

***Maageninum kanakorum* gen. nov., sp. nov.: a New Caledonian Pycnogonid (Arthropoda: Pycnogonida) with Puzzling Affinities**

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The taxonomic classification of sea spiders (Arthropoda: Pycnogonida) includes 11 distinct families, mostly characterized by different combinations of presence/absence of the cephalic appendages, the characters they display (number of articles, terminal claw, distribution of spines, etc.), and the position of gonopores in both sexes and of the cement gland pores in males. However, about 20 nominal species could not be confidently classified, and a few others were only tentatively assigned to one of these families. These taxa represent an interesting challenge to review, reshape and expand the Pycnogonida taxonomy, and thus to apprehend more comprehensively the phylogeny of the group. In this contribution, *Maageninum kanakorum* gen. nov., sp. nov. is described based on two males and two females that were sampled at 220–232 m depth in a single location off southeast of New Caledonia in 2011 during the EXBODI expedition (Tropical Deep-Sea Benthos program). A fragment of the gene coding for the first unit of the cytochrome oxidase was sequenced for three of these specimens for the purpose of DNA barcoding, and the gonopores were investigated in both sexes through scanning electron microscopy. Due to its unique combination of characters, the genus *Maageninum* cannot be confidently attributed to any of the known pycnogonid families based on the sole morphological characters: absence of chelifores; palps reduced to two articles only present in males; ovigers two-articled in males, or reduced to a conspicuous unarticulated bud in females; gonopores carried on the ventral surface of coxae 2 in legs 2–4, both in males and females. For this reason, it is to be regarded as *incertae sedis* until its position is resolved by future phylogenetic studies.

Keywords: Pantopoda, Pacific Ocean, Coral Sea, Sexual dimorphism, Diagnostic characters

BACKGROUND

Sea spiders (Arthropoda: Pycnogonida) are a group of marine chelicerates distributed worldwide. Approximately 1,400 extant species are described (Bamber et al. 2026), but this figure probably under-evaluates the actual diversity of the group (Appeltans et al. 2012) as a consequence of the lack of experts, of the geographical scarcity of studies, and of the rarity of taxonomical works integrating genetic data like DNA

barcoding (e.g., Sabroux et al. 2019b; Brenneis et al. 2020; Lee et al. 2025).

Most of extant species are assigned to one of the 11 families that are now widely accepted for the group (Bamber et al. 2026). These families are notably diagnosed by sets of characters on the cephalic appendages and legs (Bamber 2007a): the presence/absence of the chelifores, palps and ovigers (the first, second and third pair of cephalic appendages, respectively), their number of articles, whether they

carry a terminal claw, their spination or denticulation, etc.; the position of the gonopores of males and females on either of the four pairs of legs, on the ventral or dorsal surface of coxae 2 (the second proximal article of walking legs): the presence, position, number, and shape of the femoral opening of the so-called cement glands, the role of which is poorly understood (Petrova and Bogomolova 2025). The families as diagnosed by these characters are widely supported as monophyletic by phylogenetic studies, to the exception of Ascorhynchidae, Callipallenidae and Nymphonidae (Sabroux et al. 2017 2023; Ballesteros et al. 2021).

However, about 20 species included in 11 genera have so far resisted any attempt to be classified at the family rank (Bamber et al. 2026): *Bango polyonyx* Bamber, 2004; *Chonothoe hians* Nakamura & Child, 1983 and *C. verrucosa* Nakamura & Child, 1991; *Decachela discata* Hilton, 1939 and *D. dogieli* Losina-Losinsky, 1961; *Ephyrogymna circularis* Hedgepeth, 1943; six *Hannonia* Hoek, 1881 species (see Sabroux 2026 for a list and a review); *Mimipallene atlantis* Child, 1982; *Pigrogromitus timsanus* Calman, 1927; *Pycnopallene clauda* (Loman, 1908); *Pycnothoe flynni* Williams, 1940 and *P. selkirkii* Loman, 1921; *Queubus echidna* Bamber & Steffani, 2007 and *Q. jansanus* Barnard, 1946, *Bradypallene espina* Kim & Hong, 1987. In addition, the four species of the genus *Boehmia* Hoek, 1881 were only tentatively included in Ascorhynchidae by Bamber (2007a). As for fossils of the Pycnogonida crown group (= Pantopoda), most can be attributed to extant families, but one was recently suggested to belong to a family of its own (Sabroux et al. 2019a 2023).

All these taxa test the limits of the current classification of Pycnogonida. They might indicate that the current diagnoses of accepted families should be revised or extended to include these groups, or that additional lineages of sea spiders should be described into new families. Critically, many of the *incertae sedis* genera are monotypic, indicating that either their taxonomical classification is unresolved or that they represent residual lineages. Almost all these species are rarely sampled (except, to some extent, *P. timsanus*), making the chances to get new material for DNA sequencing and phylogenetic analyses very low. Material from these taxa is thus particularly interesting and critical to understand the diversity and evolution of Pycnogonida.

