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The Sea Spider Genus *Hannonia* Hoek, 1881 (Pycnogonida): A Review and Two New Species

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Hannonia is a particularly rare and poorly studied genus, which includes four species distributed along the shores of Africa and Europe. Here, two new species are described from the southern shores of Madagascar, *Hannonia arnaudae* sp. nov. and *Hannonia laurae* sp. nov. sampled during the ATIMO VATAE expedition (*Muséum national d'Histoire Naturelle* survey, 2010). DNA barcoding data were successfully obtained for the holotype of *H. arnaudae* sp. nov. Besides, additional material sampled by Bernard Thomassin at Nosy-Vé and Tuléar in July 1972 are reported: these specimens present strong affinities to the newly described *H. arnaudae* sp. nov., but consistently exhibit slight morphological deviations from the holotype description. In absence of DNA barcoding data for this material, it was not possible to estimate whether these variations were significant, preventing their formal identification to the species level. A checklist and a new identification key for the genus are also provided, together with additional morphological information for *Hannonia stocki* Munilla, 1993. All *Hannonia* species except *Hannonia typica* Hoek, 1881 were sampled in only one locality, making their geographic and bathymetric distribution range unpredictable. The genus is potentially present on the western shores of the African continent, highlighting the need for further investigation in these regions where sea spiders are rarely surveyed. The affinities of *Hannonia* with the 11 currently accepted pycnogonid families need to be investigated through phylogenetic studies to be properly understood. Morphological comparisons suggest possible affinities between this genus and two other Southern Africa pycnogonid genera of uncertain taxonomic placement, *Boehmia*, and *Queubus*, highlighting further the importance of integrating African pycnogonids to future research on sea spider diversity and evolution.

Keywords: Pantopoda, *Boehmia*, *Queubus*, Africa, Madagascar

BACKGROUND

The genus *Hannonia* Hoek, 1881 is a rare and most bizarre group among sea spiders (Pycnogonida Gerstäcker, 1863). When he uncovered the new species *Hannonia typica* Hoek, 1881 among South Africa samples collected during the HMS Challenger expedition, Hoek (1881) readily identified it as belonging to a different genus from any other known at that time. The genus is still valid today and includes three additional species to the one described by Hoek: *Hannonia spinipes* Stocki, 1956, *Hannonia echinata* Stock, 1990 and *Hannonia stocki* Munilla, 1993 (Stock 1956 1990; Munilla 1993). The species of this genus were only scarcely sampled on the shores of Africa (*H. spinipes* and *H. typica*) and Europe (*H. echinata* and *H. stocki*).

Hoek (1881) interpreted the genus as a transitional form between "chelifore-bearing" and "chelifore-lacking" groups. The concept of transitional form was later abandoned, but taxonomists kept hesitating about the familial attribution of this genus. Loman (1904) considered it to have characters of Ammotheidae Dohrn, 1881, Ascorhynchidae Hoek, 1881 and Pycnogonidae

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Wilson, 1878 altogether. It was also successively attributed or described as related to Pycnogonidae (Hoek 1881; Loman 1908; Calman 1927), Pallenidae Wilson, 1878 or Callipallenidae Hilton, 1942 (Bouvier 1907; Hedgpeth 1947; Stock 1962), and Ascorhynchidae (Bouvier 1913). Today, *Hannonia* is more pragmatically classified as *incertae sedis* (Bamber et al. 2026), pending inclusion in phylogenetic studies.

Hannonia is thus of particular interest to better understand the evolution of Pycnogonida as well as their diversity, but the genus almost never appears in publications, due to its rarity, in particular outside of South Africa. Collections of the *Muséum national d'Histoire naturelle*, Paris include several *Hannonia* specimens that were sampled in the south of Madagascar, belonging to two new species. Together with their description, this work proposes a checklist and a new identification key for the genus.

MATERIALS AND METHODS

Checklist, bathymetry and distribution map

Geographic data were extracted from the literature, completed with GBIF (2025). They were collected as GPS coordinates when possible or determined based on the geographical descriptions that were provided. The resulting dataset was used to produce a distribution map. The known bathymetrical distribution was compiled for each species based on depth indicated in the literature. Some depth records are registered as intervals, and were dealt with as in Sabroux (2025), defining for each species a minimal, and maximal known depth range. The minimal known depth range (MinKDR) corresponds to the minimal span calculated from the different sampling depth intervals; the maximal known depth range (MaxKDR), the maximal one.

Acronyms for the institutions in which cited material are hosted are as follows: MNHN: Muséum national d'Histoire naturelle, Paris, France. NHMD: Natural History Museum of Denmark, Copenhagen. NHMUK: Natural History Museum, London, UK. NBC: Naturalis Biodiversity Center, Leiden, the Netherlands. UAB: Autonomous University of Barcelona, Spain.

Sampling

The two holotypes were sampled during the ATIMO VATAE expedition (April-June 2010) in Southern Madagascar, in the vicinity of Fort-Dauphin (Taolagnaro), at station TB01 (25°0'31.7988"S, 47°0'25.8048"E; 16–22 m; 29 April 2010) and TB07 (25°2'27.7188"S, 46°59'39.9624"E; 4–5 m; 9 May 2010). The 23 specimens identified as *Hannonia* cf. *arnaudae* sp. nov. were sampled by Bernard Thomassin in the southwest of Madagascar, around Nosy-Vé and Tuléar in July 1972. Specimens were preserved in 80% ethanol and are curated at the MNHN.

DNA extraction, partial amplification, and sequencing of a fragment of the first subunit of the cytochrome *c* oxidase (CO1) were performed as described in Sabroux et al. (2017). Resulting CO1 sequence for the specimen MNHN-IU-2011-725 was deposited on GenBank under accession number PZ436599.

