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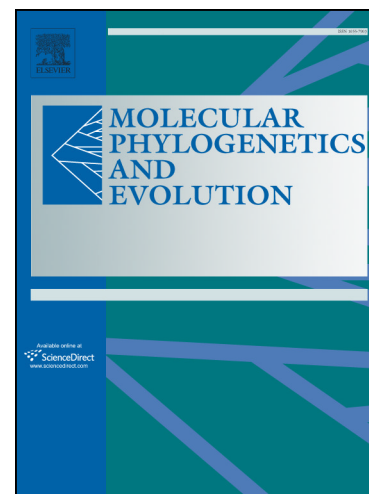
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Systematic analysis of the caridean shrimp superfamily Pandaloidea (Crustacea: Decapoda) based on molecular and morphological evidence

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Graphical Abstract

See attachment.

Abstract

One of the systematically controversial superfamilies in Caridea is the predominately deep-sea or cold water Pandaloidae, largely because this species-rich group of nearly 200 species in 25 genera exhibits a very high diversity of body forms and ecology. Although the relationships amongst the taxa within Pandaloidae have been repeatedly discussed based on morphology, no comprehensive molecular phylogeny exists. In this study, we present the first molecular phylogeny of the group, based on a combined dataset of two mitochondrial (12S and 16S rRNA) and six nuclear (ATP synthase β -subunit, enolase, glyceraldehyde-3-phosphate dehydrogenase, histone 3, phosphoenolpyruvate carboxykinase and sodium–potassium ATPase α -subunit) markers, based on 62 species (about 1/3 of known biodiversity) in 22 genera (88% of genera) of two pandaloid families (Pandalidae, Thalassocarididae) and outgroups from seven other caridean families. With generally high support, the relationships within the clade are fully resolved. Pandalidae is shown to be paraphyletic with Thalassocarididae deeply nested within as a monophyletic group, and the latter is herein considered to be a synonym of Pandalidae. Five major clades are recovered, with the shallow water genera *Anachlorocurtis*, *Chlorocurtis*, *Chlorotocella* and *Miopandalus* forming a sister clade to the remaining genera. At the genus level, the phylogeny indicates *Plesionika*, *Heterocarpus* and *Pandalus* to be not monophyletic. The validity of *Pandalopsis*, *Stylopandalus* and *Calipandalus* is challenged and these genera are considered herein to be junior synonyms of *Pandalus* (*Pandalopsis*) and *Plesionika* (*Stylopandalus* and *Calipandalus*). Although not fully resolved, some evidence potentially considers *Nothocaris* to be a valid genus. Ancestral State Reconstruction successfully recovered 15 synapomorphies for the major clades, with 11 of them reported to be of systematic significance for the first time.

Keywords: Caridea; Pandaloidae; Pandalidae; Thalassocarididae; Phylogeny; Ancestral State Reconstruction

1. Introduction

Amongst the species-rich caridean shrimps (Infraorder Caridea, > 3500 species; De Grave & Fransen, 2011), the family Pandalidae is of major economic importance (Holthuis, 1980; Wicksten, 2010). Northern Shrimp (*Pandalus borealis*) and other pandalids (e.g. *Heterocarpus reedi*) account for over 48% of worldwide shrimp capture fisheries (FAO, 2014). The family also displays a very high morphological and ecological (although primarily in deeper or colder waters) disparity. Together with the species-poor Thalassocarididae, Pandalidae comprises the superfamily Pandaloidea, which is the fifth most species-rich superfamily within Caridea, consisting of about 200 species, distributed across 25 genera (De Grave & Fransen, 2011). Morphologically, pandaloid shrimps are characterized by a non-chelate or microscopically chelate first pereopod, the carpus of the second pereopod generally being subdivided, and the presence of a rather simple endopod on the male first pleopod (Holthuis, 1993). Pandaloid shrimps are also highly diverse in their biology and life-style, such as protandrous hermaphrodites in *Pandalus* and *Pandalopsis* (Butler, 1980; Komai, 1999; Bergstrom, 2000), bioluminescence in *Stylopandalus* and *Heterocarpus* (Herring, 1985), and in forming symbiotic relationships with other invertebrates (Hayashi, 1975, Bruce, 1983, Chan & Crosnier, 1991; Horká et al., 2014).

Despite their economic importance and varied ecology, many controversies remain in the higher level systematics of Pandaloidea. In an earlier classification, Holthuis (1955) grouped three families (Pandalidae, Thalassocarididae, Physetocarididae) into the superfamily Pandaloidea. Thompson (1967), while supporting Holthuis's concept, elevated the genus *Heterocarpus* to the family Heterocarpodidae in a separate superfamily Heterocarpodoidea with two further non-pandaloid families. Bowman & Abele (1982) separated Physetocarididae (but without any argumentation) into its own superfamily Physetocaridoidea, followed in that by Chace (1992) and Holthuis (1993). In contrast, in the morphological cladistic analysis of Christoffersen (1989), a superfamily Pandaloidea was recognized and considered to be comprised of seven families: Pandalidae, Plesionikidae, Dorodoteidae, Heterocarpidae (recte Heterocarpodidae Thompson), Heterocarpoididae, Physetocarididae and Thalassocarididae. Notably, some genera were transferred to the previously monotypic Physetocarididae. This classification is generally not adopted in recent classification schemes (see discussion in Holthuis, 1993). Equally, in an unpublished, morpho-cladistic study by Komai (1994a), no support was found for Christoffersen's classification and largely the more traditional scheme of Chace (1992) and Holthuis (1993) was recovered, although with notable problems in the classification of

subordinate taxa.

Within Pandalidae itself, systematic controversies abound in the species-rich *Plesionika*, as well as the economically important *Pandalus*. *Plesionika* currently has 93 species (Chan, 2016; Chan et al., 2018), with several species groups proposed within the genus (Chan & Crosnier, 1991, 1997; Chan, 2016; Chan et al., 2018), although their true phylogenetic status remains unknown. Far from settled is also the validity of *Parapandalus* (see Chace, 1985; Holthuis, 1993) and *Nothocaris* (see Burukovsky, 1981; Chace, 1985; Chan, 2004), both currently considered as synonyms of *Plesionika*; as well as the relationship of the “*Plesionika laevis*” species group to the genus *Heterocarpus* (see Chan & Crosnier, 1997; Yang et al., 2010). For *Pandalus*, uncertainty has been highlighted as to its systematic relationship with *Pandalopsis*, with the possibility repeatedly raised that both taxa are synonyms (Komai, 1994a, 1995, 1999; Bergstromm 2000).

While morphological studies rarely reach consensus, molecular tools have so far only been used to address species status of selected taxa or for within-genus phylogenies (Zuccoa et al., 2012; Matzen da Silva et al., 2013). Some previous studies (e.g. Tsang et al., 2008; Bracken et al., 2009; Li et al., 2011; Aznar-Cormano et al., 2015) did include pandaloids, none resolved intra-familial issues due to limited taxon sampling (less than ten species across all studies).

In this study, using a comprehensive molecular dataset of two mitochondrial (12S rDNA, 16S rDNA) and six nuclear protein-coding markers (histone 3 (H3), sodium–potassium ATPase α -subunit (NaK), enolase, phosphoenolpyruvate carboxykinase (PEPCK), ATP synthase β -subunit (*atp β*), glyceraldehyde 3-phosphate dehydrogenase (GAPDH)) from 60 species belonging to 20 pandalid genera, one species each from the two thalassocaridid genera and 11 species from seven other caridean families, we endeavor to (1) examine the monophyly of the superfamily Pandaloidea as currently perceived (*sensu* De Grave & Fransen, 2011); (2) test the reciprocal monophyly of the families Pandalidae and Thalassocarididae, and (3) disentangle the phylogenetic relationships among pandalid genera. In addition, ancestral state reconstruction of morphological characters was conducted to recover synapomorphies in Pandaloidea to aid in the interpretation of morphological evolution in these shrimps.

