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PHYLOGENY OF THE DECAPODA REPTANTIA: RESOLUTION USING THREE MOLECULAR LOCI AND MORPHOLOGY

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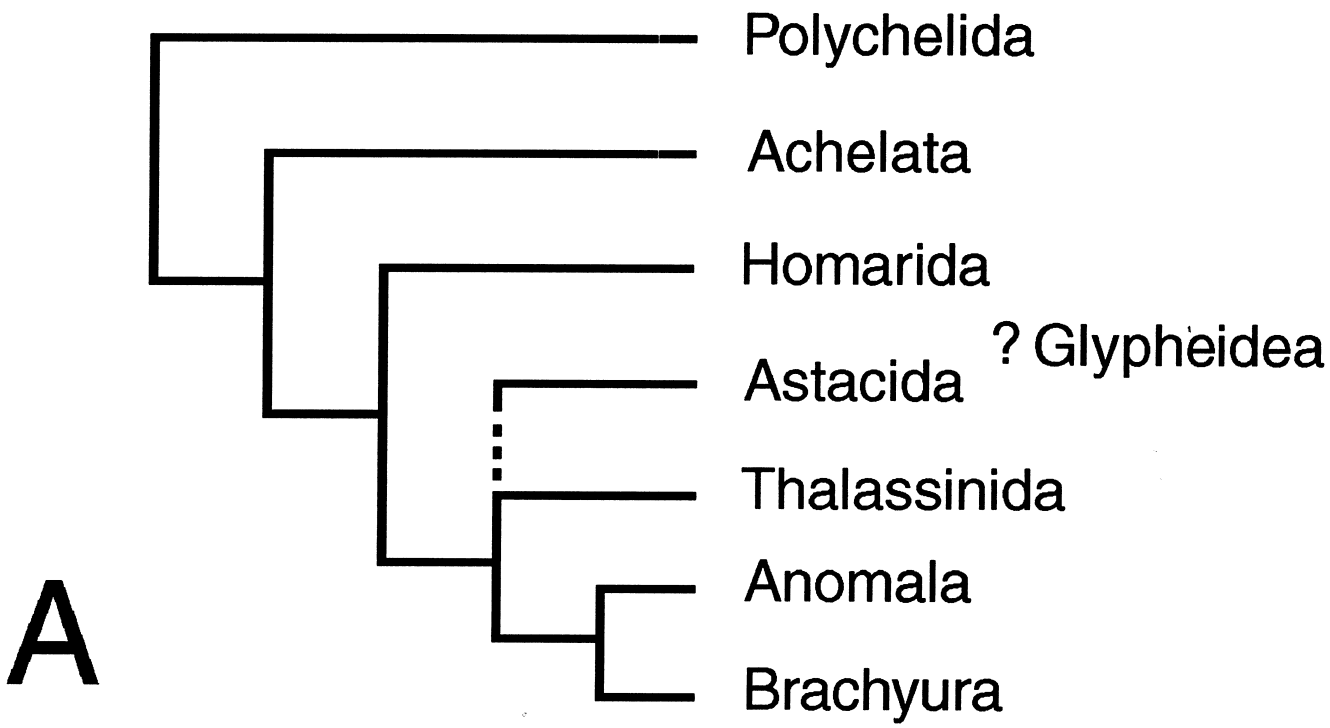
***ABSTRACT.* –** The controversial interrelationships of the major clades of the reptant decapods are resolved by simultaneous analysis of 16S, 18S, and 28S rRNA sequences in combination with morphology. All major reptant clades are represented including the first molecular data for the controversial Polychelidae, Glypheidae, and Enoplometopidae. Interrelationships of major clades in the shortest morphological cladograms were identical to those based on the molecular partition, and were congruent with those of the optimal combined analyses. The optimal tree, namely, that exhibiting minimal overall incongruence between morphological and molecular partitions was achieved under equal transition: transversion weights. Palinura, as traditionally recognised, is polyphyletic corroborating several recent studies. Infraordinal relationships are robust and insensitive to transition weight variation. For clades previously comprising the Palinura, we recognise Achelata, Polychelida and Glypheidea. Polychelida is sister to the remaining Repantia. Achelata is near basal and sister to Fractosternalia. Contrary to many previous studies, glypheideans are neither basal reptants, nor are they related to Thalassinidea, Brachyura or Anomura. Glypheidea is sister to Astacidea. A monophyletic Astacidea, comprising the freshwater crayfish (Astacida) and marine clawed lobsters (Homarida), corroborates most previous studies. The enigmatic lobster *Enoplometopus* (Enoplometopoidea) is confirmed as an astacidean rather than a possible thalassinidean. Unusual characters of the extinct uncinid lobsters, shared with enoplometopids, suggest close affinity, extending the fossil record of the Enoplometopoidea to the Lower Jurassic. The Sterropoda concept, comprising (Thalassinidea (Achelata + Meiura)) is not recognised. The clade formed by Brachyura, Anomura, and Thalassinidea is united by carapace lineae, for which we propose the new name Lineata. Internal relationships of Anomura recovered in our analyses suggest possible paraphyly of Galatheoidea and Paguroidea. Relationships within Brachyura indicate podotreme paraphyly, but greater taxonomic sampling is required to adequately test the status of Podotremata. The anomuran dromiid hypothesis is unsupported. Seven reptantian infraorders are recognised: Polychelida, Achelata, Glypheidea, Astacidea, Thalassinidea, Anomura and Brachyura.

***KEY WORDS.* –** Decapoda, Reptantia, phylogeny, molecular, morphology, Lineata new clade.

INTRODUCTION

More studies have been published on the Decapoda than any other Crustacean group. Phylogenetic relationships, however, remain contested. General consensus exists on the basal and near basal positions of the so-called 'natant' groups: Dendrobranchiata, Caridea and Stenopodidea. Similarly, the monophyly and 'high' position of Reptantia is now undisputed (e.g., Burkenroad, 1981; Scholtz & Richter, 1995; Schram, 2001; Dixon et al., 2003), but internal composition and relationships between the major clades remain some of the most contentious issues in Crustacean systematics. Reptantia contains the vast majority of decapods including the most familiar and emblematic of Crustacea: the crabs, crayfish and lobsters. The many controversies and different hypotheses of reptant interrelationships were adequately summarised by Glaessner (1969), Scholtz & Richter (1995), Martin & Davis (2001) and Dixon et al. (2003), and are not repeated here. Nevertheless, several salient issues are noteworthy. For much of the last century, four major reptant Infraorders were recognised: Palinura, Astacidea, Anomura (or Anomala) and Brachyura. Palinura comprised the Palinuroidea, Glypheoidea and Eryonoidea. The Astacidea comprised the clawed marine lobsters and freshwater crayfish. Brachyuran monophyly has been generally accepted, with the exception of the position of the some dromiaceans. Similarly, anomuran monophyly, has been uncontroversial apart from occasional uncertainty over the inclusion of thalassinideans and dromiacean crabs. Monophyly of the thalassinideans has been disputed. Particular controversy, however, has consistently surrounded internal relationships of brachyurans and anomurans, and more recently the monophyly of Astacura and Palinura (Scholtz & Richter, 1995). Following the discovery of the living glypheidean, *Neoglyphea inopinata*,



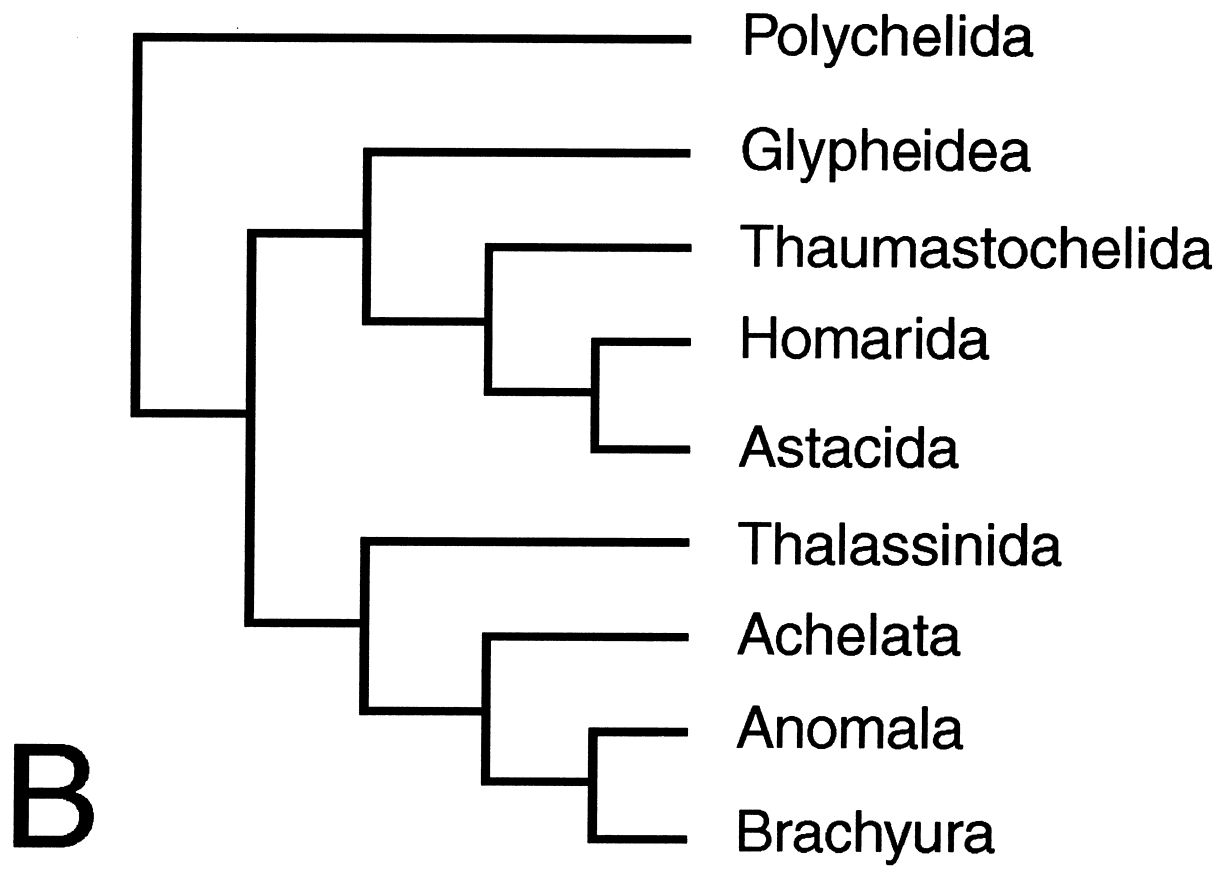


Fig. 1. Cladistic relationships of major reptant clades based on A, Scholtz & Richter (1995); and B, Dixon et al. (2003); both based on morphology.

the unity of Palinura has been increasingly challenged and the phylogenetic position of the glypheoids questioned (Burkenroad, 1981; Scholtz & Richter, 1995; Schram, 2001; Schram & Ahyong, 2002; Dixon et al., 2003; Amati et al., 2004). In corollary, infraordinal composition and interrelationships of the Reptantia, even after more than two centuries of study, are yet to reach consensus.

