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Rediscovering the unusual *Cancellus makrothrix* Stebbing, 1924 (Crustacea: Decapoda: Diogenidae) in the "Great African Seaforest"

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Abstract

The rare diogenid hermit crab *Cancellus makrothrix* Stebbing, 1924, previously known from only a few specimens collected a century ago from Algoa Bay, South Africa, has been found to be common in the kelp forest known as the "Great African Seaforest", and rocky reefs, of False Bay, South Africa. This poorly known species, considered "aberrant" by some carcinologists, is one of 17 known in the genus *Cancellus* H. Milne Edwards, 1836, and the only of the genus known to occur in the coast of southern Africa. *Cancelllus makrothrix* lives in gastropod shells, whereas all other congenerics live in a variety of petricolous dwellings that are either excavated or worn away into cylindrical cavities. The newly collected material of *C. makrothrix* in South Africa, together with the study of historical museum specimens has made possible the detailed redescription and taxonomic discussion of this species presented herein, using full illustrations, photographs, and microCT scans. For future reference, the molecular CO1 genetic barcode is reported. A lectotype is selected from Stebbing's original syntype material found to consist of two specimens: a female of which only several appendages remain, in the Natural History Museum, London, and a male, illustrated in the original description, in the Iziko South African Museum, Cape Town. Taxonomic remarks, comments on biological oddities, brief *in situ* and laboratory observations of live specimens, and a map summarizing the world distribution of species of *Cancellus*, are included.

Key words: *Cancellus*, South Africa, Hercules hermit crab, kelp forest, Indian Ocean

Introduction

Species of the diogenid genus *Cancellus* H. Milne Edwards, 1836, are specialized hermit crabs that typically live in cylindrical cavities in a variety of substrates such as calcareous rocks, pumice, granular stones, dead corals, serpulid worm tubes, calcareous algae, wood, or siliceous sponges (Mayo 1973; McLaughlin 2008; Forest & McLaughlin 2000; McLaughlin 2015). They show herculean strength in carrying or dragging their often-heavy abodes. Morphologically they are characterized by: symmetrical anterior appendages (chelipeds and ambulatory legs) that together form a tight operculum to close their home opening; a bulbous pleon; a calcified sixth pleonal tergite; symmetrical uropods and telson; lacking pleopods in males, and having unpaired pleopods 2–5 in females, which can be present on either side. Globally, 17 extant species are known (Poore & Ahyong 2023; WoRMS Editorial Board 2024), most of which have been rarely collected and thus remain taxonomically and biologically poorly known.

Along the South African coast only one species of *Cancellus* is known to occur, *C. makrothrix* Stebbing, 1924, a taxon vaguely and deficiently described a century ago presumably based on a single specimen. Barnard (1950) later examined a few more specimens believed to represent *C. makrothrix* housed in the collections of the former South African Museum in Cape Town, South Africa (now the Iziko South African Museum), and provided details of the morphology and biology of this species. Except for the listing of *C. makrothrix* by Day *et al*. (1970) in their study

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of the benthic fauna from False Bay, no other specimens of this species have been reported since the publication of Barnard's (1950) catalogue of South African crustaceans. Because the morphology of this species deviates in some respects from other congenerics, previous carcinologists have considered *C. makrothrix* to be "aberrant" or intermediate between typical pagurids and other species of *Cancellus* (Barnard 1950; Mayo 1973; Forest & McLaughlin 2000). In addition, *C. makrothrix* is the only species in the genus that uses spirally coiled gastropod shells for shelter, and as result is the only that exhibits a coiled rather than straight pleon. Despite these interesting aspects, biological knowledge about *C. makrothrix* has remained scant, and its taxonomy somewhat confusing.

Recent field work by one of us (JL), including SCUBA, has revealed that *C. makrothrix* is a common inhabitant of the southern part of the kelp forest colloquially known as the "Great African Seaforest", and associated rocky reefs and sandy bottoms of False Bay, South Africa. Based on new material collected of this species in habitats of False Bay, *in situ* and laboratory observations, together with the discovery and examination of Stebbing's (1924) original syntypes and Barnard's (1950) historical specimens deposited in the Iziko South African Museum, Cape Town, and the Natural History Museum, London, we can now provide a modern taxonomic redescription of *C. makrothrix*, including illustrations, microCT scans, and the molecular CO1 genetic barcode. In this study we discuss inconsistencies and defects in Stebbing's (1924) original description, and provide information on the morphology, distribution, unusual behavior, and brooding biology of this interesting species.

Materials and methods

Local diving knowledge was used during field work by JL to locate and collect new specimens of *Cancellus makrothrix* in the South African kelp forest and other habitats. Shallow as well as SCUBA diving depths were explored. Specimens used for this study remain deposited in Iziko South African Museum, Cape Town, South Africa (SAMC), the National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA (USNM), and in the Natural History Museum, London, UK (NHM). Morphological terminology is primarily according to that used by Forest & McLaughlin (2000). The ambulatory legs are equivalent to pereopods 2 and 3. Cephalothoracic somites and their sternites are numbered I–XIII (five cephalic and eight thoracic). The term "intersex" is applied to individuals having both male and females gonopores. Measurements indicated for specimens are of cephalothoracic shield length (sl) measured to the nearest 0.1 mm, from the tip of the rostrum to the midpoint of the posterior margin of the shield. The genetic CO1 barcode sequence is available on the Barcode of Life Data System (Bold) and GenBank. The barcode gene sequence was obtained by standard protocols as described in Landschoff & Gouws (2018). Months are abbreviated by using the first three letters; other abbreviations: ovig., ovigerous; P, pereopods 1–5; Stn., station.

Results

Taxonomy

Family Diogenidae Ortmann, 1892

Cancellus makrothrix Stebbing, 1924

(Figs. 1–7)

Cancellus makrothrix Stebbing, 1924: 240, pl. 3, figs. as, car, m, mx1, mx2, mxp1, mxp2, mxp3, prp1, prp3, prp4, prp5, T (Crustacea pl. 118) (type locality: Algoa Bay, South Africa); Barnard 1950: 447, fig. 82; Day *et al*. 1970: 56; Kensley 1974: 65; Kensley 1981: 32; Morgan 1987: 536; Forest & McLaughlin 2000: 88.

Cancellus macrothrix. — Gordan 1956: 305; Mayo 1973: 3, 11 (key), tbl. 1, fig. 22c, d; McLaughlin *et al*. 2010: 19; Wittmann & Griffiths 2017: 15; Landschoff & Gouws 2018: 783 (tree); Landschoff *et al*. 2018a: 2, fig. 1 E, F. [Misspelling]

Type material (see Taxonomic remarks). Lectotype, herein selected**:** male 16.5 mm, Bird Island Passage, Algoa Bay, SS *Pieter Faure*, 18 m, 33°51'00.0"S 26°16'58.8"E, SAMC A1541; Paratype: female, body missing except for right antennule, left cheliped, left pereopods 3–5, and right maxillipeds 1–3, same station data as lectotype, NHM 1928.12.286 (Stebbing Collection) .

