Phylogenetics of the brachyuran crabs (Crustacea: Decapoda): The status of Podotremata based on small subunit nuclear ribosomal RNA

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Abstract

The true crabs, the Brachyura, are generally divided into two major groups: Eubrachyura or 'advanced' crabs, and Podotremata or 'primitive' crabs. The status of Podotremata is one of the most controversial issues in brachyuran systematics. The podotreme crabs, best recognised by the possession of gonopores on the coxae of the pereopods, have variously been regarded as mono-, para- or polyphyletic, or even as non-brachyuran. For the first time, the phylogenetic positions of the podotreme crabs were studied by cladistic analysis of small subunit nuclear ribosomal RNA sequences. Eight of 10 podotreme families were represented along with representatives of 17 eubrachyuran families. Under both maximum parsimony and Bayesian Inference, Podotremata was found to be significantly paraphyletic, comprising three major clades: Dromiacea, Raninoida, and Cyclodorippoida. The most 'basal' is Dromiacea, followed by Raninoida and Cylodorippoida. Notably, Cyclodorippoida was identified as the sister group of the Eubrachyura. Previous hypotheses that the dromiid crab, *Hypoconcha*, is an anomuran were unsupported, though Dromiidae as presently composed could be paraphyletic. Topologies constrained for podotreme monophyly were found to be significantly worse ($P < 0.04$) than unconstrained topologies under Templeton and S–H tests. The clear pattern of podotreme paraphyly and robustness of topologies recovered indicates that Podotremata as a formal concept is untenable. Relationships among the eubrachyurans were generally equivocal, though results indicate the majoids or dorippoids were the least derived of the Eubrachyura. A new high level classification of the Brachyura is proposed.
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1. Introduction

Brachyura, the true crabs, contains more than 6500 species and is the largest clade of the decapod Crustacea. The extreme morphological diversity and probable large-scale convergence of adult features in the Brachyura has confounded consensus on phylogenetic relationships. For most of the 20th century, the brachyuran classification and its implied phylogeny reflected a scheme initiated by Milne Edwards (1834) and refined by Balss (1957), based largely on the carapace form and the buccal frame. Major subdivisions included the Dromiacea (sponge crabs and allies), Oxyrhyncha (spider crabs), Oxystomata (box crabs, pebble crabs and allies), Cancridea (cancer crabs) and Brachyrhyncha (short fronted crabs). Recognising that the prevailing view of brachyuran relationships was artificial, and building on suggestions by Gordon (1963, Guinot (1977, 1978, 1979) focused on gonopore position as a more accurate phylogenetic indicator. Guinot recognised three major groupings: Podotremata (with coxal gonopores), Heterotremata (with coxal and sternal gonopores), and

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Thoracotremata (with sternal gonopores). De Saint Laurent (1980a,b) refined Guinot's classification, recognising Dromiacea (Guinot's Podotremata) as sister to Eubrachyura (equivalent to Guinot's Thoracotremata + Heterotremata). The podotremes were recognised as 'primitive' brachyurans based on their plesiomorphic adult and larval morphology. The heterotremes and thoracotremes were recognised as the more 'advanced' with the latter most highly derived. Although Guinot's groupings have enjoyed wide usage, the interrelationships of the Brachyura remain contentious (see also Ng, 1998; Martin and Davis, 2001).

The major controversies in brachyuran phylogeny stem from two discrete but related issues: the status of Podotremata (whether mono-, para-, or polyphyletic), and the internal relationships within Eubrachyura. If Podotremata is polyphyletic, then some podotremes must lie outside Brachyura (presumably among Anomura) leading to significant instability in the high level decapod system. Several studies have suggested that Dromiidae were anomurans based on similar larval form (Williamson, 1976). Recent morphological and molecular phylogenetic studies, however, indicate that Brachyura and Anomura are reciprocally monophyletic sister clades, constituting Meiura (Scholtz and Richter, 1995; Schram, 2001; Dixon et al., 2003; Ahyong and O'Meally, 2004). Thus, the anomuran-like characters of dromiid larvae are plesiomorphies retained from the meiuran stem species (see review by McLay et al., 2001). If Podotremata is monophyletic, then, the entire Podotremata is sister to Eubrachyura. If Podotremata is paraphyletic, then the sister group to Eubrachyura lies among the podotremes. Identification of the sister to Eubrachyura, necessary for unravelling eubrachyuran interrelationships, requires resolution of the Podotremata question (see Tavares, 2003). Clearly, the interrelationships of the podotremes are the focal point of many issues. Thus, the status of Podotremata is particularly important, not only for uncovering the pattern of early brachyuran evolution, but also as a prerequisite to understanding eubrachyuran diversification.

A growing body of work has appeared treating discrete eubrachyuran clades (e.g., Schubart et al., 2000; Lai et al., 2006), but few studies have addressed the overall phylogeny of the Brachyura. The most important recent studies are Spears et al. (1992) based on 18S rRNA, Rice (1980, 1981, 1983) using larval morphology, several major studies using sperm morphology (e.g., Jamieson, 1991, 1994; Guinot et al., 1994; Jamieson et al., 1995) and analyses of foregut morphology (Brösing et al., 2002, 2006). Rice's (1980, 1983) larval studies found dromiid larvae to resemble anomurans more than eubrachyurans. Spears et al. (1992) appeared to corroborate the larval studies and even challenged Brachyuran monophyly in finding the DNA of the dromiid, *Hypoconcha*, to be anomuran. Conversely, the analyses based on sperm morphology recognised a monophyletic Brachyura with monophyletic Podotremata (Jamieson et al., 1995). Studies of foregut ossicles contradicted podotreme monophyly and even found some

podotreme groups to nest within Eubrachyura (Brösing et al., 2002, 2006). Broader studies of decapod phylogeny have also generally recovered a paraphyletic Podotremata, though none could indicate the pattern and degree of paraphyly because few podotreme exemplars were studied (e.g., Schram, 2001; Dixon et al., 2003; Ahyong and O'Meally, 2004). The controversies surrounding the early evolution of crabs are exemplified by the different phylogenetic schemes as shown in Fig. 1, with podotreme monophyly (Fig. 1a), paraphyly (Fig. 1b–e) and polyphyly (Fig. 1f). Most previous studies suffered from limited taxonomic sampling. For example, only 10 brachyuran exemplars were used in the 18SrRNA study (Spears et al., 1992). Here, in the first of a series examining the molecular phylogenetics of the Brachyura, we focus on the status of Podotremata using 18S rRNA sequences. Eight of 10 extant families of the Podotremata are represented, along with exemplars from 17 other brachyuran families.

