



Description of a new species of brooding spider crab in the genus *Paranaxia* Rathbun, 1924 (Brachyura: Majoidea), from northern Australia and Indonesia

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Abstract

A new species, *Paranaxia keesingi* sp. nov., is described based on specimens collected in northern Australia. The new species differs from its only congener, *P. serpulifera* (Guérin, 1832, in Guérin-Méneville 1829–1837), by several characters including carapace setation, sternal cavities, absence of a subhepatic spine, presence of a sharp spine on the posterodistal angle of the cheliped merus, relatively shorter chelipeds, and longer and more slender ambulatory legs. Morphological separation of the two species is supported by 12s rDNA sequence divergences of 7.4–8.2%. Like *P. serpulifera*, the newly described species exhibits direct development with females carrying juvenile individuals under the pleon. Both species are sympatric, but *Paranaxia keesingi* sp. nov. is found in deeper waters than *P. serpulifera*.

Key words: 12s ribosomal subunit, Arafura Sea, decorator crabs, direct development, Epialtidae, Majidae, Western Australia

Introduction

The genus *Paranaxia* Rathbun, 1924 has been previously placed within Mithracinae MacLeay, 1838 *sensu* Griffin and Tranter (1986) and Ng *et al.* (2008). It was nevertheless recently considered to be *incertae sedis* within Majoidea Samouelle, 1819 by Windsor & Felder (2014) when they elevated the subfamily and restricted it to genera from the Americas only.

This genus is characterised by having parallel and distally bifid rostral spines, deep orbits marked by closed fissures between the postorbital spine, supraorbital eave and suborbital floor, lacking an intercalated spine, and having pits or depressions on the sternum (Rathbun 1924).

Paranaxia is unique among spider crabs in exhibiting direct development, where the young hatch as first stage crabs and are retained under the female's pleon for at least one moult cycle (Rathbun 1914, Morgan 1987). Morgan (1987) listed the species of marine Brachyura with known or suspected direct development, which belong to the families Dromiidae de Haan, 1833, Pilumnidae Samouelle, 1819, Hymenosomatidae Macleay, 1838 and Majidae Samouelle, 1819. It should be noted that nine out of the 10 brooding species are found in Australasian waters. Recent benthic surveys in the Kimberley and Pilbara regions of Western Australia revealed the presence of a new species of *Paranaxia*, which is described herein.

Materials and methods

Terminology generally follows that of Griffin and Tranter (1986) and Davie *et al.* (2015). The carapace length (CL) was measured from the rostral apices to the posterior margin of the carapace. Postrostral carapace length (PCL) was measured from the base of the rostral sinus to the posterior margin of the carapace, this was then subtracted from the CL to determine rostral length (RL). Carapace width (CW) was measured between the lateral margins of the carapace below the epibranchial spines and just above the base of pereopod 3. Measurements in material examined is given as PCL x CW in millimetres. The length of the pereopod articles were measured along the

dorsal (extensor) margins except for the cheliped propodus, which was measured from the tip of the fixed finger to the centre of articulation with the carpus. The height of the cheliped propodus was measured at the maximum height.

Total genomic DNA was extracted from muscle tissues of specimens using Bioline ISOLATE II DNA kit following the manufacturer's instructions. Partial sequences of the mitochondrial 12s rDNA (12s) were amplified via polymerase chain reaction (PCR) using the primers 12S-F1 (5' GAAACCAGGATTAGATACCC 3') and 12S-R1 (5' TTTCCCGCGAGCGACGGCG 3') (Mokady *et al.* 1994). A standard amplification profile was performed: initial denaturation 95°C/5 min; 35 cycles of denaturation: 95°C/20 s, annealing: 50°C/20 s, and elongation: 72°C/45 s; and a final extension step: 72°C/5 min. Products were submitted to AGRF (Perth, Australia) for clean-up and sequencing.