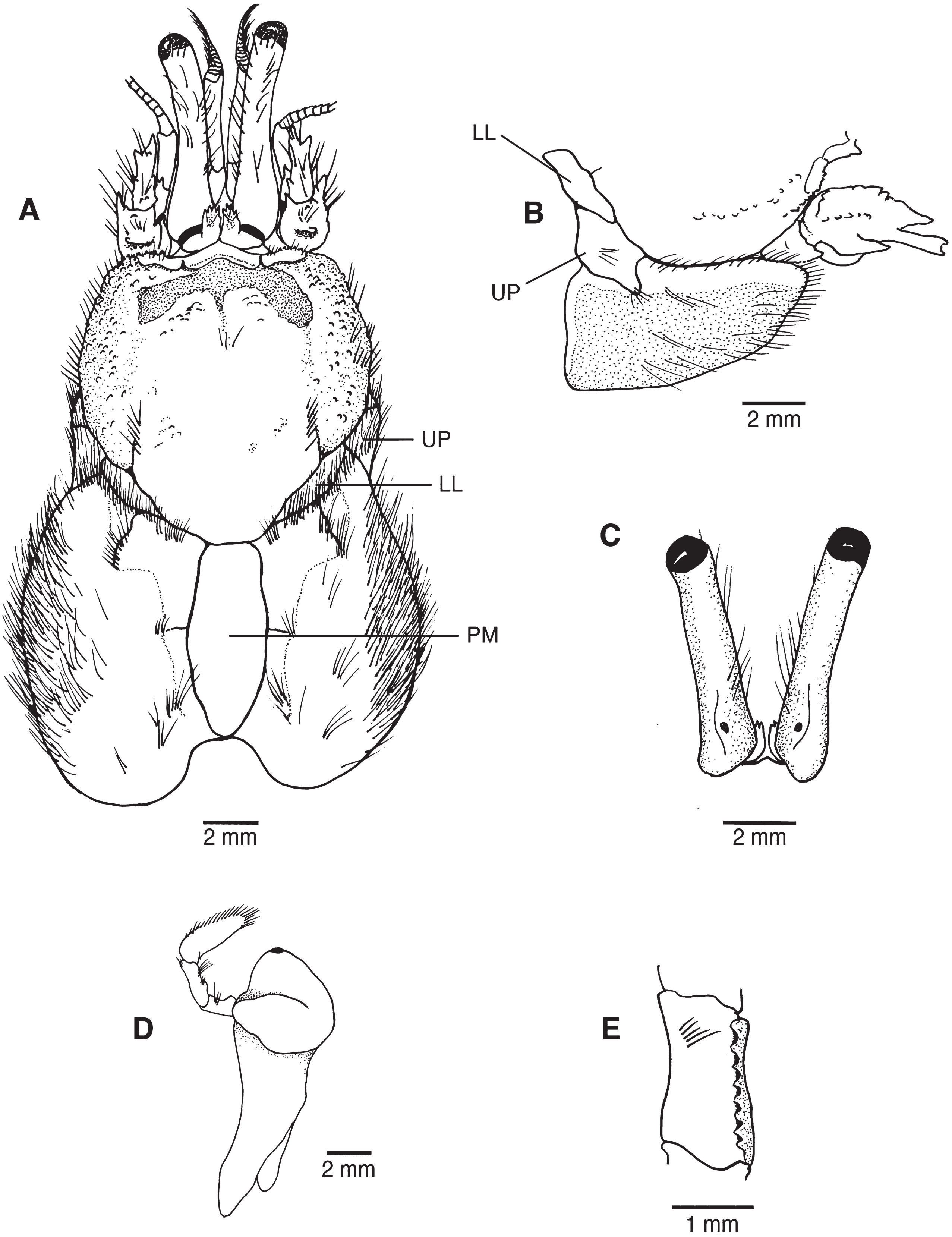

FIGURE 1. *Cancellus makrothrix* Stebbing, 1924, male (intersex), 9.5 mm, USNM 1292096: A, shield, cephalic appendages and posterior carapace, dorsal view; B, right side of cephalic shield, lateral lobe, unnamed plate, branchiostegite, and part of antennal peduncle, lateral view; C, ocular peduncles with basal 'pores', ventral view; D, mandible, internal view; E, ischium of third maxilliped with crista dentata, internal view. Abbreviations: LL, lateral lobe; PM, posteromedian plate; UP, unnamed plate.

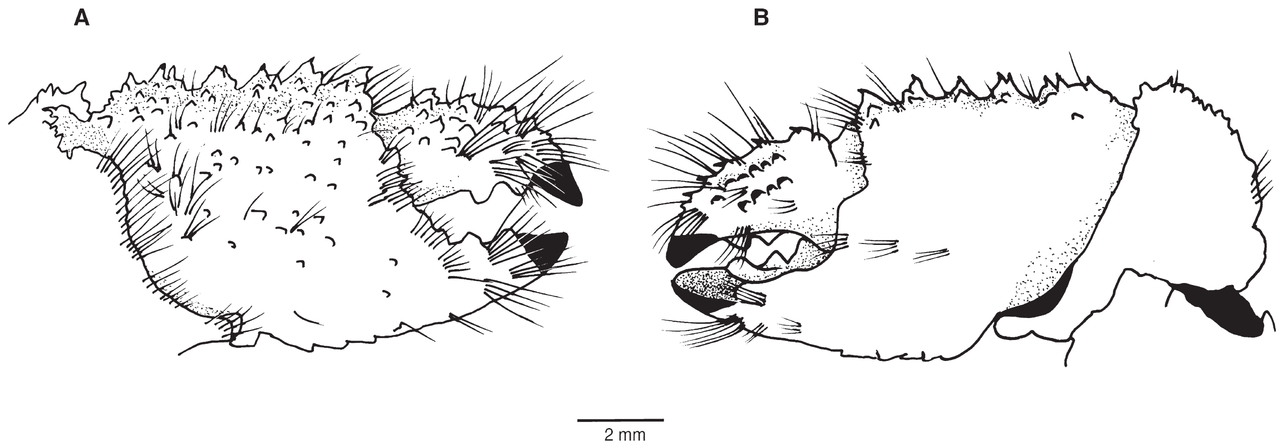

FIGURE 2. *Cancellus makrothrix* Stebbing, 1924, male (intersex), 9.5 mm, USNM 1292096, right chela: A, lateral view; B, mesial view.