Measurements

Measurements were calculated as follows: trunk + cephalon length extends from the frontal ridge of the cephalon anterior to the chelifore 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 tip; the abdomen length was measured from its base to the anus at tip; the lengths of the different article were measured from the midpoint of the proximal insertion to the midpoint of the distal insertion, in lateral view. Measurements of the leg articles are based on the third pair of legs. The main claw length was measured from the middle of its insertion in lateral view, to its tip.

RESULTS

Class Pycnogonida Latreille, 1810
Order Pantopoda Gerstäcker, 1863
Family *incertae sedis*
Genus *Hannonia* Hoek, 1881

Type species: *Hannonia typica* Hoek, 1881 by monotypy.

Diagnosis (emended from Barnard 1954): Body stout, segmented, with dorsodisal margin thickened or elevated as a bud. Lateral processes separated by less than their own diameter. Proboscis roughly ovoid, mobile, oriented ventrally. Abdomen club-shaped, elongated, segmented at base, oriented ventro-diagonally. Chelifore scapes 1-articled. Palps absent or reduced to small 1 to 3-articled appendages. Ovigers in both sexes, with 9 or 10 articles plus terminal claw. Legs stout, tarsus very short, no auxiliary claws. Some of the legs spines denticulated. Males with genital spur on ventrodistal surface of coxae 2 in legs 3 and 4. Females with gonopores on ventral surface of coxae 2 in all four pairs of legs.

Hannonia echinata Stock, 1990

Hannonia echinata Stock 1990:513–516, figs. 1–7.
Hannonia echinata—Bamber 2010:106, fig. 135.

Type material: not examined. *Holotype*: ENGLISH CHANNEL. ♂; north to Roscoff, northeast off Île de Batz, Astan Reef; 51 m; 3 Jun. 1965; coll. J. H. Stock; NBC, ZMA.PYC.3341.

Distribution: Only sampled in type locality, Astan Reef north to Roscoff, 51 m deep.

Hannonia spinipes Stock, 1956

Hannonia spinipes Stock 1956:89–92, fig. 12.

Type material: not examined. *Holotype*: SOUTHWESTERN INDIAN OCEAN. ♀; South Africa, off Durban; 64 m; 22 Aug. 1929; Java-South Africa Expedition 1929-30 st. 23; NHMD-110701.

Distribution: Only known from type locality (off Durban), 64 m deep.

Hannonia stocki Munilla, 1993

Hannonia stocki Munilla 1993:544–549, 549 [key], fig. 2, tabs 2, 3B, 4.

Type material: not examined. *Holotype*: NORTHEAST ATLANTIC. ♂; western part of the Strait of Gibraltar, south of Cape of Trafalgar; 36°4'25.8"N 6°2'51.0"W; 76–80 m; 20 Jul. 1989; FAUNA 1 Project St. 57; UAB-C22-GIB049-HanSto.

Distribution: Only known from type locality (Gibraltar Strait), sampled between 76 and 80 m deep.

Remarks: The original description of this species clearly shows that the legs are ornamented with many spines, but it was not determined whether some of them were denticulated or not like for other species of the genus. I could request pictures of these leg spines that were kindly provided, which enabled to confirm that some are indeed denticulated much like other species (Soler i Membrives comm. pers.).

Hannonia typica Hoek, 1881

Hannonia typica Hoek 1881:9 [tab], 34 [tab], 92–93, pl. 14 figs. 8–11.
Hannonia typica—Loman 1904:383–384, pl. 14 figs. 12–15; 1923:7—Hodgson 1910:227—Calman 1927:410 [text]—Barnard 1954:124–125, fig. 18—Stock 1959:561; 1962:285, fig. 10; 1982:188—Penrith & Kensley 1970: tab. 1 [p. 232]—Bakker & Sabroux 2026:207–208.

Type material: not examined. *Holotype*: SOUTHEAST ATLANTIC. ♀; Sea Point near Cape Town; on shore; Oct. 1878?; HMS Challenger expedition; NHMUK ZOO-1881.38.

Distribution: Along the coasts of South Africa (Saldanha Bay to off Durban) and on the southern coast of Namibia (Lüberitz); and from Eastern Africa (Jazeera, in Somalia). Depth range 0–40 m.

Remarks: This is by far the most sampled species among *Hannonia*, with a relatively wide distribution in the southern coasts of Africa. The sampling date of the holotype was estimated from the sampling tables of the HMS Challenger, which was in the region around that period (Tizard et al. 1885). This is only putative, as it is not clear how this specimen was sampled or obtained.

Hannonia sp.

Hannonia sp.: Stock 1959: 562, fig. 6.

Material: not examined. SOUTHEAST ATLANTIC. 1 postlarval juvenile; Saldanha Bay; 33°3'S, 17°58.5'E; 7 m; 13 Jul. 1946; UCT. Ecol. Survey SB.117.B.; NBC, ZMA.PYC.1432. 1 postlarval juvenile; Langebaan Lagoon; 33°5'S, 17°55'E; 29. Apr 1956; UCT. Ecol. Survey LB.491.A.; NBC, ZMA. PYC.1433.

Remarks: Worth to be mentioned are those two postlarval juveniles sampled in the vicinity of Saldanha Bay, and apparently parasitic of the polychaete *Acrochaetium unifilum* C.-C. Jao, 1936.

Hannonia arnaudae sp. nov.

(Fig. 1)
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Etymology: Latinization of last name "Arnaud", 1st decl. (fem.), genitive singular. This species is named after Françoise Arnaud, French sea spiders' expert who worked at the Station d'Endoume (Marseille). Françoise Arnaud contributed significantly to the knowledge of sea spiders, notably in Madagascar, and had first identified the specimens from Tuléar and Nosy-Vé as belonging to a species new to science (here included in *Hannonia* cf. *arnaudae* material), as suggested by the note she left on a label with the specimens.

