*RAFFLES BULLETIN OF ZOOLOGY* **74**: 332–358
Date of publication: 4 May 2026
DOI: 10.26107/RBZ-2026-0023
https://zoobank.org/urn:lsid:zoobank.org:pub:AC560F56-5389-4B65-97AF-332AA4E81965

# Revision of *Frodromia* McLay, 1993 (Crustacea: Brachyura: Dromiidae) and the status of Frodromiinae Števčić, 2005

Peter K. L. **Ng**

**Abstract.** The taxonomy of the West Pacific dromiid genus, *Frodromia* McLay, 1993, is revised using a suite of characters pertaining to the carapace form and armature, proportions of the ambulatory dactylus, and structures of the pereopods, thoracic sternum, male pleon, and gonopods. The identity of the poorly known type species, *F. atypica* (Sakai, 1936), is clarified and the species is rediagnosed and illustrated based on the single non-type dried specimen available. *Frodromia reticulata* (Sakai, 1974) is also rediagnosed on the basis of a series of Japanese specimens. The material identified as *F. atypica* by McLay (1993) from New Caledonia and the Indonesian Moluccas is here shown to belong to two new species, *F. granulosa* and *F. caileani*, respectively; with *F. granulosa* also reported from Vanuatu. Two other new species, *F. elegans* and *F. iners*, are described from the South China Sea and the Philippines, respectively. As a result, *Frodromia* is hereby classified in the subfamily Frodromiinae Števčić, 2005, which was originally established as a tribe in Sphaerodromiinae Guinot & Tavares, 2003, and which is here redefined and rediagnosed.

**Key words.** sponge crab, Dromioidea, systematics, subfamily definition, new species, key to taxa, Indo-West Pacific

## INTRODUCTION

McLay (1993) established *Frodromia* for two small dromiid species previously placed in *Petalomera* Stimpson, 1858: *P. atypica* Sakai, 1936, and *P. atypica reticulata* Sakai, 1974. McLay (1993) distinguished these species from *Petalomera* sensu stricto in the longer-than-wide carapace, finely granulated dorsal carapace surface, non-petaloid meri on the P1–P3, male and female uropods being dissimilar in form, and the presence of a distinctive tubercle behind the female gonopore (McLay, 1993: 171) (see also Guinot & Quenette, 2005; McLay & Ng, 2007).

The treatment by McLay (1993: 171, 172) of the two species he included in *Frodromia*, i.e., *Petalomera atypica* Sakai, 1936, and *P. atypica reticulata* Sakai, 1974, is confusing; and his key and discussion actually contradict the original description, discussion, key, and figures of the two species by Sakai (1936, 1974, 1976) in several aspects. In his key to *Frodromia*, McLay (1993: 171) writes that in *F. atypica*, the carapace is "longer than wide, anterolateral margin granulated" while in *F. reticulata*, it is "approximately as long as wide, anterolateral margin without teeth or granules". He makes no mention of the two or three larger tubercles along the lateral margin and dark brown life colour of *F. atypica* highlighted by Sakai (1974, 1976) as diagnostic characters. To this effect, he referred three males and three females from New Caledonia, the Loyalty Islands and the Moluccas to *F. atypica* without much comment. McLay (1993: 171), however, did note that "On the basis of three specimens (two males and one female) [sic], from Japan, depth 100–150 m, SAKAI (1974) described a subspecies, *Petalomera atypica reticulata*, which differs from the typical form in having a coarse network of purplish colouration on the carapace and abdomen. However there seem to be some major differences from the typical form: the illustration in SAKAI (1976, pl. 5, fig. 1) has remarkably small eyes, no evidence of teeth or granules on the anterolateral margins, carapace width approximately equal to carapace length (but according to the dimensions given, CW/CL = 0.9). Also the figure supposedly shows a male and yet it seems to have a female abdomen. There are also supposed to be differences in the rostral teeth but these are not confirmed by comparison of the illustrations of the two forms. Thus it is likely that two different species are involved, although several morphological details remain to be established."

The figure by Sakai (1976: pl. 5 fig. 1) is rather schematic so not all the characters are accurate, but his descriptions of the carapace surface (smooth) and lateral margin (lined with sharp granules) is explicit so there is no doubt for these two character sets. We agree with McLay (1993), however, that Sakai (1976) probably figured the paratype female rather than the holotype male.

The specimens McLay (1993: text-fig. 6a, fig. 17d) identified as "*F. atypica*" from New Caledonia, the Loyalty Islands

*Accepted by: Jose Christopher E. Mendoza*

Lee Kong Chian Natural History Museum, Faculty of Science, National University of Singapore, 2 Conservatory Drive, Singapore 117377, Republic of Singapore; Email: peterng@nus.edu.sg


ISSN 2345-7600 (electronic) | ISSN 0217-2445 (print)

and the Moluccas show a lateral margin which is only armed with small granules, without any trace of larger tubercles; and the lateral frontal spines are longer than the median one. This contrasts with what was described and figured by Sakai (1936, 1974, 1976) for the two taxa. The dorsal surface of the carapace of McLay's (1993) material is also covered with numerous small, rounded granules, which contradicts Sakai's (1974, 1976) observations that both *F. atypica* and *F. reticulata* have smooth carapaces (see also Nagai, 1994).

The present paper endeavours to revise the taxonomy of the two species of *Frodromia*. The identities of *Frodromia atypica* and *F. reticulata* are clarified. In addition, four new species are described from the South China Sea, the Philippines, Vanuatu, New Caledonia, and Indonesia. The revision of the species and reappraisal of characters also allows the study to recognise and rediagnose Frodromiinae Števčić, 2005, new status.

## MATERIAL AND METHODS

Specimens examined are deposited in the Zoological Reference Collection (ZRC) of the Lee Kong Chian Natural History Museum at the National University of Singapore; National Science Museum (NSMT), Tsukuba, Japan; Chiba Natural History Museum (CBM), Chiba, Japan; Wakayama Museum of Natural History (WMNH), Wakayama, Japan; and Muséum national d'Histoire Naturelle (MNHN), Paris, France.

The terminology used essentially follows that in Davie et al. (2015), Guinot & Tavares (2003), and McLay (1993). In *Frodromia*, the demarcation between the antero- and posterolateral margins is hard to define as they gradually merge; as such we use the term lateral margin instead. Measurements provided, in millimetres, are of the maximum carapace width and length, respectively. The following abbreviations are used: P2–P5 = ambulatory legs 1–4 (pereopods 2–5), respectively; G1 = male first gonopod; G2 = male second gonopod; s1/2–s7/8 = suture between thoracic sternites 1 and 2 – sternites 7 and 8, respectively.

## TAXONOMY

### Superfamily Dromioidea De Haan, 1833

### Family Dromiidae De Haan, 1833

### Subfamily Frodromiinae Števčić, 2005, new status

Frodromiini Števčić, 2005: 20.

**Diagnosis.** Carapace distinctly longer than wide, longitudinally subovate to subrectangular. Anterolateral margin not clearly separated from posterolateral margin, joins with external orbital tooth, armed with 3 teeth (including subhepatic) or lined with sharp granules (excluding external orbital tooth). Dorsal surface with regions poorly defined, distinctly convex in frontal view, may appear domed; subhepatic region not inflated. Branchial groove shallow or not visible. Front distinctly trispinate, projecting well beyond orbits; rostral spine just below level of pseudorostral spines; pseudorostral spines prominent, laterally meeting supraorbital margin as short spine. Supraorbital margin gently convex, without fissures but may be armed with several sharp granules. Orbits oblique, deeply hollowed on sides of carapace; orbital border almost continuous. Suborbital margin short, with low tooth. Proepistome relatively narrow; triangular, in front of well-defined epistome. Ocular peduncle short, thick, gradually widening distally to large cornea. Antennules with basal article large, subtrapezoidal, folding obliquely. Antenna with article 1 transversely subovate; basal article (fused articles 2 and 3) elongate, subrectangular with distal part bifurcated, inner projection stronger than outer projection. Third maxilliped not operculiform; merus subquadrate. Thoracic sternum relatively narrow; sternites 1–3 not visible; sternite 4 forming plate touching bases of third maxillipeds; when male pleon folded into sternopleonal cavity, anterior portion of sternite 4 and lateral part (episternite 4) exposed; episternite 5 completely covered by uropod, not visible. Female sternal sutures 7/8 relatively short; aperture of spermathecae small, just posterior to laterally positioned P3 gonopore. Pleon relatively long but not reaching based of third maxillipeds; pleural parts distinct, all somites and telson free; somite 6 distinctly narrower than telson; telson not elongate. Vestigial male pleopods 3-5 distinct, uniramous. Male uropods clearly visible as subovate plates, exposed but deeply inserted between pleonal somite 6 and telson, slightly mobile, obliquely positioned; weakly holds pleon by partially locking on to posterior tubercle on P2 coxa. Uropod structure sexually dimorphic: on female, uropods distinct, deeply inserted, clearly visible and transversely positioned. Epipod present on chelipeds. P2 and P3 not elongate, margins smooth or spinose. P4 and P5 reduced, shorter than preceding pereopods, P5 smaller than P4, P4 subdorsally and P5 dorsally oriented; subcheliform apparatus formed by several distal propodal spines opposing dactyli, spine may be present on outer propodal margin; inner margin of P4 and P5 dactylus entire; P5 sometimes with spine on outer dactylus margin. Male coxa of P5 strongly modified, extended, penial tube relatively long, immovable. Female P3 coxa with simple or spur-like tubercle on inner posterior angle. G1 relatively short, stout, with distal part subtruncate or with simple triangular lobe. G2 as long as or longer than G1; with styliform flagellum, short exopod may be present.

**Remarks.** In a major organisation of the Dromiiidae, Guinot & Tavares (2003) examined the known genera and recognised three subfamilies: Dromiinae De Haan, 1833, Hypoconchinae Guinot & Tavares, 2003, and Sphaerodromiinae Guinot & Tavares, 2003. The authors, however, were uncertain about several genera, one of them being *Frodromia* McLay, 1993.

Guinot & Tavares (2003: 108–110) discussed at length the subfamilial position of *Frodromia*. They noted that in the combination of characters (viz. the relatively more elongate carapace with subparallel lateral margins, relatively long P2 and P3 propodus with a gently curved dactylus, relatively

long male telson, presence of vestigial pleopods on pleonal somites 3–5, the deeply inserted male uropods with obliquely oriented dorsal plates, weak prominence in the male P3 coxae, which is covered by the closed pleon but not effective at closing it, the short female thoracic s7/8, the aperture of the spermathecae positioned relatively close to the gonopores, and the modified male P5 coxa, which lacks a movable penial tube): "*Frodromia* does not secure its position in any dromiid subfamily, and whether or not this genus belongs to the Sphaerodromiinae n. subfam. deserves further investigation." (Guinot & Tavares, 2003: 110). The female P3 coxa is distinct as the gonopore is directed anteriorly, close to the spermathecal opening, and there is a tubercle on the inner posterior edge of the coxa. In *F. granulosa*, new species, and *F. caileani*, new species, the inner posterior edge of the female P3 coxa has a prominent spur-like tubercle (Figs. 14D, 17C; Guinot & Tavares, 2003: fig. 26) but in *F. reticulata* and *F. elegans*, new species, there is only an angle (Fig. 6B) or just a low tubercle present (Fig. 9F). This tubercle or spur is present only in females, it is absent in males. The vestigial pleopods on the male pleonal somites are distinct even in the adults (Fig. 11F; Guinot & Tavares, 2003: fig. 25C). Guinot & Tavares (2003: 110) noted that the G2 has no exopod in *Frodromia*, but in *F. caileani*, new species, there is a short exopod present (Fig. 19P). It is absent in the other congeners.

Guinot & Tavares (2003: 110), however, were reluctant to transfer *Frodromia* to the Sphaerodromiinae because the structures of the rostral and lateral spines, antennal exopod, coxa of the third maxilliped, s7/8 being almost longitudinal, exposure of male thoracic sternites 1–3 when the pleon is closed, the non-expanded lateral part of male pleonal somite 6, the raised and prominent aperture of the spermatheca etc. suggested that it was not a good fit in the subfamily. As such, they left the subfamilial position unresolved, hinting that it may need to be referred to its own subfamily.

Števčić (2005: 20) followed the classification of Guinot & Tavares (2003) system for the Dromiidae but split their subfamilies into more tribes. Under his concept of Sphaerodromiinae, Števčić recognised both a tribe Sphaerodromiini and a new one, Frodromiini, for *Frodromia*. He basically adopted Guinot & Tavares' (2003) discussion points on why they were unsure if *Frodromia* was a sphaerodromiine or belonged to a separate subfamily, and summarised them into a broad diagnosis without any specimens examined.

In the present study, all the structures discussed in Guinot & Tavares' (2003) study were examined for all eight species we now recognise in *Frodromia*, including the actual type species, whose identity has been previously confused. All the characters align with Guinot & Tavares' (2003) arguments (see also Guinot & Quenette, 2005) why *Frodromia* cannot be accommodated in the Sphaerodromiinae; although several character states need to be amended. They do not support Števčić's (2005) hypothesis that *Frodromia* is in the Sphaerodromiinae; instead, it should be placed in its own subfamily. A revised diagnosis is here provided.

In subsequent years, Schweitzer & Feldmann (2010: 417) treated the Sphaerodromiinae as a full family, and this was followed by the studies of Karasawa et al. (2011: 532) and Schweitzer et al. (2012: 33). While the Sphaerodromiinae indeed has many unusual characters and is probably a good family, these studies, however, do not discuss what to do with the Hypoconchinae and if it should also be regarded as a distinct family. In this context, should the Frodromiinae also be considered as a separate family as well? Until these aspects can be resolved, we follow Guinot & Tavares (2003) in treating all these taxa as subfamilies of the Dromiidae sensu lato for the time being.

It must also be added that two other available family-level names need to be treated as junior synonyms of Dromiinae De Haan, 1833: Cryptodromiidae Watabe, 2007, and Petalomeridae Watabe, 2007. Neither taxa, however, possess diagnostic characters that warrant their recognition. Both names have not been captured in recent studies of the family because they first appeared in an unusual paper in a science policy journal by Watabe (2007), the contents bordering on metaphysics. Although both names were used as part of a discussion, they are available under the current zoological code as they were used explicitly as new names, a type genus was identified (through monotypy), and a diagnosis was made through indication (ICZN, 1999: Articles 11–13, 16.1, 16.2).

## Genus *Frodromia* McLay, 1993

*Frodromia* McLay, 1993: 170.

**Type species.** *Petalomera atypica* Sakai, 1936, by original designation.

**Diagnosis.** Carapace longitudinally ovate to subrectangular, distinctly longer than wide; dorsal surfaces of carapace, chelipeds and ambulatory legs with dense simple and plumose setae, sometimes completely obscuring surfaces and margins; dorsal carapace surface distinctly convex, without obvious regions, smooth to granular; front clearly trispinate, with 2 distinct pseudorostral spines and 1 median rostral spine; antennal exopod well-developed; small epipod present on cheliped coxa; chelipeds without petaloid merus, carpus with 2 prominent dorsal tubercles; P2 and P3 merus normal, margins not expanded, not petaloid; male and female pleons with 6 free somites and telson; vestigial pleopods present on male pleonal somites 3–5; male and female uropods deeply inserted into telson, positioned obliquely, dissimilar in form, that of male short, ovate, that of female elongate, slender; uropods part of pleonal locking mechanism, fitting in front of serrated flange on cheliped coxae; male P5 coxa without movable penial tube; female gonopore on anterior border of P3 coxa, directed anteriorly, with low tubercle or spur on inner posterior edge of coxa; G1 stout, short; G2 longer than G1, with or without short exopod; female s7/8 short; spermatheca gently sinuous, not prominently raised, aperture positioned close adjacent to gonopores. (Amended from McLay, 1993).

**Remarks.** The characters used by McLay (1993) to define *Frodromia* have been amended to reflect the present study of the type species, *F. atypica*, and consideration of the new ones described here. One character that does not work is the length of the P2 and P3 dactylus which McLay (1993) diagnosed as long but is actually quite short in *F. atypica* (Fig. 2D, E).

The kind of pubescence present on *Frodromia* species is interesting as it forms a thick tomentum which easily entangles pieces of debris under it which is not easy to remove. While the setae are not plumose, they are nevertheless densely packed. In species like *F. reticulata* and *F. granulosa*, the pubescence is very dense and almost mat-like, so much so that the margins and surface are obscured by it. The small spines or granules underneath this mat are hard to observe and cleaning the setae is tedious and the hard structures are very delicate and easily damaged. In other species like *F. elegans*, new species, and *F. iners*, new species, the setae are set further apart so the pubescence appears sparser, and the surfaces and margins are still clearly visible.

The armature on the supraorbital margin is too variable to be useful as a species-character. In *F. granulosa* for example, it varies from unarmed (Fig. 12B) to possessing four sharp granules (Fig. 14A). This variation in spination is also true for the ambulatory legs, when spines are present. Species like *F. atypica*, *F. reticulata*, *F. elegans*, and *F. iners* always have the flexor and extensor margins of the ambulatory meri and propodi completely smooth and unarmed (Figs. 8D, 11A). In taxa like *F. granulosa* and *F. caileani*, however, these margins are spinose, but the degree of spination varies quite considerably (Figs. 13A, G–J, 16G–J), although they are invariably armed with at least one or two small sharp granules.

The camouflage habits of *Frodromia* species is poorly known. According to Sakai (1936, 1976) and McLay (1993), they have been found associated with unidentified ascidians.