2. Materials and methods

2.1. Taxon sampling

A total of 31 ingroup terminals were included representing 25 brachyuran families: 8 podotreme and 17 eubrachyuran. Note that some classifications recognise two raninoid families: Raninidae and Symethidae (see Martin and Davis, 2001). We herein treat Symethidae as a junior synonym of Raninidae (see 4.1.2), though exemplars from both nominal taxa are included in the analysis. Sequences for 6 brachyuran species were derived from GenBank and 25 species were newly sequenced (Table 1).

The sister group of the Brachyura has been historically debated, though almost all recent studies have shown Anomura with this status (Scholtz and Richter, 1995; Schram, 2001; Dixon et al., 2003; Ahyong and O'Meally, 2004; Miller and Austin, 2006). The single recent exception (Porter et al., 2005), found Brachyura to be sister to the remaining reptant decapods. It should be noted, however, that support for the positions of all infraordinal reptant clades was low, and as such relationships recovered by Porter et al. (2005) are effectively equivocal. Therefore, following the results of other phylogenetic analyses, we recognised Anomura as the sister to Brachyura and rooted analyses to two anomuran exemplars representing the Galatheoidea and Paguroidea respectively: *Munida quadrispina* Benedict (GenBank accession number AF436010) and *Pylocheles macrops* Forest (AY583970).

2.2. DNA extraction and analysis

Extraction and amplification protocols follow Ahyong and O'Meally (2004). DNA was extracted from fresh or ethanol-fixed tissue samples using a modified protocol of Saghai-Maroof et al. (1984). The 18S rRNA gene was amplified in contiguous fragments, using the primer pairs 1F/4R, 3F/5r, 5F/7R and 7F/9R (primer details given
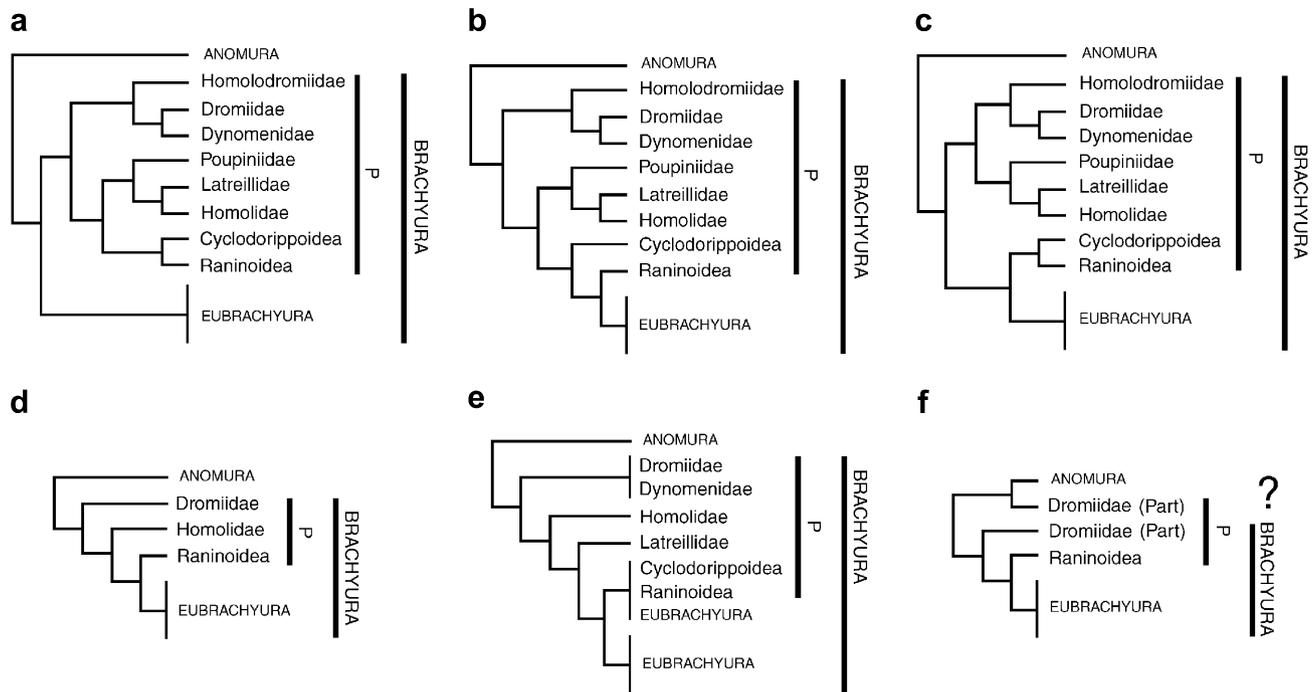
Fig. 1. Selected hypotheses of podotreme interrelationships. (a) Monophyly, based on Guinot et al. (1994: fig 7) and McLay (1999: fig 16a). (b) Paraphyly, based on McLay (1999: fig 16b). (c) Paraphyly, based on Martin and Davis (2001). (d) Paraphyly, based on Ahyong and O'Meally (2004: fig. 3). (e) Paraphyly, based on Brösing et al. (2006). P = Podotremata. (f) Polyphyly, based on Spears et al. (1992: fig. 2).

below). Amplifications were conducted in 25 μL volumes containing 1.5 mM MgCl$_2$, 0.025 mM of each dNTP, 12.5 pmol of each primer, 0.2 U of Qiagen Taq DNA polymerase, 2.5 μL of Qiagen 10× PCR buffer, 5 μL of Qiagen Q-solution and 1–100 ng of whole genomic DNA (generally a 1:20–1:50 dilution of the stock DNA extraction). Cycle parameters comprised initial denaturation at 94 °C for 1 min, 30 cycles of 94 °C for 20 s, annealing for 30 s at 49 °C, extension at 72 °C for 1.5 min, and a final extension at 72 °C for 2 min.

