

Mitochondrial phylogeny of the deep-sea squat lobsters, Munidopsidae (Galattheoidea)

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Abstract

The Munidopsidae, one of three squat lobster families in the Galattheoidea, contains the deepest dwelling squat lobsters, with some occurring at abyssal depths. Munidopsids were formerly divided into two subfamilies: Shinkaiinae, for the unusual hydrothermal vent genus *Shinkaia*; and Munidopsinae for remaining taxa. Four munidopsid genera are currently recognised (*Shinkaia*, *Leiogalathea*, *Galacantha* and *Munidopsis*) but the largest genus, *Munidopsis*, is highly diverse morphologically, with multiple genera or subgenera currently in its synonymy. Phylogenetic studies of galatheoids focussed on high level relationships indicate that *Leiogalathea* is sister to other munidopsids, but the position of *Shinkaia* with respect to *Munidopsis* and *Galacantha* is unclear, as is the reciprocal monophyly of the latter two genera. Phylogenetic analyses of the Munidopsidae based on mitochondrial 16S and COI sequences, sampling all current genera (including the majority of the formerly recognised subgenera), indicate that the generic and former subfamily classifications do not reflect the phylogeny. *Shinkaia* and *Galacantha* clades are nested within *Munidopsis* rendering the genus paraphyletic and the bi-subfamily classification phylogenetically invalid. Many of the *Munidopsis* clades recovered, however, correspond well to formerly recognised genera or subgenera, indicating good prospects for a natural subdivision of *Munidopsis*.

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1. Introduction

The squat lobster family Munidopsidae includes the deepest dwelling members of the Galattheoidea, and many have correspondingly reduced eyes for life in low light on the outer continental shelf, slope or abyssal plain. The munidopsids are sister to the remaining galatheoids and also have

the distinction of being the geologically oldest of the squat lobsters, with a fossil record dating back to the Lower Jurassic (Schweitzer and Feldmann, 2000; Ahyong et al., 2009). The Munidopsidae are distinguished from other galatheoids by their chief synapomorphy: the loss or reduction of the flagellum on maxilliped 1 (Ahyong et al., 2010).

Two munidopsid subfamilies are recognised: Shinkaiinae, for the unusual hydrothermal vent genus *Shinkaia* (Fig. 1K); and Munidopsinae for remaining taxa (Baba and Williams, 1998). Recently, the *Galathea*-like *Leiogalathea* (Fig. 1J) was shown to be a munidopsid, as sister to the *Shinkaia* + *Galacantha* + *Munidopsis* clade (Ahyong et al.,

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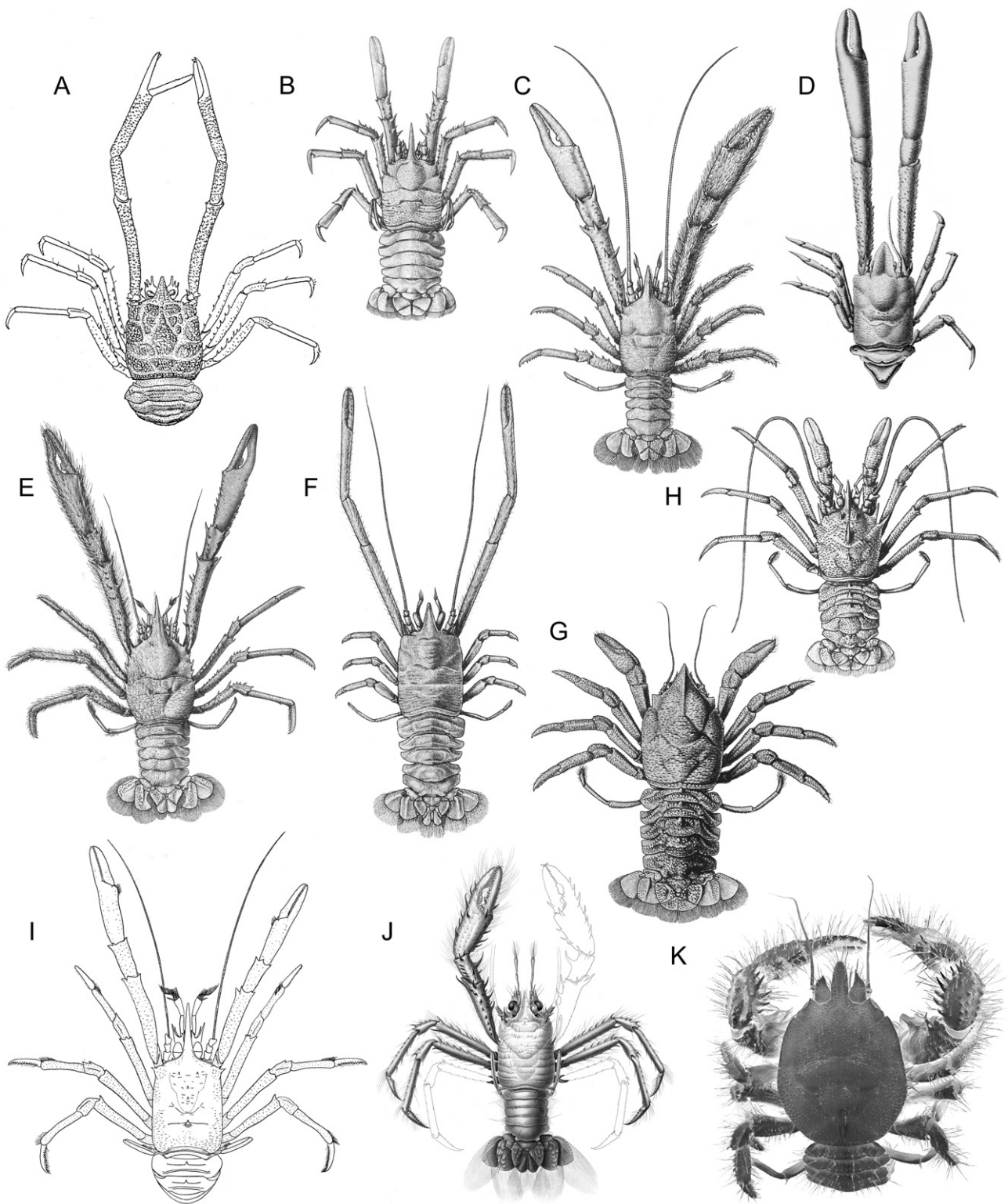


