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Description and Phylogenetic Position of a New Genus and Species of Deep-Water Alpheid Shrimp Associated with Glass Sponges off New Caledonia (Decapoda: Caridea)

Hossein Ashrafi[1,*], Zdeněk Ďuriš[1], and Arthur Anker[2,3]

[1]*Department of Biology and Ecology, Faculty of Science, University of Ostrava, Chittussiho 10, CZ-71000, Ostrava, Czech Republic.*
**Correspondence: E-mail: ashrafi.hossein.s@gmail.com (Ashrafi)*
E-mail: zdenek.duris@osu.cz (Ďuriš)
[2]*Red Sea Research Center, King Abdullah University of Science and Technology (KAUST), Thuwal, Saudi Arabia.*
E-mail: arthuranker7@gmail.com (Anker)
[3]*Universidade Federal de Pelotas, Departamento de Ecologia, Zoologia e Genética, Instituto de Biologia, Campus Universitário Capão do Leão, RS, 96010-610, Brazil*

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Batellopsis paula gen. et sp. nov., a new hexactinellid-associated alpheid shrimp, is described based on a single specimen collected at a depth of 477–503 m north of Île des Pins, New Caledonia. *Batellopsis* gen. nov. is part of a clade of four genera all containing hexactinellid-associated species, for which a molecular phylogeny is presented. The evolution of several morphological characters, including orbital teeth, a bulge-fossa system on the fingers of the first pereiopod chela, and groups of microserrulate setae on the second pereiopod chela, is discussed in light of phylogenetic results.

Key words: Alpheidae, *Batellopsis paula* gen. nov., Hexactinellida, Molecular phylogeny, Symbiosis, Tropical western Pacific

BACKGROUND

Symbiosis with sponges, particularly demosponges, is common among alpheid shrimps, commonly known as snapping shrimps (Crustacea: Caridea: Alpheidae), with a notable prevalence of sponge associations in two highly diversified genera, *Alpheus* Fabricius, 1798, and *Synalpheus* Spence Bate, 1888 (*e.g.*, Banner and Banner 1983; Ríos and Duffy 2007; Hultgren et al. 2014). However, associations with deep-sea glass sponges of the Class Hexactinellida are uncommon within the Alpheidae. Only three genera, namely *Bannereus* Bruce, 1988, *Batella* Holthuis, 1955, and *Vexillipar* Chace, 1988, with a total of six known species, have been directly recorded or are suspected to be associated with hexactinellid sponges based on indirect evidence (Bruce 1988; Chace 1988; De Grave 2004; Saito et al. 1998; Anker and Pachelle 2020; Ashrafi et al. 2022a). These three genera appear to form a monophyletic group within the Alpheidae, based on previous morphological and molecular phylogenetic analyses (Anker et al. 2006; Chow et al. 2021).

During the 2011 EXBODI expedition in the offshore waters of New Caledonia, organised by the Muséum National d'Histoire Naturelle, Paris, France (MNHN), a peculiar alpheid specimen was found in a hexactinellid sponge sample collected at the depth of 477–503 m north of Îles des Pins. Even though this specimen presented several characters of the aforementioned hexactinellid-associated genera, it could not be unambiguously assigned to any of them, suggesting that it may belong to a new genus. Therefore,

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a molecular phylogenetic analysis was performed to determine the relationships of this specimen with a selection of other alpheid genera, with emphasis on *Batella*, *Bannereus* and *Vexillipar*. The results of the molecular analysis, together with morphological data, provided enough lines of support for description of a new species assigned to a new alpheid genus. In addition, phylogenetic relationships of the hexactinellid-associated genera are clarified, with the evolution of several morphological characters discussed in light of the herein presented phylogenetic hypothesis.

MATERIALS AND METHODS

Taxon sampling

A total of seven species from the four known hexactinellid-associated alpheid genera are included in the present phylogenetic study, as follows: *Bannereus* (two species with three specimens), *Batella* (one species with one specimen), *Batellopsis* gen. nov. (one species with one specimen), and *Vexillipar* (one species with two specimens). Additionally, four species from the genera *Prionalpheus* Banner & Banner, 1960 and *Alpheopsis* Coutière, 1897 were included as outgroups. Sequences for four specimens were obtained from previous molecular studies (Chow et al. 2021; Ashrafi et al. 2022a), whereas three specimens were sequenced for the first time. For detailed information about the material, deposition institution, and GenBank accession numbers, the reader is referred to table 1.

DNA extraction, amplification, and sequencing

Third, fourth, and/or fifth pleopods were selected for total genomic DNA extraction, except for very small shrimp specimens, for which pleonal muscles were used. Genomic DNA extraction was performed using the Micro Kit (Qiagen, USA) following the manufacturer's provided instructions. The PCR reaction targeted three genes: mitochondrial large ribosomal subunit (16S) with a length of approximately 500 bp, cytochrome oxidase I (CO1) with a length of ~670 bp, and the nuclear gene Histone 3 (H3) with a length of ~340 bp. The primer sequences and thermocycler conditions used in the present study can be found in Horká et al. (2016) and Ashrafi et al. (2022b). Standard PCR reactions were performed using a total reaction volume of 22 µl. The reaction mixture included 10 µl of 2x PCRBIO Taq Mix Red, 0.8 µl of each primer (10 µM), 8.4 µl of ddH_2O, and 2 µl of DNA template. The final PCR products were purified using the GenElute PCR Clean-up kit (Sigma-Aldrich) and subsequently sent to Macrogen, Amsterdam for sequencing analysis.

Sequence alignment and tree construction

The sequencing results were visualised using CHROMAS ver. 2.6.6 (available on the Technelusium

Table 1. Hexactinellid-associated alpheid shrimps of the genera *Bannereus*, *Batella*, *Batellopsis* gen. nov. and *Vexillipar*, and four outgroup taxa from the alpheid genera *Alpheopsis* and *Prionalpheus*, used in the molecular analysis in figure 1

Species	Collection number	Locality	GenBank #			Reference
			16S	CO1	H3	
Alpheopsis labis	MNHN-IU-2016-1632	Martinique	OR886224	OR887243	OR890097	Present study
Alpheopsis paratrigona	MNHN-IU-2016-7697	Martinique	OR886225	OR887244	-	Present study
Alpheopsis yaldwyni	OUMNH.ZC.2010-15-020	French Polynesia, Moorea	MZ661635	-	MZ603129	Chow et al. 2021
Bannereus anomalus	MNHN-IU-2017-11614	New Caledonia	MZ661677	-	MZ603167	Chow et al. 2021
Bannereus chani	MNHN-IU-2017-11749 / Holotype	Taiwan	OR886227	-	-	Present study
Bannereus cf. *chani*	MNHN-IU-2010-4187	Kai Is., Indonesia	MZ661678	-	-	Chow et al. 2021
Batella praecipua	MNHN-IU-2017-2930	off New Caledonia	MZ700228	MZ695832	OR890095	Ashrafi et al. 2022; Present study
Batellopsis paula gen. et sp. nov.	MNHN-IU-2018-4937 / Holotype	off New Caledonia	OR886222	OR887241	OR890099	Present study
Prionalpheus gomezi	MNHN-IU-2016-7695	Martinique	OR886226	-	OR890098	Present study
Prionalpheus triarticulatus	MNHN-IU-2018-1035	New Caledonia	OR886223	OR887242	OR890096	Present study
Vexillipar repandum	MNHN-IU-2010-4186	Kai Islands, Indonesia	OR886221	OR887240	OR890094	Present study
Vexillipar repandum	MNHN-IU-2010-4186	Kai Islands, Indonesia	OR886220	-	OR890093	Present study

web page). Alignment of the obtained data sets for 16S, CO1, and H3 genes was performed using the MUSCLE program (Edgar 2004) implemented in MEGA ver. 10.1.7 (Kumar et al. 2018). The non-protein coding gene, 16S, was subjected to analysis using the GBLOCKS webserver ver. 0.91b (Castresana 2000) to identify highly variable positions. Default parameters were used, with the inclusion of gaps in the final blocks. This analysis retained 89% of the primary sequences, corresponding to 446 bp out of 500, for the subsequent phylogenetic analysis. For the protein coding genes, CO1 and H3, substitution saturation rates were evaluated using DAMBE ver. 7.2.102 (Xia and Xie 2001). The results indicated that all codon positions of H3 were suitable for further analysis. However, the third codon positions of CO1 exhibited substantial substitution saturation, leading to their exclusion from subsequent analyses using MEGA ver. 10.1.7 (Kumar et al. 2018). The final sequences of 16S, CO1 and H3 were concatenated using SEQUENCEMATRIX ver. 1.7.8 (Vaidya et al. 2011). The best-fitting nucleotide substitution model for each gene fragment, based on the AIC criterion, was estimated using IQ-TREE ver. 2.0.5 (Kalyaanamoorthy et al. 2017). Maximum Likelihood analyses were conducted on the IQ-TREE webserver, employing the ultrafast option and 10,000 replicates to estimate bootstrap support values. Bayesian Inference analysis was performed using MRBAYES ver. 3.2.7 (Ronquist et al. 2012) for 20 × 10^6 generations, with four chains and two independent runs. Trees were subsampled every 2500 generations, discarding the initial 20% of trees as "burn-in". Bayesian Posterior Probabilities (BPP) were calculated for the remaining trees. The final trees were visualized using the ITOL webserver.