Sequencing was performed in both directions on an Applied Biosystems (ABI)$^{®}$ 310 DNA Sequencer using the DyeDeoxy™ Terminator sequencing method according to the manufacturer's protocol except that reactions were scaled down to 10 μl using 2 μl Big Dye version 3 reaction mix. The primers (Table 2) used in the sequencing reactions were the same as those used for the amplifications with the addition of some internal primers (also listed below) needed to determine the 3′ ends of large amplification products.

Samples were run on an ABI 310 Genetic Analyser. Forward and reverse strands were combined and sequences checked for errors using Sequencher (Genecodes$^{®}$). This program was also used to assemble the separate fragments for each taxon into a single sequence. Final sequences were aligned in Clustal W using default parameters and modified by eye. The impact of retaining or excluding ambiguous regions was briefly explored in preliminary analyses. Ambiguous regions were generally defined as those where gaps of more than three bases were inferred in the ClustalX

alignment, if the inferences were not caused by an insertion in one taxon only. Topologies from analyses that included or excluded ambiguous regions were almost identical, differing only in relationships among some eubrachyurans. Therefore, regions of ambiguous alignment were excluded from final analyses. Gaps were treated as both missing and a fifth character state.

2.3. Phylogenetic analysis

Maximum parsimony analyses (MP) were conducted in PAUP* 4.0b10 (Swofford, 2002) (heuristic search, TBR, random addition sequence, 500 replicates). All characters were unordered and initial analyses were conducted under equal weights. Topological robustness was assessed using parsimony jackknifing (Farris et al., 1996). Jackknife frequencies were calculated in PAUP* using 1000 pseudoreplicates under a heuristic search with 33% character deletion. Further analyses were conducted using successive weighting and implied weights (concavity constants 1–10) in PAUP* to examine topological sensitivity to variation in character weights. We also applied the nonparametric Templeton test (Templeton, 1983) and Shimodaira–Hasegawa (S–H) tests (Shimodaira and Hasegawa, 1999) to assess whether topologies with Podotremata constrained as monophyletic were statistically different from unconstrained optimal topologies. S–H tests were performed by treating the topologies as hypotheses under a model with one substitution rate only, equal rates at different positions, no invariable sites and equal base frequencies.

Table 1
Classification of terminal taxa and GenBank accession numbers

Section	Family	Species and voucher specimen repository	GenBank Acc. No.
Dromiacea	Dromiidae	*Hypoconcha spinosissima* Rathbun, 1933 (ZRC 2006.122)	DQ925818*
	Dromiidae	*Lauridromia dehaani* (Rathbun, 1923) (AM P67928)	AY583972@
	Dynomenidae	*Metadynomene tanensis* (Yokoya, 1933) (ZRC 2002.629)	DQ925819*
	Homolodromiidae	*Homolodromia kai* Guinot, 1993 (ZRC 2006.127)	DQ925820*
	Homolidae	*Homolomannia sibogae* (Ihle, 1918) (ZRC, not vouchered)	DQ925822*
	Homolidae	*Moloha majora* (Kubo, 1936) (ZRC)	DQ925821*
	Homolidae	*Paromola japonica* Parisi, 1915 (ZRC 1998.461)	AY583973@
	Latreillidae	*Latreillia valida* de Haan, 1839 (ZRC, not vouchered)	DQ925823*
Raninoida	Raninidae	*Ranina ranina* (Linnaeus, 1758) (ZRC 2002.0342)	DQ925824*
	Raninidae	*Raninoides louisianensis* Rathbun, 1933	AF436005+
	Raninidae	*Symethis corallina* Davie, 1989 (ZRC, not vouchered)	DQ925825*
Cyclodorripoida	Cyclodorripidae	*Corycodus* sp. (ZRC 2006.0125)	DQ925827*
	Cyclodorripidae	*Tymolus brucei* Tavares, 1991 (ZRC, not vouchered)	DQ925826*
	Cymonomidae	*Cymonomoides delli* Griffin & Brown, 1976 (ZRC 2006.126)	DQ925828*
Eubrachyura	Aethridae	*Aethra scruposa* (Linnaeus, 1764) (ZRC 2003.0295)	DQ925839*
	Calappidae	*Calappa bilineata* Ng, Lai & Aungtonya, 2002 (AM P60973)	DQ925838*
	Carpiliidae	*Carpilius convexus* (Forskål, 1775) (ZRC 2006.120)	DQ925834*
	Dairidae	*Daira perlata* (Herbst, 1790) (ZRC 1998.381)	DQ925835*
	Dorippidae	*Dorippoides facchino* (Herbst, 1785) (AM P67927)	DQ925829*
	Epialtidae	*Menaethius monoceros* (Latreille, 1825) (ZRC 2000.414)	DQ925841*
	Eriphiidae	*Eriphia sebana* (Shaw & Nodder, 1803) (ZRC, not vouchered)	DQ925836*
	Grapsidae	*Leptograpsus variegatus* (Fabricius, 1793) (ZRC)	DQ925840*
	Hepatidae	*Hepatus epheliticus* (Linnaeus, 1763)	AF436004+
	Hymenosomatidae	*Amarinus paralacustris* (Lucas, 1970) (NIWA 27443)	DQ925831*
	Leucosiidae	*Tanaoa pustulosa* (Wood Mason, in Wood Mason & Alcock, 1891) (ZRC, not vouchered)	DQ925837*
	Majidae	*Schizophrys aspera* (H. Milne Edwards, 1834) (ZRC 2000.538)	DQ925842*
	Ocypodidae	*Macrophthalmus setosus* H. Milne Edwards, 1852 (AM P67934)	AY583975@
	Parthenopidae	*Rhinolambrus longispinus* (Miers, 1879) (ZRC, not vouchered)	DQ925830*
	Portunidae	*Carcinus maenas* (Linnaeus, 1758) (AM P67929)	AY583974@
	Trapeziidae	*Trapezia cymodoce* (Herbst, 1801) (NIWA 27444)	DQ925833*
	Xanthidae	*Chlorodiella nigra* (Forskål, 1775) (ZRC 1993.292–293)	DQ925832*

New sequences are marked with an asterisk (*); those from Ahyong and O'Meally (2004) are marked (@); those from Morrison et al. (2002) are marked (+). Voucher specimen repositories are abbreviated as follows: Australian Museum, Sydney (AM); National Institute of Water and Atmospheric Research, Wellington (NIWA); Raffles Museum of Biodiversity Research, Singapore (ZRC).