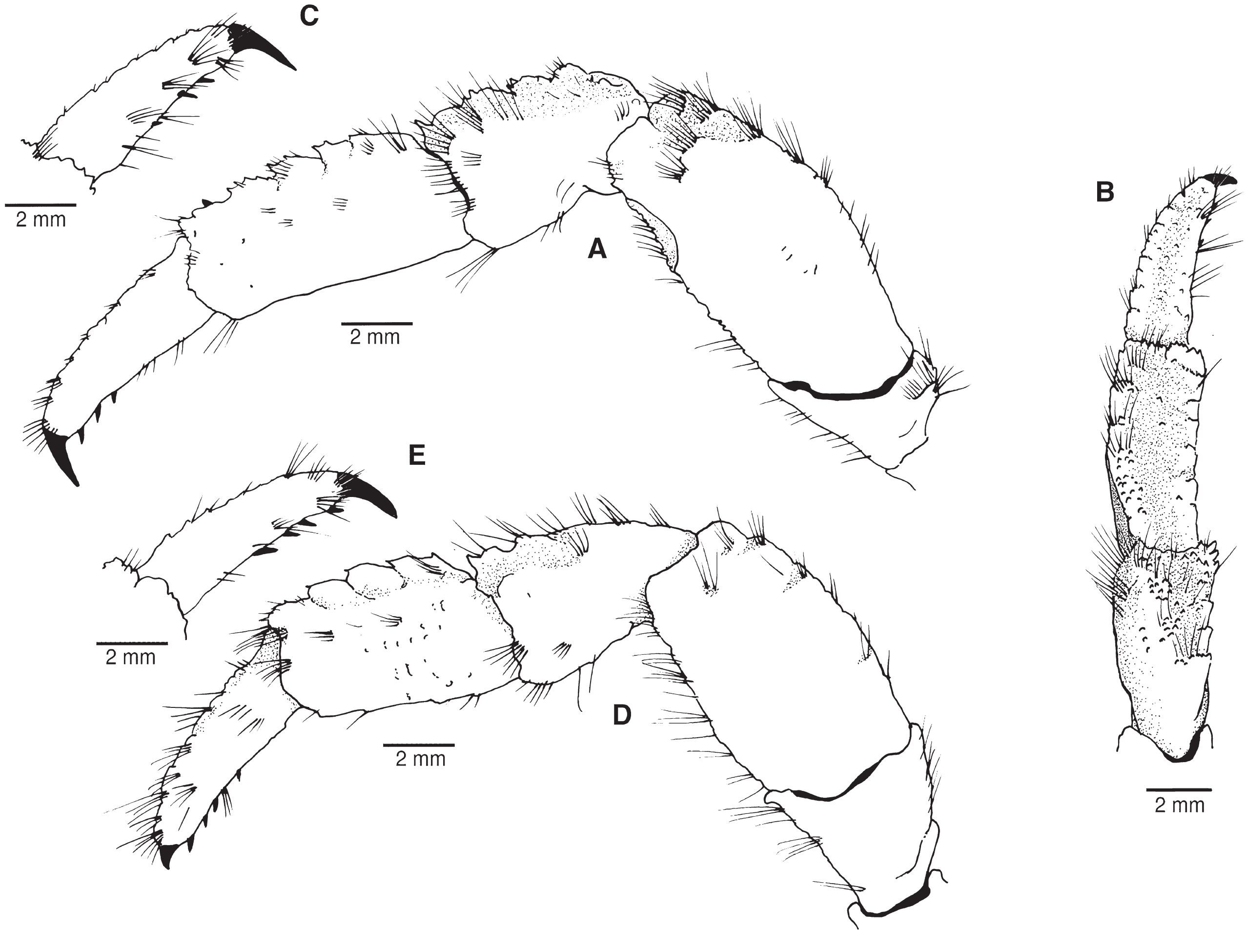

FIGURE 3. *Cancellus makrothrix* Stebbing, 1924, male (intersex), 9.5 mm, USNM 1292096: A, pereopod 2, lateral view; B, same, dorsomesial view; C, dactyl of same, mesial view; D, pereopod 3, lateral view; E, dactyl of same, mesial view.

Other material examined. Historical material. 1 female 8.1 mm, Beacon East of East London, SS *Pieter Faure*, dredge, no depth, Stn. No. 13533, "NW 0.5 W 2 min" (adapted to: 33°00'57.6"S, 27°59'06.0"E), 15 Aug 1901, SAMC A1542; 1 "brooding" female 9.5 mm (with 8 juveniles in housing), Cape Morgan, SS *Pieter Faure*, dredge, 31 m, Stn. No. 13495, "W 0.5 S, 4 min" (adapted to: 33°00'56"S, 27°59'06"E), 15 Aug 1901, SAMC

A3265; 1 male 5.5 mm, False Bay, UCT Ecological Survey, dredge, 29 m, Sta. No. FAL 4689, 34°06'S, 18°42'E, 25 Oct 1961, SAMC–A19626 (in poor condition; dried, rehydrated back in alcohol).

New material. All from False Bay, South Africa, coll. J. Landschoff: 1 male 9.0 mm (intersex, with unpaired left female gonopore), in buccinid gastropod shell, Roman Rocks (Simons Town), SCUBA, 20 m, 34°10'40.8"S, 18°27'28.8"E, 13 May 2015, SAMC A066204; 1 male 12.2 mm, Muizenberg Beach (wash-up), 34°06'21.6"S 18°28'40.8"E, 9 June 2015, SAMC A066216; 1 ovig. female 10.4 mm (with 46 eggs, ~2.3 mm mean diameter), Simons Town (Long Beach), SCUBA, 5 m, 34°11'09.6"S 18°25'37.2"E, 6 Sep 2016, USNM 1292095; 1 male (intersex, with paired female gonopores) 9.5 mm, Millers Point, freediving, 8 m, 34°13'51.6"S 18°28'40.8"E, 22 Mar 2016, in *Argobuccinum pustulosum*, USNM 1292096; 1 male 8 mm, molt of same specimen as USNM 1292096 (kept in tank), SAMC A066602; 1 male (molt) 14.3 mm, off Millers Point, SCUBA, 25 m, 34°13'40.8"S 18°29'13.2"E, 29 Sep 2017, SAMC A066603. 1 female 10.8 mm, south of A-Frame, freediving, 5 m, 34°12'40.9"S 18°27'49.2"E, 21 Mar 2023, SAMC A096852; 1 male 12.1 mm, Millers Point towards Castle Rock, freediving, 8 m, 34°14'01.2"S 18°28'37.3"E, 22 Mar 2023, SAMC A A096853.

Redescription. Cephalothoracic shield (Fig. 1A) width subequal to shield length. Rostrum obtusely triangular, terminating in small spine, distinctly overreaching lateral projections. Frontal rim consisting of flattened w-shaped ridge, weakly interrupted by fissure at each inferior angle of W-shaped ridge. Anterior margin between rostrum and lateral projections concave; lateral projections broadly rounded, armed with row of small spines and short setae; anterolateral margins sloping; lateral margins broadly rounded, moderately setose; posterior margin rounded, together with cervical grooves forming broad triangle. Dorsal surface slightly convex, uneven; with scattered tufts of setae, low rugae, and numerous small tubercles or blunt spines on each side near lateral margins; anteromedian surface with broad m-shaped flat depression directly behind rostrum and lateral projections; linea-d weakly marked. Branchiostegites (Fig. 1B) each with anterior margin rounded, setose; membranous except for well calcified dorsal portion. Presence of unnamed plate (Fig. 1A–B) between calcified dorsal portion of branchiostegite and adjacent carapace lateral lobe. Carapace lateral lobes (Fig. 1A–B) distinct, well calcified. Posterior carapace (Fig. 1A) with posteromedian plate calcified, sparsely setose; posterolateral plates dorsally calcified near posteromedian plate, with remaining portion membranous, densely setose.

Ocular peduncle (including cornea) approximately 0.68–0.84 length of cephalothoracic shield, slender, slightly curved outward, slightly broadened proximally; with moderately long setae dorsally; basal surface of ventromesial face with distinct pore (function unknown). Cornea subspherical, not dilated (subequal in diameter to width of adjacent peduncle). Ocular acicles subtriangular, mesial margins adjacent, dorsally with few setae; each terminating in strong multifid projection with 2–5 distal spines.

Antennular peduncle reaching to proximal margin of cornea when fully extended; ultimate and penultimate segments glabrous, ultimate twice as long as penultimate; basal segment with ventrodistal angle blunt, and laterodistal lobe armed distally with minute spines.

Antennal peduncle with fifth segment extending slightly beyond mid-length of ocular peduncle. Fifth segment approximately twice as long as fourth segment, unarmed except for dorsodistal setae. Fourth segment with bifid dorsodistal spine. Third segment with strong ventrodistal spine. Second segment with bristle-like setae, dorsolateral distal angle produced into strong spine-like process, dorsomesial angle with strong spine. First (basal) segment lateral face with small blunt distal spine; ventromesial angle rounded, with bristle-like setae. Acicle variably extending to approximately mid-length of ocular peduncle to slightly beyond ocular peduncle, terminating in strong bifid spine, usually with 1 dorsomesial spine proximally (at least on one side). Flagellum approximately as long as cephalothoracic shield, reaching to approximately distal margin of cheliped palm; articles bearing short setae less than 1 flagellar article in length.