A total of 67 sea spider species were reported so far from the waters of New Caledonia (Bamber 2007b; Sabroux 2025). Here, is reported a new species for the region and for science, *Maageninum kanakorum* gen. nov., sp. nov., represented by four type specimens that were sampled in a single spot upon the EXBODI

expedition during fall 2011 on the eastern coast of New Caledonia.

MATERIALS AND METHODS

Sampling and preservation

The four specimens (two males and two females) were sampled in a single location on September 8, 2011, during the EXBODI expedition organised by the Tropical Deep-Sea Benthos program in the Coral Sea between New Caledonia and Vanuatu. Sampling was performed with a trawl at station CP3827, GPS coordinates 21°58'S, 166°57'E, 220–232 m deep (Fig. 1). All four specimens were preserved in 80% ethanol and are curated at the MNHN in Paris.

Measurements

Measurements were calculated as follows: trunk + cephalon length extends from the frontal ridge of the cephalon before the chelifores' insertion, to the base of the abdomen; trunk width was calculated at the second trunk segment, lateral processes included; the proboscis was measured from its insertion to the mouth at the tip; the abdomen length was measured from its base to the anus at the tip; the different article lengths of the third leg were measured from the middle of their basal to the middle of their distal insertion in lateral view. The main claw length was measured from the middle of its insertion in lateral view, to its tip.

DNA barcoding

DNA extraction, partial amplification, and sequencing of a fragment of the first subunit of the cytochrome *c* oxidase (CO1) were done as detailed in Sabroux et al. (2017). Resulting sequences for the specimens MNHN-IU-2012-784 (holotype), MNHN-IU-2012-785 and MNHN-IU-2012-786 (paratypes) were deposited on GenBank under accession numbers PZ544956, PZ544957 and PZ544958 respectively.

Scanning Electron Microscopy (SEM)

In order to confidently assign the sex and address the position of gonopores, SEM was performed on one of each pair of legs for both sexes in paratypes MNHN-IU-2011-6515 and -2012-785. The leg was severed on the ethanol-fixated specimens with micro-scissors at coxa 1 and coxa 3 to isolate the coxa 2. The resulting fragment was dehydrated with four baths of ethanol absolute (30 minutes each) and critical-point-

dried using a Leica EM CPD300 critical point dryer. The dried coxae 2 were then mounted on SEM stubs with self-adhesive carbon stickers, ventral side facing up. The samples were then coated with platinum on a Leica EM ACE 200 vacuum coater. SEM pictures were taken using a JSM-6700F JEOL Scanning Electron Microscope.

RESULTS

Class Pycnogonida Latreille, 1810
Ordre Pantopoda Gerstäcker, 1863
Family *incertae sedis*

Genus *Maageninum* gen. nov.

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Etymology: From *Mââgenin*, a marine character depicted in some folklores of the Isle of Pines (South New Caledonia). The name is treated as neuter (2nd decl.).

Diagnosis: Ocular tubercle elongated, eyes at tip. Proboscis triradial, elongated. Abdomen long, segmented at base. Chelifores absent. Palps minute in males, absent or vestigial in females. Oviger two-articled in males; distalmost article roughly bullet-shaped with individualised pointy tip; reduced to a bud without basal articulation in females. Legs 8-articled