Examined material: *Holotype*: SOUTHWEST INDIAN OCEAN. ♂; southeastern coast of Madagascar, Fort-Dauphin (Taolagnaro), Libanona Beach; 25°2'27.7188"S, 46°59'39.9624"E; 4–5 m; 9 May 2010; ATIMO VATAE Expedition st. TB07; GenBank no: PZ436599 (CO1); MNHN-IU-2011-725.

Description (holotype ♂, MNHN-IU-2011-725): Body robust, arched. Cephalon about as long as first two trunk segments, wide, widening anteriorly as a hood above chelifores insertion, distal margin

ornamented with spines. Ocular tubercle low, rounded laterally, saddle-shaped anteriorly, kidney-like dorsally, ornamented with four eyes, spines, and small lateral sense organs. Oviger insertion as lateral knob behind cephalon, touching first lateral processes. Trunk segmented, their dorsodistal margin swollen, only slightly elevated, with small dorsal spines. Lateral processes about as long as wide, many spines laterally, dorsally and on distal margin, lateral processes of different trunk segments separated by less than half their diameter.

Proboscis not longer than cephalon, ovoid, base narrowest and bent, distal tip blunt.

Abdomen club-shaped, ornamented with spines, not reaching beyond distal margin of coxae 1 in leg 4.

Chelifore present. Scape 1-articled, short but massive, rounded distally, ornamented with spines. Chela palm round, fingers minutes.

Palp minute, 3-articled. Article 1 longest, twice as long as base width, ovoid in shape, carrying setae distally. Article 2 slenderer, about one third of article 1 length. Article 3 minute, with distal setae.

Oviger composed of 9 articles plus terminal claw. Articles 1–3 short, about as long as wide, article 2 slightly longer. Article 4 curved, about 2.8 times as long as article 3, ornamented with setae at base. Article 5 curved too, slightly shorter than article 4, ornamented with setae. Article 6 (in typical 10-articled oviger bauplan) absent or fused with article 5. Articles 7–10 a strigilis, article 7 broadest, about 1.5 times as long as wide; article 8 longest, about 1.1 times as long as article 7, about twice as long as wide; article 9 shortest, about 1.5 times as long as wide, 0.6 times as long as article 8 and 0.7 times as long as article 7; article 10 slenderest, about twice as long as wide, about 1.1 times as long as article 9 article, 0.8 as second, 0.9 as first. Strigilis spines lanceolate with many small spinules on distal half; strigilis formula 7:4:3:4. Terminal claw short, simple, curved.

Leg coxa 1 short, about as long as wide, ornamented with many short spines. Coxa 2 about 1.5 times as long as coxa 1, with lateral spines, carrying low ventrodistal genital spur on legs 3 and 4. Coxa 3 about as long as coxa 1, with dorsal and ventral spines. Femur stout, about 1.8 times as long as coxa 2, ventral surface forming an angle at second distal third. Tibia 1 stout, about 0.8 times as long as femur. Tibia 2 stout, slightly shorter than tibia 1, with ventral spines. Spines on coxae, femur, tibiae 1 and 2 carrying small denticles. Tarsus very short, grossly triangular. Propodus gently curved, about 0.7 times as long as tibia 2, with five spines on propodal sole, and setae on dorsal surface. Main claw curved, about 0.4 times as long as propodus. Auxiliary claws absent.

Measurements (mm): trunk + cephalon length 2.55; trunk width at second trunk segment (lateral processes included) 1.51; proboscis length 0.79; abdomen length 0.55; chelifore length 0.54; coxa 1 length 0.31; coxa 2 length 0.63; coxa 3 length 0.35; femur length 1.00; tibia 1 length 0.76; tibia 2 length 0.74; tarsus length 0.12; propodus length 0.48; main claw length 0.20.

Remarks: *H. arnaudae* sp. nov. is morphologically closest to *H. stocki* which presents a similar lateralisation of the ocular tubercle. However, it is readily distinguished from this species as well as every other in the genus by the absence of dorsomedian tubercles on the lateral processes and on the trunk segments and the absence of the two tubercles or projections at the base of chelifores.

Another remarkable and diagnostic character of this species is the oviger being 9- rather than 10-articled plus terminal claw. It is likely that the missing article is the 6th one, as the four articles presenting strigilis spines (normally articles 7–10 in typical oviger bauplan; *e.g.*, Sabroux et al. 2023b) and the typically long article 5 is clearly identified. Possibly, the article 6 is fused with the distal end of article 5.

Unlike *Hannonia laurae* sp. nov. and *H. echinata*, the species *H. arnaudae* presents 3-articled palps. Unlike *H. spinipes*, *H. arnaudae* presents tall tubercles on the femur, tibiae 1 and 2, and presents a short proboscis that does not reach beyond the second trunk segment when folded ventrally. Chelifores in *H. arnaudae* are conspicuously more massive than *H. typica.*

***Hannonia* cf. *arnaudae* sp. nov.**

(Fig. 2)

Examined material: MOZAMBIQUE CHANNEL. 2 ♂ ♂ ov., 6 ♂ ♂, 2 ♀ ♀, 3 juvs; Southwestern Madagascar, Nosy-Vé western beach, infralittoral, 21 m from the bank; 14 Jul. 1972; Thomassin coll. st. 870; MNHN-IU-2009-4972. 1 subadult (?); southwestern coast of Madagascar, Tuléar, Grand Récif, external front of the Grande Crique cove; 10 m; 8 Jul. 1972; Thomassin coll. st. 843B; MNHN-IU-2009-4973. 7 ♂ ♂ ov., 1 ♂, 1 ♀; southwestern coast of Madagascar, Nosy-Vé western beach, infralittoral, 28 m from the bank; 14 Jul. 1972; Thomassin coll. st. 869; MNHN-IU-2009-4974.