2. Materials and Methods

2.1. Taxon sampling

From the nearly 200 species currently described in the family Pandalidae (De Grave & Fransen, 2011), 60 species from 20 out of a total of 23 genera were included in the present study (Table 1). Three genera, *Austropandalus*, *Chelonika* and *Peripandalus*, could not be included due to a lack of samples or unsuccessful PCR amplification of decade old museum specimens. Twenty six *Plesionika* species were included, across many species groups, but particularly from the two previous synonymized genera *Nothocaris* and *Parapandalus* as well as the “*P. laevis*” group (Table 1). Additionally, one species each from the two genera of the family Thalassocarididae were also included (Table 1). The potentially allied, extremely rare monotypic family, Physetocarididae, could not be included due to lack of DNA workable samples. To examine the systematic status of Pandaloidea, we included 11 species from seven relatively closely related caridean families, based on Bracken et al. (2009), Li et al. (2011) and Aznar-Cormano et al. (2015) for which there were sequences available from at least four of the eight target markers, either from GenBank (most from previous studies by our team; Li et al., 2011; De Grave et al., 2014) or newly sequenced in this study (Table 1). In addition, *Stenopus hispidus* from the Infraorder Stenopodidea was used as a distant outgroup taxon (Table 1). All specimens used for DNA extraction were preserved in 75-95% ethanol.

2.2. DNA extraction, PCR amplification and sequencing

Total genomic DNA extraction from pleopod muscle of shrimp samples (10-15 mg) was conducted using the QIAamp DNA Mini Kit (QIAGEN, Hilden, Germany). Universal primers were utilized to amplify the targeted segments of seven of the gene markers (Table S1), including 12S rDNA (12S-FB/12S-R2, Tsang et al., 2009), 16S rDNA (16S-AR/16S-1472, Crandall and Fitzpatrick, 1996; Simons et al., 1994), H3 (AF/AR, Colgan et al., 1998), NaK (N79/N610, De Grave et al., 2014), enolase (EA2/ES1, Tsang et al., 2011), PEPCK (PA3/PR3, Tsang et al., 2008) and *atpβ* (*atpβ*-F2/*atpβ*-R2, Liao et al., 2017). The GAPDH segment was amplified by nested PCR with 1st round primers 4F/753R and subsequently 2nd round 85F/698R (Table S1); these primer sets were newly designed based on recently available sequences of carideans and other decapods in GenBank. PCR amplifications were conducted in a 50-μL reaction system that contained 1 to 5 μL of template DNA, 1x PCR reaction buffer, 2.5 mM MgCl₂, 200 nM of each primer, 200 μM dNTPs and 1.5 U of *Taq* polymerase (Takara, Japan). The thermal profile was as follows: 3 min at 94°C for initial denaturation, 35 cycles of 30 sec at 94°C, 30 sec at 48°C-55°C (depending on different markers and samples, see Table S1) and 1 min at 72°C, and finally 5 min at 72°C for final extension. After purification using Millipore MultiScreen

96-Well Filter Plates (Millipore, USA), PCR products were sequenced with the same primer sets of amplification on the ABI 3730xl Genetic Analyzer (Applied Biosystems, Foster City, CA, USA) by standard sequencing protocol. The sequencing results were checked and confirmed by eye using SeqTrace (Stucky, 2012).

2.3. *Phylogenetic analyses*

The resulting sequences were checked in NCBI web version of BLASTn (Basic Local Alignment Search Tool, National Center for Biotechnology Information, NCBI) against nt database to detect potential contamination. The nucleotide sequences were aligned and trimmed via MUSCLE program (Edgar, 2004) implemented in MEGA 7.0 (Kumar et al., 2016) with default parameters. Alignments of the six nuclear protein-coding genes were translated into the amino acids sequences to check for insertions/deletions (indels) and stop codons. The concatenated dataset was first partitioned by genes, with six nuclear protein-coding genes further divided into three codon positions (totally 20 partitions). The best partitioning scheme and the best-fit DNA substitution model for each partition were then determined by PartitionFinder v1.1.1 (Lanfear et al., 2012) according to the Bayesian information criteria (BIC; Schwarz, 1978). The final dataset was divided into six partitions with corresponding best-fit models of nucleotide substitution (Table 2). Phylogenetic trees of each individual gene and the concatenated dataset were reconstructed with maximum likelihood (ML) (Felsenstein, 1981) analyses in RAxML v8.2.4 (Stamatakis, 2014) and Bayesian inference (BI) analyses in MrBayes v3.2.6 (Ronquist et al., 2012), with both computations executed on the CIPRES Science Gateway at the San Diego Supercomputer Center (Miller et al., 2010). In ML analyses, the model GTRGAMMAI was utilized for each individual dataset and each partition in the concatenated dataset, with all free parameters estimated by RAxML with 10 independent runs. Confidence values of branches in the resulting trees were evaluated by non-parametric bootstrap estimates (Felsenstein, 1985) with 1,000 pseudoreplicates. In BI analyses, Metropolis-coupled Monte Carlo (MCMC) Markov chains were performed for the partitioned concatenated dataset, using the partitioning scheme and substitution models determined by Partition Finder (Table 2), with all free parameters estimated by MrBayes. Two independent runs, each with four chains, were executed for 10,000,000 generations. Chains sampling were performed every 1000 generations, and the burn-in frequency of trees was set to 10% to ensure that parameters had been stabilized. A 50% majority-rule consensus tree was constructed from the remaining trees to evaluate clade confidence from posterior probabilities estimation. Each

analysis was conducted three times to evaluate the consistency among runs.

Alternative systematic hypotheses were statistically examined in the concatenated dataset via approximately unbiased (AU) test (Shimodaira, 2002) and Shimodaira-Hasegawa (SH) test (Shimodaira and Hasegawa, 1999). The null hypothesis (H_0) was that there was no difference between the constrained and the best trees. Constrained trees were constructed by RAxML with topology constraint. In AU test, the per site log Likelihoods (perSiteLLs) of the trees set were calculated in RAxML and the confidence P-values of H_0 were estimated with default parameters in CONSEL (Shimodaira and Hasegawa, 2001). In the SH test, the comparison between the best tree and alternative trees was conducted in RAxML. Hypotheses tested concern the monophyly of Pandalidae, *Plesionika*, *Heterocarpus*, *Pandalus*, *Anachlorocurtis* and *Nothocaris*.

2.4. Character evolution analyses

Morphological scoring was performed for all sequenced species of Pandaloidea and four outgroup caridean species (*Saron marmoratus*, *Lysmata amboinensis*, *Macrobrachium rosenbergii* and *Ancyllocaris brevicarpalis*), since the inclusion of outgroup taxa did not materially change the majority of phylogenetic relationships within Pandaloidea (Figs. 1, S3). Ancestral State Reconstruction (ASR) was conducted to examine character evolutionary patterns and establish relevant synapomorphies within Pandaloidea. A comprehensive morphological data matrix (Appendices 1, 2) was established with 91 characters scored for 66 taxa (Appendix 2). The characters were selected based on Komai's (1994a) dataset, except autapomorphies restricted to single species. Discrete characters showing intergeneric or interspecific differences were employed, while meristic characters and counts were not included due to the difficulty of categorization. Sixty-nine out of 91 characters were binary, while 20 were three-state and two were four-state, with all states unordered. Inapplicable and missing data were indicated as “-” and “?”, respectively. To trace the evolutionary pattern of all characters, ancestral states were reconstructed using the re-rooting method of Yang et al. (1995) and the equal rate (ER) model in the R package “phytools” (Revell, 2012). Character evolution was examined across the Bayesian phylogenetic tree of the pruned taxon set (constraint to taxa included in morphological examination, Appendix 1) analyzed by MrBayes as outlined above. Marginal ancestral state was estimated for each character in each node along the phylogenetic tree.

