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Integrative approach to describe new species of squat lobsters of the genera *Heteronida* Baba & de Saint Laurent, 1996 and *Torbenella* Baba, 2008 (Decapoda, Munididae) from the Southwestern Pacific Ocean

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Abstract. Specimens of munidid squat lobsters belonging to the genera *Heteronida* Baba & de Saint Laurent, 1996 and *Torbenella* Baba, 2008 were collected in scientific expeditions made by several French cruises along the southwestern Pacific. These specimens were identified as two species (one new) of *Heteronida* and six species (four new) of *Torbenella*. The present paper provides systematic accounts of the five new species, along with new locality records of known species shown by this material and color information where available. Molecular data is provided to support the systematic status of each new species. A key to species for each of the genera is also presented.

Keywords. Pacific Ocean, integrative taxonomy, molecular characters, morphology.

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Introduction

The genera *Heteronida* and *Torbenella* were described by Baba & de Saint Laurent (1996) and Baba (2008), respectively, to include some small- to medium-sized species of squat lobsters from the western and central Pacific. Both genera belong to the group of munidids having only one pair of male gonopods

(Macpherson & Baba 2011). *Heteronida*, at present, contains three species: *H. aspinirostris* (Khodkina, 1981) from Vanuatu, New Caledonia and Tonga, *H. barunae* Baba & de Saint Laurent, 1996 from Taiwan, Kei Islands and Papua-New Guinea and *H. clivicola* Macpherson & Baba, 2006 from French Polynesia (Baba *et al*. 2008; Macpherson *et al*. 2020). This genus is characterized by the presence of a mesogastric process on the carapace and the abdominal somites 2–3 each with a strong median hump-like process (Baba & de Saint Laurent 1996). *Torbenella* also includes three species: *T. calvata* (Macpherson, 2006) from New Caledonia, *T. insolita* (Macpherson, 2004) from New Caledonia, Papua-New Guinea and Tonga, and *T. orbis* (Baba, 2005) from the Kei Islands, Papua-New Guinea, NW Australia, and Norfolk Islands (Baba *et al*. 2008; Ahyong *et al*. 2013; Macpherson *et al*. 2020). The genus is characterized by the presence of an iridescent mound mesial to the lateral limit of the orbit and a strong distomesial process on the antennal article 1 (Baba 2005, 2008).

The study material originates from the collections made by recent French expeditions to Papua-New Guinea (BIOPAPUA, PAPUA NIUGUINI, KAVIENG, MADEEP), New Caledonia (EXBODI, KANACONO) and Chesterfield Islands (EBISCO, KANADEEP), which contained specimens of these two genera. In a recent paper on the taxonomic and phylogenetic revision of the family Munididae, morphological and molecular analyses of these specimens indicated that some of them were referable to yet undescribed species (Machordom *et al*. 2022). These are hereby presented as one new species of *Heteronida* and four new species of *Torbenella*, along with new locality records for previously known species, color information where available and a key to all known species of each genera.

Material and methods

The material (including the holotype of the new species) is kept in the Museum national d'histoire naturelle, Paris (MNHN). The terminology and measurements follow Baba *et al*. (2009, 2011). The size of the specimens is indicated by the postorbital carapace length (CL), measured along the midline from the base of the rostrum to the posterior margin of the carapace. The measurements in the Material examined sections and the captions refer to the CL. The rostrum was measured from its base (situated at the level of the orbit) to the apex. Measurements of appendages were taken in dorsal (pereopod 1), lateral (antennule, maxilliped 3, pereopods 2–4) and ventral (antenna) midlines. Abbreviations used are: Mxp3, maxilliped 3; P1–4, pereopods 1–4.

Molecular data

The sequences of the different genes (COI, 16S rRNA, 18S and PEPCK) for new species and comparative material were obtained from Machordom *et al*. (2022) and some from the present material. The sequence data used for analyses are as follows, shown by GenBank accession numbers: *Heteronida ceres* sp. nov. (phosphoenolpyruvate carboxykinase -PEPCK: OP252460), *H. aspinirostris* (cytochrome oxidase subunit one -COI: OP215645, 16S rRNA -16S: OP195984, 18S: OP196233, PEPCK: OP252457), *H. clivicola* (COI: OP215646, 16S: OP195986, 18S: OP196235, PEPCK: OP252459), *H. barunae* (16S: OP195985, PEPCK: OP252458); *Torbenella aequabilis* sp. nov. (COI: OP215687, 16S: OP196026, PEPCK: OP252561), *T. crateris* sp. nov. (COI: OP215686, 16S: OP196025, 18S: OP196286), *T. lupi* sp. nov. (COI: OP215693, 18S: OP196289, PEPCK: OP252566), *T. mensae* sp. nov. (COI: OP215691, 16S: OP196030, 18S: OP196288), *T. calvata* (COI: OP215688, 16S: OP196026, PEPCK: OP252562), *T. insolita* (COI: OP215689, 16S: OP196028, 18S: OP196287, PEPCK: OP252563), *T. orbis* (COI: OP215692, 16S: OP196031, PEPCK: OP252565).

Genetic distances between species were estimated using uncorrected divergences (p) calculated using PAUP ver. 4.0 (build 167) (Swofford 2004).

Phylogenetic reconstructions were inferred based on Bayesian principles, using MrBayes ver. 3.2.6 (Ronquist *et al*. 2012), and concatenating the four genes (COI, 16S, 18S and PEPCK), when available.

Twenty million generations were generated in two runs of four chains, considering both gamma shape and invariant positions in a mixed model. Parameters and trees were sampled each 2000 generations, and the convergence of the two runs was confirmed by an average of the standard deviation of split frequencies below 0.01. The final tree was edited in FigTree (Rambaut 2009), after discarding the first 25% of the sampled trees. The support was estimated through posterior probabilities.

Results

More than 1000 sampling stations were worked during the aforementioned expeditions (http://expeditions.mnhn.fr/program/; Richer de Forges *et al*. 2013), at depth from intertidal to more than 1000 m. The present specimens were collected at depths of 120–1100 m for nine stations for species of *Heteronida* and from 15 stations for species of *Torbenella*. The morphological and molecular analyses revealed that these were identified to two species (one new) of the genus *Heteronida* and six species (four new) of the genus *Torbenella*. The Systematic account for each species is given below.

Systematic account

Phylum Arthropoda von Siebold, 1848
Subphylum Crustacea Brünnich, 1772
Class Malacostraca Latreille, 1802
Order Decapoda Latreille, 1802
Infraorder Anomura MacLeay, 1838
Family Munididae Ahyong, Baba, Macpherson & Poore, 2010
Genus *Heteronida* Baba & de Saint Laurent, 1996

Heteronida aspinirostris (Khodkina, 1981)

Bathymunida aspinirostris Khodkina, 1981: 1261, figs 1–5.

Heteronida aspinirostris – Baba & de Saint Laurent 1996: 475, figs 3d–e, 23, 32d–f. — Baba 2005: 246. — Macpherson & Baba 2006: 451. — Baba *et al*. 2008: 81.

Diagnosis

Dorsal surface of carapace finely granulate; gastric process prominently high and anteriorly produced; branchial region with distinct elevation. Rostral and supraocular spines distinct, with longitudinal ridge in midline of rostrum reaching posteriorly to gastric process, anteriorly directed strongly upward. Abdominal somites 2–3 each with strong, median hump-like process and low lateral process on each side; somite 4 with smaller median process on each of anterior and posterior ridges. P1–4 granulate. Dactyli of P2–4 relatively stout, flexor margin with 6–10 spines, distal one rather close to tip, extensor margin with plumose setae.

Material examined

NEW CALEDONIA • 1 ♂ (3.2 mm); Chesterfield Islands, EBISCO stn DW2610; 19º33.147′ S, 158º40.618′ E; 486–494 m depth; 19 Oct. 2005; MNHN-IU-2013-19874.

NEW CALEDONIA • 2 ♂♂ (3.0–3.2 mm); EXBODI stn CP3830; 22°05′ S, 167°09′ E; 400–437 m depth; 8 Sep. 2011; MNHN-IU-2016-5792 • 1 ♂ (3.4 mm); EBISCO stn DW3906; 19°50′ S, 165°33′ E; 490–580 m depth; 23 Sep. 2011; MNHN-IU-2011-7018 • 1 ♀ (3.3 mm); EBISCO stn DW3925; 18°35′ S, 164°19′ E; 388 m depth; 26 Sep. 2011; MNHN-IU-2016-5790 • 2 ♂♂ (3.2–3.3 mm); EBISCO stn DW3926; 18°35′ S, 164°20′ E; 364–473 m depth; 26 Sep. 2011; GenBank no.: COI: OP215645, 16S: OP195984, 18S: OP196233, PEPCK: OP252457; MNHN-IU-2013-1920 • 1 ♂ (3.3 mm), 2 ♀♀ (3.1–

3.2 mm); EXBODI stn CP3927; 18°36′ S, 164°20′ E; 381 m depth; 26 Sep. 2011; MNHN-IU-2013-1972 • 1 ♂ (3.2 mm), 1 ov. ♀ (3.7 mm), 1 ♀ (3.3. mm); EBISCO stn DW3930; 18°37′ S, 164°26′ E; 448–464 m depth; 26 Sep. 2011; MNHN-IU-2013-1663, MNHN-IU-2013-1662, MNHN-IU-2013-1660 • 4 ♂♂ (2.8–3.3 mm), 3 ov. ♀♀ (3.2–3.7 mm); EBISCO stn DW3937; 18°37′ S, 164°26′ E, 446–604 m depth; 27 Sep. 2011; MNHN-IU-2013-1788 to IU-2013-1790.

Distribution

Previously known from New Caledonia, Loyalty Islands, Pines Island, Norfolk Ridge, Chesterfield Islands, Vanuatu, and Tonga, between depths of 345 and 930 m. The present material was collected in New Caledonia and Chesterfield Islands, at depths of 364–604 m.

Heteronida ceres sp. nov.

urn:lsid:zoobank.org:act:A70F2B16-2C5B-47C7-AF0F-C938898D8AA8

Figs 1, 6A

Heteronida aff. *aspinirostris* – Machordom *et al*. 2022: table 2.