Maxilliped 3 endopod (Fig. 1D) ischium with well-developed, coarsely toothed crista dentata, appearing serrate, lacking accessory tooth; basis armed with weak blunt spine on mesial angle proximally. Mandible with robust calcareous molar process.

Chelipeds (Figs. 2, 5A–F, 6) symmetrical, similar in strength, armature and setation. Carpi and chelae, together with merus and dactyl of second pereopod forming operculum sealing housing when retracted; chelae positioned more or less at right angle with carpi when retracted; opercular faces of chelipeds and second pereopods forming rounded surface, with face of each second pereopod slightly flaring laterally. Fingers stout, each terminating in distinct, darkly pigmented corneous spoon-like claw; cutting edges each with 2 large, subequal blunt calcareous teeth. Dactyl gaping widely from fixed finger, dorsal (opposable) margin with row of subacute tubercles terminating in corneous tips; outer (opercular face) face with blunt tubercles, and tufts of long bristle-like setae; mesial face with 2 longitudinal rows of corneous-tipped tubercles, and scattered tufts of short setae. Fixed finger with lateral and mesial faces unarmed except for few tufts of bristle-like setae. Palm with dorsal (opposable) margin armed with strong subconiform calcareous simple or bifid spines terminating in darkly pigmented corneous tip; outer (opercular) face with scattered small tubercles and tufts of short bristle-like setae more numerous on upper half; mesial face mostly smooth, with scattered tufts of short setae; ventral margin with few low tubercles. Carpus short; dorsal (opposable) margin crest-like, with distal angle produced into lobe armed with small spines; outer (opercular) face unarmed except for scattered setae and small spines on distal margin, with distinct longitudinal groove on upper half. Merus subtriangular in cross-section, unarmed except for setose dorsal margin and minutely spinulose distolateral margin; lateral and mesial surfaces mostly smooth; lateral face with subdistal transverse groove extending nearly to ventral margin.

Pereopod 2 (Fig. 3A–C) with opercular face formed by mesial faces of dactyl, merus, dorsal face of carpus, and dorsodistal portion of merus; opercular face densely covered with bristle-like setae. Dactyl approximately as long as merus, terminating in sharp corneous claw curving ventromesially; dorsal margin uneven, with low setose rugae; lateral face smooth, naked; mesial (opercular) face with few tufts of setae; lateral face more or less smooth, with distal tuft of setae; ventromesial margin armed with 4 small corneous spines on distal half. Propodus with dorsal margin consisting of distinct, multidenticulate setose tubercles; lateral and mesial faces mostly smooth, with scattered setae; ventral margin unarmed, at most with few setae. Carpus thick, heavy, length about 1.5 times height; operculate (dorsal) face more or less flat, delimited by 2 distally diverging rows, one lateral and one mesial, of multispinose setose tubercles, distal tubercle of mesial row with distinct terminal spine; lateral and mesial faces mostly smooth, with scattered setae and tufts of setae; ventral margin unarmed. Merus dorsal margin with short setae on proximal two-thirds; opercular (dorsal) surface more or less flat, delimited my mesial and lateral ridges of multidenticulate setose tubercles; lateral and mesial faces mostly smooth, with scattered setae or bristle-like tufts of setae; ventral margin with row of minute spines. Ischium unarmed except for setae on dorsal and ventral margins.

Pereopod 3 (Fig. 3D–E) similar to pereopod 2 except for weakly marked opercular surface on segments.

Pereopod 4 (Fig. 4C) semichelate, segments robust. Dactylus subcylindrical, opposed to dorsodistal margin of propodal rasp, with ventrolateral row of 4 small blunt corneous spines, terminating in subacute corneous tip. Propodus with well-developed rasp oval in shape and covering entire distal half of segment; rasp consisting of densely packed ovate corneous scales.

Pereopod 5 (Fig. 4D) chelate; fingers with opposable surfaces spoon-like, cutting edges consisting of minute, fused corneous spinules. Dactyl slightly shorter than propodus; dorsal margin setose, with 1–3 dorsolateral rows of small ovate scales proximally. Propodus with well-developed rasp on dorsal face extending posteriorly to near margin with carpus; with mesial fringe of long setae. Coxae with ventral face convex, smooth, appearing semiglobular.

Thoracic sternum with anterior lobe of sternite XI (of third pereopods; Fig. 4A) weakly elevated, broadly rounded.

Pleon robustly subcylindrical, distinctly to weakly coiled; soft integument overall covered dorsally by fine dense pubescence (Figs. 5A–B, D, G–H), surface of left side with longitudinal fold extending full length of soft integument just below level of pleopods; dorsally with 4 distinct, separated, translucent, lightly sclerotized transverse tergites. Sixth pleonal tergite (Figs. 4E–F, 5G–H) strongly calcified, subdivided by transverse furrow into subsemicircular anterior portion and subrectangular posterior portion, dorsal face with numerous tufts of setae set on minute tubercles; anterior portion with broadly rounded distal margin armed with few subdistal spines or tubercles; posterior portion divided medially by shallow furrow, distal margin subdivided into 4 multispinose lobes (2 laterally, 2 median) armed with strong spines.

Uropods (Figs. 4F, 5G–H) weakly asymmetrical; protopod superior surface slightly excavate posterior to articulation of exopod, projection posterior to endopod bearing 2 small blunt spines; with rasp on dorsodistal face of endopod and exopod. Telson (Figs. 4F, 5G–H) symmetrical to slightly asymmetrical, ovoid, slightly broader than long; dorsal surface uneven, with many tufts of setae; posterior margin subdivided by shallow sinus into equal lobes with marginal setae.

Males without pleopods, often with female gonopores present (intersex). Females with biramous left pleopods 2–5 (all carrying eggs, Fig. 5B, D).

Genetic data. Male 9.5 mm, USNM1292096, GenBank: MH481976, BOLD: SEAKY1184-17.

Three-dimensional microCT data. Male 9.0 mm, SAMC A066204; see Landschoff *et al*. (2018b).