The longstanding instability in the reptant system is largely the product of inappropriate methods of analysis applied to inadequate data. Cladistic analyses of Reptantia have appeared only in the last decade (Scholtz & Richter, 1995; Schram, 2001; Dixon et al., 2003) (Fig. 1). The former two studies express similar patterns, being based on essentially the same data set, whereas the latter is an independent analysis. These studies recognise polyphyly of Palinura and unity of Meiura (i.e., Anomura + Brachyura) in which Polychelida is basal and Meiura 'high' in the tree. Thus, current studies find agreement at the 'base' and 'top' of the tree, but differ in the broader 'middle ground'. Two broad patterns of decapod phylogeny are evident in cladistic results, differing chiefly in monophyly or paraphyly of Astacura, and the positions of the Achelata, Thalassindea, and Glypheidea. Not surprisingly, internal relationships of most major clades are still unclear. Apart from the preliminary molecular study by Abele (1991) that included three reptant exemplars, the few existing cladistic analyses of reptant infraordinal relationships were all based on morphology (Scholtz & Richter, 1995; Schram, 2001; Dixon et al., 2003). Prior to this study, no large molecular analysis, let alone any synthetic work combining morphology with multiple sources of molecular data from representatives of all major reptant clades has been attempted. Here, we apply a 'total-evidence' approach to the phylogeny of the Reptantia, combining morphological data with 16S, 18S and 28S rRNA sequences in the largest dataset yet marshalled to study reptant phylogeny.

MATERIALS AND METHODS

***Terminal taxa.* –** Representatives of all recognised reptant infraorders were included as terminals. Special effort was made to include rare or controversial taxa such as *Neoglyphea*, *Polycheles*, *Enoplometopus*, *Thaumastochelopsis* and *Pylocheles*. As many of the recognised decapod families as practicable were represented by at least one exemplar. All extant families of Polychelida, Achelata, Glypheidea, Astacidea and Homarida were represented. For Thalassinidea, 5 of 10 families were represented, but exemplars spanned the three superfamilies recognised by Poore (1994). Thirteen of 15 families of the Anomura were represented. Of the more than 50 described families of the Brachyura, 6 were represented. Brachyuran diversity, however, was sampled via inclusion of representatives of the three major groupings proposed by Guinot (1977): Podotremata, Heterotremata and Thoracotremata. Podotremata was represented by an exemplar from the Dromiidae (*Lauridromia dehaani*), Homolidae (*Paramola orientalis*) and Raninidae (*Raninoides louisianensis*). Heterotremata was represented by an exemplar from Hepatidae (*Hepatus ephileticus*) and Portunidae (*Carcinus maenas*). Thoracotremata was represented by an exemplar from Ocypodidae (*Macrophthalmus setosus*). The ingroup comprised 44 terminals. Despite controversy over internal relationships of Reptantia, the sister group has consistently been identified as Stenopodidea (see Abele, 1991; Scholtz & Richter, 1995; Schram, 2001; Dixon et al., 2003). Therefore, the ingroup was rooted to the stenopodidean *Stenopus hispidus*. A list of terminals and their higher classification is given in Appendix 1.

***Morphological characters.* –** The morphological data matrix of 105 characters was constructed in MacClade 4.0 (Maddison & Maddison, 2000) (Appendix 2). Characters were scored from specimens in the collections of the Australian Museum, Museum and Art Gallery of the Northern Territory, Queensland Museum, Raffles Museum of Biodiversity Research (National Univerity of Singapore), and Muséum national d'Histoire naturelle, Paris. Most characters and their taxonomic distributions were discussed in previous studies (e.g., Scholtz & Richter, 1995; Schram & Ahyong, 2002; Dixon et al., 2003). Scoring of some characters herein, however, differs from those of Dixon et al. (2003). Dixon et al. (2003) coded the presence or absence of chelae on different pereopods together in a single multistate character to avoid possible 'overweighting'. In this study, we scored each pereopod separately to preserve character state homology.

Coding of most morphological features is based on exemplars used in the molecular analyses. For some histological and spermatozoal characters that are regarded as highly conserved within familial groups, however, we have made reasonable assumptions of monophyly in order that these data could be included. Thus, following Scholtz & Richter (1995), we have scored embryonic growth zone characters as identical for our astacidan exemplars, although not every freshwater crayfish species has been assayed (character 98). Features of spermatozooal morphology (characters 99-101) are unknown for *Pylocheles macrops* (Pylochelidae), but are scored according to an undescribed *Pylocheles* sp., the only pylochelid for which sperm morphology is known (Tudge et al., 2001). Similarly, Scholtz & Richter (1995) regarded the telson stretch receptor (character 43) as a shared feature of galatheoids and hippoids, though again, not every species of these groups has been studied. Obviously, for controversial taxa for which histological data are unavailable, such as *Neoglyphea*, *Polycheles*, and *Enoplometopus*, all unknowns were scored as such. Characters are listed in Appendix 3.

***Molecular data.* –** Two nuclear ribosomal genes (18S rRNA, and the D1 region of 28S rRNA) and one mitochondrial ribosomal gene (16S rRNA), were selected because of their utility in resolving phylogenetic history at different taxonomic levels (Crandall et al., 2000). We collected new sequence data for 21 taxa resulting in 56 new sequences (see Appendix 1). Other sequences were available on Genbank. In all cases except for two (*Pagurus* and *Lithodes*), sequences for each gene were derived from the same species. For *Pagurus*, the molecular partition comprised 16S and 28S sequences from the congeners *P. bernhardus* and the 18S sequence of *P.*

longicarpus. For *Lithodes* the molecular partition comprised 16S and 28S sequences from the congeners *L. maja* and the 18S sequence of *L. santolla*. The 18S and 16S sequences for *Neaxius glyptocercus*, and the 18S sequence for *Biffarius arenosus* were those used by Tudge & Cunningham (2002).

***DNA extraction and analysis.* –** Genomic DNA was extracted from fresh or ethanol-fixed tissue samples using a modified protocol of Saghai-Maroof et. al. (1984). About 0.2g of tissue was placed in 600mL 2xC-TAB buffer (100mM Tris; 1.4M NaCl; 20mM EDTA; 2% hexadecyltrimethylammonium bromide (C-TAB); and 2% 2-β-mercaptoethanol). Samples were homogenised in microfuge tubes with pestle and 20µL of Proteinase K (20mg/mL) (Amresco). After overnight incubation at 37°C, or two to three hours at 65°C, one volume of phenol:chloroform:isoamyl alcohol (24:24:1v/v/v) (Sigma) was added, tubes were mixed by inversion, and centrifuged at maximum speed for two minutes in an Eppendorf 5154D microfuge. The upper aqueous layer was removed to a fresh tube containing one volume of chloroform:isoamyl alcohol (24:1v/v) (Amresco). Tubes were again mixed by inversion and centrifuged for two minutes at maximum speed. The aqueous layer was then removed to a fresh tube containing one volume of isopropanol. The tubes were inverted several times and stored overnight at –20°C. After thirty minutes centrifuging, the supernatant was removed and the DNA pellet was washed with 500µL of 70% ethanol. After brief vortexing and a final spin for ten minutes at maximum speed, the supernatant was removed and the pellet dried under vacuum for five minutes. Depending on the size of the pellet, gauged by visual inspection, the DNA was resuspended in 100µL TE (0.1M Tris, 0.01M EDTA). The amount and quality of DNA was estimated by agarose gel electrophoresis (Sambrook et al., 1989). Sequences of two nuclear (18S and 28S expansion region D1) and one mitochondrial (16S) ribosomal RNA genes were obtained. The 18S rRNA gene was amplified and sequenced in three contiguous fragments, using the primer pairs A & L, C & Y and B & O of Apakupakul et al. (1999). A partial sequence of the 28S D1 expansion region was amplified using 28S D1F and 28S D1R primer pairs (Colgan et al., 2003). A partial sequence of the 16S rDNA gene was amplified using the primer pairs 16SLF: 5'- CGC CTG TTT ATC AAA AAC AT -3' and 16SHR: 5'- CCG GTC TGA ACT CAG ATC ACG T-3' (H. Lui, pers. comm.).

Polymerase chain reaction (PCR) conditions were the identical for all primer sets. Amplifications were conducted in 25µL volumes containing 1.5mM $MgCl_2$, 0.025mM of each dNTP, 12.5pmol of each primer, 0.2µL of Qiagen *Taq* DNA polymerase, 2.5mL of Qiagen 10X PCR buffer, 5mL of Qiagen Q-solution and 1-100ng of whole genomic DNA (generally a 1:20-1:50 dilution of the stock DNA extraction). The following cycling profile was used for all experiments: an initial denaturation at 94°C for one minute, then 30 cycles of 94°C for twenty seconds, annealing for 30 seconds (50°C for 28S *D1*, 49°C for all 18S primers and 52°C 16S), extension at 72°C for 1.5 minutes, and a final extension at 72°C for two minutes. PCRs were checked by running 5µL of the reaction on a 2% agarose gel. In most cases, a single band was obtained and purified using QIAquick spin columns (Qiagen). In the event of multiple bands, the correct sized fragment was excised from an agarose gel over UV light and purified using QIAquick columns. Forward and reverse strands were sequenced using 0.25 volume BigDye version 3 Dye Terminator premix (ABI) with the same primers used for the PCR according to manufacturer's instructions. Samples were run on an ABI 310 Genetic Analyser. Forward and reverse strands were combined and sequences checked for errors using Sequencher (Genecodes). The 16S PCR product of *Enoplometopus occidentalis* appeared to be contaminated: six pGEM-T plasmids (Promega) containing an insert from the PCR reaction were sequenced in both directions and subject to a BLAST search (Altschul et al., 1990). Two clones contained inserts most similar to fungal sequences and the remaining four (each identical) contained inserts most similar to decapod sequences and were included in subsequent analyses. Final sequences were aligned in Clustal W using default parameters and adjusted by eye. Regions of ambiguous alignment were excluded and gaps were treated as missing. The combined sequences comprised about 2.5 kilobases of nucleotide data. The alignment is available from the authors.