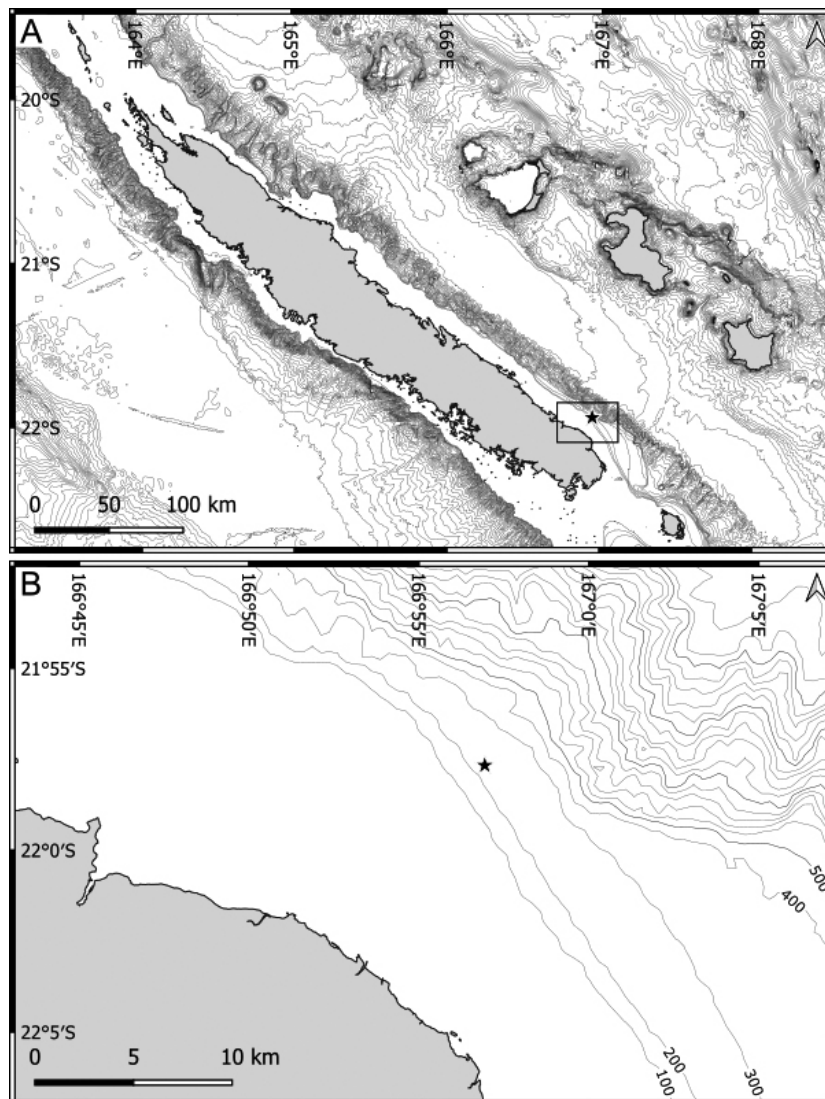


Fig. 1. Sampling locality. A: New Caledonia and surrounding waters, the framed area corresponds to B. B: Zoom-in on the Southwestern New Caledonia region. Lands (above 0 m) are filled in light grey. Bathymetry is indicated by 100 m isobath lines. The arrowhead points to the North. The sampling locality CP3827 (21°58'S, 166°57'E) is marked with a star.

plus main claw, tarsus short, one large ventral spine on propodal sole subchelate with main claw; auxiliary claws absent; ventral spur on coxa 2 in legs 2–4 in both sexes.

Type species: Maageninum kanakorum sp. nov.

***Maageninum kanakorum* sp. nov.**

(Figs. 2–5)

urn:lsid:zoobank.org:act:EAC9195B-9AC7-47CF-9DB7-BA37B62C9641

Etymology: From *kanakus*, -i, (masc., 2nd decl.), a Latin neologism referring to the Kanak people from New Caledonia. Used in the genitive plural.

Material examined: *Holotype:* CORAL SEA • ♂; Southeast of New Caledonia, off Passe d'Ounia; 21°58'S, 166°57'E; 220–232 m; 8 Sep. 2011; EXBODI st. CP3827; GenBank nos: PZ544956 (CO1); MNHN-IU-2012-784.

Paratypes: CORAL SEA • 1 ♀; same data as holotype; GenBank nos: PZ544957 (CO1); MNHN-IU-2012-785 • 1 ♀; same data as holotype; GenBank nos: PZ544958 (CO1); MNHN-IU-2012-786 • 1 ♂; same data as holotype; MNHN-IU-2011-6515.

Description (holotype ♂, MNHN-IU-2012-784; Fig. 2): Body elongated, moderately slender, trunk segments fused with suture traces, cuticle granulose. Anterior margin of cephalon widely flaring. Ocular tubercle bent forward, tall, about 2.5 times as long as base width, tip saddle-shaped in frontal view, triangular in lateral view. Eyes present, pigmented. No evidence of lateral sense organs. Lateral processes 1.2 to 1.3 times longer than wide, well separated by more than half their own diameter, marked by suture lines, one on each side laterally, and one dorsally with winged spear-shape; each carrying one long dorsomedian seta and shorter lateral setae. Insertion of ovigers and palps below first lateral processes, carried latero-ventrally on cephalon distal margin. First lateral processes elevated above cephalon. Insertion of ovigers as a small lateral process, shorter than wide.

Proboscis about as long as three first trunk segments and cephalon (*sensu* Bamber 2007a), gently curved in lateral view, grossly conical in dorsal view, distal half tubular, tip blunt, rounded.

Abdomen about as long as first two trunk segments and cephalon, oriented posteriorly, club-shaped, base articulated.

Chelifore absent.

Palp ♂ minute, 2-articled. Proximal article rounded, about as long as wide. Distal article about thrice as long as wide, tapering distally. Both articles carrying sparse short setae.