RESULTS

Phylogenetic analysis

The phylogenetic tree presented in this study was constructed based on the concatenation of three genes: 16S rRNA, mtCOI (mitochondrial cytochrome oxidase I), and nuclear H3. These genes provided a total of 1,179 base pairs of sequence data. The analysis included all sequenceable representatives of hexactinellid-associated alpheid species, namely *Bannereus anomalus* Bruce, 1988; *B. chani* Anker and Pachelle, 2020; *B.* cf. *chani* of Chow et al. (2021); *Batella praecipua* De Grave, 2004; *Batellopsis paula* gen. et sp. nov.; and *Vexillipar repandum* Chace, 1988. Four representatives from the genera *Alpheopsis* Coutière, 1897 and *Prionalpheus* Banner and Banner, 1960 were included as outgroups, since previous studies on alpheid phylogeny have shown these two genera to be part of the same smaller alpheid clade as the target genera of this study (Chow et al. 2021). Two species, *Batella leptocarpus* Chace,

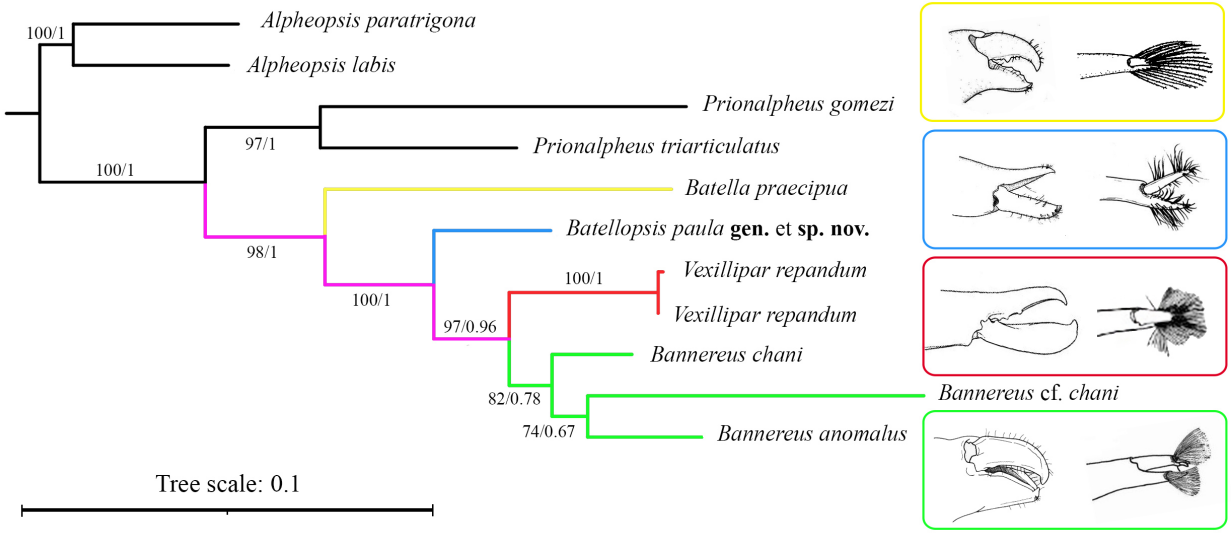

Fig. 1. Phylogenetic tree constructed using Maximum Likelihood (ML) and Bayesian Inference (BI) methods, based on the concatenation of 16S, CO1, and H3 gene sequences. The numbers above or below each branch indicate the Bootstrap support and Bayesian Posterior Probabilities, respectively. The tree represents the relationship among genera within hexactinellid-associated alpheid clades (ingroup, in colours), with two species of *Prionalpheus* and two species of *Alpheopsis* as outgroups (black lines). The genera *Batella*, *Batellopsis* gen. nov., *Vexillipar* and *Bannereus* are highlighted in yellow, blue, red, and green, respectively. Within each genus (coloured boxes), two main characters are illustrated: left, major cheliped fingers (with bulge-groove system or teeth); right, second pereiopod fingers, showing disposition of setae (organised in fan-like patterns or in simple tufts).

1988, and *B. parvimanus* Spence Bate, 1888, could not be included in the analysis due to unavailability of fresh material. To our best knowledge, these two species have not been recorded since Chace (1988), although one specimen collected by the PANGLAO 2004 expedition in the Philippines was not located in the MNHN collections (A. Anker, pers. obs.).

The phylogenetic trees resulting from Maximum Likelihood (ML) and Bayesian Inference (BI) methods showed identical topologies. The phylogenetic analysis confirmed that the four currently known hexactinellid-associated alpheid genera, viz. *Batella*, *Batellopsis* gen. nov., *Bannereus* and *Vexillipar*, form a well-supported clade (Fig. 1). This clade received high statistical support from both the maximum Bayesian Posterior Probabilities (BPP = 1) and Bootstrap support (Bs = 98). All of its members possess a combination of synapomorphic and symplesiomorphic features, which enables us to distinguish them from all other alpheid clades. The synapomorphic features of this clade are (1) an elongated second pereiopod palm, much longer than the last subdivision of the carpus; (2) the second pereiopod fingers possess dense tufts of setae, sometimes fan-shaped, with the dactylus tip biunguiculate the pollex tip in the form of a long simple unguis; (3) the mandible lacking a palp; and (4) the dactylus of the third to fifth pereiopod with the flexor margin armed with teeth of various sizes. Other important characters of this clade, mostly symplesiomorphies (shared with many other genera), are: (1) the eyes dorsally concealed by the carapace; (2) the rostrum and orbital teeth, if present, rather small, sometimes reduced; (3) the lateral plate of the third maxilliped in the form of a small rounded plate, not acutely produced; (4) the first pereiopods (= chelipeds) enlarged, equal or unequal in size, and carried extended; (5) the first pereiopod fingers lacking a distinct plunger-fossa mechanism (as in *Alpheus* or *Synalpheus*), with teeth or a with a bulge-groove system; (6) the second pereiopod with the carpus composed of five subdivisions; and (7) the sixth pleonite without articulated plate.

Within the hexactinellid-associated alpheid clade, *Batella* is in the sister position to the other three genera (*Bannereus*, *Batellopsis* gen. nov. and *Vexillipar*), which together form a robust clade (with Bootstrap support Bs = 100 and Bayesian Posterior Probability BPP = 1). The main morphological feature that differentiates *Batella* from the remaining three genera is the absence of the bulge-groove system on the major chela fingers, which is the synapomorphy of *Bannereus*, *Batellopsis* gen. nov. and *Vexillipar*. Within the clade containing *Bannereus*, *Batellopsis* gen. nov. and *Vexillipar*, the new genus was recovered in a sister position to the other two genera, which form a well-supported clade (Bs = 97 and BPP = 0.96). In *Batellopsis* gen. nov., the setae on the fingers of the second pereiopod chela are not organised in a fan-shaped manner, as in *Bannereus* and *Vexillipar*, which represents a synapomorphy of the clade containing the latter two genera. *Bannereus* can be distinguished from *Vexillipar* by the position of the major cheliped dactylus, which is in a dorsolateral position in the former genus and in a ventrolateral position in the latter genus, as well as by the reduction of the rostrum and orbital teeth in *Bannereus* and the distal armature of the incisor process of the mandible (Bruce 1988; Chace 1988; Anker and Pachelle 2020; see also below). As expected, the specimen from Indonesia tentatively identified as *Bannereus* cf. *chani* in Chow et al. (2021) was confirmed as an undescribed species.

