

A hard-earned draw: phylogeny-based revision of the deep-sea shrimp *Bentheogennema* (Decapoda: Benthescymidae) transfers two species to other genera and reveals two new species

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The phylogenetic study of the deep-sea genus *Bentheogennema* is based on four molecular markers and 79 morphological characters. All four previously recognized species and two new species of *Bentheogennema*, representatives of all other genera and species groups of Benthescymidae, and three outgroups were included in the analyses. We have examined and coded six major groups of morphological characters related to the carapace (three characters), the pleon and the telson (14), the mouthparts (nine), the armature of the pereopods (five), the thelycum (27) and the petasma (21). Results of morphological and molecular analyses were similar. Two species were transferred from *Bentheogennema* to other genera (for one of them a new genus was erected) and two new species of *Bentheogennema* were described. Three pelagic genera (*Gennadas*, *Bentheogennema* and a new genus) created a robust clade. The divergence of this clade is linked to ‘smoothing’ of the body (reduction of the branchiostegal spine on the carapace, reduction and loss of the dorsolateral spines and the end-piece on the telson) and elaboration of the copulatory structures. We provide amended diagnoses of these three pelagic genera and key to species of *Bentheogennema*.

KEYWORDS: Benthescymidae – evolution – phylogeny – plankton biology – shrimps.

INTRODUCTION

The family Benthescymidae recently encompassed two pelagic genera (mesopelagic *Gennadas* Spence Bate, 1881 and presumably bathypelagic *Bentheogennema* Burkenroad, 1936), two benthopelagic bathyal genera (*Benthescymus* Spence Bate, 1881 and *Benthonectes* Smith, 1885) and one deep-sea genus known from only a few specimens caught both in the water column and near the bottom (*Altelatipes* Crosnier & Vereshchaka, 2008). In contrast to other Dendrobranchiata, phylogeny and phylogeny-based systematics of Benthescymidae remain poorly understood. In order to fill this gap, we initiated a revision of the family with the genus *Gennadas* (16 of the 40 species of the family

(Vereshchaka *et al.*, 2017). In that paper we showed that only copulatory characters provide reliable identification of specimens and robust phylogenetic trees. Inventory of the thelyca (49 characters) and the petasmata (26 characters) retrieved several phylogenetically robust species groups. In addition, we synonymized *Gennadas crassus* Tirmizi, 1960 with *G. gilchristi* Calman, 1925. We also proposed to transfer *Bentheogennema burkenroadi* Krygier & Wasmer, 1975 to *Gennadas*, because the species was deeply nested in the *Gennadas* clade on the phylogenetic tree of Vereshchaka *et al.* (2017).

In light of these previous findings, the genus *B.* encompasses four species: *B. borealis* (Rathbun, 1902), *B. intermedia* (Spence Bate, 1888), *B. pasithea* (de Man, 1907) and *B. stephensi* Burkenroad, 1940 (WoRMS Editorial Board, 2019; *Bentheogennema burkenroadi* has not yet been transferred to *Gennadas*).

Here we take a next step and revise the second genus, *Bentheogennema*. A revision of this group

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faces several challenges. First, specimens of *Bentheogennema* are few and distributed in many collections around the world, as is the case for other deep-sea species, making comparison of characters more difficult. Second, specimens are extremely fragile and are often mutilated during retrieval by nets and trawls: most appendages, and even apical parts of the uropods, the scaphocerites and the telson, are frequently missing. Only copulatory organs and the remaining part of the telson are left for morphological analyses. However, these organs (petasmata in males and thelyca in females) are much less elaborate and informative in *Bentheogennema* than in the rest of Benthescymidae, and provide little information. The deficiency of copulatory characters poses the third problem, which makes molecular analyses desirable for confirmation of most morphological findings. Most specimens of *Bentheogennema*, including types that have been collected in the first half of the 20th century or even earlier, cannot be used for molecular analyses. Recently collected and alcohol-preserved specimens of two species from well-explored and frequently visited areas [*B. intermedia* (Spence Bate, 1888) from the Atlantic and *B. borealis* (Rathbun, 1902) from the North Pacific] are exceptions from this rule, while species from the Indian and Pacific oceans are few or absent. Fourth, original descriptions of *Bentheogennema* were made without satisfactory illustration of distinctive morphological characters (copulatory structures, spination of the telson, etc.), often resulting in inaccurate identification of *Bentheogennema* specimens. If type specimens were not available, authors often made incorrect conclusions [e.g. remarks to *Bentheogennema* in Burkenroad (1936) and Krygier & Wasmer (1975)] or this caused misidentifications [e.g. *B. intermedia* was identified as *B. pasithea* (de Man, 1907) in Vereshchaka (1990)].

Finally, the type of *Bentheogennema stephensi* has been lost: the Dendrobranchiata collected during the 'Dana' Expedition 1928–30 were sent to Dr M. Burkenroad in the 1930s and briefly described without illustrations (Burkenroad, 1940). Later, some Dendrobranchiata types, including that of *Bentheogennema stephensi*, were misplaced, while the rest of the material of *B. stephensi* dried out and was not returned. We have located some 'Dana' specimens in the collection of the Yale Peabody Museum of Natural History (USA), not in the 'home' collection at the Natural History Museum of Denmark. Luckily, we found a few additional specimens collected by French Expeditions from the area not far from the type locality (south-west Pacific), we examined them morphologically and included them in the molecular analyses.

During our examination of available material, we have found specimens that were morphologically different from all known species and presumably represented two new species. One species was represented by alcohol-preserved specimens, which could be studied by molecular methods. The second species was studied only morphologically, as it was collected during the 'Galathea' expedition (1950–52) near the Seychelles (an area not visited by deep-sea biological expeditions in recent years).

In this paper we scrutinize available information on the morphology and species composition of *Bentheogennema*, document principal morphological characters, provide scanning electron photos of thelyca and petasmata of all valid species, make morphological and (where possible) molecular phylogenetic analyses on which we base a new systematics of the genus, and analyse phylogenetic traits in the clade.

MATERIAL AND METHODS

MORPHOLOGICAL ANALYSIS

All four currently recognized, plus two new species, of *Bentheogennema* were examined morphologically (Supporting Information, Appendix S1) and considered as the in-group. In the analysis we also included representatives of all other genera and species groups of Benthescymidae: *Altelatipes* [*A. carinatus* (Smith, 1884)], *Benthescymus* group I, (*B. howensis* Dall, 2001, *B. iridescens* Spence Bate, 1881), *B.* group II (*B. altus* Spence Bate, 1881, *B. investigatoris* Alcock & Anderson, 1899), *Benthonectes* (*B. filipes* Smith, 1885) and *Gennadas* [*G. bouvieri* Kemp, 1909, *G. brevirostris* Bouvier, 1905, *G. capensis* Calman, 1925, *G. scutatus* Bouvier, 1906, *G. talismani* Bouvier, 1906 and *G. valens* (Smith, 1884)]. We chose three outgroups from different families of Penaeoidea, each representing type species of the genus: *Aristaeomorpha foliacea* (Risso, 1827) (analysis 1, Aristeidae), *Penaeus monodon* Fabricius, 1798 (analysis 2, Penaeidae) and *Solenocera membranacea* (Risso, 1816) (analysis 3, Solenoceridae).

We identified 79 binary and one multi-state morphological characters. The characters and their states are listed in the Supporting Information, Appendix S2. The dataset (Supporting Information, Appendix S3) was handled and analysed using a combination of programs using maximum parsimony settings: Winclada/Nona and TNT (Nixon, 1999; Goloboff *et al.*, 2000). Trees were generated in TNT with 30 000 trees in memory, under the 'implicit enumeration' (branch-and-bound) algorithms. Relative stability of clades was assessed by standard bootstrapping (sample with replacement) with 10 000

pseudoreplicates and by Bremer support (algorithm TBR, saving up to 10 000 trees up to 12 steps longer). In all analyses, clades were considered robust if they had synchronously Bremer support ≥ 3 and bootstrap support ≥ 70 .

MOLECULAR ANALYSIS

DNA sequence data were included for 16 species across all five genera of Benthescymidae (the same genera and species groups as in the morphological analysis) and for three species belonging to three genera that were used as outgroups in the morphological analysis. All known species of *Bentheogennema*, except *B. pasithea* and one new species, for which we failed to retrieve any sequences, were included. We had at our disposal material of 16 species from different areas of the world's oceans; sequences for outgroups were taken from NCBI GenBank (Table 1).

On the basis of the results of the Decapod Tree of Life project (Bracken *et al.*, 2009a, b; Felder & Robles, 2009; Robles *et al.*, 2009; Toon *et al.*, 2009; Bracken-Grissom *et al.*, 2014), we have selected four genetic markers proven to be informative at fine and coarse evolutionary scales: a mitochondrial ribosomal gene (16S), a mitochondrial protein-coding gene (cytochrome *c* oxidase subunit I, *COI*), a nuclear ribosomal gene (18S) and a nuclear protein-coding gene *H3*.