***Analytical methods.* –** Morphological and molecular data partitions were analysed in combination following the philosophy of 'simultaneous analysis' or 'total evidence' (e.g., Patterson, 1987; Nixon & Carpenter, 1996; Whiting et al., 1997; Schuh, 2000; Giribet et., 2001; Prendini et al., 2003). Parsimony analyses were conducted in PAUP* 4.0b10 (Swofford, 2002) (heuristic search, TBR, random addition sequence, 500 replicates). All characters were unordered. Initial analyses of the combined data were conducted under equal weights as the natural starting point (Allard & Carpenter, 1996; Edgecombe et al., 2000). Transitions are generally recognised to exhibit higher homoplasy rates than transversions, leading some to downweight or even exclude transitions (e.g., Swofford et al., 1996). The choice of any particular weighting scheme, however, is arbitary. Therefore, examination of topological stability under a range of parameters is a useful means of discerning between stable and unstable clades (i.e., those appearing under a wide range rather than under single or few parameters) (e.g., Whiting et al., 1997; Phillips et al., 2000; Giribet et al., 2002; Prendini et al., 2003). Consequently, we tested the topological sensitivity to variation in transition weights between 0 (complete exclusion) and 1 (transitions equal to transversions). Eleven transition weights were applied via step matrices in PAUP*: 0, 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9 and 1.0. Character congruence was used as an optimality criterion to select the combined analysis that minimised incongruence between data partitions. This 'optimal' cladogram is that produced under the weighting scheme that minimised overall character conflict as measured by the Incongruence Length Difference metric (ILD) (Mikevich & Farris, 1981). The incongruence among data partitions is given by dividing the difference between the combined tree length and the sum of its data partitions by the combined tree length:

Table 1. Average percentage nucleotide composition for 16S, 18S, 28S sequences, and combined sequences

	A	C	G	T
16S	33.111%	20.796%	13.156%	32.938%
18S	24.880%	23.758%	27.151%	24.211%
28S	22.526%	26.105%	33.138%	18.230%
Combined	25.977%	23.523%	25.497%	25.004%

Table 2. Tree length statistics and ILD values for separate and combined analyses under varied transition weights. (TS = transition weight, Comb = tree length for combined data, Mol = tree length for molecular partition, Morph = tree length for morphological partition, ILD = incongruence length difference, CI = consistency index, RI = retention index). Statistics for analysis with miminal ILD in bold.

TS	Morph	16S	18S	28S	Mol	Comb	ILD	CI	RI
1.00	**254**	**1649.00**	**1476.00**	**597.00**	**3820.00**	**4104.00**	**0.007310**	**0.3431**	**0.5404**
0.90	254	1558.80	1395.00	565.40	3610.30	3894.80	0.007831	0.3458	0.5432
0.80	254	1468.60	1314.00	533.80	3400.60	3685.60	0.008411	0.3436	0.5462
0.70	254	1378.40	1232.80	502.20	3190.80	3475.20	0.008748	0.3412	0.5495
0.60	254	1287.80	1151.40	470.40	2979.40	3264.40	0.009496	0.3386	0.5532
0.50	254	1194.50	1070.00	437.50	2766.50	3053.50	0.010807	0.3357	0.5572
0.40	254	1102.80	987.40	403.60	2553.80	2842.40	0.012173	0.3258	0.5617
0.30	254	1005.80	904.80	368.90	2340.10	2631.20	0.014100	0.3284	0.5667
0.20	254	913.00	822.40	332.60	2124.60	2417.60	0.016132	0.3242	0.5730
0.10	254	814.20	735.90	296.30	1908.80	2203.30	0.018382	0.3192	0.5804
0.00	254	718.00	649.00	260.00	1693.00	1989.00	0.021116	0.2875	0.5889

$$ILD = [LENGTH_{combined} - \Sigma LENGTH_{individual\ partitions}] / LENGTH_{combined}$$

Relative stability of clades was assessed using parsimony jackknifing (Farris et al., 1996) and Bremer support (Bremer, 1994). Jackknife frequencies were calculated in PAUP* using 1000 pseudoreplicates under a heuristic search with 33% character deletion. Bremer support values were determined using the 'enforce converse contraints' command in PAUP* using MacClade 4.0 (Maddison & Maddison, 2000) to generate the PAUP* converse constraints command file.

RESULTS

The aligned combined dataset contained 45 taxa and 2637 characters of which 769 are parsimony informative. The morphological data comprised 105 parsimony informative characters. The aligned 16S rRNA dataset comprised 421 characters of which 278 are variable (66%), and 220 are parsimony informative (52%). The aligned 18S rRNA dataset comprised 1811 characters with 545 variable sites (30%) and 320 parsimony informative sites (18%). The aligned 28S rRNA dataset comprised 300 characters of which 159 are variable (53%) and 115 parsimony informative (38%). As indicated by the proportions of parsimony informative sites in each gene sequence, the least conserved fragment is 16S followed by 28S and 18S. The 16S fragment is relatively AT rich compared to the other two fragments, though Chi-Squared tests of nucleotide composition for each gene fragment found no significant heterogeneity (16S, df = 132, $P = 0.99$; 18S, df = 132, $P = 1.00$; 28S, df = 132, $P = 1.00$). Mean nucleotide composition is given in Table 1.

Simultaneous analysis of morphological and molecular partitions under equal weights resulted in a single most parsimonious cladogram (4104 steps, CI 0.3431, RI 0.5404) (Figs. 2, 3). Palinura as traditionally recognised (i.e., Achelata + Glypheidea + Polychelida) is polyphyletic. Polychelida is sister to all other reptants, followed by Achelata, which is sister to Fractosternalia. Astacidea is monophyletic and sister to Glypheidea, together comprising Astacura. Within Astacidea, the freshwater crayfish (Astacida) are sister to the marine clawed-lobsters (Homarida) and within Homarida, Enoplometopoidea is sister to Nephropoidea comprising Thaumastochelidae + Nephropidae. Thalassinidea is monophyletic and sister to (Meiura (Brachyura + Anomura)). Both Anomura and Brachyura are monophyletic. Monophyly of infraordinal clades is strongly supported, with Bremer support and jackknife frequencies ranging from 7-52 steps and 96-100% respectively. Variation in transition weights resulted in identical infraordinal relationships, indicating topological stability. Minimal overall partition incongruence was achieved under equal transition:transversion weights. Tree length statistics and ILD values for sensitivity analysis are given in Table 2.

Separate analyses of the morphological data produced 12 most parsimonious trees (254 steps, CI 0.49, RI 0.86) (Fig. 2A). Separate analysis of the molecular partition under equal weights resulted in two most parsimonious trees (3820 steps, CI 0.34, RI 0.48) (Fig. 2B). Despite ambiguity within some

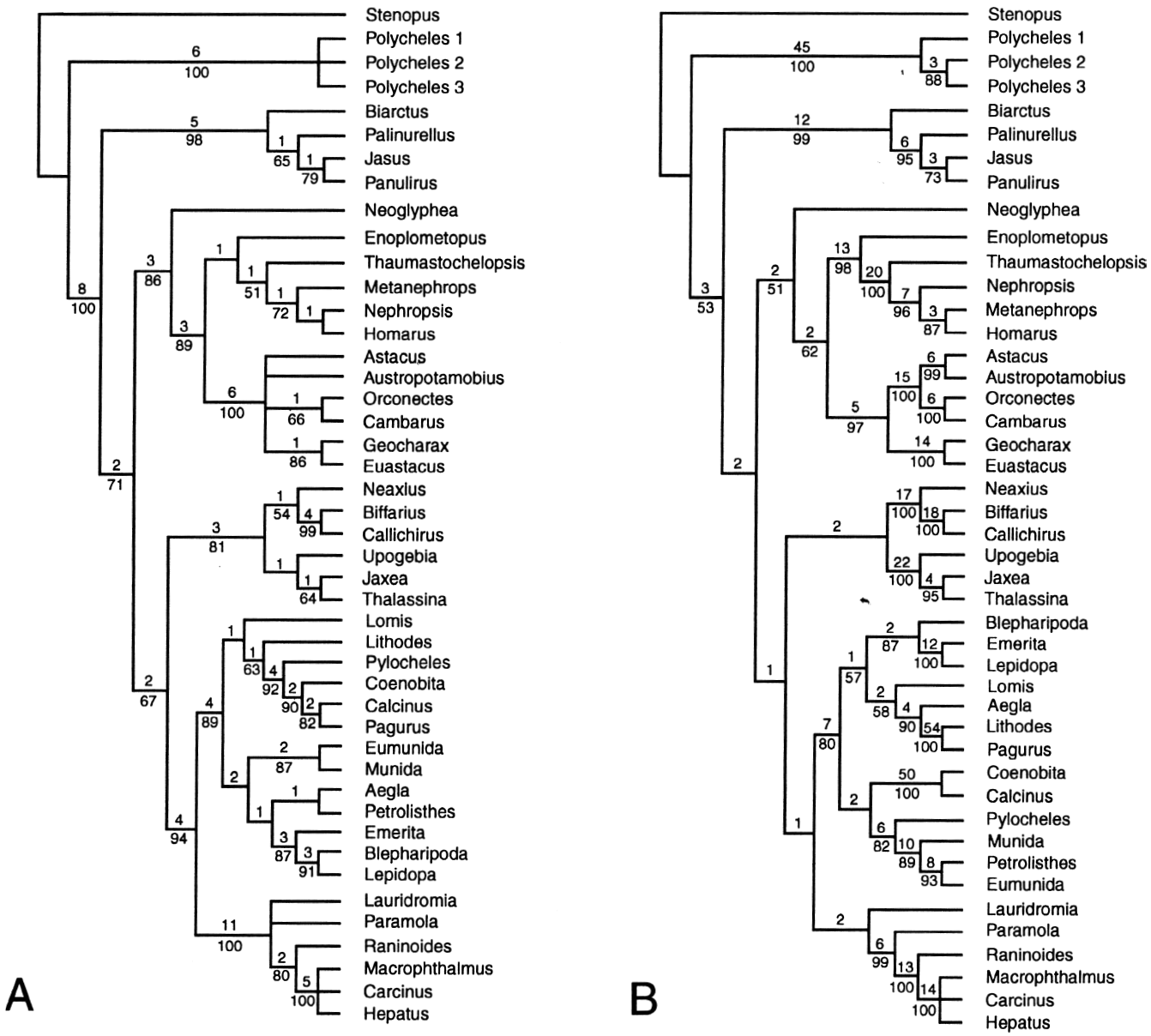


Fig. 2. A, strict consensus of 12 most parsimonious trees based on morphological partition (TL 254 steps, CI 0.49, RI 0.86). B, strict consensus of 2 most parsimonious trees based on molecular partition under equal weights (TL 3820, CI 0.34, RI 0.48). Bremer support and jackknife frequencies indicated above and below branches respectively.