TAXONOMY

Family Alpheidae Rafinesque, 1815
Batellopsis gen. nov.

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Etymology: The new genus' name is derived from the related alpheid genus *Batella*, to which the Latin suffix "*opsis*" was added, to allude to morphological similarities and phylogenetic affinities between the two genera. Gender feminine.

Diagnosis: Small alpheid shrimp. Carapace smooth; frontal margin with moderately developed, triangular rostrum and small orbital teeth; pterygostomial angle rounded; cardiac notch well developed. Pleon smooth; first to third pleonites rounded posteroventrally; fourth and fifth pleura subacute posteroventrally; sixth pleonite without articulated plate. Telson strongly tapering posteriorly; dorsal surface with two pairs of submarginal spiniform setae; posterior margin slightly convex, with one pairs of spiniform setae at each angle; anal tubercles absent. Eyes fully concealed in dorsal and lateral views. Antennular peduncle relatively stout; stylocerite slender, with subacute tip, surpassing distal margin of first antennular article; antennular flagellum with fused portion composed of four subdivisions; accessory ramus well developed. Antenna with basicerite moderately stout, armed with small distoventral tooth; scaphocerite with broad blade and strong distolateral tooth; carpocerite slender, slightly exceeding antennular peduncle. Mandible without palp; incisor process distally with four teeth. Third maxilliped slender, pediform, not operculate; coxa with rounded lateral plate; ultimate article slightly tapering distally, its tip armed with three slender spiniform setae. Chelipeds enlarged, unequal

in size, asymmetrical in shape, carried extended. Major cheliped with basis short, unarmed; merus slender, smooth, distoventral margin unarmed; carpus short, cup-shaped, with prominent tooth distolaterally; palm robust, swollen, subcylindrical, smooth; fingers subequal in length; pollex cutting edge with groove; dactylus cutting edge with distinct bulge fitting into groove of pollex. Minor cheliped slenderer and weaker than major cheliped; carpus cup-shaped, with one prominent tooth distolaterally and one smaller tooth distodorsally; palm relatively slender, subcylindrical, smooth; fingers subequal in length, no gaping when closed; finger cutting edges blade-like, without bulge-channel system. Second pereiopod with ischium unarmed; carpus composed of five subarticles, third longest; chela elongate, as long as carpus; fingers about 0.3 times as long as palm, with patchily distributed, thick, microserrulate setae; pollex slender, ending in simple tip; dactylus distally with two ungui. Third pereiopod moderately stout; ischium with one spiniform seta; merus slightly inflated, with one spiniform seta, distoventral margin projecting as subtriangular tooth; propodus with numerous spiniform setae on ventral margin; dactylus robust, distinctly subdivided into strongly biunguiculate distal part and stout proximal part, latter with minute teeth on flexor margin. Fourth pereiopod generally similar to third pereiopod, slenderer; merus unarmed. Fifth pereiopod similar to fourth pereiopod, slenderer; ischium and merus unarmed; propodus with distal half furnished with seven transverse rows of microserrulate setae on ventrolateral margin. Uropods with lateral lobe of protopod strongly projecting; distolateral tooth of exopod and small lateral tooth of diaeresis flanking slender spiniform seta, latter slightly surpassing distal margin of exopod. Gill/exopod formula: 5 pleurobranchs (above P1–P5); 1 arthrobranch (at Mxp3); 0 podobranchs; 2 epipods (Mxp1, Mxp2); 4 mastigobranchs (Mxp 3, P1–P3); 4 sets of setobranchs (P1–4); 3 exopods (Mxp 1–3).

Type species: *Batellopsis paula* sp. nov., by monotypy and present designation.

Distribution: Currently only known from the southwestern Pacific: New Caledonian archipelago (north of Île des Pins).

Remarks: Morphological, ecological and molecular data place *Batellopsis* gen. nov. within the clade also comprising *Bannereus*, *Batella* and *Vexillipar*, in the above-discussed tree topology (Fig. 1). Even though *Batellopsis* gen. nov. does not seem to have a single exclusive autapomorphic feature, the genus can be separated from *Batella*, *Bannereus* and *Vexillipar* by the distoventrally armed merus of the third pereiopod (Fig. 6D), which is unarmed in the other three genera. However, it must be noted that the distoventral armature of the third (and often also the fourth) pereiopod merus may be an intragenerically variable character in the Alpheidae (Anker et al. 2006).

Batellopsis gen. nov. can be separated from *Batella* by the following features: (1) the incisor process of the mandible distally armed with four relatively enlarged teeth (*vs*. furnished with setae in *Batella*); (2) the mastigobranchs (strap-like epipods) present on the coxae of the third maxilliped and first to third pereiopods (*vs*. absent in *Batella*); (3) the first pereiopods (= chelipeds) carried extended with the dactylus in ventrolateral position (*vs*. in the dorsolateral position in *Batella*); (4) the major cheliped fingers with a bulge-groove system (*vs*. serrated or armed with one or several stout teeth in *Batella*); (5) the second pereiopod fingers furnished with tufts of microserrulate setae in a somewhat irregular pattern (*vs*. arranged in a fan-shaped pattern in *Batella praecipua*; however, less obvious in *B. parvimanus* and *B. leptocarpus*; see Miya and Miyake 1968: fig. 4E; Chace 1988: figs. 17n, 18n; see also below); and (6) the dactylus of the third to fifth pereiopods armed with minute teeth on the flexor margin of the proximal part (homologous to corpus in some palaemonids) (*vs*. unarmed in *Batella*). Furthermore, the arthrobranch at the third maxilliped is reduced in *Batella parvimanus* (Miya and Miyake 1968: fig. 3F, as *B. bifurcata* Miya and Miyake, 1968) and absent in *B. praecipua* (Ashrafi et al. 2022a: fig 3A, B), whereas it is normally developed in the new genus (Fig. 4G); however, its presence or development remains unknown in *B. leptocarpus* (Chace 1988).

As mentioned above, *Batellopsis* gen. nov. shares with *Bannereus* (three species, including one undescribed) and *Vexillipar* the presence of a bulge-groove system on the major or both chelipeds (Fig. 5A–D; cf. Bruce 1988; Chace 1988; Anker and Pachelle 2020; A. Anker, pers. obs.), but can be readily distinguished from these two genera by the irregular pattern of microserrulate setae on the fingers of the second pereiopods, which are arranged in a fan-like manner in *Bannereus* and *Vexillipar*, similarly to *Batella*. Whether these peculiar setal fans evolved independently in *Batella* and in *Bannereus* / *Vexillipar*, or whether they evolved in the common ancestor of the hexactinellid-associated alpheid clade and then became more "disorganised" in *Batellopsis* gen. nov. remains unknown.

In the original description of *Vexillipar repandum*, Chace (1988) stated that the incisor process of the mandible lacks serrations; however, in his illustration of the mandible (Chace 1988: fig. 24p), the incisor process appears to be serrated with microscopic teeth. Our examination of two specimens of *V. repandum* (MNHN-IU-2010-4186) revealed that the incisor process of the

mandible in *V. repandum* is indeed armed with minute irregular teeth, confirming Chace's (1988) illustration. In contrast, in *Bannereus* and *Batellopsis* gen. nov. the incisor process of the mandible is distally armed with four to seven large teeth (Fig. 4A; Bruce 1988: fig. 3b). On the other hand, *Batellopsis* gen. nov. shares the same gill formula as *Vexillipar*, differing in that aspect from *Bannereus*. In *Batellopsis* gen. nov. and *Vexillipar*, the arthrobranch at the third maxilliped is normally developed or at most slightly reduced, whilst the mastigobranchs on coxae extend from the third maxilliped to the third pereiopod (Figs. 5, 6; Chace 1988). In contrast, in *Bannereus*, the arthrobranch is noticeably more reduced, whilst the mastigobranchs are absent in *B. anomalus* or reduced to only one mastigobranch on the third maxilliped in *B. chani* (Bruce 1988; Anker and Pachelle 2020).