Oviger ♂ 2-articled. Proximal article globular,

about 1.3 times as long as wide. Distal article more than twice as long as wide, roughly bullet-shaped with base slenderer, broadening until approximately its proximal two thirds, distally strongly tapering. Short setae sparsely distributed on both articles. Distal tip carrying one minute individualised extension, possibly a vestigial article or claw.

Legs cuticle faintly reticulated, with visible lateral suture line from proximal coxa 1 to distal tibia 2. Coxa 1 about 1.7 times about as long as wide, carrying one long dorsomedian seta, other long and medium-sized setae distally and medium-sized and short setae laterally. Coxa 2 longer than base width, about 1.3 times as long as its own median width laterally and 1.8 times ventrally, with long setae carried dorsally. Coxae 2 on legs 2–4 ventrally carrying one short, rounded spur carrying gonopore oriented anteriorly (see also Fig. 4C–H). Coxa 2 on first leg without spur or gonopore (see also Fig. 4A, B). Coxa 3 about as long as wide, with medium-sized setae dorsally. Femur about 5.6 times as long as wide, carrying long and medium-sized setae along its length. Tibia 1 slightly longer than femur, carrying short and medium-sized setae along its length. Tibia 2 about 1.3 times as long as femur, carrying short setae along its length. Tarsus trapezoidal, about as long as wide, with sparse short setae dorsally and ventrally. Propodus about one third of tibia 2 length, about thrice as long as tarsus, carrying dense setae dorsally, broader at base, carrying proximally on ventral side two short spines immediately followed by low propodal heel carrying one massive, curved spine. Propodal sole carrying small setae and spines. Main claw curved, about half as long as propodus length, forming subchelate structure with massive heel spine about half as long as main claw. Auxiliary claws absent. Cement gland pores absent or not observed.

Sexual dimorphism (Figs. 3, 5): Female approximately 15% larger than males in proportions, female coxae 2 stouter and proportionally shorter than in males, about 1.2 times as long as median width laterally and 1.5 ventrally. No conspicuous swelling of female leg articles among type material. Female palps absent, small anterior bud instead. Female ovigers reduced to bud with no articulation at base, less than twice as long as wide, bending anteriorly, neatly crooked with angle near its base. Spurs on coxa 2 in legs 2–4 crooked, tip bent toward article proximal part. Female gonopores larger than in males, carried on legs 2–4, oriented anteriorly.

Measurements of the holotype (mm): trunk + cephalon length 4.5, trunk width at second trunk segment (lateral processes included) 2.8, proboscis length 3.6; abdomen length 2.5; coxa 1 length 1.0; coxa 2 length 1.0; coxa 3 length 0.7; femur length 3.6; tibia 1 length 3.8; tibia 2 length 4.7; tarsus length 0.5; propodus