3. Results

3.1. Phylogenetic relationships

In total, 74 12S and 16S rDNA sequences, 72 H3 and NaK sequences, 73 enolase sequences, 70 PEPCK sequences, 64 *atpβ* sequences and 69 GAPDH sequences (including outgroups) were analyzed, including 529 new sequences. The sequences were submitted to GenBank and accession numbers are listed in Table 1, while the sequence alignment file can be found in Appendix 5. The combined dataset consisted of 3,846 bp from eight markers. The ML trees of each individual dataset (not shown) were not evidently contradictory with the ML and BI trees of the combined dataset, with the combined dataset trees exhibited better resolving power, especially in higher-level relationships. Furthermore, the final combined ML and BI trees exhibited great similarity in their overall topology, with the BI tree possessing higher statistical support (Figs. 1, S1, S2). The monophyly of the superfamily Pandaloidea *sensu* De Grave & Fransen (2011) was well supported (BP = 92%; PP = 1.0). Within Pandaloidea, the family Pandalidae, as currently defined, resolved to be paraphyletic with the monophyletic family Thalassocarididae (BP = 100%; PP = 1.0) nested within. The AU and SH tests significantly rejected the monophyly of Pandalidae ($P < 0.01$, Table 3). At a generic level, four genera, viz. *Anachlorocurtis*, *Plesionika*, *Heterocarpus* and *Pandalus* were not monophyletic in either analyses (Figs. S1, S2). The AU and SH tests significantly rejected the monophyly of *Plesionika* and *Heterocarpus* ($P < 0.01$, Table 3), but not *Anachlorocurtis* and *Pandalus* ($P > 0.05$, Table 3). On the other hand, AU and SH tests only showed moderate support ($0.01 < P < 0.05$, Table 3) for the monophyly of the currently synonymized genus *Nothocaris* (*sensu* Burukovsky, 1981), nested within *Plesionika*. Five major clades were recovered (Clades A-E, Fig. 1). Clade A comprised *Anachlorocurtis*, *Miopandalus*, *Chlorotocella* and *Chlorocurtis* (BP = 97%; PP = 1.0), being sister to the remaining Pandalidae (incl. Thalassocarididae) (BP = 100%; PP = 1.0), with *Anachlorocurtis* and *Miopandalus* most closely related (BP = 100%; PP = 1.0). Clade B comprised those *Plesionika* species belonging to the “*Nothocaris*” group (i.e. *P. hsuehyui*, *P. izumiae*, *P. lophotes*, *P. rufomaculata*, *P. erythrocyclus* and *P. grahami*) and three other genera, *Pseudopandalus*, *Pantomus* and *Notopandalus* (BP = 100%; PP = 1.0). Within Clade B, *Pantomus* occupied a sister position to the remaining taxa (BP = 82%; PP = 0.99), whilst the subclade of *Plesionika grahami* and *Notopandalus* (BP = 98%; PP = 1.0) and that of *Pseudopandalus* and the other five “*Nothocaris*” species (BP = 70%; PP = 1.0) were reciprocally monophyletic. All “*Nothocaris*” species, except *P. grahami* clustered together (BP = 100%; PP = 1.0). Clade C consisted of five genera, *Pandalina*, *Atlantopandalus*, *Dichelopandalus*, *Pandalus* and *Pandalopsis* (BP = 100%; PP = 1.0), with a

monophyletic *Pandalopsis* (BP = 73%; PP = 1.0) nested within *Pandalus* species (BP = 100%; PP = 1.0). Three out of the four informal species groups in *Pandalus*, namely, the “*P. montagui*”, “*P. hypsinotus*”, and “*P. platyceros*” groups were included in the present analyses (Fig. 1, Table 1). The monophyly of the “*P. montagui*” and “*P. hypsinotus*” groups was well supported (BP = 100%; PP = 1.0). Clade D consisted of the “*Plesionika laevis*” group (Fig. 1, Table 1), two other *Plesionika* species (*P. bifurca*, *P. spinidorsalis*), along with four further genera, *Heterocarpus*, *Proclates*, *Chlorotocus* and *Dorodotes* (BP = 100%; PP = 1.0), with *Dorodotes* in a sister position to the rest. The four species of *Heterocarpus* were separated into different clades. The grouping of the “*Plesionika laevis*” group with *H. abulbus* had moderate support (PP = 0.98), and was sister to a clade comprised of *P. bifurca* and *H. dorsalis* but with weak support (PP = 0.93). *Proclates* and *Chlorotocus* formed a clade (BP = 100%; PP = 1.0), sister to *P. spinidorsalis* (BP = 97%; PP = 1.0), and this larger clade was sister to *H. hayashi* (BP = 92%; PP = 1.0). Clade E consisted of the remaining *Plesionika* species, together with two genera (*Calipandalus*, *Stylopandalus*) nested within (BP = 100%; PP = 1.0). Among the species of *Plesionika* included in this clade, the monophyly of species referred to as *Parapandalus* by Holthuis (1993) was well supported (BP = 97%; PP = 1.0). The remaining pandalid genus, *Bitias* was clustered with *Chlorotocoides* and *Thalassocaris*, both currently placed in the family Thalassocarididae (BP = 100%; PP = 1.0), occupying a sister position to Clade E (BP = 67%; PP = 0.99). The relationships among the five clades were well resolved in both BI and ML analyses (BP > 75%; PP > 0.95), with Clade B closer to Clade C (BP = 77%; PP = 0.97) and Clade D closer to Clade E (incl. *Bitias* and Thalassocarididae; BP = 99%; PP = 1.0).

The monophyly of all other caridean families with more than one species studied was strongly supported in both analyses (BP > 95%; PP = 1.0).

3.2. Character evolution

A Bayesian phylogenetic tree was constructed for the taxa included in the morphological examination (Fig. S3), with the varied inclusion of outgroup taxa (Fig. S3) not conferring materially impact on phylogenetic relationships. From the total data set (Appendix 3; Consistency index = 0.4079, Retention index = 0.7853), 15 unambiguous synapomorphic states (i.e. character state changes consistently inferred from different optimization methods) were inferred for the majority of the major clades in the Bayesian phylogram (Fig. 2). Clade A was exclusively supported by seven unambiguous synapomorphies (characters 2-state 2, 27-1, 30-1, 36-1, 43-1, 48-1, 88-1; Fig. 2), while the sister group consisting of the remaining Pandalidae (Clades B-E) was

also supported by two unambiguous synapomorphies (characters 44-0, 68-1; Fig. 2). The subclade of *Anachlorocurtis* and *Miropandalus* within Clade A was supported by several unambiguous synapomorphies (characters 15-1, 28-1, 31-1, 36-2, 51-1, 52-1, 53-1, 56-1, 83-1; Appendix 3). The monophyly of Clade C was supported by two unambiguous derived characters (characters 49-1&2, 50-1; Fig. 2), whilst the subclade of *Pandalus* and *Pandalopsis* was supported by one unique synapomorphy (character 85-1; Fig. 2). Several synapomorphies (characters 62-2, 80-1, 86-1; Appendix 3) were also revealed within the subclade of *Pandalus* and *Pandalopsis*. The monophyletic status of Clade D and Clade E was supported by one (character 8-1; Fig. 2) and two (characters 6-1&2, 60-1; Fig. 2) unambiguous synapomorphies, respectively.

4. Discussion

In the current phylogenetic analyses of the concatenated dataset with eight markers (i.e., 12S rDNA, 16S rDNA, H3, NaK, enolase, PEPCCK, *atpβ* and GAPDH), the family Pandalidae (*sensu* De Grave & Fransen, 2011) was shown to be paraphyletic with Thalassocarididae nested within and forming a clade with *Bitias*. The remaining pandalid species were separated into five major clades, with the genera *Plesionika*, *Heterocarpus* and *Pandalus* evidently not being monophyletic. Based on the molecular phylogeny and reconstructed ancestral character states, we discuss the systematics of the superfamily Pandaloidea and family Pandalidae below.

4.1. Superfamily Pandaloidea

In earlier caridean classification schemes, three families (Pandalidae, Thalassocarididae, Physetocarididae) jointly comprised the superfamily Pandaloidea (Holthuis, 1955; Thompson, 1967). The very rare and monotypic Physetocarididae was later removed to its own superfamily Physetocaridoidea (Chace, 1992, Holthuis, 1993). This was based on the unique shape of the rostrum and structure of the chela of the second pereopod, as well as the greatly reduced maxilla and second maxilliped. On the other hand, Thompson (1967) considered that the shape and structure of the pereopodal fingers were more important than their presence or absence, and moved the pandalid genus *Heterocarpus* into a separate family Heterocarpodidae and superfamily, but maintained Physetocarididae under Pandaloidea. In contrast, the cladistic analyses of Christoffersen (1989) and Komai (1994a) showed that members of Thalassocarididae and Physetocarididae were nested within Pandalidae *sensu lato*, leading to the latter family to be divided into five or two families by these authors, respectively.

Unfortunately, due to the lack of samples of the extremely rare *Physetocaris*, the systematic placement of the family Physetocarididae could not be examined in this study.

In the present study, the members of Pandaloidea constituted a clear monophyletic group with strong support. The derived character state of the microscopic chela or non-chelate structure at the first pereopod was restricted to the Pandaloidea clade (character 64, Appendix 3), corroborating the current definition of the superfamily Pandaloidea. At a more inclusive level, the thalassocaridid species formed a highly supported subclade nested deeply within Pandalidae and sister to the rare pandalid genus *Bitias* though without identifiable synapomorphies.

The morpho-cladistic analysis of Christoffersen (1989) also suggested that Thalassocarididae is subordinated within Pandalidae. Given the strong support in the present molecular study, the synonymization of Thalassocarididae with Pandalidae is fully justified and herein formally proposed.

