lobe from the first pleonic somite.

50[†] — Symmetry. [0] ↔ [3] = 2, [1] ↔ [4] = 2, [3] ↔ [4] = 2.

[0] — symmetrical; [1] — chelae asymmetrical, pleon symmetrical; [2] — pleon and chelae asymmetrical; [3] — female asymmetrical, male symmetrical; [4] — pleon asymmetrical.

In contrast to the typical symmetrical condition of decapods [0], hermit crabs (and their putative descendants) have asymmetrical pleons, apparently in order to conform to asymmetrical mollusk shells [1 & 2]. Moreover, they often, but not always, have asymmetrical chelae [2]. Some other decapods also have asymmetrical chelae but symmetrical pleons [1]. The handedness of the animals was not considered because, in most cases, few specimens of each taxon were available for study and the handedness of a species can be variable; therefore, any observation made on the basis of two or three specimens could be misleading. Lithodids are unusual in having symmetrical males and asymmetrical females [3]. We felt that it would be better to code this as a separate state rather than scoring *Lithodes* as polymorphic for this character.

51 — Egg fate.

[0] — cast free; [1] — pleopodal incubation.

This is the defining apomorphy of Pleocyemata as erected by Burkenroad (1963). Euphausiaceans and dendrobranchiates do not generally incubate their eggs [0], but all other decapods brood the eggs on the pleopods of the female until hatching [1].

52 — Pleon cross-section.

[0] — laterally compressed; [1] — dorso-ventrally flattened.

This character was scored as inapplicable [-] for most hermit crabs, where the pleon is uncalcified and flexible, and may assume any cross-sectional shape, and also for *Callianidea* whose pleon, despite retaining clear segmentation, is flexible. All other reptants have a flattened pleon [1], compared with the laterally compressed pleon of the Natantia [0].

53 — Sexual dimorphism of pleon.

[0] — male and female pleon same size; [1] — female pleon wider than male pleon; [2] — dimorphism of telson only.

Most decapods have a similar form in both male and female [0], but almost all crabs show strong sexual dimorphism in the pleon with the male having a reduced, narrow pleon but with the female retaining a wider pleon for the incubation of eggs (see char. 51) [1]. There is sexual dimorphism in the symmetry of the pleon of lithodids but not a significant difference in size. This asymmetry is dealt with elsewhere (char. 50). Since *Calocaris macandreae* Bell, 1846 is hermaphroditic, it is scored as inapplicable [-]. The pleons of male and female *Pylocheles* are similar, but the telsons are of markedly different shapes [2].

54* — Pleonic flexion.

[0] — straight or obtusely angled - macrurous; [1] — flexed in mid-pleon (3rd somite) - anomurous; [2] — flexed in first two pleonic somites - brachyurous.

The Caridea are often characterized as having a bend in the second somite of the pleon, but similar states are found in other groups, e.g., Stenopodidea, and there does not seem to be a firm distinction from the condition in which the pleon is perfectly straight. These are, therefore, all scored equally (state [0]). Also, while many long-tailed decapods are capable of carrying their pleon flexed below them, and may habitually do so, they have been scored as [0] if it is possible for them to extend their pleon to a straight position. So, *Scyllarus* is scored as [0], but the superficially similarly-flexed *Pylocheles* is scored as [1] because it cannot fully straighten its abdomen. Most crabs and some other 'higher' decapods have their pleon flexed very close to the thorax [2]. This character was scored as inapplicable [-] for those taxa with an uncalcified pleon (see char. 55).

55* — Pleonic calcification.

[0] — strong with complete sternites; [1] — strong with incomplete sternites; [2] — weak with incomplete sternites.

In the 'lower' Decapoda, the somites of the pleon are quite distinct, and each has a sternite across the full width of the ventral surface [0]. In hermit crabs, the pleon is decalcified and the sternites are lost completely [2]. A third state exists in many anomalans and some thalassinidans, wherein the somites of the pleon are still distinct, but the sternites are either absent or fail to reach fully across the ventral side [1].

56* — Pleonic hinges.

[0] — slight; [1] — prominent; [2] — hidden.

Burkenroad (1981) confirms that Dendrobranchiata have prominent pleonic hinges [1], as well as Polychelida and Achelata. The condition in other taxa is for the hinges to be simpler joints which do not stand out from the surface of the pleon [0]. Members of Astacidea have strong hinges, but they are hidden under expansions of the pleura [2], except for one or two joints, particularly that between the first and second pleurite.

57* — Pleopods.

[0] — biramous with appendix interna; [1] — biramous without appendix interna; [2] — uniramous without appendix interna.

A structure resembling an appendix interna was seen on *Agononida*, but this is interpreted to be a segment of an unusual uniramous pleopod [2]. The form of the pleopod was scored in all cases for females, since the males of many species, notably Brachyura, have reduced pleopods. This also removed the possibility of confusing an appendix masculina with an appendix interna, whose structures are identical (De Saint Laurent, 1988).

58* — Female 1st pleopod (Pl1).

[0] — present, similar to other pleopods; [1] — present as a uniramous filament; [2] — absent.

59 — Combined male gonopod.

[0] — absent: Pl1 separate from Pl2; [1] — present: Pl1 passes through Pl2.

The distinctive gonopod of brachyuran crabs comprises a filamentous part of the second pleopod (Pl2) passing through a channel made in the first pleopod (Pl1) [1]. In no other group do the two pleopods interact in this way [0].

60* — Male Pl1.

[0] — biramous; [1] — endopod reduced; [2] — uniramous; [3] — absent.

This character was scored as inapplicable [-] for those taxa in which the first and second pleopods are linked (char. 59, state [1]).

61* — Male Pl2.

[0] — absent; [1] — uniramous; [2] — biramous, without spiral element; [3] — biramous, with spiral element.

The spiral element [3] is a characteristic feature of astacoid crayfish; other taxa lack such an element [1], have uniramous first pleopods [2], or lack the second pleopod altogether [0]. This character was scored as inapplicable [-] for those taxa in which the first and second pleopods are linked (char. 59, state [1]).

62 — Second pleomere pleura.

[0] — normal size, overlap third; [1] — expanded, overlap first.

The expansion of the second pleonic pleura has been seen as an apomorphy of Caridea, but an identical condition occurs in other groups, such as Polychelida and Astacidea. This character was scored inapplicable [-] for those animals with non-calcified pleons (char. 55).

63 — Pleonites.

[0] — rounded; [1] — pointed.

This character was scored inapplicable [-] for those animals with non-calcified pleons (char. 55), and also for those crabs in which the somites of the pleon are fused together. The state seen in some Brachyura and Thalassinida in which the lateral borders of the pleonites are straight seems to be homologous with the rounded state [0] seen in other members of the groups. It would also be unfair to code the straightened pleonites as a separate state since this is already implied by the reduction of the pleon in crabs; *Raninoides*, the only crab in this study not to have a forward-flexed pleon clearly has rounded pleonites.

64 — Sixth pleonic somite.

[0] — without furrow; [1] — with transverse furrow.

Richter & Scholtz (1994) illustrate a furrow running transversely across the tergite of the 6th pleonic somite, found in asymmetrical hermit crabs [1], and also in the male of *Pylocheles* (scored as [1]). Taxa outside Paguroidea have no such furrow dividing the sixth pleonic tergite [0].

65† — Telson. [0] ↔ [2] = 2, [0] ↔ [3] = 3, [0] ↔ [4] = 2, [1] ↔ [3] = 2, [2] ↔ [4] = 2, [3] ↔ [4] = 3.

[0] — narrow, straight, tapering; [1] — short, rounded, margin entire; [2] — short, rounded, margin indented, no X-sutures; [3] — short, rounded, margin indented, X-sutures present; [4] — convex, pointed, smooth.

A shorter, rounded telson is characteristic of Eureptantia [1 to 3], in contrast with the narrower, longer telson of the natant groups and Polychelida [0]. Anomala show further changes with an indentation at the terminal end of the telson [2 & 3], and the presence of cross-shaped sutures between the various plates which comprise the telson [3]. Hippoids are unusual in having a relatively long, pointed telson, but this is distinguished from that of natant and polychelid decapods by its smoothness and convexity [4]. The hippoid telson is part of a suite of adaptations towards efficient digging (Paul, 1981), and cannot be homologous with state [0].