### *Frodromia atypica* (Sakai, 1936)

(Figs. 1A, 2, 18A)

*Petalomera atypica* Sakai, 1936: 33, pl. 2 fig. 1; Sakai, 1976: 23, pl. 5 fig. 2.

*Frodromia atypica* – McLay, 1993: 171; Nagai, 1994: 49, pl. 1 fig. 1; Ng et al., 2008: 36; Kimura et al., 2019: 31, fig. 1-1.

**Material examined.** JAPAN: 1 dried male (4.5 × 4.8 mm) (WMNH 16), off Shionomisaki, Wakayama, 90 m, coll. S. Nagai, May 1992.

**Diagnosis.** Colour in life dark blue to brownish green (Fig. 1A). Dorsal surface of carapace and appendages with dense short setae that partially obscure surface and margins (Fig. 2A, B); dorsal surface of smooth, lateral margin lined with 3 distinct teeth, first being subhepatic, second largest (Fig. 2A, B); dorsal surface of carapace prominently convex, dome-shape in frontal view (Figs. 2A, B, 18A); posterior margin of epistome very wide (Fig. 18A); rostral spine very short, much shorter than pseudorostral (Fig. 2A, B); merus and ischium of third maxilliped smooth; adult male chela short, fingers longer than half length of palm, outer surface of palm with almost smooth or with scattered granules (Figs. 1A, 2C); female chela not known; P2 and P3 dactylus short (Fig. 2D, E); flexor margins of P2–P5 unarmed (Fig. 2A); P5 dactylus condition not known; anterior margin of sternopleonal cavity almost smooth; condition of inner posterior edge of female P3 coxa not known; male telson broadly triangular, uropods directed almost laterally (Fig. 2H); female telson not known; G1 and G2 not known.

**Colour.** "Brownish-green to dark blue" (cf. Sakai, 1976; Nagai, 1994) (Fig. 1A).

**Remarks.** *Frodromia atypica* (as a *Petalomera*) was described by Sakai (1936: 34) from one male holotype (carapace measuring 6.0 × 7.0 mm) collected from "between Ito and Hatusima" in Japan at a depth of 50 m, and an allotype (no measurement provided) from "Mituisi, off Manazuru" from 100 m. Sakai (1976: 23) later changed the spelling of the type locality to "Mitsuishi", noted that the holotype is no longer extant, and the whereabouts of the paratype female was also not stated. Sakai (1936: pl. 2 fig. 1) did not describe the colour but his colour plates shows a brownish-green specimen (present Fig. 1A). Sakai (1976: 24, pl. 5 fig. 2) later reused the same figure and in his remarks on *P. atypica reticulata*, noted that its live colour was "uniformly dark blue". Sakai (1974, 1976) added to the observations of *F. atypica* when he compared the species at length with *Petalomera atypica reticulata* Sakai, 1974 (see remarks for next species).

Nagai (1994: 49) recorded the species again from Japan and noted some morphological features of the species like the presence of three lateral teeth, and stated that the colour in life of his specimen was bluish-brown. Nagai (1994) also noted that McLay's "*F. atypica*" from New Caledonia was covered in granules and was probably misidentified because Nagai's Japanese specimen of *F. atypica* was smooth, as also originally observed by Sakai (1936, 1976).

We examined Nagai's (1994) specimen and it agrees well with Sakai's (1936, 1976) descriptions and figures. It has three distinct lateral teeth (including a subhepatic tooth) after the external orbital tooth, with the second one largest (Fig. 2A, B). The rostral spine is very short and is just visible in dorsal view (Fig. 2A, B); and the two dorsal tubercles on the cheliped carpus are large and prominent (Fig. 2A). One discrepancy is that the ambulatory dactyli are relatively short (Fig. 2D, E), not elongate as figured by Sakai (1936, 1976) (present Fig. 1A). Several aspects of the specimen cannot be examined because it is small, dried, and very delicate. To properly clean and discern the characters of the third maxilliped, cheliped and pleon would almost certainly have involved destroying parts of the animal and was deemed not justifiable, especially since it is the only known specimen of the species. On the same vein, the pleon was too stiff to attempt extracting the gonopods.

The holotype of *F. atypica* is lost, and the whereabouts of the paratype female is not known. While there is clear need for a neotype, more so since it is the type species of *Frodromia* and its identity has been unclear, it would also be pointless to select the present WMNH specimen as the replacement since it is too delicate. A neotype selection and more detailed redescription of the species will have to await the discovery of a good specimen.

The specimens identified as "*F. atypica*" by McLay (1993) from New Caledonia, Loyalty Islands and the Moluccas are clearly not this species as already observed by Nagai (1994). *Frodromia atypica* sensu stricto differs markedly from McLay's (1993) material in that the dorsal surface of the carapace is smooth, without rounded granules (Fig. 2B) (versus with numerous small, rounded granules all over the dorsal surface; Fig. 12B; McLay, 1993: fig. 6a); the lateral margin has three distinct teeth (Fig. 2B) (versus with row of small granules; Figs. 12B, 14B; McLay, 1993: fig. 6a); and the P2 and P3 dactyli are relatively short (Fig. 2D, E) (versus elongate; Figs. 12A, 13C; McLay, 1993: fig. 6d). His material was re-examined in the present study and is here referred to a new species, *F. granulosa* (see later).

The figure of the species by Kimura et al. (2019: fig. 1-1) shows a specimen from the Sea of Kumano in Japan which has not been well cleaned, and it is not possible to be sure what it is. It appears to be *F. atypica* as defined here and is provisionally included under this name. The specimen of "*F. atypica*" reported by Pratiwi & Elfidasari (2020: 1225) from the Natuna Islands in the South China Sea in very shallow waters is unlikely to be this species. No figures were provided so we cannot be certain.

**Distribution.** Known only from Japan.

### *Frodromia reticulata* (Sakai, 1974)

(Figs. 1B, 3–6, 18B, C, 19A–C)

*Petalomera atypica reticulata* Sakai, 1974: 87; Sakai, 1976: 24, pl. 5 fig. 1; Nagai, 1989: 42; Nagai, 1993: 49, pl. 1 fig. 4.

*Petalomera atypica* – Takeda, 1993: 55. (not *Petalomera atypica* Sakai, 1936).

*Frodromia reticulata* – McLay, 1993: 171; Marumura & Kosaka, 2003: 20; Ng et al., 2008: 36.

**Material examined.** JAPAN: 2 ovigerous females (6.9 × 7.8 mm, 8.2 × 9.0 mm) (NSMT-Cr-6944), station 17, Omurodashi, off Izu Islands, 87–184 m, coll. T. Okutani, 26 June 1972; 1 female (7.3 × 8.2 mm) (CBM ZC 5277), SY96 station 19, Okinoyama Bank, Sagami-nada, 34°58.47′N 139°34.15′E, 121–129 m, coll. dredge, T. Komai, TR/V *Shin'yo-maru*, 24 October 1996; 1 dried male (4.3 × 5.4 mm), 2 dried females (5.5 × 6.0 mm, 8.5 × 9.5 mm) (WMNH 17), off Shionomisaki, Wakayama, 100~200 m, coll. S. Nagai, 1974.

**Diagnosis.** Colour in life light brown to pale white with orange reticulated lines (Fig. 1B). Dorsal surface of carapace and appendages with very dense short setae that completely obscure surface and margins (Fig. 3A–D, 4A, B, 5A); dorsal surface of smooth, lateral margin lined with numerous (10–20) small granules anterior and median ones usually larger (Figs. 3A–D, 4A, B, 5A); dorsal surface of carapace prominently convex with gastric regions especially high, strongly dome-shaped in frontal view (Figs. 3A–D, 4A, B, 5A, 18B, C); posterior margin of epistome wide (Fig. 18B, C); rostral spine shorter or as long as pseudorostral spines (Figs. 3A, B, 4B, 5A); merus and ischium of third maxilliped smooth (Fig. 5B); male and female chelae short, fingers longer than half length of palm, outer surface of palm with scattered round granules (Figs. 4C, 5D); P2 and P3 dactylus elongate (Figs. 4I, 5H, I); flexor margins of P2–P5 unarmed (Fig. 5A); male and female P5 dactylus gently curved (Fig. 4E–H, 5F, G); anterior margin of sternopleonal cavity with low granules (Fig. 5J); inner posterior edge of female P3 coxa angular (Fig. 6B); male telson triangular, uropods directed more posteriorly (Fig. 4D); female telson with slender, elongate uropods (Fig. 6A); G1 distal part subtruncate, without any projection (Fig. 19A, B); G2 without exopod (Fig. 19C).

**Colour.** According to Sakai (1976: 87) the species has a "coarse network[s] of purplish colouration on the carapace and abdomen" (Fig. 1B). Nagai (1993: 49) notes that when denuded, the colour is brown with reticulated patterns.

**Variation.** The series of dried and wet-preserved specimens are consistent in the shape and physiognomy, with even the smallest specimen (a male), prominently domed in frontal view (Fig. 18B). The lateral carapace margin varies from gently convex (Fig. 3A) to almost straight (Fig. 3B). The armature of the margin varies in strength and position, sometimes with some areas smooth (Figs. 3A, B, 4B, 5A). The supraorbital margin is usually entire (Figs. 3A, 4B, 5A) but occasionally has one or two small granules (Fig. 3B). The extensor margin of the P5 dactylus is usually unarmed (Figs. 4E, F, 5G) but in some specimens, there is a spine (Figs. 4G, 5F). The presence or absence of this spine is used in dromiid taxonomy (see McLay, 1993) but it appears to be of no value in *Frodromia*. Its taxonomic value has also been questioned for some homolodromiids (see Ng & Naruse, 2007; Ng & Yang, 2021).

**Remarks.** Sakai (1974: 87) described *Petalomera atypica reticulata* (no figures provided) on the basis of a male holotype from Mimase in Tosa Bay, measuring 6.3 × 7.0 mm, and two males and a female from east of Ashizuri-zaki, Kochi Prefecture; the latter three specimens are not paratypes as they were not designated as such. He noted: "The new subspecies differs from *P. atypica* SAKAI 1936 in having coarse networks of purplish colouration on the carapace and abdomen. In *atypica*, the colouration is uniformly dark blue. The three frontal teeth are subequal in size, while in *atypica*, the lateral frontal teeth are markedly longer than the median one. The dorsal surface of carapace is markedly convex, smooth and glabrous on denudation and not at all areolated. The antero-lateral borders are parallel and entire, marked with a series of tiny spinules, of which the foremost one is sensibly larger, located a short distance from the postorbital tooth." (Sakai 1974: 87). Subsequently, in his treatment of the Japanese fauna, Sakai's (1976: 24) text for

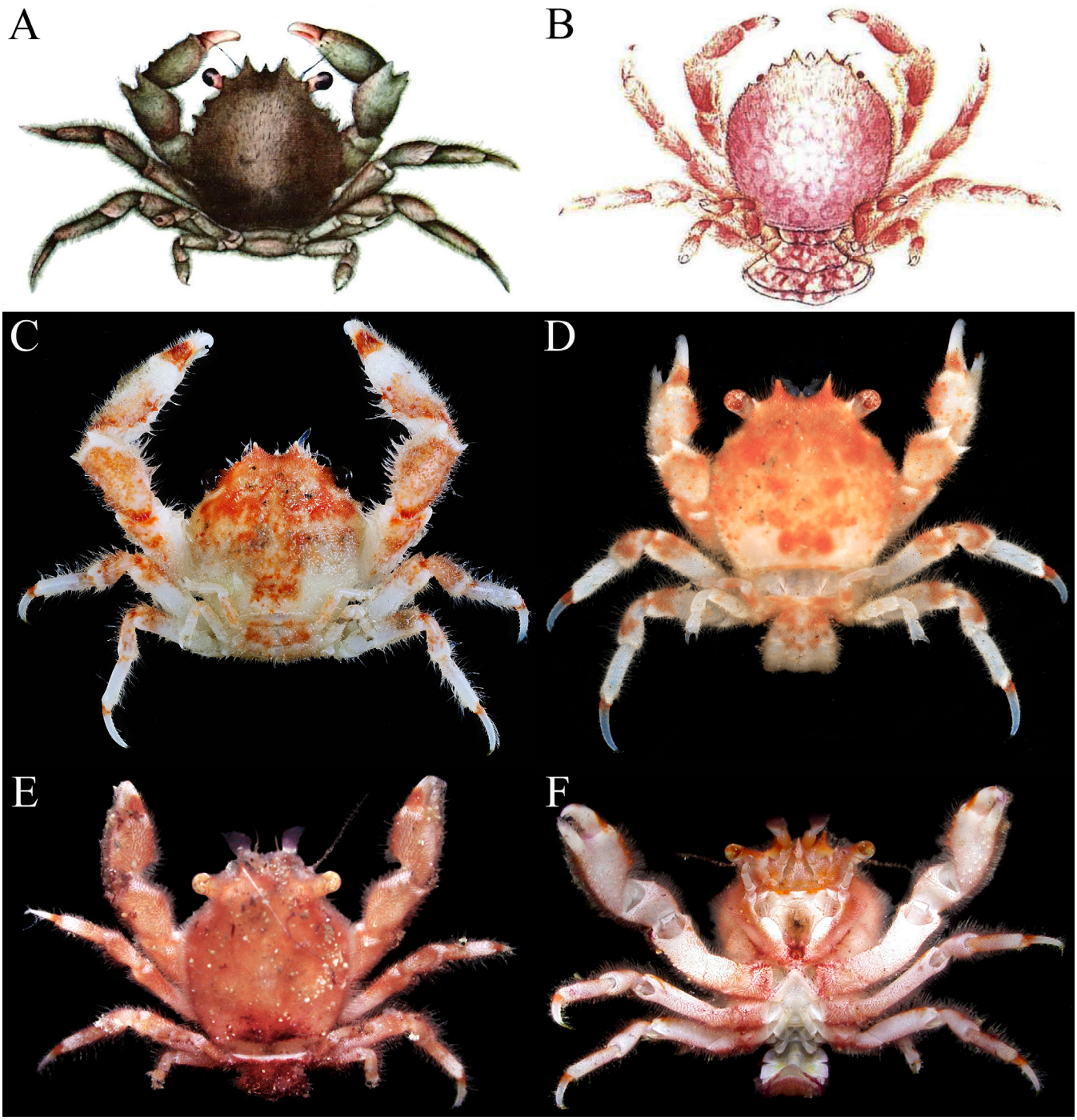


Fig. 1. Colour in life. A, *Frodromia atypica* (Sakai, 1936), after Sakai (1936: pl. 2 fig. 1); B, *F. reticulata* (Sakai, 1974), after Sakai (1976: pl. 5 fig. 1); C, *F. elegans*, new species, holotype male (6.6 × 7.5 mm) (ZRC 2024.0144), Taiwan; D, *F. granulosa*, new species, holotype male (6.5 × 7.1 mm) (ZRC 2024.0517), Vanuatu; E, F, *F. iners*, new species, holotype male (6.3 × 7.0 mm) (ZRC 2024.0518), Philippines [partly covered with sand particles and debris]. Photographs: C, T.-Y. Chan; D, J.C.E. Mendoza; E, F, P.K.L. Ng.

*F. atypica reticulata* repeated what he wrote in 1974. In his key, he writes that the two species are distinguished by their "Wrist and palm not markedly tuberculated. Carapace longer than broad, its dorsal surface smooth, extremely convex. Anterolateral borders are parallel, entire, marked with tiny tubercles or spinules. Frontal and preorbital teeth are acuminate", with *F. atypica* separated from *F. atypica reticulata* by its lateral margins being armed with two or three tubercles of a good size with the live colour dark blue (versus lateral margins armed with series of small sharp granules with the live colour dark brown with a light purple network of lines in *F. atypica reticulata*) (Sakai, 1976: 20). These notes match his figures of the two species very well (Sakai, 1976: pl. 5 figs. 1, 2) (present Fig. 1A, B).