4.2. Family Pandalidae

The present molecular phylogeny also revealed several unnatural assemblages in some pandalid genera, namely, *Plesionika*, *Heterocarpus* and *Pandalus*. In addition, the 59 studied pandalid species (excluding *Bitias*) were divided into five major clades as discussed below.

4.2.1. Clade A

Clade A consisted of *Anachlorocurtis*, *Miopandalus*, *Chlorotocella* and *Chlorocurtis*, being sister to all other Pandalidae. The inferred monophyly and phylogenetic relationships within this clade were well resolved and sufficiently corroborated by the ASR, conforming to previous conventional taxonomic characters (Holthuis, 1993) as well as morpho-cladistic analyses (Christoffersen, 1989, Komai, 1994a). The seven synapomorphies identified for this clade (Fig. 2) were: rostrum ventrally unarmed (character 2-2), fifth abdominal pleuron rounded (character 27-1), telson with lateral spiniform setae located marginally (character 30-1), stylocerite with distal margin subtruncate (character 36-1), incisor of mandible tapering to narrow point with 1 or 2 tiny teeth (character 43-1), endopod of maxilla short and rounded (character 48-1), and sixth and seventh thoracic sternites lacking protuberances (character 88-1). These characters, have so far not been considered as of particular important in the higher taxonomy of Pandaloidea, but were herein demonstrated to be of significance.

On the other hand, at least one of the characters used in traditional taxonomy for grouping Clade A (see Holthuis, 1993), e.g. the third maxilliped lacking an exopod (character 61), was shown to be homoplastic (Appendix 3).

In addition to these synapomorphies, members of Clade A share a similar ecological niche, inhabiting shallow waters in tropical-subtropical areas (Bruce, 1983; Horká et al., 2014), in sharp contrast to the other pandalids which abound in deeper and cold-water habitats. On the other hand, two unambiguous synapomorphies: mandibular palp well developed and consisting of three articles (character 44-0) and the basis of the second pereopod with dorsolateral process (character 68-1) were identified for the sister clade consisting of the remaining Pandalidae (incl. Thalassocarididae) (Fig. 2). The cladistic analyses of Christoffersen (1989) and Komai (1994a) both equally resulted in placing these genera outside of Pandalidae *sensu stricto*. Christoffersen (1989) placed *Physetocaris*, all herein Clade A genera and *Stylopandalus* into Physetocarididae. Komai (1994a) recovered all Clade A genera in a similar position to the present analyses and suggested they were deserving distinct familial status. A new family name is herein not erected for these genera, but will form the subject of a separate, more taxonomically orientated study, since both Christoffersen (1989) and Komai (1994a) suggested that *Physetocaris*, which has a bathypelagic mode of life, was closely related to Clade A, but this genus was not included in the present study.

It seems useful to mention that the subclade containing the two small-bodied, highly modified genera, *Anachlorocurtis* and *Miopandalus* yielded the highest number (9) of synapomorphies based on ASR (Appendix 3), with *Miopandalus* embedded within *Anachlorocurtis* in the phylogenetic tree (Fig. 1). Both genera are obligate commensals on antipatharian black corals (Bruce, 1983; Minemizu, 2000; Horká et al., 2014), and are generally very similar in morphology. As support against the monophyly of *Anachlorocurtis* is rather weak (AU and SH test >0.05 , Table 3), the two genera are herein not synonymized, although it is likely that in future they could be.

4.2.2. Clade B

Clade B consisted of species of *Plesionika* belonging to the “*Nothocaris*” group (those *Plesionika* with greatly unequal second pereopods), along with the monotypic genera *Notopandalus* and *Pseudopandalus*, as well as the included species of *Pantomus*. Monophyly of the genus *Plesionika*, as currently defined, has already been challenged on morphological (Christoffersen, 1989, Komai, 1994a) as well as molecular (Bracken et al.,

2009; Matzen da Silva et al., 2013) grounds, and was herein amply confirmed. Based on mitochondrial 16S and COI data, Matzen da Silva et al. (2013) equally rejected the monophyly of *Plesionika*, with the three representatives of the “*Nothocaris*” group forming a paraphyletic clade.

In this study, six “*Nothocaris*” species were included, and their recovered position suggests them to be a taxon distinct from *Plesionika*. However, the ASR analyses did not recover any defining synapomorphy for this clade, with the distinctly unequal second pereopods (character 65, Appendix 3) inferred to have evolved several times during the evolutionary history of Pandalidae. Nevertheless, the exceptional high number of subdivisions (>80) (character 70, Appendix 3) in one of the second pereopods in “*Nothocaris*” could potentially be a defining synapomorphy, depending on the status of *P. grahami*. *Plesionika grahami*, which has previously been considered to be a “*Nothocaris*”, resolved in the present analyses in Clade B (Fig. 1), away from the other “*Nothocaris*”. The AU (0.028) and SH tests (<0.05) rejected the monophyly of “*Nothocaris*”, thus this issue cannot herein be resolved and must wait for further phylogenetic analyses. Despite a lack of clear synapomorphies for Clade B, Crosnier (1997) already suggested that *Pseudopandalus* is similar to “*Nothocaris*”, whilst both Christoffersen (1989) and Komai (1994a) recovered clear affinities between *Pantomus* and *Notopandalus* in their analyses.

4.2.3. Clade C

Clade C consisted of the included species of *Pandalina*, *Pandalus* and *Pandalopsis*, as well as the monotypic *Atlantopandalus* and *Dichelopandalus*, with a monophyletic clade of *Pandalopsis* species subordinated within a wider *Pandalus*. Notably, the topology inferred herein was entirely consistent with the cladograms of Christoffersen (1989) and Komai (1994a, 1995). Two synapomorphies were identified for this clade, both on the structure of the scaphognathite (Fig. 2). *Pandalina* can be easily distinguished from other genera based on the apomorphic absence of pereopodal arthrobranchs, only being present on the third maxilliped (character 90, Appendix 3) (see Holthuis, 1993; Komai & Chan, 2010). The monophyletic group of *Pandalus* and *Pandalopsis* was supported by a single synapomorphy “endopod of pleopod 1 exhibiting sequential change related to hermaphroditism” (character 85; Fig. 2), which is associated with the unique protandric hermaphroditism of these two genera (Komai, 1994a, b, 1999). Although the presence of a broad ventral lamina on the ischium of the first pereopod was revealed to be a synapomorphy (character 62, Appendix 3) for *Pandalopsis*, this genus was nested deeply within *Pandalus*. A paraphyletic *Pandalus* with *Pandalopsis*

subordinated within, is entirely consistent with adult morphology (Komai, 1994a, b, 1999) and larval characteristics (Christoffersen, 1989), and thus *Pandalopsis* is herein formally considered to be a junior synonym of *Pandalus*.

Within *Pandalus*, four informal species groups have previously been proposed (Komai, 1999), namely, the “*P. montagui*”, “*P. stenolepis*”, “*P. hypsinotus*”, and “*P. platyceros*” groups (Table 1), with three included in the present study. The relative position of constituent species and their respective monophyly in the phylogeny (Fig. 1) consolidates these informal groupings. The ASR analyses also revealed two synapomorphies for the “*P. hypsinotus*” group (characters 80 and 86, Appendix 3).

4.2.4. Clade D

Clade D consisted of the “*Plesionika laevis*” species group, as well as *P. bifurca* and *P. spinidorsalis*, *Heterocarpus*, the included species of *Chlorotocus*, and the monotypic genera *Dorodotes* and *Procleptes*, with the clade being supported by a single synapomorphy: the relatively long postrostral carina (character 8, Fig. 2). Therefore, the proposed affinity of *Procleptes*, *Chlorotocus* and *Dorodotes* to *Heterocarpus* based on overall similarity (Chace, 1985) was confirmed herein.

The integrity of the genus *Heterocarpus* has never been questioned even though the 30 species currently known in this genus (Yang et al., 2018) display a high morphological disparity and at least five species groups can be recognized (Crosnier, 1988; Yang et al., 2010, 2018). The four species of *Heterocarpus* included in the present study each belong to different species groups, and were unexpectedly shown to form a paraphyletic assemblage. In the past, the affinity of the “*Plesionika laevis*” species group has been controversial due to its apparent intermediate position between *Plesionika* and *Heterocarpus*, and whether the group should be included in *Heterocarpus* (see Burukovsky, 1986a; Chace, 1985), *Plesionika* (see Crosnier 1986, 1988; Chan & Crosnier, 1997) or even a distinct genus (see Chace, 1989) has yet to reach consensus. Traditional morphological studies (e.g. Chace, 1985) treated the lateral carinae on the carapace and the abdominal mid-dorsal boss or carinae as defining generic characters of *Heterocarpus*. In the present study, however, these characters were not considered to be synapomorphic (e.g., character 18; Appendix 3). Equally, the phylogeny clearly showed that the three included species from the “*P. laevis*” group formed a monophyletic group with a species of *Heterocarpus*, supporting the contention that the “*P. laevis*” group was closer to *Heterocarpus* than typical *Plesionika* (i.e. Clade E, see below), even though *Heterocarpus* itself resolves to be polyphyletic.