Sequence reads were assembled, edited, and aligned using Geneious v7.1 (Kearse *et al.* 2011). Our sequences were deposited with Genbank (Table 1). Available sequences of 12s, from Majoidea, were accessed from Genbank to examine the relationship between *Paranaxia* and other majoid genera (see Teske *et al.* 2009, Windsor & Felder 2014, and Table 1 for accession numbers and locality information). Models of evolution were tested in MEGA v6 (Tamura *et al.* 2013) and the General Time Reversible model using a discrete gamma distribution (GTR+G) (Tavaré 1986) was determined to be the most appropriate. Phylogenetic relationships were inferred using maximum likelihood (ML) and neighbour-joining (NJ) methods with 1000 bootstrap replications.

The description of the new species is based on the holotype male and allotype female with variations and ranges given in parentheses. Specimens are deposited in the Western Australian Museum, Perth (WAM), Queensland Museum (QM), Lee Kong Chian Natural History Museum, Singapore (ZRC, LKCNHM), and the Muséum national d'Histoire naturelle, Paris (MNHN).

TABLE 1. Genbank accession numbers of newly sequenced specimens used in this study.

WAM catalogue number	Species	Locality in Western Australia	Genbank number
C39266	<i>Paranaxia keesingi</i> sp. nov.	Pelsaert Island, Houtman Abrolhos Islands	KU922945
C59958	<i>Paranaxia keesingi</i> sp. nov.	Passage Islands, Pilbara	KU922948
C55212	<i>Paranaxia serpulifera</i>	Woodman's Point, Cockburn Sound	KU922946
C59957	<i>Paranaxia serpulifera</i>	Abutilon Island, Pilbara	KU922947
C61241	<i>Paranaxia serpulifera</i>	Heywood Island, Bonaparte Archipelago	KU922949

Taxonomic account

Superfamily Majoidea Samouelle, 1819

Genus *Paranaxia* Rathbun, 1924

Paranaxia serpulifera (Guérin, 1832, in Guérin-Méneville 1829–1837)

(Figs 1, 3A–D, 4A–D)

Pisa serpulifera Guérin, 1832, in Guérin-Méneville 1829–1837: 9, pl. VIII, fig. 2-2d.

Naxia serpulifera—H. Milne Edwards 1834: 313.—Miers 1879: 658.—Haswell 1882: 21.—Miers 1884: 196.

Naxioides serpulifera—Rathbun 1897: 157; 1914, 661, pl. 2, figs 9, 10.

Paranaxia serpulifera—Rathbun 1924: 7.—Montgomery 1931: 417.—Griffin 1966, 266, pl. 17, fig. 2a.—Bals 1935: 127.—

Sakai 1976: 264, fig. 143.—Griffin & Tranter 1986: 280, fig. 103.—Morgan 1987: 337, figs 1, 2.—Jones 1990: 193. —

Poore 2004: 384, fig. 117g, h.—Low *et al.* 2013: 117, table 2.

Non Paranaxia serpulifera—Rahayu & Ng 2000: 889 [= *Paranaxia keesingi* **sp. nov.**].

Material examined. Lectotype herein designated: MNHN-IU-2000-4479, 1 female, 86.2×68.2 mm, “Nouvelle Hollande”.

WESTERN AUSTRALIA: WAM C5640, 1 male, 48.0 × 36.1 mm, Cottesloe, 13 Jul. 1939, L. Glauert coll.

