Zoologica Scripta

Phylogeny of eriphioid crabs (Brachyura, Eriphioidea) inferred from molecular and morphological studies

Joelle C. Y. Lai, Brent P. Thoma, Paul F. Clark, Darryl L. Felder & Peter K. L. Ng

Submitted: 20 November 2012
Accepted: 30 June 2013
doi:10.1111/zsc.12030

Lai, J.C.Y., Thoma, B.P., Clark, P.F., Felder, D.L., Ng, P.K.L. (2014). Phylogeny of eriphioid crabs (Brachyura, Eriphioidea) inferred from molecular and morphological studies. —*Zoologica Scripta*, *43*, 52–64.

The evolutionary relationships of the brachyuran crab superfamily Eriphioidea, commonly known as stone or rubble crabs, are examined. Analysis of three mitochondrial (12S, 16S and COI) and two nuclear loci (18S and Histone 3) was carried out for 51 taxa representing the Carpilioidea, Dairoidea, Eriphioidea, Goneplacoidea, Parthenopoidea, Pilumnoidea, Portunoidea, Pseudozioidea and Xanthoidea. Phylogenetic analyses of molecular data used three methods of inference that recovered similar topologies with minor differences. Maximum parsimony analysis of 20 morphological characters taken from first zoeas of 11 species yielded two equally parsimonious trees and generally supported the molecular analyses. None of the analyses recovered Eriphioidea as monophyletic, and each of the eriphioid families represented by two or more taxa was shown to be polyphyletic in both molecular and larval analyses. This study indicates that the present classification based on adult morphology is incongruent with phylogenetic relationships and that the diagnostic characters the result of convergence (particularly in feeding morphology) rather than shared ancestry.

Corresponding author: *Joelle C. Y. Lai, Department of Biological Sciences, National University of Singapore, 14 Science Drive 4, Singapore 117543, Singapore. E-mail: chiuyun@nus.edu.sg*
Brent P. Thoma, Department of Biology and Laboratory for Crustacean Research, University of Louisiana at Lafayette, Lafayette, LA, USA. E-mail: brent.thoma@gmail.com
Paul F. Clark, Department of Life Sciences, The Natural History Museum, Cromwell Road, London, SW7 5BD, England. E-mail: p.clark@nhm.ac.uk
Darryl L. Felder, Department of Biology and Laboratory for Crustacean Research, University of Louisiana at Lafayette, Lafayette, LA, USA. E-mail: dlf4517@louisiana.edu
Peter K. L. Ng, Tropical Marine Science Institute, National University of Singapore, S2S 18 Kent Ridge Road, Singapore 119227, Singapore. E-mail: peterng@nus.edu.sg

Introduction

Eriphioid crabs occupy a diverse range of habitats from intertidal rocky shores, mangrove swamps, coral reefs and the continental slope to depths below 800 m. Most of these crabs are of moderate size with the exception of *Hypothalassia armata* (De Haan, 1835) and *Pseudocarcinus gigus* (Lamark, 1818), both of which are large with the latter weighing 12 kg or more and growing up to 40 cm in carapace width. Larval development varies between five zoeal stages, for example, as for *P. gigas* (see Gardner & Quintana 1998), and four as reported by Wear (1968) and Wear and Fielder (1985) for *Ozius truncatus* H. Milne Edwards, 1834.

Some species are of commercial importance. In South-East and East Asia, *Myomenippe hardwickii* (Gray, 1831), *Menippe rumphii* (Fabricius, 1798) and *H. armata* are of economic significance in coastal communities (Ng 1998); in Australia, the Tasmanian giant crab or queen crab, *Pseudocarcinus gigas*, is the most important fishery of eriphioid crab and locally fetches ca. AUD40 to 55 per kg (Australian Department of Primary Industries, Parks, Water and Environment, online resource); *Hypothalassia acerba* Koh & Ng, 2000, is collected in large numbers for export (Ng 1998; Koh & Ng 2000); in the Americas, claws of *Menippe mercenaria* (Say, 1818) and *Platyxanthus orbignyi* (H. Milne Edwards & Lucas, 1843) are removed and the crab then

returned to the sea to regenerate a new claw; in the Atlantic and Gulf Coast of USA, the claw fishery of *M. mercenaria* and *M. adina* reached a peak of approximately 3 million pounds in weight of claws in the 2009 fishing season (Florida Fish and Wildlife Conservation Commission, online resource), and *Danielethus patagonicus* (A. Milne-Edwards, 1863) (formally *Platyxanthus*, see Thoma *et al.* 2012) in Patagonia (Carsen *et al.* 1996; Narvarte *et al.* 2007) forms a significant regional fishery.

Eriphioids can be confused with xanthoid and carpilioid crabs, and all three were taxa previously assigned to the Xanthidae. Adult eriphioid males can be distinguished from xanthoids in that all male abdominal somites are distinct and movable (vs. abdominal segments 3–5 being fused and immovable in xanthoids), the first gonopod is stout or gently curved, cylindrical (vs. slender and sinuous in xanthoids) and the second gonopod is elongate, longer than or subequal in length to first gonopod (vs. short in xanthoids). From carpilioids, eriphioids can be distinguished only by all the male abdominal somites freely moveable with visible sutures (vs. male abdominal somites 3–5 immovable and completely fused with sutures not discernible in carpilioids). Eriphioid classification has long been difficult and/or confused and has remained under almost constant review since the family Eriphiidae was established by MacLeay in 1838.

Although numerous carcinologists have considered Eriphiidae, Oziidae and Menippidae to be closely related, proposed classifications based on adult morphology have varied. This present study examines alternative classifications in the light of evolutionary relationships inferred from molecular and morphological data.

Historical review of adult systematics

MacLeay (1838) originally erected Eriphiidae (as Eriphidae) to accommodate *Eriphia* Latreille, 1817, but provided no comment on either its affinities or its composition. Dana (1851) accepted Eriphiidae (as Eriphidae) and divided it into four subfamilies, three of which were new: Aethrinae, Oziinae (as Ozinae) and Actumninae. Subsequently, Ortmann (1893) established Menippidae for Menippinae, Myomenippinae (as Panopaeinae) and Pilumninae. In addition, he established Oziidae to include Eriphiinae, Panopeinae, Oziinae and Domeciinae (as Domecinae). Ortmann assigned all these taxa to his Xanthini. This classification was modified by Alcock (1898) when he subdivided the Xanthidae into two groups distinguished by the morphology of the endostomial ridges (i.e. Hyperolissa with ridges low or absent vs. Hyperomerista with ridges well developed). Hyperomerista, which Alcock divided into four subfamilies: Menippinae, Oziinae, Pilumninae and Eriphiinae, roughly corresponded to Eriphiidae *sensu* Dana 1851; excluding Aethrinae. The classification of Borradaile (1907) agreed with Alcock (1898) who also regarded Menippinae, Oziinae and Eriphiinae as distinct taxa within Xanthidae. However, Borradaile (1907) did not subscribe to the division of Xanthidae into Hyperolissa and Hyperomerista as proposed by Alcock (1898). Although Balss (1932) accepted Xanthidae *sensu* Alcock (1898), he assigned *Eriphia*, *Eriphides*, *Menippe*, *Myomenippe* and *Ozius* to Menippinae. Balss (1957) later adapted the system of Alcock (1898) by assigning more taxa, including some fossil genera, to Menippinae.

A revolutionary brachyuran classification based on the position of male and female genital openings was proposed by Guinot (1978), who elevated Xanthidae as previously conceived to superfamily and the subfamilies therein to family rank, including Menippidae. To the latter, she referred most of the menippine genera of Balss (1957). Her menippid classification was revised in the classic monograph of xanthoids from the Red Sea and western Indian Ocean, where Crosnier (in Serène 1984) emended the Menippidae of Balss (1932) by splitting it into Oziinae, Eriphiinae and Dacryopilumninae. His Oziinae comprised of the genera *Epixanthus*, *Epixanthoides*, *Lydia*, *Sphaerozius*, *Myomenippe* and *Ozius*. This was modified by Ng *et al.* (2001) who divided Eriphiidae into four subfamilies and assigned genera as follows: *Dacryopilumnus* to Dacryopilumninae; *Eriphia* to Eriphiinae; *Hypothalassia*, *Menippe*, *Myomenippe*, *Sphaerozius* and *Pseudocarcinus* to Menippinae; *Baptozius*, *Epixanthoides*, *Epixanthus*, *Eupilumnus* (as *Globopilumnus*), *Lydia* and *Ozius* to Oziinae. In the same year, Martin & Davis (2001) published 'An updated classification of the recent Crustacea' where they recognised Menippidae within Xanthoidea, but did not list any subfamilies or genera under this taxon. In contrast, the Zoological Catalogue of Australia by Davie (2002) followed Ng *et al.* (2001) in proposing a family Eriphiidae of four subfamilies: Dacryopilumninae comprised of *Dacryopilumnus*; Eriphiinae for *Eriphia*; Menippinae for *Hypothalassia*, *Myomenippe*, *Pseudocarcinus* and *Ruppellioides*; Oziinae for *Bountiana*, *Epixanthus*, *Eupilumnus*, *Lydia* and *Ozius*.