66* — Telson spines.

[0] — absent; [1] — present, articulated; [2] — present, some articulated, some fixed; [3] — present, fixed.

Various taxa possess spines along the edge of the telson, and the homologies among them are unclear. There does seem to be a distinction to be made, however, between fixed spines [3], which are simple extensions of the telson cuticle, and articulated spines [1], which require the presence of joints at their bases. Some taxa possess both fixed spines and articulating spines at different locations on the telson [2]. Scholtz & Richter (1995) considered the spines on the astacid telson to be distinct from those of homarids based on their position on the telson, but we consider this to be better explained by a prolongation of the telson in Astacida compared to the situation in the Homarida, and that the spines are indeed homologous.

67† — Uropod form. [1] ↔ [2] = 2, [1] ↔ [3] = 2, [1] ↔ [4] = 2, [2] ↔ [3] = 2, [2] ↔ [4] = 2, [3] ↔ [4] = 2.

[0] — forming tail-fan; [1] — styliform; [2] — rasps; [3] — de-specialized; [4] — flat, recurved.

The telson and uropods of decapods fulfil a number of functions. In most taxa, they form a tail fan, used for escaping backwards with a sharp flick of the tail (caridoid escape reaction). These taxa have relatively long and flat telsons and uropods [0]. *Thalassina* is a burrowing animal in which the uropods are reduced to thin, styliform structures, useless for such an escape mechanism [1]. Many hermit crabs have rasps on the uropods in order to grip the sides of the shell that they inhabit [2], and hippoids have flattened but recurved uropods used in digging [4]. Crabs and some anomalans have telsons and uropods that are 'de-specialized', meaning that they are reduced (or absent) and apparently serve no major function [3]; this is likely to have happened convergently in more than one lineage.

68 — Distal telson cuticle.

[0] — as hard as proximally; [1] — softer than proximally; [2] — soft cuticle on telson, but not uropods.

Although soft tail fans are found convergently in both Astacida and Achelata, we found no good distinction between the two and both are scored as [1]. Whilst many crayfish do not have notably softened uropods, their telsons remain soft distally [2].

There is no conflict between this character and char. 70, since a distally soft uropod may still possess a clear line of folding, as will be seen by comparing the endopod and exopod of a parastacid crayfish uropod. Both are soft distally, but only the exopod has a diaeresis.

69* — Uropods.

[0] — biramous; [1] — uniramous; [2] — vestigial knob; [3] — absent.

70* — Diaereses.

[0] — no diaereses; [1] — exopod with spinose diaeresis; [2] — exopod and endopod with spinose diaereses.

The presence of a diaeresis on the uropodal exopod, with a spinose and distinct margin is a feature common to Astacidea and *Neoglyphea* (as well as many fossils) [1]. The soft tail fan of achelates cannot be considered a diaeresis since there is no clear line or articulation (see char. 68), whereas in Astacida the uropods are soft (char. 68), but also have a line along which they will fold. Contrary to many previous authors, we do not consider the uropods of carideans or dendrobranchiates to possess a diaeresis because the visible lines are not lines of folding [0]. *Jaxea* is unusual in having a well-formed diaeresis on both endopod and exopod [2].

RESULTS

The data matrix is given in Appendix II. The unordered analysis resulted in 96 equally most parsimonious trees, each 382 steps long (fig. 5), and the ordered analysis produced 1248 equally most parsimonious trees, each of a length of 431 steps (fig. 6).

It can be seen that the areas of least certainty are the relationships among the natant groups, with relatively little support for the clade containing Stenopodidea and Reptantia, and within Astacura. The poor support values within Astacura are largely explained by the paucity of characters effective in that region.

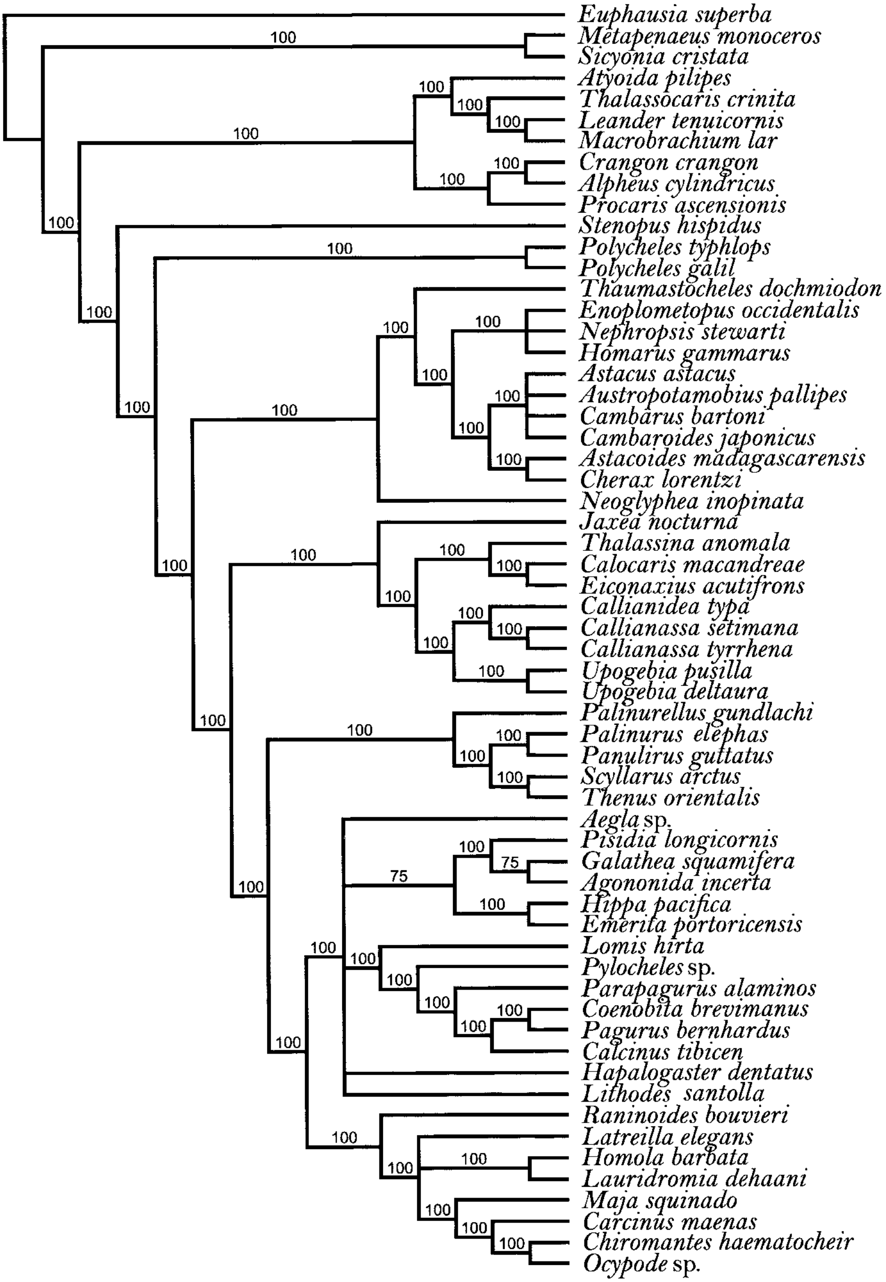

Fig. 5. Majority rule consensus of 96 equally most parsimonious trees (length = 382) from the unordered analysis.