WAM C5904, 1 female, 99.5 × 79.7 mm, 40 km north of Geraldton, 12 Mar. 1941, A.S. Carr coll. WAM C5907, 1 female, 71.6 × 56.2 mm, Mandurah, 14 Apr. 1941, W.J. Budge coll. WAM C6043, 1 female, 90.3 × 69.5 mm, South Channel, Hudson Naval Base, 22 Dec. 1944, J.H. Walleth coll. WAM C6675, 1 female, 48.7 × 37.0 mm, Broome, 17°58'S 122°14'E, 6 Mar. 1951, S. Hamilton coll. WAM C7345, 1 male, 74.7 × 59.9 mm, Mandurah, 4 Jun. 1957, R. Chalmers coll. WAM C14026, 1 male, 83.0 × 63.3 mm, South Mole, Fremantle, 32°03'00"S 115°44'00"E, Jan. 1959, W.F. Hawkins coll. WAM C16001, 1 female, 97.8 × 77.2 mm, Sunday I., Shark Bay, 14 Mar. 1986, G.J. Morgan coll. WAM C16002, 1 female, 88.7 × 68.9 mm, Sunday I., Shark Bay, 14 Mar. 1986, G.J. Morgan coll. WAM C16619, 1 female, 91.1 × 71.7 mm, Cockburn Sound, Jan. 1986, R. Beale coll. WAM C34792, 1 male, 76.9 × 61.2 mm, Shark Bay, 25°36.99'S 113°14.45'E, 15.7 m, 29 Jun. 2006, S. Morrison *et al.* coll. WAM C34793, 1 female 52.5 × 37.8 mm, Shark Bay, 25°55.50'S 113°14.02'E, 12.8 m, 24 Jun. 2006, S. Morrison *et al.* coll. WAM C38296, 1 male, 60.0 × 44.8 mm, Point Cloates, on beach, 22°43'S 113°40'E, 7 Oct. 1957. WAM C38363, 1 male 78.6 × 63.2 mm, 1 female, 68.0 × 53.4 mm, Giralia Bay, Exmouth Gulf, 22°27'S 114°20'E, 31 Mar. 1990, D.S. Jones coll. WAM C41265, 1 male, 62.4 × 42.2 mm, Admiralty Gulf, Kimberley, 14°16'S 125°52'E, 4 m, 23 Feb. 1968, E.H. Barker coll. WAM C41267, 1 female, 104.5 × 79.7 mm, Walsh Point, Admiralty Gulf, Kimberley, intertidal, 10 Aug. 1978, F.E. Wells coll. WAM C54847, 1 female, 104.9 × 83.6 mm, Green Is, 30°40'55"S 115°06'23"E, 26 Apr. 1959, R.W. George coll. WAM C54870, 1 female, 113.5 × 91.8 mm, Sandy Cape, 30°11'S 114°59'E, 2 Jan. 1960, E.P. Hodgkin & L.M. Marsh coll. WAM C55209, 1 male, 85.9 × 69.2, 1 female, 99.3 × 78.8 mm, Denham Sound, 25°46'S 113°15'E, 3 Mar. 2004. WAM C55210, 1 male, 99.6 × 73.4 mm, 1 female, 93.4 × 72.8 mm, Denham Sound, 25°46'S 113°15'E, 3 Mar. 2004. WAM C55211, 1 male, 91.3 × 72.9 mm, Jurien Bay, 30°15'S 115°01'E. WAM C55212, 1 male, 88.6 × 72.0 mm, Woodman Point, Cockburn Sound, 32°08'S 115°44'E, 10 Apr. 2013. WAM C55478, 1 male, 51.5 × 36.9 mm. WAM C55479, 1 male, 79.1 × 61.4 mm, Shark Bay, 25°32.90'S 113°13.25'E, 19.3–18.7 m, 29 Sep. 2003, S. Morrison & P. Unsworth coll. WAM C61241, 1 male, SOL56, W of Heywood Island, Bonaparte Archipelago, 15°22'35.53"S 124°11'33.98"E to 15°22'34.31"S 124°11'31.46"E, 35 m, 19 Mar. 2015, coll. J. Fromont & L. Kirkendale coll. RV *Solander*. WAM C59957, 1 male, PMCP/051, off Abutilon Island, Pilbara, 20°44'22"S 115°35'58"E, 12–8.7 m, 22 Jun. 2013, E. Morello, G. Fry, M. Miller, D. Thomson, & D. Bearham, coll. RV *Naturaliste*.