Total genomic DNA was extracted from muscle tissue of the pleon or pleopods using the Wizard SV Genomic DNA Purification Kit (Promega) in accordance with the manufacturer's protocol. One or more sets of primers were chosen to amplify targeted gene regions using polymerase chain reaction (PCR) of the *COI* gene was performed with the primers: LCOI 1490/HCOI2198 (~650 bps; Folmer *et al.*, 1994) or COL6/COH6 (the same region; Schubart & Huber, 2006; Schubart, 2009). The mitochondrial large subunit 16S rRNA was amplified by 16L2/16H3 primers (~550 bps; Schubart *et al.*, 2002; Reuschel & Schubart, 2006) and the nuclear small subunit 18S rRNA was amplified by A/L, C/Y, O/B primers (~1800 bps; Apakupakul *et al.*, 1999). Nuclear *H3* gene fragment was amplified by *H3A/H3B* primers (~330 bps; Colgan *et al.*, 1998). PCR amplification reactions were performed in 25 μ L containing 1 \times PCR buffer, 1 μ L of 10 μ M of primer pair mix, 1 μ L of DNA template, 0.2 mM of each dNTP and 0.5 units of Taq polymerase. The thermal profile used an initial denaturation for 3 min at 95 $^{\circ}$ C followed by 35–40 cycles of 20 s at 94 $^{\circ}$ C, 30 s at 45–57 $^{\circ}$ C depending on primer pair and species, 1 min at 72 $^{\circ}$ C and a final extension of 7 min at 72 $^{\circ}$ C. PCR products were purified using the PCR Purification Kit protocol (Promega) and sequenced in both

directions using BigDye Terminator v.3.1 (Applied Biosystems). Each sequencing reaction mixture, including 0.5 μ L of BigDye Terminator v.3.1, 0.8 μ L of 1 μ M primer and 1–2 μ L of purified PCR template, was run for 30 cycles of 96 $^{\circ}$ C (10 s), 50 $^{\circ}$ C (5 s) and 60 $^{\circ}$ C (4 min). Sequences were purified by ethanol precipitation to remove unincorporated primers and dyes. Products were re-suspended in 14 μ L formamide and electrophoresed in ABI Prism-3500 sequencer (Applied Biosystems). The nucleotide sequences were cleaned and assembled using CodonCode Aligner v.7.1.1. Protein-coding sequences (*COI*, *H3*) were checked for indels and stop codons to prevent the inclusion of pseudogenes. All sequences were then compared to genes reported in GenBank using BLAST (National Center for Biotechnology Information, NCBI) to check for potential contamination.

Individual gene alignments were performed using MEGA 5 (Tamura *et al.*, 2011), implementing the 'MUSCLE' option (Edgar, 2004). Missing data were designated with a '?' for any incomplete sequences. All obtained sequences were submitted to the NCBI GenBank database (Table 1).

AICc metric implemented in PartitionFinder2 (Lanfear *et al.*, 2017) was used to obtain the optimal partitioning scheme for our dataset. Results from PartitionFinder2 recommended an eight-partition scheme by gene and codon (*H3*, *COI*), which was used in the final analyses.

To assess phylogenetic relationships between species, Bayesian inference (BI) and maximum likelihood (ML) analyses were performed. The BI analysis was conducted in MrBayes v.3.2.6 (Ronquist *et al.*, 2012) for the concatenated dataset of all genes. Substitution models for each partition were used in accordance with the PartitionFinder2 results: the General Time Reversible model with a gamma-shaped rate variation across sites and with a proportion of invariable sites (GTR+I+G) was recommended for 18S and first codon partition of *COI*, GTR+I was recommended for first codon partition of *H3* and second codon partition of *COI*, GTR+G was recommended for 16S, third codon partition of *COI* and *H3*, and the Jukes–Cantor model (JC+I) was recommended for second codon partition of *H3*. Two independent runs, each consisting of four chains, were executed for this analysis. The analyses ran for 6 000 000 generations, sampled every 5000 generations, and with a relative burn-in 25%. A 1% average standard deviation of split frequencies was reached after about 1 million generations, and a 75% majority rule consensus tree was obtained from the remaining trees.

The maximum likelihood (ML) analysis was performed in RAxML GUI v.1.3 (Stamatakis, 2006)

Table 1. Individuals used in phylogenetic reconstruction with localities, voucher numbers and GenBank accession numbers

Species	Vaucher No		Locality/reference		GenBank accession numbers			
	Latitude	Longitude	Latitude	Longitude	COI	16S	18S	H3
<i>Altelatipes carinatus</i>	20°47' S	55°04' E	South-west Indian Ocean: Reunion		MK931358	MK950925	MK950909	MK931376
<i>Boreogennema borealis</i>	28°03,95'N	130°31,89'E	West Pacific: Japan		MK931359	MK950926	MK950910	MK931377
<i>Bentheogennema intermedia</i>	34°28'N	7°43' W	Gulf of Cadiz		MK931362	MK950929	MK950913	MK931380
<i>Bentheogennema intermedia</i>	01°41'N	87°06'E	Central Indian Ocean		MK931361	MK950928	MK950912	MK931379
<i>Bentheogennema stephenseni</i>	23°40'S	168°05'E	New Caledonia		MK931364	MK950931	N	MK931382
<i>Bentheogennema stephenseni</i>	22°51'S	166°23'E	New Caledonia		MK931363	MK950930	N	MK931381
<i>Bentheogennema corbariae</i>	01°43'N	87°08'E	Central Indian Ocean		MK931360	MK950927	MK950911	MK931378
<i>Benthesicymus altus</i>	20°32,7'S	55°40,9'E	South-west Indian Ocean: Reunion		MK931365	MK950932	MK950914	MK931383
<i>Benthesicymus howensis</i>	24°16'S	167°38'E	New Caledonia		MK931366	MK950933	MK950915	MK931384
<i>Benthesicymus investigatoris</i>	2°41'S	150°03'E	Papua New Guinea		MK931367	MK950934	MK950916	MK931385
<i>Benthesicymus iridescens</i>	25°45'S	162°50'E	New Caledonia		MK931368	MK950935	MK950917	MK931386
<i>Benthonectes filipes</i>	03°57'S,	153°49'E	Papua New Guinea		MK931369	MK950936	MK950918	MK931387
<i>Gennadas bouvieri</i>	14°07'N	39°31'W	Central Atlantic		MK931370	MK950937	MK950919	MK931388
<i>Gennadas</i>	5°05'N	22°00'W	Central Atlantic		MK931371	MK950938	MK950920	MK931389
<i>Gennadas capensis</i>	4°43'-4°39'N	37°09'-37°08'W	Central Atlantic		MK931372	MK950939	MK950921	MK931390
<i>Gennadas scutatus</i>	0°03'-0°01'S	36°01'W	Central Atlantic		MK931373	MK950940	MK950922	MK931391
<i>Gennadas talismani</i>	10°49'N	41°00'W	Central Atlantic		MK931374	MK950941	MK950923	MK931392
<i>Gennadas valens</i>	16°38'-16°34'N	38°15'-38°17'W	Central Atlantic		MK931375	MK950942	MK950924	MK931393
<i>Aristaeomorpha foliacea</i>	da Silva et al., 2011; Bracken et al., 2010		Mediterranean Sea; Gulf of Mexico		JQ305888	GQ487491	GQ487500	GQ487517
<i>Penaeus duorarum</i>	Unpublished; Bracken et al., 2009b		Chesapeake Bay; Gulf of Mexico		MH087613	FJ943438	FJ943445	FJ943459
<i>Solenocera necopina</i>	Bracken-Griessom et al., 2012		Gulf of Mexico		N	JX403853	JX403835	JX403894

Sequences obtained from GenBank are indicated in bold. An 'N' designates gene sequences we were unable to acquire.

and the GTR+G model was used. Bootstrap resampling with 1000 replicates was conducted using the thorough bootstrap procedure to assign support to branches in the ML tree. Final ML tree was generated using the same partitioning scheme of all concatenated genes.

We considered the clades statistically significant if they had a synchronous support of posterior probabilities ≥ 0.9 in the BI analysis and bootstrap value $\geq 70\%$ in the ML analysis.

To investigate the levels of genetic variation between *Bentheogennema* species, pairwise Kimura 2-parameter distances (K2P; Kimura, 1980) were computed in MEGA 5.

ABBREVIATIONS

Petasma: PI, pars interna; PM, pars media; PE, pars externa; LA, lobus accessories; gs, grasping structure. Thelycum: S6, sternite of the sixth thoracic segment; AS7 and PS7, anterior and posterior parts of sternite of the seventh thoracic segment; S8, sternite of the eighth thoracic segment.

RESULTS

MORPHOLOGICAL CHARACTERS

We coded six major groups of morphological characters (see Fig. 1 for character grouping and Figs 2–4 for

visualization of selected states; all represented in Supporting Information, Appendix S2):

- carapace-linked (characters 0–2), a total of three characters;
- pleon/telson-linked (characters 3–16), a total of 14 characters;
- mouthparts-linked (characters 17–25), a total of nine characters;
- pereopods-linked (characters 26–30), a total of five characters;
- thelycum-linked (characters 31–57), a total of 27 characters;
- petasma-linked (characters 58–78), a total of 21 characters.

As noted in the Introduction, only a few characters of taxonomic importance can be examined in fragile deep-sea species, because specimens are usually damaged. Among these characters the most informative were spination of the telson and morphology of the genital structures: the petasmata and the thelyca. Contribution of these characters to the character matrix was significant. We documented the characters linked to the telson (Fig. 2), the thelycum (Fig. 3) and the petasma (Fig. 4).