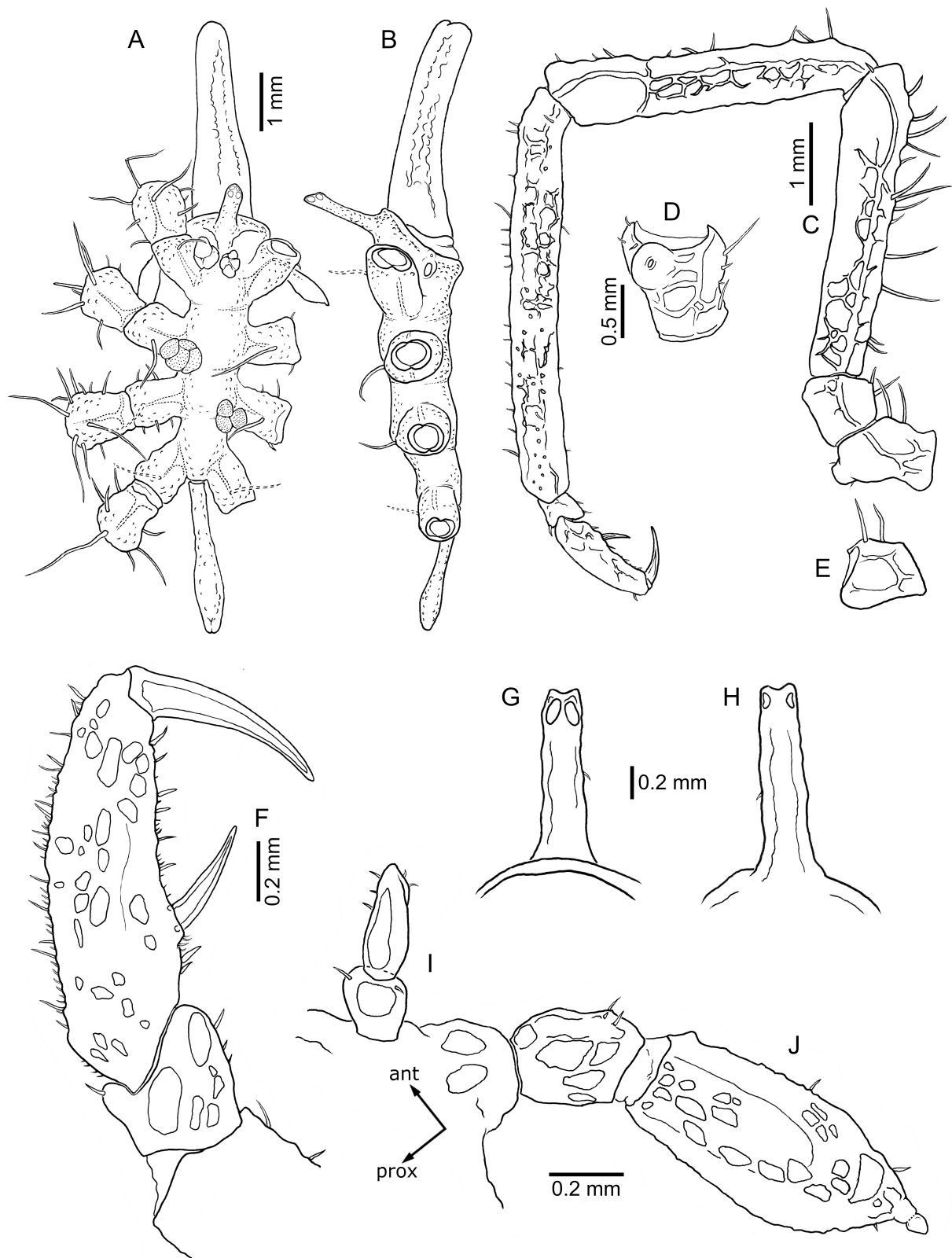


Fig. 2. *Maageninum kanakorum* gen. nov., sp. nov., holotype MNHN-IU-2012-784 (♂). A: body, dorsal view. B: body, lateral view (same scale as A). C: third leg, lateral view. D: coxa 2 of third leg, ventral view. E: coxa 2 of first leg, lateral view (same scale as C). F: terminal articles of third leg. G: ocular tubercle, anterior view. H: ocular tubercle, posterior view (same scale as H). I–J: cephalic appendages, ventral view: I: palp; J: oviger; arrows indicate orientation: ant = anterior, prox = proximal.

length 1.4, main claw length 0.7.

DNA barcode variability: All three CO1 barcoded sequences are identical (p -distance = 0).

DISCUSSION

When relying on the characters usually considered to define affinities with extant Pycnogonida families, three hypotheses can be proposed for *Maageninum*:

A superficial examination of these New Caledonian specimens could lead to regard this genus as a very slender and elongated form of Pycnogonidae Wilson, 1878. The shape of the proboscis is similar to several *Pycnogonum* species (e.g., *P. cesaiei* Sabroux, 2022; *P. clarki* Staples, 2002; *P. elephas* Stock, 1966; *P. madagascariensis* Bouvier, 1911; *P. reticulatum* Hedgpeth, 1948). As in Pycnogonidae, the chelifores are absent, and the ovigers only present in males (in the *Nulloviger* subgenus, ovigers are absent in both sexes). The structure of the ovigers in Pycnogonidae is rather variable, including in its number of articles (four to nine; Bamber 2007a), and thus does not strictly oppose to comparison with *Maageninum*. Interestingly, lateral sense organs seem to be missing, a particularity shared with Pycnogonidae (Brenneis 2022). The males also have no conspicuous cement gland pore, which is notably shared with Pycnogonidae (together with Colossendeidae and some callipallenids), and *Maageninum* shares with representatives of this family the absence of auxiliary claws. The presence of palps, however, is unseen in Pycnogonidae as it is currently accepted (Bamber et al. 2026). In addition, female Pycnogonidae have their gonopores on the dorsal surface of coxae 2, on legs 4, or on two or all pairs of legs (Bamber 2007a), while males have gonopores ventrally positioned on legs 4 only; in *Maageninum*,

gonopores are instead positioned on the ventral surface in both sexes, and on legs 2 to 4.

The family Endeidae Norman, 1908 has the same combination of cephalic appendages presence/absence as in Pycnogonidae. The slender habitus of *Maageninum* is more reminiscent of Endeidae than Pycnogonidae. However, the gonopores of Endeidae are distributed on all four pairs of legs in both sexes (Bamber 2007a), unlike in *Maageninum* which misses gonopores on the first pair. *Maageninum* notably lacks conspicuous cement gland pores, while Endeidae typically show fields or rows of glands on the posterior surface of femorae. Endeidae always miss palps, have seven-articled ovigers, and always present auxiliary claws, contrastingly with *Maageninum*. For other characters *Maageninum* hardly resembles an endeid, while this family is very homogeneous morphologically speaking.