More recently, Števčić (2005) reorganised the xanthoid classification of Guinot (1978). He separated the 'eriphiids' from Xanthoidea by creating Eriphioidea and dividing it into Eriphiidae (with three subfamilies: Eriphiinae, Platyxanthidae and Dacryopilumninae), Ladomedaeidae, Pilumnoididae and Carpiliidae. However, the new classification of Števčić (2005) did not treat Oziinae. Karasawa & Schweitzer (2006) proposed a different classification based on phylogenetic analysis of morphological data for extant and fossil taxa. They accepted Eriphioidea as proposed by Števčić (2005) but divided the superfamily into Eriphiidae, Oziidae (including Dacryopilumninae, Menippinae, Oziinae), Hypothalassiidae, Platyxanthidae and

Pseudoziidae. Most recently, in their checklist of extant brachyuran decapods of the world, Ng *et al.* (2008) retained Eriphioidea as proposed by Števčić (2005) but reorganised it by recognising only Dairoididae, Eriphiidae, Hypothalassiidae, Menippidae, Oziidae and Platyxanthidae.

Nomenclatural confusion

When Ortmann (1893) established Menippidae and raised Oziinae to family level, he considered Eriphiinae as a taxon within Oziidae, which caused nomenclatural confusion. Following Ortmann, Balss (1933) recognised Menippinae as a higher taxon and assigned to this *Eriphia* and *Ozius*. Thereafter, Balss (1957), Guinot (1978) and Crosnier (in Serène 1984) all considered the higher taxa associated with *Eriphia* to be junior synonyms of Oziinae/Oziidae. Indeed, Holthuis (1993: 619) too considered that Oziidae Dana, 1852 was the earlier available name and should be used. However, Ng (1998) stated that the name Eriphiidae MacLeay, 1838 had been overlooked and was the oldest available name for this group of brachyurans. This has been subsequently followed by Davie (2002), Števčić (2005), Karasawa & Schweitzer (2006), Koh & Ng (2008) and Ng *et al.* (2008).

Evidence from larval morphology

In his treatment of *Ozius truncatus* H. Milne Edwards, 1834, Wear (1968) briefly discussed the relevance of larval morphology to 'eriphioid' systematics and highlighted similarities in zoeal characters found in *O. truncatus*, *O. rugulosus*, *Homalaspis plana* (as *Homolaspis* [sic]) and *Menippe mercenaria*. Later, Martin (1984) proposed 'six' xanthid groups, two of which are relevant to the present study including group III, comprised in part by eriphiids, oziids and platyxanthids (i.e. *Eriphia*, *Baptozius*, *Epixanthus*, *Ozius*, *Homalaspis* and *Platyxanthus*) and group IV, which included only menippids (i.e. *Menippe* and *Sphaerozius*). Martin presented four characters that separate these two groups: antennal exopod setation, setation of the distal endopod segment on the maxillule, setation of the endopod of the maxilla and setation of the proximal endopod segment on the second maxilliped. In their treatment of *Pseudocarcinus gigas*, Gardner & Quintana (1998) discussed the relationships of Oziinae and considered the presence of a median dorsal spine on the first abdominal somite in zoeae of these two species as a diagnostic 'oziid' character, as initially suggested by Wear (1968) in his treatment of *O. truncatus*. As a result of these similarities, Gardner & Quintana (1998) suggested a possible affiliation between *P. gigas* and *Ozius*.

Present study

The objective of this study was to test the monophyly of Eriphioidea as recently proposed by Števčić (2005), Karasawa & Schweitzer (2006) and Ng *et al.* (2008) on the basis of DNA sequence data from three mitochondrial (*12S* rRNA, *16S* rRNA and *cytochrome oxidase I* [COI]) and two nuclear markers (*18S* rRNA and *histone H3* [H3]) as well as zoeal morphology.

Material and methods

Molecular phylogenetic analysis

Taxon sampling. Fifty one taxa representing Carpilioidea, Dairoidea, Eriphioidea, Goneplacoidea, Parthenopoidea, Pilumnoidea, Portunoidea, Pseudozioidea and Xanthoidea were selected for DNA analysis (see Supporting Information Table S1 for specimen details and authorities). Of these, 42 taxa have previously been referred to the Eriphioidea (Guinot 1978; Serène 1984; Števčić 2005; Karasawa & Schweitzer 2006; Ng *et al.* 2008).

DNA extraction, amplification and sequencing. Genomic DNA was extracted from muscle tissue or egg masses of ethanol-preserved specimens using DNeasy Blood and Tissue Kit (QIAGEN Inc., Valencia, CA) following the manufacturer's protocol.

Fragments of 12S, 16S and 18S ribosomal subunits, as well as the protein-coding genes *cytochrome oxidase I* and *Histone-H3* (hereafter referred to as 12S, 16S, 18S, COI and H3, respectively; see Supporting Information Table S2 for primer information) were selectively amplified using the following protocol: initial denaturation 94°C for four minutes, 34 cycles of 94°C for 30 s (denaturation), 45–52°C for 30 s (annealing; COI [45–50°C], 16S, 18S and H3 [47°C]), 12 s [52°C]) and 72°C for 60 s (extension) with a final extension of 72°C for ten minutes. PCRs were conducted using 25 μL volumes containing 2.5–3 mM $MgCl_2$, 0.025 mM of each dNTP, 12.5 pmol of each primer, 0.2 units of GoTaq DNA polymerase (Promega, Madison, WI, USA), 5 μL 5× GoTaq buffer and 1–100 ng of whole-genomic DNA. Amplicons were electrophoresed on a 1% agarose gel and subsequently purified using Agencourt AMPure system (Agencourt, Beverly, MA, USA) prior to cycle sequencing using the ABI PRISM® Dye terminator kit containing AmpliTaq and BigDye (version 3) dye terminator. Each sequencing reaction comprised 5–8 ng of PCR product, 1 μL BigDye, 0.5 μL 5× BigDye sequencing buffer and 0.4 μL sequencing primer (2 pmol/μL), topped to 5 μL with sterile Milli-Q water. Cycle sequencing parameters followed manufacturer's protocols, and all extension products were purified using CleanSEQ dye-terminator removal system (Agencourt, Beverly, MA, USA) before being read on a 3100 capillary sequencer (Applied Biosystems, Foster City, CA, USA). Sequences were read in both directions and combined in Sequencher v.4.8 (Gene Codes Corporation, Ann Arbor, MI, USA) to eliminate errors and reduce ambiguity.

Alignment. Sequences were aligned in MAFFT (Katoh *et al.* 2002) using the FFT-NS-2 strategy for COI and H3, while ribosomal sequences used the Q-INS-I strategy as described by Katoh & Toh (2008). Following alignment, GBlocks v0.9 (Castresana 2000) was subsequently used to locate and exclude ambiguously aligned regions for each ribosomal locus, using relaxed gap selection criteria (allowing gap positions within the final blocks and less strict flanking positions).

Phylogenetic analyses. Three methods were used in the inference of relationships between taxa: maximum parsimony (MP), maximum likelihood (ML) and Bayesian inference (BI). Exploratory analyses of individual gene regions indicated that single-gene data sets did not yield sufficient information to resolve phylogenetic relationships; as a result, all loci were combined using Sequence Matrix version 1.7.8 (Vaidya *et al.* 2011). Substitution saturation in COI (in total and for each codon position) was tested using the saturation index described by Xia *et al.* (2003) and implemented in DAMBE version 5.2.6 (Xia & Xie 2001).

Maximum parsimony analyses (MP) were conducted in PAUP* version 4.0a114 (Swofford 2002) with all characters equally weighted and gaps treated as a 5th character state. Heuristic search option with tree-bisection–reconnection (TBR) and random addition sequence of 1000 replicates was used. Topological robustness was assessed using parsimony jackknifing (Farris *et al.* 1996) using 1000 pseudoreplicates under a heuristic search with 30% character deletion and 50 random addition sequence replicates per pseudoreplicate.

Maximum likelihood analyses were performed using random accelerated maximum likelihood (RAxML) ver. 7.3.1 (Stamatakis 2006; Stamatakis *et al.* 2008) as implemented on the CIPRES portal (http://www.phylo.org/sub sections/portal/) (Miller *et al.* 2010) with the data set partitioned according to loci. A rapid bootstrap (BS) analysis was performed with 1000 replications to search for the best scoring ML tree using the GTRCAT model.