The present study argues strongly against the monophyly of *Heterocarpus* (AU and SH test < 0.01). The sister relationship of *Chlorotocus* and *Procleptes* was supported by a single synapomorphy (character 69, Appendix 3). This subclade was sister to *P. spinidorsalis*, already suggested on the basis of morphology (Chace, 1985), a notion herein supported by a single synapomorphy (character 87, Appendix 3). The sister relationship of this larger clade with *H. hayashii* was also supported by a single synapomorphy (character 42, Appendix 3). Such a relationship is further supported by the early larval stages of *Chlorotocus crassicornis* being very similar to those of *H. ensifer* (see Landeira et al., 2015), a closely related species to *H. hayashii* (see Crosnier, 1988). As *Heterocarpus* as currently defined was recovered to be polyphyletic, whether it is more appropriate to divide this genus or expanding it to include *Chlorotocus*, *Procleptes*, the “*Plesionika laevis*” group and selected other species of *Plesionika* cannot be resolved due to the limited taxon coverage of *Heterocarpus* in the present study.

4.2.5. Clade E

The remaining *Plesionika* species clustered in Clade E, together with the two monotypic genera, *Stylopandalus* and *Calipandalus*. Although, the type species of *Plesionika*, *P. ensis* could not be sequenced for the present study, a closely related species, *P. reflexa* was included (Chace, 1985; Chan & Crosnier 1997; Chan et al., 2018) and this clade is herein considered as *Plesionika sensu stricto*. The present study recovers *Stylopandalus* and *Calipandalus* as deeply nested within *Plesionika sensu stricto*. The generic attribution of the monotypic *Stylopandalus*, *S. richardi* has changed considerably over the decades, but a similar position of the genus was already recovered by Bracken et al. (2009) and Matzen da Silva et al. (2013). It is worth noting that a recent study also suggested that the larval characteristics of *Stylopandalus* are highly reminiscent of some *Plesionika* species (Landeira et al., 2014).

Calipandalus was recently established to accommodate a single species (Komai & Chan, 2003), with the authors already commenting that the species was morphologically similar to certain species of *Plesionika*. Although *Calipandalus* was considered to be distinct from *Plesionika* due the absence of an exopod on the third maxilliped, this character state was herein shown to be a homoplasy in Pandalidae (character 61, Appendix 3). In this study, the resolved deeply nested phylogenetic position of both *Stylopandalus* and *Calipandalus* inside *Plesionika* was supported by two synapomorphies (characters 6, 60; Fig. 2) and we herein formally consider *Stylopandalus* and *Calipandalus* as junior synonyms of *Plesionika*.

The internal status of lineages within *Plesionika* has been the subject of a long standing debate (Chace,

1985; Chan & Crosnier, 1997; Komai & Chan, 2003). *Parapandalus*, which is currently considered a junior synonym (known as the “*P. narval*” group) was characterized by the lack of epipods on all pereopods (Chace, 1985; Chan & Crosnier, 1991; Holthuis, 1993). In the present phylogeny, the four representatives agreeing with the diagnosis of *Parapandalus* (*P. narval*, *P. yui*, *P. grandis*, and *P. quasigrandis*) constituted a subordinated clade within a wider *Plesionika sensu stricto* clade. Other internal relationships within *Plesionika sensu stricto* were somewhat poorly resolved. For example, the other 11 species of *Plesionika* included in this clade were from several species groups, as well as isolated species and only *P. edwardsi* and *P. crosnieri* belong to the same species group (Chan & Crosnier, 1997). However, the herein recovered phylogeny did not reveal a sister relationship between *P. edwardsi* and *P. crosnieri*. On the other hand, two synapomorphies were identified across Clade E, even considering the exceptional high morphological disparity in the included species of *Plesionika*. We thus refrain to split Clade E into several genera and treat all the members of this clade as *Plesionika sensu stricto*, whilst acknowledging that *Plesionika sensu lato* is demonstrably a paraphyletic taxon, until the status of “*Nothocaris*” and the “*Plesionika laevis*” group is fully resolved.

4.3 Character evolution

The present ASR analyses identified 15 synapomorphies for the major clades in this superfamily, with most of these characters not previously been considered to be of systematic importance. Of these, only the shape of the stylocerite (character 36) and mandibular palp (character 44) were previously thought to be evolutionary informative by Christoffersen (1989). These two characters, together with the length of the postrostral carina (character 8) and the shape of the posterior lobe of scaphognathite (character 49), had been considered to be of taxonomic importance (e.g. Chace, 1985). On the other hand, most characters generally used for separating the genera in Pandalidae (e.g. Chace, 1985) such as the lateral carapace carinae (characters 9-11), gills and exopods on the thoracic appendages (characters 51, 52, 56, 57, 61, 90) are revealed to be apomorphic (Appendix 3). For example, it is found that on the carapace the postrostral carina instead of the lateral carinae may be more important in the evolution of these shrimps. Previous works had not considered setae in adults as of systematic importance, but setae on the rostrum (character 6), telson (character 30) and scaphognathite (character 50) are determined to be of significance (Fig. 2), as equally demonstrated in Alpheidae (Anker et al., 2006). For the mandible, it was found that changes in the incisor process (character 43, Fig. 2) were as important as the palp, equally demonstrated across Caridea by Burukovsky (1986b). The shape of the endopods of the maxilla

(character 48, Fig. 2), carpus of the third maxilliped (character 60, Fig. 2), basis of the second pereopod (character 68, Fig. 2), the protuberances on the sixth and seventh thoracic sternites (character 88, Fig. 2) also represent fundamental changes in the deeper evolution of these shrimps, even though their function is largely unknown, a statement which also applies to setal adornments.

The shallow water genera (i.e. Clade A) generally have a smoother abdomen than the deep-water genera, particularly in the rounded posteroventral angle of the fifth pleuron (character 27, Fig. 2) which was considered a significant synapomorphy, although again of unknown functionality. Although there is considerable variation in the rostral formulae in pandalids, including the presence of movable teeth and ranging from few to as many as 85 teeth, the present study revealed that the loss of ventral rostral teeth (character 2, Fig. 2) was an important early evolutionary step in this taxon, with all shallow water genera lacking these.

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Figure Captions

Figure 1. Phylogenetic tree resolved by Bayesian inference analyses of DNA sequences based on the combined dataset of eight markers, with the statistical support level indicated. The current family classification is indicated by solid bars, whilst the herein inferred clades are indicated by open bars; black and white bars denote species group or previous generic assignment, as indicated in Table 1. Differently coloured species names refer to separate genera or families, see legend.

Figure 2. Bayesian phylogram and character evolution in the Pandaloidea. The numbering on nodes represent synapomorphic characters identified via ancestral state reconstruction analyses. The matrix indicates the character states of synapomorphies, with different colors for different states. Character numbers and states follow morphological data matrix (see Appendix 2). Differently coloured species names refer to separate genera or families, see legend.

Supporting Information

Figure S1. Phylogenetic tree resolved by maximum likelihood analyses of DNA sequences based on the combined dataset of eight markers, with bootstrap values (based on 1000 pseudoreplicates) indicated at each node. The current family classification is indicated by solid bars, whilst the herein inferred clades are indicated by open bars; black and white bars denote species group or previous generic assignment, as indicated in Table 1. Different coloured species names refer to separate genera or families, see legend.

Figure S2. Phylogenetic tree resolved by Bayesian inference analyses of DNA sequences based on the combined dataset of eight markers, with Bayesian posterior probabilities indicated at each node. The current family classification is indicated by solid bars, whilst the herein inferred clades are indicated by open bars; black and white bars denote species group or previous generic assignment, as indicated in Table 1. Different coloured species names refer to separate genera or families, see legend.

Figure S3. Phylogenetic tree resolved by Bayesian inference analyses of DNA sequences based on the combined dataset of eight markers from the curated taxon set for Ancestral State Reconstruction (see Appendix 1). Bayesian posterior probabilities indicated at each node. The current family classification is indicated by solid bars, whilst the herein inferred clades are indicated by open bars. Different coloured species names refer to separate genera or families, see legend.