Table 2
Primers used in this study

Primer	Sequence	Reference
1F	TACCTGGTTGATCCTGCCAGTAG	Giribet et al. (1996)
3F	GTTCGATTCCGGAGAGGGA	Giribet et al. (1996)
4R	GAATTACCGCGGCTGCTGG	Giribet et al. (1996)
5R	CTTGGCAAATGCTTTCGC	Giribet et al. (1996)
5F	GCGAAAGCATTTGCCAAGAA	Giribet et al. (1996)
7F	GCAATAACAGGTCTGTGATGCCC	Giribet et al. (1996)
7R	GCATCACAGACCTGTTATTGC	Giribet et al. (1996)
9R	GATCCTTCCGCAGGTTCACCTAC	Giribet et al. (1996)
18Sa2.0	ATGGTTGCAAAGCTGAAAC	Whiting et al. (1997)
18Sbi	GAGTCTCGTTCGTTATCGGA	Whiting et al. (1997)

For comparison with results of MP, analyses conducted under Bayesian inference (BI) were conducted using MrBayes Version 3.1.2 (Huelsenbeck and Ronquist, 2001). Metropolis coupled Monte Carlo Markov Chains were run for 2,000,000 generations. Four differentially heated chains were run in each of two simultaneous runs. Topologies were sampled every 100 generations. Likelihood settings were determined during the run. Base frequencies were estimated, as were the rates of the six substitution types (nst = 6). A discrete gamma distribution was assumed for variation in the rate of substitution between nucleotide positions in the alignment and the shape parameter of this distribution was estimated during the run. After inspection of the likelihoods of the sampled trees, the first 10,000 generations of each were discarded as 'burn in'. All remaining topologies had likelihoods within 0.1% of the long-term asymptote in each run suggesting that these were sampled after the Markov Chain's convergence to a stable posterior probability distribution. The standard deviation of split frequencies converged to a value of 0.009745. All trees remaining after the discarding were used in calculation of posterior probabilities using a majority rule consensus.

3. Results

3.1. Sequence data

We obtained new 18S sequences for 25 brachyuran species (GenBank Accession numbers DQ925818–DQ925842, Table 1). The aligned 18S dataset including areas of uncertain alignment contained 33 terminals and 2020 characters. After excluding ambiguous regions, 1830 characters

remained of which 347 (19%) were variable and 163 (9%) were parsimony informative. The alignment is available online as an entry in TreeBASE. The 18S sequence is slightly GC rich, though a χ^2 test of nucleotide composition found no significant heterogeneity between sequences (df = 96, P = 1.00). Mean nucleotide composition is A 0.2399, C 0.2705, G 0.2422, T 0.2474.

3.2. Maximum parsimony and Bayesian inference

Treating gaps as either a fifth character state or missing data resulted in identical topologies. Therefore, results discussed below refer to analyses with gaps treated as missing. Maximum parsimony searches resulted in a single minimal length topology (length 758, CI 0.4793, RI 0.5027) (Figs. 2 and 4). Zero-length branches caused ambiguity among two homolid exemplars and four eubrachyurans. Podotremata was not monophyletic but comprised three clades forming a grade leading to the eubrachyurans: a dromiacean clade followed by a raninoid clade and then a cyclodorippoid clade. The dromiacean clade comprises dromiids, dynomenids, homolodromiids, homolids and latreilliids (jackknife proportion 98%). The raninoid clade comprises the repre-

sentatives of all three studied subfamilies, Ranininae (*Ranina*), Raninoidinae (*Raninoides*) and Symethinae (*Symethis*) (jackknife proportion 93%). The cyclodorippoid clade comprises cymonomids and cyclodorippids (jackknife proportion 100%). Although Podotremata is paraphyletic, the monophyly and positions of the three podotreme clades are robust. Within the dromiacean clade, *Lauridromia* is sister to *Metadynomene* rather than *Hypoconcha* suggesting dromiid paraphyly. Similarly, *Latreillia* is nested within the homolids, with moderate jackknife support, suggesting homolid paraphyly. The thoracotreme clade (*Macrophthalmus* + *Leptograpsus*) is nested among the heterotremes indicating a paraphyletic Heterotremata. Interrelationships of the podotreme clades was insensitive to successive weighting and implied weights (concavity constant ranging from 1–10) recovering an identical pattern of podotreme paraphyly as the equally weighted analysis. Templeton and S–H tests also rejected the hypothesis of podotreme monophyly. Topologies in which Podotremata was constrained as monophyletic (length 772) were significantly worse ($P < 0.04$) than unconstrained topologies.