The whereabouts of Sakai's holotype and other specimens are not known. They are not in Japanese repositories where his material has been found (e.g., see Muraoka, 1998). Nevertheless, the present specimens from Japan agree very well with the description and figures of *F. reticulata* and it is clearly a distinct species (see McLay, 1993). The specimens show no trace of the original colours. As in Sakai's (1976)

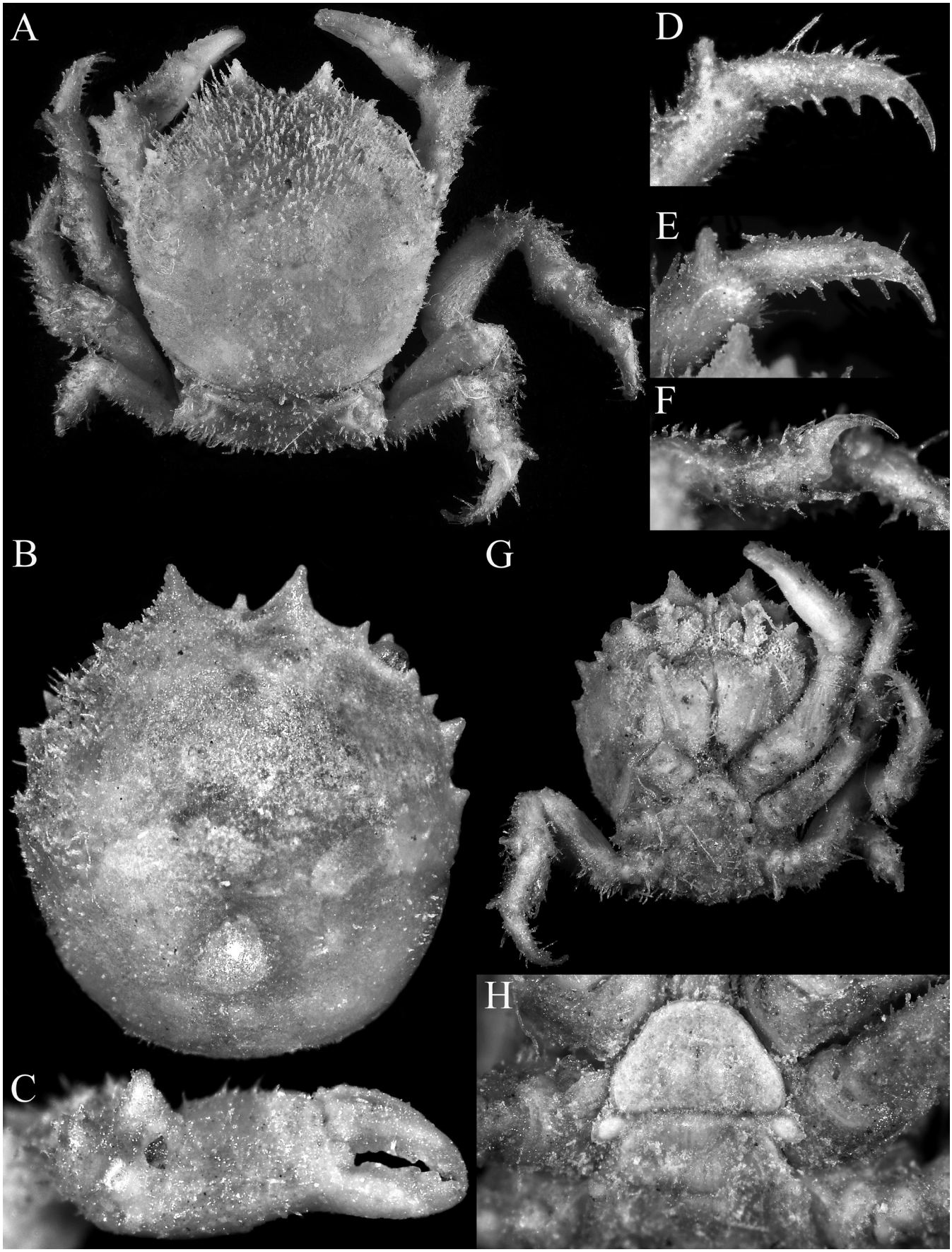


Fig. 2. *Frodromia atypica* (Sakai, 1936), male (4.5 × 4.8 mm) (WMNH 16), Japan. A, overall dorsal habitus; B, dorsal view of carapace (right side denuded); C, right chela; D, left P2 propodus and dactylus; E, left P3 propodus and dactylus; F, right P4 carpus, propodus and dactylus (distal spine missing); G, ventral surface of habitus; H, pleonal somite 6 and telson.

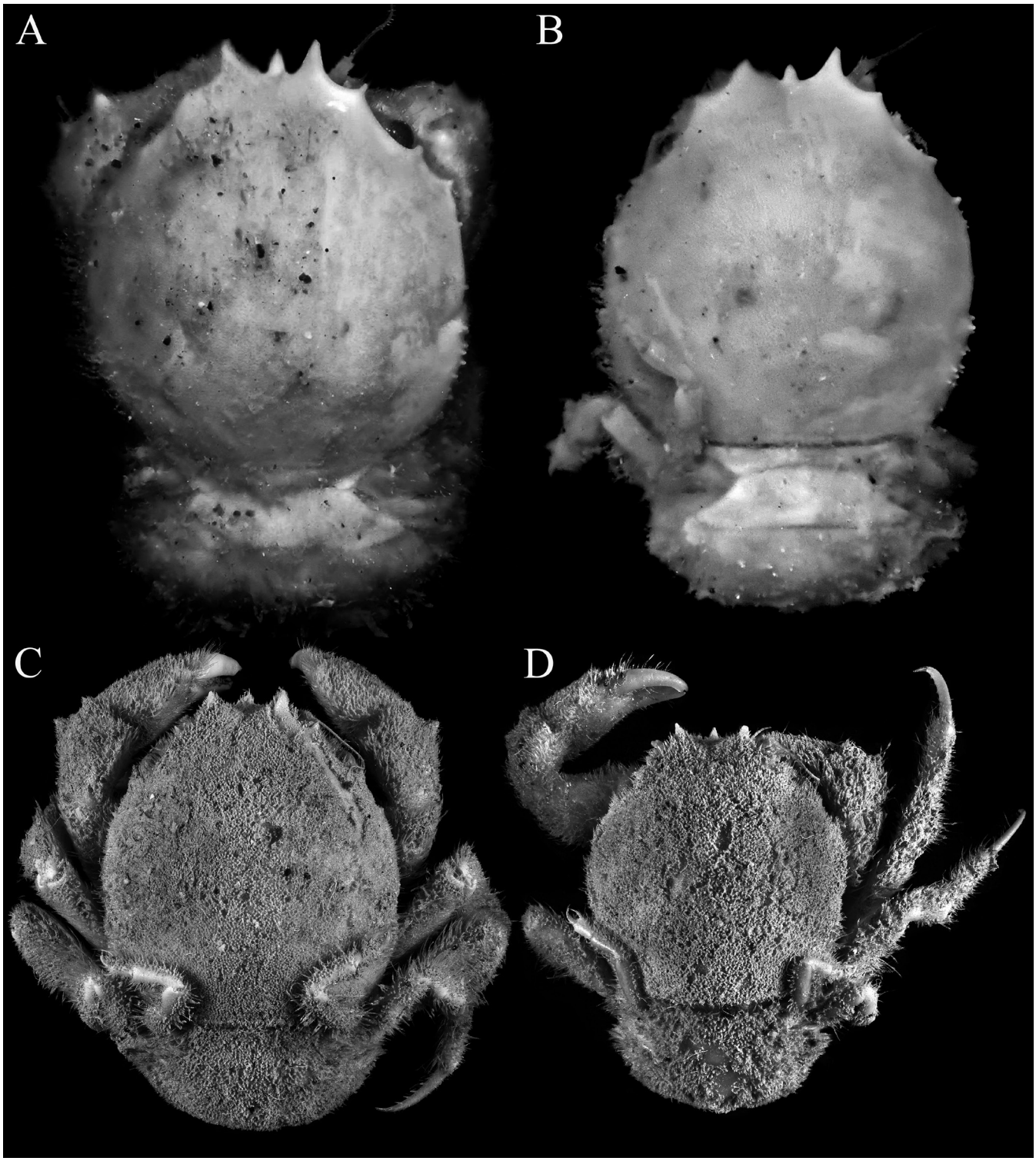


Fig. 3. *Frodromia reticulata* (Sakai, 1974). A, ovigerous female (8.2 × 9.0 mm) (NSMT-Cr-6944), Japan; B, ovigerous female (6.9 × 7.8 mm) (NSMT-Cr-6944), Japan; C, female (8.5 × 9.5 mm) (WMNH 17), Japan; D, female (5.5 × 6.0 mm) (WMNH 17), Japan. A, B, dorsal view of carapace (right side denuded); C, D, overall dorsal habitus.

figure (present Fig. 1B), the pseudorostral spines are generally longer than the prominent rostral spine (Figs. 3A–D, 5A) but in the male specimen, the rostral spine is actually slightly longer (Fig. 4B).

**Distribution.** Known only from Japan.

***Frodromia elegans*, new species**
(Figs. 1C, 7–9, 18D, 19D–F)

**Material examined.** Holotype: male (6.6 × 7.5 mm) (ZRC 2024.0144), station CP4136, continental slope, sandy-coral substrate, 19°57.0127′N 114°35.735′E – 19°56.50′N 114°33.88′E, 249–250 m, South China Sea, Taiwan, coll. ZHONG SHA 2015 Cruise, 23 July 2015.

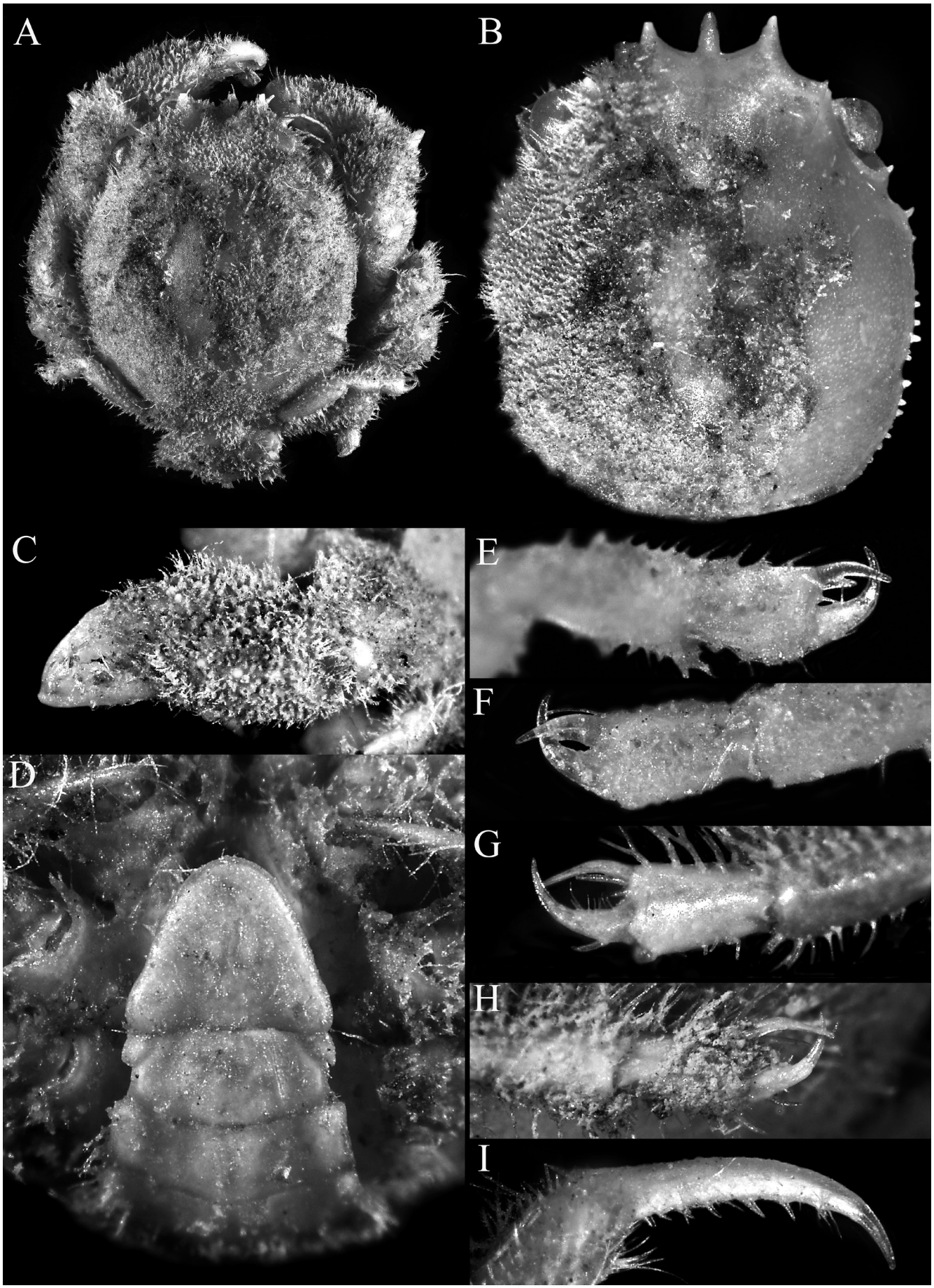


Fig. 4. *Frodromia reticulata* (Sakai, 1974). A–F, male (4.3 × 5.4 mm) (WMNH 17), Japan; G, female (5.5 × 6.0 mm) (WMNH 17), Japan; H, I, female (8.5 × 9.5 mm) (WMNH 17), Japan. A, overall dorsal habitus; B, dorsal view of carapace (right side denuded); C, left chela; D, male pleon; E, H, right P5 carpus, propodus and dactylus; F, G, left P5 carpus, propodus and dactylus; I, right P3 propodus and dactylus.

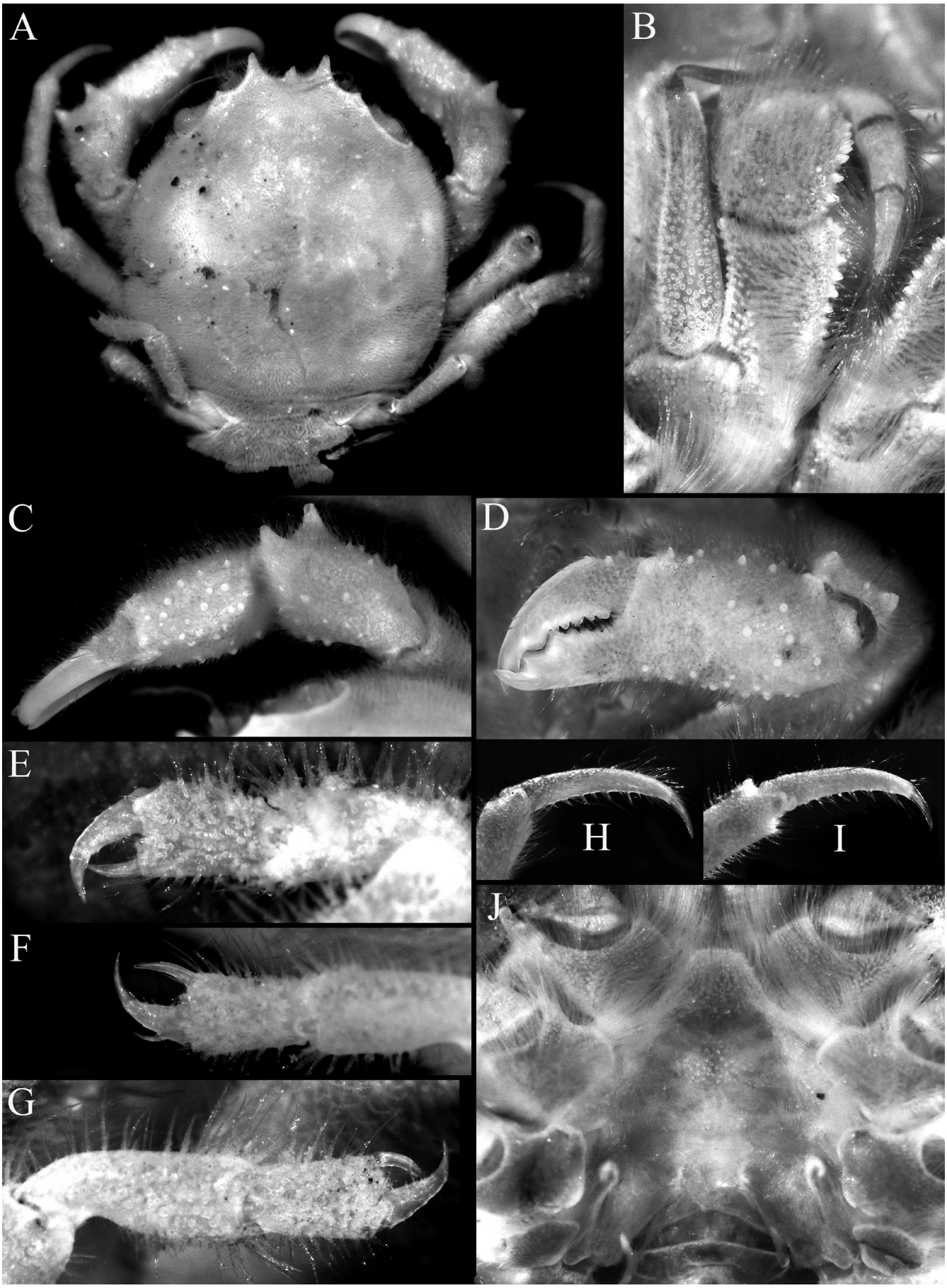


Fig. 5. *Frodromia reticulata* (Sakai, 1974), female (7.3 × 8.2 mm) (CBM ZC 5277), Japan. A, overall dorsal habitus (right side partially denuded); B, right third maxilliped; C, dorsal view of right cheliped; D, right chela; E, left P4 carpus, propodus and dactylus; F, left P5 carpus, propodus and dactylus; G, right carpus, propodus and dactylus; H, right P3 propodus and dactylus; I, right P2 propodus and dactylus; J, sternopleonal cavity showing spermatheca.