Fig. 1. Representatives of genera of Munidopsidae and groups within *Munidopsis*. (A) *Anoplnotus* group (*M. granulata* Miyake and Baba, 1967); (B) *Bathyanankyristes* group (*M. levis* Alcock and Anderson, 1894); (C) *Dasyopus* group (*M. dasyopus* Alcock, 1894); (D) *Elasmonotus* group (*M. longimanus* Milne-Edwards, 1880); (E) *Galathodes* group (*M. trifida* Henderson, 1885); (F) *Galathopsis* group (*M. cylindrophthalma* Alcock, 1894); (G) *Orophorhynchus* group (*M. granosa* Alcock, 1901); (H) *Galacantha rostrata* Milne-Edwards, 1880; (I) *Munidopsis curvirostra* Whiteaves, 1874; (J) *Leiogalatea laevirostris* (Balss, 1913); (K) *Shinkaia crosnieri* Baba and Williams, 1998 (A, modified from Miyake and Baba, 1967; B, from Alcock and McArdle, 1901; C and E, from Alcock and MacGilchrist, 1905; D, from Milne-Edwards and Bouvier, 1897; F and H, from Alcock and Anderson, 1895; G, from Alcock and McArdle, 1902; I, from Selbie, 1914; J, from Doflein and Balss, 1913; K, modified from Baba and Williams, 1998).

2009; Schnabel et al., 2011). Thus, Munidopsidae currently includes four genera: *Leiogalathea* and members of the subfamilies, Shinkaiinae (*Shinkaia*) and Munidopsinae (*Munidopsis* and *Galacantha*). Only one and two extant species *Shinkaia* and *Leiogalathea* are known, respectively, but there are more than 230 species of *Galacantha* and *Munidopsis* worldwide (Baba et al., 2008). In particular, *Munidopsis* is highly diverse morphologically with as many as seven genera or subgenera recognised by past workers for species now placed there (Fig. 1A–I).

Phylogenetic relationships within Munidopsidae have not been examined in detail and studies within *Munidopsis* have focused only on small species clusters or small regional groups (e.g., Creasey et al., 2000; Cubelio et al., 2007; Jones and Macpherson, 2007). Although *Leiogalathea* has been identified as sister to other munidopsids, the position of *Shinkaia* with respect to *Munidopsis* and *Galacantha* is unclear, as is the reciprocal monophyly of the latter two genera. In addition, several Mesozoic fossil munidopsid genera appear to fall within the currently broad concept of *Munidopsis* (Ahyong et al., 2010) and may represent diagnosable clades within the genus. Generic names aside, determining the phylogenetic placement of these fossils is necessary for the most reliable estimates of munidopsid divergence times. A well-resolved phylogeny of the munidopsids is thus a necessary first step in understanding the evolution of the group. Here, we assess whether the generic and subfamily classification of the Munidopsidae reflects phylogenetic relationships inferred from mitochondrial 16S and COI sequences of selected munidopsid species.

2. Materials and methods

2.1. Terminal taxa

Representatives of all recognised munidopsid genera were included as ingroup terminals (Table 1). COI and 16S sequences of *Shinkaia*, *Leiogalathea* and selected *Munidopsis* and *Galacantha* species derived from GenBank. The voucher specimen corresponding to a published GenBank sequence EU920928, originally identified as *Munidopsis rostrata* (see Toon et al., 2009) was re-identified as *Galacantha valdiviae* based on photographs provided by H. Bracken (Brigham Young University, Utah). Mitochondrial DNA sequences of remaining *Munidopsis* and *Galacantha* terminals were derived from ethanol preserved specimens in the collections of Museum Victoria, Melbourne (NMV), the National Institute of Water and Atmospheric Research, Wellington (NIWA), the University of Louisiana at Lafayette, Louisiana (ULL), and the Universidad Católica del Norte, Coquimbo (UCN). The Munidopsidae is sister to the remaining galatheoids (Ahyong et al., 2009; Schnabel et al., 2011), so analyses were rooted to selected Galatheidae and Munididae.