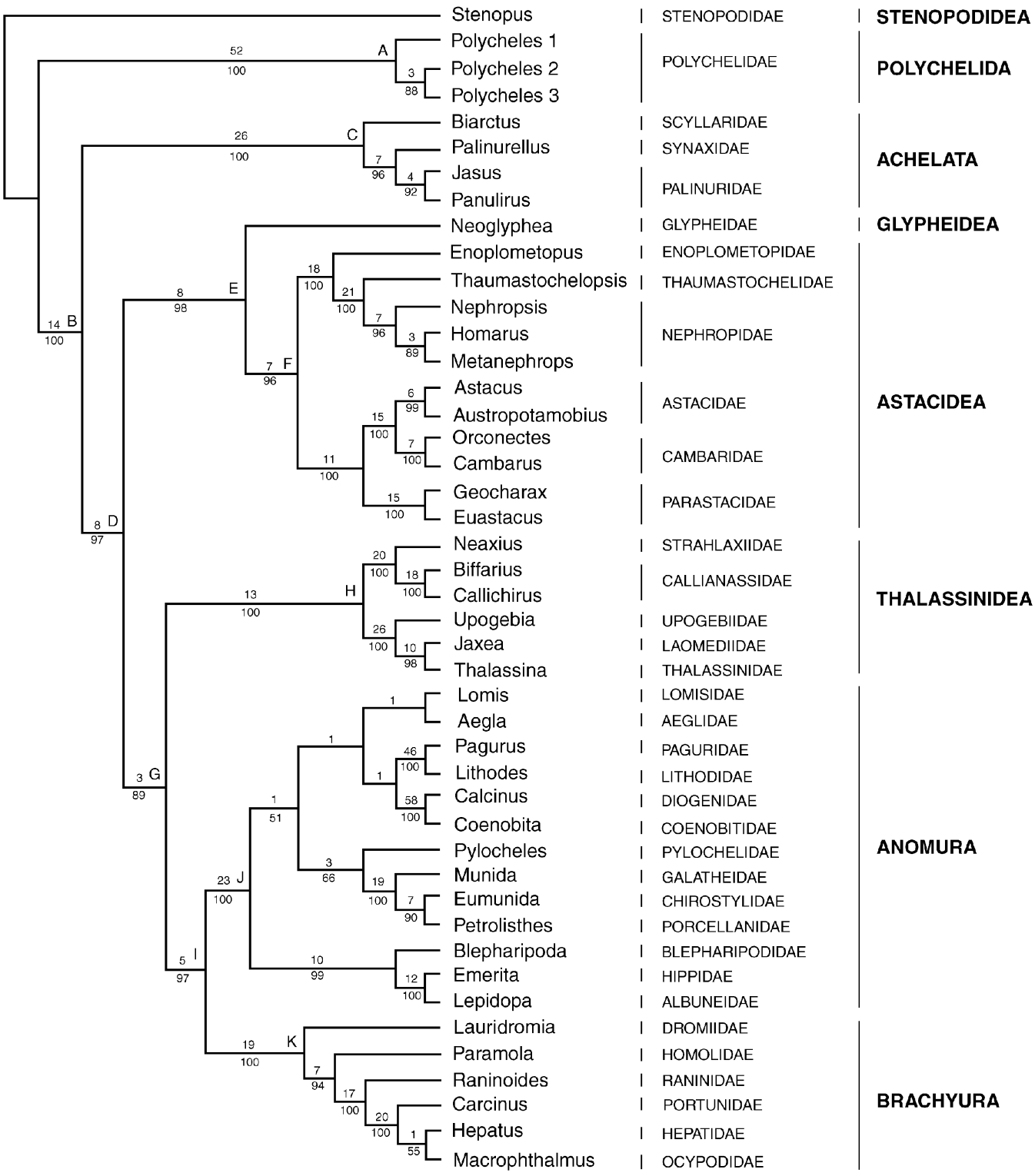


Fig. 3. Single most parsimonious cladogram of combined data using weighting that minimises incongruence (transition: transversion weights equal, TL 4104, CI 0.34, RI 0.54). Bremer support and jackknife frequencies indicated above and below branches respectively. Character optimisations for labelled nodes given in Table 2.

Table 3. Unambiguous morphological character state transformations for major nodes in the optimal cladogram (Fig. 3).

Node A (Polychelida): **5**: 0→1, **7**: 0→1, **31**: 0→1, **67**: 0→2, **85**: 0→1.
Node B (Eureptantia): **39**: 0→1, **58**: 0→1, **62**: 0→1, **69**: 0→1, **74**: 0→1, **84**: 0→1, **88**: 0→1, **97**: 0→1.
Node C (Achelata): **15**: 0→1, **20**: 0→1, **41**: 0→1, **42**: 2→0, **44**: 0→1, **64**: 0→1, **66**: 0→1.
Node D (Fractosternalia): **18**: 0→1, **21**: 0→1, **30**: 0→1, **53**: 0→1, **77**: 0→1, **104**: 0→1.
Node E (Astacura): **1**: 0→1, **47**: 0→1, **48**: 0→1, **49**: 0→1, **76**: 0→1, **79**: 0→1, **82**: 0→1.
Node F (Astacidea): **12**: 0→1, **78**: 0→1, **84**: 0→1.
Node G (Lineata): **2**: 0→1, **9**: 0→1, **11**: 0→1.
Node H (Thalassinidea): **17**: 0→1, **32**: 0→1, **34**: 0→1, **75**: 0→2, **83**: 0→1.
Node I (Meiura): **7**: 0→1, **27**: 0→1, **33**: 1→0, **36**: 0→1, **54**: 0→1, **90**: 0→1.
Node J (Anomura): **28**: 0→1, **59**: 0→1, **69**: 0→1, **89**: 0→1, **93**: 0→1, **99**: 0→1.
Node K (Brachyura): **13**: 0→1, **15**: 0→1, **18**: 1→0, **21**: 1→0, **26**: 1→2, **37**: 0→1, **39**: 1→0, **46**: 0→2, **57**: 0→1, **60**: 0→1, **78**: 1→0, **81**: 0→1, **88**: 1→3, **91**: 0→1.

major clades, relationships between infraordinal clades in partitioned morphological and molecular analyses were congruent with those of the combined analyses. Morphological topologies differed from the molecular topologies in resolution within Polychelida, relative positions of *Metanephrops* and *Nephropsis* within Homarida, internal resolution of Astacida and Brachyura, and in internal relationships of the Anomura. In most instances, the combined analysis resolved ambiguity present in the morphological topologies in line with the molecular signal, but internal relationships of Anomura differed from those recovered under both partitioned analyses. Morphological character optimisations and topological stability measures for the optimal cladogram are given in Table 3 and Figure 3 respectively.

DISCUSSION

The value of simultaneous analysis is exemplified in the present results: cladograms derived from combined datasets were better resolved than those of separate analyses, and combination has permitted emergence of secondary signal within Anomura. Monophyly and interrelationships of the major 'infraordinal' reptant clades are robust, being both insensitive to parameter variation and well corroborated (as measured by jackknifing and Bremer support). Our results verify the positions of Polychelida and Meiura as determined by previous cladistic studies (Scholtz & Richter, 1995; Schram, 2001; Dixon et al., 2003) but also arbitrate areas of conflict. Thus, Achelata is near basal instead of sister to Meiura (contra Dixon et al., 2003); Thalassinidea is sister to Meiura instead of Achelata + Meiura (contra Dixon et al., 2003); Astacidea is monophyletic (contra Scholtz & Richter, 1995), with inclusion of enoplometopoids in Homarida (contra Schram, 2001); and Glypheoidea is sister to Astacidea (contra Scholtz & Richter, 1995, and Schram, 2001). Although relationships within most infraordinal clades will remain unsettled for sometime, the broad pattern of reptant evolution appears to be emerging. Major clades are discussed in more detail below.

ACHELATA and POLYCHELIDA

The basal position of Polychelida in Reptantia, and polyphyly of Palinura *sensu lato* in our analyses, corroborates previous cladistic studies (Scholtz & Richter, 1995; Schram, 2001; Schram & Ahyong, 2002; Dixon et al., 2003). The relationships of the three polychelid exemplars reflect taxonomic expectations. *Polycheles* 1 corresponds to *Polycheles* sensu stricto and *Polycheles* 2 and 3 correspond to the old genus *Stereomastis*. Owing to the removal of polychelids and glypheoids from Palinura, we follow Scholtz & Richter (1995), Richter & Scholtz (2001), Dixon et al. (2003) and Poore (2004) in applying Achelata to the clade containing nominate palinuran taxa and allies. Amati et al. (2004) suggested achelate paraphyly (by uniting polychelids with scyllarids) based on two shared characters: the first pereopod being larger than the others, and the presence of a dorsal median ridge on the abdomen. This unusual relationship is, however, unlikely. The characters identified by Amati et al. (2004) are present in other achelates (e.g., *Justitia*, with an enlarged first pereopod; *Linuparus* and *Palinustus*, with a median dorsal abdominal ridge). Moreover, Polychelida and Achelata are the most strongly supported infraordinal clades in our analysis.

The near basal position of Achelata, recognised by Scholtz & Richter (1995) and Schram (2001) was not recovered by Dixon et al. (2003). Dixon et al. (2003) proposed Eurysternalia for the clade Meiura + Achelata, united by the broad sternum, antennal and antennular similarities. In placing Achelata 'down tree', our results indicate that the putative synapomorphies of Eurysternalia are convergent. Accordingly, Eurysternalia is not recognised herein.

The status of Synaxidae, whether distinct from or synonymous with Palinuridae, is disputed (cf. Davie, 1990; Holthuis, 1991; Martin & Davis, 2001). Synaxidae is not contradicted by our results — our synaxid exemplar, *Palinurellus wieneckii*, is sister to the palinurid exemplars in the analysis. However, a recent, comprehensive cladistic analysis of palinurids and synaxids, using morphological and molecular data, indicated

synaxid polyphyly and in most analyses found both extant synaxid genera to be nested among other palinurans (Patek & Oakley, 2002).