Prior to BI analyses, best-fit model for individual loci was selected using MrModeltest version 2.2 (Nylander 2004) under Akaike information criterion (AIC).

Bayesian analyses were carried out using MrBayes version 3.1.2 (Ronquist & Huelsenbeck 2003) on Gordon, available via CIPRES portal (http://www.phylo.org/portal2/). Analyses included 2 independent runs of 4 chains (3 heated and 1 cold) run for 50 million generations with trees sampled every 1000 generations. The first 12.5 million generations were discarded as 'burn-in', and posterior probabilities were estimated from the remaining sampled generations. Log-likelihood values and posterior probabilities were checked to warrant that chains had reached stationarity (SD < 0.03).

Larval phylogenetic analyses

A matrix of larval morphology (Supporting Information Table S3) was constructed in MacClade 4.08 (Maddison & Maddison 2000) from zoea hatched under laboratory conditions (Supporting Information Appendix S1). Trees were inferred using MP inference in PAUP* 4.0a114. Heuristic search option with tree-bisection–reconnection (TBR) and random addition sequence of 100 replicates was used with characters all equally weighted, unordered and scored as irreversible-up. Character states were polarised using *Charybdis helleri* (A. Milne-Edwards, 1867) as the outgroup because this portunoid has six zoeal stages (see Dineen *et al.* 2001), and no xanthoid to date has been described with this number of larval stages (see also Clark 2001, 2005, 2009; Clark & Guerao 2008). Support for resulting topologies was assessed using decay indices (DI) (Bremer 1988) calculated in PAUP* using TreeRot version 3 (Sorenson & Franzosa 2007).

Results

Molecular phylogenetics

Although data were obtained for 51 taxa, sequencing for some taxa was not successful for all markers. Sequences were obtained for all 51 taxa for 12S, 16S and H3 but only 44 and 47 sequences were obtained for COI and 18S, respectively. The aligned 12S, 16S and 18S data sets were 428, 556 and 1807 base pairs in length prior to the removal of ambiguously aligned regions using Gblocks, which yielded final lengths of 349 characters (79% retention), 490 (89% retention) and 1725 base pairs (98% retention). The final concatenated data set consisted of 3272 characters (12S: 349, 16S: 490, 18S: 1725, H3: 338, COX1: 370 [3rd codon position removed]). There were 2510 constant characters, 210 variable characters that were parsimony-uninformative and 552 parsimony-informative characters.

While the I_{ss} value for COI as a whole and the first and second codon was significantly less than the $I_{ss.c}$ value, the third codon was found to be saturated (I_{ss} 0.680 vs. $I_{ss.c}$ 0.696, P-value = 0.65) and therefore removed in subsequent analyses. The models suggested by MrModeltest were HKY+I+G (Hasegawa *et al.* 1985) for 12S and H3; SYM+I+G (Zharkikh 1994) for 18S; and GTR+I+G (Tavaré 1986; Rodríguez *et al.* 1990) for 16S and COI.

Three methods of phylogenetic inference used in this study recovered topologies with minor differences.

Several clades were recovered in all three analyses (Fig. 1) including:

1. A clade with BI/ML/MP support values of 1.0/92/96 comprised of *Baptozius vinosus*, *Epixanthus corrosus*, *Epixanthus helleri*, *Ozius rugolusus*, *Ozius tenuidactylus*, *Ozius reticulatus*, *Epixanthus dentatus*, *Ozius guttatus*, *Lydia annulipes* and *Epixanthus frontalis*. Within this clade,

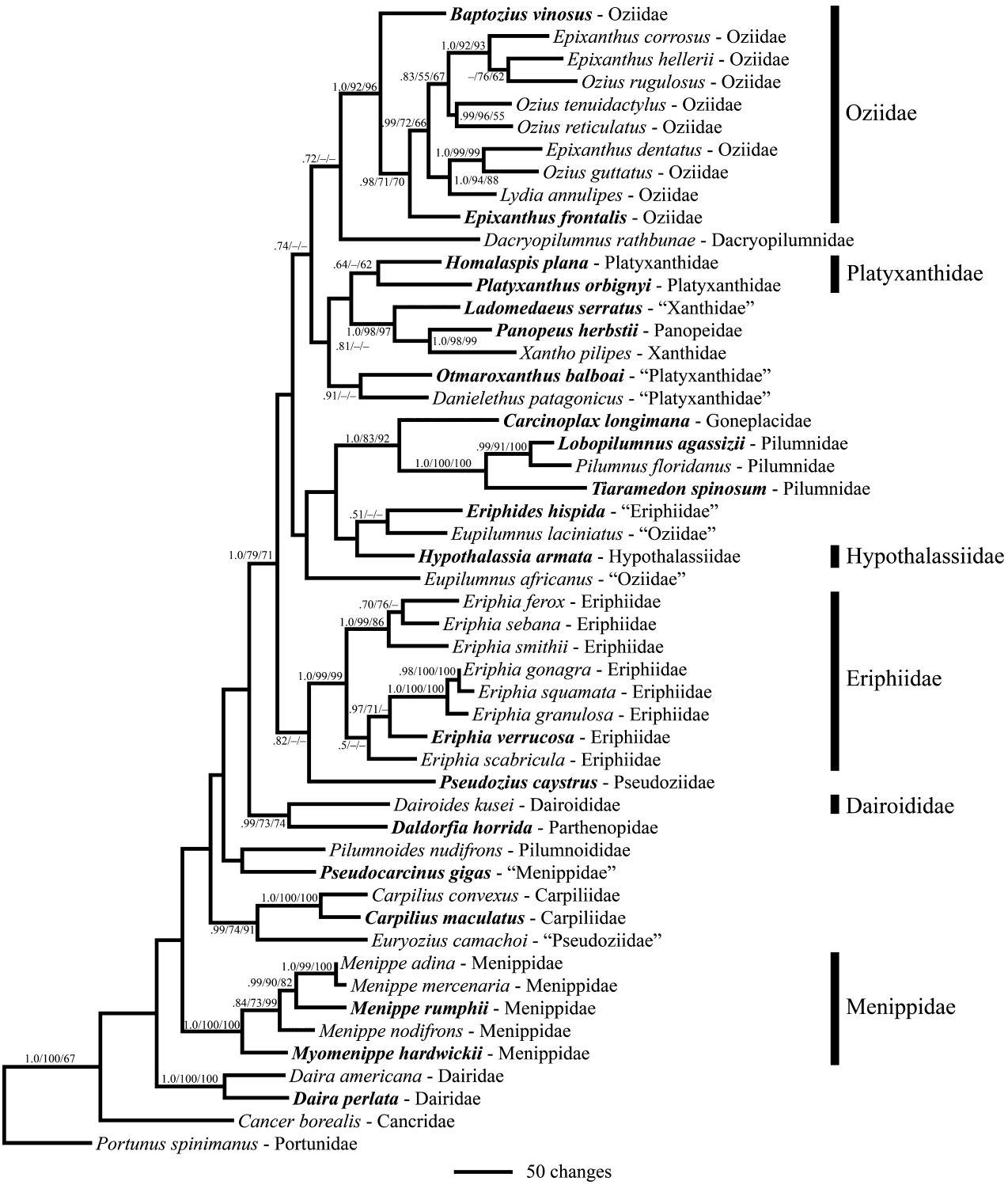

Fig. 1 Maximum likelihood phylogram with posterior probabilities/ML bootstrap/MP jackknife support. Taxa in bold indicates type species of genus. Family names following species names represent current classification (Ng *et al.* 2008). Names in quotation marks indicate that the taxon is recovered as not monophyletic. Annotations indicate families of Eriphioidea *sensu* Ng *et al.* (2008) as recovered here.

Baptozius is recovered as a sister taxon to the other genera, while *Ozius* and *Epixanthus* are recovered as not monophyletic with nearly every species of *Ozius* being recovered as sister to a species of *Epixanthus*. Support for terminal clades is generally high, with the exception of the *E. helleri* and *O. rugolosus* clade, which is recovered in ML and MP analyses, but not in BI analysis, in which *E. corrosus* and *O. rugolosus* are sister species but this arrangement was not statistically supported.