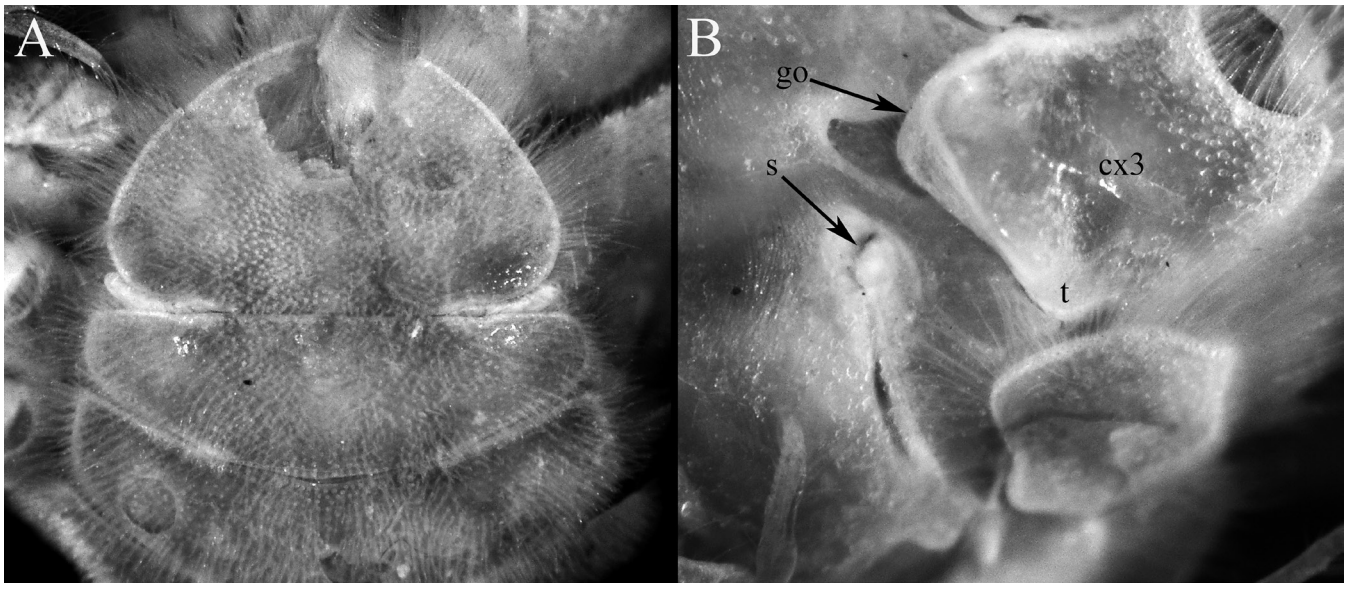


Fig. 6. *Frodromia reticulata* (Sakai, 1974), female (7.3 × 8.2 mm) (CBM ZC 5277), Japan. A, pleonal somites 5, 6 and telson; B, left sternopleonal cavity showing spermatheca and enlarged P3 coxa. Abbreviations: ap = spermathecal aperture; cx3 = coxa of P3; go = female gonopore; s = aperture of spermatheca; tubercle on P3 coxa.

Paratypes: TAIWAN: 2 males (6.4 × 7.1 mm, 6.8 × 7.4 mm) (ZRC 2024.0141), 1 male (6.3 × 7.4 mm) (MNHN-IU-2023-635), station CP4135, continental slope, sandy coral substrate, many solitary corals, 19°58.42′N 114°32.93′E – 19°58.94′N 114°37.70′E, 211–218 m, South China Sea, Taiwan, coll. ZHONG SHA 2015 Cruise, 23 July 2015; 1 ovigerous female (5.9 × 6.5 mm) (ZRC 2024.0143), station CP4136, continental slope, sandy-coral substrate, 19°57.0127′N 114°35.735′E – 19°56.50′N 114°33.88′E, 249–250 m, South China Sea, Taiwan, coll. ZHONG SHA 2015 Cruise, 23 July 2015.

**Diagnosis.** Colour in life dirty white with patches of orange (Fig. 1C). Dorsal surface of carapace and appendages with dense short setae that partially obscure surface and margins (Fig. 7A, B); dorsal surface smooth; lateral margin lined with numerous (7–20) small granules, anterior ones usually larger (Figs. 7A, B, 9A); dorsal surface of carapace gently convex in frontal view (Figs. 7A, B, 9A, 18D); posterior margin of epistome wide (Fig. 18D); rostral spine shorter or as long as pseudorostral spines (Fig. 7B); merus and ischium of third maxilliped smooth (Fig. 8A); male chelipeds elongate, chela long, fingers longer than half length of palm, outer surface of palm with scattered round granules (Fig. 9D); P2 and P3 dactylus elongate (Figs. 8C, 9B); flexor margins of P2–P5 unarmed (Fig. 8D); male P5 dactylus sharply bent medially with prominent angle (Fig. 8D, F); female P5 dactylus gently curved (Figs. 4E–H, 5F, G); anterior margin of sternopleonal cavity smooth (Fig. 9F); inner posterior edge of female P3 coxa with low tubercle (Fig. 9F); male telson triangular, uropods directed almost laterally (Fig. 8H); female telson with uropods slender, elongate (Fig. 9E); G1 distal part with acute projection (Fig. 19D, E); G2 without exopod (Fig. 19F).

**Etymology.** The species epithet, *elegans* (L. elegant, refined), is a reference to the graceful appearance of the new species; used here as an adjective.

**Colour.** Dirty-white background with uneven patches of orange on the dorsal surface (denser on the anterior half), and patches on the chelipeds and P2 and P3; base of dactylar finger orange (Fig. 1C).

**Variation.** The lateral armature varies to some degree. In the holotype male specimen (ZRC 2024.0144), there is a relatively larger spine behind the external orbital spine, followed by 10–14 sharp granules with more smaller ones on the marginal surfaces of the posterolateral margin (Fig. 7B). The lateral margin of the female paratype (ZRC 2024.0143) is less well armed overall, with only about 7 or 8 sharp granules, with only one of these on the lateral margin which is otherwise almost unarmed (Fig. 9A). The three males (ZRC 2024.0141) has the lateral margin variously armed with many small granules.

**Remarks.** Morphologically, *Frodromia elegans*, new species, superficially agrees with Sakai's (1974, 1976) descriptions and figure of *F. reticulata*; the colour in life is an uneven pattern of orange patches and lines on a dirty white background (Fig. 1D), similar to that figured for *F. reticulata* (Sakai, 1976: pl. 5 fig. 1), although no obvious reticulated lines are visible. *Frodromia elegans*, however, can easily be separated by its carapace and appendages covered with a soft pubescence that only partially obscures the surface and margins (Figs. 1D, 7A) (versus covered with a very thick pubescence that completely obscures the surface and margins in *F. reticulata*; Figs. 3C, D, 4A); has a distinctly less inflated carapace, with the lateral margins and the dorsal surface gently convex (Figs. 7A, 9A, 18D) (versus lateral margins strongly convex and the dorsal surface is prominently domed in *F. reticulata*; Figs. 3, 4A, B, 5A, 18B, C); the adult male chelipeds are elongate, with the chela long, slender and the fingers are shorter than the palm (Figs. 7A, C, 8B) (versus chelipeds relatively short with shorter chela and the fingers subequal in length to the

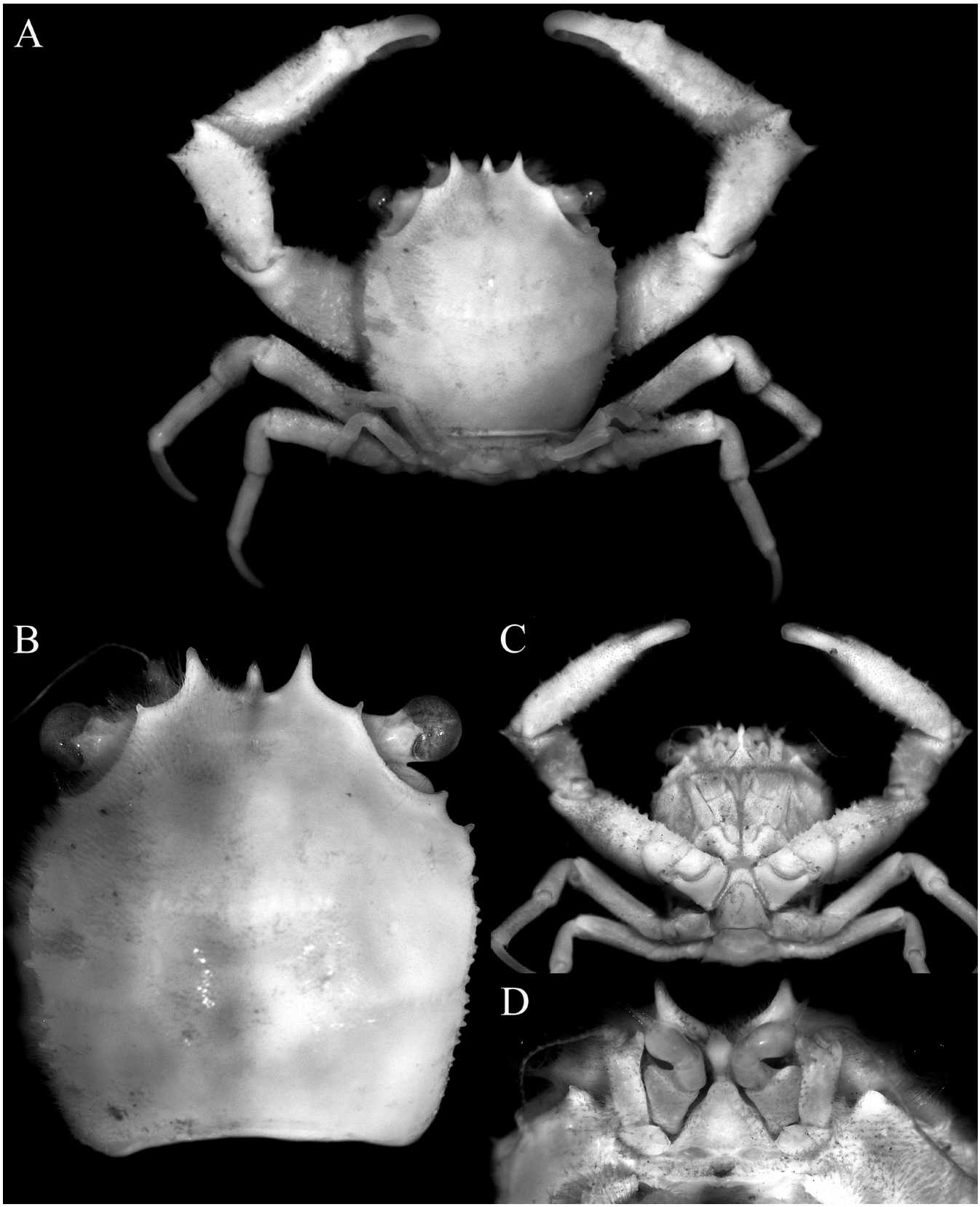


Fig. 7. *Frodromia elegans*, new species, holotype male (6.6 × 7.5 mm) (ZRC 2024.0144), Taiwan. A, overall dorsal habitus (right side denuded); B, dorsal view of carapace (right side denuded); C, ventral surface of cephalothorax; D, epistome, antennules and antennae (anteroventral view).

palm in *F. reticulata*; Fig. 4C); the female chela is relatively shorter (Fig. 9D) (versus longer in *F. reticulata*; Fig. 5D); the P2 and P3 dactyli are proportionately longer and more slender (Figs. 8C, 9B) (versus dactyli relatively shorter and stouter in *F. reticulata*; Fig. 4E–H); the bent dactylus of the male P5 has a prominent median angle (Fig. 8D, F) (versus dactylus gently curved in *F. reticulata*; Fig. 4E–G); and the distal part of the G1 has a small projection (Fig. 19D, E)

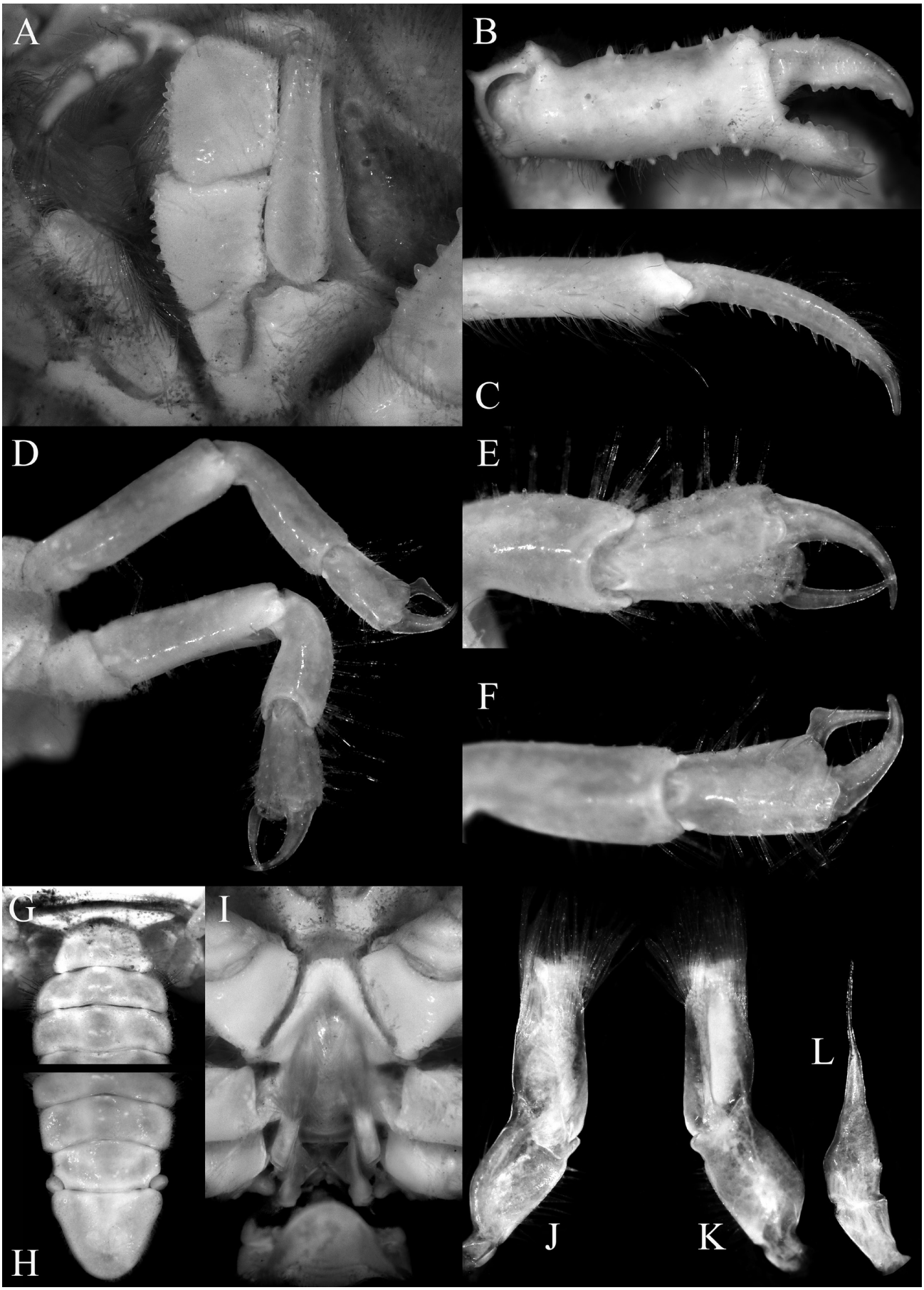


Fig. 8. *Frodromia elegans*, new species, holotype male (6.6 × 7.5 mm) (ZRC 2024.0144), Taiwan. A, left third maxillipeds (denuded); B, right chela (partially denuded); C, right P3 propodus and dactylus; D, right P4 and P5; E, right P4 carpus, propodus and dactylus; F, right P5 carpus, propodus and dactylus; G, pleonal somites 1–4; H, pleonal somites 5–6 and telson; I, sternopleonal cavity with G1s; J, left G1 (ventral view); K, left G1 (dorsal view); L, left G2 (dorsal view).

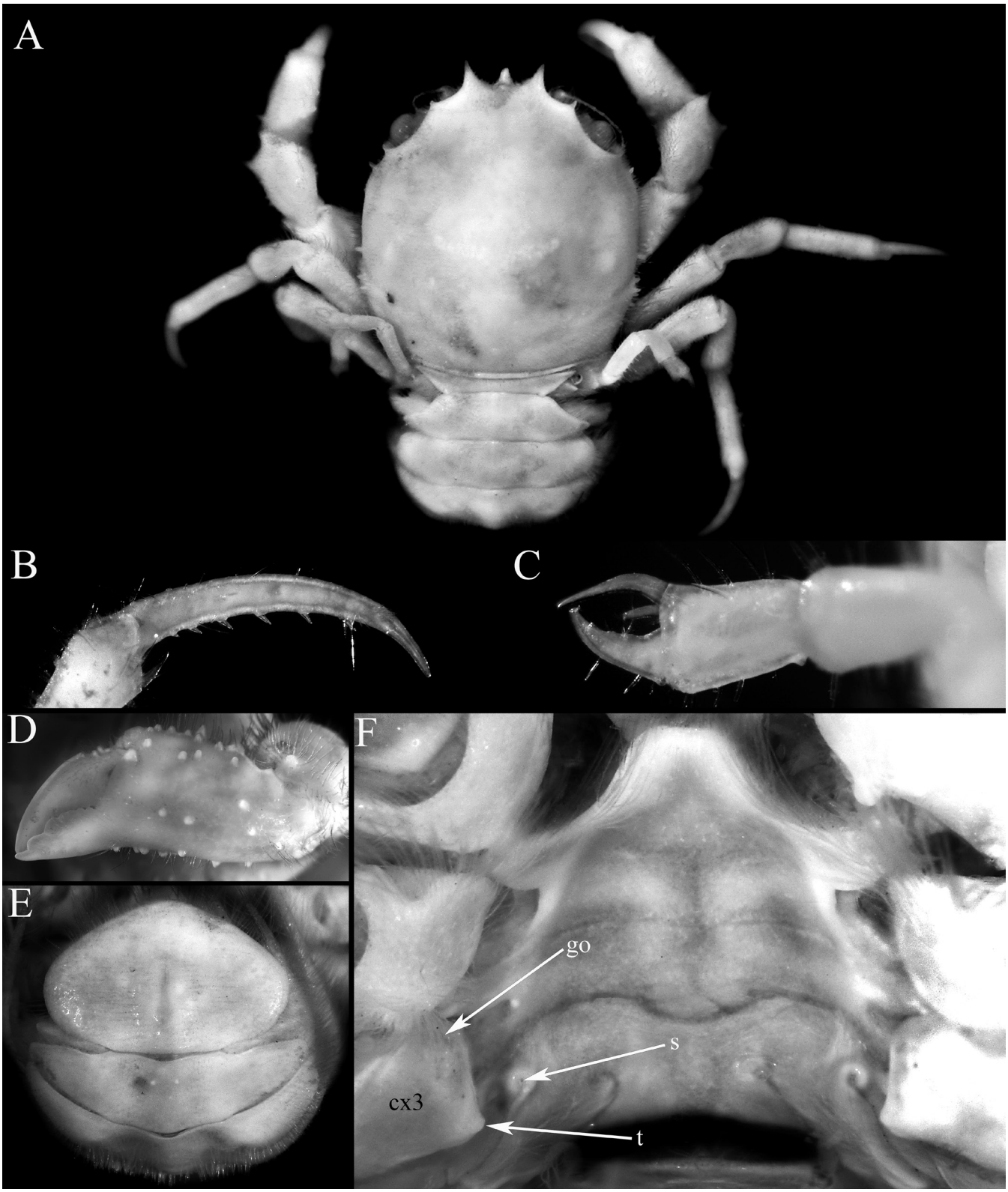


Fig. 9. *Frodromia elegans*, new species, paratype ovigerous female (5.9 × 6.5 mm) (ZRC 2024.0143), Taiwan. A, overall dorsal habitus (right side denuded); B, right P3 propodus and dactylus; C, left P5 carpus, propodus and dactylus; D, left chela (partially denuded); E, pleonal somites 5 and 6, and telson; F, sternopleonal cavity showing spermatheca. Abbreviations: cx3 = coxa of P3; go = female gonopore; s = aperture of spermatheca; t = tubercle on P3 coxa.