Bayesian results (Fig. 3) resemble MP topologies in recovering a paraphyletic Podotremata. The position of
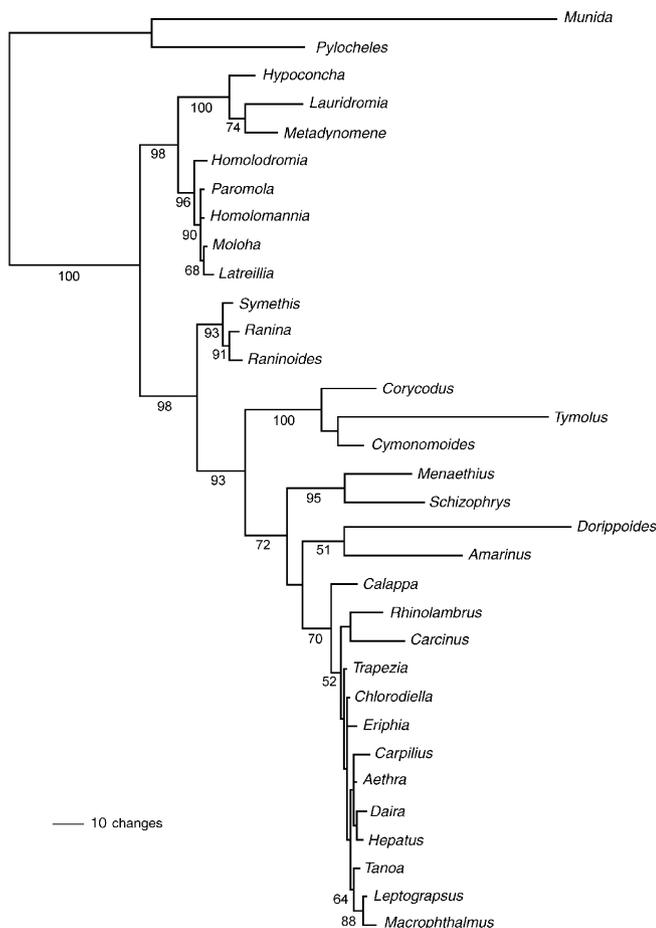

Fig. 2. Single minimal length MP topology (length 758, CI 0.4793, RI 0.5027). Rooted to two anomuran outgroups, *Munida* and *Pylocheles*. Jackknife proportions indicated at nodes.
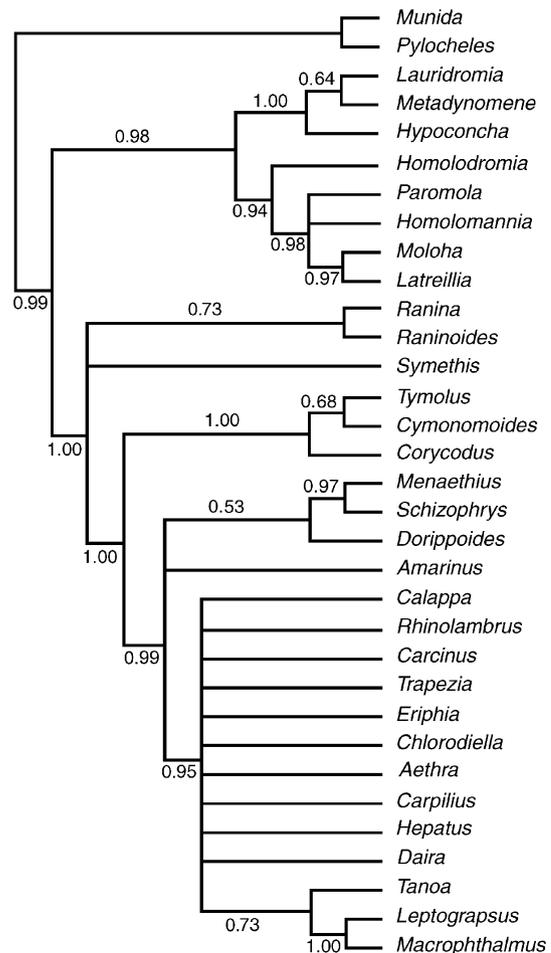
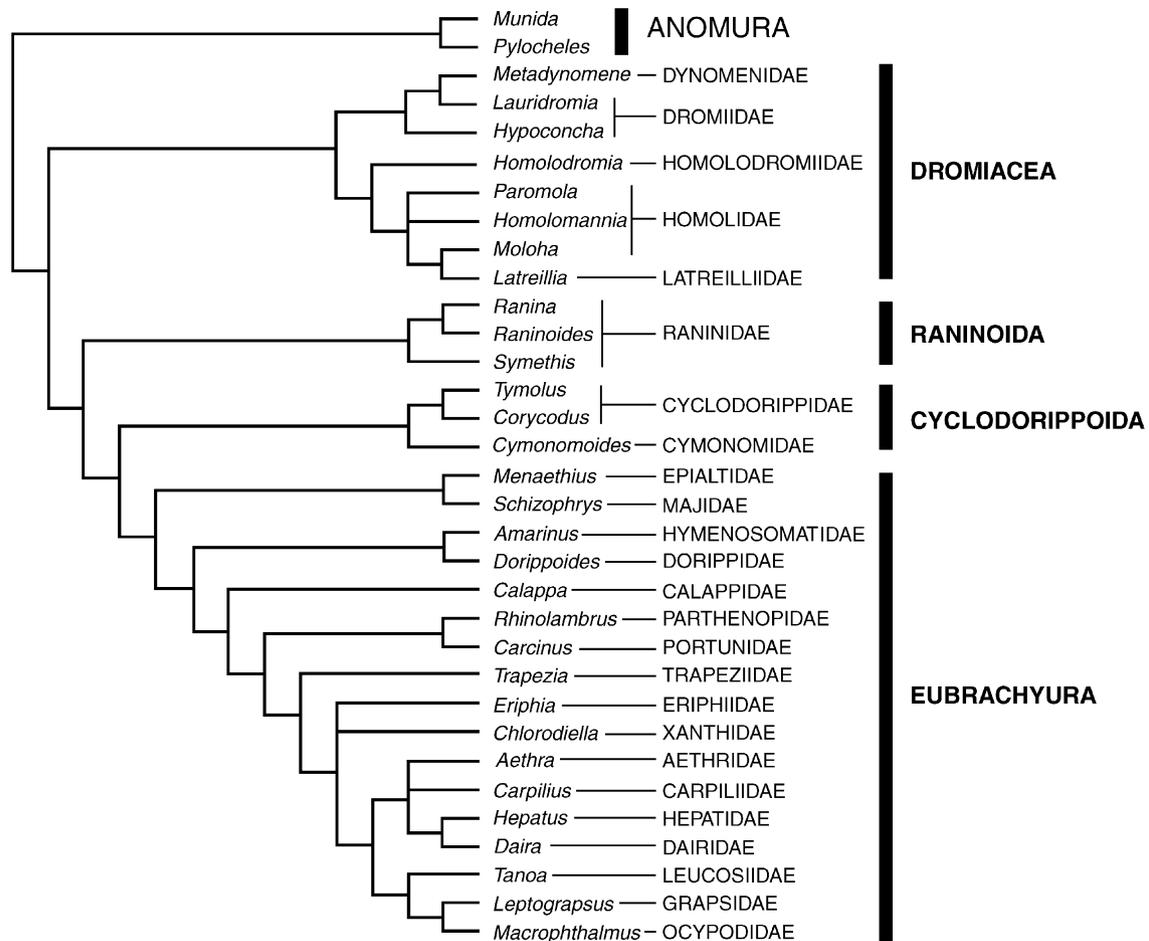Fig. 3. Bayesian topology. Posterior probabilities indicated at nodes.