2.2. DNA extraction, PCR amplification and sequencing

Total DNA was extracted from ca. 50 mg ethanol preserved abdominal tissue or pereopod of the target specimen following the salt-based extraction procedure described by Aljanabi and Martinez (1997) with minor modifications. Quantity and quality of DNA were examined by means of 1% agarose TAE buffer gel electrophoresis against known standards. Partial COI and 16S sequences were PCR-amplified using the primer pair LCO1490-HCO2198 described by Folmer et al. (1994) and 16Sar1–16Sbrh described by Palumbi and Benzie (1991), respectively. Standard PCR reactions were performed in 30 μ l of medium containing approximately 10 ng DNA, 1.5 mM MgCl₂, 0.2 mM dNTPs, 1 μ M of forward and reverse primers each, 1 \times PCR reaction buffer and 1.25 units of *iTaq* DNA polymerase (Scientifix). The amplification cycle for the partial COI marker included an initial denaturation at 94 °C for 4 min followed by 35 cycles of 94 °C 1 min, 50 °C 1 min and 72 °C 1.5 min followed by a final extension cycle at 72 °C for 7 min. The partial 16S gene was amplified under the same conditions except for the lower annealing temperature (45 °C). Quantity and length of the PCR-products were examined by 1% gel electrophoresis as described above. Multiple amplification products were never observed. PCR reactions were sent to Macrogen Inc. (Korea; www.macrogen.com) for purification and direct sequencing on both directions.

2.3. Sequence alignments and phylogenetic analysis

Electropherograms were assembled in Sequencher 4.9 (Gene Codes) and partial COI sequences aligned manually in Bioedit v7.0.9 (Hall, 1999). Since many regions of the partial 16S gene are extremely divergent and may produce unreliable alignments, sequences were either aligned in Bioedit using ClustalW algorithm (Thompson et al., 1994) with several gap openings and extension penalties or in MUSCLE (<http://www.ebi.ac.uk/Tools/muscle/index.html>), the latter known to achieve the highest accuracy scores (Edgar, 2004). Three alignments (COI, 16S and concatenated COI–16S) were considered for phylogenetic analysis; 16S and COI–16S alignments were refined by eye. Alignment gaps were treated as missing data.

Phylogenetic information content in each partition was assessed by calculating g_1 statistics as a measure of the skewness of distribution of tree-lengths among 10,000 random maximum parsimony trees (Hillis and Huelsenbeck, 1992) in PAUP*4.0b10 for Windows (Swofford, 2002). The significance of the g_1 value was compared with critical values ($p=0.01$) for four state characters given the number of distinct sequences and the number of parsimony informative sites. Hierarchical Likelihood Ratio Tests (hLRTs) were run in Modeltest Version 3.7 (Posada and Crandall, 1998) to identify the best-fitting model and parameters (gamma distri-

Table 1. Classification of terminal taxa and GenBank accession numbers. Collecting locality and institutional registration numbers given for voucher specimens of new sequences. Abbreviations: Museum Victoria, Melbourne (NMV); National Institute of Water and Atmospheric Research, Wellington (NIWA); the University of Louisiana at Lafayette, Louisiana (ULLZ); Universidad Católica del Norte, Coquimbo (UCN); Brigham Young University, Utah (BYU). Note: the 16S sequence of *Galacantha valdiviae* (EU920928) was originally published as *Munidopsis rostrata* (see Toon et al., 2009).

Taxon	COI	16S	Locality	Museum no.
Munidopsidae				
<i>Galacantha diomedea</i>	JN166758 ^a	JN166748 ^a	Chile	UCN G3b
<i>Galacantha rostrata</i> 1	JN166755 ^a	JN166751 ^a	Tasman Sea	NIWA 28060a
<i>Galacantha rostrata</i> 2		HQ380261	Tasman Sea	NIWA 28060b
<i>Galacantha quiqueti</i>	JN166754 ^a	JN166744 ^a	Tasman Sea	NIWA 28088
<i>Galacantha spinosa</i> 1	JN166769 ^a	JN166752 ^a	N Gulf of Mexico	ULL Z-10852
<i>Galacantha spinosa</i> 2	JN166768 ^a	JN166753 ^a	N Gulf of Mexico	ULL Z-8023
<i>Galacantha subspinosa</i> 1	JN166760 ^a	JN166745 ^a	NW Australia	NMV J56403a
<i>Galacantha subspinosa</i> 2	JN166756 ^a	JN166746 ^a	NW Australia	NMV J56403b
<i>Galacantha subspinosa</i> 3	JN166761 ^a	JN166750 ^a	NW Australia	NMV J56403c
<i>Galacantha subspinosa</i> 4	JN166762 ^a	JN166747 ^a	NW Australia	NMV J56403d
<i>Galacantha subspinosa</i> 5	JN166757 ^a	JN166749 ^a	NW Australia	NMV J56403e
<i>Galacantha valdiviae</i>		EU920928	Japan	BYU KC3102
<i>Leiogalatea laevirostris</i> 1	AY351055	EU821541		
<i>Leiogalatea laevirostris</i> 2		AY351252		
<i>Munidopsis abbreviata</i>	JN166771 ^a	JN166724 ^a	N Gulf of Mexico	ULLZ-10848
<i>Munidopsis bairdii</i>		EU821542		
<i>Munidopsis bracteosa</i>	DQ677689			
<i>Munidopsis comarge</i>	JN166772 ^a	JN166732 ^a	New Zealand	NIWA 53792
<i>Munidopsis crenatirostris</i> 1	JN166783 ^a	JN166736 ^a	NW Australia	NMV J56399
<i>Munidopsis crenatirostris</i> 2	JN166781 ^a	JN166738 ^a	NW Australia	NMV J57252
<i>Munidopsis crenatirostris</i> 3	JN166778 ^a	JN166733 ^a	NW Australia	NMV J56397
<i>Munidopsis crenatirostris</i> 4	JN166780 ^a		NW Australia	NMV J55009a
<i>Munidopsis crenatirostris</i> 5	JN166779 ^a	JN166742 ^a	NW Australia	NMV J55009b
<i>Munidopsis crenatirostris</i> 6	JN166782 ^a	JN166743 ^a	NW Australia	NMV J55009c
<i>Munidopsis curvirostra</i> 1	FJ581770			
<i>Munidopsis curvirostra</i> 2	FJ581769			
<i>Munidopsis curvirostra</i> 3	FJ581768			
<i>Munidopsis cylindrophthalma</i>	JN166784 ^a	JN166737 ^a	NW Australia	NMV J55128
<i>Munidopsis dasypus</i> 1	JN166774 ^a	JN166727 ^a	NW Australia	NMV J56121
<i>Munidopsis dasypus</i> 2	JN166776 ^a		NW Australia	NMV J57251
<i>Munidopsis dasypus</i> 3	JN166777 ^a	JN166729 ^a	NW Australia	NMV J57250a
<i>Munidopsis dasypus</i> 4	JN166773 ^a	JN166730 ^a	NW Australia	NMV J57250b
<i>Munidopsis erinacea</i>	JN166767 ^a	JN166731 ^a	N Gulf of Mexico	ULLZ-7810
<i>Munidopsis kensleyi</i>	JN166775 ^a	JN166728 ^a	NW Australia	NMV J62313
<i>Munidopsis levis</i>		JN166723 ^a	NW Australia	NMV J55125
<i>Munidopsis longimanus</i>	JN166770 ^a	JN166741 ^a	N Gulf of Mexico	ULL Z-10851
<i>Munidopsis opalescens</i> 1		JN166739 ^a	Chile	UCN G4
<i>Munidopsis opalescens</i> 2	JN166759 ^a	JN166740 ^a	Chile	UCN G7
<i>Munidopsis polymorpha</i>	DQ860146			
<i>Munidopsis quadrata</i> 1	JN166766 ^a	JN166734 ^a	Chile	UCN G1
<i>Munidopsis quadrata</i> 2	DQ882093			
<i>Munidopsis recta</i>	DQ677702	EF428964		
<i>Munidopsis trifida</i> 1	JN166764 ^a	JN166725 ^a	Chile	UCN G9
<i>Munidopsis trifida</i> 2	JN166765 ^a	JN166726 ^a	Chile	UCN G10
<i>Munidopsis</i> sp.	JN166763 ^a	JN166735 ^a	Chile	UCN G8
<i>Shinkaia crosnieri</i> 1	EU420129	EU420129		
<i>Shinkaia crosnieri</i> 2	NC011013	NC011013		
Outgroups				
<i>Alainius crosnieri</i> 1	AY351050	AY351238		
<i>Alainius crosnieri</i> 2		AY351239		
<i>Galathea</i> sp. 1	GQ260875	EU821544		