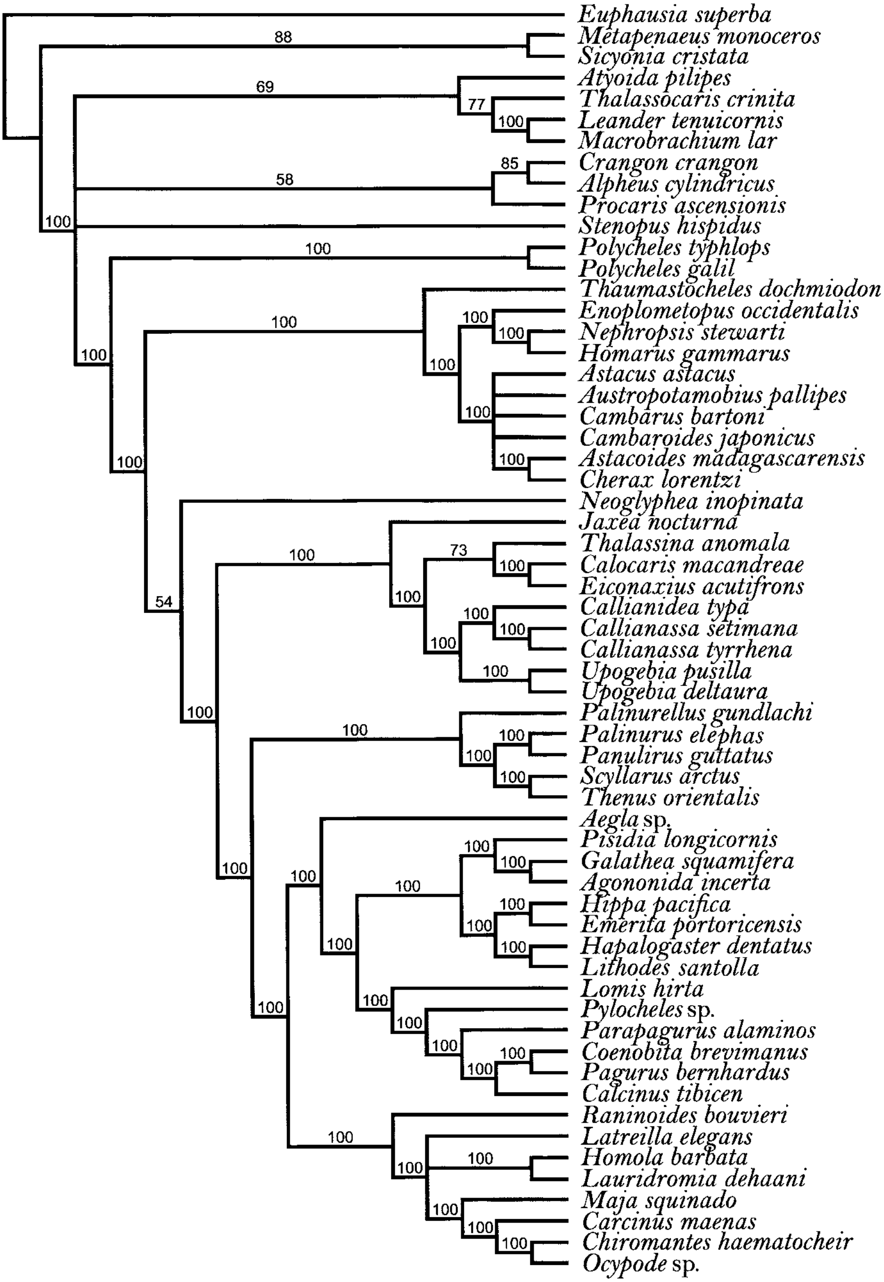

Fig. 6. Majority rule consensus of 1248 equally most parsimonious trees (length = 431) from the ordered analysis (see text for details). This differs from the unordered analysis (fig. 5) chiefly by the uncertainty among natant groups, the resolution within Anomala, and the uncertainty of the position of *Neoglyphea inopinata* Forest & De Saint Laurent, 1975.

Only Homarida was found not to be monophyletic, with *Thaumastocheles* separate from the other clawed lobsters. The relationships among the major groups are summarized in fig. 7, in which *Thaumastocheles* and its sister genus *Thaumastochelopsis* are placed in a clade of their own, Thaumastochelida, separate from the remaining Homarida.

When PAUP* was constrained to produce trees in agreement with the cladogram published by Scholtz & Richter (1995), the resulting 8899 most parsimonious trees were 401 steps long; when constrained to produce trees containing a monophyletic Palinura (comprising Polychelida, Achelata, and Glypheoidea), 4527 most parsimonious trees of length 395 were produced. Both analyses were performed with all characters unordered, and the results are, respectively, 19 and 13 steps longer than the most parsimonious unconstrained trees.

On the basis of the above tree, we propose a new classification, in which we have deliberately avoided connotations of Linnaean rank. The sister group to Reptantia is not specified, nor are relationships within Astacidea. It remains to be seen whether *Thaumastocheles* belongs with the remaining Homarida.

Proposed classification

- DECAPODA
  - DENDROBRANCHIATA
  - PLEOCYEMATA
    - Caridea
    - [Un-named clade]
      - Stenopodidea
      - Reptantia
        - Polychelida
        - Eureptantia
          - Astacura
            - Glypheoidea
            - Astacidea
              - Thaumastochelida
              - Homarida (Enoplometopidae + Nephropidae)
              - Astacida
          - Sterropoda
            - Thalassinida
            - Eurysternalia
              - Achelata
              - Meiura
                - Anomala
                - Brachyura

Nodes

Using *Euphausia* as an out-group, the ground pattern of the Decapoda includes the presence of chelae (char. 21), the presence of a rostrum (char. 39), and the

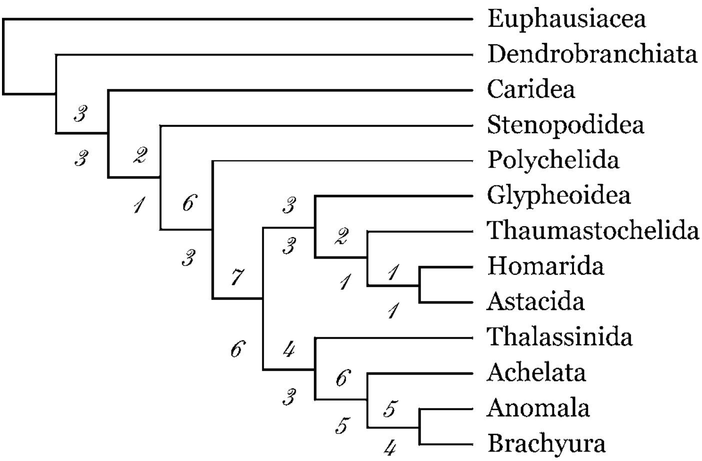

Fig. 7. Cladogram showing relationships between the major groups under study. Figures above branches refer to branch length, and figures below the branches are Bremer Support (Decay Index); both derive from the unordered analysis.

presence of spines on the telson (char. 66). A greater number and diversity of out-group taxa would be needed, however, to draw any firm conclusions. The remaining nodes relevant to the distribution of the major groups are discussed, in order, below.

1. — DENDROBRANCHIATA Bate, 1888. Dendrobranchiata is probably a monophyletic group, although this clade is not recovered in all of the most parsimonious trees in the ordered analysis. Prawns are united by the unique presence of dendrobranchiate gills (char. 47), and by the prominent nature of the hinges between their pleonic somites (char. 56) (Burkenroad, 1981). A further apomorphy, not included in this analysis is the presence of a petasma in male dendrobranchiates (Burkenroad, 1963).

2. — PLEOCYEMATA Burkenroad, 1963. Whilst Dendrobranchiata may not be monophyletic, Pleocyemata certainly is, and its defining characteristic is the brooding of eggs on the female's pleopods (char. 51). A shortening of the first pleonic somite (char. 48), and the presence of lobes overlapping the carapace from the first pleonic somite (char. 49) also unite this group.

3. — CARIDEA Dana, 1852. One feature that is purported to define Caridea is the presence of a "caridean lobe" on the first maxilliped, although it also occurs in some paguroids (Felgenhauer & Abele, 1983). We could find no qualitative difference, however, between the state in carideans and that in other decapods, and have not included such a lobe in this analysis. Caridean monophyly could not be confirmed in the ordered analysis.

Carideans share phyllobranchiate gills (char. 47), lack a chela on the third pereiopod, and almost all possess a chela on the second pereiopod. The ground state of this character for Caridea seems to be chelate first and second pereiopods but an achelate third pereiopod (char. 21, state [2]). Even if this is not phylogenetically significant, it does help to distinguish caridean shrimp from other natant decapods, since both dendrobranchiates and stenopodids have chelate third pereiopods.