Diagnosis. Body, pereopods completely covered in dense pubescence, hooked setae present on rostrum, preorbital spines, anterolateral carapace margins, dorsal tubercles, all ambulatory leg articles, except dactyls. Rostral length 0.1–0.45 times CW. Subhepatic spine large, directed anteroventrally. Pterygostomian region unarmed. Intestinal tubercle rarely produced beyond posterior carapace margin. Anterior most sternal pit reniform, deep, well defined in both sexes; paired lateral sternal pits shallow poorly defined relative to anterior pit in males, absent in mature females. Chelipeds of mature males (>80 mm CW) elongate, merus extends beyond rostral apices, prominent posterodistal tubercle blunt; propodus length up to 1.32 times CW. Pereopods 2–5 stout, pereopod 2 (P2) dactyl up to 0.48 times CW.

Description. Males. Carapace pyriform, PCL 1.23–1.50 times CW, regions well defined, densely covered in short pubescence; hooked setae present on tubercle apices, anterior branchial, hepatic margins. Rostral horns parallel, distally bifid, 0.24–0.50 times CW; tufts of hooked setae on lateral, dorsal, mesial surfaces. Orbits closed dorsally, ventrally; preorbital angle produced into large anterodorsally directed spine with hooked setae, postorbital lobe anteriorly cupped, dorsal orbital hiatus a narrow fissure. Gastric region elevated, slightly higher than other regions; 13 small tubercles distributed in anterior gastric region; apex with 3 large, blunt tubercles.

Hepatic region inflated, with acute stout spine on subhepatic margin directed anteroventrally, approximately same size as preorbital, branchial spines, visible in dorsal view.

Pterygostomian region unarmed. Branchial region inflated with 2 low mesial tubercles, lateral margin with large laterally directed spine above pereopod 3, apex rounded. Cardiac region elevated, apex bluntly rounded. Intestinal tubercle large, apex rounded.

Eyestalks sparsely setose anteriorly, cornea terminal, retractable into orbit. Antenna basal article laterally expanded to form suborbital floor; flagellum inserted ventral to rostrum, not visible dorsally.

Maxilliped 3 with dense pubescence, thicker, longer along borders of articles; ischium narrower than merus, mesial margin dentate, lateral margin approximately 0.7 mesial margin length, outer surface with shallow longitudinal depression; merus subtriangular, anterolateral angle produced.