Nymphonoidea Wilson, 1878 includes two families, Callipallenidae Hilton, 1942 and Nymphonidae Wilson, 1878. Callipallenids are paraphyletic (so are probably nymphonids; see Ballesteros et al. 2021 and Sabroux et al. 2023). Nonetheless, they have very reduced palps (with zero to four articles) in males, and no palp at all in females, which could suggest affinities between *Maageninum* and Nymphonoidea. However, all species included among Nymphonoidea have, so far, functional three-articled chelifores, which are often massive. Ovigers in Nymphonoidea are also typically 10-articled (although see Staples 2021) with terminal claw either present or absent. Male nymphonoids have two or four pairs of gonopores and females four pairs, unlike *Maageninum*.

While arguments in favour of an affinity with Pycnogonidae are more numerous, none of the aforementioned hypotheses are plainly satisfactory, mostly as a consequence to the unusual number and position of gonopores, the presence/absence combination of the cephalic appendages and the unique structure of the ovigers. To test the new species' phylogenetic position with available molecular data, Bayesian Inference analyses were performed integrating the new DNA barcode sequences to a dataset composed of the CO1 sequences published by Sabroux et al. (2017 2019b) and Lee et al. (2025), but the resulting topologies (data not shown) expectably turned out to be totally unsupported and inconclusive, whether third codon positions were coded as purine/pyrimidine or not.

Phylogenetic studies have underlined that cephalic appendages in adult sea spiders have appeared/disappeared several times through the evolution of the group, a lability that is probably facilitated by that they remain invariably present at the larval stage (Ballesteros et al. 2021; Sabroux et al. 2023). The structure of ovigers and palps can also be very variable

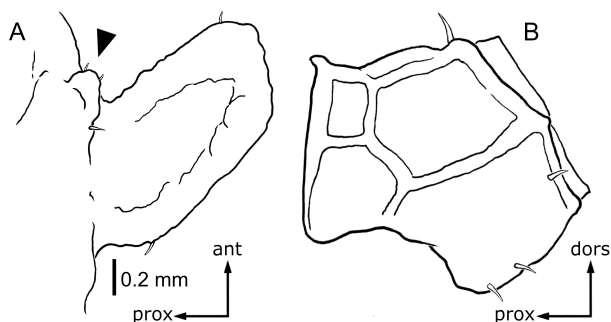


Fig. 3. *Maageninum kanakorum* gen. nov., sp. nov., paratype MNHN-IU-2012-786 (♀). A: vestigial oviger, ventral view; the arrowhead shows the small anterior bud. B: coxa 2 of third leg (same scale as A). Arrows indicate orientation: ant = anterior, dors = dorsal, prox = proximal.