Remarks: Thomassin's specimens are overall very similar to the holotype described above, although slight but consistent differences must be reported. Firstly, setae tend to be less dense and shorter in Thomassin's material, notably on lateral processes (Fig. 2). Second, the abdomen in Thomassin's specimens tends to reach beyond the first coxa of leg 4, and thus to be longer than

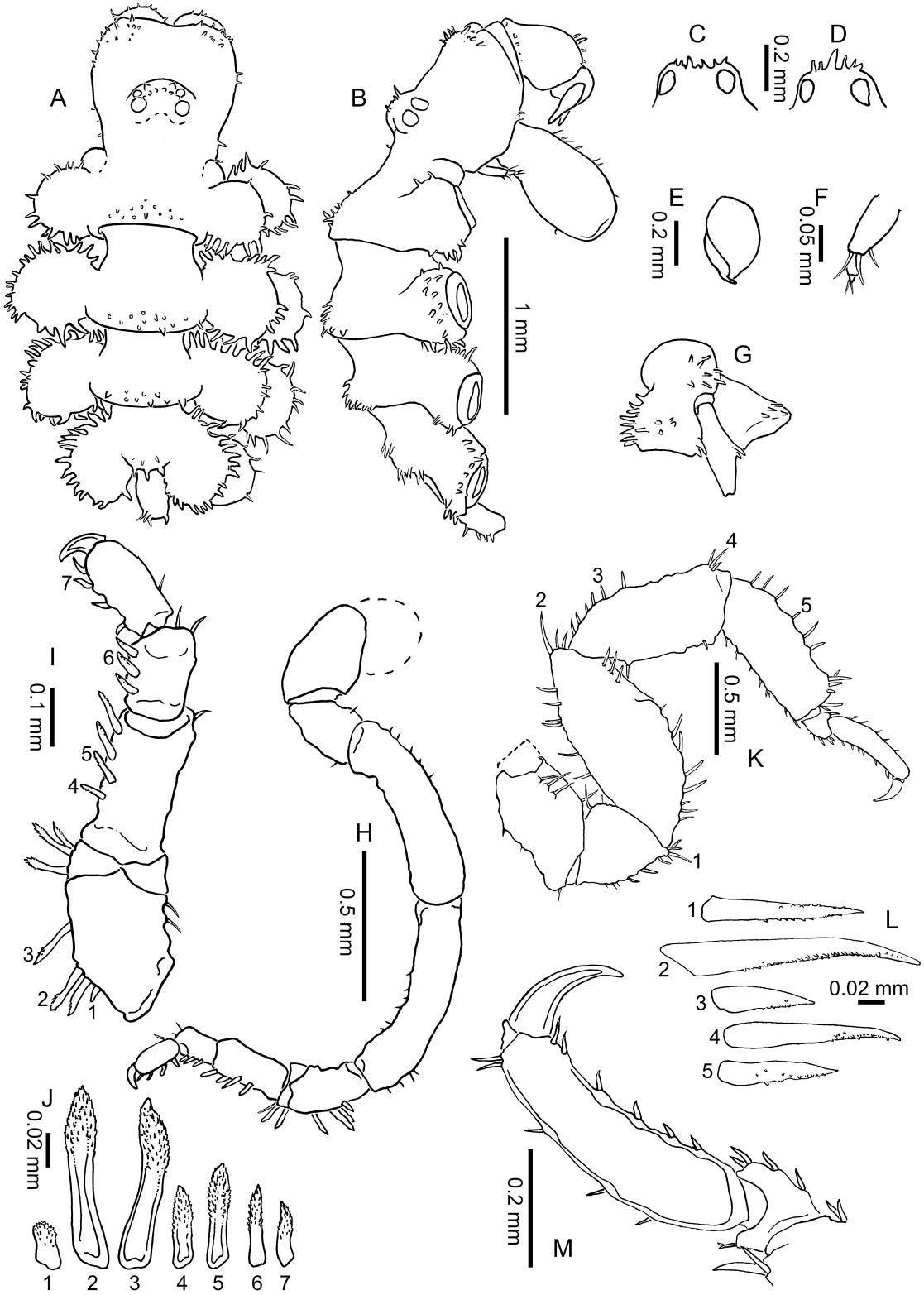

Fig. 1. *Hannonia arnaudae* sp. nov., holotype MNHN-IU-2011-725 (♂). A: dorsal view of the body (same scale as B). B: lateral view of the body. C: anterior view of the ocular tubercle. D: posterior view of the ocular tubercle (same scale as C). E: chela. F: oviger. G: last trunk segment and abdomen, diagonal view (same scale as B). H: oviger. I: strigilis. J: ovigeral spines (numbers in J correspond to numbered spines in I). K: third leg (the black arrowhead indicates the ventral spur and gonopore of coxa 2). L: leg denticulated spines (numbers in L correspond to numbered spines in K). M: tarsus, propodus and main claw of the third leg.

in the holotype. However, the antiquity of Thomassin's material did not enable to produce barcoding data that could have ruled out the hypothesis of variability between reciprocally isolated populations. Therefore, I refrain from describing this material as another new species based on these sole morphological variations. Recently sampled material from Tuléar and/or Nosy-Vé should be examined and barcoded to get a clearer insight.

Males and females are very similar for all characters observed. Males have the same sexual characters as the holotype of *H. arnaudae*. Females do not present genital spurs on legs 3 and 4, and exhibit gonopores on the coxae 2 of all four pairs of legs. One specimen (MNHN-IU-2009-4973; fig. 2A, B), probably a subadult, is particularly slender and small, with longer distance between lateral processes.