Table 1 (Continued)

Taxon	COI	16S	Locality	Museum no.
<i>Galathea</i> sp. 2	GQ260877			
<i>Munida compressa</i>	AY350944	AY351114		
<i>Munida rubridigitalis</i>	AF283887	AY351163		
<i>Munida thoe</i>	AY351009	AY351182		
<i>Pleuroncodes monodon</i> 1	AY351062	AY351259		
<i>Pleuroncodes monodon</i> 2		EU821545		
<i>Sadayoshia</i> sp.		EU821547		

^aNew sequences are marked.

bution, proportion of invariable sites, transition–transversion ratio) for Bayesian inference (BI) and maximum likelihood (ML) analyses given the alignment. The GTR substitution model was used when the Modeltest output could not be implemented in MrBayes. In these cases model parameters were treated as unknown variables with uniform default priors and were estimated as part of the analysis. Maximum likelihood phylogenies were computed in PAUP*. Bayesian inference was implemented in MrBayes v3.1.2 (Huelsenbeck and Ronquist, 2001). Optimal models of nucleotide evolution for BI and ML were identified by Modeltest. ML heuristic searches were run in PAUP* (random addition sequence; TBR branch swapping; 10 replicates). BI was conducted for 5,000,000 generations of two parallel runs of four chains each, starting from a random tree and sampling every 1000 generations. The convergence of the parameter estimates was graphically confirmed by plotting values of likelihood against the generation time in Tracer v1.5 (Rambaut and Drummond, 2007). Non-parametric bootstrap support (Felsenstein, 1985) for individual clades was estimated in PhyML v3.0 (Guindon and Gascuel, 2003) on 1000 pseudoreplicates using the same methods, options and constraints used for the ML tree-inferences.

3. Results

3.1. Sequences and alignments

Sixty-two new sequences (31 each of COI and 16S rDNA) obtained from 18 species were merged with publically available munidopsid and outgroup sequences to create three alignments: COI, 16S and a concatenated COI-16S (see Table 1 for specimen information and Table 2 for alignment length, model selection and summary statistics). The COI and 16S partitions comprised 503 (43% parsimony informative) and 513 positions (44% parsimony informative), respectively. Both COI and 16S sequences were AT rich. Average base composition was A = 27.1%, C = 18.1%, G = 17.9%, T = 36.9% for COI; A = 35.8%, C = 10.1%, G = 18.0%, T = 36.1% for 16S. The length distribution of 10,000 random trees computed for each alignment was considerably left-

skewed indicating significant amount of phylogenetic signal in the datasets (Table 2).