Examination of available material resulted in a discovery of two new species. One of these (*B. corbariae*) is similar to *B. stephenseni* in having a single pair of

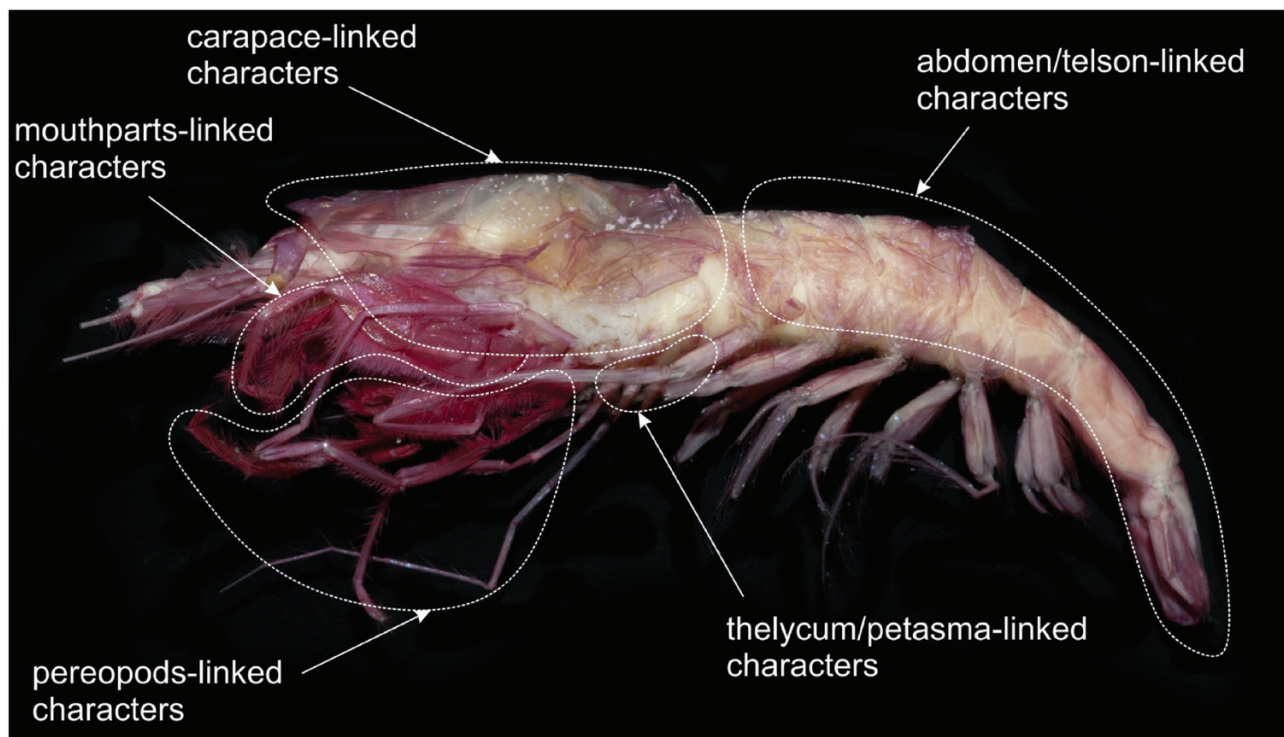


Figure 1. General view and grouping of morphological characters of *Bentheogennema*.

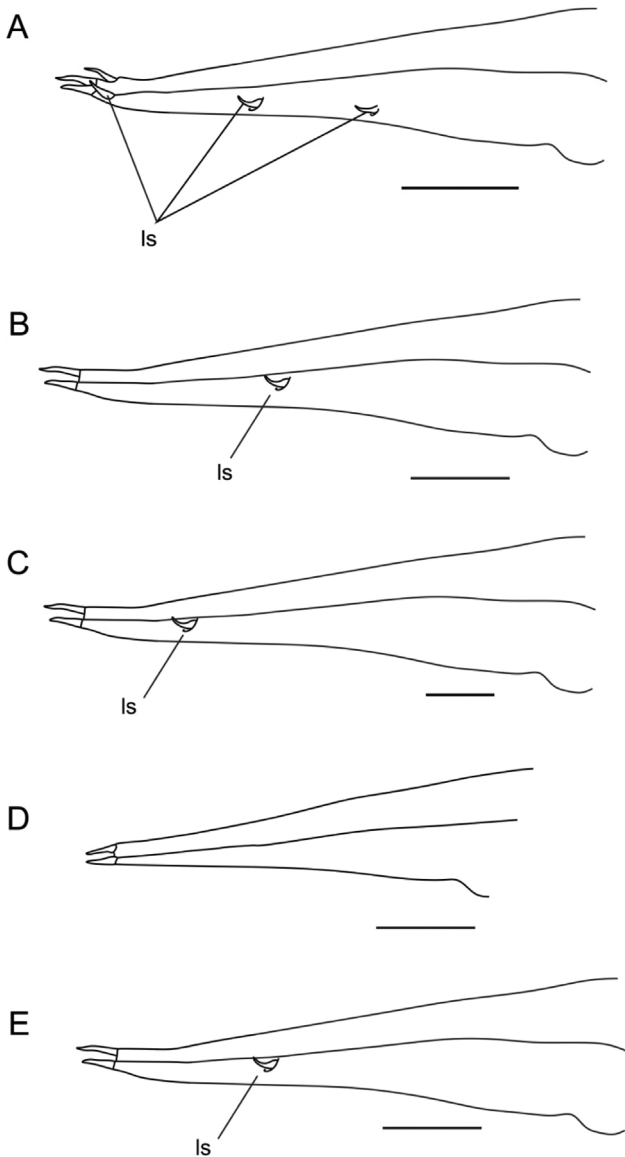


Figure 2. Telsons of *Bentheogennema intermedia* (Spence Bate, 1888), A, NHMD 228678; *Bentheogennema stephensi* Burkenroad, 1940, B, MNHN-Na-6453; *Bentheogennema corbariae*, C, MNHN-Na-6453; *Bentheogennema torbenwolffi*, D, NHMD 228678, and *Boreogennema borealis* (Rathbun, 1902), E, MNHN-IU-2016-9205. Abbreviations: ls, lateral spines. Scale bars 1 mm.

the dorsolateral spines near dorsal surface, but both species differ in the position of the spines along the length of the telson (Fig. 2) and in the morphology of the thelycum (Fig. 3). The other new species (*B. torbenwolffi*) differs from all *Bentheogennema* in the absence of the dorsolateral spines and in the unique, wide, rounded, labrum-like, posterior scutum on S6 of the thelycum (Figs 2, 3). Males of *B. torbenwolffi* have not been found.

MORPHOLOGICAL ANALYSES

Analysis 1 with *Aristaeomorpha foliacea* as outgroup retrieves a single most parsimonious (MP) tree (Fig. 5; Supporting Information, Appendix S4) with a score of 99 (Ci = 77, Ri = 87). The tree shows five major robust clades: (1) *Benthesicymus* group II (*B. altus* and *B. investigatoris*); (2) *Altelatipes* + *Benthesicymus* group I + *Benthonectes* (*A. carinatus*, *B. howensis*, *B. iridescens* and *B. filipes*); (3) *Bentheogennema* (*B. intermedia*, *B. stephensi*, *B. corbariae* and *B. torbenwolffi*); (4) *Boreogennema* (*B. borealis*); (5) *Gennadas* (*G. bowieri*, *G. brevirostris*, *G. capensis*, *G. pasithea*, *G. scutatus*, *G. talismani* and *G. valens*). Clades 3–5 are combined in a robust clade.

Analysis 2 with *Penaeus monodon* as outgroup also retrieves a single MP tree (Fig. 5; Supporting Information, Appendix S4) with a score of 100 (Ci = 79, Ri = 88) and with the same clades having slightly different (but statistically significant) support.

Analysis 3 with *Solenocera membranacea* as outgroup also retrieves a single MP tree (Fig. 5; Supporting Information, Appendix S4) with a score of 100 (Ci = 79, Ri = 88). The tree topology is similar to that of analyses 1 and 2.

In all three analyses, genera of Benthesicymidae are monophyletic except *Benthesicymus*, which is represented by two clades (group I and group II). Species of *Gennadas* always encompass four clades: (1) robust *G. brevirostris* + *G. pasithea* + *G. scutatus*; (2) *G. talismani* + *G. valens*, supported by bootstrap but not by Bremer analysis; (3) *G. bowieri* and (4) *G. capensis*.

Relationships within *Bentheogennema* were not resolved.

MORPHOLOGICAL SYNAPOMORPHIES

Morphological synapomorphies supporting clades are mapped on Figure 6. The clade *Bentheogennema* + *Boreogennema* + *Gennadas* is supported by the following synapomorphies:

- Pleon: loss of the carina on the fourth and fifth somites (characters 5 and 6).
- Telson: simplification of the end of the telson: apically truncate (11), without triangular end-piece between terminal spines (14).
- Mouthparts: distally suboval exopod of first maxillipeds (18).
- Petasma: PM as a simple straight lamina (65), development of PE (74).

The clade *Bentheogennema* was supported by:

- Carapace: reduction of branchiostegal spine (1, 2).
- Thelycum: development of posterior protuberances on S6 (35), simple trapezoid S7 (44).