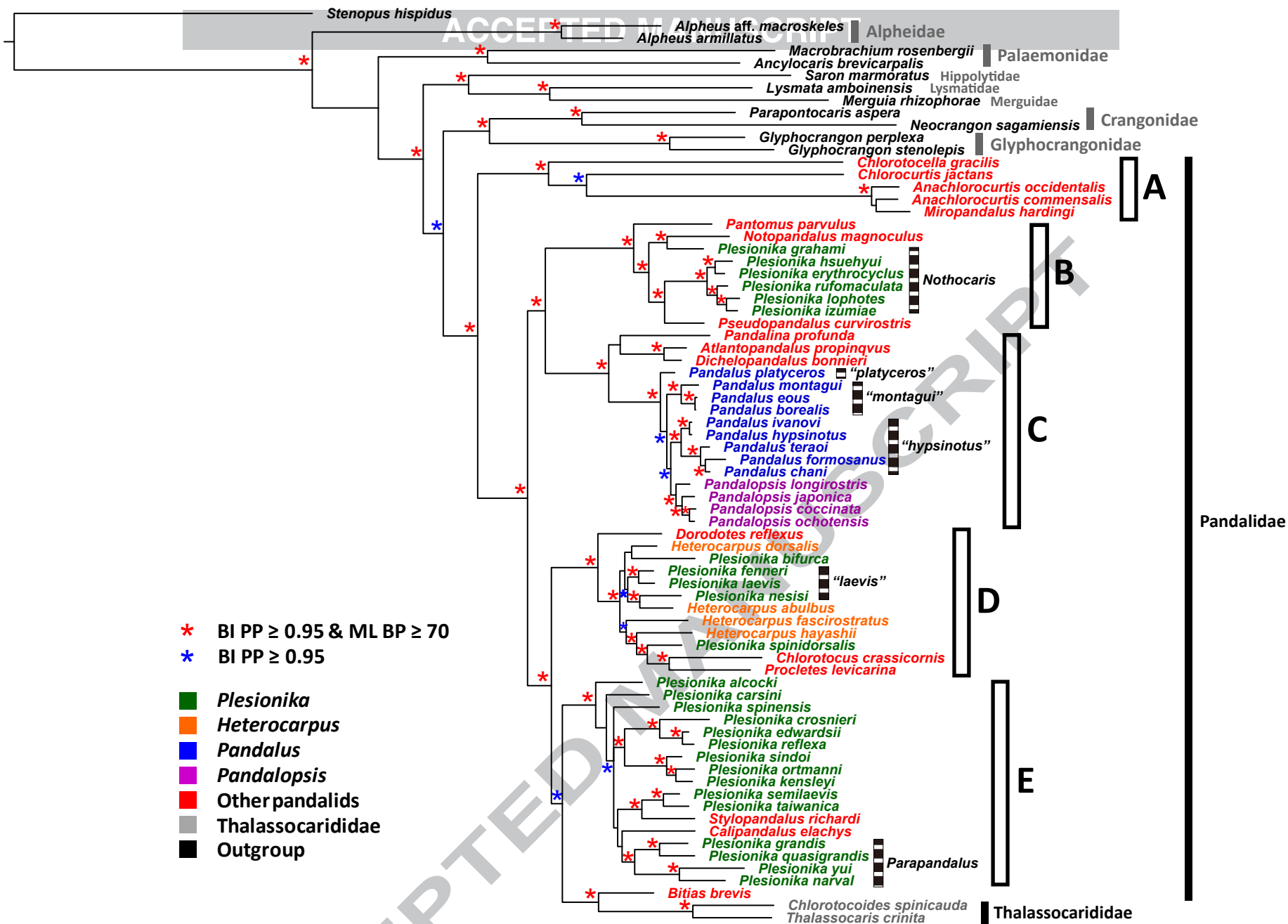
Appendix 1. Morphological data matrix.

Appendix 2. Morphological characters and states

Appendix 3. Ancestral state reconstruction for 91 morphological characters.

Appendix 4. List of material examined for morphological examination.

Appendix 5. Sequence alignment file in nexus format.



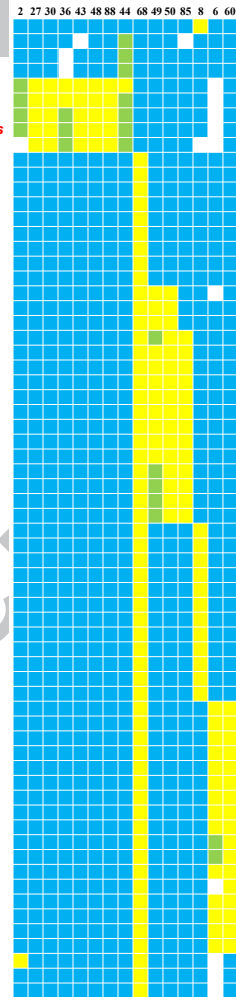
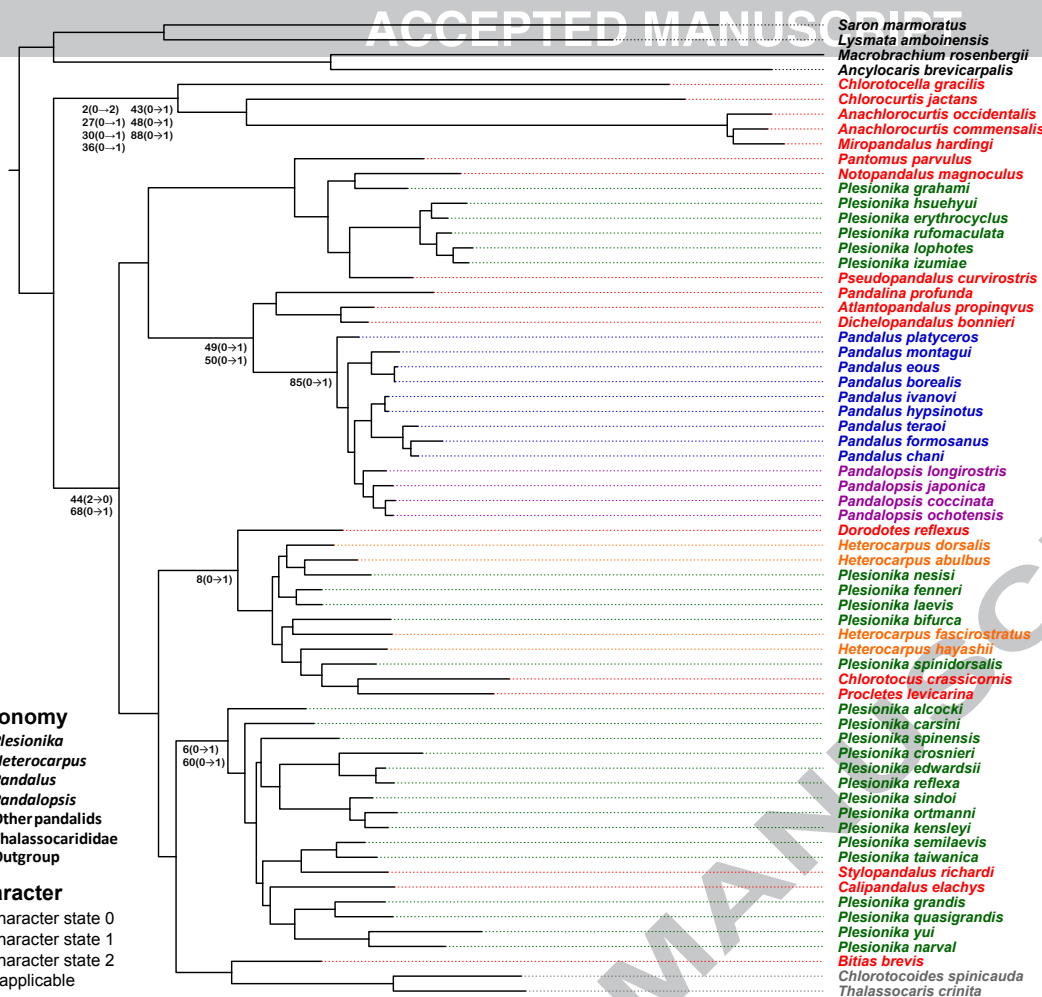


Table 1 Classification, sampling localities and GenBank accession numbers of species used in the present study.