3.2. Phylogenetic analyses

Topologies derived from individual genes under ML and BI were similar to those derived from combined analyses, all of which show that *Munidopsis* is not monophyletic (Figs. 2 and 3). The chief differences between the COI and 16S topologies are in the composition of *Galacantha* and positions of *Leiogalathea* and *Shinkaia*. The phylogenies inferred from the COI gene (Fig. 2A) resolve a *Galacantha* clade that includes *Munidopsis abbreviata* (Milne-Edwards, 1880) (although with equivocal nodal support for its position); *Shinkaia* is sister to the clade of hydrothermal vent species [*Munidopsis bairdii* (Smith, 1884) and *Munidopsis bracteosa* Jones and Macpherson, 2007]; and *Leiogalathea* is nested between the hydrothermal vent clade and the remaining munidopsids. In the 16S topologies (Fig. 2B), *Galacantha* is monophyletic, apart from *Galacantha diomedae* Faxon, 1893, which stands as sister to all other munidopsids; *Shinkaia* is not sister to the hydrothermal vent clade of *Munidopsis*, although the two clades are in ‘close’ proximity.

The combined analysis resolves *Galacantha* as monophyletic (to the exclusion of *G. diomedae*); *Shinkaia* and hydrothermal vent species of *Munidopsis* form a distinct clade in line with the single-gene topologies; and *Leiogalathea* is resolved as sister to the remaining munidopsids corroborating previous studies based on combined nuclear and mitochondrial markers (Ahyong et al., 2009; Schnabel et al., 2011). Our discussion to follow focuses on the results of the combined analyses, being based on the most substantial dataset.

4. Discussion

The phylogeny of Munidopsidae inferred herein is not compatible with relationships implied by the former subfamily classification (Baba and Williams, 1998). *Shinkaia* is nested within the *Munidopsis*–*Galacantha* clade irrespective of the data partition or analysis method used. Thus, Shinkaiinae and

Table 2. Sequence and alignment statistics. *l*, alignment length; *n*, number of sequences; *h*, number of unique haplotypes; *g*₁, phylogenetic informativeness of the data; *m*, evolutionary model selected by Modeltest; *i*, proportion of invariant sites; *a*, Gamma distribution shape parameter; *v*, variable, parsimony uninformative sites; *p*, parsimony informative sites.

	<i>l</i>	<i>n</i>	<i>h</i>	<i>g</i> ₁	<i>m</i>	<i>i</i>	<i>a</i>	<i>v</i>	<i>p</i>
COI	503	45	41	−0.68	GTR+I+G	0.4740	0.7620	19	216
16S	513	45	39	−0.61	TVM+G	0.3918	0.3496	51	226
COI-16S	1016	51	50	−0.64	TVM+I+G	0.4324	0.8037	82	462

Munidopsinae are not reciprocally monophyletic, although based on the complete dataset (16S+COI), they form a clade that is sister to *Leiogalatea*, corroborating analyses of higher level anomuran interrelationships based on combined 16S + nuclear 18S and 28S sequences (Ah Yong et al., 2009; Schnabel et al., 2011).

The ‘basal’ position of *Leiogalatea* (Fig. 1J) follows morphological expectations given its plesiomorphic, well-developed eyes and *Galathea*-like habitus. Of all munidopsids, *Leiogalatea* has the most *Galathea*-like body form – the broad triangular rostrum, well-developed eyes, and sparsely ornamented carapace and abdomen, leading