The clade *Boreogennema* was supported by:

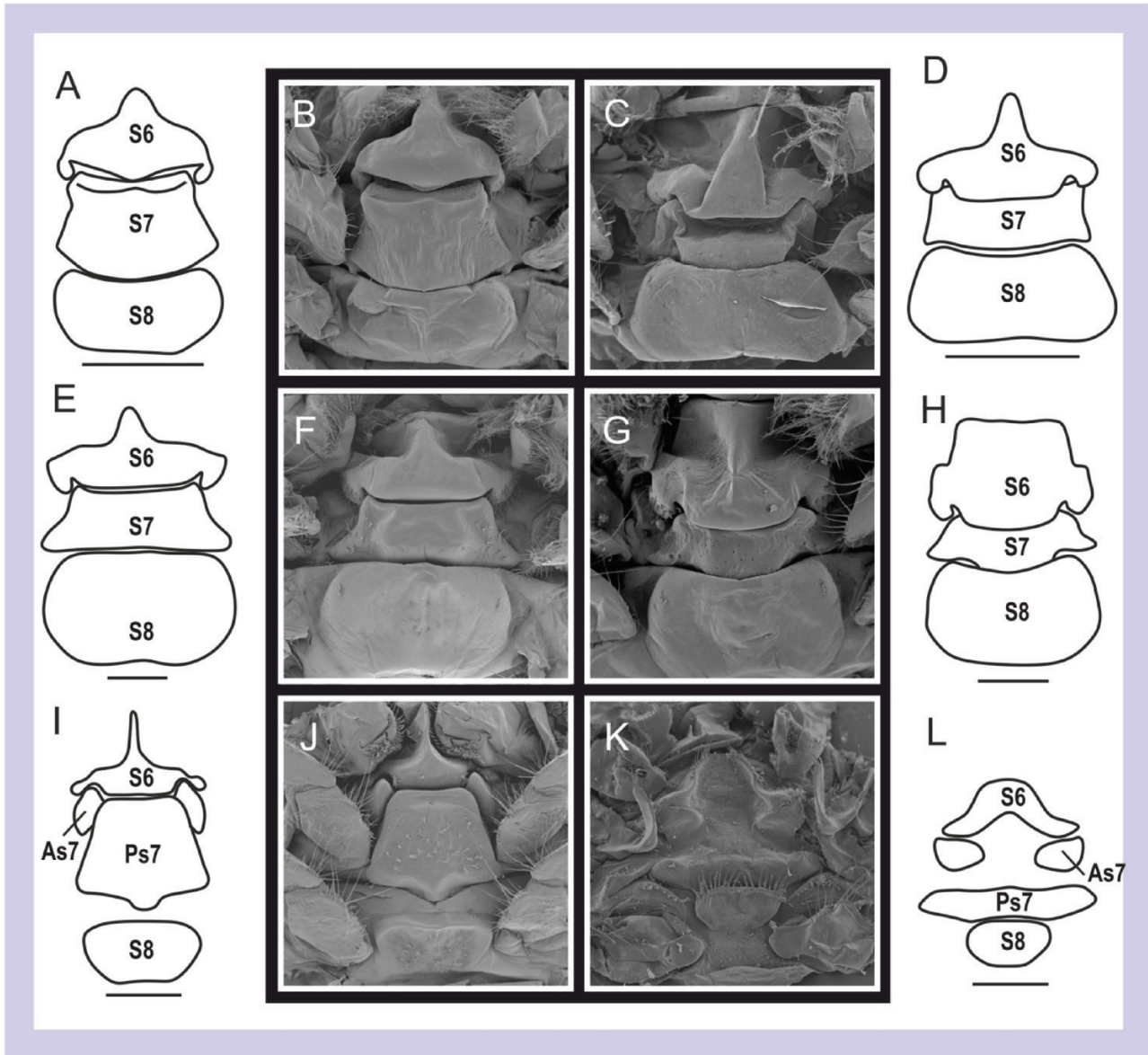


Figure 3. Thelyca (SEMs and schemes) of *Bentheogennema intermedia* (Spence Bate, 1888), A, B, MNHN-Na-12445; *Bentheogennema stephensi* Burkenroad, 1940, C, D, YPM 40240; *Bentheogennema corbariae*, E, F, MNHN-Na-6453; *Bentheogennema torbenwolffi*, G, H, ZMUK-NHMD 228683; *Boreogennema borealis* (Rathbun, 1902), I, J, MNHN-IU-2016-9205, and *Gennadas pasithea* de Man, 1907, (K, L, NHMD-263611). Abbreviations: S6, sternite of the sixth thoracic segment; AS7 and PS7, anterior and posterior parts of sternite of the seventh thoracic segment; S8, sternite of the eighth thoracic segment); sc, scutum. Scale bars 1 mm.

- Telson: reduction of dorsolateral spines (a single pair set near dorsal margin – 16).
- Thelycum: division of S7 (49).

The clade *Gennadas* was supported by:

- Telson: loss of dorsolateral spines (12).
- Pereopods: a specialized distal tooth on the basis of the first pair (26).

- Thelycum: elaborate S6 (31).
- Petasma: modified (divided or scoop-like) PE (75).

MOLECULAR ANALYSES

We successfully obtained 18 *COI* sequences, 18 16S sequences, 16 18S sequences and 18 *H3* sequences. The four-marker dataset comprised 3859 bp. Both

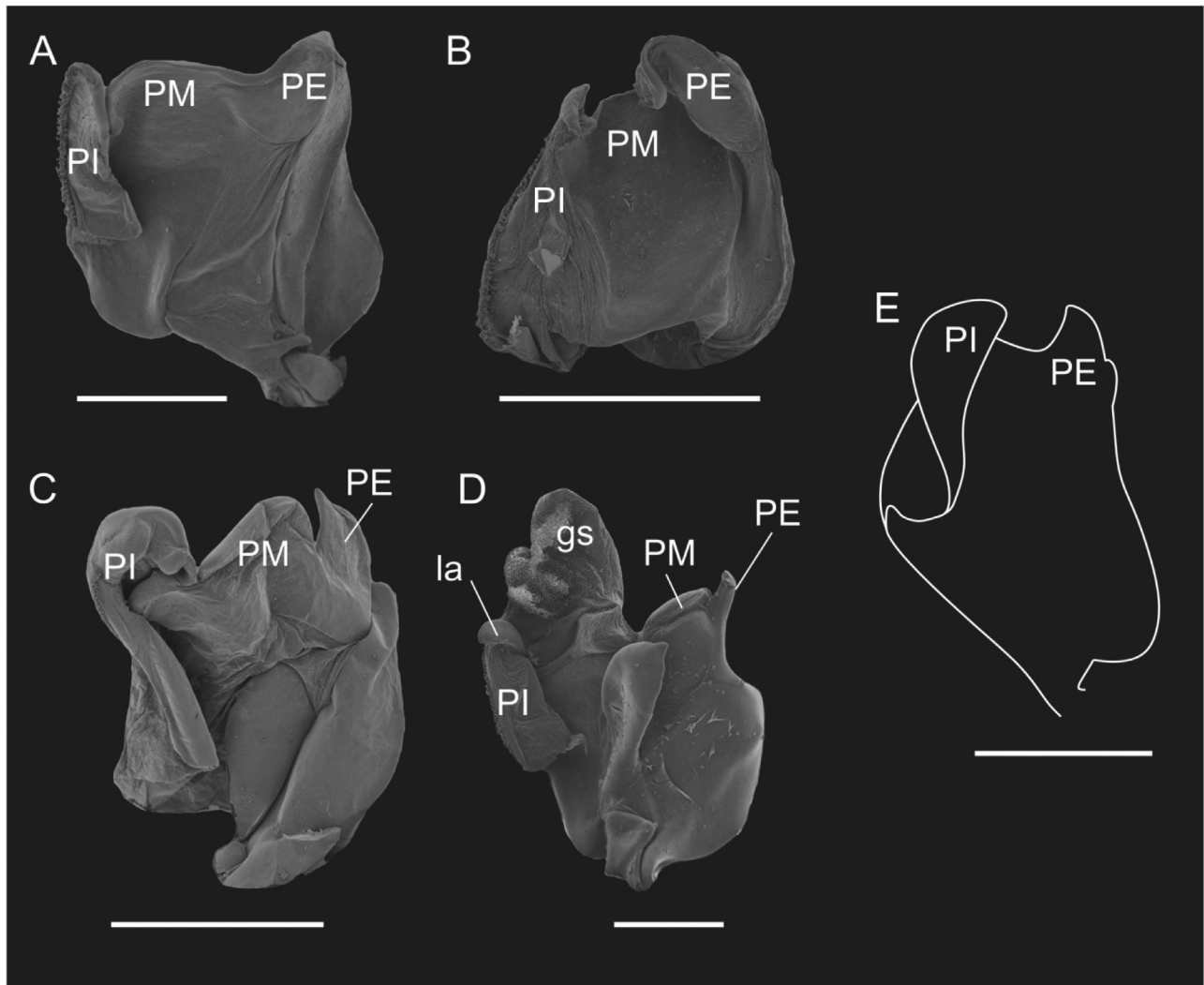


Figure 4. Petasmata of *Bentheogennema intermedia* (Spence Bate, 1888), A, MNHN-Na-12445; *Bentheogennema stephensi* Burkenroad, 1940, B, YPM 40240; *Boreogennema borealis* (Rathbun, 1902). C, MNHN-IU-2016-9205; *Gennadas pasithea* de Man, 1907, D, NHMD-263610; *Bentheogennema corbariae*, E, MNHN-IU-2016-11805). Abbreviations: PI, pars interna; PM, pars media; PE, pars externa; LA, lobus accessories; gs, grasping structure. Scale bars 1 mm.