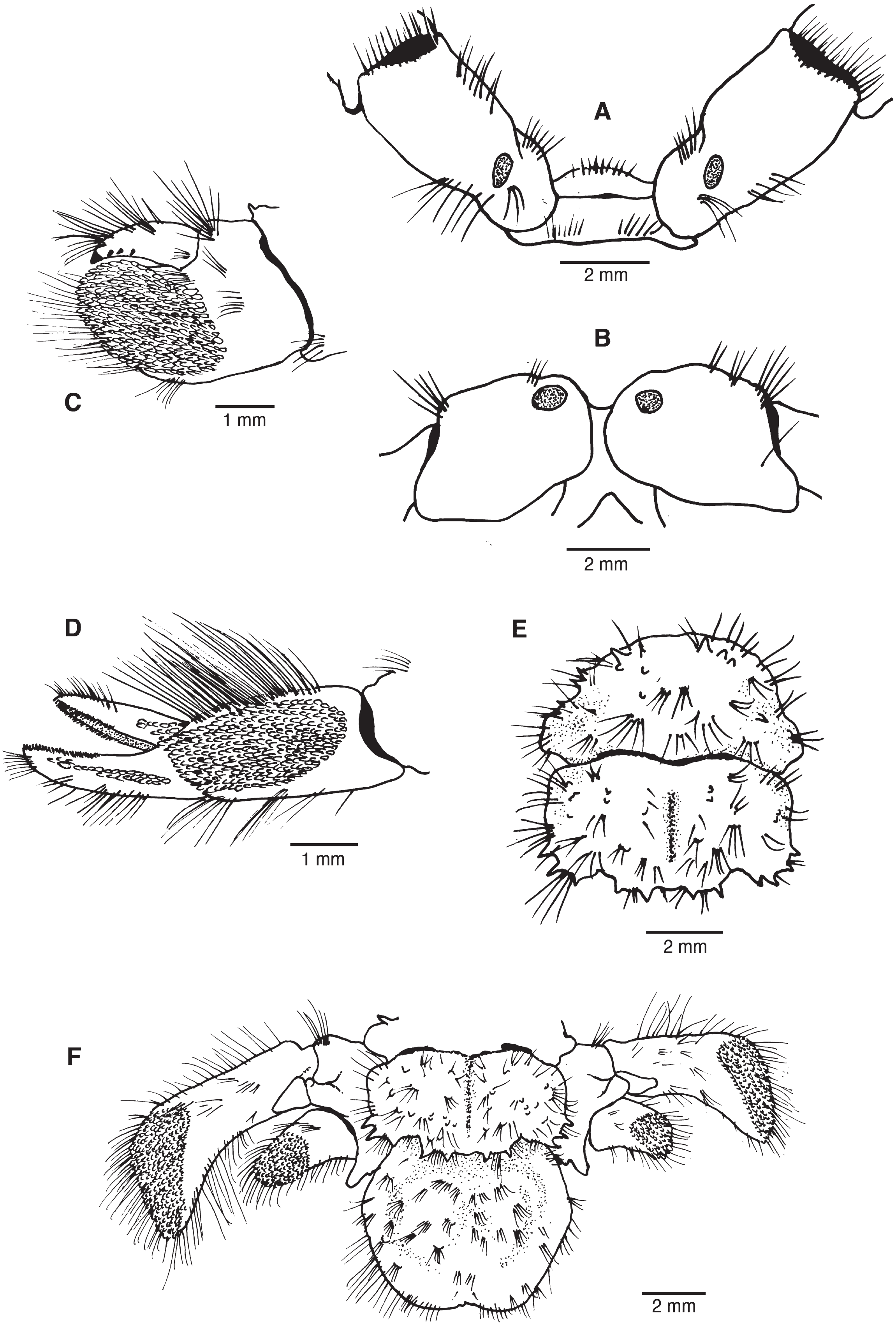

FIGURE 4. *Cancellus makrothrix* Stebbing, 1924, male (intersex), 9.5 mm, USNM 1292096: A, sternite XI and coxae of pereopod 3, ventral view; B, sternite XIII and coxae of pereopod 5, ventral view; C, propodus and dactyl of pereopod 4, lateral view; D, propodus and dactyl of pereopod 5, lateral view; E, sixth pleonal somite, dorsal view; F, posterior portion of sixth pleonal somite, uropods, and telson, dorsal view.

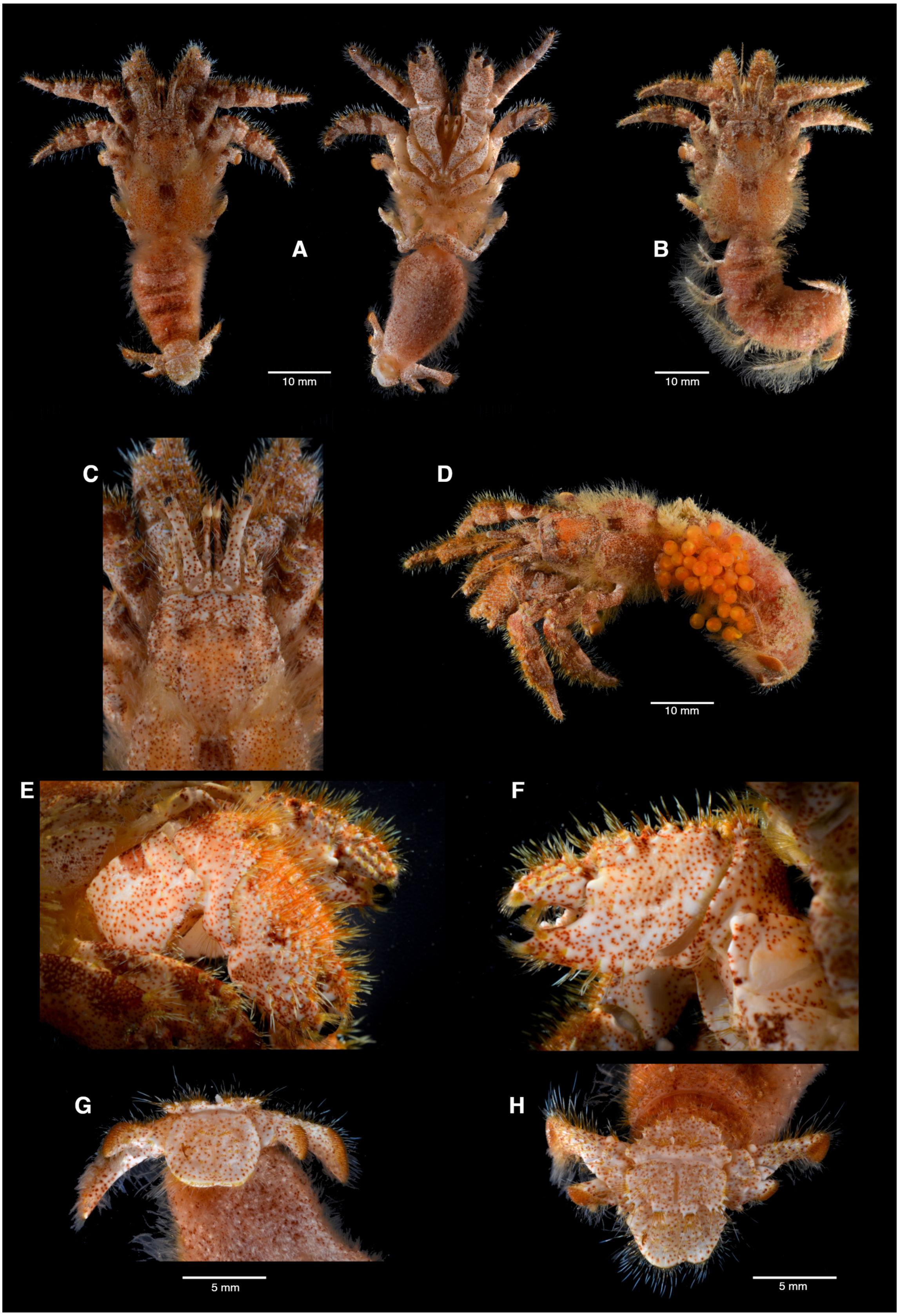

FIGURE 5. *Cancellus makrothrix* Stebbing, 1924, colour in life: A, dorsal view (left) and ventral view (right) male (intersex), 9.5 mm, USNM 1292096; B, dorsal view female 10.8 mm, SAMC-A096852; C shield and cephalic appendages, same as A; D, left lateral view, ovig. female 10.4 mm, USNM 1292095; E, right cheliped, lateral view; F, same as E, mesial view, male 12.1 mm SAMC-A096853; G, uropods and telson, dorsal view, USNM 1292096; H, posterior portion of sixth pleonal somite, uropods, and telson, dorsal view, same as G.