Batellopsis gen. nov., *Bannereus*, and *Vexillipar* can be differentiated using several characteristics of the chelipeds. In *Batellopsis* gen. nov. and the two known species of *Bannereus*, the chelipeds are unequal in size and moderately dissimilar in shape (Figs. 2, 5A, 5E; Bruce 1988: figs. 1, 4a, 4g). In contrast, in *Vexillipar*, the chelipeds are equal in size and symmetrical in shape (Chace 1988). Furthermore, the cheliped dactyli are ventrolateral position in *Batellopsis* gen. nov. and *Vexillipar*, whereas they appear to be in dorsolateral position in *Bannereus* (Fig. 2; Chace 1988: fig. 23; Bruce 1988: fig. 1).

***Batellopsis paula* sp. nov.**

(Figs. 2–6)

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Material examined: Holotype: ovigerous female (CL 4.0 mm); MNHN-IU-2018-4937, north of Île des Pins, New Caledonia; EXBODI sta. CP3841, 22°24'S, 167°24'E; depth 477–503 m; 09.10.2011; coll. MNHN team.

Etymology: The new species is named after Paula Martin-Lefèvre (MNHN) for her immense help and hospitality during the authors' visit(s) to the MNHN collection; used as a noun in apposition.

Description: Small alpheid shrimp (holotype: CL 4.0 mm). Carapace (Fig. 2) glabrous, somewhat swollen, not compressed laterally, unarmed. Frontal margin (Fig. 3A, B) between rostrum and orbital teeth slightly concave; rostrum moderately developed, triangular in dorsal view, with subacute tip, reaching distal margin of first article of antennular peduncle, slightly wider than long; rostral carina obsolete, reaching posteriorly level of anterior margin of eyes; orbito-rostral process moderately developed; orbital teeth small, subacute, reaching to about mid-length of rostrum, slightly longer than wide, approximately 0.3 times as wide as rostrum, slightly descendant in lateral view; pterygostomial angle rounded, slightly protruding anteriorly; cardiac notch well developed.

Pleon (Fig. 2) glabrous; pleura of first and second pleonites rounded anteroventrally and posteroventrally; third pleuron rounded posteroventrally, fourth and fifth pleura projecting as small subacute tooth posteroventrally; sixth pleuron with small subtriangular projection on posterolateral margin, flanking each side of telson, without articulated plate.

Telson (Fig. 3C, D) subrectangular, tapering distally, about 1.8 times as long as proximal width, posterior margin 2.8 times as broad as anterior margin; dorsal surface armed with two pairs of small spiniform setae located approximately at 0.7 and 0.9 telson length, anterior and posterior respectively; posterior margin relatively narrow, furnished with six long plumose setae and two pairs of stouter spiniform setae, mesial about 1.7 times as long as lateral, latter slightly longer than dorsal spiniform setae.

Eyes (Fig. 3A, B) fully concealed in both dorsal and lateral views; cornea somewhat reduced; anteromesial margin rounded.

Antennule (Fig. 3A, B) with peduncle relatively stout; visible portion of first article slightly longer than broad; stylocerite slender, distinctly overreaching distal margin of first article but falling short of mid-length of second article; second antennular article slightly longer than wide; third article as long as second article, about 1.6 times as long as wide; lateral antennular flagellum thicker than mesial antennular flagellum, fused portion composed of four subdivisions, accessory ramus about half as long as fused portion, with six groups of aesthetascs on distal subdivisions and secondary ramus.

Antenna (Fig. 3A, B) with basicerite short, stout, its distoventral margin armed with small, triangular tooth, superior margin rounded; scaphocerite well developed, broad, ovate, slightly overreaching end of antennular peduncle, distolateral tooth stout, distinctly surpassing blade, blade broad, falling short of end of antennular peduncle; carpocerite slightly compressed dorsoventrally, slender, slightly surpassing end of antennular peduncle.

Mandible (Fig. 4A) with robust molar process; incisor process distally with four teeth, lateral slightly more robust than mesial; palp absent. Maxillule (Fig. 4B) with bilobed endopod, dorsal lobe stronger than and distinctly surpassing ventral lobe, with four long setae, ventral lobe with one seta; dorsal endite almost square-shaped, with long spiniform setae; ventral endite rounded at tip, with slender spiniform and slender setae. Maxilla (Fig. 4C) with moderately broad

scaphognathite; dorsal endopod simple, with two setae near tip; dorsal endite with shallow cleft; ventral endite short, furnished with several setae. First maxilliped (Fig. 4D) with deep cleft between dorsal and ventral endites; dorsal endite with slender spiniform setae; ventral endite without setae; caridean lobe of exopod narrow, furnished with three long, thick, plumose setae; endopod not subdivided, with four long, thick, plumose setae on distal third; epipod shallowly trilobed. Second maxilliped (Fig. 4E) with family-typical endopod; exopod with one long, thick seta located at about 0.3 of its length; epipod small, narrow. Third maxilliped (Fig. 4F, G) slender, pediform; coxa with shallow, rounded lateral lobe and strap-like epipod (mastigobranch); antepenultimate article slender, about seven times as long as broad; penultimate article slender, about three times as long as broad, about half as long as antepenultimate article; ultimate article slender, slightly tapering distally, approximately eight times as long as proximal width, about as long as antepenultimate article, armed with three spiniform setae on apex; arthrobranch normally developed.

First pereiopods (Fig. 5) enlarged, unequal in size, asymmetrical in shape, carried extended with dactylus in ventrolateral position. Major cheliped (Fig. 5A–D) with coxa moderately stout, with strap-like epipod and setobranch; basis and ischium short, unarmed; merus slender, smooth, about four times as long as broad, slightly concave on distal fourth of its length; carpus short, cup-shaped, smooth; palm robust, swollen, subcylindrical, about 1.9 times as long as wide, smooth; fingers relatively stout, subequal in length, about 0.4 times as long as palm, not gaping when closed; pollex with cutting edge with deep groove; dactylus with cutting edge distinctly bulging, this bulge fitting into groove of pollex. Minor cheliped (Fig. 5E–G) much weaker and shorter than major cheliped; coxa similar to that of major cheliped; basis and ischium short, unarmed; merus slender, about five times as long as broad, smooth, unarmed; carpus small, cup-shaped, with one prominent tooth distolaterally and one smaller tooth distodorsally; palm somewhat elongate, subcylindrical in cross-section, about three times as long as wide; fingers subequal, about half as long as palm, not twisted, not gaping when closed; cutting edges without bulge-groove system.

Second pereiopod (Fig. 7A–C) with all articles relatively slender; coxa with strap-like epipod and setobranch; basis short; ischium about 5.5 times as long as broad, unarmed ventrally; merus about 0.9 times as long as ischium; carpus approximately as long as merus, with five subdivisions, approximate ratio of articles equal to: 2 : 1 : 1 : 1 : 3; chela elongate, as long as carpus; palm long, tapering distally, about four times