(versus distal part subtruncate, without any projection in *F. reticulata*; Fig. 19A, B).

The male P5 dactylus of *F. elegans* has a distinctive shape, curving sharply medially, forming an angular corner on the outer margin (Fig. 8D, F), and is present in all the male specimens examined. This condition is unique for *F. elegans* and easily distinguishes it from all congeners. In female specimens, the P5 dactylus is gently curved (Fig. 9C) like those of other species.

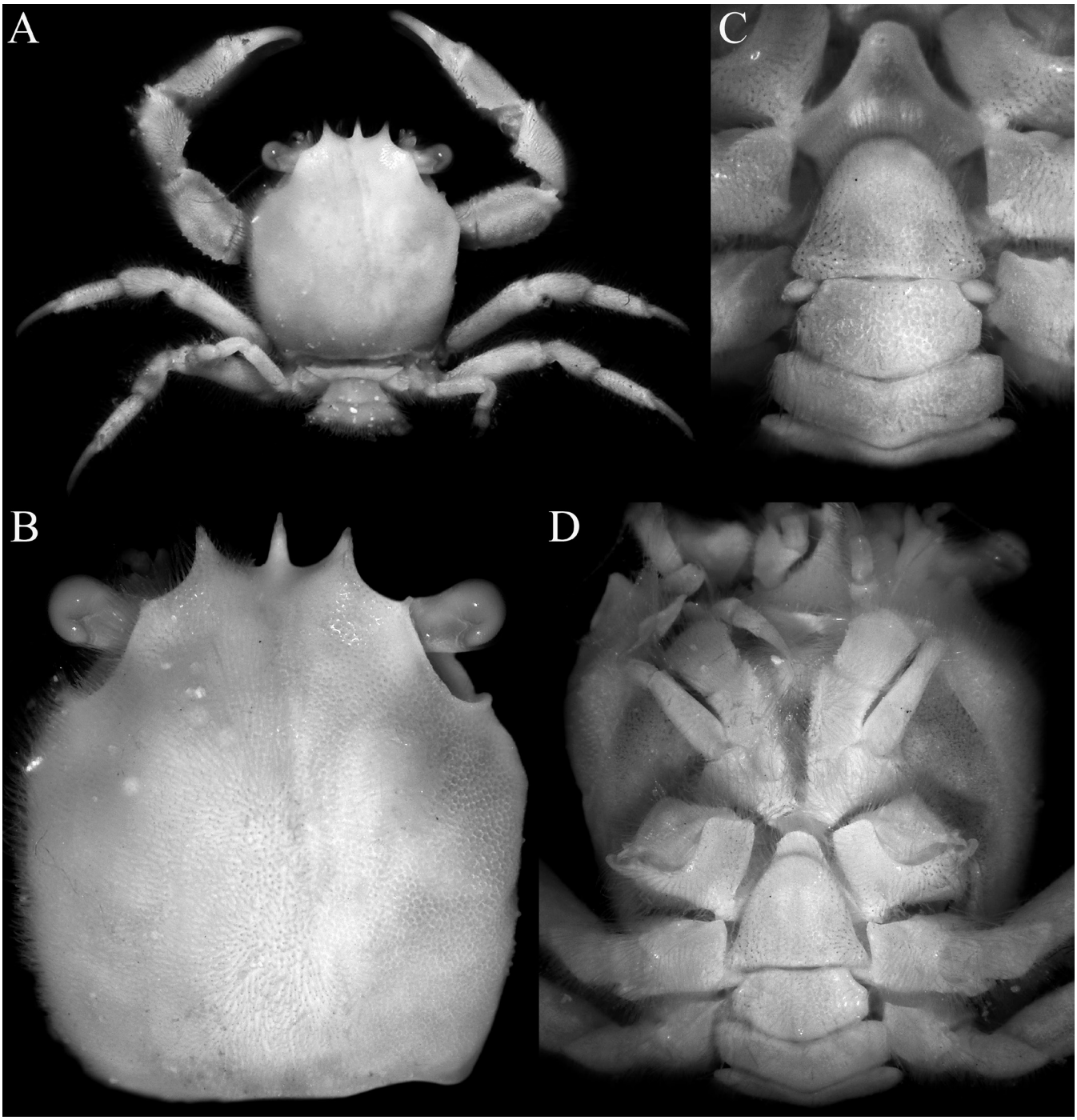


Fig. 10. *Frodromia iners*, new species, holotype male (6.3 × 7.0 mm) (ZRC 2024.0518), Philippines. A, overall dorsal habitus (right side denuded); B, dorsal view of carapace (right side denuded); C, pleonal somites 5–6 and telson; D, ventral view of cephalothorax.

The eggs of *F. elegans* are numerous and relatively small, measuring only 0.5 mm in diameter (preserved), and as such, the species probably has planktotrophic larvae.

**Distribution.** Known only from several locations in the northern part of the South China Sea.

***Frodromia iners***, **new species**
(Figs. 1E, F, 10, 11, 18E, 19G–I)

**Material examined.** Holotype: male (6.3 × 7.0 mm) (ZRC 2024.0518), station T31, between Panglao and Balicasag islands, Bohol Sea, Philippines, 9°33.0′N 123°42.0′E, 100–140 m, coll. PANGLAO 2004 Expedition, 2 July 2004.

**Diagnosis.** Colour in life uniformly orange (Fig. 1E, F). Dorsal surface of carapace and appendages with dense short setae that partially obscure surface and margins (Fig. 10A, B); dorsal surface of smooth; lateral margin appears almost entire, with only 5 or 6 very small granules (Fig. 10B); dorsal surface of carapace gently convex in frontal view (Figs. 10A, B, 18E); posterior margin of epistome wide (Fig. 18E); rostral spine longer than pseudorostral spines (Fig. 10B); merus and ischium of third maxilliped

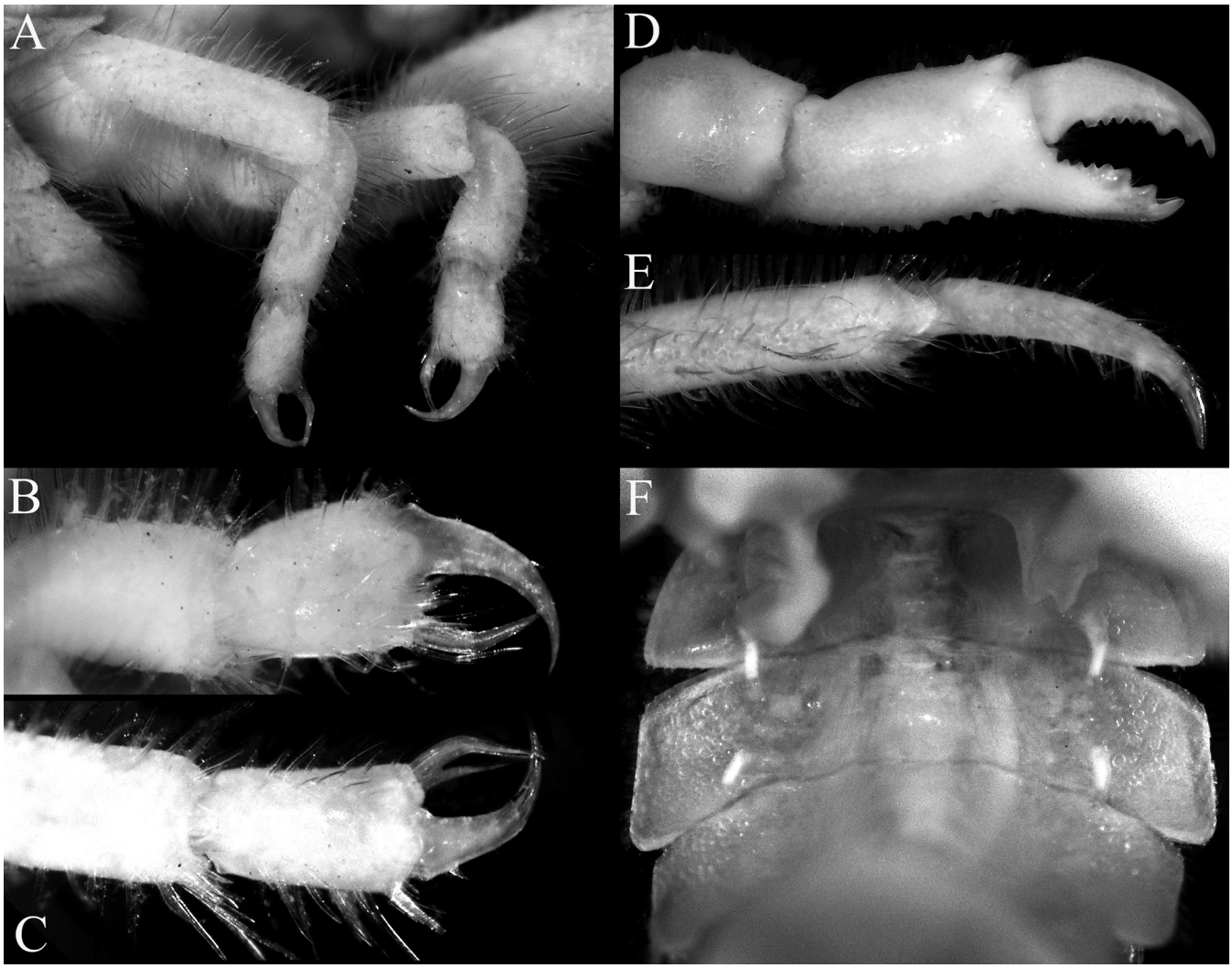


Fig. 11. *Frodromia iners*, new species, holotype male (6.3 × 7.0 mm) (ZRC 2024.0518), Philippines. A, right P4 and P5; B, right P4 carpus, propodus and dactylus; C, right P5 carpus, propodus and dactylus; D, right chela (denuded); E, right P3 propodus and dactylus; ventral surface of pleonal somites 3 and 4 showing vestigial pleopods.

smooth (Fig. 10D); adult male chelipeds not elongate, merus and carpus with rounded granules only along margins (Fig. 10A); male chela relatively short, fingers about half length of palm, outer surface of palm smooth (Fig. 11D); female chela not known; P2 and P3 dactylus relatively shorter (Fig. 11E); flexor margins of P2–P5 unarmed (Fig. 11A); P5 dactylus gently curved (Fig. 11A, C); anterior margin of sternopleonal cavity smooth (Fig. 10D); condition of inner posterior edge of female P3 coxa not known; male telson triangular, uropods directed almost laterally (Fig. 10C, D); female telson not known; G1 distal part with acute projection (Fig. 19G, H); G2 without exopod (Fig. 19I).

**Etymology.** The species epithet, *iners* (L. unassuming, docile), alludes to the simple characters of the new species, which distinguish it from its closest congener, *F. elegans*, new species; used here as an adjective.

**Colour.** Dorsal surfaces evenly orange with joints red; ventral surfaces white with red flecks (Fig. 1E, F).

**Remarks.** *Frodromia iners*, new species, is morphologically most similar to *F. elegans*, new species, from the South China Sea, it can easily be separated by its distinctively much longer rostral spine which reaches beyond the tips of the pseudorostral spines (Fig. 10A, B) (versus rostral spine distinctly shorter than pseudorostral spines in *F. elegans*; Figs. 7A, B, 9A); the lateral carapace margin is almost entire except for five or six small granules (Fig. 10A, B) (versus with 7–20 large and small granules in *F. elegans*; Figs. 7A, B, 9A); the male chela and fingers are relatively shorter and the outer surface of the chela is smooth (Fig. 11D) (versus chela and fingers distinctly longer with distinct row of median granules in *F. elegans*; Fig. 8B); the P2 and P3 dactyli are proportionately shorter (Fig. 11E) (versus elongate in *F. elegans*; Figs. 8C, 9B); and the male P5 dactylus is gently curved (Fig. 11A, C) (versus with distinct median angle in *F. elegans*; Fig. 8D, F). Significantly, the colour in life is also different, with *F. iners* a uniform orange on all its dorsal surfaces (Fig. 1E); *F. elegans* has a white background with irregular orange lines (Fig. 1C).

**Distribution.** Known only from the Philippines.

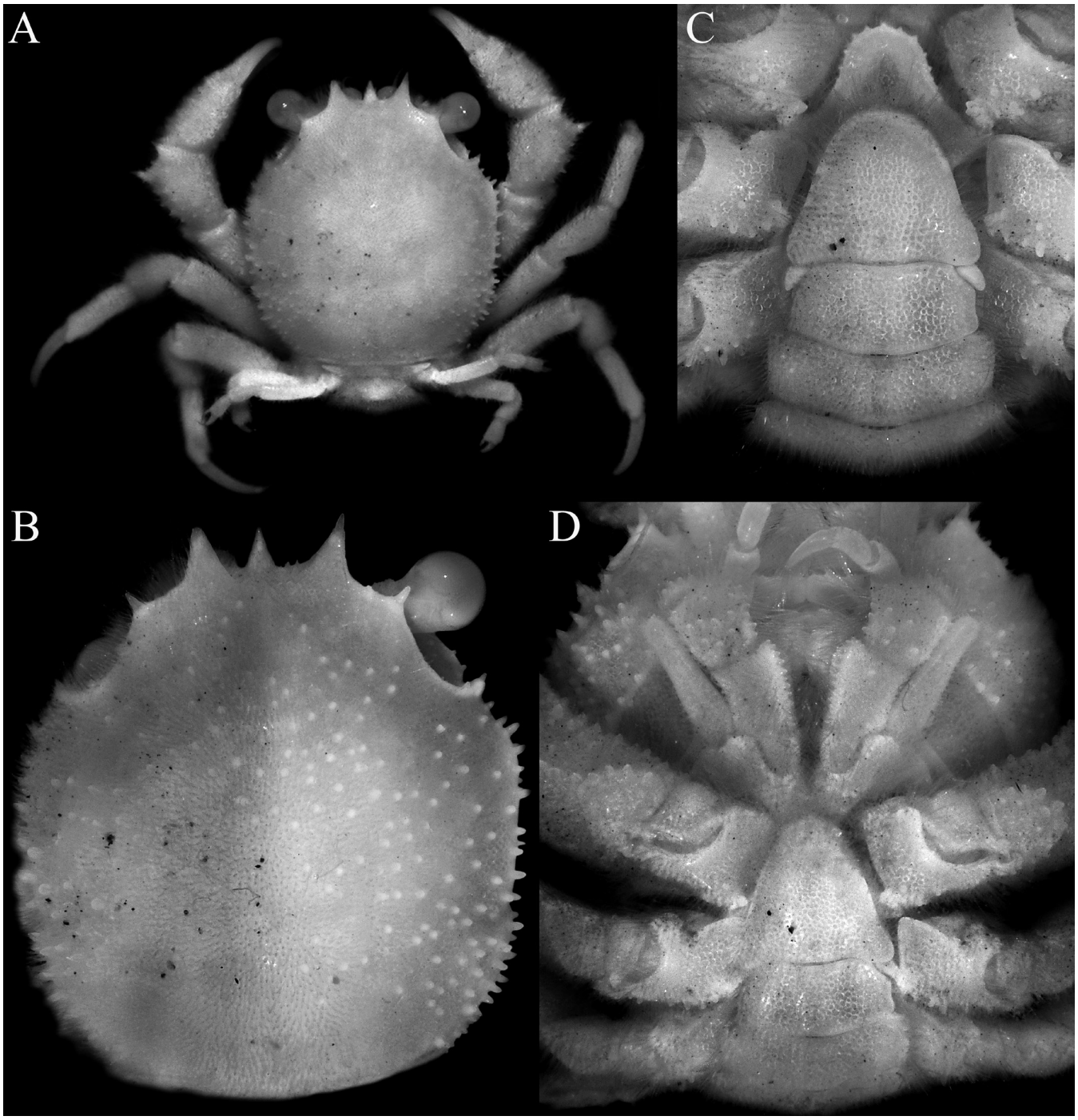


Fig. 12. *Frodromia granulosa*, new species, holotype male (6.5 × 7.1 mm) (ZRC 2024.0517), Vanuatu. A, overall dorsal habitus (right side denuded); B, dorsal view of carapace (right side denuded); C, pleonal somites 5–6 and telson; D, ventral view of cephalothorax.