Family	Species	Previous generic assignment/ Species group/other remarks	Voucher	Sampling locality	12S	16S	H3	NaK	enolase	PEPCK	atp β	GAPDH
Pandalidae	<i>Anachlorocurtis commensalis</i> *		OUMNH.ZC.2010-02-010	Taiwan	MK471256	MK470767	MK471096	MK470901	MK470835	MK470965	MK471160	MK471028
	<i>Anachlorocurtis occidentalis</i>		RMNH.CRUS.D.56174	Jordan	MK471257	MK470768	MK471097	MK470902	MK470836	MK470966	MK471161	MK471029
	<i>Atlantopandalus propinquus</i> *		OUMNH.ZC.2004-21-030	Norway	MK471258	MK470769	MK471098	MK470903	MK470837	MK470967	MK471162	MK471030
	<i>Bitias brevis</i>		MNHN-IU-2014-6330	Solomon Island	MK471259	MK470770	MK471099	MK470904	MK470838	MK470968	MK471163	MK471031
	<i>Calipandalus elachys</i> *		NTOU M02104	South China Sea	MK471260	MK470771	MK471100	MK470905	MK470839	MK470969	MK471164	MK471032
	<i>Chlorocurtis jactans</i> *		OUMNH.ZC.2011-05-028	Israel	MK471261	MK470772	MK471101	MK470906	MK470840	MK470970	MK471165	MK471033
	<i>Chlorotocella gracilis</i> *		MNHN-IU-2014-6329	New Caledonia	MK471262	MK470773	MK471102	MK470907	MK470841	MK470971	MK471166	MK471034
	<i>Chlorotocus crassicornis</i> *		NTOU M01869	Taiwan	MK471263	MK470774	MK471103	MK470908	MK470842	MK470972	MK471167	MK471035
	<i>Dichelopandalus bonnieri</i> *		OUMNH.ZC.2004-21-002	Norway	MK471264	MK470775	MK471104	MK470909	MK470843	MK470973	MK471168	MK471036
	<i>Dorodotes reflexus</i> *		NTOU M02105	South China Sea	MK471265	MK470776	MK471105	MK470910	MK470844	MK470974	MK471169	MK471037
	<i>Heterocarpus abulbus</i>		NTOU M01878	Taiwan	MK471266	MK470777	MK471106	MK470911	MK470845	MK470975	MK471170	MK471038
	<i>Heterocarpus dorsalis</i>		NTOU M02098	Taiwan	MK471267	MK470778	MK471107	MK470912	MK470846	MK470976	MK471171	MK471039
	<i>Heterocarpus hayashii</i>	Close to type species <i>H. ensifer</i>	NTOU M02099	Taiwan	MK471268	MK470779	MK471108	MK470913	MK470847	MK470977	MK471172	MK471040
	<i>Heterocarpus fascirostratus</i>		NTOU M02078	South China Sea	MK471269	MK470780	MK471109	MK470914	MK470848	MK470978	MK471173	MK471041
	<i>Miropandalus hardingi</i> *		NTOU M01205	Taiwan	MK471270	MK470781	MK471110	MK470915	MK470849	MK470979	MK471174	MK471042
	<i>Notopandalus magnoculus</i> *		NIWA 103449.1	New Zealand	MK471271	MK470782	MK471111	MK470916	MK470850	MK470980	MK471175	MK471043
	<i>Pandalina profunda</i>		OUMNH.ZC.2004-21-041	Norway	MK471272	MK470783	MK471112	-	-	-	-	-
	<i>Pandalopsis coccinata</i>		OUMNH.ZC.2014-01-051	Japan	MK471273	MK470784	MK471113	MK470917	MK470851	MK470981	MK471176	MK471044
	<i>Pandalopsis japonica</i>		CBM-ZC 7765	Japan	MK471274	MK470785	MK471114	MK470918	MK470852	MK470982	MK471177	MK471045
	<i>Pandalopsis longirostris</i>		CBM-ZC 14936	Japan	MK471275	MK470786	MK471115	MK470919	MK470853	MK470983	MK471178	MK471046
	<i>Pandalopsis ochotensis</i>		OUMNH.ZC.2011-11-034	Japan	MK471276	MK470787	MK471116	MK470920	MK470854	MK470984	MK471179	MK471047
	<i>Pandalus borealis</i>	montagui group	OUMNH.ZC.2004-21-006	Norway	MK471277	MK470788	MK471117	MK470921	MK470855	MK470985	MK471180	MK471048
	<i>Pandalus chani</i>	hypsinotus group	NTOU M02103	Taiwan	MK471278	MK470789	MK471118	MK470922	MK470856	MK470986	MK471181	MK471049
	<i>Pandalus eous</i>	montagui group	CBM-ZC 7756	Russia	MK471279	MK470790	MK471119	MK470923	MK470857	MK470987	MK471182	MK471050
	<i>Pandalus formosanus</i>	hypsinotus group	NTOU M02120	Taiwan	MK471280	MK470791	MK471120	MK470924	MK470858	MK470988	MK471183	-
	<i>Pandalus hypsinotus</i>	hypsinotus group	OUMNH.ZC.2014-01-052	Japan	MK471281	MK470792	MK471121	MK470925	MK470859	MK470989	MK471184	MK471051
	<i>Pandalus ivanovi</i>	hypsinotus group	CBM-ZC9223	Russia	MK471282	MK470793	MK471122	MK470926	MK470860	MK470990	MK471185	MK471052
	<i>Pandalus montagui</i> *	montagui group	OUMNH.ZC.2006-14-006	United Kingdom	MK471283	MK470794	MK471123	MK470927	MK470861	MK470991	MK471186	MK471053
	<i>Pandalus platyceros</i>	platyceros group	OUMNH.ZC.2008-07-005	USA	MK471284	MK470795	MK471124	MK470928	MK470862	MK470992	MK471187	MK471054
	<i>Pandalus teraoi</i>	hypsinotus group	OUMNH.ZC.2013-05-062	Japan	MK471285	MK470796	MK471125	MK470929	MK470863	MK470993	MK471188	MK471055