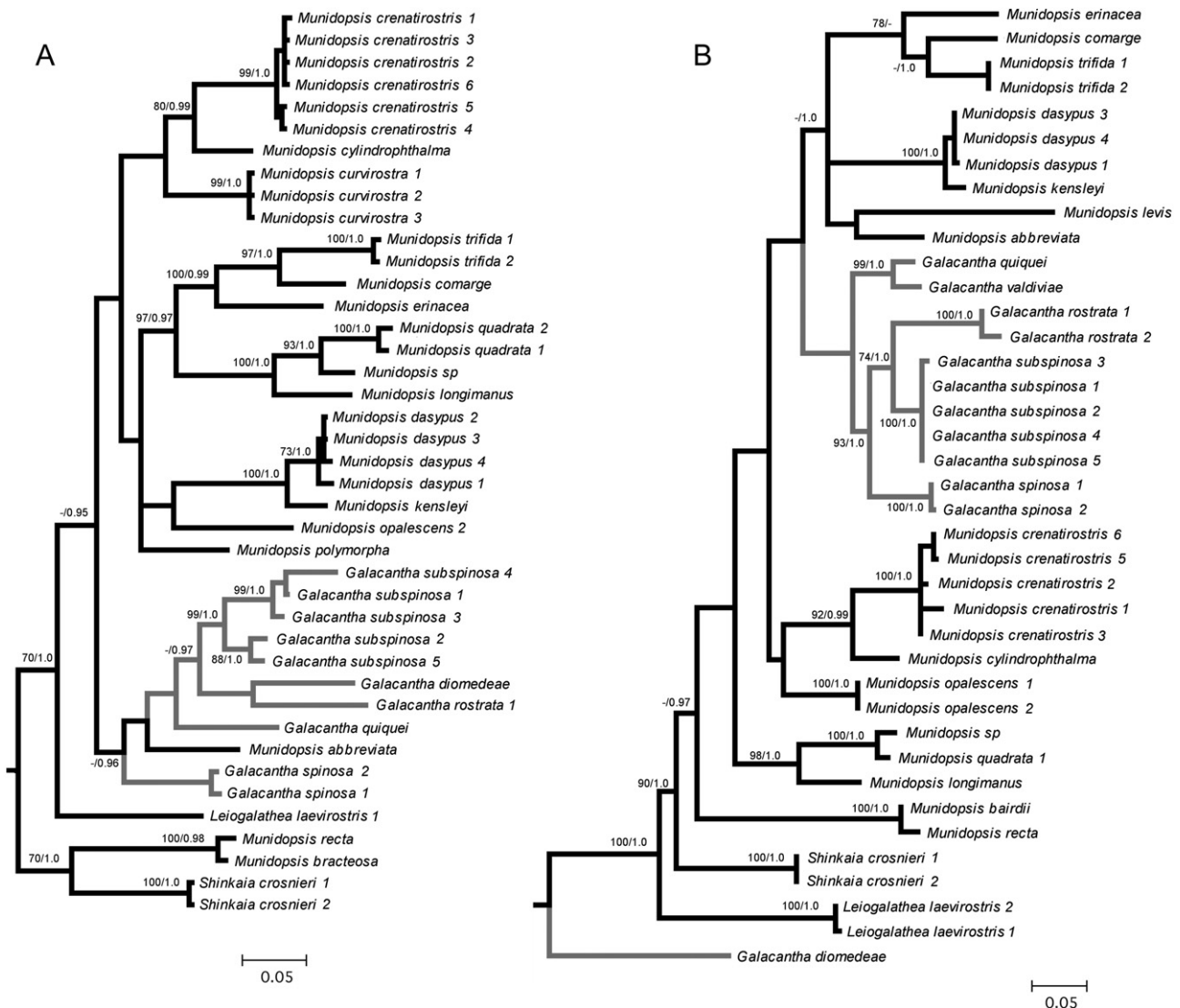


Fig. 2. Phylogeny of Munidopsidae. (A) Bayesian phylogram based on partial COI sequences ($\ln L = -5520.28165$); (B) maximum likelihood phylogram based on partial 16S rDNA sequences ($\ln L = -12160.17532$). Species of *Galacantha* are marked in gray. Numbers on nodes indicate non-parametric bootstrap support (maximum likelihood) and posterior probabilities (Bayesian inference). Only values at or above 70% and 0.95 for bootstrap and posterior probability, respectively, are reported. Slight differences in taxonomic representation between COI and 16S topologies reflect incomplete sampling of both amplicons for some species.

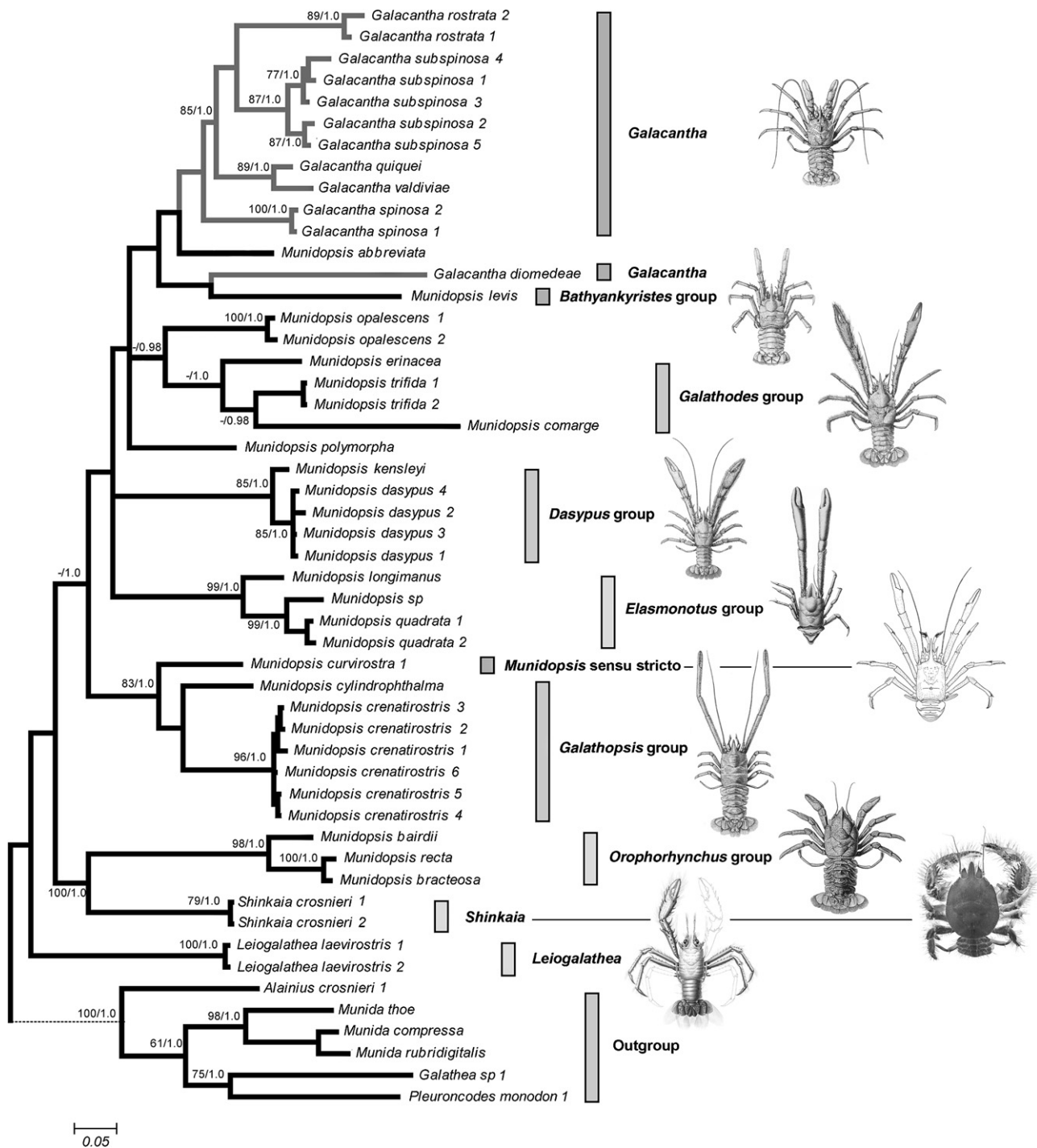


Fig. 3. Bayesian phylogram of Munidopsidae based on combined COI and 16S rDNA gene sequences ($\ln L = -10960.98154$). Species of *Galacantha* are marked in gray. Numbers on nodes indicate non-parametric bootstrap support (maximum likelihood) and posterior probabilities (Bayesian inference). Only values above at or above 60% and 0.95 for bootstrap and posterior probability, respectively, are reported.