Fig. 4. Classification of the Brachyura based on single minimal length topology derived by MP analysis.

Symethis, however, is ambiguous, probably being an arte-fact of the incomplete 18S sequence for that terminal. Interrelationships of the eubrachyurans are largely unre-solved, though the majoids and *Dorippoides* lie outside of the remaining eubrachyurans. The position of *Dorippoides* is weakly supported in MP and Bayesian analyses as sister to either *Amarinus* (MP, jackknife proportion 51%) or the majids (BI, posterior probability 0.53). As in the MP anal-ysis, Heterotremata is paraphyletic on the basis of the internally nested thoracotreme clade.

A similar pattern of podotreme paraphyly is common to all analyses. The dromiacean clade is herein recognised as Dromiacea, the raninoid clade as Raninoida, and the cycl-odorippoid clade as Cyclodorippoida.

4. Discussion

4.1. Status of Podotremata

Guinot's (1977, 1978) original tripartite concept, Podo-tremata, Heterotremata and Thoracotremata, aimed pri-marily to recognise levels of organization that correspond to evolutionary transitions, rather than formally delimiting monophyla. De Saint Laurent (1980a,b), however, with slight compositional modifications, recognised Guinot's

three divisions as monophyletic groups, with Heterotre-mata and Thoracotremata as sister taxa. Since then, debate has continued over the status of Podotremata, Heterotre-mata and Thoracotremata (Tavares, 2003).

Several morphological characters have been advanced in favour of podotreme monophyly. Most obvious are the coxal gonopores in both sexes, reduction of the fifth and usually fourth pereopods, absence of a *sella turcica*, and aspects of sperm morphology (Jamieson, 1994; Guinot et al., 1994; Jamieson et al., 1995). Most recently, Guinot and Quenette (2005) proposed the unusual 'paired sperma-theca' of females (paired seminal receptacles independent of the oviduct, associated with sternites 7/8) as a podo-treme synapomorphy, distinguished from the vulva of female eubrachyurans (paired oviducal seminal receptacles on sternite 6). Within Podotremata, three major groups are currently recognised: Dromiacea (homolodromiids, dromi-ids and dynomenids), Archaeobrachyura (containing the raninoids and cyclodorippoids) and Homolidea (homo-loids) (Guinot and Tavares, 2001). Guinot and Tavares (2001) proposed synapomorphies for each clade, with Dromiacea united by the presence of uropods forming a ventral lobe or dorsal plate, Homolidea united by the uro-pod transformed into a socket, and Archaeobrachyura uni-ted by the absence of uropods (see also Guinot and

Bouchard, 1998). Though Jamieson et al. (1995) recovered a monophyletic Podotremata using spermatozoal morphology, evidence from foregut ossicles (Brösing et al., 2002, 2006), somatic morphology and molecular sequences (Dixon et al., 2003; Ahyong and O'Meally, 2004; present data) all contradict podotreme monophyly.

The three major podotreme clades recognised here are not congruent with Guinot's divisions and in many respects more closely reflect the classification proposed by Martin and Davis (2001). Four major brachyuran clades are recognised here corresponding to Dromiacea, Raninoidea, Cyclodorippoidea and Eubrachyura.

4.1.1. Dromiacea

The major podotreme clade recovered herein is sister to the remaining Brachyura comprising Dromioidea (Dromiidae, Dynomenidae), Homolodromioidea (Homolodromiidae) and Homoloidea (Homolidae, Latreilliidae and Poupiniidae). Most previous workers have recognised a close relationship between dromiaceans and homoloids (e.g., Bouvier, 1896; Balss, 1957; Gordon, 1963; Števčić, 2005), though early conceptions of Archaeobrachyura included homoloids to the exclusion of other dromiaceans (e.g., Guinot, 1977, 1978, 1991). Most recently, Guinot and Quenette (2005) also recognised the close relationship between dromiaceans and homoloids. Guinot's Dromiacea comprises Dromioidea + Homolodromioidea, which is sister to Homolidea. Martin and Davis (2001) recognised a similar pattern of relationship, though with Homolidea subordinated to an expanded Dromiacea. Thus, apart from Brösing et al. (2006) who found homoloids and dromioids to belong in separate clades, the validity of a clade comprising Dromioidea, Homolodromioidea and Homoloidea is currently widely accepted, despite different conceptions of higher taxa. Present results, however, differ from Guinot and Quenette (2005) and Martin and Davis (2001) in the internal relationships of the dromicacean clade. Homolodromioidea is sister to Homoloidea rather than Dromioidea, rendering Dromiacea *sensu* Guinot paraphyletic. This indicates that the socket-like uropod of homolideans derives from the lobed or plate-like uropod of the remaining dromiaceans. Of further interest is the condition of the endophragmal skeletal junctions in dromiaceans. The endophragmal skeletal junctions of homolodromioids and homoloids are formed by interdigitation rather than fusion as in all other Brachyura (Guinot and Quenette, 2005). Thus, the fused skeletal junctions of dromiaceans and eubrachyurans are independent derivations, whereas the interdigitate condition is apparently plesiomorphic, being present also in Anomura (Secretan, 1983). Further study of endophragmal morphology is required to evaluate whether the skeletal fusion in dromiaceans and eubrachyurans is comparable, and whether the skeletal interdigitation of homoloids and anomurans can be homologised. Should the skeletal fusion in dromiaceans prove different from that of eubrachyurans, and should the homoloid interdigitation prove different from that of anomurans, then additional synapomorphies for the aforementioned groups could be proposed.