Etymology

The name ‘*ceres*’ (Roman goddess of grains and agriculture) refers to the numerous granules covering the carapace, abdomen, and pereopods.

Material examined

Holotype

NEW CALEDONIA • ♂ (3.5 mm); EXBODI stn CP3927; 18°36′ S, 164°20′ E; 381 m depth; 26 Sep. 2011; MNHN-IU-2013-1847.

Paratypes

WALLIS AND FUTUNA • 1 ov ♀ (3.1 mm); MUSORSTOM 7 stn DW610; 13°22.5′ S, 176°08.9′ W; 286 m depth; 26 May 1992; MNHN-IU-2017-8968.

TONGA • 1 ov. ♀ (3.5 mm); BORDAU 2 stn DW1586; 18°34.20′ S, 173°54.93′ W; 400–487 m depth; 13 Jun. 2000; GenBank no.: PEPCK: OP252460; MNHN-IU-2013-19955.

Description

Carapace. Slightly longer than wide, greatest width measured behind end of anterior cervical groove; dorsal surface densely granulate. Gastric region with strong median process anteriorly blunted, not produced, height less than one-fifth that of carapace (measured in lateral view between dorsal surface and linea anomurica). Cardiac region with somewhat elevated transverse ridge preceded by distinct cervical groove. One low process on each branchial area, near posterolateral angle. Front margins strongly concave. Anterolateral spines strong, blunt, horizontal, directed straight forward, not reaching anterior margin of rostrum. Lateral branchial margins somewhat convex, convergent behind end of posterior cervical groove, with a few small processes, minute anteriormost process bluntly, produced laterally. Rostrum much wider than long, horizontal, dorsal surface with weak median carina; rostral spine absent or obsolescent. Lateral margins convergent anteriorly, ending in minute or obsolescent supraocular spines; anterior margin transverse.

Thoracic sternum. Sternal plastron 0.7 as long as wide, successively broadened posteriorly. Sternite 3 having anterior margin slightly convex, surface depressed medially, width slightly less than half that of sternite 4; anterior margin of sternite 4 contiguous with entire posterior margin of sternite 3, surface depressed medially

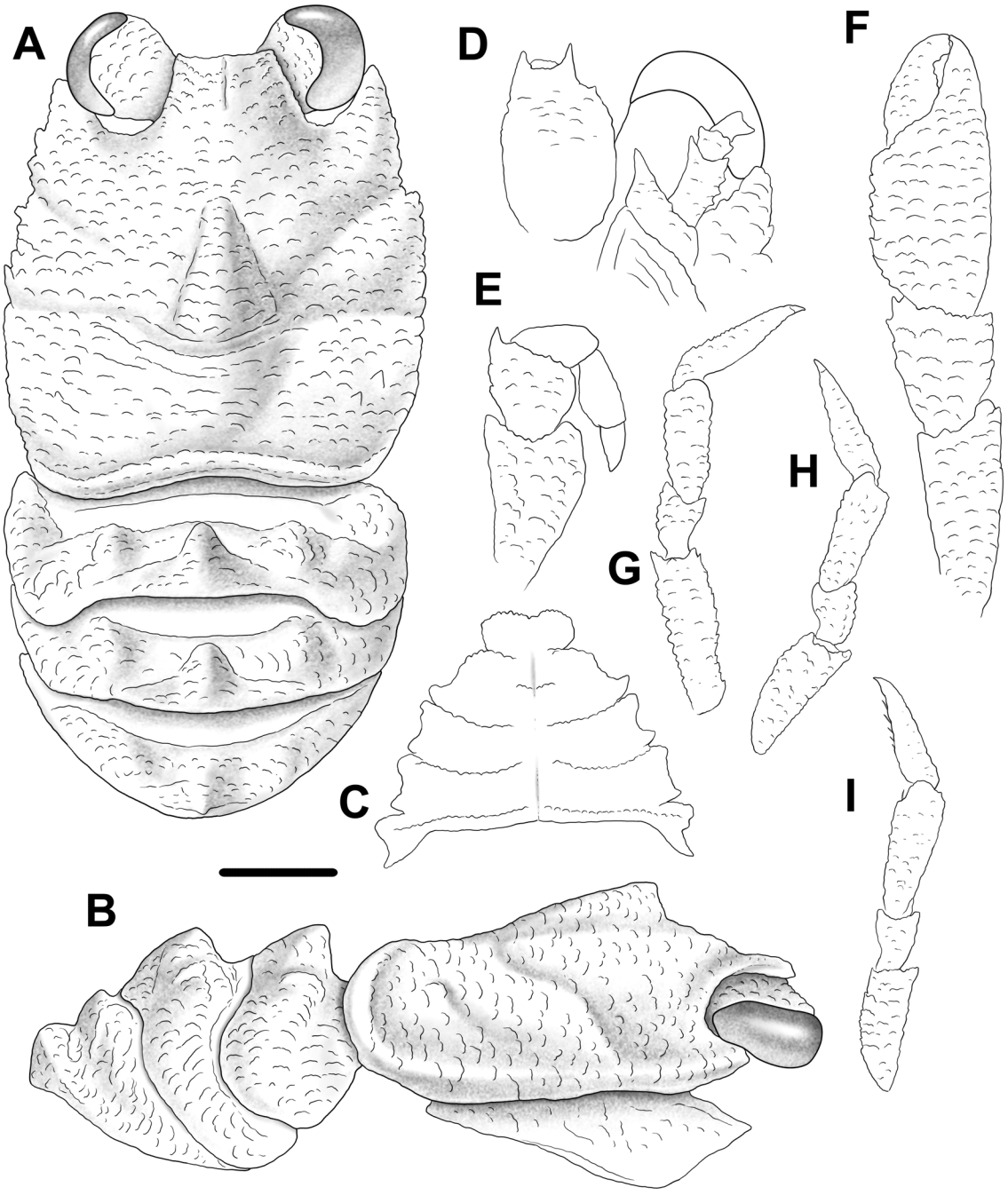

Fig. 1. *Heteronida ceres* sp. nov., holotype, ♂, CL = 3.5 mm (MNHN-IU-2013-1847), New Caledonia. **A**. Carapace and abdomen, dorsal view. **B**. Carapace and abdomen, lateral view. **C**. Sternal plastron. **D**. Cephalic region, showing antennular and antennal peduncles, ventral view. **E**. Right Mxp3, lateral view. **F**. Right P1, dorsal view. **G**. Right P2, lateral view. **H**. Left P3, lateral view. **I**. Left P4, lateral view. Scale bar: A–C, F–I = 1.0 mm; D–E = 0.5 mm.

Abdomen. Abdominal somites 2–3 each with low process flanking median process. Telson subdivided into 7 platelets.

Eyes. Cornea strongly dilated, without eyelashes; dorsal surface of peduncle granulate.

Antennule. Antennular article 1 squamate, with 2 distal spines (distolateral larger than distomesial), and 1 minute lateral spine.

Antenna. Squamate. Article 1 with stout distomesial process not reaching end of article 2; article 2 elongate, longer than wide, with distomesial and distolateral spines, distomesial larger, not reaching end of article 3; articles 3 and 4 unarmed.

Mxp3. Ischium 1.5 times as long as merus, with rounded distal process on each of flexor and extensor margins; merus with strong distal spine on extensor margin, a few acute granules on flexor border.

P1.1.4–1.7 times as long as carapace, squamate, subcylindrical; merus and carpus with small distomesial spine; palm 1.3–1.4 times as long as fingers.

P2–4. Squamate; P2 exceeding P1 carpus. Meri successively shorter posteriorly; extensor margin moderately cristate, with blunt distal spine; flexor margin granulate. Extensor margin of carpi tuberculate, with blunt distal spine. Propodi occasionally somewhat widened distally; flexor margin with movable distal spine; length 0.6 that of merus, as long as or slightly shorter than dactylus on P2, slightly longer than dactylus on P3 and P4. Dactyli slender, somewhat curved; flexor margin with 5–9 minute spines, distal one rather close to tip; extensor margin with plumose setae.

Colour. Body and P1–P4 light orange.

Genetic data

Unfortunately, there is no data for the most common and variable markers (COI, 16S). Sequence data was only available for 18S and PEPCK. These genes were almost not variable within the genus *Heteronida*. The maximum divergence values found were for 18S, but for PEPCK *H. ceres* sp. nov. did not show any clear divergence when compared to the other species, except for *H. clivicola*. The new species is different from *H. barunae* with 1.84% and from *H. aspinirostris* with 0.15% sequence divergence for 18S, and from *H. clivicola* up to 0.32% for 18S and 0.17% for PEPCK. In any case, *H. ceres* sp. nov. forms a well-supported clade (pp = 1) with the other species of the genus *Heteronida* (Fig. 7).

Remarks

The new species is closely related to *H. aspinirostris* (Khodkina, 1981), but it differs in the following features:

– The dorsal carapace surface is densely granulated in the new species, whereas it is finely granulated, and not densely so in *H. aspinirostris*.

– The gastric process is low and not anteriorly produced in *H. ceres* sp. nov., whereas it is prominently high and anteriorly produced in *H. aspinirostris*.

– The rostral and supraocular spines are obsolescent in the new species, whereas these spines are distinct in *H. aspinirostris.*

The abdominal processes are stronger in *H. aspinirostris* than in *H. ceres* sp. nov.

Distribution

New Caledonia, Wallis and Futuna and Tonga, between depths of 286 and 487 m.

Key to species of the genus *Heteronida*

1. Body densely granulated, with numerous large granules ..... ***H. ceres*** sp. nov.
– Body not densely granulated, with minute or small granules 2

2. Rostrum without ridge in midline ..... ***H. barunae*** Baba & de Saint Laurent, 1996
– Rostrum with longitudinal ridge in midline 3

3. Branchial region of carapace with distinct elevation. Gastric process prominently high and anteriorly produced ..... ***H. aspinirostris*** (Khodkina, 1981)
– Branchial region of carapace without elevation. Gastric process low and rounded .... ***H. clivicola*** Macpherson & Baba, 2006

Genus *Torbenella* Baba, 2008

Torbenella aequabilis sp. nov.
urn:lsid:zoobank.org:act:C00CBABF-A072-4153-BF27-A2FEFCDF002C
Fig. 2

Torbenella aff. *calvata*2 – Machordom *et al*. 2022: table 2.