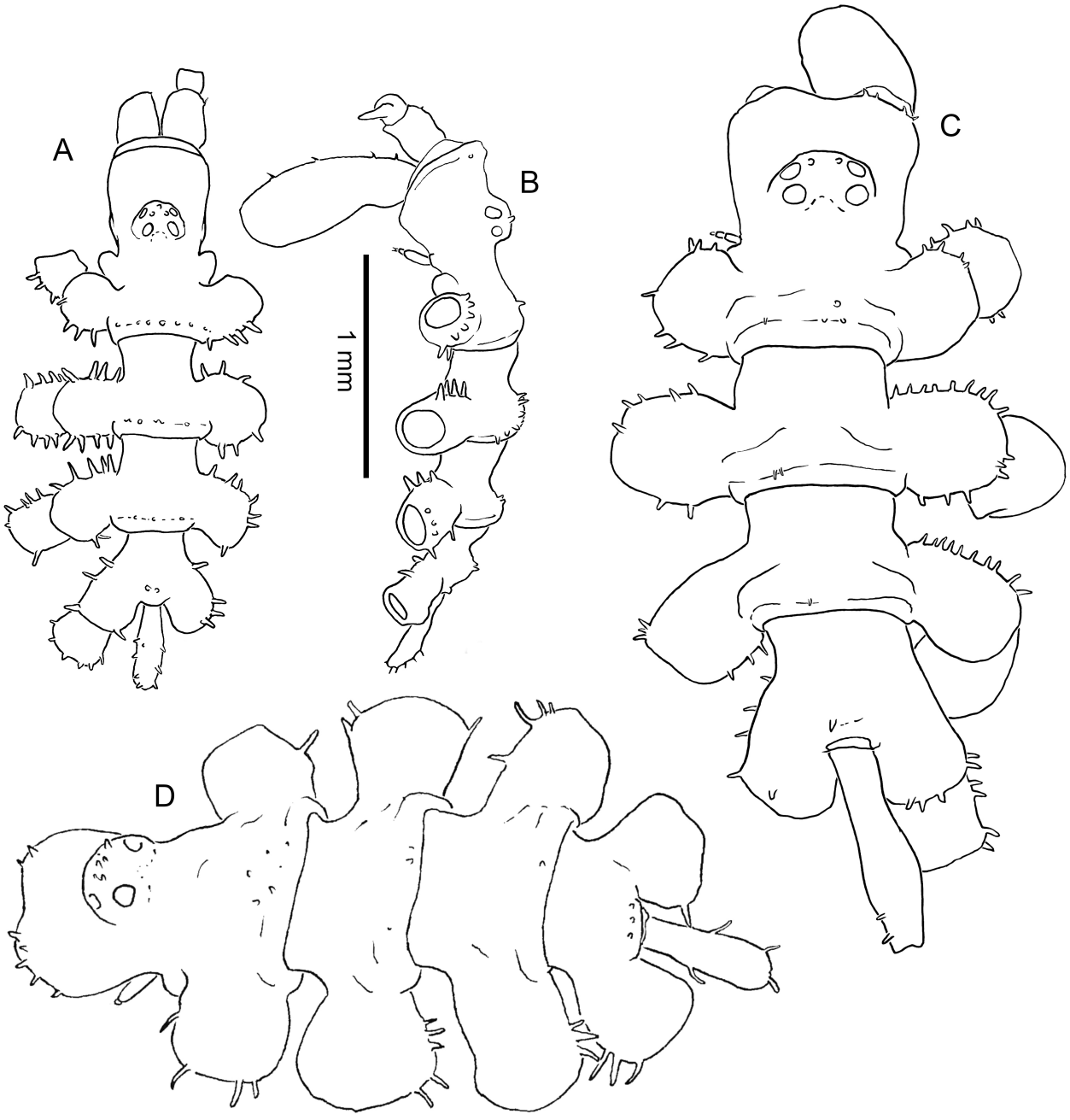

Fig. 2. *Hannonia* cf. *arnaudae* sp. nov., specimens MNHN-IU-2009-4973 (subadult?; A-B) and MNHN-IU-2009-4974 (♀: C, and ♂: D). A, C, D: dorsal view of the body (same scale as B). B: lateral view of the body.

***Hannonia laurae* sp. nov.**

(Fig. 3)

urn:lsid:zoobank.org:act:18F4C1AB-2C44-4CFF-A5B2-296E5A4C7469

Etymology: From "*Laura*", latinization of French first name "Laure" (simplified to avoid the long diphthong), 1st decl. (fem.), genitive singular. This species is named after Laure Corbari (MNHN), who participated to the ATIMO VATAE expedition, and there, initiated the systematic sampling of sea spiders by the *Planète Revisitée* expeditions that was continued ever since. This allowed for the accumulation of a remarkable scientific collection of sea spiders in the MNHN and thus a significant contribution to our knowledge of sea spiders.

Examined material: *Holotype*: SOUTHWEST INDIAN OCEAN. ♀; southeastern coast of Madagascar, Fort-Dauphin (Taolagnaro), Fort-Dauphin Bay; 25°0'31.7988"S, 47°0'25.8048"E; 16–22 m; 29 Apr. 2010; ATIMO VATAE Expedition st. TB01; MNHN-IU-2011-749.

Description (holotype ♀, MNHN-IU-2011-749): Body robust, covered of low pointy tubercles. Cephalon about as long as two first trunk segments, prolongated anteriorly as a wide hood covering dorsally chelifores and proboscis insertion, distal tip with a pair of bifurcated anterior projections, and a pair of low pointy tubercles medially. Ocular tubercle split in a lateral pair joining at base, one anterior and one posterior eye on each tubercle, tip with low pointy tubercles, lateral sense organs absent or inconspicuous. Lateral projection of cephalon just behind ocular tubercle on which articulate ovigers touching first lateral processes. Trunk fully segmented, trunk segments 2 to 4 anterior margin with two (trunk segments 2 and 3) or one (trunk segment 4) low pointy tubercle. Every trunk segment posterior margin ornamented with dense low pointy tubercles, thickened and elevated as a tall bead, posterior margin of fourth trunk segment as a dorsal tubercle. Lateral processes about 1.5 times as long as wide, covered in many low pointy tubercles that form a dorsomedian protuberance.