Somatic morphology would predict a close relationship between latreilliids and homolids—despite the strikingly different carapace shape, members of both families share a modified P5 only and an eye in which the cornea articulates with the peduncle (Ng, 1998). Of the Brachyura that carry camouflage, only the Homolidae and Latreilliidae have only the last ambulatory leg (P5) modified for carrying. All other podotremes that are known to carry objects have the last two pairs of legs modified. The close relationship between the homolids and latreilliids is reflected in present results. Notably, however, *Latreillia* is nested among the homolid exemplars as sister to *Moloha*, suggesting the possibility that latreilliids are merely highly modified homolids.

The orthodox placement of *Hypoconcha* as brachyuran rather than anomuran is corroborated by present results, contradicting Spears et al. (1992). Moreover, *Hypoconcha* is unambiguously a dromioid, so its aberrant anomuran position recovered by Spears et al. (1992) is enigmatic. Our *Hypoconcha* sequence exhibits a 6% pairwise difference from that of Spears et al. (1992), contrasting with a 2% difference between our *Hypoconcha* and *Lauridromia* sequences. Moreover, Spears et al.'s (1992) 18S *Hypoconcha* sequence closely resembles that of the diogenid hermit crab *Clibanarius albidigitatus* (GenBank accession number AF438751), not only in overall similarity (1% pairwise difference), but also in the presence of numerous identical synapomorphic substitutions. The '*Hypoconcha*' sequence of Spears et al. (1992) may represent a diogenid hermit crab, possibly *Clibanarius*, rather than a brachyuran. The lack of both morphological and molecular evidence indicates that the *Hypoconcha*-Anomuran hypothesis should be abandoned. Although *Hypoconcha* is unambiguously a dromioid, reciprocal monophyly of the constituent dromioid families, Dromiidae and Dynomenidae, is less secure. Paraphyly of Dromiidae with respect to Dynomenidae, implied by our results, is consistent with the high degree of somatic morphological diversity among dromiids, and the results of spermatozoal and foregut studies (Guinot et al., 1994; Jamieson et al., 1995; Guinot et al., 1998; Brösing et al., 2006). Further study using a larger suite of dromiid exemplars is required to resolve the internal structure of Dromioidea.

4.1.2. Raninoidea

Previous studies have generally placed the raninoids either in close proximity to the cyclodorippoids within a monophyletic Podotremata (e.g., Guinot and Tavares, 2001), or associated with Eubrachyura (e.g., Martin and Davis, 2001; Brösing et al., 2006). Thus, the position of the raninoid clade is somewhat unexpected in occupying the 'intermediate' position in the podotreme grade. Placement of raninoids 'between' dromiaceans and cyclodorippoids renders the Archaeobrachyura concept untenable. The absence of uropods in archaeobrachyurans, advanced by Guinot and Tavares (2001) as a synapomorphy of the

group, is not unique. Rather, absence of uropods unites raninoids and cyclodorippoids with Eubrachyura. Thus, the molecular data are consistent with morphological observations—that no morphological characters are uniquely shared by archaeobrachyurans.

Goeke (1981) established a new subfamily, Symethinae, for *Symethis* Weber, 1795. In reappraising the Raninidae, Guinot (1993) retained Symethinae as one of six subfamilies, but commented briefly that its many morphological peculiarities indicate that the symethines probably require familial status. Martin and Davis (2001), following Tucker (1998), formally recognised the family Symethidae. Examination of a good series of *Symethis corallina* Davie, 1989 (ZRC, Philippines), however, revealed little evidence to warrant a separate family for symethines distinct from the Raninidae *sensu stricto*. *Symethis* certainly bears some unusual apomorphies, but it otherwise differs little from other raninids, and is plausibly nested among the other five raninoid subfamilies, of which three are represented in our analyses (Ranininae, Raninoidinae, Symethinae). Therefore, until comprehensive phylogenetic analyses of Raninidae *sensu lato* become available, we follow Davie (2002) in recognising Symethinae rather than Symethidae.

4.1.3. Cyclodorippoidea

The Cyclodorippoidea is monophyletic and sister to the eubrachyurans. The cyclodorippoid + eubrachyuran clade has not been recovered by previous studies, though some older classifications aligned some taxa now placed in Cyclodorippoidea with the eubrachyuran dorippoids based essentially on similar body form (e.g., Balss, 1957). Martin and Davis (2001) also speculated on a possible cyclodorippoid + eubrachyuran relationship citing T. Spears (personal communication). The topologies recovered by most analyses, with *Tymolus* as sister to *Cymonomoides* rather than *Corycodus*, suggests paraphyly of Cyclodorippidae. Whilst monophyly of Cyclodorippidae warrants further investigation, robustness of the *Tymolus* + *Cymonomoides* clade is low under both MP and BI.

An unusual feature of cyclodorippoids, otherwise present only in eubrachyurans, is the development of a true 'abdominal-sternal cavity' with wide sternal plate. Thus, cyclodorippoids stand out as aberrant within the framework of 'Archaeobrachyura' being more highly carcinized. Under an 'Archaeobrachyura' concept, cyclodorippoids and eubrachyurans are only distantly related, requiring independent evolution of the true 'abdominal-sternal cavity'. Recognition of the cyclodorippoid + eubrachyuran clade, however, parsimoniously accounts for the unusual abdominal-sternal morphology of cyclodorippoids. Rather than being convergent, the true 'abdominal-sternal cavity' originated once—in the common ancestor of the cyclodorippoids and eubrachyurans.