2. *Dacryopilumnus rathbunae* (Dacryopilumnidae) is recovered as sister to the clade comprised of taxa representing *Baptozius*, *Ozius*, *Epixanthus* and *Lydia* (see 1 above) in both BI (0.72) and ML (<50) analyses but is recovered as sister to *P. caystrus* in MP analyses (<50).
3. A clade comprised of three xanthoids, *Xantho pilipes*, *Panopeus herbstii* and *Ladomedaeus serratus* (1.0/98/97), which is sister to a poorly supported clade comprised of *Homalaspis plana* and *Platyxanthus orbignyi* (0.64/–/62). Sister to this is a clade comprised of *Otmaroxanthus balboai* and *Danielethus patagonicus* (0.91/-/-). This arrangement is not statistically supported but is recovered in all three analyses.
4. *Carcinoplax longimana* (Goneplacidae) is recovered as the moderately well-supported sister (1.0/83/92) to a clade comprised of three pilumnoids: *Lobopilumnus agassizii*, *Pilumnus floridanus* and *Tiaramedon spinosum* (1.0/100/100).
5. A clade comprised of *Eriphides hispida* (Eriphiidae), *Eupilumnus laciniatus* (Oziidae) and *Hypothalassia armata* (Hypothalassiidae) was recovered in all three analytical methods but this arrangement was not statistically supported. This clade was recovered as the sister to the goneplacid/pilumnoid clade (4) but again this arrangement was not statistically supported.
6. A clade that comprised all included species of Eriphiidae, omitting *Eriphides hispida*, was well supported (1.0/99/99). *Eriphides hispida* was recovered as sister to *Eupilumnus laciniatus* (0.51/-/-).
7. A well-supported clade (1.0/100/100) made up of *Carpilius maculatus* and *Carpilius convexus* (Carpiliidae) was recovered as sister to *Euryozius camachoi* (Pseudoziidae) (0.99/74/91).
8. A moderately well-supported clade (0.84/73/99) comprised of *Menippe adina*, *Menippe mercenaria*, *Menippe rumphii* and *Menippe nodifrons* is recovered as sister to *Myomenippe hardwickii* (1.0/100/100). This clade includes all species of Menippidae included in the analyses except *Pseudocarcinus gigas*, which was recovered in a clade with *Pilumnoides nudifrons* (Pilumnoididae) in all three analyses, but the relationship is not statistically supported.
9. A well-supported clade (1.0/100/100) comprised of *Dairoides kusei* (Dairoididae) and *Daldorfia horrida* (Parthenopidae).

Trees recovered by BI and ML analyses differed only in the position of *Cancer borealis* Stimpson, 1859 (Cancridae) relative to the outgroup, *Portunus spinimanus* Latreille, 1819 (Portunidae). Maximum parsimony (MP) yielded topologies that differed from those inferred using BI and ML methods in the position of *Dacryopilumnus rathbunae* and *Pseudozius caystrus*, with these two taxa found in a single poorly supported clade in MP analyses. In ML and BI analyses, *D. rathbunae* was recovered as a poorly supported sister taxon to the main oziid clade and *P. caystrus* was recovered as a poorly supported sister taxon to the main eriphiid clade. The phylogenetic relationships of *Eupilumnus africanus* were also indeterminate as its placement in MP analyses differed from those recovered in ML and BI analyses, in addition to being poorly supported in all analyses. In all cases, the superfamily Eriphioidea was not recovered as a monophyletic clade.

Zoeal morphological analysis

Maximum parsimony analysis of zoeal morphology yielded two equally parsimonious trees with 45 steps and consistency index of 0.53 (Fig. 2). Three major clades are recovered in both trees:

1. *Lydia annulipes* and *Pseudocarcinus gigas* are sister to *Ozius truncatus*. Sister to this clade is *Dacryopilumnus rathbunae* and *Epixanthus frontalis*. All nodes within this clade have a decay index (DI) of 1.
2. *Eriphia smithii* and *Hypothalassia armata* (DI = 1).
3. *Myomenippe hardwickii* is recovered as sister to *Menippe mercenaria* (DI = 1), and while this relationship is recovered in both of the two equally parsimonious trees, the remainder of clade varies. In one topology, *Menippe nodifrons* is recovered as sister to this clade (DI = 0) with *Menippe rumphii* as sister to that. In the alternative topology, *M. rumphii* is recovered as sister to the clade of *M. hardwickii* and *M. mercenaria*, while *M. nodifrons* is sister to these three taxa. Despite the differences between the two topologies, composition of the group is stable (DI = 7).

Discussion

Phylogenetic analyses of both molecular and larval data are largely congruent. There were no attempts to undertake a combined molecular and morphological analysis due to a lack of overlap in taxon sampling. In addition, adult morphology was not analysed due to a lack of suitable characters that differed from characters traditionally used in delineating eriphioid taxa. As demonstrated by Lai *et al.* (2011) in their study of the Xanthidae, using 'conventional' adult morphology as character sets presents limitations on the data set.

In all analyses, the superfamily Eriphioidea, as well as the families Oziidae and Menippidae, is not recovered as

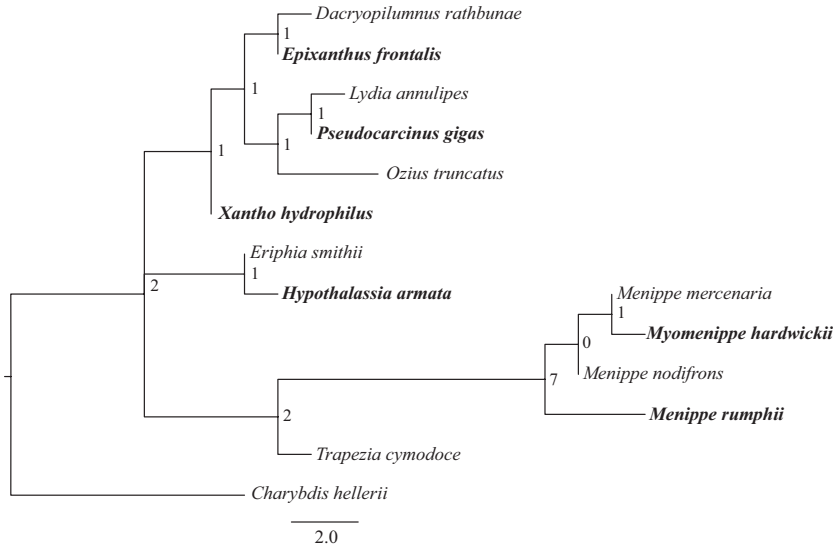

Fig. 2 Phylogram inferred from first-stage zoeal morphology using maximum parsimony. Taxa in bold indicate type species of genera. Tree length 45, consistency index 0.5333. Numbers on branches indicate decay indices.

monophyletic. While analyses of molecular data indicate that Eriphiidae and Platyxanthidae are not monophyletic, Platyxanthidae is not represented in the larval data and Eriphiidae is represented by only a single species (*Eriphia smithii*). These analyses suggest that the morphological characters used in defining the superfamily, particularly the characters of the chelipeds, may reflect convergence in feeding behaviour or other behaviour related to cheliped morphology rather than shared ancestry and that the concepts of this group proposed by Števčić (2005), Karasawa & Schweitzer (2006), and Ng *et al.* (2008) are not reflective of evolutionary relatedness.

Three of five genera presently attributed to Menippidae are represented in both molecular and larval data sets, and analyses indicate that the family is not monophyletic. *Pseudocarcinus gigas* is recovered as sister to *Lydia annulipes* in the analysis of larval data, while analyses of molecular data suggest an affiliation to *Pilumnoides* Lucas, in H. Milne Edwards & Lucas, 1844. *Menippe* and *Myomenippe* are recovered in a well-supported clade (1.0/100/100 DI = 7) that appears to represent Menippidae *sensu stricto* (s. s.) as it contains the type species, *Menippe rumphii*; however, relationships within this clade are less clear. Analyses of molecular data indicate that *Myomenippe* is a well-supported sister (0.84/73/99) to a monophyletic *Menippe*, while analysis of zoeal morphology indicates *Menippe* is paraphyletic, *Myomenippe hardwickii* being recovered within the clade comprised of species of *Menippe*. This relationship is not recovered in any of the molecular analyses and is not well supported in analysis of zoeal data (DI = 0), which suggests that while zoeal morphology may be useful in diagnosing the family, it is not a reliable tool for distinguishing between closely related menippids.

The recovery of *Pseudocarcinus* outside of Menippidae s. s. was unexpected as it has been long recognised as a menippid since its description by H. Milne Edwards (1834). Although zoeal characters indicate an affiliation between *P. gigas* and *Ozius* with both representing group III xanthid larvae (Martin 1984), Gardner & Quintana (1998) concluded that megalopal morphology of *P. gigas* more closely fits the criterion established by Martin (1988) for *Menippe* spp. They then suggested that this change in affinities between early zoeal and megalopal stages may reflect the increase in setation that takes place as the number of larval stages increases, coupled with the fact that both *Pseudocarcinus* and *Menippe* have five zoeal stages, while *Ozius* only has four. The present analysis of zoeal morphology supports the findings of Gardner & Quintana (1998) and indicates a relationship between *Pseudocarcinus gigas*, *Ozius truncatus* and *Lydia annulipes*; however, this arrangement is not well supported (DI = 1). Furthermore, this relationship has not been indicated by previous examinations of adult morphology and is not supported by present molecular analyses where *P. gigas* is associated with *Pilumnoides nudifrons*. Although the relationship between *P. gigas* and *P. nudifrons* is not statistically supported, it is recovered in all three analyses. In any case, analyses of both data sets indicate that *P. gigas* is only distantly related to Menippidae s. s.