Etymology

From the Latin '*aequabilis*', 'equal', in reference to the similar morphology to *Torbenella crateris* sp. nov.

Material examined

Holotype

NEW CALEDONIA • ♀ (6.6 mm); KANACONO stn DW4785; 22°48′ S, 167°41′ E; 388–403 m depth; 29 Aug. 2016; GenBank no.: COI: OP215687, 16S: OP196026, PEPCK: OP252561; MNHN-IU-2017-8750.

Paratype

NEW CALEDONIA • ♀ (6.8 mm); same collection data as for holotype; MNHN-IU-2014-13980.

Description

Carapace. As long as wide. Transverse ridges usually interrupted, except several on gastric region and posterior part of carapace, with dense very short setae. Scales and secondary striae absent between main striae. Gastric region with 2 main epigastric spines, each behind supraocular spine; 4–6 additional minute spines on each side and 2–3 between median spines; several small spines at base of rostrum and in parahepatic, hepatic and anterior branchial regions; one small postcervical spine on each side. Orbit with lateral limit slightly defined. Frontal margins concave. Lateral margins slightly convex. Anterolateral spine well developed, at anterolateral angle, barely reaching level of sinus between rostrum and supraocular spines. One or 2 very small marginal spines anterior to cervical groove. Branchial margins with 4 small spines. Rostrum spiniform, 0.4 times carapace length, not exceeding end of corneae, carinated dorsally, straight, and directed slightly upwards. Supraocular spines not reaching midlength of rostral spine and falling far short of end of corneae, subparallel, directed slightly upwards.

Thoracic sternum. Smooth, without striae, except a few on sternite 4. Anterior part of sternite 4 slightly narrower than sternite 3; anterior margin widely contiguous to sternite 3. Sternite 3 2.5 times as wide as long; sternite 4 3 times as wide as long, and 2.3 times as wide as sternite 3.

Abdomen. Somite 2 unarmed; somites 3–4 with 2 median spines on anterior ridge; posterior ridge of somite 4 with median small spine. Somites 2–3 each with 3 transverse ridges and several scales in addition to anterior ridge. Somite 4 with a few striae.

Eyes. Eyes large, maximum corneal diameter half distance between bases of anterolateral spines.

Antennule. Article 1 (distal spines excluded) about one-third carapace length, elongate, slightly exceeding end of corneae, with 2 short distal spines, mesial spine shorter than lateral spine; lateral margin unarmed, bearing numerous long plumose setae.

Antenna. Article 1 with prolonged, strong mesial process, slightly exceeding antennular peduncle, lateral border with numerous long plumose setae; article 2 with 2 subequal distal spines, barely reaching end of article 3; article 3 with small distomesial and distolateral spine; ultimate segment unarmed.

Mxp3. Ischium about 1.5 times length of merus, distoventrally bearing spine. Merus with well-developed median spine on flexor margin, extensor margin unarmed.

P1. Squamous, with dense short setae on scales, with scattered long setae, length 3.0–3.5 times that of carapace. Merus slightly longer than carpus, armed with some mesial spines, distalmost strongest. Carpus slightly longer than palm, 3 times as long as wide, with several spines along mesial margin. Palm slightly longer than fingers, unarmed. Fingers unarmed, distally curving and crossing, ending in a sharp point.

P2–4. Moderately long and slender, squamous, with dense short setae on scales, with some long iridescent setae along extensor margins of all articles. P2 twice carapace length. Meri successively shorter posteriorly (P3 merus 0.7 length of P2 merus, P4 merus 0.7 times length of P3 merus); P2 merus as long as carapace, 5.5–6.0 times as long as wide, 1.7–1.8 times as long as P2 propodus; P3 merus 4.2–4.5 times as long as wide, 1.5 times as long as than P3 propodus; P4 merus 3.5 times as long as wide, 1.3 times as long as P4 propodus. Extensor margins of meri with row of small, proximally diminishing, spines on P2–3, distal spine only on P4; flexor margins with distal spines followed proximally by several eminences; lateral sides unarmed. Carpi with several spines on extensor margin; flexor margin ending in blunt point. Propodi 4.0–4.5 times as long as wide; extensor margin unarmed; flexor margin with 5–7 slender movable spines, without fixed distal spine. Dactyli slender, length 0.8–0.9 times that of propodi; flexor margin with 2–4 movable spinules along entire length; dactylus 6 times as long as wide.

Genetic data

Sequence data for COI, 16S and PEPCK could be included. The greatest discrimination was shown by COI, with the smallest pairwise sequence divergence of 4.86% between *T. aequabilis* sp. nov. and *T. lupi* sp. nov., and the highest (15.42%) between *T. aequabilis* and *T. calvata. Torbenella aequabilis* was a sister species of *T. orbis* (pp = 0.9; Fig. 7).

Distribution

New Caledonia, between depths of 388 and 403 m.

Remarks

The new species is morphologically closely related to *T. calvata* (Macpherson, 2006) and *T. crateris* sp. nov. from New Caledonia, having the abdominal somite 2 unarmed. Characters distinguishing these species are outlined under the account of *T. crateris* (see below).

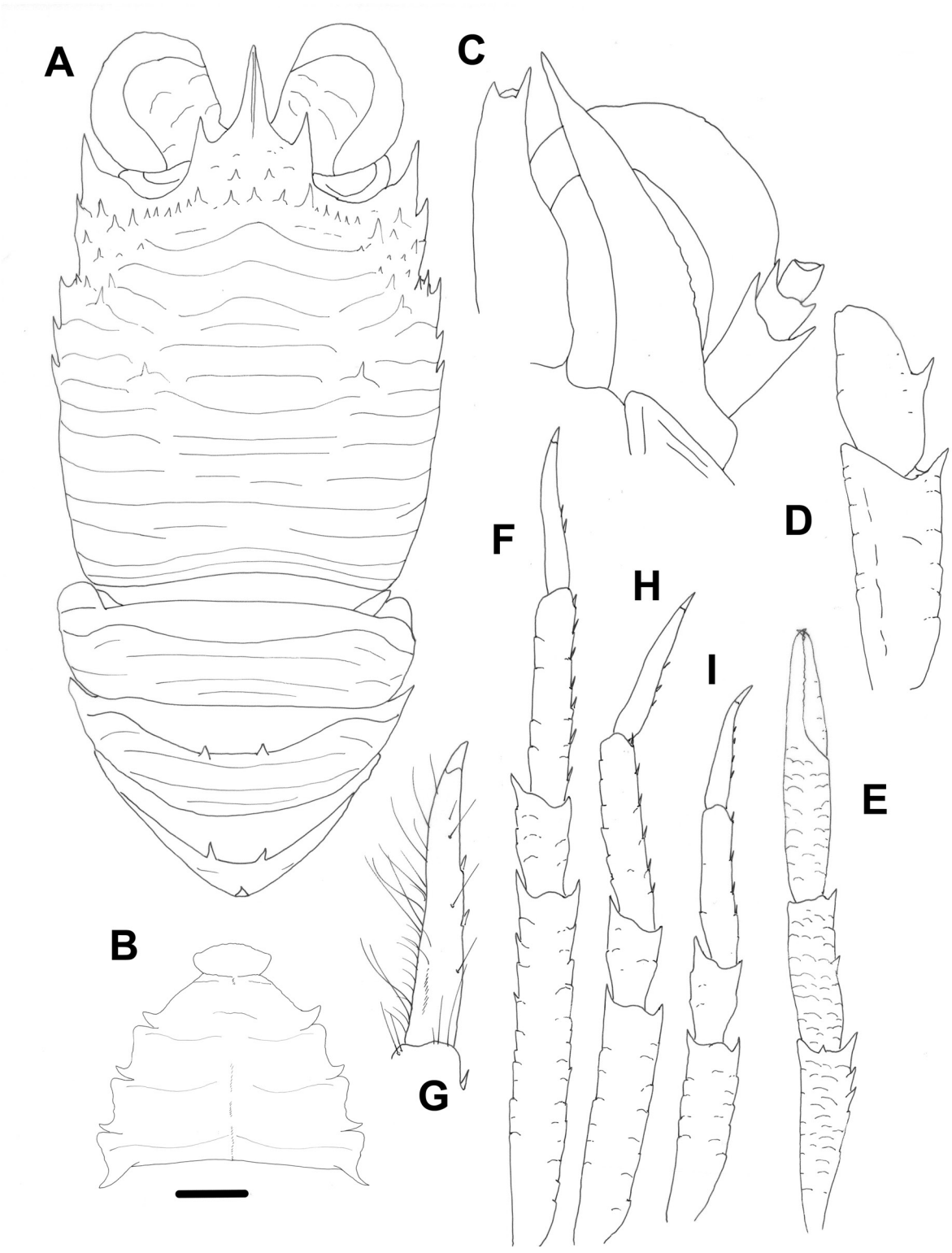

Fig. 2. *Torbenella aequabilis* sp. nov., holotype, ♀, CL = 6.6 mm (MNHN-IU-2017-8750), New Caledonia. **A**. Carapace and abdomen, dorsal view. **B**. Sternal plastron. **C**. Cephalic region, showing antennular and antennal peduncles, ventral view. **D**. Right Mxp3, lateral view. **E**. Left P1, dorsal view. **F**. Right P2, lateral view. **G**. Dactylus of right P2, lateral view. **H**. Right P3, lateral view. **I**. Right P4, lateral view. Scale bar: A–B, F, H–I = 1.0 mm; C–D, G = 0.5 mm; E = 2 mm.

Torbenella calvata (Macpherson, 2006)

Torbenia calvata Macpherson, 2006: 678, fig. 4 (New Caledonia, 260–950 m).

Torbenella calvata – Baba 2008: 1021 (new combination). — Baba *et al*. 2008: 181 (compilation).