ML and BI trees have identical topology and receive high support at most nodes (Fig. 7). Benthescyidae is monophyletic and well-supported on both trees. It encompasses five robust clades, the same as found in the morphological analysis: (1) *Benthescyimus* group II (*B. altus* and *B. investigatoris*); (2) *Altelatipes* + *Benthescyimus* group I + *Benthonectes* (*A. carinatus*, *Benthescyimus howensis*, *Benthescyimus iridescens* and *Benthonectes filipes*); (3) *Bentheogennema* (*B. intermedia*, *B. stephensi* and *B. corbariae*); (4) *Boreogennema* (*B. borealis*); (5) *Gennadas* (*G. bouvieri*, *G. brevirostris*, *G. capensis*, *G. scutatus*, *G. talismani* and *G. valens*). The clades *Benthescyimus* group I + *Benthonectes* and *B. intermedia* + *B. stephensi* gain statistical support

either on BI or on ML trees and are not considered here as robust. As in the morphological analyses, clades 3–5 were combined in a single robust clade. In addition, clade *Gennadas* + *Boreogennema* also gains statistical support.

As in the morphological analysis, all genera of Benthescyidae are monophyletic, except paraphyletic *Benthescyimus*. Species of *Gennadas* form three robust clades: (1) *G. brevirostris* + *G. scutatus*; (2) *G. bouvieri* + *G. talismani* + *G. valens*; and (3) *G. capensis*.

In order to gain a deeper insight into relationships between *Bentheogennema*, *Boreogennema* and *Gennadas*, we calculated interspecific K2P distances among available specimens of these genera (Table 2).

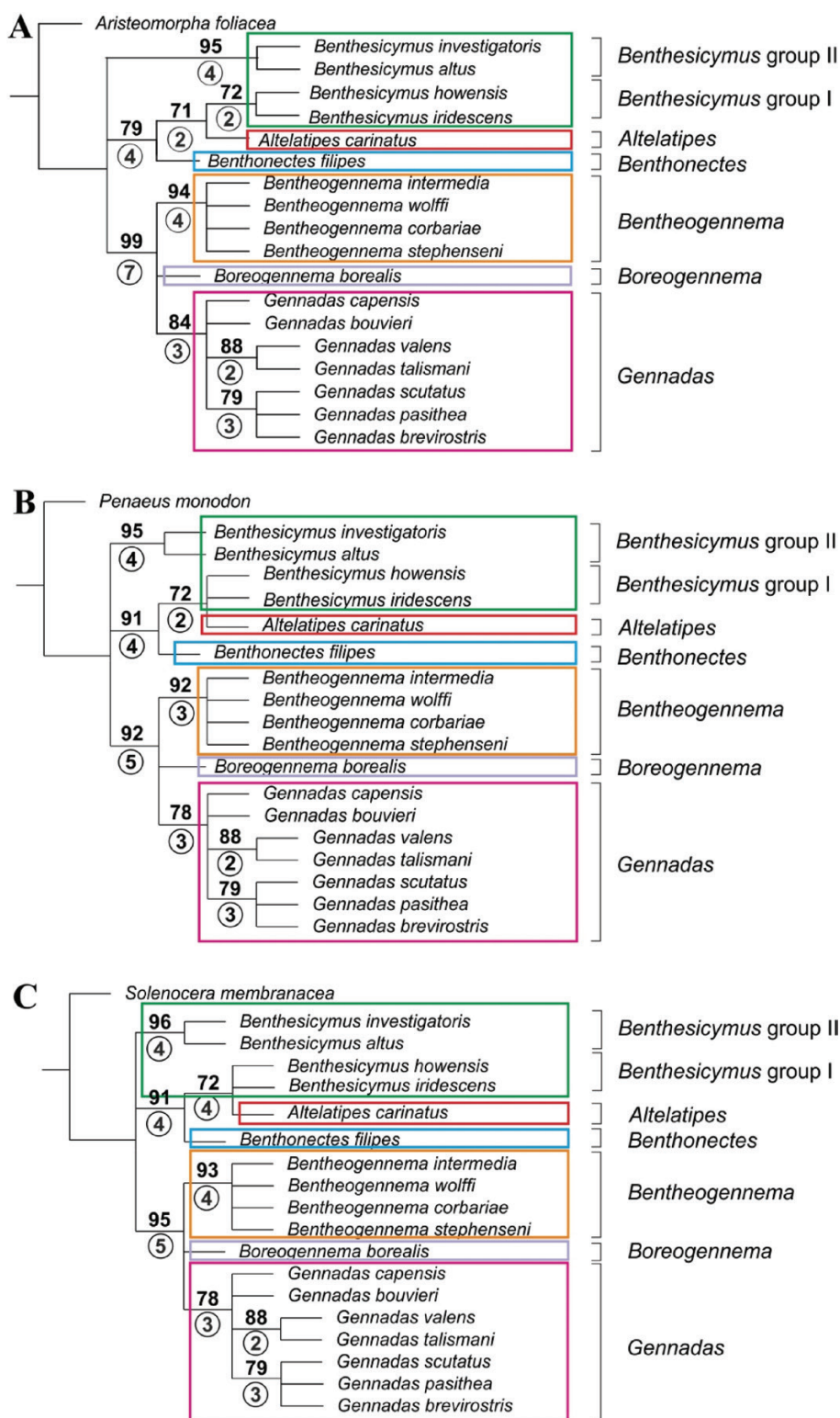


Figure 5. Statistical support on morphological MP trees with *Aristaeomorpha foliacea* (Risso, 1827) (analysis 1, A), *Penaeus monodon* Fabricius, 1798 (analysis 2, B) and *Solenocera membranacea* (Risso, 1816) (analysis 3, C) as outgroups. Different colours indicate genera. Only clades supported by either Bremer values (in circles, below branches) or bootstrap values (above branches) are shown.

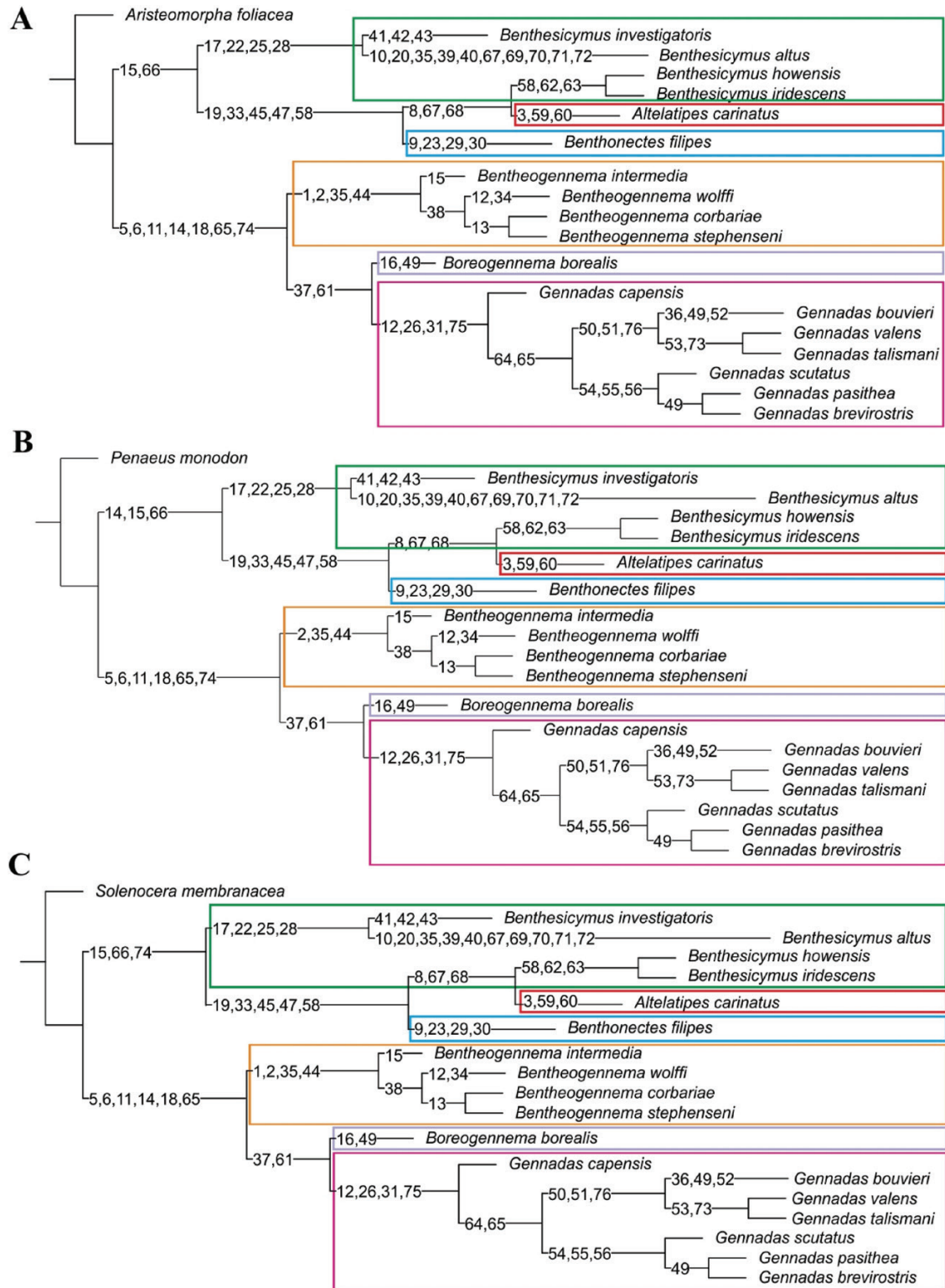


Figure 6. Synapomorphies on morphological MP trees with *Aristaeomorpha foliacea* (Risso, 1827) (analysis 1, A), *Penaeus monodon* Fabricius, 1798 (analysis 2, B) and *Solenocera membranacea* (Risso, 1816) (analysis 3, C) as outgroups. Different colours indicate genera (see character coding in Supporting Information, Appendix S2).