4. — [Un-named clade: STENOPODIDEA + REPTANTIA]. The relationships between Stenopodidea, Reptantia, and Caridea have been very unstable, and so we could not find any suitable name proposed by any author that comprised only these animals, nor have we proposed one. Stenopodidea was included in the suborder Reptantia by De Saint Laurent (1979), and in the Macrura Reptantia by Gurney (1942), but herein Reptantia retains its usual, more restricted meaning, excluding the Stenopodidea. The placement of the Stenopodidea as the sister group to the Reptantia (s. s.) is widely supported among recent authors (Gurney, 1942; De Saint Laurent, 1979; Abele & Felgenhauer, 1986; Schram, 1986; Kim & Abele, 1990; Abele, 1991; Schram, 2001; Richter & Scholtz, 2001), but not without some dissent. Burkenroad (1963, 1981) believed Stenopodidea (Euzygida in his terminology) to be the sister group to Caridea (Eukyphida in his terminology), a situation that would result in a tree only one step longer than the most parsimonious trees, with only the presence of articulating spines on the telson (char. 66) as a synapomorphy of that clade. Felgenhauer & Abele (1983), on the other hand, inferred a reptantian origin for both Stenopodidea and Caridea, an idea that has received little support.

Members of this group share a mandible that has a curved palp and has a strong molar process (char. 14, ambiguous in the ordered analysis) and also a shallow groove on the carapace (char. 42). Since there is so much debate about homologies of carapace grooves, this may seem to be a weak character, but carapace grooves probably represent the sites of muscle attachment (see Tshudy & Babcock, 1997, for discussion). Uniramous male first pleopods (char. 60) seem to be synapomorphic for this group, but this is ambiguous in the unordered analysis. Further evidence, not used in this study, for a sister-group relationship between stenopodids and reptants is provided by the fusion of the protocephalon with the carapace and the zoeal morphology of the two groups (De Saint Laurent, 1979).

5. — STENOPODIDEA Claus, 1872. Since only one stenopodidean taxon was studied, it is difficult to draw conclusions about what features characterize the entire group. Of the three groups traditionally placed in Natantia, Stenopodidea is the only one whose members have trichobranchiate gills (char. 47), but this is probably plesiomorphic, since trichobranchiate gills are also found in euphausiaceans, other decapods, and other malacostracans. The enlargement of the third pereiopod (char. 20), instead of the first or second, is unique. *Stenopus* also has spines on its eyestalks (char. 3).

6. — REPTANTIA Boas, 1880. Reptantia was not included as a clade in the "Updated classification of the Recent Crustacea", but the authors refer to this omission on their part as "curious, and possibly a mistake" (Martin & Davis, 2001: 44). Almost every other author since Boas (1880) has included Reptantia as a natural group. Exceptions to this include Felgenhauer & Abele (1983), who considered Caridea and Stenopodidea to be derived from reptants, and Beurlen & Glaessner (1930), who believed Caridea to be derived specifically from thalassinidan rootstock.

The pereiopods of reptants articulate in a medio-lateral manner, enabling them to walk (char. 22), and the first two segments of P1 are fused together (char. 29). The carapace is calcified (char. 40) and flattened (char. 52) and the telson lacks spines (char. 66). The mandible of reptants has a long articulation along its anterior edge (char. 13). Other homoplastic characters, ambiguously supported, include the shortening of the third maxilliped relative to the other thoracopods (char. 16, unambiguous in the ordered analysis), and the enlargement of the first pereiopod (char. 20). When ordered, char. 56 (prominent pleonic hinges) becomes a reptant synapomorphy.

Reptants are also united by their possession of a widened brain (Sandeman et al., 1993), by spermatozoal characters (Scholtz & Richter, 1995), by the fusion and rigidity of the epistome (De Saint Laurent, 1979), and probably by a parallel mating position (see Scholtz & Richter, 1995, for discussion of the mating position of *Polycheles*).

Burkenroad (1963) considered the stem-reptant to possess achelate legs (char. 21, state [0]), uniramous first pleopods (characters 58 and 60, states [1] and [2], respectively), a reduced first pleonic somite (char. 47, state [1]) and expanded second pleonic somite (char. 62, state [1]). We agree, except that we conclude that the ancestral reptant had three pairs of chelate limbs (char. 21, state [1]).

7. — POLYCHELIDA De Haan, 1841. Polychelida comprises a single extant family (Polychelidae) of extant animals and a number of fossil taxa. The name Eryonoidea is used for a wider group that may not be monophyletic (Schram & Ahyong, 2002: 634). The monophyly of the extant examples is without doubt and is supported by a number of characters.

The opening of the antennal gland is directed dorsally, on to a surface of the antennule, rather than ventrally (char. 11). Unlike their close relatives, polychelids possess a mandible that has a curved palp but no molar process (char. 14). The exopod of the third maxilliped is absent (char. 17), the basis, ischium, and merus of each pereiopod are fused together (char. 31), and the fourth pereiopod is chelate (char. 35). The carapace is dorso-ventrally depressed (char. 41), lacks a large rostrum (char. 39), and its posterior edge forms a strong V-shape towards the anterior of the animal (char. 43). Furthermore, a knob arising from the first pleonic somite (char. 45) holds down the carapace (see also section on Achelata), and the pleopods are biramous and lack appendices internae (char. 57).

In the ordered analysis, the chela on P5 (char. 36) is an unambiguous synapomorphy, but it is ambiguous when unordered. In the unordered analysis, the prominent pleonic hinges (char. 56) are a synapomorphy. In addition to the characters used here, the members of the Polychelida have a characteristic larval form, known as the eryoneicus larva (Gurney, 1942).

8. — EUREPTANTIA Scholtz & Richter, 1995. Eureptantia is defined by a number of characters and is undoubtedly monophyletic. Their antennae have the sensilla arranged in a broad row towards the end of the flagellum instead of distributed across the whole flagellum (char. 5). This has sometimes been recognized in only a few taxa, but is present in almost all eureptants. Indeed, Boas' definition of Reptantia included "setæ olfactoriæ in parte distali flagelli exterioris" (Boas, 1880: 134 (= 156)). Eureptants lack a stylocerite (char. 7), but possess a crista dentata (char. 18) on a third maxilliped with a blunt-tipped dactylus (char. 15). The hinge between the carpus and the propodus of the first pereiopod is a stable double-hinge instead of a flexible single articulation (char. 26). The first pleopod of the female is reduced (char. 58), and a rounded, short telson is found in eureptants, in contrast with the elongate, triangular telson of polychelids and natant taxa (char. 65). Further evidence for eureptant monophyly is provided by the presence of an accessory lobe in the deutocerebrum (Sandeman et al., 1993), and from the thoracic endoskeleton (Scholtz & Richter, 1995). Character 38, the fractostern, can also be interpreted as a synapomorphy of Eureptantia (see Discussion).

9. — ASTACIDEA Latreille, 1802. This is a relatively weak clade in the analysis, which is united by only two characters. The first of these is the depth of the transverse groove on the carapace (char. 42), and the second is the existence of a diaeresis on the exopods of the uropods (char. 70). This latter character is also found in certain members of the Thalassinida as well as in many fossils, and seems quite likely to be a plesiomorphic feature for these taxa. A line of contact between the epistome and carapace (char. 21) is unambiguous in the unordered analysis, but ambiguous in the ordered analysis. Martin & Davis (2001) included Glypheoidea in Astacidea for the first time, a finding confirmed by this study.

10. — GLYPHEOIDEA Winkler, 1883. While it is tempting to draw conclusions about the positioning of Glypheoidea from the location of *Neoglyphea*, this is, as pointed out by Schram & Ahyong (2002), unwise. The unity of the three families in Glypheoidea is not certain; the palaeontologists Beurlen & Glaessner (1930), for instance, separated Pemphicidae from Glypheidae and Mecochiridae. Both Glypheidae (cf. Forest & De Saint Laurent, 1989) and Mecochiridae (cf. Feldmann et al., 2002) have been moved from Palinura to Astacidea, but the position of

Pemphicidae, and therefore the unity of Glypheoidea, remains uncertain. Further study is needed to confirm the relationships between the three families and other decapods.