Diagnosis

Carapace with transverse ridges usually interrupted, except several on gastric region and posterior part of carapace; gastric region with 2 epigastric spines, behind supraocular spines, and several minute spines on each side; parahepatic, anterobranchial and postcervical spines present on each side. Anterolateral spine of carapace short, not reaching sinus between rostral and supracocular spines. Rostrum spiniform, less than half as long as remaining carapace, slightly carinated dorsally, straight, and slightly upwards directed. Abdominal somite 2 unarmed; posterior ridge of abdominal somite 4 unarmed. Thoracic sternite 3 wide, more than 3 times as wide as long. Antennal article 1 with unusually prolonged mesial process, not exceeding antennular peduncle, distolateral spine of article 2 very strong, exceeding article 3; article 3 with small distolateral spine; article 4 unarmed. P1–4 moderately long and slender; P2–4 dactyli with extensor margin slightly convex, slightly curving distally, each with 1–2 movable spinules on median portion of flexor margin.

Material examined

NEW CALEDONIA • 1 ♂ (4.6 mm); Chesterfield Islands, EBISCO stn DW2632; 21º03.655′ S, 160º44.673′ E; 297–378 m depth; 21 Oct. 2005; MNHN-IU-2013-19909 • 1 ov. ♀ (5.0 mm); KANADEEP stn CP4947; 24º08′ S, 159º37′ E; 275–276 m depth; 5 Sep. 2017; GenBank no.: COI: OP215688, 16S: OP196026, PEPCK: OP252562; MNHN-IU-2017-2839 • 1 ♂ (4.3 mm); KANADEEP stn CP4948, 24º07′ S, 159º40’ E; 275 m depth; 5 Sep. 2017; MNHN-IU-2017-2636.

Distribution

New Caledonia, Chesterfield Islands between depths of 260 and 950 m.

Torbenella crateris sp. nov.
urn:lsid:zoobank.org:act:6CBF6B31-504B-4688-8EAB-E1D94F433791
Fig. 3

Torbenella aff. *calvata*1. — Machordom *et al*. 2022: table 2.

Etymology

The name ‘*crateris*’ refers to one of the southern hemisphere constellations (the Cup).

Material examined

Holotype

NEW CALEDONIA • ov. ♀ (7.2 mm); EXBODI stn CP3927; 18°36′ S, 164°20′ E; 381 m depth; 26 Sep. 2011; MNHN- IU-2013-1858.

Paratypes

NEW CALEDONIA • 1 ov. ♀ (5.4 mm); EXBODI stn CP3849; 22°03′ S, 168°41′ E; 360–560 m depth; 13 Sep. 2011; MNHN-IU-2011-7609 • 2 ov. ♀♀ (6.7–8.4 mm), 1 ♀ (6.0 mm); EXBODI stn CP3927; 18°36′ S, 164°20′ E; 381 m depth; 26 Sep. 2011; MNHN-IU-2011-7921 • 1 ov. ♀ (8.8 mm); EBISCO stn DW3932; 18°32′ S, 164°21′ E; 500–1100 m depth; 27 Sep. 2011; GenBank no.: COI: OP215686, 16S: OP196025, 18S: OP196286; MNHN-IU-2011-8600 • 2 ov. ♀♀ (7.2–7.3 mm); SPANBIOS stn DW5247; 18°36.1′ S, 164°24.4′ E; 352–376 m depth; 23 Jul. 2021; MNHN-IU-2021-2960 •

1 ov. ♀ (5.3 mm); SPANBIOS stn DW5264; 20°28.6′ S, 164°49.9′ E; 332–335 m depth; 26 Jul. 2021; MNHN-IU-2020-907 • 1 ♂ (8.6 mm), 1 ♀ (3.5 mm); Chesterfield Islands, KANADEEP stn DW5026; 20º22′ S, 158º40′ E; 360–410 m depth; 21 Sep. 2017; MNHN-IU-2017-8927, MNHN-IU-2017-2821 • 1 ♀ (3.3 mm); KANADEEP stn DW5037; 19º54′ S, 158º35’′E; 340 m depth; 22 Sep. 2017; MNHN-IU-2017-2824.

Description

Carapace. As long as wide. Transverse ridges laterally or medially interrupted, with dense very short setae. Few scales and secondary striae between main striae. Gastric region with 2 main epigastric spines, each behind supraocular spine; 4–6 flanking minute spines and 2–3 small spines between median spines; several small spines at base of rostrum and in parahepatic, hepatic and anterior branchial regions; one small postcervical spine on each side. Orbit with lateral limit slightly defined. Frontal margins concave. Lateral margins slightly convex. Anterolateral spine well developed, at anterolateral angle, nearly reaching level of sinus between rostral and supraocular spines. One very small marginal spine directly anterior to cervical groove. Branchial margins with 4–5 small spines. Rostrum spiniform, 0.4 carapace length, not exceeding end of corneae, carinated dorsally, straight, and slightly upwards directed. Supraocular spines barely reaching midlength of rostral spine and falling short of end of corneae, subparallel, directed slightly upwards.

Thoracic sternum. Smooth, without striae, except a few on sternite 4. Anterior part of sternite 4 slightly narrower than sternite 3, anterior margin widely contiguous to sternite 3. Sternite 3 2.5 times as wide as long; sternite 4 2.5–2.7 times as wide as long, and 2.4–2.5 times as wide as sternite 3.

Abdomen. Somite 2 unarmed; somites 3–4 with 2 median spines on anterior ridge; posterior ridge of somite 4 with median spine small, rarely obsolescent. Somites 2–3 each with 1–2 transverse ridges in addition to anterior ridge. Somite 4 with a few striae.

Eyes. Eyes large, maximum corneal diameter half distance between bases of anterolateral spines.

Antennule. Article 1 (distal spines excluded) about one-third carapace length, elongate, slightly exceeding corneae, with 2 short distal spines, mesial spine shorter than lateral spine; lateral margin unarmed, bearing numerous long plumose setae.

Antenna. Article 1 with prolonged and strong mesial process, slightly exceeding antennular peduncle, lateral border with numerous long plumose setae; article 2 with 2 distal spines, distomesial spine longer than distolateral, not reaching end of article 3; article 3 with small distomesial spine, article 4 unarmed.

Mxp3. Ischium about 1.5 times length of merus, distoventrally bearing spine. Merus with well developed median spine on flexor margin, extensor margin unarmed.

P1. Squamous, with dense short setae on scales, with scattered long setae, length 3.5–4.0 times that of carapace. Merus 1.2 times carapace length, slightly longer than carpus, armed with some mesial spines, distalmost strongest. Carpus slightly longer than palm, and 4 times as long as wide, with several spines along mesial margin. Palm 1.2 times as long as fingers, unarmed. Fingers unarmed, distally curving and crossing, ending in a sharp point.

P2–4. Moderately long and slender, squamous, with dense short setae on scales, with some long iridescent setae along extensor margins of all articles. P2 2.0–2.5 times carapace length. Meri successively shorter posteriorly (P3 merus times 0.8 length of P2 merus, P4 merus 0.8 times length of P3 merus); P2 merus as long as carapace, 6.0 times as long as wide, 1.7–1.8 times as long as P2 propodus; P3 merus 4.5–5.0 times as long as wide, 1.5 times as long as P3 propodus; P4 merus 4.0 times as long as wide, 1.3 times

as long as P4 propodus. Extensor margins of meri with row of small proximally diminishing spines on P2–3, distal spine only on P4; flexor margins with distal spines followed proximally by several eminences; lateral sides unarmed. Carpi with distal spine on extensor margin; flexor margin ending in blunt point. Propodi 4.5–5.0 times as long as wide; extensor margin unarmed; flexor margin with 5–6 slender movable spines, without fixed distal spine. Dactyli slender, length 0.8–0.9 times that of propodi; flexor margin with 2 movable spinules on median part; dactylus 7.0 times as long as wide.

Genetic data

sequence data could be generated for COI, the partial ribosomal 16S and 18S genes. *Torbenalla crateris* sp. nov. is resolved as the sister species of the clade formed by *T. aequabilis* sp. nov., *T. lupi* sp. nov., *T. orbis*, and *T. insolita* (Fig. 7). High values of COI divergence were found between this new species and the rest of representative of the genus: from 10.46 % respect to *T. lupi* sp. nov. to 13.27% with respect to *T. calvata* and *T. insolita*. The divergence respect to *T. aequabilis* was slightly smaller (12.29%).

Remarks

The new species is morphologically closely related to *T. calvata* (Macpherson, 2006) and *T. aequabilis* sp. nov., having the abdominal somite 2 unarmed. The three species differs from each other in the following aspects:

The anterolateral spine of the carapace falls far short of the sinus between rostral and supraocular spines in *T. calvata*, whereas these spines are longer and barely reaching the level of this sinus in *T. aequabilis* and *T. crateris*.

The posterior ridge of the abdominal somite 4 has a median spine, usually small, rarely obsolescent in *T. aequabilis* and *T. crateris*, always absent in *T. calvata*.

The thoracic sternite 3 is clearly wider in *T. calvata* than in *T. crateris* and *T. aequabilis* (3.5 times vs 2.5 times as wide as long). The anterior margin of sternite 4 is wider than sternite 3 in *T. calvata*, whereas it is slightly narrower in *T. crateris*. Furthermore, the sternite 4 is 2.4–2.5 times as wide as sternite 3 in *T. aequabilis* and *T. crateris*, whereas it is only twice as wide in *T. calvata*.

The distolateral spine of the antennal article 2 is very strong, exceeding article 3 in *T. calvata*, whereas this spine is much smaller and never reaching the end of article 3 in *T. aequabilis* and *T. crateris*.

The differences between *T. crateris* and *T. aequabilis* are as follows:

The transverse ridges of the carapace are not usually interrupted except several on gastric region and posterior part of carapace in *T. aequabilis*, whereas all ridges are medially or laterally interrupted in *T. crateris*.

The abdominal somites 2–3 each bear 3 transverse ridges and several scales in addition to the anterior ridge in *T. aequabilis*, whereas there are only one or two additional ridges in *T. crateris.*

The P2–4 dactyli are more elongate in *T. crateris* (7 times as long as wide) than in *T. aequabilis* (6 times as long as wide) .