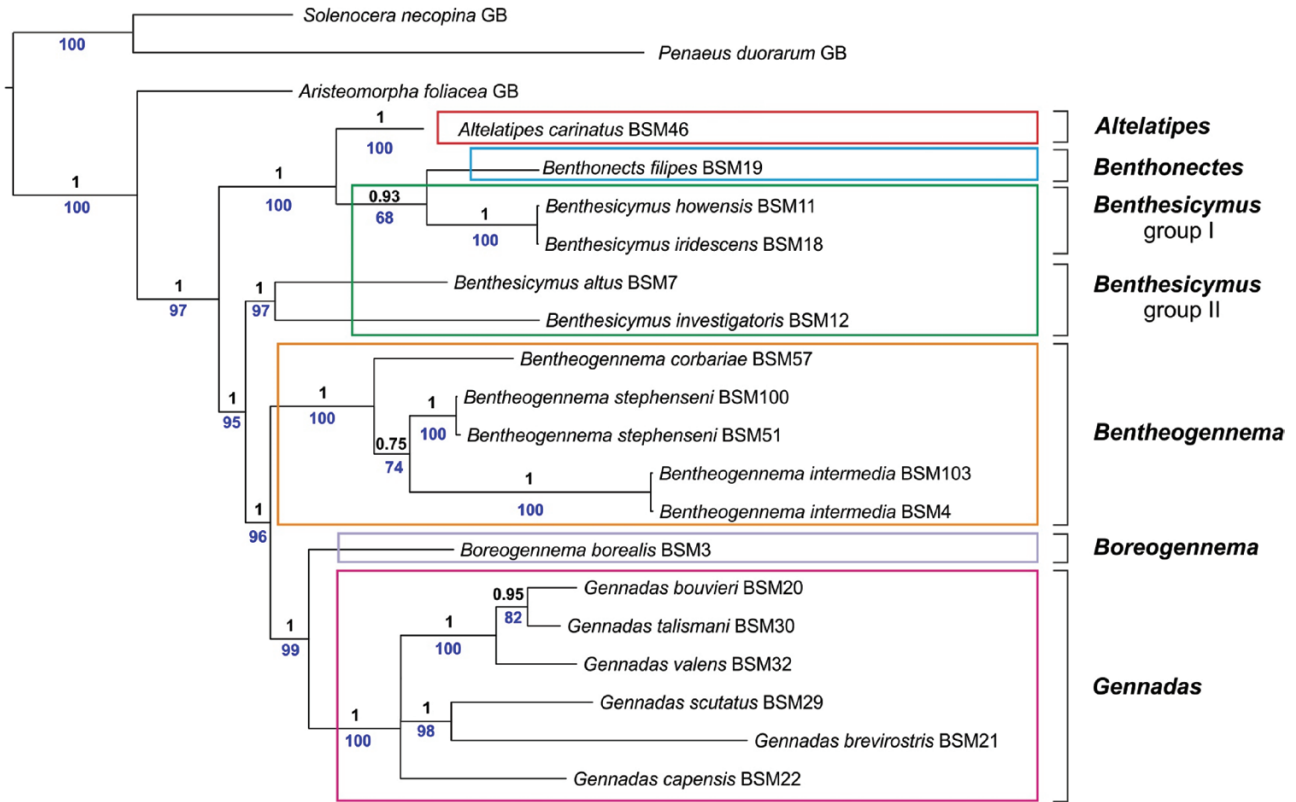


Figure 7. Molecular tree with *Aristaeomorpha foliacea* (Risso, 1827), *Penaeus duorarum* Burkenroad, 1939 and *Solenocera necopina* Burkenroad, 1939 as outgroups. The horizontal scale bar marks the number of expected substitutions per site. Statistical support indicated as Bayesian posterior probabilities (black, above branches) and ML bootstrap analysis with 1000 replicates (blue, below branches). Different colours indicate genera.

Bentheogennema and *Boreogennema* are relatively distantly related: for 16S, the distances were 2.8–4.4% between species of *Bentheogennema* and 6.6–8.3% between each species of *Bentheogennema* and *B. borealis*. For *COI*, the distances between species of *Bentheogennema* were also shorter than between each of them and *B. borealis* (13.8–15.6% and 19.1–20.4%, respectively). Relationships between *Boreogennema* and *Gennadas* are less clear owing to higher genetic heterogeneity in *Gennadas*. For *COI* and 16S, the distances overlap: 13.3–18.8% between *Gennadas* species, 17.0–21.6% between *Gennadas* species and *Boreogennema* for *COI*, 7.5–9.0% between *Gennadas* species and *Boreogennema* for 16S.

Relationships within *Bentheogennema* are not resolved: *B. intermedia* and *B. stephenseni* form a common clade on the ML tree, but this clade was not robust in the BI tree (Fig. 7).

DISCUSSION

IMPACT OF PHYLOGENETIC ANALYSES ON CLASSIFICATION

Both morphological and molecular analyses provide similar results and nearly identical sets of supported clades. Retrieved trees are alike in topology and mostly differ in clade support: in general, clade support on molecular trees is more robust than those on the morphological trees (see Figs 6, 7). Both morphological analyses 1–3 and molecular analyses (BI and ML) call for modification of the taxonomy of Benthesicymidae.

The status of Bentheogennema pasithea

We examined available material of *B. pasithea*, including the types, and found both the thelycum and the petasma of this species to be greatly elaborate and structurally similar to those seen in the core species of *Gennadas* (Vereshchaka *et al.*, 2017). Our phylogenetic

Table 2. Pairwise nucleotide divergence (%) under the Kimura two-parameter model based on cytochrome c oxidase subunit I (COI; below the diagonal) and 16S (above the diagonal) sequences between *Bentheogennema*, *Boreogennema* and *Gennadas*. n/d – data are not available. Different colours mark different genera

Genus	Bentheogennema			Boreogennema			Gennadas				
	Species	<i>B. intermedia</i>	<i>B. stephenseni</i>	<i>B. corbariae</i>	<i>B. borealis</i>	<i>G. bouvieri</i>	<i>G. breviostris</i>	<i>G. capensis</i>	<i>G. scutatus</i>	<i>G. talismani</i>	<i>G. valens</i>
Bentheogennema											
	<i>B. intermedia</i>	4.4	4.0	8.3	11.8	11.5	13.4	11.2	10.6	11.3	
	<i>B. stephenseni</i>	13.8	2.8	7.4	9.9	8.9	13.1	9.2	8.5	9.2	
	<i>B. corbariae</i>	14.7	15.6	6.6	10.2	10.1	12.4	9.2	8.1	9.7	
Boreogennema	<i>B. borealis</i>	19.1	19.6	20.4	8.6	9.0	9.0	8.3	8.3	7.5	
Gennadas	<i>G. bouvieri</i>	22.6	21.5	21.9	21.6	9.7	10.8	9.4	7.0	6.8	
	<i>G. breviostris</i>	22.5	19	22.3	18.5	17.1	11.3	8.7	8.1	9.2	
	<i>G. capensis</i>	19.8	20.6	18.6	17.1	16.9	16.4	10.1	11.5	10.3	
	<i>G. scutatus</i>	22.5	19.6	20.7	18.4	18.3	14.8	15.4	9.0	9.7	
	<i>G. talismani</i>	21.2	21.7	20.7	18.7	14.9	16.1	18.7	15.8	6.2	
	<i>G. valens</i>	22.9	20.3	19.8	17.0	17.6	14.4	16.8	15.8	13.3	

analysis showed that this species is deeply nested into the *Gennadas* clade. It is remarkable that this species was originally described as *Gennadas* (de Man, 1907) and later transferred to *Bentheogennema* by Burkenroad (1936). Here we transfer *B. pasithea* back to *Gennadas* and provide an emended diagnosis of this species.

GENNADAS PASITHEA DE MAN, 1907

(FIGS 3KL, 4D)

Type material: Female, carapace length 8 mm, ZMA.CRUDS.D.102591, ‘Siboga’, St. 230, 03°58’ S, 128°20’ E, 0-2000 m (holotype); male, carapace length 11 mm, ZMA.CRUDS.D.102591, ‘Siboga’, St. 230, 03°58’ S, 128°20’ E, 0-2000 m (paratype).