11. — ASTACURA Borradaile, 1907. Scholtz & Richter (1995) were unable to find any character that would unite Homarida and Astacida into a single clade, Astacura. Apart from those character states which are also present in Glypheoidea (see Astacidea, above), we found two characters which may bring these two similar groups together. Telson spines (char. 66) are not found in *Thaumastocheles*, but are present in all other Astacura. While Scholtz & Richter (1995) considered the spines to be different in Astacida and Homarida because of their different positions, we take a different view (see char. 66). The presence of a long process emanating from the ischium of the first pereiopod that articulates with the coxa of the first pereiopod (char. 27), however, must be seen as good evidence of monophyly of the two taxa (see fig. 3). No comparable structure exists in other taxa, even those with similarly strong first pereiopods. This ischio-coxal process provides the best evidence that the two groups are closely related. Whilst *Neoglyphea* does not possess a process that extends from the ischium to the coxa, it is interesting to note a smaller process originating in the same place in the illustration of Forest & De Saint Laurent (1981, fig. 19a), but articulating only with the basis. This raises the possibility that this character is a synapomorphy of Astacidea, but has been either reduced or incipiently developed in *Neoglyphea*. Study of fossil glypheoids with reference to this character should help to clarify its nature vis-à-vis the process seen in Astacura. A horizontal position of the first pereiopod (char. 25) is also a synapomorphy of the Astacura.

12. — HOMARIDA Bate, 1888. Homarida was not resolved as a monophyletic group, with *Thaumastocheles* emerging as a sister group to clawed lobsters and crayfish. This does not prevent Nephropidae and Enoplometopidae being closely related. Intriguingly, *Thaumastocheles* resembles *Neoglyphea* in the forms of both the epistome and the pleurites. Of the five apomorphies given by Scholtz & Richter (1995) for Homarida, two are not found in Enoplometopidae, one excludes *Thaumastocheles*, and the other two refer to juveniles. It is possible that the crescent-shaped larval telson with a median spine will prove to be found throughout Homarida, or maybe just in Nephropidae; it has not been studied in Enoplometopidae and Thaumastochelidae.

If Homarida were monophyletic, it may be united by the loss of the fractostern (char. 38). The development of lobsters from fractosternate forms (see Discussion) may explain the separation between P5 and P4, which is not present in polychelids or natants.

Tshudy & Babcock (1997) performed a cladistic study of clawed lobsters including many fossil taxa, mostly using characters based on spines and grooves, which are often subject to homoplasy. Among their findings was the suggestion that Thaumastochelidae was indistinguishable from Nephropidae and should be abandoned. This study contradicts that view, not just finding Thaumastochelidae to be distinct from Nephropidae, but from Homarida as a whole.

13. — ASTACIDA Latreille, 1802. Although not strongly supported in this analysis, there is considerable evidence for the monophyly of the freshwater crayfish. The gastrulation of crayfish is an invagination process, in contrast with that of their close relatives, they show a unique ring of about forty ectoteloblasts in contrast to the plesiomorphic number of nineteen, and they undergo direct development (Scholtz, 2002). Among the characters we were able to use in this analysis, the perpendicular ischium-merus boundary of the first pereiopod (char. 28), the loss of a median ridge or suture in the posterior carapace (char. 44), and the presence of soft cuticle in the distal part of the telson (char. 68) all point towards Astacida as a monophyletic group.

14. — STERROPODA new clade. The name of this clade is derived from the Greek words "στερρος", meaning stiff or grown together, and "πους", meaning foot or leg, in reference to the fusion of the first three segments of each pereiopod (char. 31), although this is ambiguous in the ordered analysis. Scholtz & Richter (1995) considered the fused state to have been attained convergently in Achelata, Meiura, and Polychelida, but that view is not supported in this analysis; the state in polychelids differs in that three segments are fused instead of only the first two. Sterropoda is also characterized by the loss of the chela of the third pereiopod (char. 21, ambiguous in the ordered analysis), the double-bent form of the third maxilliped (char. 16), and the loss of the male first pleopod (char. 60). It is also possible that the presence of lineae is an apomorphy for this group (char. 46), if it is considered that different lineae are indeed homologous.

15. — THALASSINIDA Burkenroad, 1981. The monophyly of Thalassinida, though doubted in the past (Gurney, 1942), is confirmed by the curved articulation between the ischium and merus of P1 (char. 28), by the presence of a row of setae on P2 (char. 30), and by a distinctive form of the seventh thoracic sternite (char. 33). The Thalassinida are further unified by their possession of apposition eyes, in contrast to the reflecting superposition eyes found in most other groups (Gaten, 1998; Richter, 2002), probably in relation to their burrowing behaviour. Scholtz & Richter (1995) considered the construction of complex burrows to be a synapomorphy of Thalassinida, but we believe this may be plesiomorphic (see Discussion).

The infraorder Thalassinida is currently divided into three superfamilies: Thalassinoidea, Axioidea, and Callianassoidea. This study is in accordance with that classification but for the position of *Jaxea*. This is a member of Laomediidae, and so Callianassoidea, but is found in this analysis to be basal to Thalassinida. The position of *Jaxea* in this study is stable and well supported, and if this were indeed its true position, then the systematics of Thalassinida would need to be revised.

16. — EURYSTERNALIA new clade. We have chosen not to use the term Gastralida of Beurlen & Glaessner (1930) for this clade, since that group also includes Polychelida, which is not closely related to the members of this group. Tudge & Cunningham (2002) found some evidence in support of this group from molecular data. Since neither they nor any other authors have given this clade a name, we chose to erect a new name that would encapsulate some characteristic of its members. 'Eurysternalia' is derived from the Greek "εὐρυστερνος", meaning 'broad-chested', in reference to the wide, flat sternum that its members possess (char. 19) (see fig. 2).

In addition, the antennules of eurysternalians are strongly recurved, with sensilla concentrated on one side (char. 5) and the flagella are of similar length to the middle peduncular segment (char. 6), the peduncle is Z-shaped and lacks a stylocerite (char. 7) (see fig. 1). Scholtz & Richter (1995) noted the similarities between the antennules of achelates and meiurans, but did not consider the two groups to be closely related. Their observation, that achelate antennules have two flagella twisted around each other whereas meiuran antennules do not, seems unreliable; we note variation in this respect not only within both achelates and meiurans, but even upon the same specimen. One may also argue that the antennules bend in different directions in different taxa, i.e., that they bend down and then up again in scyllarids, for instance, but up, and then down again in meiurans. This, however, does not prevent their being homologous, particularly since it is only scyllarids among Achelata that show such a pattern; the other families have antennules that are a straighter Z-shape and capable of bending in a number of directions.

The scaphocerite of the second antenna is generally lost in Eurysternalia (char. 8), although it does re-appear in Anomala, and the depressed, or flattened, nature of the carapace unites eurysternalians (char. 41). This may be related to the widening of the sternites (char. 19, above) although other taxa, such as polychelids, have distinctly depressed carapaces but narrow sternites.

Two homoplastic characters, which may be apomorphies for this group, are the loss or reduction of the rostrum (char. 39) and the fusion of the epistome to the carapace (char. 12). The epistome of anomalans is reported to be fused, but with this fusion hidden (Burkenroad, 1981; Števčić, 1995). If anomalans had been scored as having this fusion, this would be an unambiguous synapomorphy for Eurysternalia.

17. — ACHELATA Scholtz & Richter, 1995. There is little doubt that Achelata forms a monophyletic group. The eyestalks of achelates have a row of hairs alongside the eye (char. 3). The second antenna is greatly enlarged (char. 9),

resulting in the greatly thickened form found in Synaxidae and Palinuridae, and the enlarged, flattened form found in Scyllaridae. The basal articles of the second antennae are fused with the epistome (char. 10), the pereiopods (except the fifth) are achelate (char. 21). The carapace is held to the body by a knob emanating from the last thoracic somite (char. 45), which was shown by Scholtz & Richter (1995) not to be homologous with the knob in Polychelida. The pleon has prominent hinges (char. 56) (except in the ordered analysis) and the pleurites are pointed (char. 63). The tail fan is soft distally (char. 68), and the telson (char. 66) possesses fixed lateral spines. If the lineae of thalassinids and those of meiurans are homologous, then achelates have lost the lineae (char. 46). As well as the various external characters used in this analysis, Achelata is also united by a unique and distinctive larval form, the phyllosoma larva (Gurney, 1942).