ASTACURA: GLYPHEIDEA + ASTACIDEA

Following Dixon et al. (2003), we recognise Astacura for Glypheidea + Astacidea. The glypheideans have a diverse fossil record dating from the Triassic. The mosaic of characters possessed by most glypheoids, such as the thalassinidean- or astacidean-like habitus and palinuran-like achelate limbs have variously allied them to all major reptant groups. Glypheideans have even been accorded a central role in decapod evolution (Glaessner, 1969), and the view that they are primitive reptants has persisted even into very recent literature (Martin & Davis, 2001). Many workers in the latter 20th century treated glypheoids as palinurans because of their achelate or subchelate pereopods, but discovery of the rare 'living fossil' *Neoglyphea inopinata* reinvigorated studies into the glypheoids (Forest & de Saint Laurent, 1975, 1981, 1989). Consistent findings of recent morphological (Forest & de Saint Laurent, 1989; Schram & Ahyong, 2002; Feldmann & de Saint Laurent, 2002; Dixon et al., 2003; Amati et al., 2004) and now molecular analyses indicate that glypheoids must be considered astacuran. The position of the achelate glypheoids within Astacura poses the question — is the lack of chelae in Glypheoidea and Achelata of the same origin and are the chelae of Astacideans homologous with those of other Reptantia? The first pereopod is chelate in almost all decapods. The most parsimonious interpretation of our results indicates that the achelate condition of Achelata and Glypheidea are independent derivations and that the major chelae of other reptants are primary homologies. Moreover, Amati et al. (2004) recently described a new Middle Triassic genus and family, *Chimerastacus* (Chimerastacidae), as sister to the Glypheidae. The well-developed chelae in *Chimerastacus* indicate that stem lineage glypheoids were probably also chelate. Further, shared carapace groove patterns show that the extinct clawed lobsters, Erymoidea, are sister to Glypheoidea instead of Nephropoidea as previously thought (Amati et al., 2004). Thus, the phylogenetic position of Erymoidea, as sister to Glypheoidea, further indicates that the achelate pereopods of glypheids and achelates are convergent.

The original concept of Fractosternalia included Glypheidea, Astacida, Thalassinidea and Meiura, united by the possession of fused rather than articulated posterior thoracic sternites, and a bi- rather than tri-partite secula (Scholtz & Richter, 1995; Schram & Ahyong, 2002). The bipartite secula and fused posterior thoracic sternites placed Homarida as sister to, but excluded from, Fractosternalia (Scholtz & Richter, 1995). Present recognition of a monophyletic Astacidea, however, corroborates the conclusions of Crandall et al. (2000) and Dixon et al. (2003), and thus places Homarida within Fractosternalia. As in Brachyura, the absence of fractostern synapomorphies in Homarida is a derivation, acquired independently in both clades. Internal relationships of the Astacida were comprehensively treated by Crandall and colleagues (e.g., Crandall et al., 2000)

Homarida comprises Nephropoidea and Enoplometopoidea. Recent molecular (Tam & Kornfield, 1998) and morphological analyses of selected lobster genera (Tshudy & Babcock, 1997; Tshudy & Sorhannus, 2000a, b) challenged the validity of the nephropid subfamilies of Holthuis (1974, 1991). In addition, Tshudy & Babcock (1997) and Tshudy & Sorhannus (2000a, b) disputed the validity of Thaumastochelidae, whilst Dixon et al. (2003) found thaumastochelids to be outside of Homarida. Nephropoidea in our analyses comprises a nephropid group as sister to *Thaumastochelopsis* sp. Accordingly, we recognise Thaumastochelidae and Nephropidae. The status of the nephropid subfamilies certainly requires close scrutiny, but the status of Thaumastochelidae seems secure.

Enoplometopoidea, the sister to Nephropoidea, is a small, apparently relict group, comprising 11 tropical marine species assigned to *Enoplometopus* (see Poupin, 2003). The systematic position of enoplometopoids has been disputed owing to their unusual combination of morphological features, such as the suppressed carapace grooves, semichelate second and third pereopods, astacoid-like abdominal pleura, non-fractostern condition, and articulated posterolateral telson spines. *Enoplometopus* has been treated as an astacidean (de Saint Laurent, 1988; Scholtz & Richter, 1995; Dixon et al., 2003; Amati et al., 2004), an axiid thalassinidean (Holthuis, 1974, 1983; Fransen et al., 1997) or sister to Fractosternalia + Homarida (Schram, 2001). Our results corroborate the bulk of decapod studies by indicating an enoplometopoid-nephropoid affinity. Until now, the enoplometopoid fossil record was unknown, although Schram (2001) speculated on a possible connection with the Upper Devonian *Palaeopalaemon newberryi* Whitfield. On the basis of excellent revisionary studies of the fossil lobsters (Schweigert & Garassino, 2003; Schweigert et al., 2003), however, we suggest that enoplometopids have strong affinities with the extinct Uncinidae, notably *Malmuncina* Schweigert & Garassino. Both groups share indistinct or suppressed carapace grooves, similar abdominal pleura, a dorsally and laterally dentate rostrum, and spinose margins of the propodus and dactylus of the chelae. Uncinidae is thus assigned to the Enoplometopoidea, extending the 'enoplometopoid' fossil record back to the Lower Jurassic.

THALASSINIDEA

Some authors treated thalassinideans as part of the Anomura (e.g., Borradaile, 1907; Glaessner, 1969), but most regard the two groups as distinct. Current debates over Thalassinidea largely concern monophyly, phylogenetic position and internal relationships. Monophyly of Thalassinidea has oft been disputed, primarily on the basis of larval and spermatozoal features (see Poore, 1994; Scholtz & Richter, 1995; Schram, 2001; Dixon et al., 2003 for monophyly; and Gurney, 1938; de Saint Laurent, 1973; Tudge, 1997; Tudge & Cunningham, 2002; Morrison et al., 2002 for non-monophyly). The most recent and most comprehensive morphological cladistic analysis of Thalassinidea indicates monophyly (Poore, 1994). Tudge & Cunningham (2002),

using 16S and 18S sequences, found low support for overall monophyly but recovered two, separate, strongly supported clades. Our analyses recover Tudge & Cunningham's (2002) two major clades, but as a strongly supported monophylum. Callianassoid exemplars, however, are ranged in both major clades, suggesting that Callianassoidea sensu Poore (1994) might not be monophyletic. Interestingly, the two main thalassinidean clades recovered herein and by Tudge & Cunningham (2002) correspond to the superfamilial groupings proposed by de Saint Laurent (1979a, b): Axioidea comprising Axiidae (sensu lato), Callianassidae and Callianideidae; and Gebiidea comprising Laomediidae, Upogebiidae and Thalassinidae.

The unsettled position of Thalassinidea in Reptantia has largely revolved around disputed homologies of carapace lineae in thalassinideans (*linea thalassinica*), anomurans (*linea anomurica*) and brachyurans (*linea dromica*). Analyses finding a sister relationship between thalassinideans and anomurans (e.g., Martin & Abele, 1986; Poore, 1994) treated the lineae of both groups as homologous. In contrast, Scholtz & Richter (1995) regarded *linea anomurica* and *linea thalassinica* as independent because some thalassinideans lack carapace lineae, and because the lineae of thalassinideans terminates at the posterior margin of the carapace whereas the lineae of paguroids terminates in an uncalcified field. Consequently, Scholtz & Richter (1995) could not resolve the position of thalassinideans, although the connection between Anomura and Brachyura was recognised in a new clade, Meiura. Rather than refuting the primary homology of the lineae, however, we suggest that Scholtz & Richter's (1995) observations show that the posterior portion of the lineae is merely modified differently in the two clades. Moreover, the absence of lineae in axioids, herein represented by *Neaxius glyptocercus*, is a secondary loss as shown by its internal position in Thalassinidea. Thus, the most parsimonious interpretation of the data indicates that carapace lineae in thalassinideans, anomurans and brachyurans are homologous, being a synapomorphy of Thalassinidea + Meiura. Dixon et al. (2003) introduced Sterropoda for Thalassinidea + Achelata + Meiura, named for the fused ischium and basis of the pereopods. Return of Achelata to a near basal position in Reptantia invalidates the original concept of Sterropoda. Although Sterropoda could be redefined to refer to Thalassinidea + Meiura, the nominate synapomorphy is not unique to the clade. Therefore, for Thalassinidea + Meiura, we propose a new name, Lineata, alluding to the shared carapace lineae. The presence of carapace lineae in the oldest known decapod, *Palaepalaemon newberryi* from the Upper Devonian, suggests that it is sister to, if not within the Lineata (Schram & Dixon, 2003). If this association is correct, then Lineata, and possibly the entire Reptantia, could be considerably older than presently known.

MEIURA: ANOMURA + BRACHYURA

As determined by recent cladistic studies (e.g., Scholtz & Richter, 1995; Schram, 2001; Dixon et al., 2003), Anomura and Brachyura are sisters rather than having evolved independently from separate macrurous forms as previously thought (Glaessner, 1969). Our results corroborate previous somatic morphological and molecular analyses of Anomura in strongly supporting monophyly (Martin & Abele, 1986; Scholtz & Richter, 1995; Schram, 2001; Dixon et al., 2003). Internal relationships are less stable, and despite generally low internal support, patterns recovered in the combined analysis reflect those emerging from several other studies. Hippoidea is sister to the remaining anomurans as found by Martin & Abele (1986) and the most recent molecular analysis (Pérez-Losada et al., 2002). Paguroidea and Galatheoidea are sisters but neither is strictly monophyletic. The symmetrical paguroid *Pylocheles macrops* (Pylochelidae) is sister to the remaining galatheoids, albeit with weak support. In this context, the dissimilarity between pylochelid sperm and that of other paguroids is noteworthy (Tudge et al., 2001). Previous workers have regarded pylochelids as possibly paraphyletic, but certainly paguroid (Richter & Scholtz, 1994), so the unusual position of Pylochelidae in our results is unexpected based on somatic morphology.

The position of Aeglidae in our results is significant, as sister to Lomisidae, and together with the latter being sister to the paguroids instead of the galatheoids. Aeglids have almost universally been aligned with the Galatheoidea (Martin & Davis, 2001) owing to superficial similarities with galatheids, but several studies have challenged prevailing wisdom. Two non-cladistic studies (Dana, 1852; Martin & Abele, 1988) recognised a remarkable resemblance between carapace suture patterns of aeglids and paguroids. Other similarities between aeglids, and at least some paguroids, include asymmetrical chelae and trichobranchiate gills (Martin & Abele, 1988). Morrison et al. (2002) (using molecular data) and Tudge & Scheltinga (2002) (using sperm morphology) recognised a close relationship between *Aegla* and *Lomis* (Lomisoidea) although the former study also recognsied a close association of aeglids and lomisids with galatheoids instead of paguroids. Most recently, Pérez-Losada et al. (2002) found Aeglidae to be independent of both Galatheoidea and Paguroidea, supporting superfamily status for aeglids. Clearly, the galatheoid position of Aeglidae in the Anomura seems questionable as several independent lines of evidence now suggest.