***Frodromia granulosa*, new species**
(Figs. 1D, 12, 13, 18F, 19J–L)

*Frodromia atypica* – McLay, 1993: 171 (in part), figs 6 a–j, 17 d; Guinot & Tavares, 2003: 108, figs. 25, 26; Richer de Forges et al., 2005: 60; Ng & Richer de Forges, 2007: 280; Poupin, 2010: 44 (not *Petalomera atypica* Sakai, 1936).
*Frodromia* ? *atypica* – Guinot & Quenette, 2005: 290, fig. 12.

**Material examined.** Holotype: 1 male (6.5 × 7.1 mm) (ZRC 2024.0517), station AT8, west Malo Island, Santo, Vanuatu, 15°40.5′S 167°01.5′E, 366–389 m, coll. SANTO 2006 Expedition, 17 September 2006.

Paratypes: 1 male (7.2 × 8.3 mm) (MNHN-IU-2021-9847 = MNHN-B26403), station CP1091, east of Santo, Vanuatu, 15º13′S 167°13′E, 344–350 m, coll. P. Bouchet & B. Richer de Forges, MUSORSTOM 8 cruise, 6 October 1994; 1 male (7.3 × 8.2 mm), 1 female (8.4 × 9.2 mm) (MNHN-IU-2021-9848 = MNHN-822559), station CP171, Grand Passage, New Caledonia, 18°59′S 163°15′E, 435 m, coll. P. Bouchet & B. Richer de Forges, MUSORSTOM 4 cruise, 17 September 1995; 1 male (7.4 × 8.4 mm) (MNHN-IU-2021-9849 = MNHN-826358), station CP867, Loyalty Basin, New Caledonia, 21°26′S 166°18′E, 720–950 m, coll. B. Richer de Forges, HALIPRO 1 cruise, 22 March 1994; 1 male

(6.0 × 7.1 mm) (MNHN-IU-2021-9850), station CP670, east coast, New Caledonia, 20°54′S 165°53′E, 394–397 m, coll. P. Bouchet & B. Richer de Forges, BATHUS I cruise, 14 March 1993; 1 female (10.0 × 10.9 mm) (MNHN-IU-2021-9851 = MNHN-822560), station CP464, east of Cape of Pines, Lifou, Loyalty Islands, New Caledonia, 21°01′S 167°32′E, 420–430 m, coll. P. Bouchet, B. Métivier & B. Richer de Forges, MUSORSTOM 6 cruise, 21 February l989; 2 males (4.5 × 5.2 mm, 5.8 × 6.3 mm), 1 female (6.5 × 7.2 mm) (MNHN-IU-2021-9853), station CP707, east coast, New Caledonia, 21°43′S 66°36′E, 347–375 m, coll. P. Bouchet & B. Richer de Forges, BATHUS I cruise, coll. 19 March l993; 1 male (7.1 × 8.0 mm) (ZRC 2024.0710, ex MNHN-IU-2021-9854 = MNHN-B22558), station CP464, east of Cape of Pines, Lifou, Loyalty Islands, New Caledonia, 21°01′S 167°32′E, 420–430 m, coll. P. Bouchet, B. Métivier & B. Richer de Forges, MUSORSTOM 6 cruise, 21 February 1989; 1 female (9.7 × 10.5 mm) (MNHN-IU-2021-9855), station CP742, Boulari Pass, New Caledonia, 22°33′S l66°26′E, 340–470 m, coll. B. Richer de Forges, BATHUS 2 cruise, 14 May 1993; 1 female (7.3 × 8.5 mm) (MNHN-IU-2021-9856 = MNHN-B27893), station CP412, northwest of Lifou, Loyalty Islands, New Caledonia, 20°41′S 167°04′E, 437 m, coll. B. Richer de Forges, MUSORSTOM 6 cruise, 15 February 1989; 3 females (8.5 × 9.2 mm, 9.2 × 10.3 mm, 8.9 × 9.7 mm) (MNHN-IU-2021-9857), station CP737, Kouaré Pass, New Caledonia, 23°03′S 167°00′E, 350–400 m, coll. P. Bouchet & B. Richer de Forges, BATHUS 2, 13 May 1993; 1 male (8.2 × 9.4 mm), 1 female (7.1 × 8.3 mm) (MNHN-IU-2021-9858 = MNHN-826357), station CP464, east of Cape of Pines, Lifou, Loyalty Islands, New Caledonia, 21°01′S 167°32′E, 420–430 m, coll. P. Bouchet, B. Métivier & B. Richer de Forges, MUSORSTOM 6 cruise, 21 February 1989; 1 female (10.0 × 10.8 mm) (ZRC 2024.0711, ex MNHN-IU-2021-9859 = MNHN-26359), station CP868, Loyalty Basin, New Caledonia, 21°15′S 165°56′E, 430–550 m, coll. B. Richer de Forges, HALIPRO I cruise, 23 March 1994; 1 male (6.0 × 6.9 mm), 1 female (7.7 × 8.5 mm) (MNHN-lU-2021-9860 = MNHN-826360), station CP868, Loyalty Basin, New Caledonia, 21°15′S 165°56′E, 430–550 m, coll. B. Richer de Forges, HALIPRO I cruise, 23 March l994.

**Diagnosis.** Colour in life pale yellow with patches of orange (Fig. 1D). Dorsal surface of carapace and appendages with dense short setae that partially obscure surface and margins (Fig. 12A, B); dorsal surface of carapace with numerous sharp and round granules; lateral margin with numerous prominent sharp granules, uniformly distributed along length (Fig. 12A, B; McLay, 1993: fig. 6a, b); dorsal surface of carapace strongly convex in frontal view (Figs. 12A, B, 18F); posterior margin of epistome wide (Fig. 18F); rostral spine shorter or as long as pseudorostral spines (Figs. 12A, B, 14A, B); merus and ischium of third maxilliped with distinct sharp granules (Fig. 12D); adult male chelipeds not elongate, merus and carpus with numerous sharp granules (Fig. 12A, D); male chela relatively short, fingers about half length of palm, outer surface of palm covered with numerous sharp tubercles and granules (Fig. 13B; McLay, 1993: fig. 6c); female chela similar to male (Fig. 14B, C); P2 and P3 dactylus elongate (Fig. 13C; McLay, 1993: fig. 6d); flexor margins of P2–P5 with sharp granules (Fig. 13A); P5 dactylus gently curved (Fig. 13E, F; McLay, 1993: fig. 6f); anterior margin of sternopleonal cavity lined with sharp granules (Fig. 12C); inner posterior edge of female P3 coxa with prominent spur-like tubercle (Fig. 14D); male telson triangular, uropods directed almost posteriorly (Fig. 12C; McLay, 1993: fig. 6i); female telson with narrow, elongate uropods (Fig. 14C; McLay, 1993: fig. 6j); G1 distal part with broadly triangular projection (Fig. 19J, K); G2 without exopod (Fig. 19L).

**Etymology.** The species epithet, *granulosa* (L. granulous, granular) alludes to the prominent granules on the carapace of the new species; used here as an adjective.

**Colour.** Background pale yellowish with uneven patches of orange, some forming oval patterns (Fig. 1D).

**Variation.** The granules on the dorsal surface are less pronounced on the anterior surface in large specimens but are always distinct on the posterior part (Fig. 14B). The extent and strength of the spination on the flexor and extensor margins of the P2–P5 meri and propodi is very variable, but some spines or granules are always present (Fig. 13G–J).

**Remarks.** The diagnostic characters of *F. granulosa*, new species, are the dorsal surface of the carapace, suborbital, subhepatic and pterygostomial surfaces, surfaces and margins of the thoracic sternum, chelipeds and ambulatory legs, and merus of the third maxilliped being covered with distinct sharp granules (Figs. 12A–D, 13A, B).

McLay (1993) identified six specimens from New Caledonia (one male and one female), the Loyalty Islands (one male and two females) and the Moluccas (one male); describing and figuring the taxon in detail. His diagnoses and figures leave no doubt that they are conspecific with *F. granulosa*. The G1 shape of the species is similar to that figured by McLay (1993: fig. 6g) and there is a distinct distal projection formed by the subdistal part of one of the folds (Fig. 19J, K). A re-examination of the structure showed that it is almost identical in form to the holotype of *F. granulosa* (Fig. 19J, K).

*Frodromia granulosa*, together with *F. caileani*, new species (see below), are distinct among known species in the genus in that there is a prominent spur-like tubercle on the inner posterior edge of the P3 coxa of the female (Fig. 14D, 17C). In other congeners, only a low tubercle is present (Figs. 6B, 9F).

All the records of "*F. atypica*" from the West Pacific by Richer de Forges et al. (2005), Ng & Richer de Forges (2007), and Poupin (2010) were based on McLay (1993), and as such should be referred to *F. granulosa*.

**Distribution.** Known from Vanuatu, New Caledonia and Loyalty Islands.

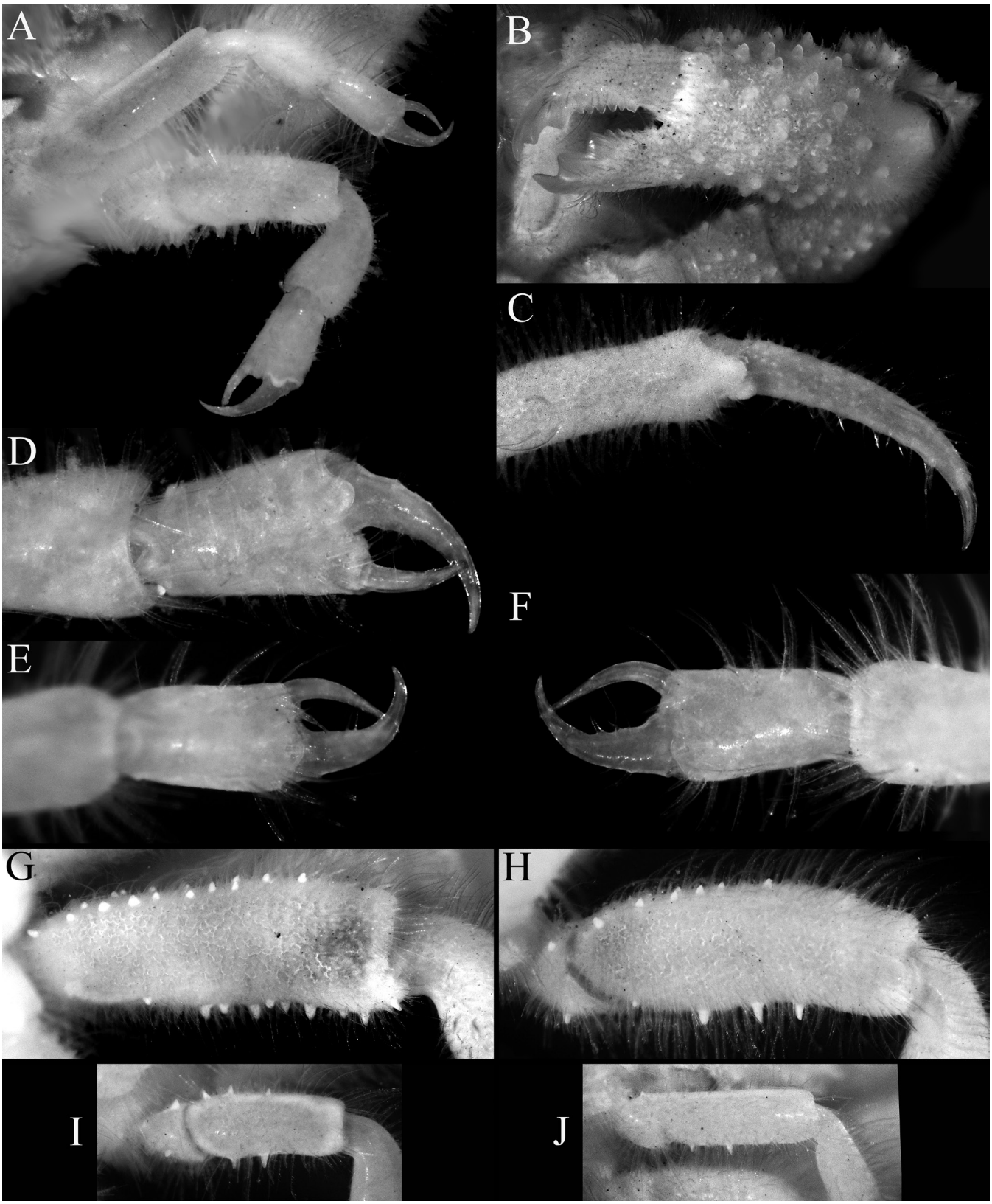


Fig. 13. *Frodromia granulosa*, new species, holotype male (6.5 × 7.1 mm) (ZRC 2024.0517), Vanuatu. A, right P4 and P5; B, left chela (partially denuded); C, right P3 propodus and dactylus; D, right P4 propodus and dactylus; E, right P5 propodus and dactylus; F, left P5 propodus and dactylus; G–J, P2–P5 merus, respectively. G–J photographed to same scale.

***Frodromia caileani*, new species**
(Figs. 15–17, 18G, 19M–P)

*Frodromia atypica* – McLay, 1993: 171 (in part) (not *Petalomera atypica* Sakai, 1936).

**Material examined.** Holotype: male (6.4 × 7.0 mm) (MNHN-IU-2021-9846a = MNHN-B26362), station DW49, Tanimbar Islands, Moluccas, Indonesia, 08°00′S 132°59′E, 206–210 m, coll. P. Bouchet, W. Kastoro & B. Métivier, KARUBAR cruise, 29 October 1991.

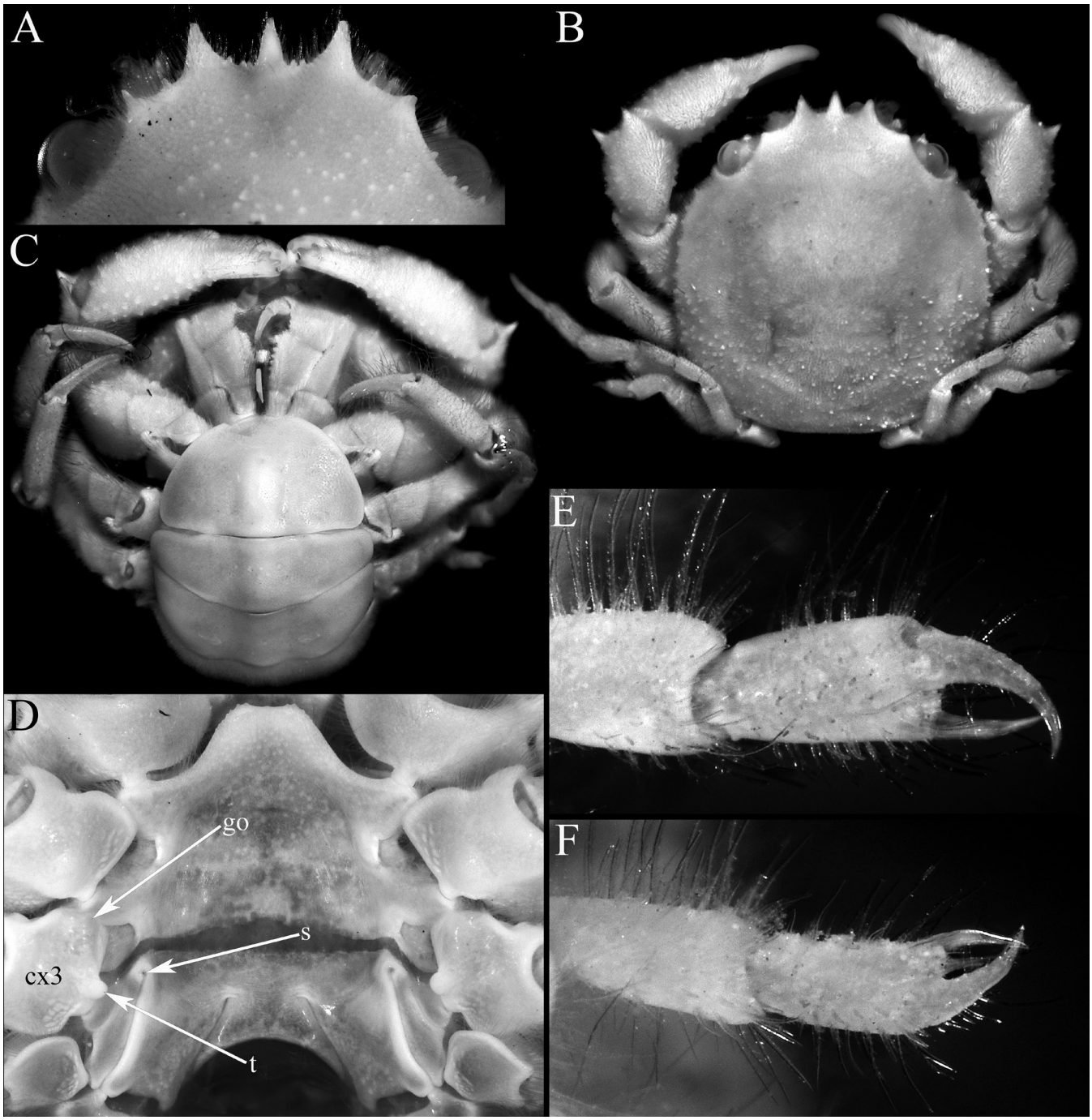


Fig. 14. *Frodromia granulosa*, new species. A, paratype male (6.0 × 7.1 mm) (MNHN -IU-2021-9850), New Caledonia; B–F, paratype female (10.0 × 10.9 mm) (MNHN -IU-2021-9851), New Caledonia. A, frontal margin and orbits; B, overall dorsal habitus; C, ventral surface of cephalothorax and pleon; D, sternopleonal cavity showing spermatheca; E, right P4 propodus and dactylus; F, right P5 propodus and dactylus. Abbreviations: cx3 = coxa of P3; go = female gonopore; s = aperture of spermatheca; t = tubercle on P3 coxa.