It has been suggested (Martin & Davis, 2001) that Palinura would be an equally good name for this group, but we reject this. Palinura has for many decades been used to include Glypheoidea, which were for much of that time known only as fossils, and Polychelida. The removal of these last two groups nullifies the joining together of the three groups in Palinura, and so retention of the name seems unjustified and likely to cause confusion. Following Scholtz & Richter (1995), we prefer to use Achelata, which is free from confusion and clearly refers to the three extant families Scyllaridae, Synaxidae, and Palinuridae.

We found Synaxidae to be basal, and Scyllaridae and Palinuridae to be united by the loss of the female first pleopod (char. 58) and also by the presence of matchstick gills rather than the similar trichobranchiate gills (char. 47) (see fig. 4).

18. — MEIURA Scholtz & Richter, 1995. The first pleonic somite, or 'waist', of meiurans is narrow (char. 48, unordered analysis only), and lacks lobes overlapping the carapace (char. 49); the pleon is flexed (char. 54) and its sternites are incomplete (char. 55). It is unclear under this optimization whether the ancestral meiuran had its fifth pereiopod held dorsally, as in the ancestral brachyuran, or internally, as in the ancestral anomalan (char. 34). Either way, there is a reduction in the size of the fifth pereiopod, which is therefore a meiuran apomorphy. The distinct bend in the Mxp3 exopod (char. 17) is also likely to be an apomorphy for the Meiura. In the ordered analysis, the loss of prominent pleonic hinges (char. 56) is an apomorphy.

19. — ANOMALA De Haan, 1839. In common with Burkenroad (1981), we prefer the older and more precise term Anomala to Anomura, which often refers to Anomala + Thalassinida. Four unambiguous characters unite Anomala: the notch in the carapace into which the basal articles of the second antenna fit (char. 10), the reversal of the coxosternal joints of the thoracopods (char. 22), the rotation of the cheliped so that the dactylus is horizontal (char. 25), and the loss of the first pleopod of the female (char. 58).

Within Anomala, not all the traditional groupings are preserved, given the current character list. Four superfamilies are currently recognized (Martin & Davis, 2001): Galatheoidea, Paguroidea, Hippoidea, and Lomisoidea. Of these, only Hippoidea and the monotypic Lomisoidea are found to be monophyletic. The family Aeglidae is separated from the remainder of the Galatheoidea (as was found by Pérez-Losada et al., 2002), and the family Lithodidae is separated from the remaining Paguroidea. Much of this latter shift may, however, be due to the remarkable derived form of the lithodids, which is the best example of carcinization outside Brachyura. The characters which link Lithodidae to Paguroidea are persuasive. DNA sequences (Cunningham et al., 1992), gene rearrangements (Morrison et al., 2002), spermatozoa (Tudge et al., 1998), and macro- and micro-morphology (Richter & Scholtz, 1994) all point to an origin for Lithodidae among the Paguroidea, often close to the genus *Pagurus*.

A hermit crab origin for lithodids is not universally accepted, however: Martin & Abele (1986) considered the lithodids' closest relative to be *Lomis hirta* (Lamarck, 1818), while McLaughlin & Lemaître (1997) considered Lithodidae to be the sister group to the remaining Paguroidea, with a reversal of the usual explanation of lithodid evolution. One character that Richter & Scholtz (1994) used to link Lithodidae to *Pagurus* may need to be re-assessed. They reported a synapomorphy of the antennule where the two rows of sensilla on each annulus are displaced laterally relative to each other. We have also found this state in *Galathea squamifera* Leach, 1814, suggesting that it might be the plesiomorphic condition in Anomala if not in the whole of Meiura.

20. — BRACHYURA Latreille, 1802. True crabs (Brachyura, including Dromiacea), undoubtedly form a monophylum with several characters changing state at the base of the clade. Crabs possess an orbito-antennularis fossa, formed by the carapace and one or more antennae (char. 1), their third maxillipedes are operculiform (char. 16), the uropods are absent (char. 69), and the telson loses any specialization for escape or digging (char. 67) (ambiguous if unordered). The posterior edge of the carapace is straight (char. 43), and the second pleomere is not expanded (char. 62). The gills are phyllobranchiate (char. 47) (the most primitive crab, *Homolodromia*, not included in this study, has trichobranchiate gills). A further synapomorphy is the form of the first and second male pleopods, which are arranged so that the second pleopod passes through the first pleopod, the two forming collectively a single gonopod (char. 59). While the presence of a structure holding the telson to the sternum may be seen as a synapomorphy of Brachyura, many different devices in fact exist and are not homologous (Guinot & Bouchard, 1998).

Števčić (1995, 1998) has argued that Raninidae is an advanced group among Dromiacea, not the most basal branch, as depicted in the cladograms above (figs. 5, 6). Martin & Davis (2001) go further and include Raninidae in Eubrachyura. If it is true that the raninids are not the most primitive crabs, then two further characters are synapomorphies for Brachyura. Crabs (except raninids) have sexually dimorphic pleons (char. 53) and their pleons are strongly reflexed under the cephalothorax (char. 54). Each of these is apparently reversed in Raninidae.

The argument that dromiaceans belong in Anomala on the basis of larval morphology is spurious. It is unsurprising that dromiacean larvae should resemble those of anomalans, but this is undoubtedly due to symplesiomorphies, not apomorphies, and this is only further evidence for eubrachyuran monophyly.

DISCUSSION

Systematics

The cladogram we present (fig. 7) is in broad agreement with previously published trees, particularly that of Scholtz & Richter (1995). We were able to confirm their finding that the Polychelida is the most basal branch of the Reptantia, and a sister group to Eureptantia. As a result, Palinura, which contains Polychelida, Glypheoidea, and Achelata, cannot be monophyletic. This cladogram differs from that of Scholtz & Richter (1995), however, in two important respects. Firstly, Astacidea is re-united, with Astacida and Homarida (excluding Thaumastochelida) now as sister groups. This contradicts the view that Astacida represent a more advanced form by virtue of their fractured sternum. The second difference concerns the positioning of Achelata, which, in this analysis, is the sister group to Meiura in a new clade, Eurysternalia.

The former point is unlikely to be contentious since a close relationship between the two groups has been assumed by all authors with the exception of Scholtz & Richter (1995, and later papers by each author). The similarities of form between a crayfish and a lobster seem too close to deny such a grouping, although this could all too easily be based on plesiomorphies. We feel, however, that the process from the ischium of the first pereiopod is so constant among the two groups that it must represent evidence of common descent, especially since no similar process occurs in any other group.

In contrast to the re-unification of Astacidea, the new position of Achelata seems likely to cause more concern. Spiny lobsters and their allies have traditionally been classified nearer the true lobsters because of superficial similarities such as overall body shape and size, and lifestyle. Carcinology has now progressed beyond simply classifying animals into "long-tailed" and "short-tailed" forms, and we no longer see such an association as justified. Nor do we accept the grouping of achelates with glypheoids and/or polychelids to form Palinura. No character seems to unify these three groups, except, again, the long tail. Glypheoidea has now been moved from Palinura (cf. Martin & Davis, 2001), and Polychelida should follow, to a basal position among Reptantia, as suggested by all the recent cladistic studies (Scholtz & Richter, 1995; Schram, 2001; this study).

Since Achelata is not closely related to Astacidea or Polychelida, Eurysternalia appears to be a natural group. The similarities in antennular morphology seem too close for the constituent groups not to be related, and this, together with the wide sternum, argues strongly in favour of the monophyly of Eurysternalia. The fact that the antennules of Brachyura and Anomala are more similar to each other than they are to those of Achelata is no argument against eurysternalian monophyly, but only serves to confirm that Meiura is also a monophyletic group.