Proboscis roughly pyriform, folded ventrally, not reaching posterior margin of the second segment. Abdomen club-shaped, segmented at base, directed ventrodiagonally, ornamented with many low pointy tubercles, not reaching beyond coxa 2 of legs 4. Chelifore reduced, scapes 1-articled, about twice as long as wide. Chela residual, without movable finger.

Palp absent.

Ovigers damaged, not preserved beyond article 5. Articles 1 and 2 short, about as long as wide, article 3 short, damaged in holotype, article 4 long, about 4 times as long as wide, article 5 only fragmentarily preserved in holotype.

Legs coxa 1 as long as wide. Coxa 2 about 1.5 times as long as wide and 1.5 times as long as coxa 1, carrying denticulated spines. Coxae 2 of all legs carrying gonopore. Coxa 3 shorter than coxae 1 and 2, slightly longer than wide, carrying denticulated spines. Femur stout, about 1.6 times as long as coxa 2. Tibia 1 stout, cylindrical, 0.7 times as long as femur. Tibia 2 cylindrical, slenderer than tibia 1, 0.85 times as long as tibia 1. Femur, tibia 1 and tibia 2 ornamented with low tubercles carrying denticulated spines. Tarsus as long as wide, with distal spines ventrally and dorsally. Propodus 0.9 times as long as tibia 2 and more than 3 times longer than tarsus. Main claw strongly curved, 0.4 times as long as propodus. Auxiliary claws absent.

Measurements (mm): trunk + cephalon length 1.88; trunk width at second trunk segment (lateral processes included) 1.45; proboscis length 0.85; abdomen length 0.60; chelifore length 0.23; coxa 1 length 0.32; coxa 2 length 0.44; coxa 3 0.21; femur length 0.72; tibia 1 length 0.76; tibia 2 length 0.56; tarsus length 0.16; propodus length 0.53; main claw length 0.20.

Remarks: Unfortunately, the specimen has both ovigers almost entirely missing (broken), but the unique morphology of this species makes it easily recognisable even without the characters these appendages might carry. It was also not possible to obtain a DNA barcode sequence.

Hannonia laurae sp. nov. is made unique by the dense low pointy tubercles on the trunk dorsoposterior margins and the lateral processes, the pair of dorsal spines in the middle of the cephalon, and the bifurcated head distal prolongations. It is furthermore readily distinguished from *H. arnaudae*, *H. spinipes*, *H. stocki*, and *H. typica* by the absence of palps. It finally differs from *H. echinata* by the proboscis being smooth rather that spinous, and by the absence of the spines on the body.

Geographical and bathymetrical distribution

Hannonia species appear to be relatively shallow dwellers, since they were all recorded above 100 m (Table 1). The distribution of the genus can be roughly described in two groups (Fig. 4): four species (*H. arnaudae*, *H. laurae*, *H. spinipes*, *H. typica*) are mostly distributed south of the African continent; however, *H. typica* is also recorded further north, from the coast of Somalia, about 200 km north of the Equator. The two remaining species (*H. echinata* and *H. stocki*) were exclusively recorded in the Northern Hemisphere, around Europe, in the English Channel (*H. echinata*), and west of the Gibraltar Strait (*H. stocki*). No sampling