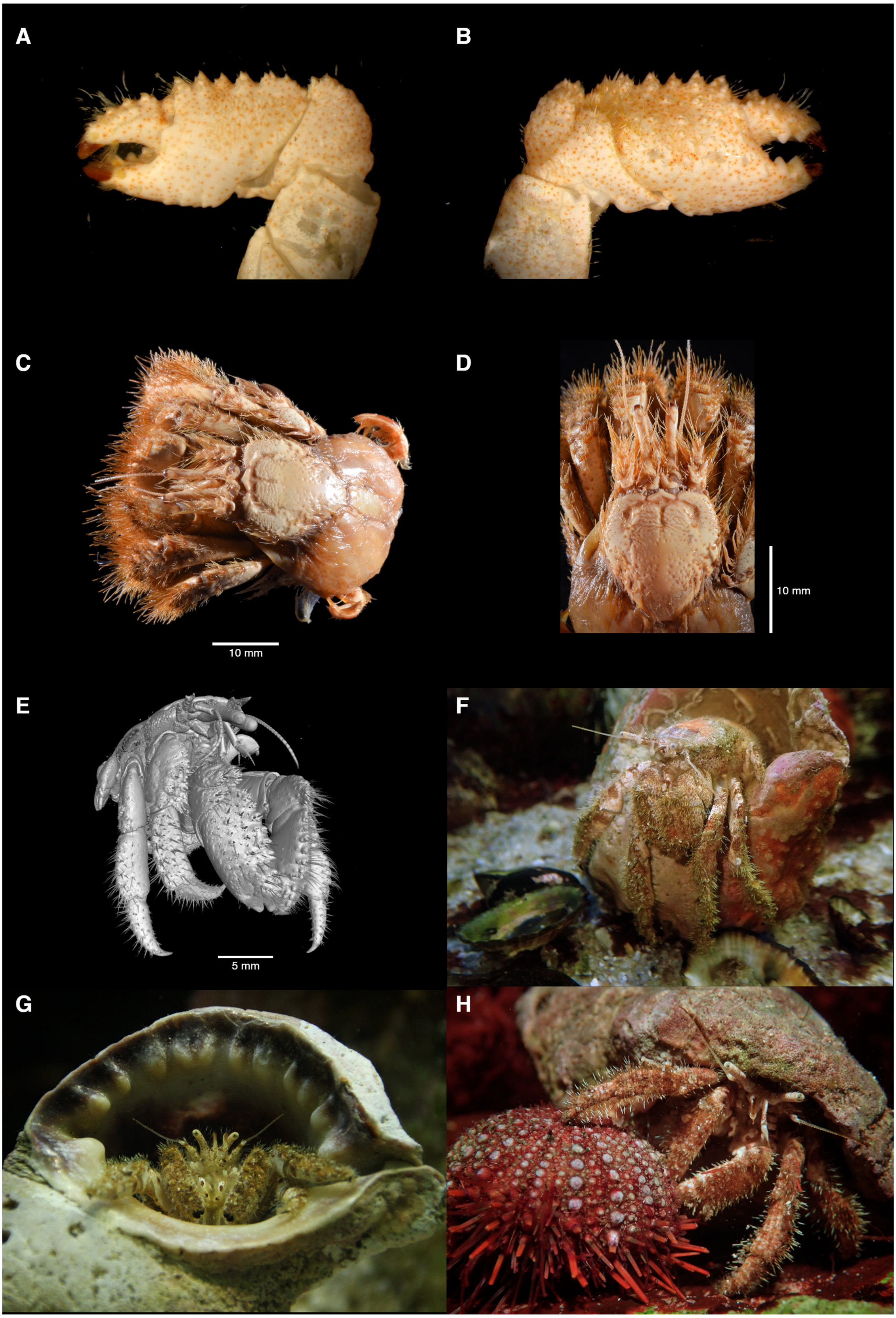

FIGURE 6. *Cancellus makrothrix* Stebbing, 1924: A, mesial and B, lateral view of right cheliped (in alcohol), male (intersex), 9.5 mm, USNM 1292096; C dorsal view of male paratype (pleon missing), 16.5 mm, SAMC 1541; D, shield, dorsal view of the same as C; E, three-dimensional reconstruction of microCT scan, male 9.0 mm, SAMC A066204; F, specimen in life extended from shell (in tank), male 14.3 mm, SAMC A066603; G, specimen in natural habitat, Millers Point, False Bay, Cape Town; H, specimen in tank eating Cape Urchin (identity unclear), ~9.5 mm, USNM 1292096. Photographs F, G, by Craig Foster.

Colour. General colour in life (Figs. 5, 6F–G): cream to orange brown and darker patches, sprinkled with small brown-red dots; strong setae appear orange-yellow at base, white on distal half, plumose setae cream. Shield cream to orange near midline, with usually two dark brown patches on anterior one-third and darker areas laterally; evenly to irregularly covered with small brown-red dots. Anterior half or calcified part of cardiac region dark brown, remainder of carapace and pleon somewhat uniformly cream to orange-brown and with the usual red dots. Ocular peduncles cream with irregularly spaced brown-red dots, often in groups of 3–5, becoming smaller distally, less intense in colour, and less dense; corneas light blue; acicles as proximal part of peduncles, with white calcareous spines. Antennular and antennal peduncles like proximal ocular peduncles, but with spines and tubercles cream to white; antennular peduncles with white dorsal flagellum, ventral flagellum with light and small brown-orange yellowish dots; antennal peduncles without dots, semi-transparent to cream. Chelipeds and pereopods primary color as carapace, but usually each segment with proximal broad dark brown patch on dorsal inner and outer face, sometimes as ring around entire segment; brown patches less pronounced on chelipeds, and obscured by setation, most pronounced on second pereopod. Ventral surfaces, uropods and telson as primary color. Eggs of later developmental stage orange.

Distribution and habitat. South coast of South Africa from East London to False Bay, Cape Town. Depth range: 5–31 m; commonly found at diving depths of 5–25 m on various habitats from sandy substrate to rocky reefs in kelp forest. Typically inhabits oversized gastropods shells such as those of the genus *Murex* as reported by Barnard (1950) or large buccinids in False Bay.

Proposed common name. “Hercules hermit crab”.

Taxonomic remarks. As previously mentioned, Stebbing’s (1924) description of *Cancellus makrothrix* is brief and lacks morphological details, a situation exacerbated by the confusion on the number, fate and condition of his original material. A first problem during this study was to locate the type material of Stebbing’s taxon. In his description Stebbing (1924: 241) stated that “The specimen is a female, with the sexual openings conspicuous at the bases of the third paraeopods”, and he did not mention any other specimens. Stebbing indicated the locality of his female specimen to be Algoa Bay, and stated that the specimen was deposited in the South African Museum with registration number “A 1541” (currently SAMC A1541). However, examination of the specimen deposited in that museum under that registration number showed that it is actually a male (not intersex with both male and female gonopores, which could have been mistaken for a female by Stebbing in his description). In view of this discrepancy in the sex of the specimen, we searched the handwritten record in the Iziko South African Museum pertaining to the *SS Pieter Faure* collections used by Stebbing (1924), and confirmed Barnard’s (1950) discovery that lot “A1541” originally contained two specimens, of which only a male was found during our study in that SAMC lot. On the suspicion that the missing female type might have been transported to London to be worked on by the Rev. T.R.R. Stebbing (1835–1926; Mills 1976), we requested a search at the Natural History Museum, London, where indeed their “Stebbing Collection” was found to include a lot (NHM 1928.12.286) from Algoa Bay with the appendages of a specimen that unquestionably is of *C. makrothrix*, the only species of *Cancellus* known to occur in South African waters. Although the body of that specimen is missing and thus the sex cannot be ascertained, the appendages left in the jar (a right antennule, a left cheliped, left pereopods 3–5, and right maxillipeds 1–3, see “Type material”) must belong to Stebbing’s (1924) female mentioned in his description. So it is clear that Stebbing worked with two specimens, a female and a male that must be considered as syntypes. From these syntypes, the male (sl = 16.5 mm, SAMC A1541) is herein selected as lectotype for Stebbing’s taxon.