Strong support for brachyuran monophyly in our analyses reflects results of other cladistic studies (Scholtz & Richter, 1995; Jamieson et al., 1995; Schram, 2000; Dixon et al., 2003). Although Spears et al. (1992) proposed transfer of dromiids to Anomura based analysis of 18S sequences, all podotremes in our analysis, including a dromiid, are unambiguously brachyuran. The unexpected position of the dromiid *Hypoconcha arcuata* Stimpson according to Spears et al. (1992) lacks morphological support and is perhaps best interpreted as aberrant behaviour of incomplete sequence data. Resequencing of *Hypoconcha* is recommended. As indicated by Scholtz & Richter (1995), other similiarities between basal brachyurans and anomurans cited as evidence of affinity, such as larval and spermatozoal morphology, are plesiomorphic. We find no support for the anomuran dromiid hypothesis.

A different explanation of the anomuran-like dromiid larvae

was proposed by Williamson (1988, 1992) in horizontal gene transfer between an anomuran and brachyuran. Since cladistic analyses show Anomura and Brachyura to be sister groups, larval similarities are hardly surprising. Therefore, Scholtz & Richter (1995) dismissed Williamson's hypothesis as a failure to recognise dromiid larval plesiomorphy. The core of the problem, however, was not a simple error of method because Williamson's hypotheses were grounded in phylogeny. The widely held view at the time indicated that, rather than being sister groups, Brachyura and Anomura were independently derived from separate lobster-like ancestors (Glaessner, 1969; Williamson, 1988, 1992). In that context, instead of suggesting retention of plesiomorphies, the anomuran-like larval morphology of dromiids either indicated radical convergence or unrecognised affinity. Williamson favoured the latter and proposed horizontal gene transfer instead of questioning the phylogeny. Unfortunately, the phylogenetic models used by Williamson were the result of unrepeatable, intuitive methods of construction. Williamson & Rice (1996) again invoked horizontal gene transfer to account for significant morphological disparity between pelagic larvae of two supposedly closely related groups — achelates and polychelids, both previously placed in Palinura. Cladistic analyses, however, consistently indicate palinuran polyphyly. Polychelids and achelates are not close relatives, so larval dissimilarity is not unexpected. Clearly, erroneous patterns used by Williamson led to dubious hypotheses of process. These examples underscore the potential impact of phylogeny on biological theory, and therefore the fundamental need for robust, well-corroborated phylogenetic hypotheses. Had phylogenetic research been adequate, Williamson's (1988, 1992) radical theory would probably not have been suggested, at least for Decapoda.

Most workers accept monophyly of Guinot's Thoracotremata and paraphyly of Heterotremata but are divided over Podotremata (Guinot & Bouchard, 1998; McLay, 1999; Tavares, 2003). Analyses of sperm morphology (Guinot et al., 1994; Jamieson et al., 1995) support podotreme monophyly. In contrast, our data and a recent study of foregut morphology suggest paraphyly with dromiids as basal Brachyura (Brösing et al., 2002). Our sampling of podotremes is preliminary, however, and additional brachyuran exemplars are required to robustly test the status of Podotremata. Indeed, the internal relationships of the massively diverse Brachyura, together with integration of the diverse fossil record (Feldmann, 2003) remain among the greatest challenges currently facing reptant phylogenetics.

Classification of the Reptantia

We propose a revised classification of the Reptantia below. It resembles that of Dixon et al. (2003) but with obvious differences in the position of Achelata, return of Thaumastochelidae to Nephropoidea, suppression of Sterropoda, use of Anomura instead of Anomala (following common usage), and proposal of Lineata for the Thalassinidea + Meiura clade.

Accommodating phylogenetic information within a Linnaean classification is difficult because of the limited number of available rank categories. These and other limitations of the Linnaean system have led some to propose its abandonment (e.g., Cantino et al., 1999). Despite the problems of the Linnaean system, however, its practical value remains, and continues to be almost universally accepted. Obviously, Linnaean categories have no ontological meaning and taxa of equal rank are equivalent only in the sense that their compositions are mutually exclusive. Thus, providing that taxa are monophyletic, rank assignments should be no more than issues of taxonomic utility. If our classification of Reptantia is placed in a Linnaean framework, we propose the following Infraorders (indicated below in bold): Polychelida, Achelata, Glypheidea, Astacidea, Thalassinidea, Anomura and Brachyura. Most of these groups have long been treated as Infraorders. Achelata, Polychelida and Glypheidea, however, are recognised in view of the polyphyly of the traditional Palinura. Forest & de Saint Laurent (1989) proposed infraordinal status for Glypheidea, but several subsequent authors (and only recently at that) formally placed glypheoids within Astacidea (Martin & Davis, 2001; Feldmann & de Saint Laurent, 2002; Amati et al., 2004). Either scheme is equally consistent phylogenetically, but the latter alters long established use of Astacidea. Therefore, we apply Astacidea in its traditional sense, for homaridans and astacidans, and recognise Glypheidea as a separate Infraorder.

DECAPODA
Reptantia Boas
Polychelida de Haan
Eureptantia Scholtz & Richter
Achelata Scholtz & Richter
Fractosternalia Scholtz & Richter
Astacura Borradaile
Glypheidea Winckler
Astacidea Latreille
Astacida Latreille
Homarida Bate
Lineata *new clade*
Thalassinidea Latreille
Meiura Scholtz & Richter
Anomura MacLeay
Brachyura Latreille

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APPENDIX 1. Classification of exemplars with GenBank accession numbers for gene sequences. New sequences are indicated (*). T & C are from Tudge & Cunningham (2002).

	16S	18S	28S
STENOPODIDEA Claus			
Stenopodidae Claus			
Stenopus hispidus (Olivier)	AY583884*	AY583958*	AY583976*
POLYCHELIDA de Haan			
Eryonoidea de Haan			
Polychelidae Wood-Mason			
Polycheles aculeatus Galil (*Polycheles* 2)	AY583885*	AY583959*	AY583977*
Polycheles baccatus Bate (*Polycheles* 1)	AY583886*	AY583960*	AY583978*
Polycheles suhmi (Bate) (*Polycheles* 3)	AY583887*	AY583961*	AY583979*
ACHELATA Scholtz & Richter			
Palinuroidea Latreille			
Palinuridae Latreille			
Panulirus argus (Latreille)	AF337966	U19182	AF436000
Jasus edwardsii (Hutton)	AF192866	AF235972	
Scyllaridae Latreille			
Biarctus sordidus (Stimpson)	AY583888*	AY583962*	AY583980*
Synaxidae Bate			
Palinurellus wieneckii (de Man)	AY583889*	AY583963*	AY583981*
GLYPHEIDEA Winckler			
Glypheoidea Winckler			
Glypheidae Winckler			
Neoglyphea inopinata Forest & de St Laurent	AY583894*	AY583968*	AY583986*
ASTACIDEA Latreille			
Nephropoidea Dana			
Nephropidae Dana			
Homarus americanus H. Milne Edwards	AF370876	AF236971	
Metanephrops armatus Chan & Yu	AY583890*	AY583964*	AY583982*
Nephropsis stewarti Wood-Mason	AY583891*	AY583965*	AY583983*
Thaumastochelidae Bate			
Thaumastochelopsis sp.	AY583893*	AY583967*	AY583985*
Enoplometopoidea de St Laurent			
Enoplometopidae de St Laurent			
Enoplometopus occidentalis (Randall)	AY583892*	AY583966*	AY583984*
Astacoidea Latreille			
Astacidae Latreille			
Astacus astacus (Linnaeus)	AF235983	AF235959	AF235973
Austropotamobius torrentium (Schrank)	AF235984	AF235960	AF235974
Camabaridae Hobbs			
Cambarus maculatus Hobbs & Pflieger	AF235988	AF235964	AF235978
Orconectes virilis Hagen	AF235989	AF235965	AF235979
Parastacoidea Huxley			
Parastacidae Huxley			
Geocharax gracilis Clark	AF235992	AF235968	AF235982
Euastacus bispinosus Clark	AF235991	AF235967	AF235981
THALASSINIDEA Latreille			
Callianassoidea Dana			
Callianassidae Dana			
Biffarius arenosus (Poore)	AY583895*	T&C	AY583987*
Callichirus major (Say)	AF436041	AF436002	
Upogebiidae Borradaile			
Upogebia affinis (Say)	AF436047	AF436007	AF435987
Laomediidae Borradaile			
Jaxea nocturna Nardo	AF436046	AF436006	AF435986
Axioidea Huxley			
Strahlaxiidae Poore			
Neaxius glyptocercus von Martens	T&C	T&C	
Thalassinoidea Latreille			
Thalassinidae Latreille			
Thalassina anomala (Herbst)	AY583896*	AY583969*	AY583988*

APPENDIX 1 (continued)

ANOMURA MacLeay			
Paguroidea Latreille			
Coenobitidae Dana			
Coenobita compressus H. Milne Edwards	AF436059	AF436023	AF435999
Diogenidae Ortmann			
Calcinus obscurus Stimpson	AF436058	AF436022	AF435998
Lithodidae Samouelle			
Lithodes maja (Linnaeus)	AF425330		AF425350
Lithodes santolla (Molina)		AF439385	
Paguridae Latreille			
Pagurus bernhardus (Linnaeus)	AF425335		AF425354
Pagurus longicarpus Say		AF436018	
Pylochelidae Bate			
Pylocheles macrops Forest	AY583897*	AY583970*	AY583989*
Lomisoidea Bouvier			
Lomisidae Bouvier			
Lomis hirta (Lamarck)	AF436052	AF436013	AF435993
Galatheoidea Samouelle			
Chirostylidae Ortmann			
Eumunida sternomaculata de St Laurent & Macpherson		AF436011	AF435991
Galatheidae Samouelle			
Munida quadrispina Benedict	AF436050	AF436010	AF435990
Porcellanidae Haworth			
Petrolisthes armatus (Gibbes)	AF436049	AF436009	AF435989
Hippoidea Latreille			
Albuneidae Stimpson			
Lepidopa californica Efford	AF436054	AF436015	AF435996
Blepharipodidae Boyko			
Blepharipoda occidentalis Randall	AF436053	AF436014	AF435994
Hippidae Latreille			
Emerita emeritus (Linnaeus)	AY583898*	AY583971*	AY583990*
Superfamily Uncertain			
Aeglidae Dana			
Aegla uruguyana Schmitt	AF436051	AF436012	AF435992
BRACHYURA Latreille			
Dromioidea de Haan			
Dromiidae de Haan			
Lauridromia dehaani (Rathbun)	AY583899*	AY583972*	AY583991*
Homoloidea de Haan			
Homolidae de Haan			
Paramola japonica Parisi	AY583900*	AY583973*	AY583992*
Raninoidea de Haan			
Raninidae de Haan			
Raninoides louisianensis Rathbun	AF436044	AF436005	AF435985
Calappoidea Milne Edwards			
Hepatidae Stimpson			
Hepatus ephileticus (Linnaeus)	AF436043	AF436004	AF435984
Portunoidea Rafinesque			
Portunidae Rafinesque			
Carcinus maenas (Linnaeus)	AY583901*	AY583974*	AY583993*
Ocypodoidea Rafinesque			
Ocypodidae Rafinesque			
Macrophthalmus setosus H. Milne Edwards	AY583902*	AY583975*	AY583994*