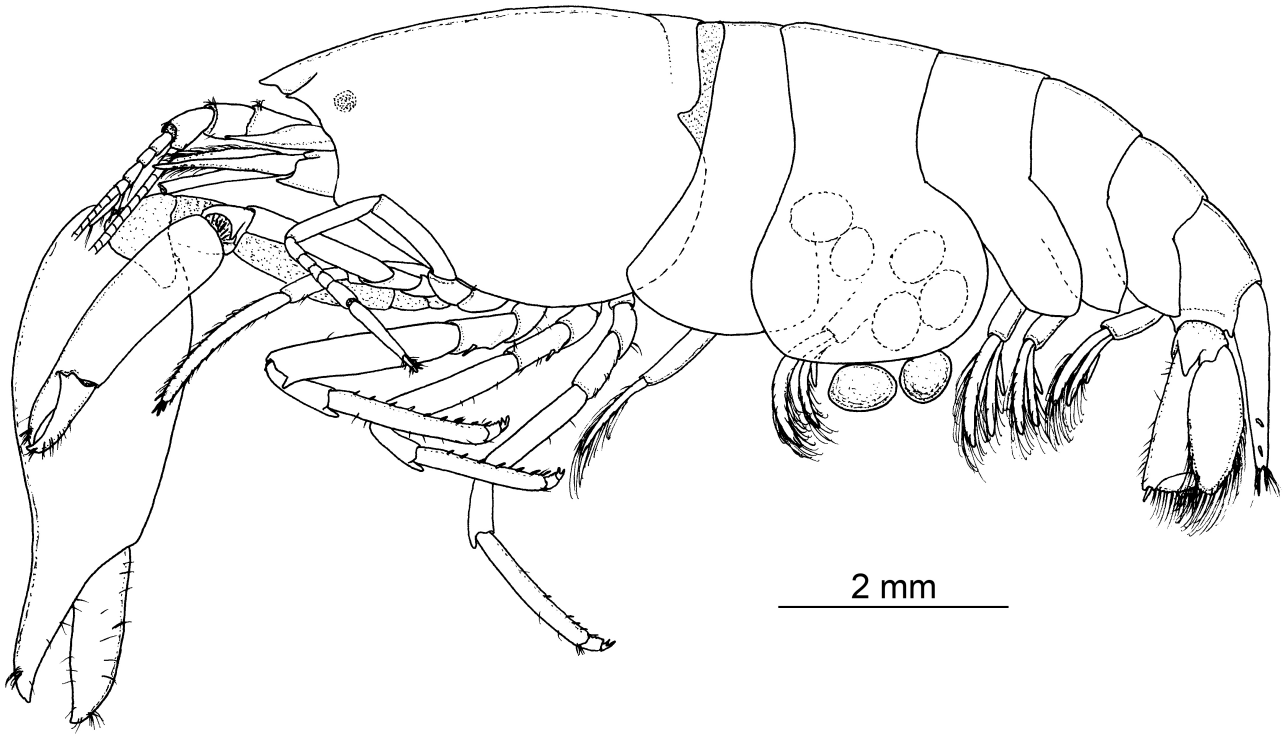

Fig. 2. *Batellopsis paula* gen. et sp. nov., holotype, ovigerous female (CL 4.0 mm), north of Île des Pins, New Caledonia (MNHN-IU-2018-4937): habitus, left lateral view [right side appendages omitted, except for major cheliped].

as long as wide; fingers short, about 0.3 times as long as palm, furnished with patchily distributed microserrulate setae, some in tufts; pollex very slender, ending in simple tip; dactylus also slender, ending in two hook-shaped ungui.

Third pereiopod (Fig. 6D, E) moderately slender; coxa bearing strap-like epipod and setobranch; basis short; ischium short, slightly widening distally, armed with one spiniform seta on ventrolateral surface; merus slightly inflated, about 4.5 times as long as wide, armed with one spiniform setae on ventral margin at about proximal third, distoventral margin projecting as sharp, subtriangular tooth; carpus slightly widening distally, about three times as long as wide, with unarmed distoventral margin; propodus relatively slender, subequal to merus, about eight times as long as wide, ventral margin armed with nine spiniform setae in addition to one distal pair of spiniform setae flanking dactylar base; dactylus robust, subdivided by suture into proximal portion (corpus) and distal portion with two large, sharp ungui, ventral unguis about twice as broad as base of dorsal (main) unguis and slightly shorter, proximal portion with distal half of flexor margin armed with several small teeth, latter decreasing in size

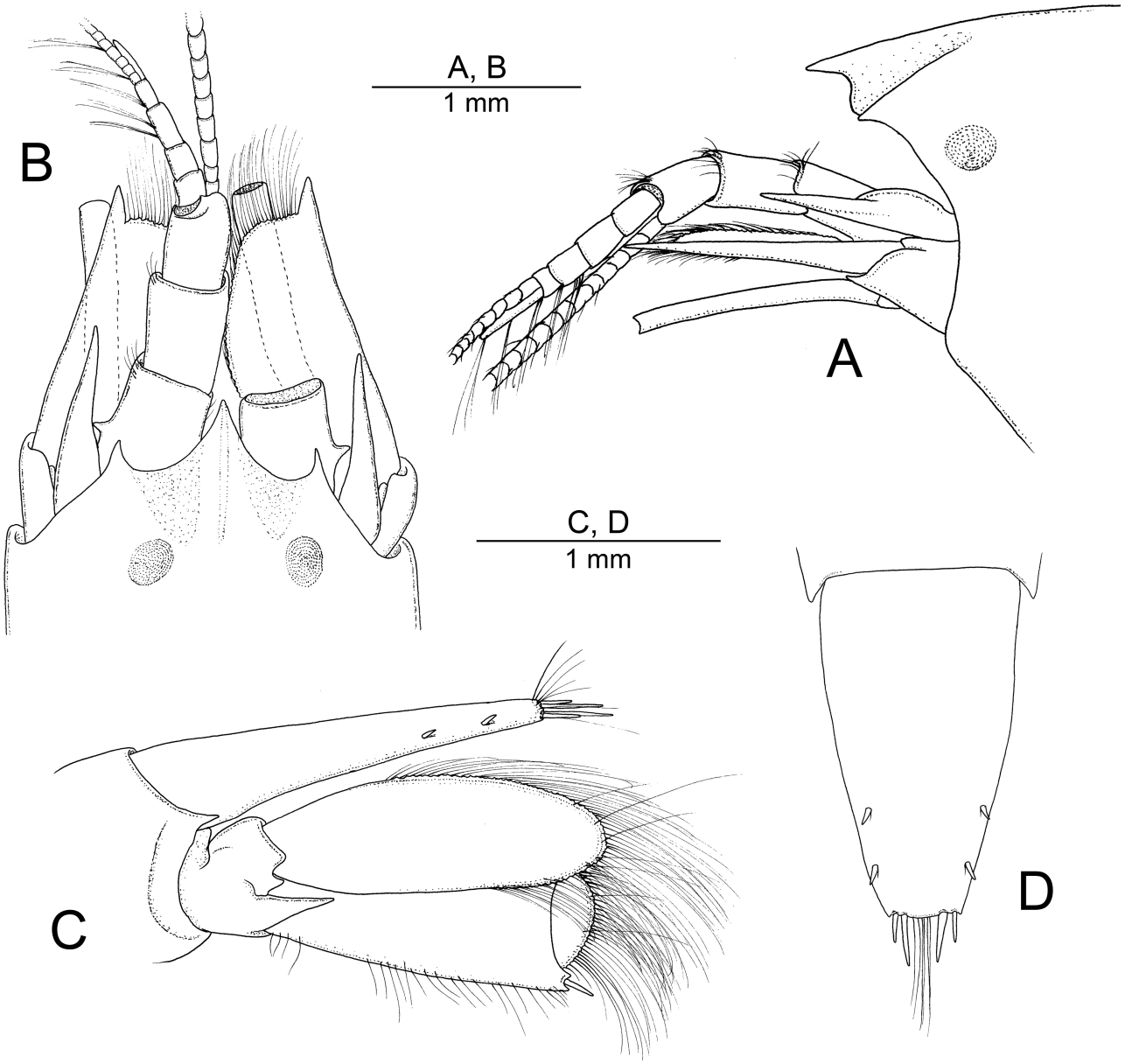

Fig. 3. *Batellopsis paula* gen. et sp. nov., holotype, ovigerous female (CL 4.0 mm), north of Île des Pins, New Caledonia (MNHN-IU-2018-4937): A, frontal region (right antennular peduncle broken), lateral view; B, same, dorsal view; C, telson and uropods, lateral view; D, telson, dorsal view.