Distribution

New Caledonia and Chesterfield Islands, between depths of 340 and 1100 m.

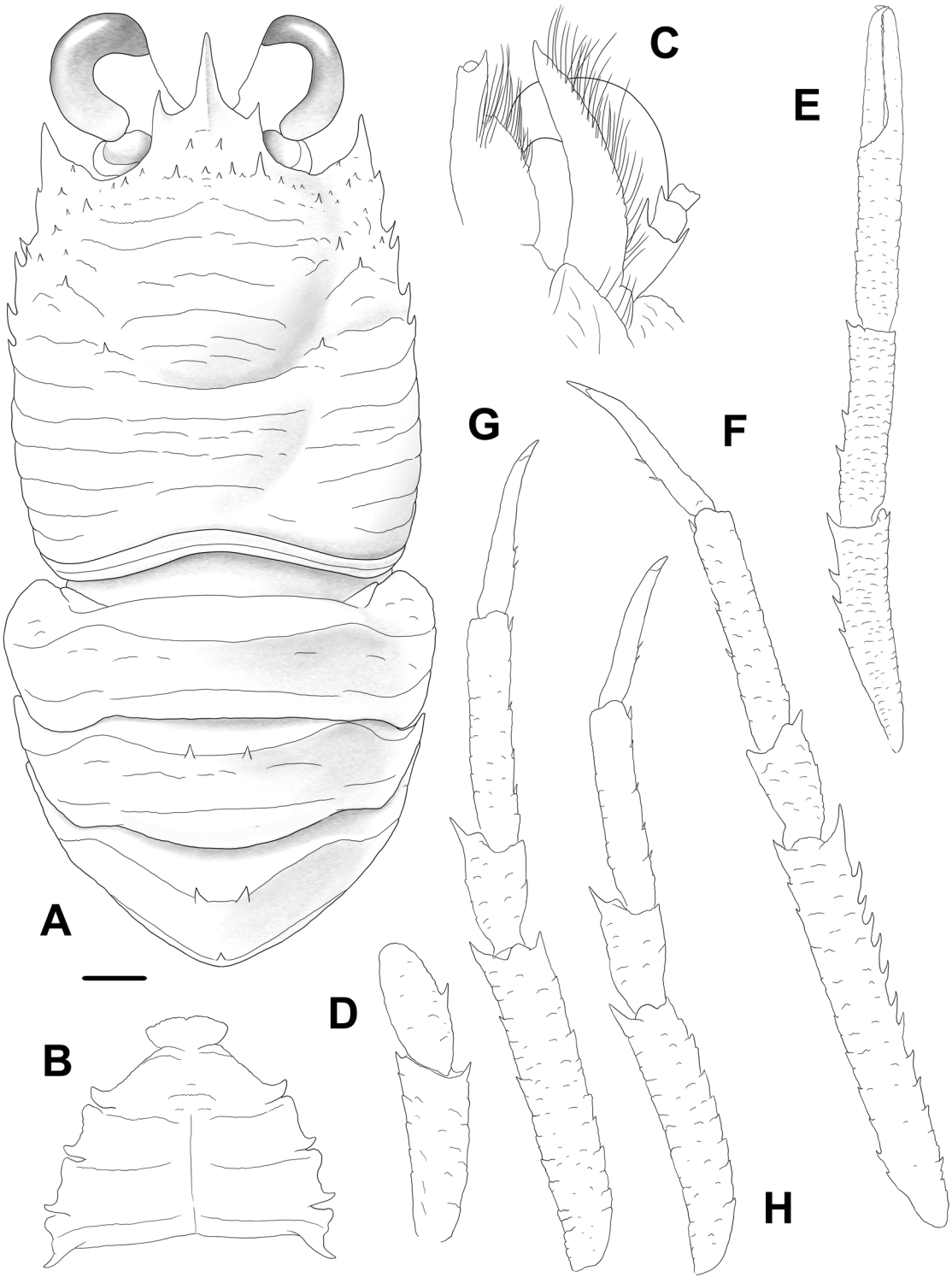

Fig. 3. *Torbenella crateris* sp. nov., holotype, ov. ♀, CL = 7.2 mm (MNHN-IU-2013-1858), New Caledonia. **A**. Carapace and abdomen, dorsal view. **B**. Sternal plastron. **C**. Cephalic region, showing antennular and antennal peduncles, ventral view. **D**. Right Mxp3, lateral view. **E**. Right P1, dorsal view. **F**. Left P2, lateral view. **G**. Right P3, lateral view. **H**. Right P4, lateral view. Scale bar: A–B, F–H = 1.0 mm; C–D = 0.5 mm; E = 2 mm.

Torbenella insolita (Macpherson, 2004)
Fig. 6B

Agononida insolita Macpherson, 2004: 242, fig. 2.

Torbenia insolita – Baba 2005: 308.
Torbenella insolita – Baba 2008: 1021. — Baba *et al*. 2008: 181. — Macpherson *et al*. 2020: 91.

Diagnosis

Carapace with gastric region with 2 epigastric spines behind supraocular spines, and several minute spines on each side; parahepatic, anterobranchial and postcervical spines present on each side. Anterolateral spine strong, at anterolateral angle, nearly reaching level of sinus between rostrum and supraocular spines. Rostrum spiniform, less than half as long as remaining carapace, slightly carinated dorsally, straight, and slightly upwardly directed. Supraocular spines overreaching midlength of rostrum and not overreaching end of corneas, parallel, directed slightly upwards. Abdominal somites 2–4 with 2 median spines on anterior ridge; posterior ridge of abdominal somite 4 unarmed. Thoracic sternite 3 wide, about 3 times as wide as long. Antennal article 1 with unusually prolonged mesial process, exceeding antennular peduncle, article 2 with distomesial spine strong, overreaching midlength of article 4; article 3 with small distolateral spine; article 4 unarmed. P1–4 moderately long and slender; P2–4 dactyli with extensor margin slightly convex, slightly curving distally, each with 3–6 movable spinules along entire or proximal two-thirds of flexor margin.

Material examined

NEW CALEDONIA • 3 ♂♂ (5.8–9.5 mm), 5 ov. ♀♀ (7.2–8.1 mm), 1 ov. ♀ (7.5 mm); EXBODI stn CP3927; 18°36′ S, 164°20′ E; 381 m depth; 26 Sep. 2011; GenBank no.: COI: OP215689, 16S: OP196028, 18S: OP196287, PEPCK: OP252563; MNHN-IU-2011-6942, MNHN-IU-2014-13981, MNHN-IU-2013-1857 • 1 ♀ (4.1 mm); Chesterfield Islands, KANADEEP stn DW5015; 21°14′ S, 159°13′ E; 210–470 m depth; 20 Sep. 2017; MNHN-IU-2017-2755.

Description

Colour. Body and appendages whitish. Carapace with some yellowish bands on gastric area and posterior and lateral margins. Orange stripes on distal part of P1 palm, carpus and merus, and P2–4 propodi.

Distribution

Previously known from New Caledonia, Papua-New Guinea and Tonga, at depths of 120–386 m. The present material was caught in New Caledonia and Chesterfield Islands at depths of 210–470 m.

Torbenella lupi sp. nov.
urn:lsid:zoobank.org:act:FE41E3F0-3236-4B3D-AB95-CC190C43A233
Fig. 4

Torbenella aff. *orbis*1. — Machordom *et al*. 2022: table 2.

Etymology

The name ‘*lupi*’ refers to one of the southern hemisphere constellations (the Wolf).

Material examined

Holotype

PAPUA-NEW GUINEA • ov. ♀ (10.2 mm); KAVIENG stn CP4418; 02º27′ S, 150º40′ E; 335–340 m depth; 28 Aug. 2014; GenBank no.: COI: OP215693, 18S: OP196289, PEPCK: OP252566; MNHN-IU-2014-10024.

Paratypes

PAPUA-NEW GUINEA • 3 ♂♂ (6.5–8.0 mm), 3 ov. ♀ (7.5–8.0 mm), 1 ♀ (5.9 mm); KAVIENG stn DW4495; 02º24′ S, 149º55′ E; 272–274 m depth; 6 Sep. 2014; MNHN-IU-2014-9900 • 1 ♀ (7.2 mm); KAVIENG stn CP4496; 02º25′ S, 149º54′ E; 269–274 m depth; 6 Sep. 2014; MNHN-IU-2014-13983.

Description

Carapace. Slightly wider than long. Transverse ridges usually interrupted, except several on gastric region and posterior part of carapace, with dense very short setae. Main transverse striae on posterior part of carapace interrupted in cardiac region. Scales and secondary striae absent between main striae. Gastric region with 2 main epigastric spines each behind supraocular spine; with row of 4–5 minute flanking spines and some small spines at base of rostrum and in parahepatic, hepatic and anterior branchial regions; one small postcervical spine on each side. Orbit with lateral limit weakly defined. Frontal margins concave. Lateral margins slightly convex. Anterolateral spine well developed, at anterolateral angle, reaching level of sinus between rostrum and supraocular spines. One or 2 very small marginal spines anterior to cervical groove. Branchial margins with 4 (rarely 5) small spines. Rostrum spiniform, less than half as long as remaining carapace, not exceeding end of corneae, carinated dorsally, straight, and directed slightly upwards. Supraocular spines barely reaching midlength of rostral spine and falling short of end of corneae, subparallel, directed slightly upwards.

Thoracic sternum. Smooth, without striae, except a few on sternite 4. Sternite 3 2.5 times as wide as long; sternite 4 2.8 times as wide as long, and 2.3 times as wide as sternite 3. Anterior part of sternite 4 slightly narrower than sternite 3; anterior margin widely contiguous to sternite 3.

Abdomen. Somites 2–4 with 2 median spines on anterior ridge; posterior ridge of somite 4 with small median spine. Somites 2–3 each with 3 transverse ridges and several scales in addition to anterior ridge. Somite 4 with a few striae.

Eyes. Eyes large, maximum corneal diameter 0.4 times distance between bases of anterolateral spines.