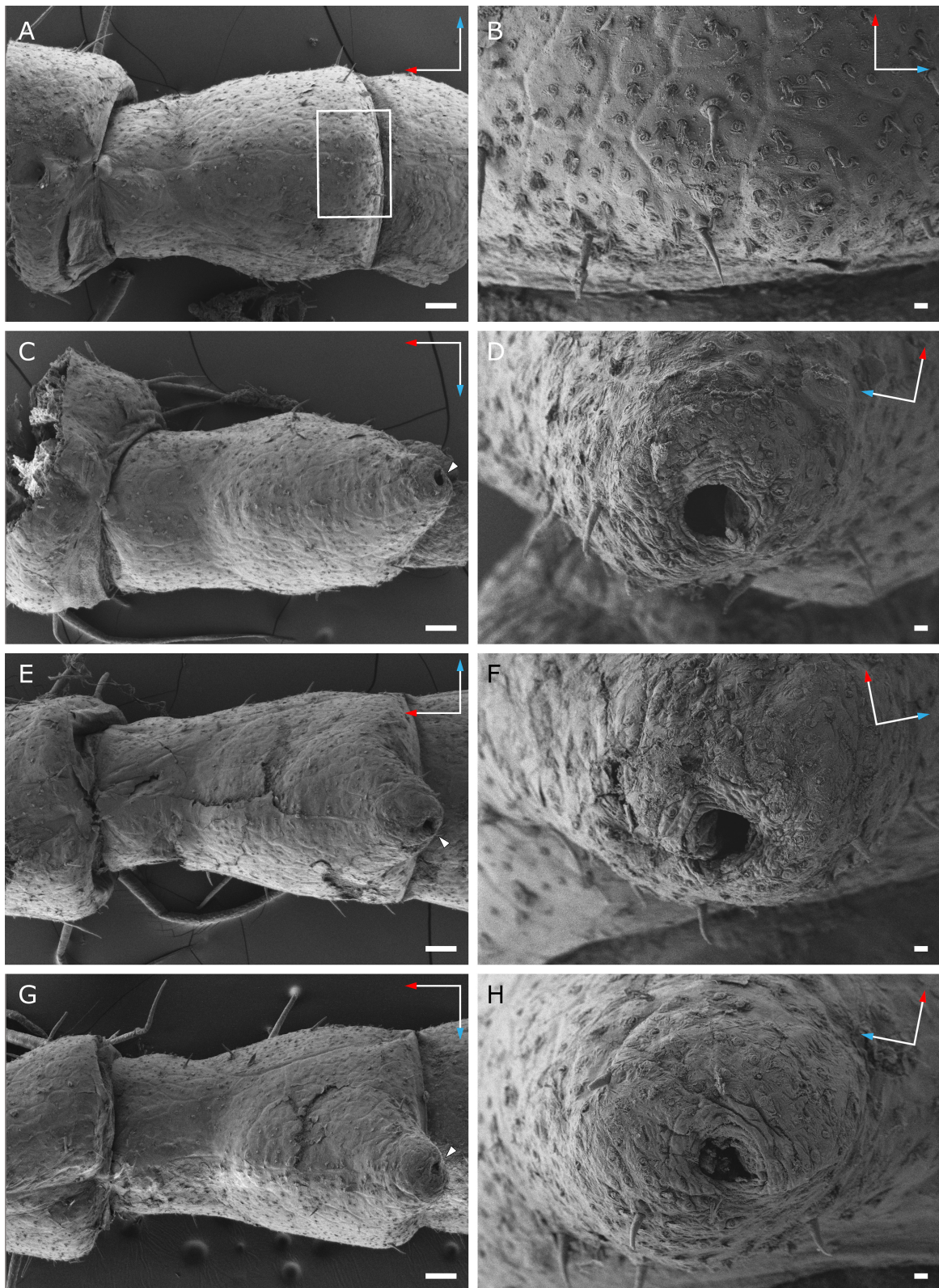


Fig. 4. ventral view of coxae 2 in *Maageninum kanakorum* gen. nov., sp. nov., paratype MNHN-IU-2011-6515 (♂), Scanning Electron Microscopy. A, C, E, G: general view of coxa 2, ventral view (white arrowheads point to the gonopore ♂; scale bar 100 μm); B, D, F, H: focus on the gonopore ♂, or the absence thereof (scale bar 10 μm). A, B: right leg 1 (the white frame in A corresponds to the field in B). C, D: left leg 2. E, F: right leg 3. G, H: left leg 4. Red arrowhead indicates proximal direction, blue arrowhead posterior direction. Scales are the same as in figure 5.