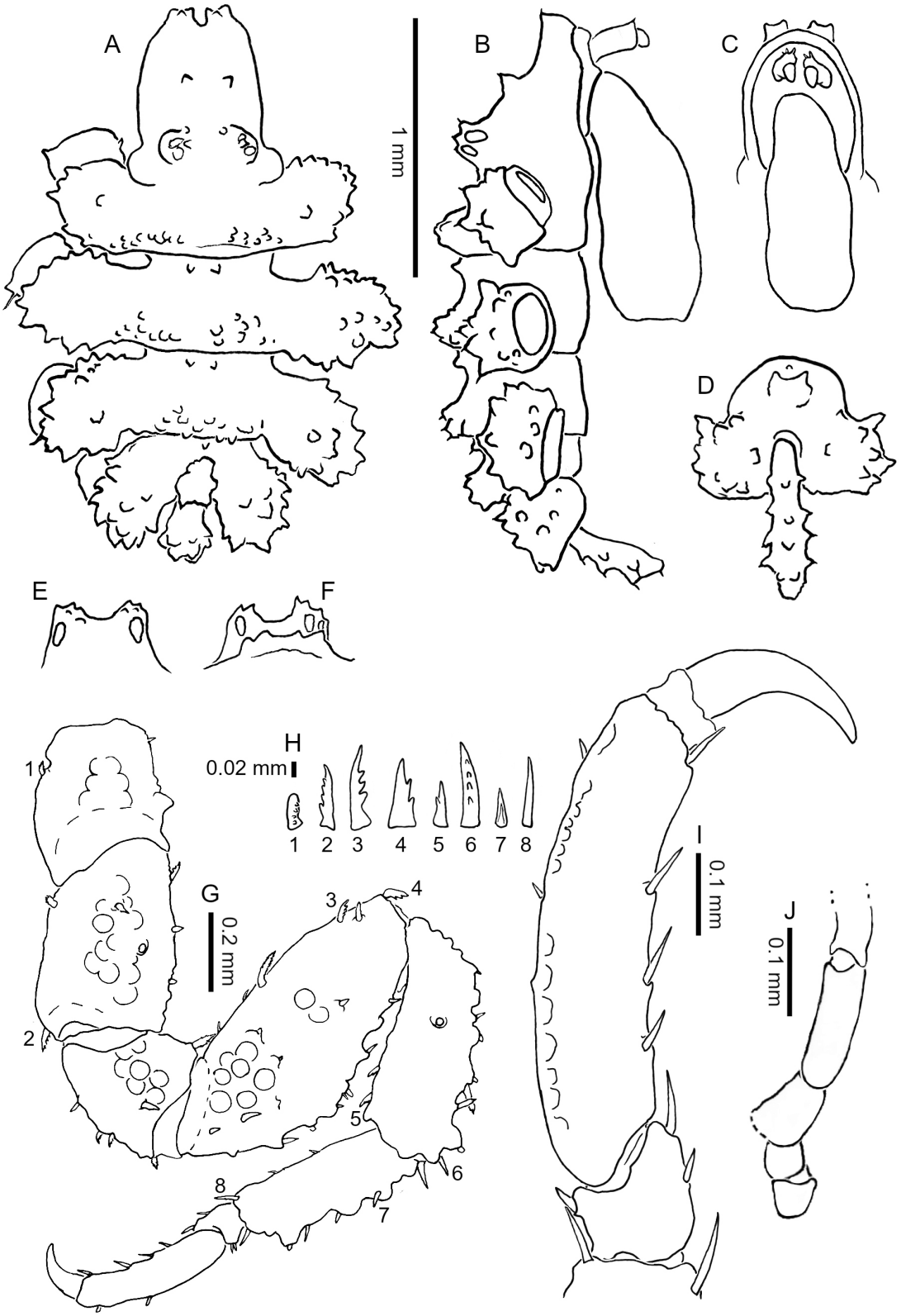

Fig. 3. *Hannonia laurae* sp. nov., holotype MNHN-IU-2011-749 (♀). A: dorsal view of the body. B: lateral view of the body (same scale as A). C: ventral view of the cephalon and proboscis (same scale as A). D: last trunk segment and abdomen, posterior view (same scale as A). E: anterior view of the ocular tubercle (same scale as A). F: posterior view of the ocular tubercle (same scale as A). G: third leg. H: leg spines (numbers in H correspond to numbered spines in G). I: tarsus, propodus and main claw of the third leg. J: oviger (only proximally preserved).

is known from the Mediterranean Sea, the Western African coast down to Southern Namibia or the Red Sea.

Identification key to worldwide *Hannonia* species

A previous identification key was proposed by Munilla (1993), that includes the four species that were known at that time. As it was not possible to examine the holotype of *Hannonia typica*, it was decided to not rely on the characters used by Munilla to distinguish this species, *e.g.*, the pubescent cuticle and the smooth proboscis, owing to that these characters are not conspicuous in earliest illustrations:

1. Tiny palp present, elongated, generally composed of a few articles 2
- Palp absent or reduced to a short vestigial bud 4
2. Setae on the tibiae 1 and 2 shorter than the tubercle on which they stand ..... *H. spinipes*
- Setae on the tibiae 1 and 2 as long or longer than the tubercle on which they stand 3
3. Dorsodistal margin of trunk segments low, dorsomedian tubercles on lateral processes absent ..... *H. arnaudae* sp. nov.
- Dorsodistal margin of trunk segments as elevated bead or dorsomedian tubercles, legs with rounded spinous dorsomedian tubercles on lateral processes ..... *H. stocki*
4. Ocular tubercle bipartite, divided into two lateral parts ..... *H. laurae* sp. nov.
- Ocular tubercle monopartite, tip possibly bifide 5
5. Setae of tibiae 1 and 2 on long digitiform tubercles ..... *H. echinata*
- tibiae 1 and 2 without conspicuous digitiform tubercles ..... *H. typica*

Fig. 4. Distribution of *Hannonia* species around Africa. Each colour is attributed to one of the six species, names indicated on the map: "arnaudae" = *Hannonia arnaudae*, "echinata" = *H. echinata* etc. Type locality is indicated with a star, other known sampling localities (when they exist) are indicated with a circle. The question mark stands from *Hannonia* cf. *arnaudae* sp. nov. specimens described in the present work. Distribution based on data from the literature and GBIF (2025). A cross over a circle indicates a record from GBIF for which the identifier could not be confirmed as an expert in sea spiders and is thus, to some extents, less reliable than other records.

DISCUSSION

Hannonia distribution

Hannonia representatives are all coastal species exclusively found above 100 m deep as far as the rare sampling events enable to tell (Table 1). Some species occur at very shallow depths (*H. arnaudae*: 4–5 m, *H. laurae*: 16–22 m, *H. typica*: 0–40 m) while others were only sampled at greater depths (*H. echinata*: 51 m, *H. spinipes*: 64 m, *H. stocki*: 76–80 m), but the actual bathymetrical distribution for these species cannot be reliably determined due to the scarcity of their sampling. The known geographic distribution of this genus (Fig. 4) is uneven: most records are from the region of Cape Town, but concern only one species, *H. typica*. This species shows a wide distribution: it was collected on the southern coast of Namibia, in the vicinity of Durban, or even more distantly, south to the Somalian coast. Other species have been only sampled in one locality. These observations highlight the lack of knowledge for the distribution for those species.

It is also questionable whether the isolation of northern species (*H. echinata* and *H. stocki*) is representative of the distribution of the genus or is artefactual due to a lack of comprehensive survey. Arguably, if the distribution of *Hannonia* is to be extended, it is not to be expected in the Mediterranean Sea and the Red Sea, which were relatively well sampled also for Pycnogonida (*e.g.*, Carpenter 1910; Stock 1958 1964; Arnaud 1987; Chimenz Gusso and Lattanzi 2003; Lehmann et al. 2014). Instead, very little is known about species of the western coast of the African continent, where known or new species of the *Hannonia* genus could be uncovered. *H. typica*, which already shows a wide distribution, could arguably be expected in these regions.