to its original classification alongside *Galathea* and *Allogalathea* (Galatheidae). The reduced maxilliped 1 flagellum of *Leiogalatea* is transitional between the well-developed condition (plesiomorphic) of munidids and galatheids, and the complete loss of the flagellum in remaining munidopsids (derived). *Leiogalatea* could also be considered to be ecologically transitional, occurring on the continental shelf and

upper slope as in munidids, rather than the outer slope or abyssal habitats of most other munidopsids.

Galacantha and *Shinkaia* stand deeply nested among clades of *Munidopsis* indicating that the current concept of *Munidopsis* (Baba et al., 2008) is not monophyletic. This result is not unexpected given the high morphological diversity within *Munidopsis* sensu lato. Past workers have

attempted to represent this diversity through many generic divisions for those species now placed in *Munidopsis* or *Galacantha*: *Anoplomotus* Smith, 1883; *Bathyankyristes* Alcock and Anderson, 1894; *Elasmonotus* Milne-Edwards, 1880; *Galathopsis* Henderson, 1885; *Galathodes* Milne-Edwards, 1880; and *Orophorhynchus* Milne-Edwards, 1880 (Fig. 1). Most workers in the 19th and early 20th centuries variously used some or all of these generic names (e.g. Milne-Edwards, 1880; Faxon, 1893; Alcock, 1901; Balss, 1913; Tirmizi, 1966), although all recognised difficulties in ‘satisfactorily’ subdividing *Munidopsis*. For convenience, Alcock (1901) used several such names for informal groupings or subgenera within the single genus *Munidopsis*. Chace (1942), however, “failed to reveal any natural grouping” and synonymised all of the aforementioned generic names with *Munidopsis*. Apart from the recent resurrection of *Galacantha* (Macpherson, 2007), most subsequent workers have followed Chace. Although our representation of morphological diversity in *Munidopsis* is not yet comprehensive, our topologies already recover several major clades corresponding to previously recognised genera or subgenera.

Shinkaia (Fig. 1K) is sister to a clade of *Orophorhynchus*-group species of *Munidopsis* (Fig. 1G), characterised by a triangular rostrum, a mesially placed distal eye-spine, squamae or short striations on the carapace, and chelipeds that are usually shorter than the second pereopods. In addition, the *Shinkaia* and *Orophorhynchus* clades may share a similar habitat – hydrothermal vents. Many, though not all, species of the *Orophorhynchus* group are known hydrothermal vent associates, but the sister relationship with *Shinkaia* suggests that the vent habitat could be ancestral. If the common ancestor of *Shinkaia* and the *Orophorhynchus* group was a hydrothermal vent associate, colonisation of deepwater vent habitats can be inferred to have occurred early in the evolution of the munidopsids. At present, the fossil record of munidopsids from chemosynthetic environments is limited to *Shinkaia katapsyxis* Schweitzer and Feldmann, 2008, from the Eocene Humptulips formation, Western Washington, USA (Schweitzer and Feldmann, 2008). The hydrothermal vent clade (*Shinkaia* + *Orophorhynchus* group) is sister to the clade containing *Galacantha* and the remaining species of *Munidopsis*, most of which are associated with corals or other complex non-chemosynthetic habitats.

Galacantha (Fig. 1H) is substantially monophyletic and most species form a clade, except for *G. diomedae*, which is weakly allied to the *Bathyankyristes* group [diagnosed by the subchelate walking legs and represented by *Munidopsis levis* (Alcock and Anderson, 1894)] (Fig. 1B). The nodal support excluding *G. diomedae* from other species of *Galacantha* is weak, however, so the position may reflect a limitation in the data or an analytical artefact. Morphologically, *G. diomedae* differs from other *Galacantha* in having a scarcely elevated rostrum. In other members of *Galacantha* the rostrum is distinctly elevated. Additionally the rostrum of *G. diomedae* lacks any trace of the horizontal portion, which is either distinct or rudimentary in all other species of *Galacantha*. The

taxonomic position of *G. diomedae* requires reassessment, but is retained in *Galacantha* pending further corroboration by more extensive analyses.

Interrelationships of the remaining *Galacantha* exemplars correlate biogeographically, with Western Atlantic (*Galacantha spinosa* Milne-Edwards, 1880) and Indo-Pacific clades (*Galacantha quiquei* Macpherson, 2007; *Galacantha subspinosa* Macpherson, 2007; *Galacantha rostrata* Milne-Edwards, 1880; *G. valdiviae* Balss, 1913). *G. quiquei* and *G. valdiviae* uniquely share single rather than double anterolateral spines on the carapace, and are sister taxa as expected morphologically. In contrast, *G. subspinosa* and *G. spinosa* are morphologically similar, and were formerly considered conspecific (Macpherson, 2007). They apparently have a more distant molecular relationship, however, with *G. subspinosa* more closely allied to its Indo-Pacific congeners than to the western Atlantic *G. spinosa*.