APPENDIX 2. Morphological data matrix

Stenopus	1000000000	1000000000	0000110000	0000000000	2100000000
Polycheles 1	0000101000	1000000000	0000110000	1010000100	02?0000000
Polycheles 2	0000101000	1000000000	0000110000	1010000100	02?0000000
Polycheles 3	0000101000	1000000000	0000110000	1010000100	02?0000000
Jasus	0000000000	1300100001	0000310000	0010000010	1001000000
Panulirus	0000000000	1300100001	0000310000	0010000010	1001000000
Palinurellus	1000000000	1000100001	0000110000	0010000010	1001000000
Biarctus	0000001000	1000100001	0000310000	0010000010	1001000000
Homarus	1111000000	1200000000	0000100001	0010000010	2000001110
Nephropsis	1111000000	1200000000	0000100001	0010000010	2000001110
Metanephrops	1111000000	1100000000	0000100001	0010000010	2000001110
Thaumastochelopsis	1010000000	1201000000	0000100001	0011000010	02?0001110
Neoglyphea	1000000000	1001000100	100011?001	0011000010	02?0001110
Enoplometopus	1100000000	1100000000	0000100001	0010000110	21?0001110
Orconectes	1000000000	0101000100	1000100001	0010000110	1001001110
Cambarus	1000000000	0101000100	1000100001	0010000110	1001001110
Astacus	1000000000	0101000100	1000100001	0010000110	1001001110
Austropotamobius	1000000000	0101000100	1000100001	0010000110	1001001110
Geocharax	1000000000	0101000100	1000110001	0010000110	1001001110
Euastacus	1000000000	0101000100	1000110001	0010000110	1001001110
Biffarius	0100010010	0000001100	1000110001	0111000010	0200000000
Jaxea	0100010011	0000001100	1000110001	0111000010	0200001110
Neaxius	1100000001	0100001100	1000110001	0111000010	0200000000
Upogebia	1100010010	0000001100	1000110001	0111000010	0200000000
Callichirus	0100010010	0000001100	1000110001	0111000010	0200000000
Thalassina	0100000011	1000001100	1000110001	0111000010	0200000000
Lomis	0100001110	0000100100	1000111101	0010010010	0200000000
Munida	1100001010	1000110100	1000211101	0010010011	0210000000
Eumunida	1100001010	1000110100	1000211101	0010010010	0210100000
Petrolisthes	0100101110	0000110100	1000211101	0010010011	0210000000
Aegla	0100001010	0000100100	1000111101	0010010010	0210000000
Blepharipoda	0100001010	0000000100	1000111101	0000010010	0210000000
Emerita	0100000010	0000000100	1000211101	0010010000	0210000000
Lepidopa	0100001010	0000000100	1000211101	0000010010	0210000000
Pylocheles	0100011010	0000010100	1000111101	0000000010	0200100001
Pagurus	0100021010	0000020110	1000211111	0001100010	0200100001
Calcinus	0100021010	0000020100	1000211111	0001100010	0200100001
Coenobita	0100011010	0000010100	1000211111	0001100010	0200100001
Lithodes	1100101110	0000100110	1000211111	0011010010	0200010000
Paramola	0100001010	0010100000	0000221001	0000011000	0200020000
Lauridromia	0100001010	0010100000	0000221001	0000011000	0200020000
Carcinus	0100101100	0010100000	0111221001	0001011000	0200020000
Raninoides	0100001000	0010100000	0000221001	0001011000	0200020000
Hepatus	0100101100	0010100000	0111221001	0001011000	0200020000
Macrophthalmus	0100101100	0010100000	0111221001	0001011000	0200020000

APPENDIX 2. Morphological data matrix (continued).

Stenopus	0000000000	0000000010	0000100100	0000000000	0000000000	00000
Polycheles 1	0000000000	0000002010	0010000100	0000100000	00?0000???	?0???
Polycheles 2	0000000000	0000002010	0010000100	0000100000	00?0000???	?0???
Polycheles 3	0000000000	0000002010	0010000100	0000100000	00?0000???	?0???
Jasus	0000100100	0101010000	1121010120	0101000100	0000001000	10101
Panulirus	0000100100	0100010000	1121010120	0101000100	0000001000	10101
Palinurellus	0000100100	0111010000	1121010120	0101000100	0000001000	10101
Biarctus	0000000100	1111110000	0121010100	0101000100	0000001000	10101
Homarus	0010100100	0100000000	0001001012	0000000100	0000001001	10111
Nephropsis	0010100100	0100000000	0001001012	0000000100	0000001001	10111
Metanephrops	0010100100	0100000000	0001001012	0000000100	0000001001	10111
Thaumastochelopsis	0010100100	0100000000	0001001012	0000000100	00?0001?01	10111
Neoglyphea	0010100100	0100000000	0001011111	0011000102	00?0000???	?0???
Enoplometopus	0010100100	0100000000	0001001012	0000000100	0000001?00	10???
Orconectes	0010100100	0000000000	0001101012	0000000200	0000001100	11111
Cambarus	0010100100	0000000000	0001101012	0000000200	0000001100	11111
Astacus	0010100100	0100000000	0001101012	0000000200	0000001100	11111
Austropotamobius	0010100100	0100000000	0001101012	0000000200	0000001100	11111
Geocharax	0010100100	0100000000	0001101012	0000000200	0001001100	11111
Euastacus	0010100100	0100000000	0001101012	0000000200	0001001100	11111
Biffarius	0010000110	0100001000	0121101100	0011000100	0000000000	10111
Jaxea	0011100100	0100000000	0121201100	0111000100	0000001000	10111
Neaxius	0010100100	0100000000	0021201100	0011000100	0000000000	10111
Upogebia	0010100100	0100001000	0121201100	0111000100	0000001000	10111
Callichirus	0010000110	0100001000	0121101100	0011000100	0000000000	10111
Thalassina	0011100100	0000000000	0121201100	0111000100	0000001000	10111
Lomis	1011100110	1111100011	0121001100	0101000111	0010001010	10111
Munida	0011100100	1111100011	0121001100	0101000111	0010011010	10111
Eumunida	0011100100	1111100011	0121001100	0101000111	0010011010	10111
Petrolisthes	0011100110	1101100011	0121001000	0101000111	0010011010	10111
Aegla	0011100100	1101100011	0121001000	0101000111	0010011010	11111
Blepharipoda	0011100110	0100000011	0021001120	0001000111	0010011010	10111
Emerita	0011100100	0100000011	0021010120	0101000111	0010011010	10111
Lepidopa	0011100110	0100000011	0021001120	0001000111	0010011010	10111
Pylocheles	1011100110	0111100011	0021001100	0101011111	0110001010	10111
Pagurus	2111110110	1111100111	0021001100	0101011111	0110101010	10111
Calcinus	2111100110	1111100011	0021001100	0101011?11	0110101010	10111
Coenobita	2111100110	1111000011	0121001100	0101111111	0110101011	10111
Lithodes	2011110110	1111100111	0021001100	0101000111	0110111010	10111
Paramola	4011101101	1111100000	0121001000	1001000301	1000001000	10111
Lauridromia	3011101101	1111100000	0121001000	1001110301	1000001000	10111
Carcinus	4011002101	1111100000	0121001020	1001000300	0000001000	10111
Raninoides	?011001101	1111100000	0121001020	1001000300	1000001000	10111
Hepatus	4011002101	1111100000	0121001000	1001000300	0000001000	10111
Macrophthalmus	4011002101	1111100000	0121001000	1001000300	0000001000	101?1

APPENDIX 3. Morphological characters.