Of the seven genera presently assigned to Oziidae, five are represented in our molecular data set and three in our larval data set. Analyses of both data sets indicate that the family is not monophyletic, and molecular data suggest

many of the oziid genera are in need of revision. Analyses of molecular data recovered a well-supported clade (1.00/92/96) made up of four of the five oziid genera, while the fifth, *Eupilumnus*, is recovered as paraphyletic and well outside the oziid clade. As the type species of the genus, *Eupilumnus actumnoides*, is not included here, it is unclear whether *Eupilumnus* s. s. is representative of Oziidae or an undetermined lineage. Zoeal data corroborate molecular analyses and provide additional evidence supporting the polyphyly of the family with *Pseudocarcinus* and *Dacryopilumnus* both being recovered within a larger oziid clade; however, the arrangement of these taxa is not well supported (DI = 1).

The present analyses suggest the genera *Ozius*, *Epixanthus* and *Eupilumnus* are not monophyletic. Molecular data indicate that the species presently attributed to *Ozius* and *Epixanthus* represent at least four lineages: (i) *Ozius rugulosus*, *Epixanthus corrosus* and *Epixanthus hellerii*; (ii) *Ozius reticulatus* and *Ozius tenuidactylus*; (iii) *Ozius guttatus* and *Epixanthus dentatus*; and (iv) *Epixanthus frontalis* (the type species of the genus). These findings are congruent with previous analyses of larval morphology that called attention to differences between larvae of *E. frontalis* and *E. dentatus* (Saba *et al.* 1978; Clark 2001; Clark & Paula 2003). Molecular data also suggest that these taxa may be geographical structured, with a split between American (*O. reticulatus* and *O. tenuidactylus*) and Indo-West Pacific (*O. guttatus* and *E. dentatus*) taxa. Interestingly, *E. helleri*, known from the eastern Atlantic, is recovered in a clade with two taxa known primarily from the western Indian Ocean and Red Sea (*E. corrosus* and *O. rugulosus*). Although both of these species are presently considered relatively widespread (western Indian Ocean to French Polynesia), the relationship between biogeography and phylogeny, suggested by these analyses, requires a thorough study of these taxa across their known ranges.

Analyses of molecular data also indicate that *Eupilumnus* is not monophyletic, with *Eupilumnus laciniatus* being recovered as sister to an atypical eriphiid, *Eriphides hispida*, in a clade with *Hypothalassia armata*, which is sister to representatives of Goneplacidae and Pilumnidae. Although not well supported statistically, this clade is consistently recovered in all three analyses and is partially supported by adult morphology. These findings are not entirely unexpected as *E. laciniatus* is an atypical eupilumnid with extremely spinose features and carapace characters, much like those exhibited by *Hypothalassia* (Ng & Tan 1985; Ng 1992; Koh & Ng 2000). Previous studies have also suggested that *Eupilumnus africanus* may not be closely related to its congener, differing in a number of characters (see Guinot-Dumortier 1959), a finding supported here as well. As stated above, until the type species of the genus is included in the analyses, it is unclear whether either of these lineages represent *Eupilumnus* s. s. Regardless, these analyses suggest that detailed review of the genus is required.

A number of authors have discussed relationships between *Daira*, *Dacryopilumnus* and *Dairoides* with no clear consensus (Serène 1984; Guinot 1967; Sakai 1976; Ng & Tan 1984, 1985; Dai & Yang 1991; Ng *et al.* 2001; Števčić 2005; Ng *et al.* 2008 – for a summary see Ng *et al.* 2008: 57). Superficially resembling many xanthids, *Daira* was long considered a member of that group despite having a number of unusual features, including unique cuticular ornamentation (Guinot 1967, 1979). Guinot (1978) commented on the similarities of *Dairoides* to *Daira*, but pointed out that *Dairoides* more closely resembled parthenopids. Ng & Rodríguez (1986) described the family Dairidae in the superfamily Parthenopoidea to accommodate *Daira* and *Dairoides*, and Števčić (2005) defined Dairoididae for the latter and placed both families in the superfamily Dairoidea. Serène (1984) established Dacryopiluminae (as a subfamily of Eriphiidae) for *Dacryopilumnus* but provided no comment on its relationship to either *Daira* or *Dairoides*. Citing characters of the sterno-abdominal cavity, male abdomen and chelipeds, Ng *et al.* (2008) placed Dairoididae (with only the genus *Dairoides*) within Eriphioidea and recognised the superfamily Dairoidea to include the families Dacryopilumnidae and Dairidae. The similarities between *Dairoides* and many parthenopid genera have been regarded as convergence (see Ng *et al.* 2008), but our results suggest that there may be a phylogenetic basis for their relationship. The only parthenopid included here, *Daldorfia horrida* (Parthenopidae), is recovered as a moderately well-supported sister to *Dairoides kusei* (0.99/73/74). This suggests that the characters of the chelipeds, press button and male abdomen that unite *Dairoides* with eriphioids may be the result of convergence, and *Dairoides* is actually part of Parthenopoidea.

Analyses of larval and molecular data suggest a relationship between *Dacryopilumnus* and Oziidae, with *Dacryopilumnus rathbunae* being recovered as sister to a clade representative of Oziidae in molecular analyses. Although this relationship is not well supported (0.72/-/-), a similar relationship is recovered in analysis of larval morphology, with *D. rathbunae* being grouped with the other oziids and *Pseudocarcinus gigas*. Again, this relationship is not well supported (DI = 1), but an affiliation between *Dacryopilumnus* and the oziids is recovered in all analyses except MP, wherein it is instead associated with *P. caystrus* as sister to *Eriphia*. As originally suggested by Serène (1984), it appears that *Dacryopilumnus* is a representative of Eriphioidea; however, its affinities are far from certain, and additional investigation is warranted. Its position in Dairoidea is in question until further investigation.

Both genera presently attributed to Eriphiidae were included in the present study, and while analyses indicate that the genus *Eriphia* is monophyletic, the family is not. In all analyses of molecular data, *Eriphides hispida* is recovered as sister to *Eupilumnus laciniatus*. As only a single species representing the family is included in our larval data set, it is unclear whether larval morphology supports these findings or further confounds the relationships of the group. Although the association between *Eriphides* and *Eriphia* has never been questioned given their shared adult morphology, these results suggest that morphological similarities uniting these taxa (e.g. completely closed orbital margin, antenna positioned away from orbit and antennule, major chela with molariform tooth and others; see Koh & Ng 2000; Ng *et al.* 2008: 62) are the result of convergence.

As in the case of *Ozius*, molecular analyses suggest congruence between geography and phylogeny in *Eriphia*. A well-supported American clade (1.00/100/100) comprising *Eriphia gonagra*, *Eriphia squamata* and *Eriphia granulosa* is sister to *Eriphia verrucosa*, a species known from the Mediterranean Sea and East Atlantic. Positioned as sister to this Atlantic and eastern Pacific clade is *Eriphia scabricula* from the western Indian Ocean and Red Sea, but this relationship is not supported. In addition, analyses recovered a well-supported clade (1.00/99/86) comprised of species from the Indian and Indo-West Pacific Oceans (*Eriphia sebana*, *Eriphia smithii* and *Eriphia ferox*). The relationship between geography and phylogeny, suggested by these analyses, warrants a thorough study of these taxa across their known ranges to better understand the suspected historical and contemporary factors that have led to present-day distributions.

Previously recognised as part of Menippidae (as Menippinae) by Ng *et al.* (2001) and Davie (2002), the family Hypothalassiidae was erected by Karasawa & Schweitzer (2006) (in their superfamily Xanthoidea) to accommodate *Hypothalassia* based on differences in the frontal margin and upper orbital fissures. Ng *et al.* (2008) provided additional evidence to separate *Hypothalassia* from Menippidae (see also Koh & Ng 2000) and recognised Hypothalassiidae as part of Eriphioidea. In the present study, the family is represented by a single species, *H. armata*, in both data sets, and although our analyses support recognising Hypothalassiidae, they do not suggest a clear affinity with other Eriphioidea families. Instead, *Hypothalassia* is positioned in a 'mixed' clade along with *Eupilumnus laciniatus* and *Eriphides hispida*, although this arrangement is not supported statistically. Regardless, additional investigations into the affinities of *Hypothalassia* are warranted, particularly its relationship to *Eupilumnus*.