	<i>Pantomus parvulus*</i>	MNHN-IU-2014-6333	French Guiana	MK471286	MK470797	MK471126	MK470930	MK470864	MK470994	MK471189	MK471056
	<i>Plesionika alcocki</i>	NTOU M01599	Philippines	MK471287	MK470798	MK471127	MK470931	MK470865	MK470995	MK471190	MK471057
	<i>Plesionika bifurca</i>	NTOU M02101	South China Sea	MK471288	MK470799	MK471128	MK470932	MK470866	MK470996	MK471191	MK471058
	<i>Plesionika carsini</i>	NTOU M02102	Taiwan	MK471289	MK470800	MK471129	MK470933	MK470867	MK470997	MK471192	MK471059
	<i>Plesionika crosnieri</i>	NTOU M02083	Taiwan	MK471290	MK470801	MK471130	MK470934	MK470868	MK470998	MK471193	MK471060
	<i>Plesionika edwardsii</i>	NTOU M02106	Taiwan	MK471291	MK470802	MK471131	MK470935	MK470869	MK470999	MK471194	MK471061
	<i>Plesionika erythrocyclus</i>	<i>Nothocaris</i>	Taiwan	MK471292	MK470803	MK471132	MK470936	MK470870	MK471000	MK471195	MK471062
	<i>Plesionika fenneri</i>	<i>laevis</i> group	French Polynesia	MK471293	MK470804	-	MK470937	MK470871	MK471001	MK471196	MK471063
	<i>Plesionika grahami</i>	<i>Nothocaris</i>	New Caledonia	MK471294	MK470805	MK471133	-	MK470872	-	MK471197	-
	<i>Plesionika grandis</i>	<i>Parapandalus</i>	Taiwan	MK471295	MK470806	MK471134	MK470938	MK470873	MK471002	MK471198	MK471064
	<i>Plesionika hsuehyui</i>	<i>Nothocaris</i>	Taiwan	MK471296	MK470807	MK471135	MK470939	MK470874	MK471003	MK471199	MK471065
	<i>Plesionika izumiae</i>	<i>Nothocaris</i>	Taiwan	MK471297	MK470808	MK471136	MK470940	MK470875	MK471004	MK471200	MK471066
	<i>Plesionika kensleyi</i>		Philippines	MK471298	MK470809	MK471137	MK470941	MK470876	MK471005	MK471201	MK471067
	<i>Plesionika laevis</i>	<i>laevis</i> group	Guadeloupe	MK471299	MK470810	-	MK470942	MK470877	MK471006	MK471202	MK471068
	<i>Plesionika lophotes</i>	<i>Nothocaris</i>	Taiwan	MK471300	MK470811	MK471138	MK470943	MK470878	MK471007	MK471203	MK471069
	<i>Plesionika narval</i>	<i>Parapandalus</i>	Taiwan	MK471301	MK470812	MK471139	MK470944	MK470879	MK471008	MK471204	MK471070
	<i>Plesionika nesi</i>	<i>laevis</i> group	Taiwan	MK471302	MK470813	MK471140	MK470945	MK470880	MK471009	MK471205	MK471071
	<i>Plesionika ortmanni</i>		Taiwan	MK471303	MK470814	MK471141	MK470946	MK470881	MK471010	MK471206	MK471072
	<i>Plesionika quasigrandis</i>	<i>Parapandalus</i>	Philippines	MK471304	MK470815	MK471142	MK470947	MK470882	MK471011	MK471207	MK471073
	<i>Plesionika reflexa</i>	Closest to the type species <i>P. ensis</i>	Taiwan	MK471305	MK470816	MK471143	MK470948	MK470883	MK471012	MK471208	MK471074
	<i>Plesionika rufomaculata</i>	<i>Nothocaris</i>	Taiwan	MK471306	MK470817	MK471144	MK470949	MK470884	MK471013	MK471209	MK471075
	<i>Plesionika semilaevis</i>		Taiwan	MK471307	MK470818	MK471145	MK470950	MK470885	MK471014	MK471210	MK471076
	<i>Plesionika sindoi</i>		Taiwan	MK471308	MK470819	MK471146	MK470951	MK470886	MK471015	MK471211	MK471077
	<i>Plesionika spinensis</i>		Philippines	MK471309	MK470820	MK471147	MK470952	MK470887	MK471016	MK471212	MK471078
	<i>Plesionika spinidorsalis</i>		South China Sea	MK471310	MK470821	MK471148	MK470953	MK470888	MK471017	MK471213	MK471079
	<i>Plesionika taiwanica</i>		Taiwan	MK471311	MK470822	MK471149	MK470954	MK470889	MK471018	MK471214	MK471080
	<i>Plesionika yui</i>	<i>Parapandalus</i>	Taiwan	MK471312	MK470823	MK471150	MK470955	MK470890	MK471019	MK471215	MK471081
	<i>Proclites levicarina*</i>		Taiwan	MK471313	MK470824	MK471151	MK470956	MK470891	MK471020	MK471216	MK471082
	<i>Pseudopandalus curvirostris*</i>	MNHN-IU-2014-12729	New Caledonia	MK471314	MK470825	MK471152	MK470957	MK470892	MK471021	MK471217	MK471083
	<i>Stylopandalus richardi*</i>	NTOU M02119	South China Sea	MK471315	MK470826	MK471153	MK470958	MK470893	MK471022	MK471218	MK471084
Thalassocarididae	<i>Chlorotocoides spinicauda</i>	NTOU M02124	Vanuatu	MK471316	MK470827	MK471154	MK470959	MK470894	-	MK471219	MK471085
	<i>Thalassocaris crinita</i>	NTOU M02123	Madagascar	MK471317	MK470828	MK471155	MK470960	MK470895	MK471023	MK471220	-
Alpheidae	<i>Alpheus</i> aff. <i>macroseles</i>	NTOU M02122	Taiwan	MK471318	MK470829	MK471156	MK470961	MK470896	MK471024	MK471221	MK471086
	<i>Alpheus armillatus</i>	OUMNH.ZC.2007-20-014	Honduras	MK471319	MK470830	MK471157	MK470962	MK470897	MK471025	MK471222	MK471087

Crangonidae	<i>Parapontocaris aspera</i>	NTOU M02100	Taiwan	MK471320	MK470831	MK471158	MK470963	MK470898	MK471026	MK471223	MK471088
	<i>Neocrangon sagamiensis</i>	NTOU M01011	Taiwan	MK471321	<u>KF023106</u>	<u>JF346301</u>	<u>JF346337</u>	<u>JF346265</u>	<u>JF346373</u>	-	MK471089
Glyphocrangonidae	<i>Glyphocrangon perplexa</i>	NTOU M00706	Taiwan	MK471322	<u>KF023104</u>	<u>JF346325</u>	<u>JF346361</u>	MK470899	<u>JF346397</u>	-	MK471090
	<i>Glyphocrangon stenolepis</i>	NTOU M01013	Taiwan	MK471323	<u>KF023103</u>	<u>JF346308</u>	<u>JF346344</u>	<u>JF346272</u>	<u>JF346380</u>	-	MK471091
Hippolytidae	<i>Saron marmoratus</i>	NTOU M01144	Japan	MK471324	MK470832	MK471159	MK470964	MK470900	MK471027	-	MK471092
Lysmatidae	<i>Lysmata amboinensis</i>	MSLKHC-CA23Lyamb	Hong Kong	MK471325	<u>KF023091</u>	<u>JF346318</u>	<u>JF346354</u>	<u>JF346282</u>	<u>JF346390</u>	-	MK471093
Merguidae	<i>Merguia rhizophorae</i>	OUMNH.ZC.2009-06-05	Panama	-	<u>EU861508</u>	<u>KF178857</u>	<u>KJ701251</u>	<u>KJ701252</u>	-	-	-
Palaemonidae	<i>Macrobrachium rosenbergii</i>	MSLKHC-Maros	Hong Kong	MK471326	MK470833	<u>JF346320</u>	<u>JF346356</u>	<u>JF346284</u>	<u>JF346392</u>	-	MK471094
	<i>Ancyllocaris brevicarpalis</i>	MSLKHC-CA22Pebre	Hong Kong	MK471327	MK470834	<u>JF346324</u>	<u>JF346360</u>	<u>JF346288</u>	<u>JF346396</u>	-	MK471095
Stenopodidae	<i>Stenopus hispidus</i>	MSLKHC-Sthis	Hong Kong	<u>KX086354</u>	<u>KF023075</u>	<u>JF346323</u>	<u>JF346359</u>	<u>JF346287</u>	<u>EU427247</u>	-	-

Classification generally follows De Grave & Fransen (2011). Species with asterisk suffix represent type species in corresponding genera. Underlined species were included in the morphological scoring. Previous generic assignment/Species group follows Burukovsky (1981); Chace (1985); Chan & Crosnier (1997); Komai (1999). “-” represents missing data; underlined accession numbers represent sequences obtain from GenBank. Voucher specimens are deposited as follows: NTOU (National Taiwan Ocean University, Keelung), OUMNH-ZC (Oxford University Museum of Natural History, Zoological Collection), MNHN (Muséum national d’Histoire naturelle, Paris), CBM (Natural History Museum and Institute, Chiba), MSLKHC (Simon F.S. Li Marine Science Laboratory, The Chinese University of Hong Kong), RMNH (Naturalis Biodiversity Center, Leiden), NIWA (National Institute of Water and Atmospheric Research, Wellington).

Table 2 Best partitioning scheme and best-fit substitution model selected by PartitionFinder.

Partition	Model
12S, 16S	GTR + I + G
H3 1, <i>atpβ</i> 1	GTR + I
H3 2, NaK 2, <i>enolase</i> 2, <i>PEPCK</i> 2, <i>atpβ</i> 2, <i>GAPDH</i> 2	GTR + I + G
H3 3, NaK 3, <i>enolase</i> 3, <i>atpβ</i> 3, <i>GAPDH</i> 3	GTR + G
NaK 1, <i>enolase</i> 1, <i>PEPCK</i> 1, <i>GAPDH</i> 1	GTR + I + G
<i>PEPCK</i> 3	GTR + G

Table 3 AU test and SH test of phylogenetic hypotheses. P-Value < 0.05 indicates significant support against the monophyly of a particular group.

Hypotheses	Tree Scores	P-Value	
		AU test	SH test
Unconstrained tree	-54579.957		
Monophyletic Pandalidae	-54647.797	<0.01	<0.01
Monophyletic <i>Plesionika</i>	-55781.926	<0.001	<0.01
Monophyletic <i>Heterocarpus</i>	-54650.089	<0.01	<0.01
Monophyletic <i>Pandalus</i>	-54595.411	0.269	>0.05
Monophyletic <i>Anachlorocurtis</i>	-54581.073	0.553	>0.05
Monophyletic <i>Nothocaris</i>	-54615.896	0.028	<0.05



Highlights

- The first molecular phylogeny of the caridean Pandaloidea is reconstructed.
- Genetic data from eight markers are generated for most Pandaloidea genera.
- A derived placement of Thalassocarididae renders Pandalidae paraphyletic and should be considered a junior synonym of the clade.
- Synapomorphies are recovered for the major clades.