The alternative theory, that Thalassinida is the sister group to Meiura, would be upheld by only one character in this study, which is the presence of lineae (char. 46). It would not be surprising that such lineae should be absent from achelates, since lineae are lines of softening to allow the carapace to bend. Spiny lobsters and their allies rely on the hardness and inflexibility of their carapace for protection, and so may well have lost any lineae their ancestors may have had.

It is perhaps unfortunate that achelates are so derived in so many ways, leaving external morphology as perhaps the best guide to their relationships. The brains of achelates are folded and compressed (Sandeman et al., 1993), and their phyllosoma larvae are unique (Gurney, 1942). It is therefore difficult to use data from brain or larval morphology to compare with other taxa. Spermatozoal and molecular data may be necessary to finally confirm any phylogeny. Relatively little is known about the variations in decapod spermatozoa, and no phylogeny of higher groups such as Reptantia or Decapoda has been attempted with spermatological data. Tudge & Scheltinga (2002) did note, however, that the resemblance between the spermatozoa of *Aegla* (Meiura) and *Jasus* (Achelata) was stronger than that between *Aegla* and Thalassinida.

Molecular data are similarly scant. No single study has attempted to uncover the relationships within Reptantia. Morrison et al. (2001) used genes and mitochondrial rearrangements to confirm the monophyly of Anomala, and Crandall et al. (2001) used genes to study freshwater crayfish origins. In both cases, relationships outside the particular group in question remained sketchy. Complete mitochondrial DNA sequences are available for only three decapod taxa: *Penaeus monodon* Fabricius, 1798 (Dendrobranchiata), *Pagurus longicarpus* Say, 1817 (Anomala) and *Panulirus japonicus* (Von Siebold, 1824) (Achelata) (Yamauchi et al., 2002). The addition of a single astacidean or thalassinidan to the dataset could confirm which group is the sister group to Meiura.

Fractosterns, lifestyles, and ancestral forms

Under the hypothesis presented here of decapod evolution, the fractostern of Scholtz & Richter (1995) (char. 38) must have been lost several times, i.e., in the Homarida, Palinura, and the Brachyura. The separation of the last two thoracic sternites is a complex feature that also entails changes to the secula that are found in all fractosternate animals. Therefore, it is more probable that the fractostern, along with the complex secula, evolved only once and was then lost a number of times. Such a loss of the fractostern was implicit in Scholtz & Richter's (1995) hypothesis, since they included the Brachyura in the Fractosternalia, assuming that the brachyuran ancestor was fractosternate but lost the articulation during carcinization. If the fractostern evolved on a single occasion, then it must have been in the ancestral eureptant. Borradaile (1906) also considered the fractostern to be primitive to the Reptantia, but he considered *Stenopus* to be fractosternate, which is clearly not the case. The fractostern would then have been lost in the following lineages: Homarida, Thaumastochelida (if considered separate from Homarida), Achelata, and Brachyura. Whilst this hypothesis is one step longer than the structure evolving four times, it is more plausible.

Those taxa in which the fractostern was lost are all largely free-living animals, relying less on burrows, crevices, or shells for protection. Much of their protection derives from the rigidity and strength of their exoskeleton. It is our belief that it is a disadvantage for such animals to have an extra articulation in the sternum, or at least that it confers no advantage. For a burrower, however, such as a thalassinidan or astacidean, the extra flexibility is useful in the confined spaces of the burrows. One might conclude, therefore, on the basis of its supposed fractostern, that the ancestral eureptant was not an epibenthic animal like some lobsters, spiny lobsters, and crabs of today, but had a more sheltered lifestyle, probably living in some sort of burrow.

Simple vertical burrows, tentatively assigned to Astacida, have been found dating from the Carboniferous period (Hasiotis, 1999). By the Triassic, complex, multi-branched systems derived from an initial, U-shaped tunnel were constructed. These resemble the burrows of current thalassinidans in gross topology (see, for example, Dworschak, 2001), but no work has been done to compare the burrow morphologies of different decapod taxa. One should not assume that the Carboniferous burrows are necessarily those of crayfish; such burrows could have been dug by thalassinidans, or by a distant ancestor of both. Even some marine lobsters retain a burrowing habitus; Holthuis (1974) reports surprise that *Acanthacaris* lives in a burrow, since its morphology did not suggest such a lifestyle.

Polychelids show no sign of a burrowing lifestyle, but are instead adapted to a deep-sea benthic environment. We suspect that the ancient Reptantia divided into two branches, one living on the surface of the sea-bed (Polychelida), and one burrowing beneath it (Eureptantia). This may also help to explain the paucity of decapod fossils over much of geological time; animals living in burrows or in the deep sea are rarely preserved.

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[Note that Appendices I-II follow on pp. 973-975.]

APPENDIX I — TAXA

Euphausiacea: *Euphausia superba* Dana, 1852
Dendrobranchiata: *Metapenaeus monoceros* (Fabricius, 1798), *Sicyonia cristata* (De Haan, 1844)
Caridea: *Alpheus cylindricus* Kingsley, 1878, *Atyoida pilipes* (Newport, 1847), *Crangon crangon* (Linnaeus, 1758), *Leander tenuicornis* (Say, 1818), *Macrobrachium lar* (Fabricius, 1798), *Procaris ascensionis* Chace & Manning, 1972, *Thalassocaris crinita* (Dana, 1853)
Stenopodidea: *Stenopus hispidus* (Olivier, 1811)
Polychelida: *Polycheles typhlops* Heller, 1862, *Polycheles galil* Ahyong & Brown, 2002
Glypheoidea: *Neoglyphea inopinata* Forest & De Saint Laurent, 1975
Homarida: *Enoplometopus occidentalis* (Randall, 1840), *Homarus gammarus* (Linnaeus, 1758), *Nephropsis stewarti* Wood-Mason, 1872, *Thaumastocheles dochmiodon* Chan & De Saint Laurent, 1999
Astacida: *Astacoides madagascarensis* (H. Milne Edwards & Audouin, 1839), *Astacus astacus* (Linnaeus, 1758), *Austropotamobius pallipes* (Lereboullet, 1858), *Cambaroides japonicus* (De Haan, 1842), *Cambarus bartonii* (Fabricius, 1798), *Cherax lorentzi* J. Roux, 1911
Thalassinida: *Callianassa setimana* (De Kay, 1842), *Callianassa tyrrhena* (Petagna, 1792), *Callianidea typa* H. Milne Edwards, 1837, *Calocaris macandreae* Bell, 1846, *Eiconaxius acutifrons* Bate, 1888, *Jaxea nocturna* Nardo, 1847, *Thalassina anomala* (Herbst, 1804), *Upogebia deltaura* (Leach, 1815), *Upogebia pusilla* (Petagna, 1792)
Achelata: *Palinurellus gundlachi* Von Martens, 1878, *Palinurus elephas* (Fabricius, 1787), *Panulirus guttatus* Latreille, 1804, *Scyllarus arctus* (Linnaeus, 1758), *Thenus orientalis* (Lund, 1793)
Anomala: *Aegla* sp., *Agononida incerta* (Henderson, 1888), *Calcinus tibicen* (Herbst, 1791), *Coenobita brevimanus* Dana, 1852, *Emerita portoricensis* Schmitt, 1935, *Galathea squamifera* Leach, 1814, *Hapalogaster dentatus* (De Haan, 1844), *Hippa pacifica* (Dana, 1872), *Lithodes santolla* (Molina, 1782), *Lomis hirta* (Lamarck, 1818), *Pagurus bernhardus* (Linnaeus, 1758), *Parapagurus alaminos* Lemaître, 1989, *Pisidia longicornis* (Linnaeus, 1767), *Pylocheles* sp.
Brachyura: *Carcinus maenas* (Linnaeus, 1758), *Chiromantes haematocheir* (De Haan, 1833), *Homola barbata* (Fabricius, 1793), *Latreilla elegans* Roux, 1830, *Lauridromia dehaani* (Rathbun, 1923), *Maja squinado* (Herbst, 1788), *Ocypode* sp., *Raninoides bouvieri* Capart, 1951

APPENDIX II — DATA MATRIX

(See table I on pp. 974-975.)