Material examined: Nine females and eight males (details in Supporting Information, Appendix S1).

Type locality: Equatorial Indian Ocean, 03°58’ S, 128°20’ E.

Emended diagnosis: Integument membranous; rostrum not reaching distal corneal margin, armed with one apical and one dorsal tooth; carapace with developed branchiostegal spine set on anterior margin, hepatic spine absent; pleon with first to fifth somites dorsally rounded and sixth somite dorsally carinate; telson posteriorly truncate, with a single pair of apical spines, dorsolateral spines absent. Eyestalks with long tubercle. First maxilliped with exopod not segmented distally; fourth and fifth pereopods with dactyl slender, not articulated. Petasma (Fig. 4D) subrectangular, LA and grasping structure present, PM and PE entire. Thelycum (Fig. 3K, L): S6 subtriangular, bearing setose shield directed forward; S7 divided, AS7 as two subtriangular protrusions with sharp anterior angles, PS as long chitinized strip, laterally produced beyond coxae, with two groups of lateral setae in addition to two groups of sublateral setae, coxae with long setose protuberances; S8 with setose shield directed forward.

Geographical distribution: The type material and the examined material from the Dana Expeditions derive from a narrow strip between 12° S and 4° N and 56° E and 138° E in the Indian Ocean and the West Pacific. This species is probably associated with the Equatorial waters of this region; records from other oceanic areas (e.g. Pérez Farfante & Kensley, 1997) may be a result

of misidentification due to an incomplete original description.

Vertical distribution: Meso- and bathypelagic.

The status of Bentheogennema borealis

Like *B. pasithea*, this species was described as *Gennadas* and later transferred to *Bentheogennema* by Burkenroad (1936). Morphological analysis shows that this species shares characters of both *Gennadas* and *Bentheogennema*. The structure of the thelycum (S7 divided) resembles that of *Gennadas*, while the structure of the petasma (grasping structure absent, simple unspecialized PE) and the presence of the dorsolateral movable spines on the telson, both make the species similar to *Bentheogennema*. Furthermore, *B. borealis* does not form a clade with *Bentheogennema* in morphological or molecular trees. Interspecific K2P distances (Table 2) also support the molecular divergence of *B. borealis* from species of core *Bentheogennema*. Relations between *B. borealis* and *Gennadas* are more ambivalent: they create a robust clade on molecular trees and can be formally combined in a single genus. However, this clade is not robust on any of the morphological trees: Bremer and bootstrap supports are always low (Fig. 5A–C). In respect that *B. borealis* and *Gennadas* also show significant morphological difference, notably in copulatory structures, we propose a new genus for it: *Boreogennema*.

BOREOGENNEMA LUNINA ET.AL. GEN. NOV.

(Figs 2E, 3 IJ, 4C)

Diagnosis: Integument membraneous; rostrum not reaching distal corneal margin, armed with one apical and one dorsal tooth; carapace with developed branchiostegal spine set on anterior margin, hepatic spine absent; pleon with first to fifth somites dorsally rounded and sixth somite dorsally carinate; telson posteriorly truncate, with a single pair of movable dorsolateral spines near dorsal margin and a single pair of apical spines (Fig. 2E). Eyestalks with long tubercle; first maxilliped with exopod not segmented distally; fourth and fifth pereopods with dactyl slender, entire. Petasma (Fig. 4C) subrectangular, grasping structure absent, PM as convex lamina, PE as entire lash. Thelycum (Fig. 3IJ): S6 pentagonal (sharp angle directed forward), no posterior setose protuberances; S7 divided, AS7 as a pair of widely separated subtriangular elevations, PS7 as pentagonal shield; S8 as simple subrectangular plate.

LSID: urn:lsid:zoobank.org:act:D1B577FE-102B-4220-B502-03018569E52F, 12.07.2019.

Species included: *Boreogennema borealis* (Rathbun, 1902), comb. nov.

Type species: *Gennadas borealis* Rathbun, 1902, by monotypy.

Geographical distribution: North Pacific.

Vertical distribution: Meso- and bathypelagic.

Composition and diagnosis of Bentheogennema

In light of our findings, the composition of *Bentheogennema* should be corrected: two species (*B. pasithea* and *B. borealis*, see above) should be removed and two new species (described below) should be added. Characters such as the presence of 1–3 pairs of dorsolateral spines on the telson, which was traditionally diagnostic for *Bentheogennema*, is no longer supported: spines may not only range in number, but can be absent altogether. Moreover, a detailed examination shows that these spines are probably not homologous: they are set at different positions along the longitudinal axis of the telson, either near its dorsal (*B. corbariae* and *B. stephensi*) or ventral (*B. intermedia*) margin. It is notable that all Benthescymidae, except *Gennadas* (in which the spines are absent), always have three pairs of the dorsolateral spines set close to the ventral margin of the telson at fixed positions along the longitudinal axis of the telson (Fig. 2A–C). It is likely that these spines in all *Bentheogennema*, except *B. intermedia*, are not homologous to the dorsolateral spines in the rest of Benthescymidae and thus probably evolved independently.

The only set of diagnostic characters of *Bentheogennema* is now associated with the morphology of the copulatory structures, the thelycum and the petasma. Other external characters in greatly mutilated specimens cannot be described with certainty (see photos of specimens in Supporting Information, Appendix S5). Here we provide the emended diagnosis of *Bentheogennema* along with the synopsis of the species included.

BENTHEOGENNEMA BURKENROAD, 1936

Emended diagnosis: Integument membraneous; rostrum not reaching distal corneal margin, armed with one apical and one dorsal tooth; carapace with rudimentary branchiostegal spine set on anterior margin, hepatic spine absent; pleon with first to fifth

somites dorsally rounded and sixth somite dorsally carinate; telson posteriorly truncate, with 0–3 pairs of movable dorsolateral spines and a single pair of apical spines. Eystalks with long tubercle. First maxilliped with exopod not segmented distally; fourth and fifth pereopods with dactyl slender, not articulated. Petasma subrectangular, LA and grasping structure absent, PM as straight lamina between PI and PE, PE as entire unspecialized lash. Thelycum: S6 subtriangular, bearing a pair of posterior setose protuberances; S7 as simple undivided nearly trapezoid plate; S8 as simple subrectangular plate.

Species included: ***B. corbariae* sp. nov.**, *B. intermedia* (Spence Bate, 1888), *B. stephensi* Burkenroad, 1940 and ***B. torbenwolffi* sp. nov.**

Type species: *Gennadas intermedius* Spence Bate, 1888 (type by original designation).

BENTHEOGENNEMA INTERMEDIA
(SPENCE BATE, 1888)

(FIGS 2A, 3 AB, 4A)

Type material: Female, NHMUK:ecatalogue:1256676, ‘Challenger’ Exp., off Sierra Leone (holotype).

Material examined: Four females and eight males (details in Supporting Information, Appendix S1).

Type locality: Off Sierra Leone (no further details).

Diagnosis: Telson with three (rarely two) pairs of dorsolateral spines near ventral surface (Fig. 2A). Thelycum: S6 without posterior scutum; S7 not shortened, nearly as long as S6 (Fig. 3AB). Petasma as in the genus diagnosis (Fig. 4A).

Remarks: This species differs from other *Bentheogennema* in having 2–3 pairs of the dorsolateral spines. Like all other genera of Benthescymidae, *B. intermedia* has S7 nearly as long as S6, while in the rest of *Bentheogennema* S7 is shortened (half as long as S6).

Geographical distribution: Atlantic, Indian and probably Pacific Ocean. Molecular data show low variance between Atlantic and Indian Ocean populations (Fig. 7).

Vertical distribution: Bathypelagic.

***BENTHEOGENNEMA STEPHENSI* BURKENROAD,**
1940

(FIGS 2B, 3 CD, 4B)

Type material: Male, NHMD-79464, lost (holotype).

Material examined: 17 females and 15 males (details in Supporting Information, Appendix S1).

Type locality: 760 km N of New Zealand, 28°17.6′ S, 177°1.0′ E.

Diagnosis: Telson with a single pair of the dorsolateral spines set near dorsal surface at 60% of telson length (Fig. 2B). Thelycum: S6 without posterior scutum; S7 shortened, half as long as S6 (Fig. 3CD). Petasma as in the genus diagnosis (Fig. 4B).

Geographical distribution: Western Pacific. The examined material from the Dana Expeditions derives from the west Pacific. Records from other areas (e.g. Pérez Farfante & Kensley, 1997) are likely a result of misidentification due to an inadequate original description. At least, similar specimens from the Indian Ocean appeared to be different species.

Vertical distribution: Bathypelagic.

***BENTHEOGENNEMA CORBARIAE* LUNINA ET AL. SP.**
NOV.

(FIGS 2C, 3 EF)

Type material: Female MNHN-Na-6453, ‘Marion Dufresne’, SAFARI II, St. CP 10, 1°43′ N; 87°08′ E, 02.08.1981, bottom depth 4350 m (holotype); male MNHN-IU-2016-11805, ‘Marion Dufresne’, Madagascar Exp., St. GS 2 13:30–14:00, Grand Shmidt, 0–2000 m, 4 December 1974 (paratype).