Although recent summaries have treated Platyxanthidae as an eriphioid lineage (Karasawa & Schweitzer 2006; Ng *et al.* 2008; Thoma *et al.* 2012), Guinot (1979) suggested that it might be more closely related to the Xanthidae s. s. The present study, which includes four representatives of the family, suggests that Platyxanthidae is closely associated with the Xanthoidea and that the family is not monophyletic. While the results presented here should be treated with caution as the clade is unstable and has no statistical support, they do support findings of previous studies that examined the morphology of the group (Guinot 1968; Thoma *et al.* 2012). In particular, Thoma *et al.* (2012) provided a suite of adult characters that support splitting *Platyxanthus* into three genera (*Platyxanthus*, *Danielethus* Thoma, Ng & Felder, 2012, and *Otmaroxanthus* Števčić, 2011) and suggested that differences in gonopod morphology (among other characters) may indicate that *Otmaroxanthus* represents a lineage distinct from the other platyxanthids.

In the summary provided by Števčić (2005), Ladomedaeidae, Pilumnoididae and Carpiliidae were considered to be part of the Eriphioidea. Later, Manuel-Santos & Ng (2007) synonymised Ladomedaeidae with the Euxanthinae (Xanthidae) and Ng *et al.* (2008) recognised Pilumnoididae and Carpiliidae in the superfamilies Pseudozioidea and Carpilioidea, respectively, on the basis of adult morphology. In addition, present analyses support recognition of Carpiliidae as a lineage distinct from eriphioids with *Carpilius convexus* and *Carpilius maculatus* (the type species of the genus) recovered in a well-supported clade (1.00/100/100) as the sister to *Euryozius camachoi* and well separated from other eriphioids (see also Wetzer *et al.* 2003). The relationship between *E. camachoi* and *Carpilius*, as well as that between *Pseudozius caystrus* and *Eriphia*, suggests that Pseudoziidae is polyphyletic as presently defined. In particular, the affinities of *Euryozius* to Pseudoziidae s. s. require re-examination as adult morphology does not support a close affiliation between *Carpilius* and *Euryozius* (Ng & Liao 2002). In addition, the molecular data do not suggest an affiliation between *Euryozius* and Pseudoziidae s. s. as was indicated by Ng *et al.* (2008).

Aside from the in-group families of Eriphioidea, the present analyses further confirm the paraphyly of the Xanthidae (Thoma *et al.* 2009; Lai *et al.* 2011). Lai *et al.* (2011) provided evidence that Euxanthinae is not monophyletic and that *Ladomedaeus* Števčić 2005 is only distantly related to Euxanthinae s. s. While the present analyses clearly indicate that *Ladomedaeus serratus* is affiliated with Xanthoidea and not part of Eriphioidea, it provides no insights into the potential affinities of the genus to Euxanthinae; they also do not clarify status of Ladomedaeidae, with *L. serratus* being recovered as sister to a clade comprised of *Panopeus herbstii* (Panopeidae) and *Xantho pilipes* (type genus of Xanthidae).

© 2013 The Norwegian Academy of Science and Letters, **43**, 1, January 2014, pp 52–64

The monophyly of Pilumnidae is supported and the family appears to be sister to *Carcinoplax longimana* (Goneplacidae).

Conclusions

Present analyses indicate that Eriphioidea is not monophyletic. Eriphioid families represented by two or more taxa were shown to be not monophyletic in both molecular and larval analyses. This study suggests that the present classification of the group, based upon adult morphology, reflects similarity due to convergence in feeding or other behaviour related to cheliped morphology or symplesiomorphies in sterno-abdominal cavity features, gonopods and other features. Adult morphology alone does not appear to resolve the phylogenetic relationships of the group as the 'xanthoid' shape appears to be a recurrent habitus among brachyurans and assumptions of phylogenetic proximity based on similarities in carapace shape alone can be misleading (e.g. see Ng & Clark 2000; Castro *et al.* 2004; Lai *et al.* 2011). The present study further confirms the need for studies that combine all available data (larval and adult morphology, molecular, ecological and geographical). This approach has already been productive in similar studies of Xanthidae (Lai *et al.* 2011), where molecular and larval data sets compelled morphologists to re-examine the adult characters used in delineating taxa. This resulted in a number of new character suites being uncovered, which allowed many of the groups to be redefined to better reflect natural groupings (e.g. Mendoza & Guinot 2011; Mendoza & Manuel-Santos 2012). Although recent systematic reviews have increased subdivision within the taxa formerly attributed to the superfamily Xanthoidea (Guinot 1978; Serène 1984; Martin & Davis 2001; Davie 2002; Števčić 2005; Karasawa & Schweitzer 2006; Ng *et al.* 2008), the present study suggests that many taxa warrant further division. Lastly, a correlation between geography and phylogeny was suggested in several groups (e.g. Oziidae s. s., *Eriphia*), which indicates that careful study of these taxa across their known ranges is warranted.

Acknowledgements

Exchange of researchers between the Muséum national d'Histoire naturelle, Paris (MNHN), National University of Singapore, National Museum of Natural History (Smithsonian Institution), Washington, D.C., The Natural History Museum, London (NHM) and University of Louisiana at Lafayette was supported by a European Distributed Institute of Taxonomy (EDIT) Integrating Research Grant, and we are grateful to the Invertebrate Zoology Department staff of the Museum Support Center, Smithsonian Institution, for facilitating our visit in January 2011. Joelle Lai thanks Jacqueline Mackenzie-Dodds of the Wolfson Wellcome Biomedical Laboratories, Julia Llewellyn-Hughes of the sequencing facility, and Peter Foster of the Molecular Biology Computing Facility at the Department of Zoology (NHM) for their support and help during her visit in January 2010. For fieldwork and analyses of zoeal data, Paul Clark acknowledges support from Smithsonian Short Term Visitor Grant to the Smithsonian Marine Station at Link Port, Fort Pierce Florida (via Ray Manning); European research project INCO-DC no. IC18-CT96-0127 (via José Paula); Conservation Fund of NUS and Nanyang Technological University, Singapore; Research Fellowship from NUS (via Peter Ng); two Visiting Scientist grants from MNHN (via Alain Crosnier); British Airways for logistical support; Zoology Research Fund, Zoology Department (NHM); and Enhancement Grant (NHM). Darryl Felder acknowledges support from U.S. National Science Foundation grants NSF/BS&I DEB-0315995, NSF/AToL EF-0531603 and NSF/RAPID DEB 1045690. Additional funding for fieldwork was obtained under various expeditions, notably PANGLAO 2004, 2005 and AURORA 2007 (via Philippe Bouchet, funded and supported by various sources including MNHN, University of San Carlos [Cebu], Philippine Department of Agriculture's Bureau of Fisheries and Aquatic Resources, National Museum of the Philippines, National Taiwan Ocean University, NUS and TOTAL Foundation). Participation of Brent Thoma was partially supported under a Louisiana Board of Regents doctoral fellowship. This is contribution number 163 of the UL-Lafayette Laboratory for Crustacean Research.

References

Alcock, A. (1898). Materials for a carcinological fauna of India. No. 3. The Brachyura Cyclometopa. Part I. The family Xanthidae. *Journal of the Asiatic Society of Bengal*, *67*, 67–233.

Australian Department of Primary Industries, Parks, Water and Environment (2013, March). Available via http://www.dpiw.tas.gov.au/inter/nsf/WebPages/SCAN-6Q48RF?open.

Balss, H. (1932). Über einige systematisch interessante Xanthidae (Crustacea, Decapoda, Brachyura) der Harmsschen Reisen nach dem Sundaarchipel. *Zeitschrift für Wissenschaftliche Zoologie*, *142*, 510–519.

Balss, H. (1933). Über zwei interessante Xanthidae (Crustacea Dekapoda) des Naturhistorischen Museums in Wien. *Annalen des Naturhistorischen Museums in Wien*, *46*, 297–301.

Balss, H. (1957). Decapoda. In H. G. Bronns (Ed.) *Klassen und Ordnungen des Tierreichs. Fünfter Band 5*, *Abteilung 1*, *Buch* 7 (pp. 1505–1672). Leipzig: Akademische Verlagsgesellschaft.

Borradaile, L. A. (1907). On the classification of the decapod crustaceans. *Annals and Magazine of Natural History*, *Series*, 7, 457–486.

Bremer, K. (1988). The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. *Evolution*, *42*, 795–803.

Carsen, A. E., Kleinman, S. & Scelzo, M. A. (1996). Fecundity and relative growth of the crab *Platyxanthus patagonicus* (Brachyura: Platyxanthidae) in Patagonia, Argentina. *Journal of Crustacean Biology*, *16*, 748–753.