TABLE I
Data Matrix

[		10		20		30		40		50		60		70]
[		.		.		.		.		.		.		.]
Euphausia superba	00001	00001	10000	02000	0010-	00000	00000	00000	00000	01000	00000	01?00	20000	00000
Metapenaeus monoceros	00000	01001	10000	02000	1010-	00000	00000	00010	00000	00000	00000	11002	20000	00000
Sicyonia cristata	00101	00001	10000	00000	1010-	00000	00000	00010	00010	00000	00000	12002	20100	10000
Atyoida pilipes	00000	01001	10020	02000	20101	10000	00000	00010	00000	02110	10000	00?01	21000	10000
Thalassocaris crinita	00000	00001	10000	02002	4010-	00000	00000	00010	00000	02010	10000	00001	21000	10000
Leander tenuicornis	00001	00001	10001	12002	20101	10000	00000	00010	00000	02110	10000	00001	21000	10000
Macrobrachium lar	00000	00001	10000	12002	20102	10000	00000	00010	00000	02110	10000	00001	21000	10000
Crangon crangon	00000	00001	10010	02001	20101	10000	00000	00000	00000	02110	10000	01001	21000	10000
Alpheus cylindricus	00000	00001	10010	02001	20101	10000	00000	00000	00000	02111	10000	00001	21000	10000
Procaris ascensionis	00000	00001	10010	02000	0010-	000?0	00000	00000	01010	02110	10000	01001	21000	10000
Stenopus hispidus	00200	00001	10030	02003	10101	10000	00000	00010	01000	01110	10000	01002	20000	10000
Polycheles typhlops	---00	00001	20110	10001	11101	10010	20002	10001	11112	01110	11000	10002	21000	00000
Polycheles galil	---00	00001	20110	10001	11101	10010	20002	20001	11112	01110	11000	10?02	21000	00000
Neoglyphea inopinata	00001	01001	11131	02101	01101	30001	00000	00111	02010	01110	11000	?0102	21001	00001
Thaumastocheles dochmiodon	---01	01001	11111	12101	11100	31010	00000	20011	02010	01111	11?00	21?02	21002	00001
Enoplometopus occidentalis	00001	01001	10131	12101	11100	31010	00001	10011	00010	01110	11000	21102	21101	10001
Nephropsis stewarti	00001	01101	10131	12101	11100	31010	00000	00011	02010	01110	11000	2110?	?1101	30001
Homarus gammarus	00001	01001	10131	12101	11100	31010	00000	00011	02010	01111	11000	21102	21101	30001
Astacus astacus	00001	01001	11131	12101	11100	31110	00000	00111	02000	01110	11000	21102	31001	20201
Austropotamobius pallipes	00001	01001	11131	12101	11100	31110	00000	00111	02000	01110	11000	21202	31001	20201
Cambarus bartonii	00000	01001	11131	12101	11110	31110	00000	00111	02000	01110	11000	21102	31001	20201
Cambaroides japonicus	00001	01001	11131	12101	11110	31110	00000	00111	02000	01110	11000	21202	31001	20201
Astacoides madagascarensis	00000	01001	11131	11101	11100	31110	00000	00111	02000	01110	11000	21203	21001	30101
Cherax lorentzi	00001	01001	11131	12101	11100	31110	00000	00111	02000	01110	11000	21203	21001	30101
Jaxea nocturna	03001	01001	10131	22101	31101	30211	10100	?0111	01000	11110	11000	21?03	21001	00002
Thalassina anomala	00000	01101	10131	23101	21101	30211	10100	00112	02200	13311	11000	01102	20001	01000
Calocaris macandreae	0--01	01101	11131	22101	21101	30211	10100	00113	02010	01311	11-00	00-0-	20001	30001
Eiconaxius acutifrons	00001	01001	10131	22101	21101	30210	10100	?0113	02000	01311	11000	00?03	20101	00001
Callianidea typa	02001	01001	00131	22101	21001	30011	10101	20103	02300	12301	1-001	00102	20001	00000
Callianassa setimana	02001	01101	00131	30101	31001	30011	10101	20103	02300	12301	11000	00103	00001	00000

TABLE I
(Continued)

[		10		20		30		40		50		60		70]
[		.		.		.		.		.		.		.]
Callianassa tyrrhena	02001	01101	00131	30101	31001	30011	10101	20103	02000	12301	11000	00103	00001	00000
Upogebia pusilla	03001	01001	001?1	22001	31101	30211	10100	20113	02000	11300	11001	01?03	20001	00000
Upogebia deltaura	03001	01001	00131	22001	31101	30211	10100	20113	02000	11300	11001	01?03	20001	00000
Palinurellus gundlachi	00102	13112	12131	11121	011?1	32010	10000	?0011	11001	01110	11000	1110?	?1101	30100
Palinurus elephas	00102	13112	12131	22111	011?0	32010	10000	00001	02001	04110	11000	1120?	?0101	30100
Panulirus guttatus	00101	03112	1-131	21120	01100	30010	10000	10001	02001	04110	11000	12203	20101	30100
Scyllarus arctus	20102	13122	1-111	22021	01101	10010	10000	?0001	10001	04110	11000	11?03	21101	30100
Thenus orientalis	40002	13122	1-111	22120	01101	30010	10000	00001	21001	04110	11000	11203	21101	30100
Aegla sp.	00001	23100	10131	23221	32100	300?0	10020	00110	11000	11300	11011	0?203	01002	00000
Pisidia longicornis	00002	22100	10131	33021	32100	30010	10020	20101	21300	12100	11011	02203	20003	00000
Galathea squamifera	00102	12100	10131	23121	32100	30010	10020	20111	21300	12100	11011	02202	21003	00000
Agononida incerta	00002	12100	10131	23121	321?0	30010	10020	20111	21300	12100	11011	02203	21003	00000
Lomis hirta	00002	13?00	?0131	23131	32100	300?1	10020	20202	21000	11320	?1011	01202	21001	03010
Hippa pacifica	00002	03100	?0030	20011	02200	32110	10020	20201	00300	12320	11011	02103	01004	04000
Emerita portoricensis	00001	03100	1???1	00011	0?2?-	22111	10020	?0?01	01300	12320	11011	02?03	01004	04000
Hapalogaster dentatus	00002	13000	?0131	23221	32100	300?0	1?020	20202	21000	12301	?1?12	-??03	0--01	0303-
Lithodes santolla	00002	13100	10131	23220	321?0	30010	10020	00211	21000	12303	11021	02203	00001	0303-
Pylocheles sp.	00101	13000	10131	23101	32100	300?1	10041	21102	11000	11300	?1210	01102	10012	02000
Parapagurus alaminos	01002	13000	10131	13101	32100	30010	10040	21203	11000	113-2	1-0-2	-1?02	2--12	02000
Coenobita brevimanus	01101	13000	?0131	13111	32100	30010	10040	21203	11000	123-2	1-0-2	-1203	0--13	02000
Pagurus bernhardus	01002	13000	10131	13211	32100	30010	10040	21203	11000	123-2	1-0-2	-1?03	2--12	02000
Calcinus tibicen	01002	13000	10131	13101	32100	30010	10040	21203	11000	123-2	1-0-2	-1203	2--12	02000
Raninoides bouvieri	10002	23101	12111	31121	31201	32010	10010	00001	10303	12000	11011	0111-	-0001	0303-
Latreilla elegans	30002	13101	12131	33120	31100	300?0	10010	00001	11300	0?300	11121	0111-	-0-01	0303-
Homola barbata	10102	13101	12131	33121	31101	300?0	10010	00002	11000	12200	11121	011??	?0001	0303-
Lauridromia dehaani	10002	13101	12131	33111	31101	32110	10030	20002	21300	12300	11121	0111-	-0001	0302-
Maja squinado	20012	13102	1-131	33120	31101	30010	11000	00001	11300	12300	11120	0121-	-0001	0303-
Carcinus maenas	20012	13102	1-131	33121	31101	32010	11050	00001	21300	12301	11121	0121-	-0-01	0303-
Chiromantes haematocheir	20012	13102	1-131	33021	31101	30010	12050	00001	21300	12300	11121	0121-	-0-01	0303-
Ocypode sp.	10012	?3102	1-131	31021	31100	30010	12050	00001	21300	12301	11121	0121-	-0001	0303-