4.1.4. Eubrachyura

Relationships among the eubrachyurans, though well resolved, are generally not robust. Under MP, the majoids are sister to the remaining eubrachyurans followed by a dorippid + hymenosomatid clade. Interrelationships and positions of the majoids and dorippids are more ambiguous under BI. All analyses, however, indicate that majoids and dorippids are 'low' in the Eubrachyura. Notably, the 'low' position of majids in the Eubrachyura was also suggested by Spears et al. (1992), Jamieson et al. (1995), Rice (1983) and Brösing et al. (2006) on the basis of molecular, spermatozoal, larval and foregut data, respectively.

Recently, Guinot and Richer de Forges (1997) proposed a close relationship between majids and hymenosomatids. Our results are indecisive regarding a hymenosomatid-majid alliance, either in terms of topological robustness (MP, BI) or resolution (BI), although majoids and hymenosomatids are always in proximity to or near the 'base' of the eubrachyurans. Significantly, dorippids are always associated with the majoid–hymenosomatid assemblage. Thus, the sister to the remaining eubrachyurans lies among the majoids–hymenosomatids–dorippids. In favour of the low position of majoids is larval morphology (Rice, 1983), and in favour of dorippoids are the cyclodorripoid-like facies, particularly in carapace form and the reduced fourth and fifth pereopods adapted for carrying camouflage. In a review of carrying behaviour in brachyurans, Guinot et al. (1995) observed that carrying camouflage in certain brachyuran groups is phylogenetically significant. Camouflage carrying is a common tendency of podotremes, dorippoids and majoids, paralleling that of some anomurans. Wicksten (1982: 307) observed that use of only the second and third pereopods for locomotion in the cyclodorippid *Deilocerus* (=*Clythrocerus*) *planus* (Rathbun, 1900) produced similar movements to those of the shell-carrying anomurans. "Dorippids and majids can...be considered as primitive in the Heterotremata–Thoracotremata assemblage" and in brachyurans, "the loss of the camouflage may be regarded as an advanced behaviour" (Guinot et al., 1995: 407). Notably, the 'behavioural link' between podotremes, dorippids and majids discussed by Guinot et al. (1995) reflects the pattern detected by present analyses (albeit requiring further corroboration), namely in the 'low' position of majoids and dorippids in the Eubrachyura.

Among the 'higher' eubrachyurans, several interesting hypotheses are suggested. For instance, the close relationship between the portunids and parthenopids (i.e., *Carcinus* + *Rhinolambrus*) recognised by MP was also suggested by larval morphology (Rice, 1983). More significantly, the dispersed positions of *Daira*, *Carpilius*, *Eriphia*, *Trapezia* and *Chlorodiella*, all currently placed in Xanthoidea by most workers, add weight to the growing challenge to monophyly of the superfamily (e.g., Schubart et al., 2000; Wetzer et al., 2003; Castro et al., 2004; Schweitzer, 2005; Karasawa and Schweitzer, 2006). Schweitzer (2005), reflecting Wright and Collins (1972) and Glaessner (1980), revisited a possible dynomenid ancestry for Xanthidae. Indeed, the carapace of some xanthids superficially resembles Recent dynomenids. However, the carapace of these xanthids resembles that of the extinct podotrematous

Etyidae to an even greater extent (Guinot and Tavares, 2001). Though xanthoid interrelationships remain elusive, all are unambiguously eubrachyurans, so a Xanthidae-podotreme alliance is not presently supported. More recently, Karasawa and Schweitzer (2006) accepted a more orthodox interpretation of xanthoid evolution, and proposed a new classification of the xanthoids including explicit recognition of paraphyly of Xanthoidea through changes to the superfamilial classification.

The equivocal support for internal relationships of most eubrachyurans is probably due to insufficient variability in the 18S sequences of these more recently diverged taxa. The Eubrachyura is the largest clade in the Decapoda and will require considerably more taxonomic sampling before its internal relationships can be resolved. Importantly, however, identification of Cyclodorippoidea as sister to Eubrachyura lays the foundation for future phylogenetic analyses of the latter clade. Study of eubrachyuran interrelationships is ongoing using a larger suite of terminals and more rapidly evolving markers.

4.2. Classification

The pattern of podotreme paraphyly recovered herein is not fully compatible with any of the existing classifications proposed for Brachyura. Non-monophyly of the 'primitive crabs' renders Guinot's Podotremata untenable as a formal taxonomic category. Similarly, the classification of Števčić (2005), also with a monophyletic Podotremata (as Dromiacea), cannot be accepted. A revised higher classification of the Brachyura is proposed below. Though such classificatory changes might be criticized for reliance on a single locus, 18S rRNA is appropriate for reconstructing deep divergences, and resulting topologies are robust. Moreover, the proposed classification reflects morphological patterns, some of which have been foreshadowed in previous classifications. Our Dromiacea is essentially congruent with that of Martin and Davis (2001) in containing Dromioidea, Homolodromioidea and Homoloidea. Martin and Davis (2001) Raninoida, however, comprising cyclodorippoids + raninoids, is precluded by the pattern of podotreme paraphyly. Although in 'close proximity', cyclodorippoids and raninoids do not form a clade. Cyclodorippoids and raninoids could still be included within an expanded Eubrachyura (*sensu* Martin and Davis, 2001), but such a scheme seems counterproductive. Including podotreme clades in Eubrachyura will significantly complicate diagnosis of the latter (see Guinot and Quenette, 2005) and render the clade name meaningless with respect to the degree of structural organization of the heterotreme–thoracotreme assemblage. Thus, we apply Eubrachyura in its traditional sense, to the clade comprising only heterotremes and thoracotremes. For taxonomic consistency, we propose that the three major podotreme clades be each recognised as separate sections, Dromiacea, Raninoida and Cyclodorippoida, alongside section Eubrachyura.

Brachyura
   Dromiacea
   Raninoida
   Cyclodorippoida
   Eubrachyura

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