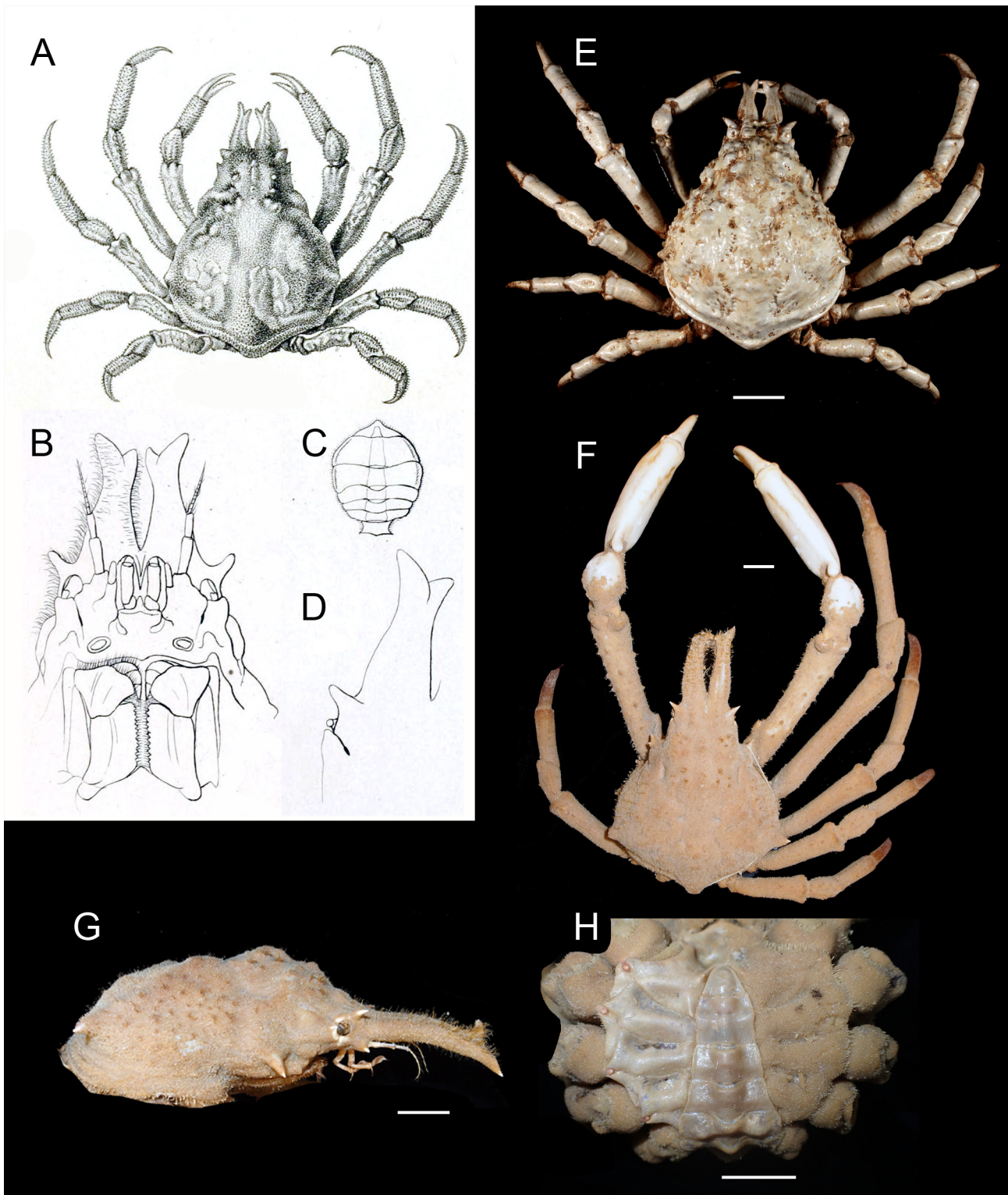


FIGURE 1. *Paranaxia serpulifera* (Guérin, 1832, in Guérin-Méneville 1829–1837). A–D reproduction of original figures published by Guérin (1832, in Guérin-Méneville 1829–1837); A, whole female dorsal view; B, anterior portion, ventral view; C, pleon; D, orbit and rostrum, dorsal view; E, MNHN-IU-2000-4479, proposed lectotype female, photo credit: François Baptiste (MNHN); F, G, WAM C828 male; F, whole individual, dorsal view; G, carapace, lateral view; H WAM C55210, male, sternum, and pleon, half denuded. Scale bars: E–H, 20 mm.

Chelipeds equal, becoming elongate in males >80 mm CW, length up to 1.23 P2, merus extending beyond apices of rostrum, medial dorsal tubercle, blunt posterodistal tubercle; carpus smooth about as long as dactyl;

propodus length 2.62–3.91 times height, 0.5–1.32 CW; smooth; dactyl with prominent tooth in gape, occludent margins of fingers crenulate.

Ambulatory legs stout, unarmed, covered in dense pubescence except at distal extremities of dactyls, hooked setae present dorsally on all articles except dactyls. P2 longest, 1.44–2.62 times CW. Dactyls evenly curved, P2 dactyl 0.28–0.48 times CW, unarmed on ventral surface.