1. Rostrum: absent or obsolete (0); well-developed (1). (Dixon et al., 2003).
2. Branchiocardiac groove: present (0); absent (1).
3. Cervical and hepatic grooves of carapace: not forming 'W' (0); forming 'W' (1). The conjunction of the cervical and hepatic grooves of the carapace form a W-like pattern, uniting nephropoid lobsters (Scholtz & Richter, 1995).
4. Carapace clavicular incision: absent (0); present (1). The clavicular incision in the lower anterior carapace unites many nephropoid lobsters (Holthuis, 1974).
5. Carapace margins: indistinct (0); distinct (1). (Scholtz & Richter, 1995).
6. Posterior portion of carapace: well-calcified (0); soft or poorly calcified, membranous (1).
7. Carapace shape: subcylindrical (0); depressed (1). The subcylindrical carapace form is present primarily in astacurans, thalassinideans and some achelates. The carapace in most other taxa is dorsoventrally depressed.
8. Carapace proportions: elongate (0); as long as wide or wider (1).
9. Carapace lineae: absent (0); present (1). In the absence of evidence to the contrary, carapace lineae in thalassinids (*linea thalassinica*), anomurans (*linea anomurica*) and brachyurans (*linea dromica*) are scored as homologous following Dixon et al. (2003).
10. Carapace cardiac notch: absent (0); present (1).
11. Antennal spine: absent (0); present (1).
12. Supraorbital ornamentation: absent (0); longitudinal carina (1); reduced to a small spine (2); large, horn-like tooth (3). Many reptants possess supraorbital ornamentation in the form of spines or carinae. Astacidans almost universally possess a longitudinal supraorbital carina.
13. Carapace epistomial ridge: unfused with anterior carapace (1); fused with anterior carapace (1). (Scholtz & Richter, 1995).
14. Lateral margin of epistome and carapace: not in broad contact (0); in broad contact (1). (Schram & Ahyong, 2002; Dixon et al., 2003).
15. Thoracic sternal plastron: narrow (0); broadening posteriorly (1). (Dixon et al., 2003)
16. Branchiostegites: fully calcified (0); partially calcified (1); membranous (2).
17. Thoracic sternite 7 with large pair of lobes: absent (0); present (1). (Scholtz & Richter, 1995).
18. Fusion between thoracic sternites 7-8: fused (0); articulating (1). (Scholtz & Richter, 1995; Schram & Ahyong, 2002; Dixon et al., 2003).
19. Fusion between thoracic sternite 8 and abdominal somite 1: unfused (0); fused (1). A feature of some paguroids (McLaughlin & Lemaitre, 1997).
20. Articulation between thoracic sternite 8 and carapace: absent (0); present (1). In achelates, the carapace and last thoracic segment are connected by a knob-like structure. A similar type of holding structure is present between the carapace and first abdominal segment in polychelids (character 31). Functional similarities led Dixon et al. (2003) to treat the two types of articulation as states of the same character. As shown by Scholtz & Richter (1995), however, the two types of articulation are not homologous; we treat them as separate characters.
21. Secula sclerite number: two or fewer (0); three (1). (Scholtz & Richter, 1995; Schram & Ahyong, 2002; Dixon et al., 2003).
22. Female gonopore position: coxal (0); sternal (1).
23. Telson locking device: absent (0); sternal (1); coxal (2). The abdomen in many Brachyura is held in position by a locking device of the sixth abdominal segment that engages a counterpart on the thoracic sternum (Guinot & Bouchard, 1998).
24. Sella turcica: absent (0); present (1). The sella turcica is a feature of the endophragmal skeleton uniting the sternitreme Brachyura (i.e., Eubrachyura) (Secretan, 1998).
25. Gill type: dendrobranchiate (0); trichobranchiate (1); phyllobranchiate (2); 'match-stick' (3). (Dixon et al., 2003).
26. Seminal receptacle: medial (0); absent (1); paired (2). Seminal receptacles are present in achelates, most astacideans, anomurans and brachyurans. A synapomorphy of brachyurans is pairing of the seminal receptacles. In other reptants, the seminal receptacle lies on the sternal midline. We avoid the term 'paired spermatheca' because of its specific reference to podotreme seminal receptacles (Tavares & Secretan, 1993).
27. Posterior thoracic and anterior abdominal ganglia: unfused (0); fused (1). (Scholtz & Richter, 1995).
28. Joints between pereopodal coxae and sternites: regular (0); inverted (1). (Scholtz & Richter, 1995; Dixon et al., 2003).
29. Abdomen symmetry: symmetrical (0); assymetrical (1). (Scholtz & Richter, 1995; Dixon et al., 2003).
30. Pleonic hinges: lateral (0); midlateral (1). (Scholtz & Richter, 1995; Dixon et al., 2003).
31. Abdominal somite 1 and carapace with knob-like articulation: absent (0); present (1). A synapomorphy of polychelids (see discussion of character 20).
32. Abdominal somite 1 width: as wide as adjacent somites (0); forming a narrow waist (1). (Scholtz & Richter, 1995; Dixon et al., 2003).
33. Abdominal somite 1 overlapping lobes: absent (0); present (1). (Dixon et al., 2003).
34. Abdominal pleura: well developed (0); reduced (1).

35. Abdominal segmentation: somites distinct (0); somites ill-defined (1). In most decapods, the abdominal tagmatization is distinct. In asymmetrical hermit crabs, however, the abdominal somite boundaries may be ill-defined.
36. Pleon position: straight (0); ventrally flexed (1).
37. Pleon sexual dimorphism: slight (0); strong (1).
38. Second pleomere pleuron: normal size, overlapping third (0); inflated, overlapping first and third (1).
39. Telson shape: narrow, triangular (0); wide, rounded (1). (Scholtz & Richter, 1995; Dixon et al., 2003).
40. Telson undivided (0); composed of plates in X-like pattern (1). (Scholtz & Richter, 1995; Dixon et al., 2003).
41. Telson posterolateral spine position: absent (0); present midlaterally (1); present distally (2). (Dixon et al., 2003).
42. Telson posterolateral spines mobility: fixed (0); articulated (1); absent (2).
43. Telson stretch receptor: absent (0); present (1). (Scholtz & Richter, 1995).
44. Tail fan cuticle: hard (0); soft (1). (Scholtz & Richter, 1995; Dixon et al., 2003).
45. Telson lateral margin: entire (0); indented (1). The laterally indented telson margin is a feature of some paguroids.
46. Uropods: biramous (0); vestigial (1); uniramous (2).
47. Uropodal exopod diaeresis: absent (0); present (1).
48. Uropod exopod diaeresis: margin not spinose (0); margin spinose (1).
49. Uropod endopod outer spine: absent (0); present (1).
50. Uropod rasp: absent (0); present (1).
51. Uropod shape: foliaceous, symmetrical, forming tailfan (0); segments reduced, narrowed, symmetrical (1); segments reduced, narrowed, asymmetrical (2); small lobe (3); fused with abdominal somite 6, forming socket (4). Uropod form varies markedly in Reptantia. Most bear the typical tailfan, but in many taxa, such as paguroids, the uropod segments are narrowed and may be symmetrical or asymmetrical. In Brachyura, the uropods are highly reduced, being vestigial and present as a small plate or even fused to the sixth abdominal segment forming a minute socket involved in the 'telson locking device' (Guinot & Bouchard, 1998).
52. Ocular acicles: absent (0); present (1).
53. Mandible molar process: weak (0); trapezoidal (1); round (2). (Scholtz & Richter, 1995; Dixon et al., 2003).
54. Maxilliped 3 flagella: straight (0); double bent (1). (Dixon et al., 2003).
55. Maxilliped 3 crista dentata: absent (0); present (1). (Dixon et al., 2003).
56. Crista dentata accessory tooth: absent (0); present (1). (Dixon et al., 2003).
57. Maxilliped 3 merus/ischium: slender (0); pediform (1); operculiform (2). (Dixon et al., 2003).
58. Maxilliped 3 dactylus apex: sharp (0); blunt (1). (Dixon et al., 2003).
59. Maxilliped 3 epipod: present (0); absent (1).
60. Orbito-antennularis fossa: absent (0); present (1). (Dixon et al., 2003).
61. Antennular flagella: straight (0); strongly curved (1). (Dixon et al., 2003).
62. Antennular flagella sensilla: on all surfaces (0); one-sided (1). (Dixon et al., 2003).
63. Antennular flagella segment proportions: annuli subequal (0); annuli wider than long (1). (Dixon et al., 2003).
64. Antennular flagella length: longer than antennular peduncle segment 2 (0); similar to antennular peduncle segment 2 (1). (Dixon et al., 2003).
65. Antennular peduncle shape: straight (0); Z-shaped (1). (Dixon et al., 2003).
66. Antennal basal articles: articulating (0); fused with carapace and epistome (1). (Scholtz & Richter, 1995; Dixon et al., 2003).
67. Antennal gland position: ventral (0); lateral (1); dorsal (2). (Dixon et al., 2003).
68. Antennular outer flagellum: basal segments free (0); some basal segments fused (1). A feature shared by pagurids and lithodids (Richter & Scholtz, 1994).
69. Antennular stylocerite: absent (0); present (1).
70. Antennal basal article position: not in notch (0); in carapace notch (1). (Dixon et al., 2003).
71. Antennal size: small (0); large, strongly calcified (1).
72. Scaphocerite: present, well developed (0); absent or reduced (1). (Dixon et al., 2003).
73. Basis, ischium and merus of pereopods 3-5: all separate (0); all fused (1); basis-ischium fused (2). (Dixon et al., 2003).
74. Pereopod 1 propodus dactyl articulation: simple (0); double hinge (1). (Scholtz & Richter, 1995; Dixon et al., 2003).
75. Pereopod 1 ischium: oblique (0); perpendicular (1); curved (2). (Dixon et al., 2003).
76. Pereopod 1 condition: chelate or semichelate (0); simple (1).
77. Pereopod 1 size: not greatly inflated (0); greatly inflated (1).
78. Pereopod 1 dactylus orientation: horizontal or oblique (0); vertical (1). (Scholtz & Richter, 1995).

79. Pereopod 1 ischial process: absent (0); distinct (1); slight bulge (2). (Dixon et al., 2003).
80. Pereopod 1 ischial process length: negligible (0); short (1); long (2).
81. Pereopod 1 dactylus: internal (0); external (1). (Scholtz & Richter, 1995).
82. Pereopod 2 condition: chelate or semichelate (0); absent (1).
83. Pereopod 2 ischium setal row: absent (0); present (1). (Poore, 1994; Dixon et al., 2003).
84. Pereopod 3 condition: chelate or semichelate (0); simple (1).
85. Pereopod 4 condition: simple (0); chelate or subchelate (1).
86. Pereopod 4 size: normal, similar to preceding limb (0); reduced (1).
87. Pereopod 4 rasp: absent (0); present (1).
88. Pereopod 5 dactylar teeth: few triangular teeth (0); many scale-like teeth (1); comb-teeth (2); absent (3). (Scholtz & Richter, 1995).
89. Pereopod 5 location: external (0); partially concealed (1).
90. Pereopod 5 size: large (0); markedly reduced (1); reduced (2).
91. Pereopod 5 position: normal (0); dorsal or subdorsal (1)
92. Pereopod 5 rasp: absent (0); present (1).
93. Pereopod 5 position in late zoea: aligned with other pereopods (0); reduced, in anteromedian position (1). (Scholtz & Richter, 1995).
94. Male pleopod 1: present (0); absent (1).
95. Pleopod pairing: paired (0); unpaired (1).
96. Pleopod 2-5 rami: biramous (0); uniramous (1).
97. Pleopod appendix interna: present (0); absent (1); vestigial (2).
98. Embryonic growth zone: 19 ectoteloblasts (0); 40 ectoteloblasts (1). Scholtz (1992, 1993) and Scholtz & Richter (1995) recognised the embryonic growth zone consisting of about 40 ectoteloblasts to be a synapomorphy of Astacida.
99. Spermatophores: unstalked (0); stalked (1). (Scholtz & Richter, 1995; Jamieson & Tudge, 2000; Tudge et al., 2001; Tudge & Scheltinga, 2002).
100. Sperm acrosome: spherical (0); elongated (1). (Scholtz & Richter, 1995; Jamieson & Tudge, 2000; Tudge et al., 2001; Tudge & Scheltinga, 2002).
101. Sperm nuclear arms: absent (0); present (1). (Scholtz & Richter, 1995; Jamieson & Tudge, 2000; Tudge et al., 2001; Tudge & Scheltinga, 2002).
102. Development: indirect (0); direct (1). (Scholtz & Richter, 1995).
103. Brain accessory lobes: absent (1); present (1). (Scholtz & Richter, 1995).
104. Protocerebrum: raised (0); not raised (1). (Scholtz & Richter, 1995).
105. Brain proportion: longer than wide (0); wider than long (1). (Scholtz & Richter, 1995).

ERRATUM

Phylogeny of the Decapoda Reptantia: resolution using three molecular loci and morphology. Raffles Bulletin of Zoology 52(2): 673-693

Appendix 3, character 26, sentence 1 should read: "Seminal receptacles are present in brachyurans and most astacideans."