Paratypes: 1 male (5.6 × 4.8 mm) (ZRC 2024.0712, ex MNHN-IU-2021-9846b), 1 ovigerous female (6.6 × 6.9 mm) (MNHN-IU-2021-9846b = MNHN-B26362), same data as holotype; 1 male (4.8 × 5.6 mm) (MNHN-IU-2021-9852 = MNHN-826361), station DW44, Tanimbar Islands, Moluccas, Indonesia, 07°52′S 132°48′E, 291–295 m, coll. KARUBAR cruise, coll. P. Bouchet, W. Kastoro & B. Métivier, 29 October 1991.

**Diagnosis.** Colour in life not known. Dorsal surface of carapace and appendages with dense short setae that partially obscure surface and margins (Figs. 15A, 16A, 17A); dorsal surface of carapace smooth; lateral margin with numerous prominent sharp granules especially dense on posterolateral margin (Fig. 15, B); dorsal surface of carapace strongly convex in frontal view (Figs. 15A, 16A, 17A, 18G); posterior margin of epistome wide (Fig. 18G); rostral spine shorter or as long as pseudorostral spines (Figs. 15A, B, 16A, 17A); merus and ischium of third maxilliped smooth, unarmed (Fig. 15C); adult male chelipeds not elongate, merus and carpus with numerous sharp granules (Figs. 15A, 16A, 17A); male chela relatively short, fingers about half length of palm, outer

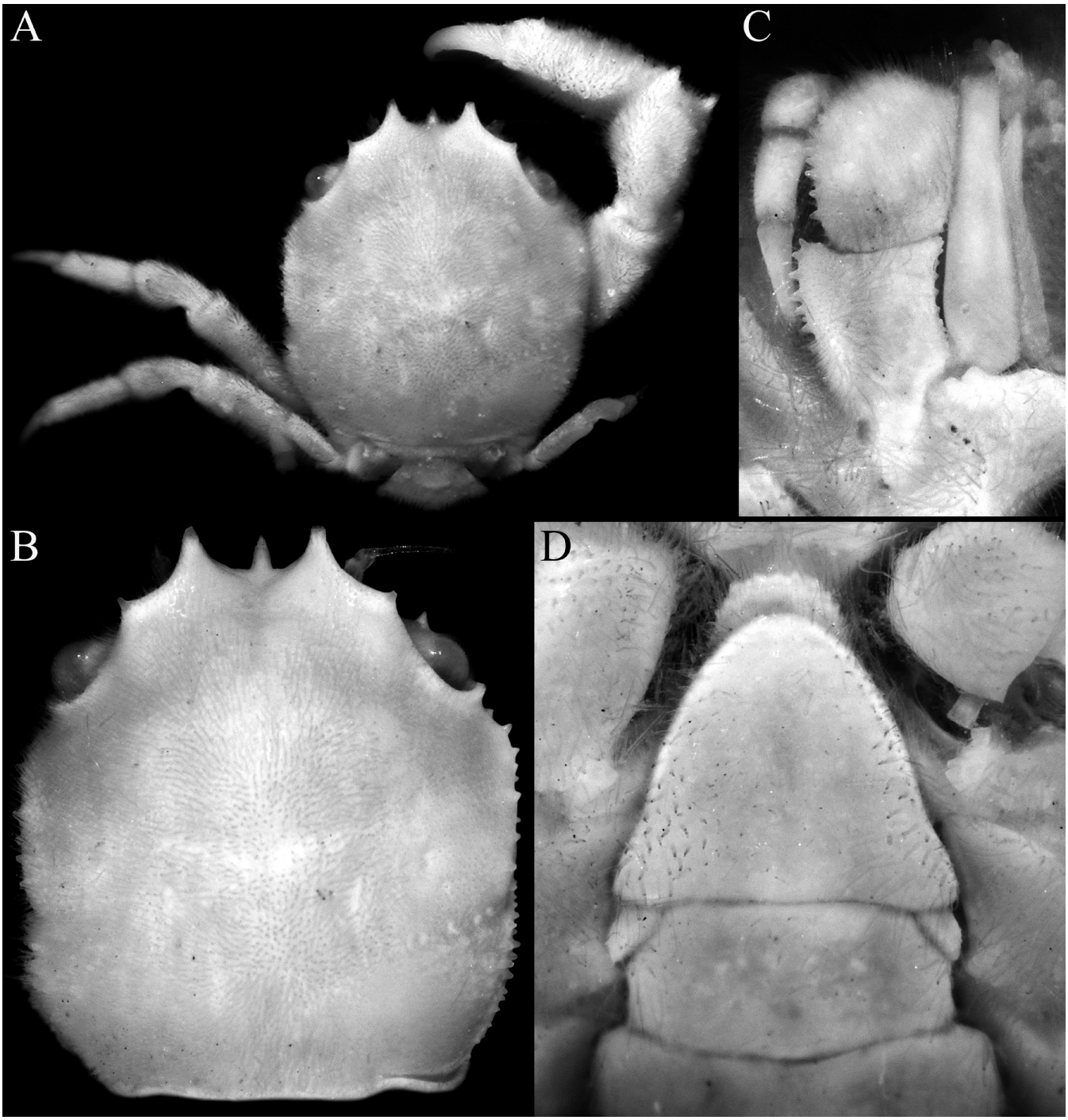


Fig. 15. *Frodromia caileani*, new species, holotype male (6.4 × 7.0 mm) (MNHN-IU-2021-9846a), Moluccas. A, overall dorsal habitus; B, dorsal view of carapace (right side denuded); C, left third maxillipeds; D, pleonal somites 5 and 6, and telson.

surface of palm covered with numerous sharp tubercles and granules (Figs. 16B, 18G); female chela similar to male but palm relatively shorter (Fig. 17A); P2 and P3 dactylus elongate (Fig. 16D); flexor margins of P2–P5 with sharp granules of varying extent (Fig. 16G–K); P5 dactylus gently curved (Fig. 16F); male anterior margin of sternopleonal cavity lined with low sharp granules (Fig. 15D); inner posterior edge of female P3 coxa with spur-like tubercle (Fig. 17C); male telson triangular, uropods directed almost posteriorly (Fig. 15D); female telson with narrow, elongate uropods (Fig. 17B); G1 distal part with broadly triangular projection (Fig. 19M–O); G2 with short exopod (Fig. 19P).

**Etymology.** The name honours an old friend, the recently departed Colin McLay, whose revision of the Dromiidae is a major landmark in the study of these animals. The name is derived from the Scottish version of his name, "Cailean" (for Colin) and alludes to his ancestral roots; he was always a proud Scotsman, and New Zealander.

**Colour.** Not known.

**Variation.** Like in *F. granulosa*, the strength of the spination on the flexor and extensor margins of the P2–P5 meri and propodi in *F. caileani* is quite variable, but some spines or sharp granules are invariably present (Fig. 16G–K).

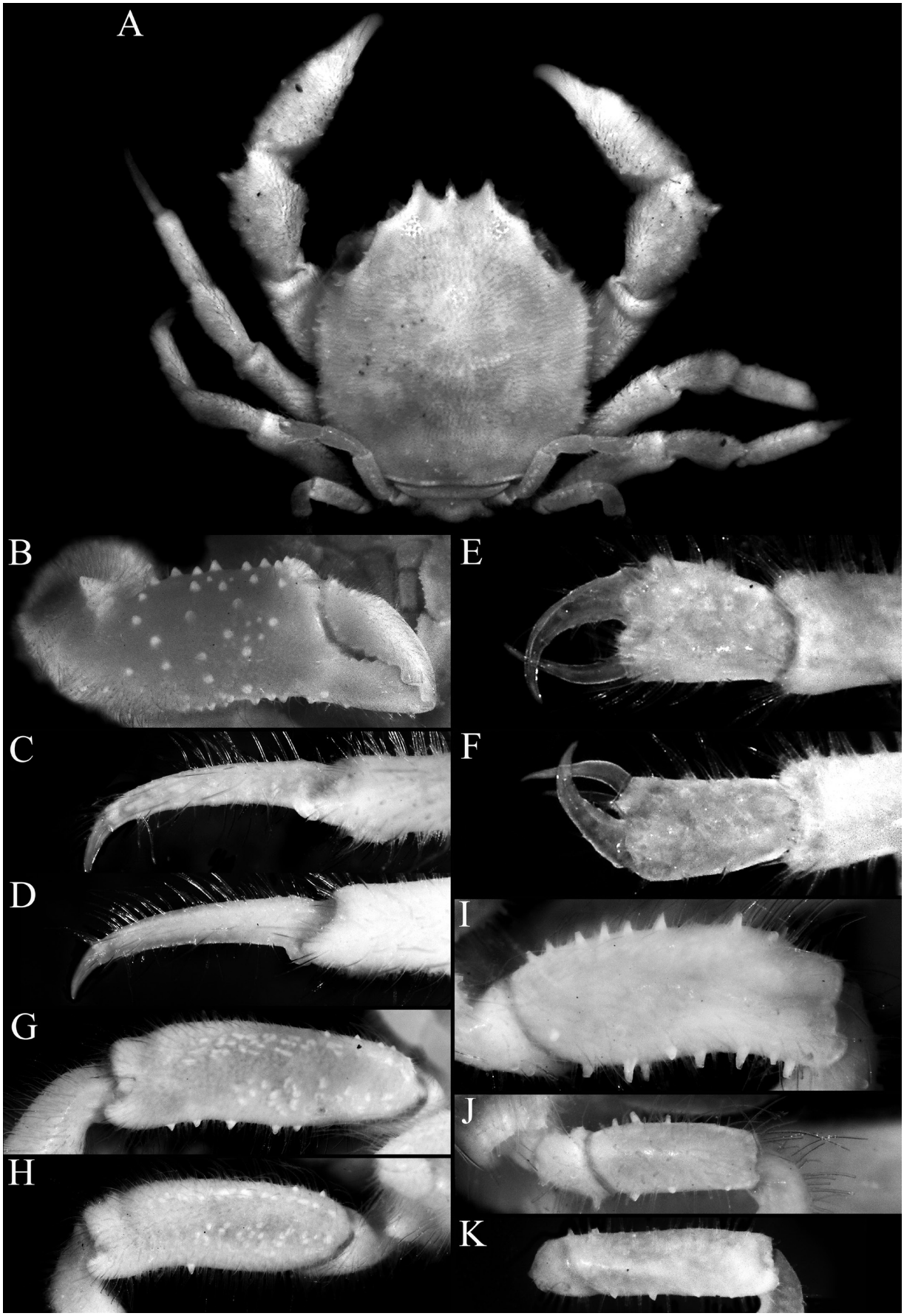


Fig. 16. *Frodromia caileani*, new species. A, paratype male (5.6 × 4.8 mm) (ZRC 2024.0712, ex MNHN-IU-2021-9846b), Moluccas; B–H, holotype male (6.4 × 7.0 mm) (MNHN-IU-2021-9846a), Moluccas; I–K, paratype male (4.8 × 5.6 mm) (MNHN-IU-2021-9852), Moluccas. A, overall dorsal habitus; B, D, right chela (denuded); C, left P2 propodus and dactylus; D, left P3 propodus and dactylus; E, left P4 carpus, propodus and dactylus; F, left P5 carpus, propodus and dactylus; G, left P2 merus; H, left P3 merus; I, right P3 merus; J, right P4 merus; K, right P5 merus.

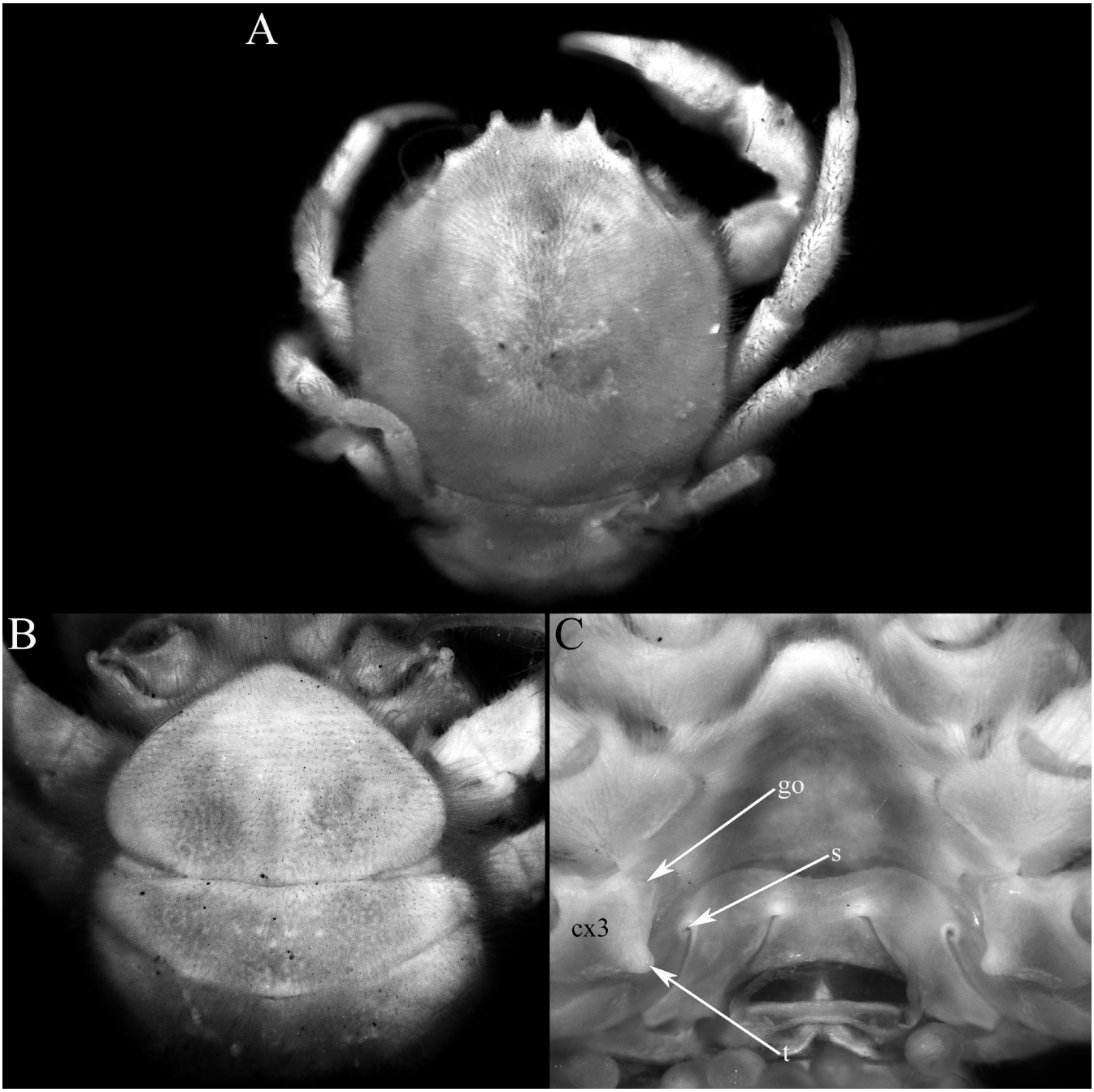


Fig. 17. *Frodromia caileani*, new species, paratype female (6.6 × 6.9 mm) (MNHN-IU-2021-9846c), Moluccas. A, overall dorsal habitus; B, pleon; C, sternopleonal cavity showing spermatheca. Abbreviations: cx3 = coxa of P3; go = female gonopore; s = aperture of spermatheca; t = tubercle on P3 coxa.

**Remarks.** Although McLay (1993: 171) treated the material from Tanimbar Islands and New Caledonia as conspecific, a close examination shows otherwise. The New Caledonian material is strongly granulated on the surfaces of the carapace, third maxilliped and ambulatory legs (Figs. 12A, B, D, 13A, 14A, B); in the Tanimbar specimens, the dorsal surface, third maxillipeds and ambulatory legs are smooth and unarmed (Figs. 15A–C, 16A, 17A). The only characters they share is the distinctive spur-like tubercle on the posterior edge of the female P3 coxa and the strongly granulated chela (Figs. 14D, 17C). Externally, *F. caileani*, new species, is most similar to *F. elegans*, new species, and *F. iners*, new species. *Frodromia caileani* can be separated from *F. elegans* by its relatively shorter male chelipeds (Figs. 15A, 16A) (versus male chelipeds elongate; Fig. 7A), the P2 and P3 dactyli are proportionately shorter (Fig. 16C, D) (versus with proportionately longer dactyli; Figs. 7A, 8C); the posterior edge of the female P3 coxa has a spur-like tubercle (Fig. 17C) (versus with a low tubercle; Fig. 9F); and the P5 dactylus is gently curved (Fig. 16F) (versus P5 dactylus bent at sharp angle; Fig. 8F). From *F. iners*, *F. caileani* can be distinguished by its rostral spine being shorter or subequal to the pseudorostral spines (Figs. 15A, B, 16A, 17A) (versus rostral spine distinctly longer than the pseudorostral spines; Fig. 10A, B); and the more prominently granulated lateral margins (Figs. 15B, 16A, 17A) (versus almost smooth with only scattered granules; Fig. 10A, B).