A second problem during this study was to determine which specimen was illustrated by Stebbing (1924, pl. 3, [Crustacea pl. 118]). Stebbing’s illustrations are few and crudely executed. The illustration (Stebbing 1924: pl. 3 fig. T) of the posterior part of the pleon shows a nearly symmetrical telson, what appears to be an inaccurately drawn posterior part of the sixth pleonal somite, and incomplete or mutilated uropods; the illustrations (Stebbing 1924: pl. 3 figs. prp 1, prp 3, prp 4) of a cheliped and pereopods 3 and 4 appear distorted and do not show any surface ornamentation. Those illustrations could possibly belong to either the female or male syntypes, except for the mouthparts, which should belong to the female syntype as the male syntype (SAM-C 1541) is still intact and its mouthparts clearly were not dissected. The illustration (Stebbing 1924: pl. 3, fig. car) of the anterior portion of the cephalic shield and ocular peduncles initially appeared to be erroneous as it shows ocular acicles that are distally bifid (left) or simple (right), whereas all specimens we studied and believed to represent Stebbing’s *C. makrothrix* have ocular acicles that are distally multifid. However, examination of the male syntype specimen catalogued as SAMC-1541 showed exactly the same spinulation on the ocular acicles as depicted by Stebbing (1924: pl. 3, fig.

car). We thus consider that Stebbing's illustration (pl. 3, fig. car) is of the male catalogued as SAMC-1541. Given the unusually large size of this male (cephalothoracic shield length 16.5 mm), the largest known of *C. makrothrix*, we attribute the morphology of its ocular acicles to size variation, a condition frequently seen (pers. observation) in many other paguroids.

In summary, we conclude that Stebbing's (1924: pl. 3) illustrations of *Cancellus makrothrix* represent a composite of both the female syntype now at the Natural History Museum, London (NHM 1928.12.286) and the male syntype herein selected as lectotype at Iziko South African Museum, Cape Town (SAMC-1541).

Since Stebbing's (1924) description of *Cancellus makrothrix*, this species was not reported again until Barnard (1950) remarked on the lack of details in the original description. Based on three specimens of *C. makrothrix* found in SAMC, i.e., the male syntype (now lectotype) from Algoa Bay and two more specimens from East London, Barnard (1950) provided details about the morphology, habitat, and presumed development of Stebbing's species. As previously mentioned, Barnard (1950: 449) considered *C. makrothrix* to be a "very aberrant" species of the genus *Cancellus*. He observed that in contrast to other congenerics *C. makrothrix* lives in gastropod shells (*Murex*) instead of excavated burrows in corals, soft rocks, and sponges; has a coiled rather than straight pleon; the chelipeds as well as pereopods 2 and 3 (instead of just the chelipeds and pereopods 2) together tightly form a closure for the aperture of the gastropod shell used as housing; and the upper surface of the carpus of the chelipeds do not form a strong knuckle-like projection. Furthermore, Barnard's (1950, fig. 82) illustration shows slightly asymmetrical uropods and a distinctly asymmetrical telson. This unusual morphology for a species of *Cancellus* led Mayo (1973) to consider *C. makrothrix* to be more primitive than other symmetrical congenerics, and consequently intermediate between the more typical pagurids and species of *Cancellus*. Presumably, according to Mayo, the slightly asymmetrical uropods, flattened opercular surfaces of the chelipeds, and the spirally coiled pleon in *C. makrothrix*, reflected incomplete evolution from the use of asymmetrical to tubular housing.

It appears that Gordan (1956) was the first to change the spelling of Stebbing's (1924) species epithet to "*macrothrix*" rather than "*makrothrix*", most likely in order to Latinize the Greek letter "k". Since then, the spelling "*macrothrix*" was used by several carcinologists (Mayo 1973; McLaughlin *et al.* 2010; Wittmann & Griffiths 2017; Landschoff & Gouws 2018; Landschoff *et al.* 2018a, b). Forest & McLaughlin (2000) correctly reverted to Stebbing's original spelling.

Mayo (1973) provided an in-depth review of the taxonomic literature, morphological features, and life history information available for the nine species of *Cancellus* known at that time. However, Mayo did not have any material of *C. makrothrix* available for examination and thus did not add any new information on the morphology or biology of this species, although she pointed out that Stebbing's (1924: pl. 3, fig. car) rough illustrations of the anterior part of the cephalothoracic shield and eyestalks did not agree with the expanded description of this species provided by Barnard (1950) and in fact appeared more like that in species of other genera of pagurids.

Kensley (1974: 65) provided more precise information about the type locality of *Cancellus makrothrix* in Algoa Bay as "Bird Island passage, Cape Province, 10 fathoms", and also added that the original sample was collected by the "S.S. *Pieter Faure*", a Cape Government trawler that investigated the coast of what is now South Africa (Barnard, 1964). Subsequently, Kensley (1981) indicated that *C. makrothrix* occurred from False Bay to East London, in a depth range of 34–80 m. While the distribution remains correct, the depth information is an error as this information provided by Kensley (1974, 1981) was based on the few previously reported specimens, all listed above and all from shallower waters. Except for one additional specimen listed in Day *et al* (1970), no new material of *C. makrothrix* has been taxonomically reported since Barnard's report until the present study. In an apparent oversight, Emmerson's (2016) did not include *Cancellus makrothrix* in his recent guide and checklist to the decapods from the south African coasts of Namibia to Mozambique.

Morphological and biological oddities. As previously mentioned under "Taxonomic Remarks", *C. makrothrix* stands out morphologically among species of *Cancellus* in that the outer surfaces of the chelipeds (palm and carpi) that form part of the opercular surface are flattened or slightly convex rather than concave; both pereopods 1 and 2, instead of only pereopod 1, together with the chelipeds, form the opercular surface; the coiled pleon; and the slightly asymmetrical uropods. In addition, *C. makrothrix* differs from other species of *Cancellus* in the use of gastropod shells for housing rather than straight burrows in a variety of petriculous substrates, a condition which presumably has caused the slight asymmetry present on pleon and uropods.

The study of specimens of *Cancellus makrothrix* revealed the puzzling presence of what appears to be a pore on the basal surface of the ventromesial face of each ocular peduncle (Fig. 1C). Such pore, if indeed our anatomical interpretation is correct, has not been reported on the ocular peduncles in any species of *Cancellus*, or to our knowledge in any other paguroid. The function of this pore, if any, can only be speculated on at this point.