Castresana, J. (2000). Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Molecular Biology and Evolution*, *17*, 540–552.

Castro, P., Ng, P. K. L. & Ahyong, S. T. (2004). Phylogeny and systematics of the Trapeziidae Miers, 1886 (Crustacea: Brachyura), with the description of a new family. *Zootaxa*, *643*, 1–70.

Clark, P. F. (2001). Interpreting patterns in chaetotaxy and segmentation associated with abbreviated brachyuran zoeal development. *Invertebrate Reproduction and Development* [2000], *38*, 171–181.

Clark, P. F. (2005). The evolutionary significance of heterochrony in the abbreviated zoeal development of pilumnine crabs (Crustacea: Brachyura: Xanthoidea). *Zoological Journal of the Linnean Society*, *143*, 417–446.

Clark, P. F. (2009). The bearing of larval morphology on brachyuran phylogeny. In J. W. Martin, K. A. Crandall & D. L. Felder (Eds) *Decapod Crustacean Phylogenetics* (pp. 221–241). Boca Raton, London, New York: CRC Press, Taylor & Francis Group.

Clark, P. F. & Guerao, G. (2008). A description of *Calocarcinus africanus* Calman, 1909 (Brachyura, Xanthoidea) first zoeal stage morphology with implications for Trapeziidae systematics. *Proceedings of the Biological Society of Washington*, *121*, 475–500.

Clark, P. F. & Paula, J. (2003). Descriptions of ten xanthoidean (Crustacea: Decapoda: Brachyura) first stage zoeae from Inhaca Island, Mozambique. *Raffles Bulletin of Zoology*, *51*, 323–378.

Dai, A.-Y. & Yang, S.-L. (1991). *Crabs of the China Seas*. Berlin: Springer-Verlag.

Dana, J. D. (1851). On the classification of the Cancroidea. Scientific Intelligence, III. Zoology. *American Journal of Science and Arts Second Series*, *12*, 121–131.

Davie, P. J. F. (2002). Crustacea: Malacostraca: Eucarida (Part 2): Decapoda - Anomura, Brachyura. *Zoological Catalogue of Australia*, *19*, xiv+636.

Dineen, J. F., Clark, P. F., Hines, A. H., Reed, S. A. & Walton, H. P. (2001). Life history, larval description, and natural history of *Charybdis hellerii* (Decapoda, Brachyura, Portunidae), an invasive crab in the western Atlantic. *Journal of Crustacean Biology*, *21*, 774–805.

Farris, J. S., Albert, V. A., Källersjö, M., Lipscomb, D. & Kluge, A. G. (1996). Parsimony jackknifing outperforms neighbour-joining. *Cladistics*, *12*, 99–124.

Florida Fish and Wildlife Conservation Commission (March 2013). Available via http://myfwc.com/research/saltwater/crustaceans-marine-arthropods/stone-crabs/.

Gardner, C. & Quintana, R. (1998). Larval development of the Australian giant crab *Pseudocarcinus gigas* (Lamarck, 1818) (Decapoda: Oziidae) reared in the laboratory. *Journal of Plankton Research*, *20*, 1169–1188.

Guinot, D. (1967). Recherches préliminaires sur les groupements naturels chez les Crustacés Décapodes Brachyoures. III. A propos des affinités des genres Dairoides Stebbing et Daira De Haan. *Bulletin du Muséum national d'Histoire naturelle*, *Paris*, *2e série*, *39*, 540–563.

Guinot, D. (1968). Recherches préliminaires sur les groupements naturels chez les Crustacés Décapodes Brachyoures. IV. Observations sur quelques genres de Xanthidae. *Bulletin du Muséum national d'Histoire naturelle*, *Paris*, (1967), *39*, 695–727.

Guinot, D. (1978). Principes d'une classification évolutive des Crustacés Décapodes Brachyoures. *Bulletin Biologique de la France et de la Belgique*, *Paris*, *112*, 211–292.

Guinot, D. (1979). Données nouvelles sur la morphologie, la phylogenèse et la taxonomie des Crustacés Décapodes Brachyoures. *Mémoires du Muséum national d'Histoire naturelle*, *Paris*, *(A) Zoologie*, *112*, 1–354.

Guinot-Dumortier, D. (1959) Les espéces indo–pacifiques du genre *Globopilumnus* (Crustacea Brachyura Xanthidae). *Mémoires de l'Institut scientifique de Madagascar (F)*, *3*, 97–118.

Hasegawa, M., Kishino, H. & Yano, T. (1985). Dating of the human-ape splitting by a molecular clock of mitochondrial DNA. *Journal of Molecular Evolution*, *22*, 160–174.

Karasawa, H. & Schweitzer, C. (2006). A new classification of the Xanthoidea *sensu lato* (Crustacea: Decapoda: Brachyura) based on phylogenetic analysis and traditional systematics and evaluation of all fossil Xanthoidea *sensu lato*. *Contributions to Zoology*, *75*, 23–73.

Katoh, K. & Toh, H. (2008). Recent developments in the MAFFT multiple sequence alignment program. *Briefings in Bioinformatics*, *9*, 286–298.

Katoh, K., Misawa, K., Kuma, K. & Miyata, T. (2002). MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Research*, *30*, 3059–3066.

Koh, S. K. & Ng, P. K. L. (2000). A revision of the shore crabs of the genus *Hypothalassia* Gistel, 1848 (Crustacea: Decapoda: Brachyura: Eriphiidae). *Raffles Bulletin of Zoology*, *48*, 123–141.

Koh, S. K. & Ng, P. K. L. (2008). A revision of the shore crabs of the genus *Eriphia* Latreille, 1817 (Crustacea: Decapoda: Brachyura: Eriphiiidae). *Raffles Bulletin of Zoology*, *56*, 327–355.

Lai, J. C. Y., Mendoza, J. C., Guinot, D., Clark, P. F. & Ng, P K. L. (2011). Xanthidae MacLeay, 1838 (Decapoda: Brachyura: Xanthoidea) systematics: a multi-gene approach with support from adult and zoeal morphology. *Zoologischer Anzeiger*, *250*, 407–448.

MacLeay, W. S. (1838). On the Brachyurous Decapod Crustacea. Brought from the Cape by Dr. Smith. Illustrations of the Zoology of South Africa; consisting chiefly of figures and descriptions of the objects of natural history collected during an expedition into the interior of South Africa, in the years 1834, 1835, and 1836; fitted out by "The Cape of Good Hope Association for Exploring Central Africa." together with a summary of African Zoology, and an inquiry into the geographical ranges of species in that quarter of the globe, Published under the Authority of the Lords Commissioners of Her Majesty's Treasury, Invertebratae. A. Smith. London, Smith, Elder and Co.: [1849] IV: 53–71, pls 2, 3. [For dates of publication see Waterhouse 1880: 489–491].

Maddison, D. R. & Maddison, W. P. (2000). '*MacClade. Analysis of Phylogeny and Character Evolution. Version 4.0*.' Sunderland, Massachusetts: Sinauer Associates.

Manuel-Santos, M. R. & Ng, P. K. L. (2007). On the genus *Ladomedaeus* Števčić, 2005, from the Philippines and Japan, and the status of the Ladomedaeidae Števčić, 2005 (Decapoda: Brachyura: Xanthoidea). *Raffles Bulletin of Zoology*, Suppl 16, 177–185.

Martin, J. W. (1984). Notes and bibliography on the larvae of xanthid crabs, with a key to the known xanthid zoeae of the western Atlantic and Gulf of Mexico. *Bulletin of Marine Science*, *34*, 220–239.

Martin, J. W. (1988). Phylogenetic significance of the brachyuran megalopa: evidence from the Xanthidae. *Symposia of the Zoological Society of London*, *59*, 69–102.

Martin, J. W. & Davis, G. E. (2001). An updated classification of the Recent Crustacea. *Natural History Museum of Los Angeles County, Science Series*, *39*, 1–124.

Mendoza, J. C. E. & Guinot, D. (2011). Revision of the genus *Glyptoxanthus* A. Milne-Edwards, 1879, and establishment of Glyptoxanthinae nov. subfam. (Crustacea: Decapoda: Brachyura: Xanthidae). *Zootaxa*, *3015*, 29–51.

Mendoza, J. C. E. & Manuel-Santos, M. R. (2012). Revision of *Garthiella* Titgen, 1986 (Crustacea: Decapoda: Brachyura: Xanthidae), with description of a new subfamily and a new species from the central Philippines. *Zootaxa*, *3446*, 32–48.

Miller, M. A., Pfeiffer, W. & Schwartz, T. (2010). Creating the CIPRES Science Gateway for inference of large phylogenetic trees. *Proceedings of the Gateway Computing Environments Workshop (GCE) New Orleans, LA*. pp. 1–8.