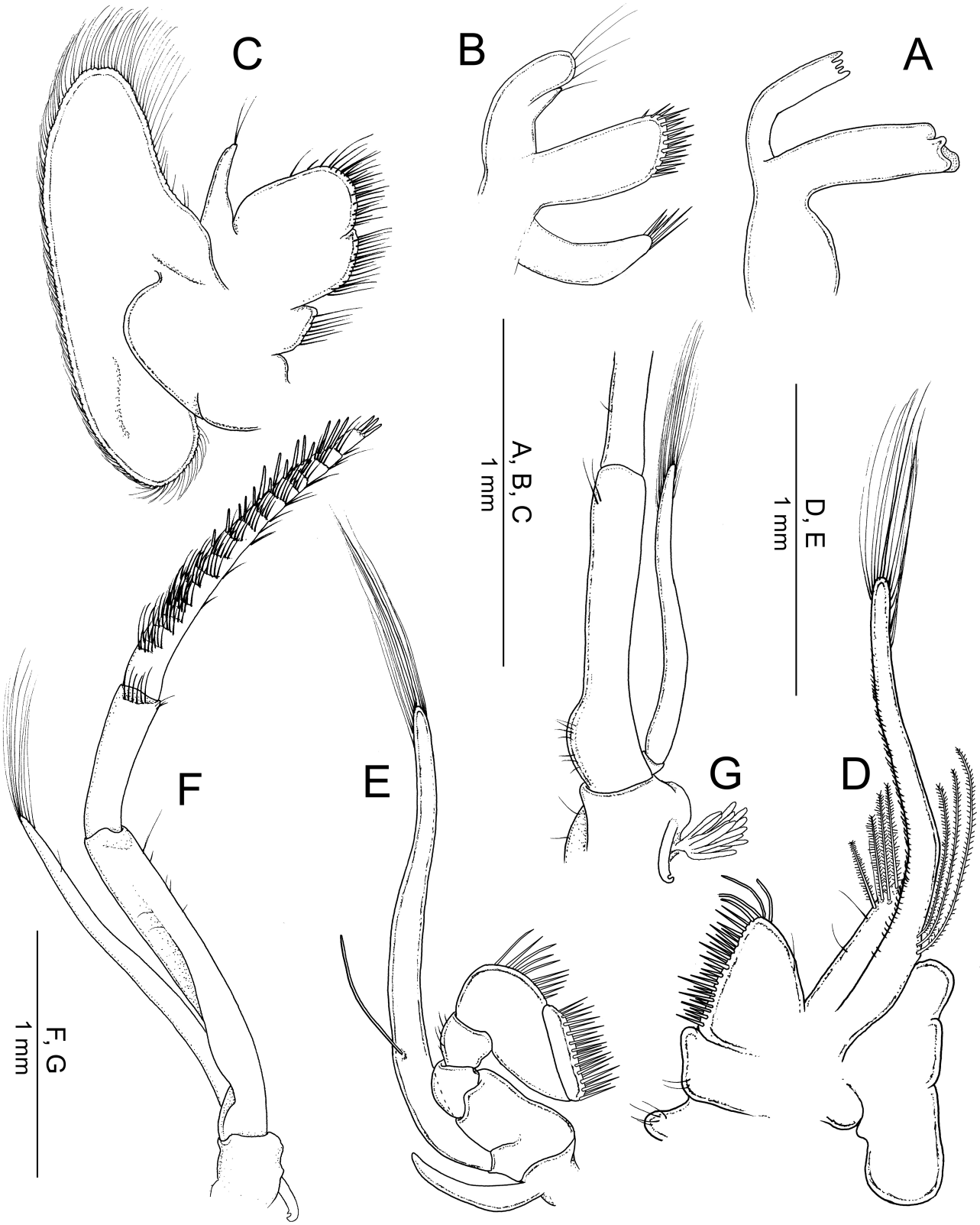

Fig. 4. *Batellopsis paula* gen. et sp. nov., holotype, ovigerous female (CL 4.0 mm), north of Île des Pins, New Caledonia (MNHN-IU-2018-4937): A, mandible, lateral view; B, maxillule, lateral view; C, maxilla, lateral view; D, first maxilliped, lateral view; E, second maxilliped, lateral view; F, third maxilliped, mesial view; G, same, proximal half, lateral view.

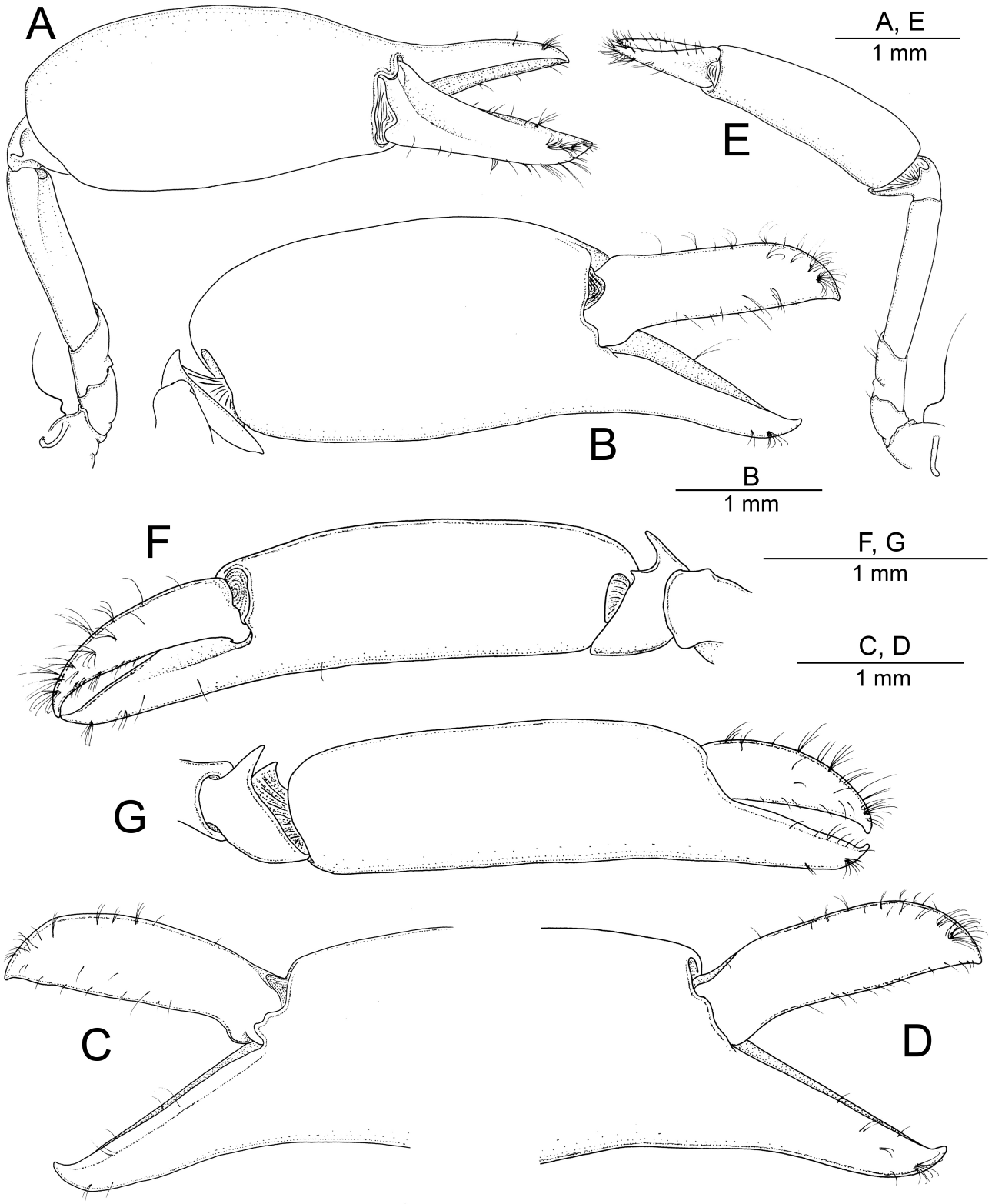

Fig. 5. *Batellopsis paula* gen. et sp. nov., holotype, ovigerous female (CL 4.0 mm), north of Île des Pins, New Caledonia (MNHN-IU-2018-4937): A, major cheliped, lateral view; B, same, chela, dorsolateral view; C, same, fingers, lateral view; D, same, mesial view; E, minor cheliped, lateral view; F, same, carpus and chela, mesial view; G, same, lateral view.