Among the specimens examined of *Cancellus makrothrix*, we encountered two specimens with both male and female gonopores. In one (USNM 1292096) these were both paired, and in the other (SAMC A066204) the female gonopore was observed only on the left. In these specimens the pores are not as wide or as well-developed as in true females and they have been sexed as males here also, given the lack of pleopods as in strictly functional males. To our knowledge, intersex individuals have not been previously reported for species of *Cancellus*. However, the occurrence of intersex individuals in paguroids, often considered "aberrant", has been known since the late 19th century although only in the diogenid *Dardanus deformis* (H. Milne Edwards, 1836) has this phenomenon regularly been observed (Hilgendorf 1879; Fize & Serène 1955; Lewinsohn 1982; McLaughlin & Lemaitre 1993). It has been hypothesized that this condition might indicate a functional hermaphroditism or perhaps latent sex reversal (McLaughlin & Lemaitre 1993), although only in the last 25 years have authors focused on studying intersexuality in paguroids (Turra & Leite 2000, 2001; Turra 2004, 2007; Fantucci *et al.* 2007; Gusev & Sabotin 2007; Sant'Anna *et al.*, 2010; Obuid-Allah *et al.*, 2019). Sant'Anna *et al.* (2010) have shown that at least in one species of the diogenid genus *Clibanarius* Dana, 1852, a portion of the population consists of intersex individuals that have both male and female functional reproductive systems, meaning they can reproduce as males and females, and thus supporting the existence of sequential hermaphroditism. Whether the same is true in *C. makrothrix*, or possibly other species of *Cancellus,* as well as the evolutionary factors that explain hermaphroditism in these paguroids, remains to be investigated.

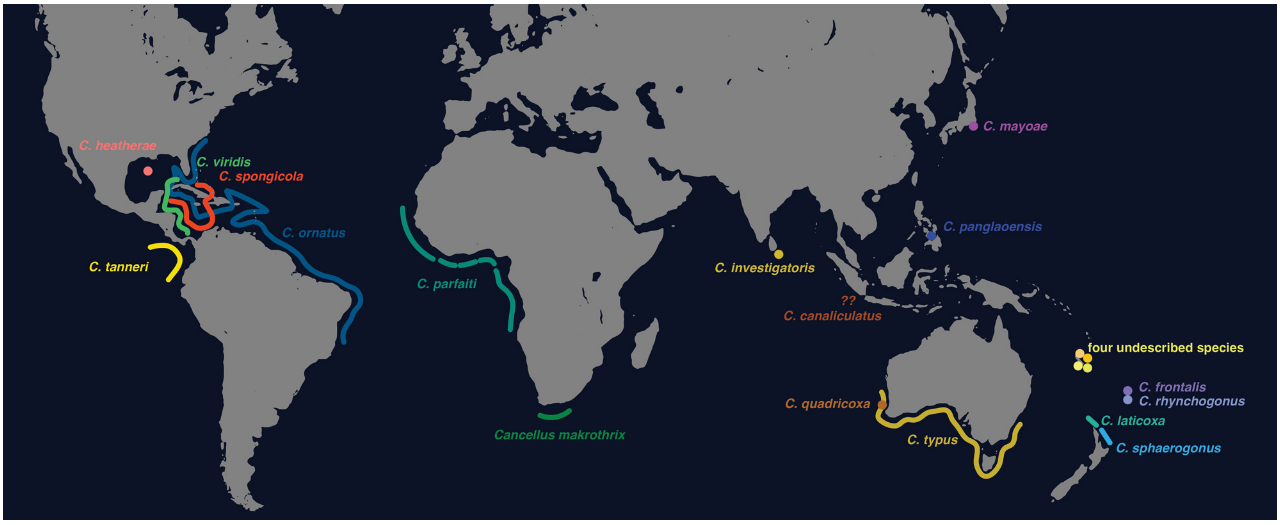

FIGURE 7. World distribution of species of *Cancellus* H. Milne Edwards, 1836.

Cancelllus makrothrix is one of only four species of paguroid in which abbreviated development has been reported, the others being *C. typus* H. Milne Edwards, 1836, *Areopaguristes abbreviatus* (Dechancé, 1963a), and *Paguristes frontalis* (H. Milne Edwards, 1836) (Hale 1927, 1941; Barnard 1950; Dechancé 1963b as *Paguristes abbreviatus*; Morgan 1987), although we have observed abbreviated development, and indeed brooding, of several other diogenid hermit crabs in the genus *Paguristes* and *Areopaguristes* from South African waters (J. Landschoff, unpubl. data). Glaucothoë larvae as well as juveniles have been reported in the former four species from inside the housing of the hermit crab or attached to the pleopods, an indication of parental care. Barnard (1950) observed "juveniles" already hatched as glaucothoë larvae or still inside the egg adhering to the pleon and sides of the carapace in one female (SAMC A3265), and concluded that in this species the free-swimming zoeal larval stage was suppressed and the young developed inside the housing occupied by the female. A similar conclusion indicating direct development was reported earlier by Hale (1941) in the Australian species *C. typus* H. Milne Edwards, 1836.

The ovigerous female specimens we collected contained 46 large sized eggs with an ~2.3 mm average in diameter. Although no more juveniles were found inside the shell or the back of a female adult, these large eggs add to Barnard's observation of glaucothoë stage post-larvae living inside the gastropod shell used as housing. The specimens we found carried shells that seemed enormous for such a small crab, and the free space in the spire of the gastropod shell provides a safe environment for the post-larvae to grow to juvenile stages (Figs. 6F–H).

Ecological and behavioral notes. The preference of *Cancellus makrothrix* for heavy, thick and usually greatly oversized shells is noteworthy, and this behaviour is indeed the best way to locate adult specimens in the field. Smaller individuals are probably overlooked among other hermit crab species. In the waters around Cape Town *C. makrothrix* co-occurs with several other paguroids, of which *Paguristes gamianus* (H. Milne Edwards, 1836) is highly abundant but commonly occupies smaller and lighter *Bunupena, Turbo* or *Bullia* shells despite a similar adult body size. From our experience in the field, inhabited shells larger than 100 mm are nearly always occupied by *C. makrothrix.*_The thick and strongly developed pereopods allow them to even climb highest or vertical reef structures. The habit of using heavy and difficult-to-carry petricolous dwellings might explain the evolutionary adaptation of *C. makrothrix* to easily carry these large and thicker gastropod housings, a specialization that is likely to provide better protection from predation.

The shells *Cancellus makrothrix* occupies in False Bay are generally overgrown by and/or pervaded by boring invertebrates and a detailed study of the associated fauna would make an intriguing study on its own. Additionally, the preference of *C. makrothrix* of large homes (Fig. 6F, G) quite literally creates, as previously noted, room for its developing young inside the shell after hatching, and the cavity provides shelter and habitat for smaller crustaceans. In fact, the collection of samples that led to this present study already led to the discovery and description of *Heteromysis cancelli* Wittmann & Griffiths, 2017, an obligatory commensal shrimp that exclusively lives inside the shells utilized by *C. makrothrix.*

By keeping *Cancellus makrothrix* for several months in the aquaria (Fig. 6H), it was repeatedly observed how *C. makrothrix* climbed onto the back of a sea urchin, holding on to the urchin test with its strong legs, and one-by-one clipped off and fed on the spines, tube feet, and pedicellaria. Initially we were inclined to think that the spines were only cut away to expose the tube feet for consumption, but over a period of >2 h *C. makrothrix* slowly clipped away and ingested all parts. The specimen molted a short time later but it is speculative if this food preference (the animal was fed with mussel meat as well) was related to perhaps increase calcium intake. Furthermore, it remains to be discovered if this predation occurs in the wild. Given the low abundance of *C. makrothrix* it seems unlikely that this species would have any noteworthy impact on wild urchin populations. *Cancellus makrothrix* might be an opportunistic generalist feeder as the paratype male specimen still has the remains of a polychaete worm held between its mouthparts.

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