Antennule. Article 1 (distal spines excluded) about one-third carapace length, elongate, barely reaching end of corneae, with 2 short distal spines, mesial spine shorter than lateral spine; lateral margin unarmed, bearing numerous long plumose setae.

Antenna. Article 1 with prolonged, strong mesial process exceeding antennular peduncle, lateral border with numerous long plumose setae; article 2 with 2 distal spines, distomesial longer than distolateral, barely reaching end of article 3; article 3 with distomesial spine, article 4 unarmed.

Mxp3. Ischium about 1.5 times length of merus, distoventrally produced to spine. Merus with well-developed median spine on flexor margin, extensor margin unarmed.

P1. 2.5–3 times carapace length, squamous, with dense short setae on scales, with scattered long setae. Merus 1.3–1.5 times carpus length, armed with some mesial spines, distalmost strongest. Carpus slightly longer than palm, 3 times as long as wide, with several spines along mesial margin. Palm slightly longer

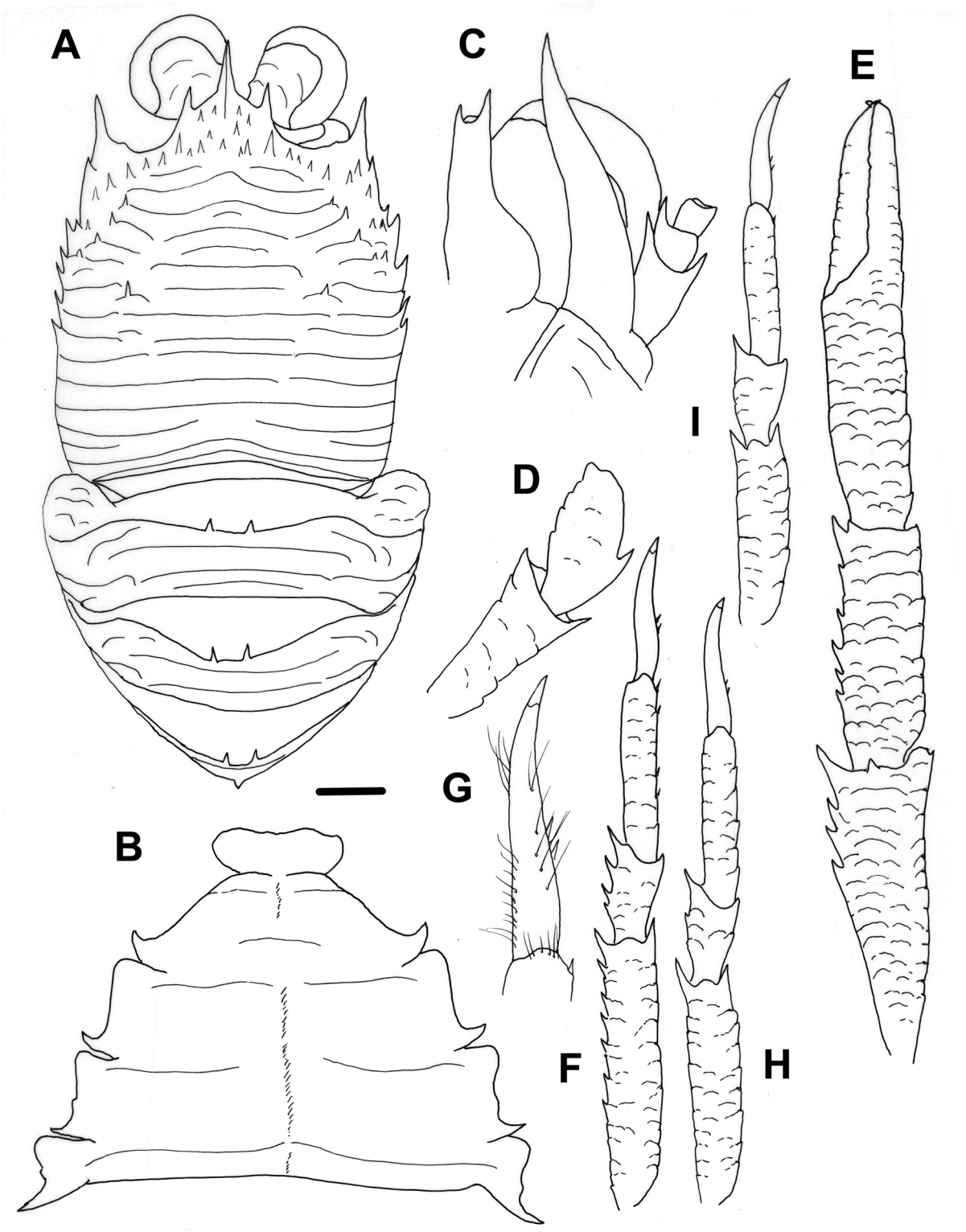

Fig. 4. *Torbenella lupi* sp. nov., holotype, ov. ♀, CL = 10.2 mm (MNHN-IU-2014-10024), Papua-New Guinea. **A**. Carapace and abdomen, dorsal view. **B**. Sternal plastron. **C**. Cephalic region, showing antennular and antennal peduncles, ventral view. **D**. Right Mxp3, lateral view. **E**. Right P1, dorsal view. **F**. Right P2, lateral view. **G**. Dactylus of right P2, lateral view. **H**. Right P3, lateral view. **I**. Right P4, lateral view. Scale bar: A, E–F, H–I = 2.0 mm; B–D, G = 1.0 mm.

than fingers, with few small spines on mesial border. Fingers unarmed, distally curving and crossing, ending in sharp point.

P2–4. Moderately long and slender, squamous, with dense short setae on scales, with some long iridescent setae along extensor margins of all articles. P2 twice carapace length. Meri successively shorter posteriorly (P3 merus 0.8 times length of P2 merus, P4 merus 0.8 times length of P3 merus); P2 merus 0.8 times carapace length, 4.5–5.0 times as long as wide, 1.7 times as long as P2 propodus; P3 merus 4.0–4.5 times as long as wide, 1.5 times as long as P3 propodus; P4 merus 3.5–4.0 times as long as wide, 1.3 times as long as P4 propodus. Extensor margins of meri with row of small, proximally diminishing spines on P2–3, distal spine only on P4; flexor margins with distal spines followed proximally by several eminences; lateral sides unarmed. Carpi with several spines on extensor margin; flexor margin ending in blunt point. Propodi 4.0–4.5 times as long as wide; extensor margin unarmed; flexor margin with 4–5 slender movable spines, without fixed distal spine. Dactyli slender, length 0.9 times that of propodi; flexor margin with 2 median movable spinules; P2 dactylus 5.5 times as long as wide.

Genetic data

Partial genes of COI, 18S and PEPCK were successfully sequenced. As usual, the COI sequence showed the highest levels of divergence, 4.86% comparing *T. aequabilis* sp. nov. and *T. orbis*, and 15.42% to *T. calvata*. *Torbenella lupi* sp. nov. formed a well-supported cluster (pp = 1) with *T. aequabilis* and *T. orbis* (Fig. 7).

Remarks

The new species is morphologically closely related to *T. orbis* (Baba, 2005) and *T. mensae* sp. nov., sharing the presence of median spines on the anterior ridge of the abdominal somite 2. Characters distinguishing the three species are outlined under the Remarks of *T. mensae* (see below).

Distribution

Papua-New Guinea, between depths of 269 and 340 m.

Torbenella mensae sp. nov.
urn:lsid:zoobank.org:act:1D01DE3B-C8B9-4316-8457-33EE2B7B9526
Fig. 5

Torbenella aff. *orbis*2.— Machordom *et al*. 2022: table 2.

Etymology

The name '*mensae*' refers to one of the southern hemisphere constellations (the Table Mountain).

Material examined

Holotype

PAPUA-NEW GUINEA • ♂ (7.2 mm); MADEEP stn DW4312; 09°50′ S, 151°34′ E; 120–280 m depth; 3 May 2014; GenBank no.: COI: OP215691, 16S: OP196030, 18S: OP196288; MNHN-IU-2016-3004.

Description

Carapace. Slightly wider than long. Transverse ridges with dense, very short setae, not medially interrupted. Scales and secondary striae absent between main striae. Gastric region with 2 main epigastric spines, each behind supraocular spine; 3–5 additional minute spines on each lateral side; some small spines at base of rostrum and in parahepatic, hepatic and anterior branchial regions; one small postcervical spine on each side. Orbit with iridescent mesial, rounded mound, lateral limit slightly

defined. Frontal margins concave. Lateral margins slightly convex. Anterolateral spine well developed, at anterolateral angle, reaching level of sinus between rostrum and supraocular spines. One small marginal spine anterior to cervical groove. Branchial margins with 4 small spines. Rostrum spiniform, less than half as long as remaining carapace, reaching end of corneae, straight, and directed slightly upwards. Supraocular spines not reaching midlength of rostral spine and falling short of end of corneae, subparallel, directed slightly upwards.

Thoracic sternum. Smooth, without striae, except a few on sternite 4. Sternite 3 3.2 times as wide as long; sternite 4 3.6 times as wide as long, twice wider than sternite 3. Anterior margin of sternite 4 contiguous to entire posterior margin of sternite 3.