Hannonia affinities

The morphological characters of *Hannonia* do not indicate obvious affinities with any of the 11 families that are currently accepted by most taxonomists (Bamber 2007; Bamber et al. 2026): the proboscis shape and the segmentation at the abdomen's base are reminiscent of what is found in Ascorhynchidae; chelifores are developed like in Callipallenidae, Nymphonidae, Pallenopsidae and Phoxichilidiidae, and in some Ammotheidae and Ascorhynchidae; the reduction and/or absence of palps is also observed in Callipallenidae and Pallenopsidae; ovigers are similar in shape to Ammotheidae, Ascorhychidae, Callipallenidae, Nymphonidae and Pallenopsidae, the oviger terminal claw is present like in Ascorhynchidae, Nymphonidae, and some Callipallenidae and Ammotheidae; they lack auxiliary claws like in Ascorhynchidae. This hesitation is well illustrated in the literature, where the group has been associated to different families or compared with various genera: it was regarded as close to *Pycnogonum* (Hoek 1881) or more explicitly included within Pycnogonidae (Loman 1908) based on the body robustness and the presence of dorsomedian tubercles on the trunk and lateral processes. It was regarded as belonging to Callipallenidae *sensu* Stock (1954 1962) based on the presence of chelifores, the reduction of palps, the typically 10-articled ovigers present in two sexes and their structure, the shortness of the tarsus, the shape of the propodus, the distribution of the female gonopores (Bouvier 1907; Hedgpeth 1947; Stock 1962). It was associated by Bouvier (1913) to Eurycydidae Sars, 1891 [= Ascorhynchidae Hoek, 1881] because of the elongation of the body, the presence of a terminal ovigeral claw, and the absence of auxiliary claws. Munilla (1993) seems to have followed Bouvier's view, as he included *Hannonia* within Ammotheidae *sensu* Munilla (1999) [≈ Ascorhynchoidea *sensu* Bamber 2007], a paraphyletic group (Ballesteros et al. 2021, Sabroux et al. 2023a) which includes Ascorhynchidae species. Bamber (2007) also included *Hannonia* within Ascorhynchoidea *sensu* Bamber (2007) but classified it as *incertae sedis* within the paraphyletic superfamily. Loman (1908) even considered the genus as intermediate between Pallenidae [= Callipallenidae *sensu* Stock (1954 1962)] and Phoxichildiidae. Today, the most up-to-date classification is that proposed by Bamber (2007); due to the paraphyly of Ascorhynchoidea *sensu* Bamber (2007), *Hannonia* should be regarded as Pantopoda *incertae sedis*.

It is worth noting that *Hannonia* could be divergent from all described sea spider families and belong to a family on its own that is still to be described. Sea spider families are mostly defined by an original set of cephalic appendages and a characteristic distribution of gonopores on legs in both sexes; to this regard, *Hannonia* diverges from other families, and the possibility of describing a new family thus deserves some consideration. Two genera could be more closely related to *Hannonia*: *Queubus* Barnard, 1946, regarded as *incertae sedis* by Bamber (2007) and Bamber et al. (2026); and *Boehmia* Hoek, 1881, that was only speculatively included into Ascorhynchidae by Bamber (2007). Those two genera share a lot of common traits with *Hannonia*: body compact and segmented, gently arched, abdomen base segmented, absence of auxiliary claws, ovigers 10-articled with scarce strigilis spines and terminal claw; furthermore, *Queubus* has its palps either reduced (*Queubus echidna* Bamber and Steffani, 2007) or absent (*Queubus jamesanus* Barnard, 1946); while *Boehmia* has chelifores with 1-articled scapes. It is worth noting that *Proboehmia* Stock, 1991 from New Caledonia is morphologically similar to *Boehmia* and differs from the latter by the two-articled scapes.

Interestingly, both *Queubus* and *Boehmia* are exclusively known from southern coasts of the African continent, where most *Hannonia* species are recorded: *Queubus echidna* is recorded from Chameis

Table 1. Known bathymetric range for *Hannonia* species. The depth at which was 2 collected the type specimen is also indicated. The minimal known depth range (MinKDR) 3 corresponds to the minimal span calculated from the different sampling depth intervals; the 4 maximal known depth range (MaxKDR), the maximal one

	MinKDR (m)	MaxKDR (m)	Holotype depth (m)
H. arnaudae	-	4–5	4–5
	(5–10 with cf. specimens)	(4–10 with cf. specimens)	
H. echinata	51	*idem*	51
H. laurae	-	16–22	16–22
H. spinipes	64	*idem*	64
H. stocki	-	76–80	76–80
H. typica	0–40	*idem*	0

Deep, Namibia (Bamber and Steffani 2007); *Queubus jamesanus* from St James in False Bay (Barnard 1946) and East London (Barnard 1955); *Boehmia chelata* (Böhm, 1879) from Cape Town (Flynn 1928); *Boehmia tuberosa* Möbius, 1902 from Cape Town, Agulhas bank, East London, and the Transkei area (Arnaud and Child 1988); *Boehmia longirostris* Stock, 1957 was sampled between Mossel Bay and Natal (Stock 1957a). *Boehmia dubia* Hedgpeth, 1950 that was sampled near Ross Island (Hedgpeth 1950), is most probably an austrodecid juvenile (Stock 1957b). Therefore, new sampling and research on the sea spiders along the Southern African shores could provide valuable insights into the evolution of pycnogonids through future phylogenetic studies.

CONCLUSIONS

This is the first occurrence of the rare and poorly known genus *Hannonia* Hoek, 1881 from Madagascar. The descriptions of *Hannonia arnaudae* sp. nov. and *Hannonia laurae* sp. nov. are based on the two holotypes sampled at Fort Dauphin. These species are discriminated from other representatives of *Hannonia* by the nine-articled ovigers, and the unique ornamentation of the body and legs, respectively. Additional material sampled at Nosy-Vé and Tuléar might also belong to *H. arnaudae* sp. nov., although the morphological variations from the type material, together with the absence of DNA barcode data, do not allow a confident taxonomic assignment.

The geographical distribution and phylogenetic affinities of *Hannonia* remain widely unexplored. The genus shares several morphological traits with two genera typically found in Southern Africa, *Queubus* Barnard, 1946 and *Boehmia* Hoek, 1881, which may indicate closer phylogenetic affinities. This highlights the importance of including more African pycnogonids in future studies of Pycnogonida phylogeny.

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