The type species of *Munidopsis*, *Munidopsis curvirostra* Whiteaves, 1874 (Fig. 1I), is sister to a clade of two species corresponding to the *Galathopsis* group (Fig. 1F). These two species, *Munidopsis cylindrophthalma* (Alcock, 1894) and *Munidopsis crenatirostris* Baba, 1988, share a flattened or medially sulcate rostrum, unarmed carapace margins and unarmed abdominal tergites. Neither *M. cylindrophthalma* nor *M. crenatirostris* were originally placed in *Galathopsis*, but they closely resemble the two species for which the genus was originally proposed, *Munidopsis debilis* (Henderson, 1885) and *Munidopsis laevigata* (Henderson, 1885), respectively. Although, Henderson (1888) subsequently regarded *Galathopsis* as a junior synonym of *Elasmonotus* because of the similar carapace shape, our results recovered both groups in separate clades, which differ from each other in abdominal ornamentation. The *Elasmonotus* group recovered here, containing *Munidopsis quadrata* Faxon, 1893, *M. sp.* and *Munidopsis longimanus* (Milne-Edwards, 1880) (Fig. 1D), is similar to the *Galathopsis* group in the laterally unarmed, rectangular carapace and broad, simple rostrum, but differs in the medially gibbose anterior abdominal tergites.

The *Galathodes* group (Fig. 1E) (*Munidopsis comarge* Taylor et al., 2010, and *Munidopsis trifida* Henderson, 1885), united by a distally tridentate rostrum is sister to *Munidopsis erinacea* (Milne-Edwards, 1880) followed by *Munidopsis opalescens* Benedict, 1902. Although *M. erinacea* was originally placed in the *Galathodes* group because of the tridentate rostrum, the rostrum is slender as in *M. opalescens*, rather than broad and flattened as in *M. comarge* and allies such as *Munidopsis serricornis* (Lovén, 1852) and *Munidopsis treis* Ahyong and Poore, 2004. The extinct munidopsid genera *Paragalathea* (lower Jurassic to Paleocene) and *Eomunidopsis* (Upper Jurassic to Upper Cretaceous) (Schweitzer and Feldmann, 2000), also with broad, distally tridentate rostra may be closely related to the *Galathodes* group.

Munidopsis dasypus Alcock, 1894 and *Munidopsis kensleyi* Ahyong and Poore, 2004, form a clade sharing a spiniform rostrum, a subrectangular, transversely convex carapace with anterolateral spines and no eyespines, herein

referred to as the *Dasypus* group (Fig. 1C). The fossil munidopsid genus, *Gastrosacus* (Upper Jurassic to Cretaceous), with a slender rostrum and minimally ornamented carapace, is possibly closely related to the *Dasypus* group. *Munidopsis polymorpha* Koelbel, 1892, is ambiguously positioned in our results, but could belong to the *Dasypus* group; it too has a slender rostrum and minimally armed carapace.

The only *Munidopsis* synonym not represented in our results is the *Anoplnotus* group (Fig. 1A), erected for *Munidopsis polita* (Smith, 1883), but which also includes *Munidopsis bruta* Macpherson, 2007, *Munidopsis granulata* Miyake and Baba, 1967, *Munidopsis palmatus* Khodkina, 1973, *Munidopsis truculenta* Macpherson and Segonzac, 2005 and *Munidopsis vesper* Taylor et al., 2010. In these species, the rostrum is simple and narrow, eye-spines are absent, sternite 3 is entirely fused to sternite 4, the carapace regions are well marked, abdominal tergites unarmed and the dactyli of the walking legs are falcate with smooth margins. Henderson (1888) regarded *Anoplnotus* as a synonym of *Elasmonotus* because of the similar general carapace outline and elongate chelipeds. The affinities of the *Anoplnotus* group are not clear, however, but we suspect that similarities to the *Elasmonotus* group are superficial.

As is evident from the foregoing results, the classification of the munidopsids, both at superfamilial and generic levels requires significant revision. *Munidopsis* sensu lato is not monophyletic given the phylogenetic positions of *Galacantha* and *Shinkaia*. Thus, Shinkaiinae and Munidopsinae cannot be simultaneously maintained without compromising the monophyly of the latter. If a subfamilial structure is to be proposed within Munidopsidae, the most natural division would be between the *Leiogalatea* clade, and the clade containing *Munidopsis*, *Galacantha* and *Shinkaia*, both of which have synapomorphies and exhibit sufficient morphological disparity to support taxonomic division.

The major challenge facing generic revision of the Munidopsidae is identifying diagnosable clades within *Munidopsis*. Chace (1942) regarded meaningful subdivisions of *Munidopsis* as virtually impossible, but present topologies show that most of the previously proposed genera or subgenera correspond to *Munidopsis* clades identified herein. These may translate relatively easily into a natural classification. Resurrecting the old generic system, however, would be premature at this stage. The number of known species of *Munidopsis* sensu lato has doubled since Chace wrote in 1942 and a wider range of forms remains to be analysed to test the validity of the clades identified herein. Many of the old genera will probably prove valid, but their diagnoses and composition require refinement to accommodate the range of forms now known. The generic system of extant species will need to be coordinated with fossil munidopsid genera and new genera will almost certainly be required. To this end, we are extending our sampling of species and molecular markers with the addition of morphological data toward a comprehensive revision of *Munidopsis* sensu lato.

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