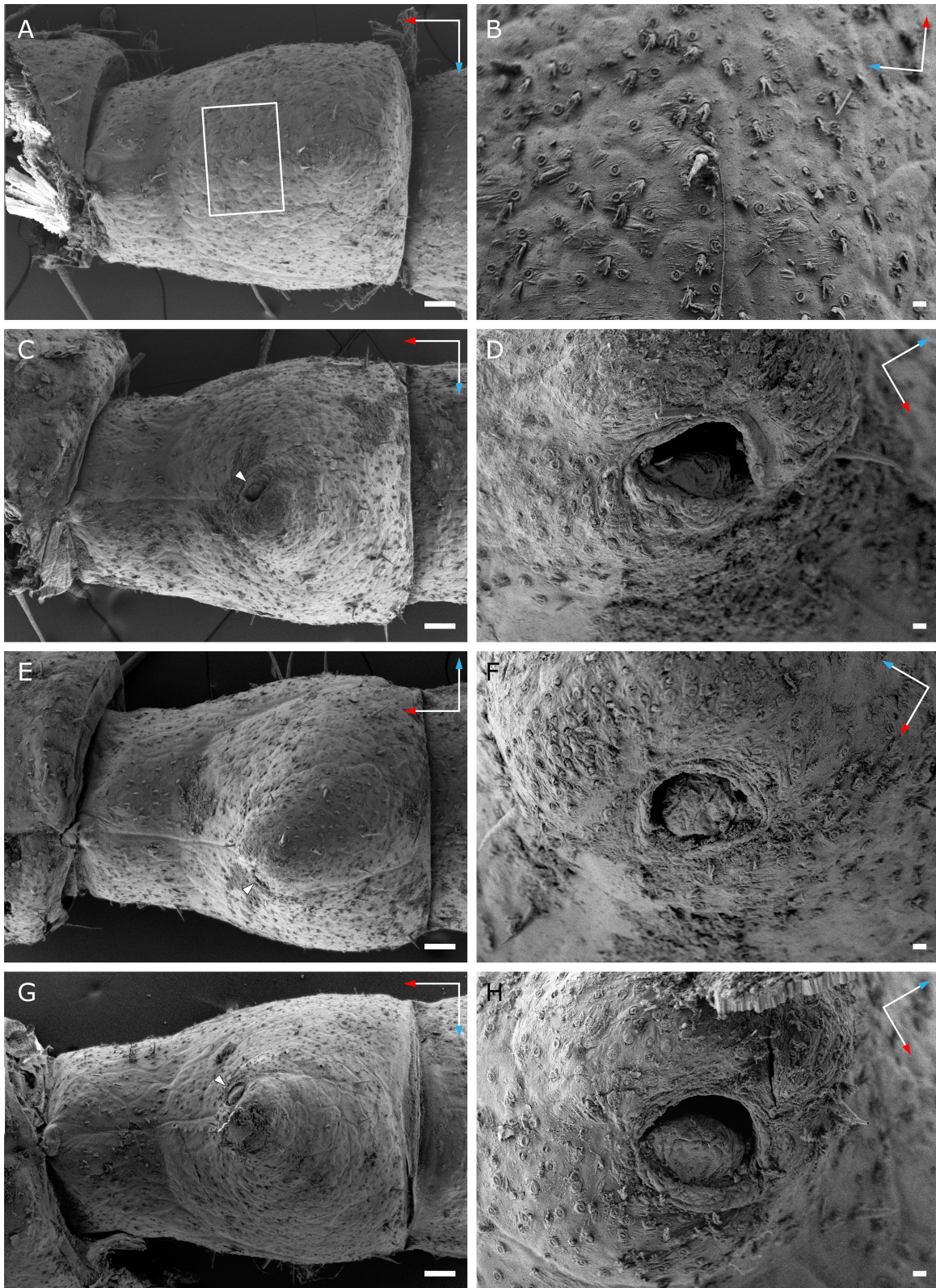


Fig. 5. ventral view of coxae 2 in *Maageninum kanakorum* gen. nov., sp. nov., paratype MNHN-IU-2012-785 (♀), Scanning Electron Microscopy. A, C, E, G: general view of coxa 2, ventral view (white arrowheads point to the gonopore ♀; scale bar 100 µm); B, D, F, H: focus on the gonopore ♀, or the absence thereof (scale bar 10 µm). A, B: left leg 1 (the white frame in A corresponds to the field in B). C, D: left leg 2. E, F: right leg 3. G, H: left leg 4. Red arrowhead indicates proximal direction, blue arrowhead posterior direction. Scales are the same as in figure 4.

in some lineages as noted above for Pycnogonidae (for ovigers) or Callipallenidae (for palps). The number and position of gonopores and cement gland pores are often undescribed, meaning that we might not know the full extent of variations presented in described lineages. On the top of that, the relatively poor resolution of sea spider phylogeny at interfamilial rank makes it difficult to evaluate which of these characters are autapomorphic in modern sea spiders.

Thus, it cannot to be excluded that *Maageninum* is a highly derived species within one of the 11 described families. Alternatively, it could represent a distinct lineage of sea spiders, well separated from the described families. In that case, and depending on taxonomic strategies, *Maageninum* could be integrated into the most closely related described family, that is yet to be determined, by drastically emending the said family diagnosis. Or the unique morphology of *Maageninum*, involving key characters for the higher ranks taxonomy of sea spiders, could motivate the erection of a new, monotypic family. Either way, *Maageninum* illustrates the increasing complexity of our picture of Pycnogonida diversity and evolution, as already well illustrated by the diagram of Hedgpeth (1947, fig. 1). Therefore, phylogenetic studies that will include *incertae sedis* taxa such as *Maageninum* will be critical for understanding the evolution of sea spiders and of the morphological characters that are traditionally used to determine their higher ranks classification.

CONCLUSIONS

This is the description of a new sea spider species and genus, sampled for the first time off the coast of New Caledonia in the Coral Sea. The four specimens, two males and two females, allow for a complete description including sexual dimorphism. The combination of morphological characters in *Maageninum kanakorum* gen. nov., sp. nov.—namely, the absence of chelifores, the palps minute in males and absent or vestigial in females, the ovigers minute in males and residual in females, the gonopores on the ventral surface of coxae 2 in legs 2–4 in both sexes, the abdomen articulated at base—does not allow this new species to be assigned to any of the 11 widely accepted sea spider families. This finding highlights that the diversity of Pycnogonida remains largely unexplored and that the current taxonomy of the group does not yet reflect its phylogenetic diversity.

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Authors' contributions: RS conducted all aspects of this work.

Competing interests: RS declares no conflict of interest.

Availability of data and materials: the new material cited in this reference is curated at the *Muséum national d'Histoire naturelle*, Paris (France) under the collection numbers that are indicated in the material list. DNA barcode sequences are available on GenBank at the specified accession numbers.

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Ethics approval consent to participate: Not applicable.

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