LSID: urn:lsid:zoobank.org:act:3909BDDE-76A5-4D20-BOBF-2AB8020F19FC, 12.07. 2019

Material examined: Holotype and paratype.

Type locality: Central Indian Ocean, 1°43′ N; 87°08′ E.

Diagnosis: Telson with a single pair of the dorsolateral spines set near dorsal surface at 80% of telson length (Fig. 2C). Thelycum: S6 without posterior scutum; S7 shortened, half as long as S6 (Fig. 3EF). Petasma as in the genus diagnosis (Fig. 4E).

Etymology: Named after Dr Laure Corbari, Museum National d’Histoire Naturelle, Paris, who re-initiated the international carcinological hub of the Laboratoire

des Arthropodes. She inspires researchers from many countries to work with the collections, in which the new species was found.

Remarks: *Bentheogennema corbariae* is similar to *B. stephensi* in most characters, including the morphology of the copulatory structures. Both species differ from other *Bentheogennema* in having a single pair of dorsolateral spines on the telson. *Bentheogennema corbariae* differs from *B. stephensi* in the position of the dorsolateral spines: 80% and 60% of the telson length, respectively.

The petasma of *B. corbariae* differs from other petasmata of Benthescymidae in the absence of cincinnuli on PI (Fig. 4E and SEM in Supporting Information, Appendix S5). We did not include this character in the morphological analyses and in the diagnosis of the species, because only a single individual was observed and further material is necessary for better insight in this phenomenon.

Genetic distance between specimens supports validity of the new species (Fig. 7), which are parapatric: *B. corbariae* occurs in the north-east Indian Ocean, while *B. stephensi* has only been recorded from the West Pacific.

Vertical distribution: Bathypelagic.

***BENTHEOGENNEMA TORBENWOLFFI* LUNINA ET.AL.
SP. NOV.**

(FIGS 2D, 3 GH)

Material: Female ZMUK-NHMD-228683, ‘Galathea’ St. 266, 3° 38’ S; 52° 43’ E, 27.03.1951, bottom depth 4700–4970 m (holotype); ZMUK-NHMD-228681,

‘Galathea’ St. 266, 3° 38’ S; 52° 43’ E, 27.03.1951, bottom depth 4700–4970 m (paratype).

LSID: urn:lsid:zoobank.org:act:396E6F3C-D38E-422B-8D69-9172B23D5980, 12.07.2019

Material examined: Holotype and paratype.

Type locality: Western Indian Ocean, 3° 38’ S; 52° 43’ E.

Diagnosis: Telson without dorsolateral spines (Fig. 2D). Thelycum: S6 bearing wide rounded larbrum-like posterior scutum; S7 shortened, half as long as S6 (Fig. 3G, H).

Etymology: Named after late Dr Torben Wolff, Natural History Museum of Denmark, Copenhagen, who has supported our research on the Danish collections in the 1990s and 2000s and participated in the Galathea Expedition, which yielded this new species.

Remarks: Morphologically *B. torbenwolffi* differs from all other species of the genus in the absence of the dorsolateral spines on the telson (like in *Gennadas*) and in having a unique labrum-like posterior scutum on S6. Tissues of the available specimens cannot be used for molecular analyses and there is little hope to sample new specimens in the near future. Even without molecular data, morphological characters give a significant support for a description of the new species.

Geographical distribution: West Indian Ocean, near the Seychelles.

KEY TO SPECIES OF *BENTHEOGENNEMA*

1. Three (rarely two) pairs of dorsolateral spines in addition to apical spines on telson (Fig. 2A). S7 of thelycum not shortened, as long as S6 (Fig. 3A, B) *B. intermedia*
- At most a single pair of dorsolateral spines in addition to apical spines on telson. S7 of thelycum shortened, half as long as S6.....2
2. Dorsolateral spines in addition to apical spines on telson absent (Fig. 2D). S6 of thelycum with wide rounded larbrum-like posterior scutum (Fig. 3G, H) *B. torbenwolffi*
- One pair of dorsolateral spines set near dorsal margin in addition to apical spines on telson present. S6 of thelycum without wide rounded labrum-like posterior scutum3
3. Dorsolateral spines set at 60% of length of telson (Fig. 2B). West Pacific..... *B. stephensi*
- Dorsolateral spines set at 80% of length of telson (Fig. 2C). Indian Ocean *B. corbariae*

After all taxonomical modifications in the *Bentheogennema* + *Boreogennema* + *Gennadas* clade, we provide a new key to the genera of Benthescymidae.

KEY TO GENERA OF BENTHESICYMIDAE

1. Fourth and fifth pleonic somites not carinate; telson apically truncate.....2
- Fourth and fifth pleonic somites carinate; telson with apical triangular endpiece between terminal spines..... 4
2. Thelycum: S7 sternite divided; petasma: PM divided or convex (if entire).....3
- Thelycum: S7 sternite entire; petasma: PM entire, as straight nearly truncate lamina*Bentheogennema*
3. Telson without dorsolateral spines; thelycum: PS7 trapezoid, subtriangular, or as a narrow strip; petasma: gs and LA present, PE divided or scoop-like *Gennadas*
- Telson with a pair of dorsolateral spines; thelycum: PS7 pentagonal; petasma: gs and LA absent, PE as simple subtriangular lash..... *Boreogennema*
4. Dactyli of fourth and fifth pereopods greatly elongate and subsegmented.....*Benthonectes*
- Dactyli of fourth and fifth pereopods ordinary, unisegmented5
5. Rostrum dorsally unarmed or bearing a single rudimentary dorsal tooth. Third pleonic segment with well-developed dorsal carina. Petasma: PE greatly overreaching PI.....*Altelatipes*
- Rostrum dorsally armed with one or more well-developed dorsal teeth. Third pleonic segment without well-developed dorsal carina. Petasma: PE not overreaching PI..... *Benthesicymus*

Vertical distribution: Bathypelagic.

MORPHOLOGICAL TRAITS IN *BENTHEOGENNEMA* AND RELATED CLADES

The clade *Bentheogennema* + *Boreogennema* + *Gennadas* is robust in all trees and represents the pelagic branch of Benthescymidae. This clade is supported by several synapomorphies, which are merely adaptive to the pelagic realm. Loss of the carinae on pleonic somites and ‘smoothing’ of the telson (reducing of the dorsolateral spines and loss of the triangular end-piece) may enhance the escape function owing to the reduction of turbulence during backward flips. Mouthparts-linked synapomorphies (distally suboval exopod of maxillipeds) may reflect feeding type on pelagic objects, which are different from those occurring on or near the bottom. Finally, elaboration of the petasma (enlarged laminar PM and developed PE) may represent the first step in the enhancing of fixation and stimulation of mates during spermatophore transfer in the turbulent and hydrographically dynamic pelagic zone: these processes are important for successful copulation, as was shown for other pelagic taxa (Lunina & Vereshchaka, 2017; Vereshchaka et al., 2017).

Further divergence in the *Bentheogennema* + *Boreogennema* + *Gennadas* clade is linked to enhanced ‘smoothing’ of the body and elaboration of the copulatory structures. The first trait may be illustrated by the reduction of the branchiostegal spine on the carapace (*Bentheogennema*), by the reduction (*Boreogennema*) or loss (*Gennadas*) of the dorsolateral spines on the telson. The second trait is reflected in

various scenarios of elaboration of the copulatory structures. In *Bentheogennema*, elaboration is more remarkable in the S6 sternite (development of posterior protuberances). In *Boreogennema* and *Gennadas*, the S7 sternite becomes divided and further gains complex relief (*Gennadas*). In addition, in *Gennadas* the petasma also gains complex structure including modification and specialization of PE (divided or scoop-like) and PI (development of a specialized grasping structure covered with cincinnuli (Fig. 4D) and hypothetically adapted to carrying a spermatophore (see details in Vereshchaka et al., 2017)).

CONCLUSIONS

Comparison of morphological and molecular phylogenetic trees of *Bentheogennema* and related genera shows that both methods provide similar results, although molecular clades in general gain better statistical support. Similarities in the tree topologies have made possible scrutinizing of the phylogenetic systematics of *Bentheogennema*. However, retrieved results pose new questions about phylogenetics of related genera. First, both morphological and molecular phylogenetic trees suggest paraphyly of the genus *Benthesicymus*: *Benthesicymus* group II creates a separate clade, while *Benthesicymus* group I is combined with *Altelatipes* and *Benthonectes*, both in molecular and morphological trees. The clade *Benthesicymus* group I, although robust in the molecular tree, never gains statistical support in morphological trees. Further studies incorporating additional species are necessary to resolve relations

between and within *Benthesicymus*, *Altelatipes* and *Benthonectes*. Furthermore, morphological and molecular analyses result in slightly different tree topology in *Gennadas*: robustness of retrieved clades differs on the trees. A wide range of K2P distances in this genus also suggests significant diversity of *Gennadas* and call for future molecular analyses of the genus.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site.

Appendix S1. Material used for morphological analyses. MNHN, National Museum of Natural History (Paris, France); NMNH, National Museum of Natural History, Washington, DC, United States; NHMD, National History Museum, Copenhagen, Denmark; YPM, Yale Peabody Museum.

Appendix S2. Character scoring.

Appendix S3. Data matrix.

Appendix 4. Retrieved trees.

Appendix 5. Supplementary morphological data.