Fig. 18. Frontal view of cephalothorax of *Frodromia* species. A, *F. atypica* (Sakai, 1936), male (4.5 × 4.8 mm) (WMNH 16), Japan; B, *F. reticulata* (Sakai, 1974). A–F, male (4.3 × 5.4 mm) (WMNH 17), Japan; C, female (8.5 × 9.5 mm) (WMNH 17), Japan; D, *F. elegans*, new species, male (6.6 × 7.5 mm) (ZRC 2024.0144), Taiwan; E, *F. iners*, new species, holotype male (6.3 × 7.0 mm) (ZRC 2024.0518), Philippines (left side of carapace damaged); F, *F. granulosa*, new species, holotype male (6.5 × 7.1 mm) (ZRC 2024.0517), Vanuatu; G, *F. caileani*, new species, holotype male (6.4 × 7.0 mm) (MNHN-IU-2021-9846a), Moluccas.

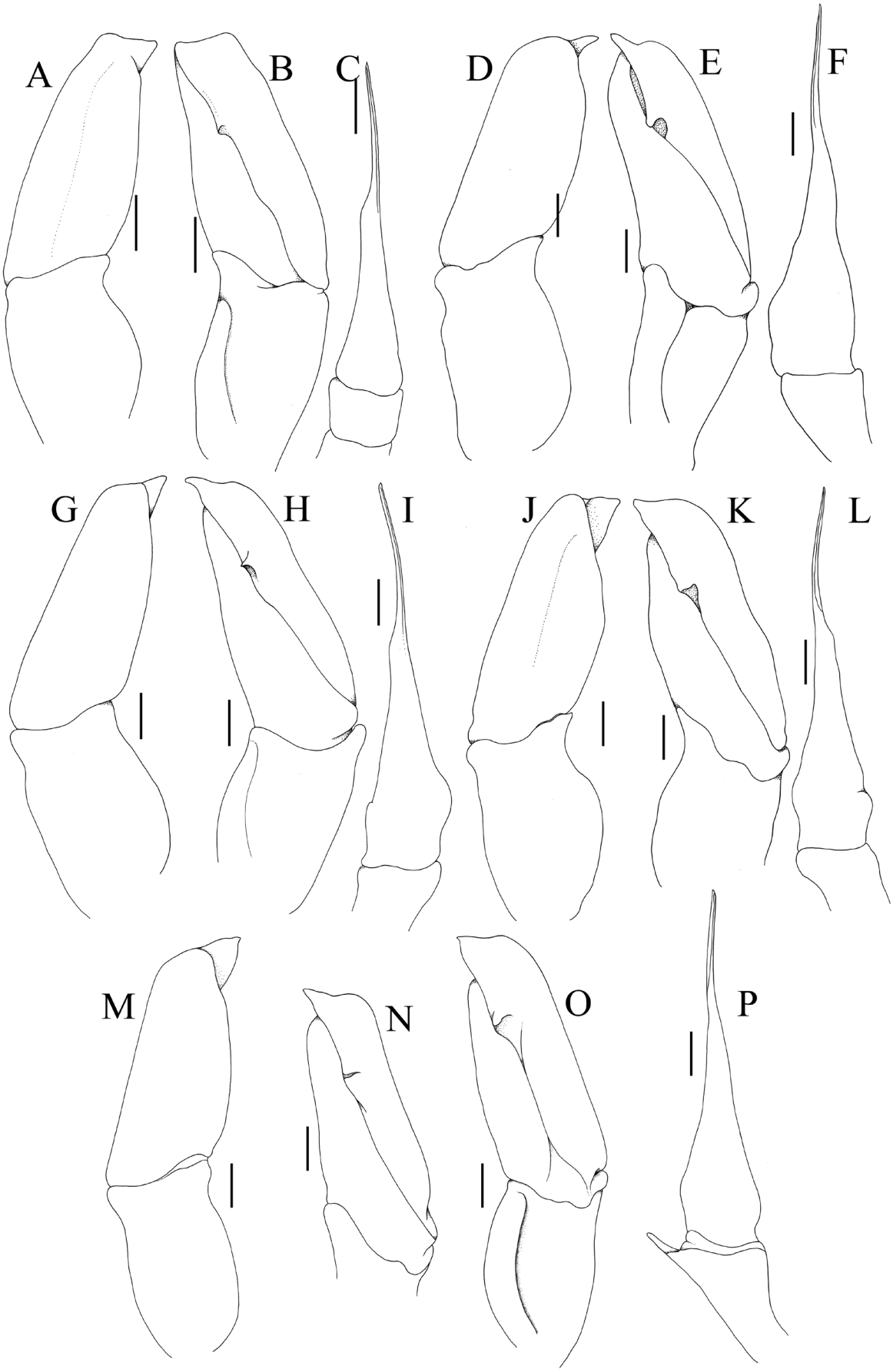


Fig. 19. Gonopods. A–C, *Frodromia reticulata* (Sakai, 1974), male (4.3 × 5.4 mm) (WMNH 17), Japan; D–F, *F. elegans*, new species, male (6.6 × 7.5 mm) (ZRC 2024.0144), Taiwan; G–I, *F. iners*, new species, holotype male (6.3 × 7.0 mm) (ZRC 2024.0518), Philippines; J–L, *F. granulosa*, new species, holotype male (6.5 × 7.1 mm) (ZRC 2024.0517), Vanuatu; M–P, *F. caileani*, new species, holotype male (6.4 × 7.0 mm) (MNHN-IU-2021-9846a), Moluccas. A, D, G, J, M, left G1 (subdorsal view); B, E, H, K, N, O, left G1 (subventral view); C, F, I, L, P, left G2. Scales: 0.2 mm.

**Distribution.** Known only from the Indonesian Moluccas.

## KEY TO SPECIES IN THE GENUS *FRODROMIA*

1. Lateral margin with 3 prominent, distinct teeth after external orbital angle (including hepatic tooth) (Fig. 2B); P2 and P3 dactylus short (Fig. 2A, D, E) ..... *F. atypica* (Sakai, 1936)
– Lateral margin without distinct teeth, with only sharp granules present (e.g., Fig. 7B); P2 and P3 dactylus long (e.g., Fig. 8C) ..... 2
2. Margins of P2–P5 merus and/or propodus always armed with sharp granules (e.g., Fig. 13G–J)..... 3
– Margins of P2–P5 merus and/or propodus smooth, unarmed (e.g., Figs. 7A, 8D) ..... 4
3. Dorsal surface of carapace covered with numerous small rounded and sharp granules (Fig. 12B); merus of third maxilliped covered with distinct sharp granules (Fig. 12D); base of G2 without exopod (Fig. 19L) ..... *F. granulosa*, new species
– Dorsal surface of carapace smooth, unarmed (Fig. 15B); merus of third maxilliped smooth (Fig. 15C); base of G2 with short exopod (Fig. 19P) ..... *F. caileani*, new species
4. Dorsal surface of carapace strongly inflated, prominently domed in frontal view; covered with dense mat-like pubescence that completely obscures surfaces and margins (e.g., Fig. 18B, C) ..... *F. reticulata* (Sakai, 1974)
– Dorsal surface of carapace convex but not prominently domed in frontal view; setae on carapace less dense. Surfaces and margins partially visible (e.g., Fig. 18D–F)..... 5
5. Rostral spine shorter or as long as pseudorostral spines (e.g., Fig. 7B); lateral margins with 7–20 small and large granules or small sharp granules (e.g., Fig. 7B); adult male chelipeds elongate (Fig. 7A); male P5 dactylus sharply bent medially at an angle (Fig. 8F)..... *F. elegans*, new species
– Rostral spine longer than pseudorostral spines (Fig. 10B); lateral margins with 5 or 6 very small granules (Fig. 10B); adult male chelipeds not elongate (Fig. 10A); male P5 dactylus curved (Fig. 11C) ..... *F. iners*, new species

## ACKNOWLEDGEMENTS

The author is grateful to Chan Tin-Yam who sent me his specimens from the South China Sea, which started this study. He also thanks Paula Martin-Lefreve and Laure Corbari (MNHN), and Tomoyuki Komai (CBM) for loan of material. The PANGLAO 2004 Expedition was organised by Philippe Bouchet (MNHN) with University of San Carlos (Cebu), National Fisheries Research and Development Institute (Manila), the Bureau of Fisheries and Aquatic Resources (Manila), NMCR, the National University of Singapore, and the Taiwan National Ocean University; and supported by TOTAL Foundation, the French Ministry of Foreign Affairs, and the ASEAN Regional Centre for Biodiversity and Conservation. The SANTO 2006 expedition to Vanuatu was organised by MNHN, Pro Natura International (PNI), and Institut de Recherche pour le Développement (IRD); with a permit issued to Philippe Bouchet (MNHN) and was part of the Census of Marine Life's Reefs programme funded by the Total Foundation and Sloan Foundation. He also thanks Hironori Komatsu (NSMT), Yusuke Yamana (WMNH), and Tohru Naruse (University of the Ryukyus) for their kind help in studying specimens. He is very grateful to Marcos Tavares and an anonymous reviewer for kindly reviewing the manuscript and their many helpful comments which have greatly improved the text.

## LITERATURE CITED

Davie PJF, Guinot D & Ng PKL (2015) Anatomy and functional morphology of Brachyura. In: Castro P, Davie PJF, Guinot D, Schram FR & von Vaupel Klein JC (eds.) Treatise on Zoology – Anatomy, Taxonomy, Biology. The Crustacea. Volume 9C–I. Decapoda: Brachyura (Part 1). Brill, Leiden, pp. 11–163.

De Haan HM (1833–1849) Crustacea. In: von Siebold PF (ed.) Fauna Japonica, sive Descriptio animalium, quae in itinere per Japoniam, jussu et auspiciis superiorum, qui summum in India Batavia imperium tenent, suscepto, annis 1823–1830 collegit, notis, observationibus a adumbrationibus illustravit. Apud Auctorem, Lugduni Batavorum, fasc. 1–8, I–xxi+vii–xvii+ix–xvi+1–243 pp., pls. 1–55, A–Q, circ., pl. 2.

Guinot D & Quenette G (2005) The spermatheca in podotreme crabs (Crustacea, Decapoda, Brachyura, Podotremata) and its phylogenetic implications. Zoosystema, 27(2): 267–342, figs. 1–29.

Guinot D & Tavares M (2003) A new subfamilial arrangement for the Dromiidae De Haan, 1833, with diagnoses and description of new genera and species (Crustacea, Decapoda, Brachyura). Zoosystema, 25(1): 43–129.

ICZN, International Commission on Zoological Nomenclature, 1999. International Code of Zoological Nomenclature. International Commission of Zoological Nomenclature. Fourth Edition. Adopted by the XXI General Assembly of the International Union of Biological Sciences. International Trust for Zoological Nomenclature, in association with the British Museum (Natural History), London, 338 pp.

Kimura T, Kimura S, Jimi N, Kuramochi T, Fujita T, Komai T, Yoshida R, Tanaka H, Okanishi M, Ogawa A, Itaru Kobayashi, Masafumi Kodama, Saito M, Kiyono Y, Katahira H, Nakano H, Yoshikawa A, Uyeno D, Tanaka M, Oya Y, Maekawa Y, Nakamura T, Okumura J & Tanaka K (2019) Benthic deep-sea fauna in south of the Kii Strait and the Sea of Kumano, Japan. Bulletin of the Graduate School of Bioresources Mie University, 45: 11–50.

Marumura M & Kosaka A (2003) Catalogue of the brachyuran and anomuran crabs donated by the late Mr. Seiji Nagai to the Wakayama Prefectural Museum of Natural History. Wakayama Prefectural Museum of Natural History, Kainan, pp. 1–73.

McLay CL (1993) Crustacea: Decapoda: The Sponge Crabs (Dromiidae) of New Caledonia and the Philippines with a review of the genera. In: Crosnier A (ed.) Résultats des campagnes MUSORSTOM 10. Mémoires du Muséum national d'Histoire naturelle, 156: 111–251.

McLay CL & Ng PKL (2007) Revision of the Indo-West Pacific sponge crabs of the genus *Petalomera* Stimpson, 1858 (Decapoda: Brachyura: Dromiidae). Raffles Bulletin of Zoology, 55(1): 107–120.

Muraoka K (1998) Catalogue of the brachyuran and anomuran crabs donated by Prof. Dr. Tune Sakai to the Kanagawa Prefectural Museum. Catalogue of the collection in the Kanagawa Prefectural Museum of Natural History, Odawara, No. 11, 1–67 pp, 16 pls.

Nagai S (1989) Some remarkable crabs of Wakayama Prefecture I. Nankiseibutu: The Nanki Biological Society, 31(1): 39–44.

Nagai S (1993) Some remarkable crabs of Wakayama Prefecture II. Nankiseibutu: The Nanki Biological Society, 35(1): 49–53.

Nagai S (1994) Some remarkable crabs of Wakayama Prefecture II. Nankiseibutu: The Nanki Biological Society, 36(1): 49–53.

Ng PKL, Guinot D & Davie PJF (2008) Systema Brachyurorum: Part I. An annotated checklist of extant brachyuran crabs of the world. Raffles Bulletin of Zoology, Supplement 17: 1–286.

Ng PKL & Naruse T (2007) On two species of deep sea homoloid crabs of the genus *Dicranodromia* (Crustacea: Decapoda: Brachyura: Homolodromiidae) from the Philippines, with description of a new species. Raffles Bulletin of Zoology, Supplement 16: 47–53.

Ng PKL & Richer de Forges B (2007) The Brachyura of New Caledonia. In: Payri CE & Richer de Forges B (eds.) Compendium of marine species from New Caledonia. Documents Scientifiques et Techniques, Volume Spécial, deuxième édition Institut de recherché pour le développement, Noumea, pp. 315–331.

Ng PKL & Yang C-H (2021) On two new species of deep-sea carrier crabs (Crustacea: Brachyura: Homolodromiidae: *Dicranodromia*) from Taiwan and the Philippines, with notes on other Indo-West Pacific species. Zookeys, 1071: 129–165.

Poupin J (2010) Biodiversité de l'Indo-Pacifique tropical français 2514 espèces de Crustacés Décapodes et Stomatopodes. IRENav, Institut de Recherche de l'Ecole Navale, 76 pp.

Pratiwi R & Elfidasari D (2020) The crustaceans fauna from Natuna Islands (Indonesia) using three different sampling methods. Biodiversitas, 21(3): 1215–1226.

Richer De Forges B, Hoffschir C, Chauvin C & Berthault C (2005) Inventaire des espèces de profondeur de Nouvelle-Calédonie. Census of deep-sea species of New Caledonia. Documents Scientifiques et Techniques, 116 (volume special), Noumea, pp. 1–103.

Sakai T (1936) Studies on the crabs of Japan. I. Dromiacea. Scientific Reports of the Tokyo Bunrika Daigaku, Section B, 3, supplement 1: 1–66, figs. 1–13, pls. 1–9.

Sakai T (1974) Notes from the Carcinological Fauna of Japan (V). Researches in Crustacea, 6: 86–95 (English text), 96–102 (Japanese text), 1 frontispiece plate.

Sakai T (1976) Crabs of Japan and Adjacent Seas. Tokyo, Kodansha Ltd., pp. i–xxix+1–773 (English text), figs. 1–379: pp. 1–461 (Japanese text): 1–16, pls. 1–251.

Karasawa H, Schweitzer CE & Feldmann RM (2011) Phylogenetic analysis and revised classification of podotrematous Brachyura (Decapoda) including extinct and extant families. Journal of Crustacean Biology, 31(3): 523–565.

Schweitzer CE & Feldmann RM (2010) The Sphaerodromiidae (Brachyura: Dromiacea: Dromioidea) in the fossil record. Journal of Crustacean Biology, 30: 417–429.

Schweitzer CE, Feldmann RM & Karasawa H (2012) Treatise Online no. 51: Part R, Revised, Volume 1, Chapter 8M: Systematic descriptions: Infraorder Brachyura, Section Dromiacea. Treatise Online. KU Paleontological Institute, The University of Kansas, pp. 1–43. https://doi.org/10.17161/to.v0i0.4336.

Števčić Z (2005) The reclassification of Brachyuran Crabs (Crustacea: Decapoda: Brachyura). Natura Croatica (Fauna Croatica), 14(1): 1–159.

Stimpson W (1858) Crustacea Anomura. Prodromus descriptionis animalium evertebratorum, quae in Expeditione ad Oceanum Pacificum Septentrionalem, a Republica Federata missa, Cadwaladaro Ringgold et Johanne Rodgers Ducibus, observavit et descripsit. Pars VII. Proceedings of the Academy of Natural Sciences of Philadelphia, 10(7): 225–252.

Takeda M (1993) Catalogue of crab specimens (Crustacea: Decapoda: Brachyura). Part 1. National Science Museum, Tokyo, 93 pp.

Watabe H (2007) Metabiology of decapods: construction of axiomatic system of the autopoiesis theory. Ocean Policy Studies, 5: 31–125.