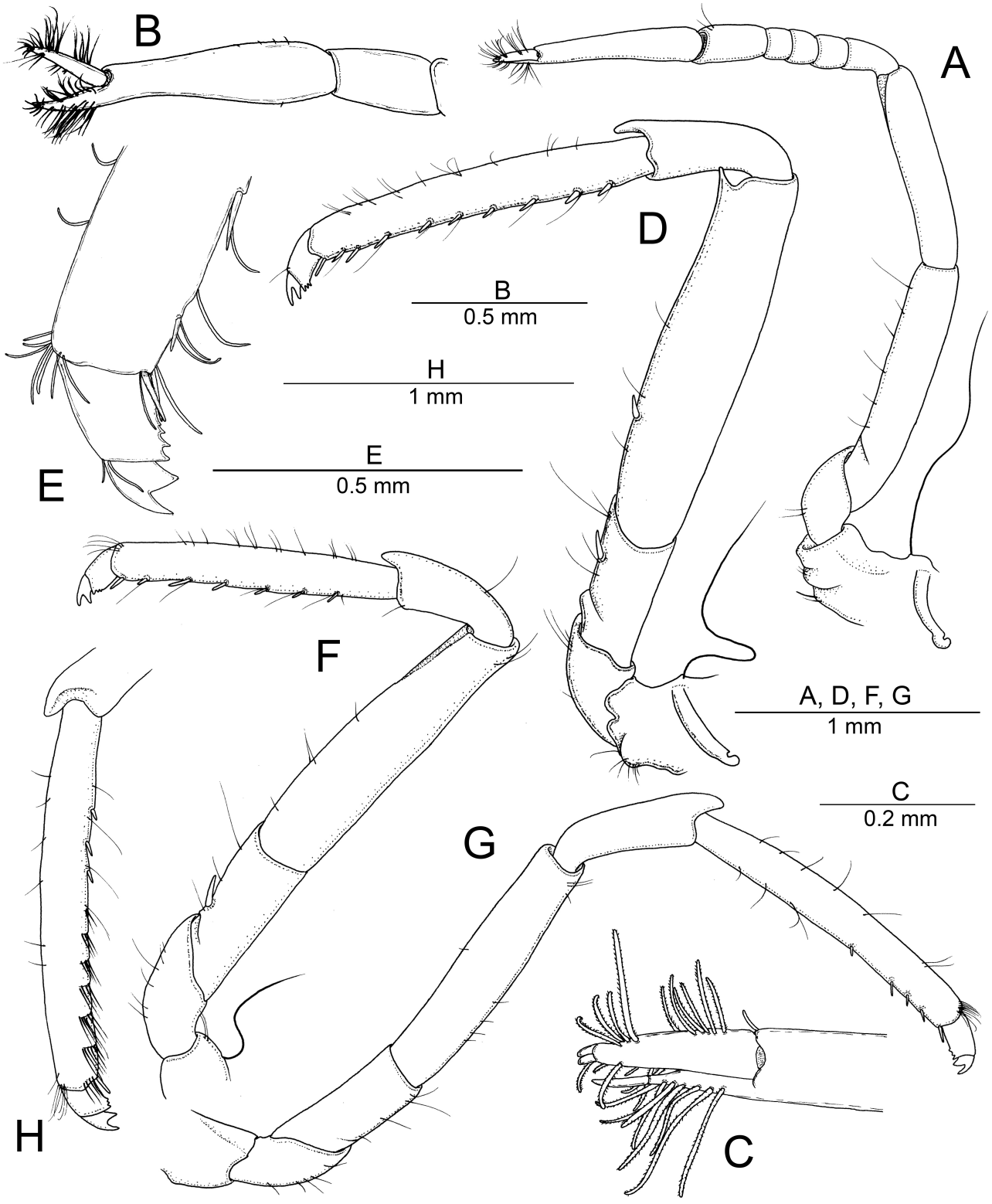

Fig. 6. *Batellopsis paula* gen. et sp. nov., holotype, ovigerous female (CL 4.0 mm), north of Île des Pins, New Caledonia (MNHN-IU-2018-4937): A, second pereiopod, lateral view; B, same, chela, mesial view; C, same, fingers with some microserrulate setae removed to show details of distal portion of fingers, mesial view; D, third pereiopod, lateral view; E, same, distal portion of propodus and dactylus, lateral view; F, fourth pereiopod, lateral view; G, fifth pereiopod, mesial view; H, same, propodus and dactylus, lateral view.

towards proximal margin, with most proximal teeth being microscopic. Fourth pereiopod (Fig. 6F) generally similar to third pereiopod in proportions, slenderer; coxa without strap-like epipod, with setobranch only; ischium with spiniform seta on ventrolateral surface; merus unarmed, i.e., without spiniform seta on ventral margin and without sharp distoventral tooth; propodus armed with six spiniform setae on ventral margin and one distal pair of spiniform setae flanking dactylar base. Fifth pereiopod (Fig. 6G, H) slenderest of three ambulatory legs; coxa without setobranch; ischium unarmed ventrally; merus unarmed; propodus with seven spiniform setae on ventral margin in addition to distal pair of spiniform setae flanking dactylar base, distal half furnished with seven transverse rows of microserrulate setae on ventrolateral surface.

Uropods (Fig. 3C) with lateral lobe of protopod strongly projecting; exopod ovoid, distolateral margin with small tooth adjacent to slender spiniform seta, latter slightly exceeding distal margin of endopod; diaresis almost straight, with small lateral lobe; endopod subequal to exopod in length, ovoid, without specific features.

Type locality: North of Île des Pins, New Caledonia.

Distribution: Presently only known from the type locality.

Ecology: The trawl haul contents from the EXBODI station CP3841 shows a significant number of hexactinellid sponges (Fig. 7). Since the holotype of *Batellopsis paula* gen. et sp. nov. was found in the same lot as several spongicolid shrimp specimens (probably *Spongicola* sp.), it can be assumed that this alpheid shrimp, too, was most likely associated with a hexactinellid sponge.

DISCUSSION

The molecular phylogenetic analysis confirms that *Batellopsis* gen. nov. is part of a morphologically and genetically well-supported clade, which also includes *Batella*, *Bannereus*, and *Vexillipar*. These genera are also characterised ecologically, being associated with hexactinellid sponges at depths ranging from 156 m for *Batella parvimanus* (Miya and Miyake 1968) and 296–875 m for *Vexillipar repandum* (Chace 1988). Indeed, eight out of a dozen or so records of species within this clade mentioned a confirmed or supposed association with hexactinellid sponges. The ecological affinity of these four genera with deep-water hexactinellid sponges, together with the undisputable monophyly of the clade that these genera compose (Anker et al. 2006 for *Batella*, *Bannereus*, and *Vexillipar*; Chow et al. 2021 for *Bannereus* and *Vexillipar*; present study for all four genera), allows us to define a small hexactinellid-associated clade (hereafter HA clade) within the Alpheidae.

All members of the HA clade share a number of exclusive or non-exclusive synapomorphic characters: (1) mandible lacking palp; (2) second pereiopod chela unusually elongate; (3) second pereiopod fingers furnished with patches of thick, microserrulate setae, sometimes arranged in a fan-shaped pattern (*Batella praecipua*, *Bannereus*, *Vexillipar*); (4) second pereiopod dactylus terminating in a strongly biunguiculate tip; (5) second pereiopod pollex very slender, with a simple tip; and (6) third to fifth pereiopods with dactylus

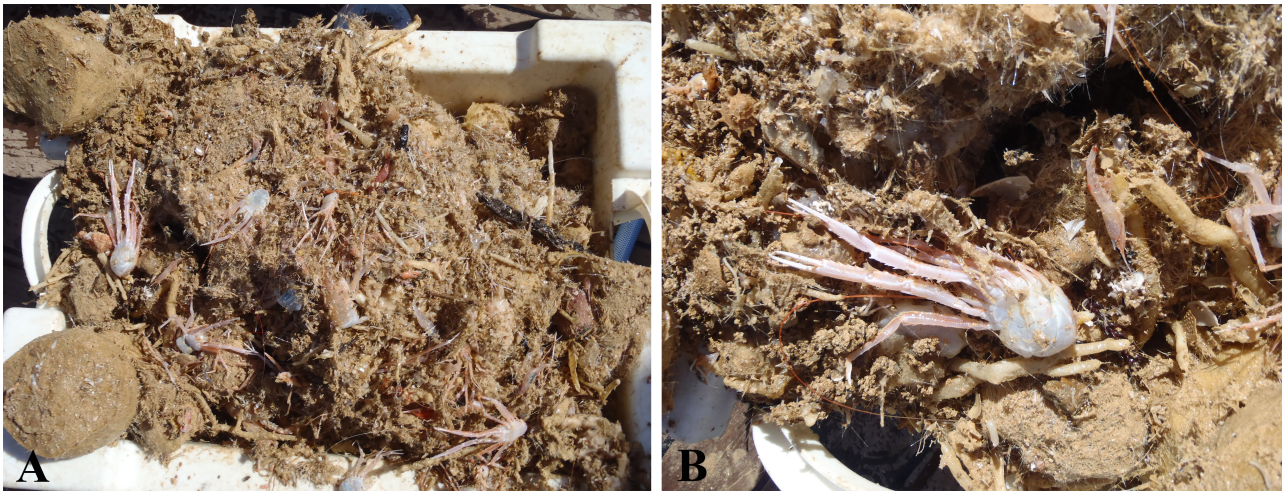

Fig. 7. Trawl haul from EXBODI station CP3841 (depth: 477–503 m), north of Île des Pins, New Caledonia, type locality of *Batellopsis paula* gen. et sp. nov. Note the presence of several sponges, predominantly Hexactinellida, including the presumed host of *Batellopsis paula* gen. et sp. nov. and several spongicolid shrimps and galatheids. Photo credit: Laure Corbari et al., MNHN.