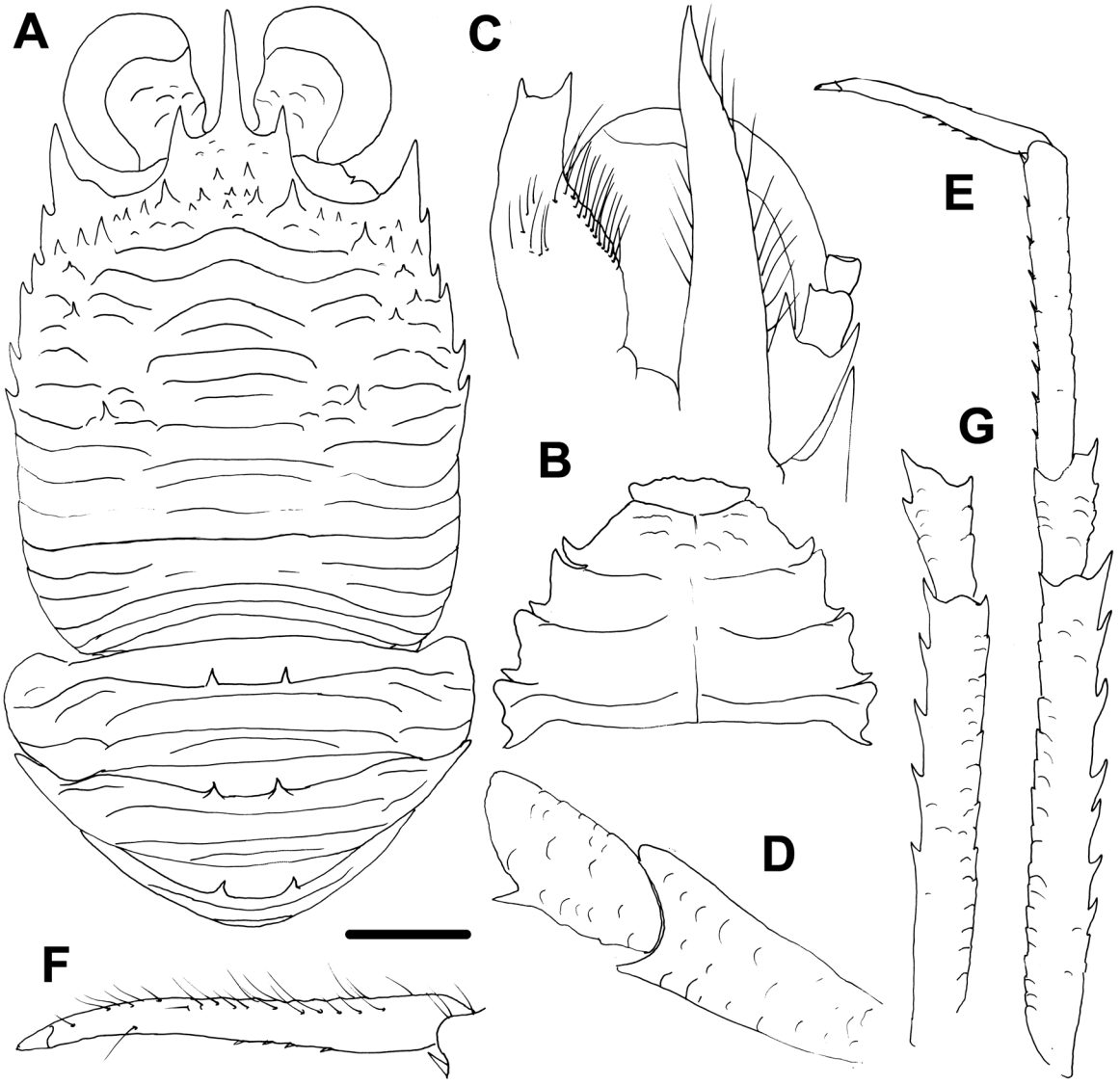

Fig. 5. *Torbenella mensae* sp. nov., holotype, ♂, CL = 7.2 mm (MNHN-IU-2016-3004), Papua-New Guinea. **A**. Carapace and abdomen, dorsal view. **B**. Sternal plastron. **C**. Cephalic region, showing antennular and antennal peduncles, ventral view. **D**. Left Mxp3, lateral view. **E**. Left P2, lateral view. **F**. Dactylus of left P2, lateral view. **G**. Right P3, lateral view. Scale bar: A–B, E, G = 2.0 mm; C–D, F = 1.0 mm.

Abdomen. Somites 2–4 each with 2 median spines on anterior ridge; posterior ridge of somite 4 unarmed. Somites 2–3 each with 3 transverse ridges and several scales in addition to anterior ridge. Somite 4 with a few striae.

Eyes. Eyes large, corneae dilated, maximum diameter 0.4 times distance between bases of anterolateral spines.

Antennule. Article 1 (distal spines excluded) about one-third carapace length, elongate, barely reaching end of corneae, with 2 short distal spines, distomesial spine shorter than distolateral spine; lateral margin unarmed, bearing numerous long plumose setae.

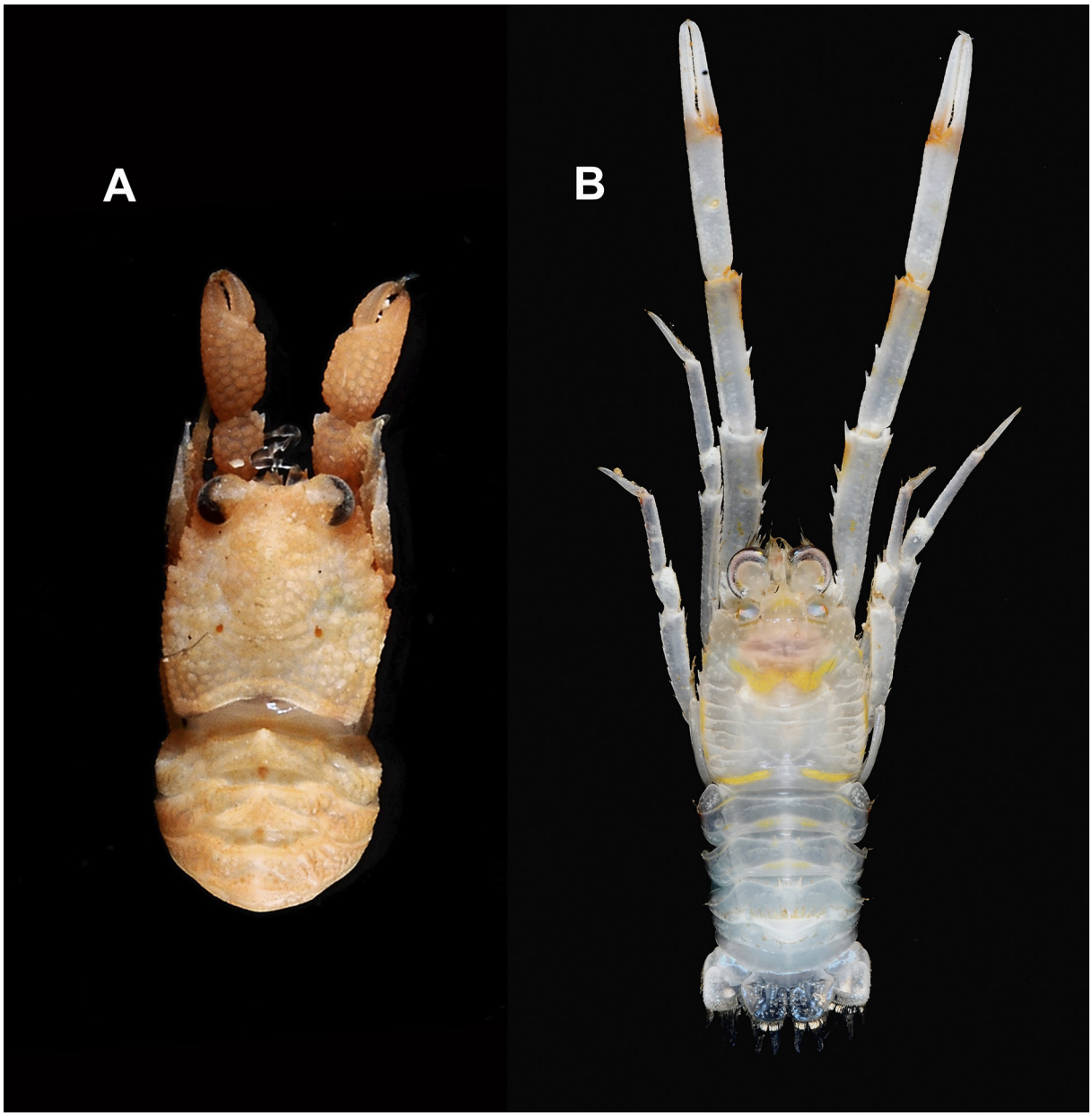

Fig. 6. Dorsal view. Colours in life. **A**. *Heteronida ceres* sp. nov., holotype, ♂, CL = 3.5 mm, New Caledonia, EXBODI, stn CP3927. **B**. *Torbenella insolita* (Macpherson, 2004), ov. ♀, CL = 7.2 mm, New Caledonia. EXBODI, stn CP3927.

Antenna. Article 1 with prolonged, strong mesial process, exceeding antennular peduncle, lateral border with long plumose setae; article 2 with 2 distal spines, distomesial slightly larger than distolateral, not reaching end of article 3; article 3 with minute distomesial spine, article 4 unarmed.

Mxp3. Ischium about 1.5 times length of merus, distoventrally produced to spine. Merus with well developed median spine on flexor margin, extensor margin unarmed.

P1. Lost.

P2–3 (P4 lost). Moderately long and slender, squamous, with dense short setae on scales, and some long iridescent setae along extensor margins of all articles. P2 2.8 times carapace length. Meri shorter posteriorly (P3 merus 0.9 times length of P2 merus); P2 merus 1.2 times carapace length, 8.5 times as long as wide, 1.6 times as long as P2 propodus; P3 merus 4.0 times as long as wide. Extensor margins of P2–3 meri with row of small proximally diminishing spines; flexor margins with distal spines followed proximally by several eminences; lateral sides unarmed. Carpi with several spines on extensor margin; flexor margin ending in blunt point. P2 propodus 8 times as long as wide; extensor margin unarmed; flexor margin with 9 slender movable spines, without fixed distal spine. P2 dactylus long and slender, 7.5 times as long as wide, length 0.8 times that of propodus; flexor margin with 4 movable spinules along proximal half.

Genetic data

COI, 16S and 18S were successfully sequenced. CO1 provided the maximum divergence between *T. mensae* sp. nov. and *T. aequabilis* sp. nov. (15.17%). The minimum value for this gene and species was 12.87% with respect to *T. crateris* sp. nov. *Torbenella mensae* sp. nov. appeared in the phylogenetic reconstruction as a sister species of *T. calvata* (Fig. 7), but with a low support (pp = 0.62).