Milne Edwards, H. (1834). *Histoire naturelle des Crustacés, comprenant l'anatomie, la physiologie et la classification de ces animaux*. Paris: Roret.

Narvarte, M., González, R., Osovnikar, P., Camarero, M., Curtolo, L. & Reinaldo, M.O. (2007). Experimental trap fishery for the crabs *Platyxanthus patagonicus* and *Ovalipes trimaculatus* in the San Matías Gulf, Patagonia, Argentina. *Journal of the Marine Biological Association of the UK*, *87*, 1235–1242.

Ng, P. K. L. (1992). The Indo-Pacific Pilumnidae VIII. Pilumnus laciniatus Sakai, 1980 a senior synonym of Globopilumnus multituberosus Garth & Kim, 1983 (Crustacea: Decapoda: Brachyura). *Crustaceana*, *63*, 221–222.

Ng, P. K. L. (1998). Crabs. In K. E., Carpenter & V. H. Niem (Eds) *FAO species identification guide for fishery purposes. The living marine resources of the Western Central Pacific. Volume 2. Cephalopods, crustaceans, holothurians and sharks*. (pp. 1045–1155). Rome: FAO.

Ng, P. K. L. & Clark, P. F. (2000). The Indo–Pacific Pilumnidae XII. On the familial placement of Chlorodiella bidentata (Nobili, 1901) and Tanaocheles stenochilus Kropp, 1984 using adult and larval characters with the establishment of a new subfamily, Tanaochelinae (Crustacea: Decapoda: Brachyura). *Journal of Natural History*, *34*, 207–245.

Ng, P. K. L. & Liao, L. (2002). On a new species of *Euryozius* Miers, 1886 (Crustacea: Decapoda: Brachyura: Pseudoziidae) from the Philippines, with notes on the taxonomy of the genus. *Proceedings of the Biological Society of Washington*, *115*, 585–593.

Ng, P. K. L. & Rodríguez, G. (1986). New records of *Mimilambrus wileyi* Williams, 1979 (Crustacea: Decapoda: Brachyura), with notes on the systematics of the Mimilambridae Williams, 1979 and Parthenopoidea MacLeay, 1838 *sensu* Guinot, 1978. *Proceedings of the Biological Society of Washington*, *99*, 88–99.

Ng, P. K. L. & Tan, L. W. H. (1984). The 'shell peeling' structure of the box crab *Calappa philargius* (L.) and other crabs in relation to mollusc shell architecture. *Journal of the Singapore National Academy of Science*, *13*, 195–199.

Ng, P. K. L. & Tan, L. W. H. (1985). Right Handedness' in heterochelous calappoid and xanthoid crabs – suggestion for a functional advantage. *Crustaceana*, *49*, 98–100.

Ng, P. K. L., Wang, C.-H., Ho, P.-H. & Shih, H.-T. (2001). An annotated checklist of brachyuran crabs from Taiwan (Crustacea: Decapoda). *National Taiwan Museum Special Publication Series*, *11*, Iv+86.

Ng, P. K. L., Guinot, D. & Davie, P. (2008). Systema Brachyurorum: Part I. An annotated checklist of extant brachyuran crabs of the world. *Raffles Bulletin of Zoology*, *17*, 1–286.

Nylander, J. A. A. (2004). *MrModeltest v2. Program Distributed by the Author*. Evolutionary Biology Centre: Uppsala University.

Ortmann, A. (1893). Die Decapoden-Krebse des Strassburger Museums. VII. Theil. Abtheilung: Brachyura (Brachyura genuina Boas) II. Unterabtheilung: Cancroidea, 2. Section: Cancrinea, 1. Gruppe: Clyclometopa. *Zoologische Jahrbücher. Jena. Abteilung für Systematik*, *7*, 411–495.

Rodríguez, F., Oliver, J. L., Marín, A. & Medina, J. R. (1990). The general stochastic model of nucleotide substitution. *Journal of Theoretical Biology*, *142*, 485–501.

Ronquist, F. & Huelsenbeck, J. P. (2003). MrBayes version 3.0: Bayesian phylogenetic inference under mixed models. *Bioinformatics*, *19*, 1572–1574.

Saba, M., Takeda, M. & Nakasone, Y. (1978). Larval development of *Epixanthus dentatus* (White, 1847). *Bulletin of the National Science Museum, Tokyo Series A (Zoology)*, *4*, 151–161.

Sakai, T. (1976). *Crabs of Japan and the Adjacent Seas*. Tokyo: Kodansha Ltd.

Serène, R. (1984). Crustacés Décapodes Brachyoures de l'Océan Indien occidental et de la Mer Rouge, Xanthoidea: Xanthidae et Trapeziidae. Avec un addendum par Crosnier, A.: Carpilliidae et Menippidae. *Faune Tropicale*, *24*, 1–400.

Sorenson, M. D. & Franzosa, E. A. (2007). *TreeRot, version 3*. Boston, MA: Boston University.

Stamatakis, A. (2006). RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics*, *22*, 2688–2690.

Stamatakis, A., Hoover, P. & Rougemont, J. (2008). A rapid bootstrap algorithm for the RaxML web servers. *Systematic Biology*, *57*, 758–771.

Števčić, Z. (2005). The reclassification of brachyuran crabs (Crustacea: Decapoda: Brachyura). *Natura Croatica*, *1*, 1–159.

Swofford, D. L. (2002). '*PAUP*. Phylogenetic Analysis Using Parsimony (* and Other Methods)*. Version 4.0b10. Sunderland, Massachusetts, USA: Sinauer Associates.

Tavaré, S. (1986). Some probabilistic and statistical problems in the analysis of DNA sequences. *Some Mathematical Questions in Biology—DNA Sequence Analysis*, *17*, 57–86.

Thoma, B. P., Schubart, C. D. & Felder, D. L. (2009). Molecular phylogeny of western Atlantic representatives of the genus *Hexapanopeus* (Decapoda: Brachyura: Panopeidae). In J. W. Martin, K. A. Crandall & D. L. Felder (Eds) *Decapod Crustacean Phylogenetics* (pp. 551–565). Boca Raton, London, New York: CRC Press, Taylor & Francis Group.

Thoma, B. P., Ng, P. K. L. & Felder, D. L. (2012). Review of the family Platyxanthidae Guinot, 1977 (Crustacea, Decapoda, Brachyura, Eriphioidea), with the description of a new genus and a key to genera and species. *Zootaxa*, *3498*, 1–23.

Vaidya, G., Lohman, D. J. & Meier, R. (2011). SequenceMatrix: concatenation software for the fast assembly of multi-gene datasets with character set and codon information. *Cladistics*, *27*, 171–180.

Wear, R. G. (1968). Life–history studies on New Zealand Brachyura 2. Family Xanthidae. Larvae of Heterozius rotundifrons A. Milne Edwards, 1867, Ozius truncatus H. Milne Edwards, 1834 and

Heteropanope (Pilumnopeus) serratifrons (Kinahan, 1856). *New Zealand Journal of Marine and Freshwater Research*, *2*, 293–332.

Wear, R. G. & Fielder, D. R. (1985). The marine fauna of New Zealand: Larvae of the Brachyura (Crustacea, Decapoda). *New Zealand Oceanographic Institute Memoir*, *92*, 1–90.

Wetzer, R., Martin, J. W. & Trautwein, S. E. (2003). Phylogenetic relationships within the coral crab genus *Carpilius* (Brachyura, Xanthoidea, Carpiliidae) and of the Carpiliidae to other xanthoid crab families based on molecular sequence data. *Molecular Phylogenetics and Evolution*, *27*, 410–421.

Xia, X. & Xie, Z. (2001). DAMBE: data analysis in molecular biology and evolution. *Journal of Heredity*, *92*, 371–373.

Xia, X., Xie, Z., Salemi, M., Chen, L. & Wang, Y. (2003). An index of substitution saturation and its application. *Molecular Phylogenetics and Evolution*, *26*, 1–7.

Zharkikh, A. (1994). Estimation of evolutionary distances between nucleotide sequences. *Journal of Molecular Evolution*, *39*, 315–329.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Parental females of larvae used for morphological analysis of first stage zoea.

Fig. S1. Telson: lateral & medial spines; a. *Quadrella maculosa* Alcock, 1898; b. *Tanaocheles bidentata* (Nobili, 1901); c. *Rhinolambrus pelagicus* (Rüppell, 1830); d. *Ozius truncatus* H. Milne Edwards, 1834; e. *Hexapanopeus paulensis* Rathbun, 1930.

Table S1. List of species used in DNA analysis with locality data and Genbank accession numbers.

Table S2. Primers used in this study.

Table S3. Data matrix for 'eriphiid' first stage zoea analysis, comprising 14 taxa and 20 characters.