conspicuously subdivided by a suture, with a simple (*B. anomalus*, *B. praecipua*) or strongly biunguiculate (*B. parvimanus*, *B. leptocarpus*, *B. chani*, *V. repandum*) distal portion and a stouter proximal portion (corpus), the latter unarmed (*Batella*) or armed with minute teeth (remaining genera).

Our phylogenetic analysis recovered *Batella* as a sister to the remaining genera of the HA clade. *Batella* does not have the bulge-groove system on the cheliped fingers, which appears to be a synapomorphy of the subclade consisting of *Batellopsis* gen. nov., *Bannereus* and *Vexillipar*. Within this subclade, *Batellopsis* gen. nov., was recovered as a sister to *Bannereus* and *Vexillipar*, in which the microserrulate setae of the second pereiopod fingers are organised in a fan-shaped pattern, contrary to the patchily distributed setae in the new genus. However, the inclusion of *Batella parvimanus* (type species of the genus) and *B. leptocarpus* will be necessary to shed more light on the position and taxonomic status of *B. praecipua*, which displays at least two major discrepancies with the other two species, namely the general shape of the chelipeds and the configuration of the dactylus of the third to fifth pereiopods (De Grave 2004; Ashrafi et al. 2022a).

List of abbreviations

CL, carapace length.
HA clade, hexactinellid-associated clade.
MNHN, Muséum National d'Histoire Naturelle, Paris, France.
Mxp, maxilliped.
P, pereiopod.

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Authors' contributions: HA: Conceptualisation, methodology, molecular analysis, original draft. ZĎ: Resources, review, editing. AA: Conceptualisation, review, editing.

Competing interests: The author declare that there are no competing interests.

Availability of data and materials: All sequences used in the study are submitted to GenBank, with their respective registration numbers provided in table 1.

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Ethics approval consent to participate: Not applicable.

REFERENCES

Anker A, Ahyong ST, Noël PY, Palmer AR. 2006. Morphological phylogeny of alpheid shrimps: parallel preadaptation and the origin of a key morphological innovation, the snapping claw. Evolution **60:**2507–2528. doi:10.1111/j.0014-3820.2006.tb01886.x.

Anker A, Pachelle PP. 2020. Description of a second deep-water species in the alpheid shrimp genus *Bannereus* Bruce, 1988 (Malacostraca: Caridea). Zootaxa **4894:**133–142. doi:10.11646/zootaxa.4894.1.8.

Ashrafi H, Anker A, Ďuriš Z. 2022b. *Salmoneus shojaei*, a new species of mangrove-dwelling alpheid shrimp (Decapoda: Caridea) from Iran. Zootaxa **5165:**121–132. doi:10.11646/zootaxa.5165.1.7.

Ashrafi H, Ďuriš Z, Anker A. 2022a. The first complete specimen of the deep-water shrimp *Batella praecipua* De Grave, 2004 (Crustacea: Decapoda: Alpheidae). Zootaxa **5092:**378–386. doi:10.11646/zootaxa.5092.3.8.

Banner AH, Banner DM. 1983. An annotated checklist of the alpheid shrimp from the western Indian ocean. Travaux et Documents de l'ORSTOM **158:**1–164.

Bruce AJ. 1988. *Bannereus anomalus*, new genus, new species, a deep-sea alpheid shrimp from the Coral Sea. Pac Sci **42:**139–149.

Castresana J. 2000. Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. Mol Phylogenet Evol **17:**540–552. doi:10.1093/oxfordjournals.molbev.a026334.

Chace FAJr. 1988. The caridean shrimps (Crustacea: Decapoda) of the Albatross Philippine expedition, 1907–1910, part 5: family Alpheidae. Smithsonian Contributions to Zoology **466:**1–99. doi:10.5479/si.19436696.391.1.

Chow LH, De Grave S, Anker A, Poon KKY, Ma KY, Chu KH, Chan TY, Tsang LM. 2021. Distinct suites of pre-and post-adaptations indicate independent evolutionary pathways of snapping claws in the shrimp family Alpheidae (Decapoda: Caridea). Evolution **75:**2898–2910. doi:10.1111/evo.14351.

De Grave S. 2004. A new species of *Batella* (Crustacea, Decapoda, Alpheidae) from New Caledonia. Zoosystema **26:**503–510.

Edgar RC. 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Res **32:**1792–1797. doi:10.1093/nar/gkh340.

Holthuis LB. 1955. The recent genera of the caridean and stenopodidean shrimps (class Crustacea, order Decapoda,

supersection Natantia) with keys for their determination. Zoologische Verhandelingen **26:**1–157.

Horká I, De Grave S, Fransen CHJM, Petrusek A, Ďuriš Z. 2016. Multiple host switching events shape the evolution of symbiotic palaemonid shrimps (Crustacea: Decapoda). Sci Rep-UK **6:**26486. doi:10.1038/srep26486.

Hultgren KM, Hurt C, Anker A. 2014. Phylogenetic relationships within the snapping shrimp genus *Synalpheus* (Decapoda: Alpheidae). Mol Phylogenet Evol **77:**116–125. doi:10.1016/j.ympev.2014.03.008.

Kalyaanamoorthy S, Minh BQ, Wong TKF, Haeseler A, Jermiin LS. 2017. ModelFinder: Fast model selection for accurate phylogenetic estimates. Nat Methods **14:**587–589. doi:10.1038/nmeth.4285.

Kumar S, Stecher G, Li M, Knyaz C, Tamura K. 2018. MEGA X: Molecular evolutionary genetics analysis across computing platforms. Mol Biol Evol **35:**1547–1549. doi:10.1093/molbev/msy096.

Miya Y, Miyake S. 1968. Redefinition of the genus *Batella* (Crustacea, Decapoda, Alpheidae), with description of a new species from Kyushu, Japan. *Ohmu*. Occasional papers of Zoological laboratory, Faculty of Agriculture, Kyushu University, Fukuoka, Japan **1:**113–120.

Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP. 2012. MRBAYES 3.2: Efficient Bayesian phylogenetic inference and model selection across a large model space. Syst Biol **61:**539–542. doi:10.1093/sysbio/sys029.

Ríos R, Duffy JE. 2007. A review of the sponge-dwelling snapping shrimp from Carrie Bow Cay, Belize, with description of *Zuzalpheus*, new genus, and six new species. Zootaxa **1602:**3–89. doi:10.11646/zootaxa.1602.1.1.

Saito T, Nakajima K, Konishi K. 1998. First zoea of a rare deep-sea shrimp *Vexillipar repandum* Chace, 1988 (Crustacea, Decapoda, Caridea, Alpheidae), with special reference to larval characters of the family. P Seto Mar Biol Lab **38:**147–153. doi:10.5134/176279.

Vaidya G, Lohman DJ, Meier R. 2011. SequenceMatrix: concatenation software for the fast assembly of multi-gene datasets with character set and codon information. Cladistics **27:**171–180. doi:10.1111/j.1096-0031.2010.00329.x.

Xia X, Xie Z. 2001. DAMBE: software package for data analysis in molecular biology and evolution. J Hered **92:**371–373. doi:10.1093/jhered/92.4.371.