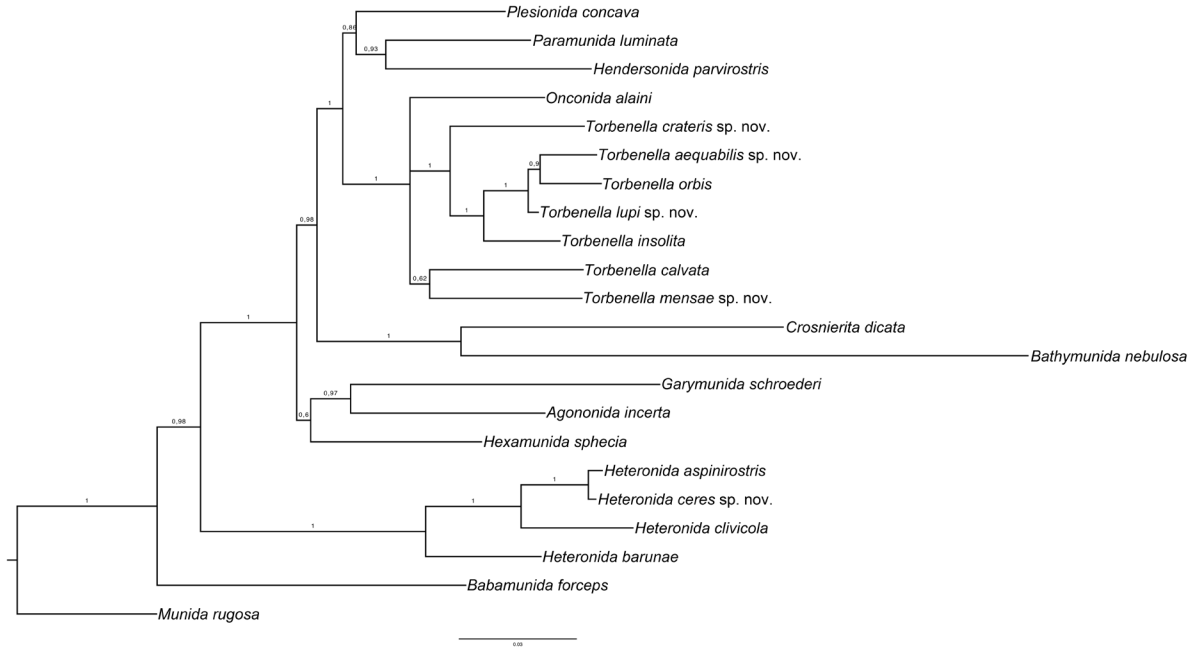

Fig. 7. Bayesian phylogenetic inference based on four concatenated gene fragments (COI, 16S, 18S and PEPCK). Numbers on branches indicated the posterior probability supports.

Remarks

Torbenella lupi sp. nov., *T. mensae* sp. nov. and *T. orbis* (Baba, 2005) are unique in the genus in having the presence of spines along the anterior ridge of the abdominal somite 2. *Torbenella mensae* is easily distinguished from the other 2 species by the wider thoracic sternite 3 (more than 3 times as wide as long) and the absence of spines on the posterior ridge of the abdominal somite 4. The other species have the thoracic sternite 3 moderately wide, less than 3 times as wide as long, and the posterior ridge of the abdominal somite 4 usually with small median spines.

Torbenella lupi sp. nov. and *T. orbis* were found at the same station in Papua-New Guinea. *Torbenella lupi* is distinguished from *T. orbis* by having spinules on the flexor margin of the P2–4 dactyli, which are absent in *T. orbis*. Furthermore, these articles are more slender in *T. orbis* than in the new species (7.5 vs 5.5 times as long as wide).

The genetic differences among the three species were: 13.28% for COI between *T. mensae* and *T. lupi* sp. nov., and 14.70% between *T. mensae* and *T. orbis* (COI), and pairwise distance of 11.12% for 16S between *T. mensae* and *T. orbis*; sequence data for 16S was not available for *T. lupi*.

Distribution

Papua-New Guinea, between depths of 120 and 280 m.

Key to species of *Torbenella*

1. Second abdominal somite unarmed 2
– Second abdominal somite with 2 median spines on anterior ridge 4

2. Thoracic sternite 3 wide, more than 3 times as wide as long. Posterior ridge of abdominal somite 4 unarmed. Anterolateral spine of carapace short, not reaching sinus between rostral and supracocular spines ..... ***T. calvata*** (Macpherson, 2006)
– Thoracic sternite 3 narrow, less than 3 times as wide as long. Posterior ridge of abdominal somite 4 usually with small median spine. Anterolateral spine of carapace well developed, barely reaching sinus between rostral and supracocular spines 3

3. Some transverse ridges of carapace uninterrupted. Abdominal somites 2–3 each with 3 transverse ridges in addition to anterior ridge ..... ***T. aequabilis*** sp. nov.
– All transverse ridges of carapace laterally or medially interrupted. Abdominal somites 2–3 each with 1 or 2 transverse ridges in addition to anterior ridge .....***T. crateris*** sp. nov.

4. Antennal article 2 with distomesial spine strong, overreaching midlength of article 4. P2–4 dactyli armed with row of spinules on proximal two-thirds of flexor margin .... ***T. insolita*** (Macpherson, 2004)
– Antennal article 2 with distomesial spine of moderate size, reaching midlength of article 3. P2–4 dactyli unarmed or with a few spinules on proximal half of flexor margin 5

5. Thoracic sternite 3 wide, more than 3 times as wide as long. Posterior ridge of abdominal somite 4 unarmed .....***T. mensae*** sp. nov.
– Thoracic sternite 3 moderately wide, less than 3 times as wide as long. Posterior ridge of abdominal somite 4 usually with small median spine 6

6. P2–4 dactyli slender, 7.5 times as long as wide; flexor margin unarmed ..... ***T. orbis*** (Baba, 2005)
– P2–4 dactyli moderately slender, 5.5 times as long as wide; flexor margin with a few spinules on proximal half .....***T. lupi*** sp. nov.

Discussion

The results obtained in this study support previous findings that the species richness in most genera of squat lobsters is still underestimated, as it has been demonstrated for a number of other genera (e.g., Baba 2018; Rodríguez-Flores *et al*. 2019; Macpherson *et al*. 2020; McCallum *et al*. 2021). Furthermore, species records of *Heteronida* and *Torbenella* are mainly from the southwestern Pacific (Baba *et al*. 2008), from Kei Islands to New Caledonia and French Polynesia, highlighting the importance of this area as a 'hot spot' in squat lobster diversity (Schnabel *et al*. 2011; Cabezas *et al*. 2012). The species are recorded on the continental shelf and upper slope, at depths of ca 200–700 m (*Heteronida*) and ca 150–900 m (*Torbenella*) (Macpherson *et al*. 2010). Three species of *Heteronida* have a moderately wide geographic distribution: *H. aspinirostris* and *H. ceres* sp. nov., from New Caledonia to Tonga, *H. barunae* from Papua-New Guinea and Kei Islands to Taiwan, whereas *H. clivicola* is restricted to French Polynesia. In contrast, the species of *Torbenella* have, in general, a reduced distribution range: three species (*T. aequabilis* sp. nov., *T. calvata* and *T. crateris* sp. nov.) are only found in New Caledonia and surrounding waters, and two species (*T. lupi* sp. nov. and *T. mensae* sp. nov.) are only found in Papua-New Guinea. *Torbenella insolita* and *T. orbis* occur from Tonga to Papua-New Guinea and New Caledonia, and from Kei Islands to Norfolk Islands, respectively. Most species of these genera are found in allopatry, although in a few cases two species can be found in the same station, e.g., *H. aspinirostris–H. ceres* and *T. crateris–T. insolita* in New Caledonia, *T. orbis–T. lupi* in Papua-New Guinea (Macpherson *et al*. 2020 and this study).

Previous phylogenetic studies have suggested that *Heteronida* and *Torbenella* are probably monophyletic and both originated during the Miocene (Machordom *et al*. 2022). These taxa are included in the clade of munidids having only one pair of gonopods in the males (Machordom & Macpherson 2004; Machordom *et al*. 2022). *Heteronida* is not phylogenetically close to other small-sized species, e.g., *Bathymunida* Balss, 1914, *Onconida* Baba & de Saint Laurent, 1996, whereas *Torbenella* is closely related to other genera of small or moderate size species, e.g., *Onconida*, that is included in a non-resolved clade together with *Torbenella* (Machordom *et al*. 2022). On the other hand, the molecular analyses undertaken allowed us to identify a number of phylogenetically informative characters (Knowlton 2000). There are few morphological characters of phylogenetic value in *Heteronida.* For instance, the species of this genus are easily differentiated from each other by the armature of the carapace and abdomen: covered by large size granules in *H. ceres* sp. nov. vs few and small-sized granules in the other species. *Heteronida ceres* is genetically very different from the other species, suggesting that the granulation could have a phylogenetic value in this genus. A similar pattern is observed in the species of *Torbenella*, where there are few morphological characters with a phylogenetic value. For instance, species from a well-supported clade (*T. aequabilis* sp. nov., *T. crateris* sp. nov., *T. insolita* and *T. orbis*) (see Machordom *et al*. 2022) possess a narrow thoracic sternite 3, whereas this sternite is very wide in a separate clade (*T. calvata* and *T. mensae* sp. nov.). However, characters used in the key to species, for instance, the absence/presence of spines on the anterior ridge of the abdominal somite 2 and the posterior ridge of somite 4 are observed in both clades indicating a low phylogenetic value although it can be used to separate species. Similar patterns are observed in other diagnostic characters, e.g., the size of the anterolateral spine of the carapace, the presence or absence of spinules in the flexor margin of the P2–4 dactyli. These results confirm the difficulty in identifying diagnostic characters with phylogenetic signal in taxa where morphological homoplasy is high, as it has been observed in other munidids (e.g., Macpherson & Machordom 2001; Cabezas *et al*. 2012; Poore & Andreakis 2014). Therefore, morphological conservatism has important consequences and must be taken into account in taxonomic studies of squat lobsters (Puillandre *et al*. 2011).

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