Sternum with series of prominent pits surrounding pleon, each pit placed across junction of sternal segments, anterior-most pit on sternite 3, 4 reniform, posterior margin concave; 8 pits present adjacent to articulation with each pereopod, sternite 8 pit smallest, all shallower than anterior-most pit. Pleonal-locking tubercles prominent, on sternite 5 near suture with sternite 4.

Pleon with 6 free somites plus telson, widest at somites 2, 3, somite 6 lateral margins convex, width 1.2 times length, longer than somite 5; telson triangular, width 1.25 times length, apex rounded. Raised ridge running length of pleon, all pleonal somites with transverse ridge, giving slight, paired lateral depressions present at junctions of each somite.

Gonopod 1 slightly curved laterally, tapering distally into an acute point, aperture subapical, basally with very short setae on lateral margins. Gonopod 2 stout, curved laterally, apex inflated, fabiform, with minute scattered subapical, stout setae. Penis coxal emerging from P5.

Females. Surface details of carapace, pereopods 2–5 same as males. Subhepatic spine not always visible in dorsal view. Chelipeds much smaller, slender than males, propodus length 2.39–3.64 times height, 0.17–0.57 times CW, merus with blunt posterodistal tubercle. P2 1.30–2.05 times CW, dactyl 0.18–0.40 times CW. Sternal cavity on sternite 3, 4 same as male; lacking cavities on sternites 5–8. Pleon covering whole of sternum except sternites 1–3; broadest at somites 5, 6, telson short, broad width 3.0 length. Vulvae ovate, narrowing laterally, positioned in anterior half of sternite 6 submedially, blocked internally by chitinous vulvar valve.

Distribution. Australia: Western Australia (south to Perth), Northern Territory, Queensland. Depth: 0–20 m.

Remarks. The specimen herein designated as lectotype (MNHN-IU-2000-4479) is presumed to be the individual figured by Guérin (Fig. 1A–D). This specimen was labelled simply as “*Naxia serpulifera* Milne Edwards Nouvelle Hollande”. Although no dates are on the label, Nouvelle Hollande was no longer the official name of the Australian continent after 1824, suggesting that the specimen pre-dates Guérin’s publication. The female measures 116.7 mm CL, 86.2 mm PCL and 68.2 mm CW, which roughly corresponds to H. Milne Edwards’ measurements of “4 inches”. The specimen agrees with the original figures as well as the females examined during this study and is in good condition except in that it is missing the pleon. Many of the specimens figured by Guérin, were deposited in the Academy of Natural Sciences of Philadelphia, but no specimens of *Paranaxia serpulifera* are listed in the catalogues of Spamer & Bogan (1992; 1994), further supporting the present designation.

Holthuis & Manning (1990) and Low *et al.* (2013) have shown that Guérin’s plate 8 was published no later than February 1832 and we have followed Low *et al.*’s recommendation in citing 1832 as the publication date. Guérin (1832, in Guérin-Méneville 1829–1837), however, credited H. Milne Edwards with the authority of *Pisa serpulifera*, but H. Milne Edwards’ description (under the name *Naxia serpulifera*) was not published until 1834.

Our attribution of *P. serpulifera* to the specimens described by H. Milne Edwards (1834) is supported by his description of the size of the pterygostomial spine and comparison of the length of the ambulatory legs. He mentioned the presence of a spine on the pterygostomial region, of a similar size as the branchial and preorbital spines. The positioning of this spine is not shown in Guérin’s figures (Guérin 1832: Figs 1A, B), but can be clearly seen above the suture in the newly designated lectotype. This spine is always found above the suture line between the pterygostomial and the subhepatic regions in the examined specimens of *P. serpulifera*. In contrast, the spine is found below this suture and is clearly smaller than the branchial and preorbital spines in *P. keesingi* **sp. nov.** No subsequent description of *P. serpulifera* even mentions this spine. In relation to the legs, H. Milne Edwards describes the first pair being longer than the second in males (shorter in females). The chelipeds of male *P. keesingi* **sp. nov.**, however, are always shorter than P2 (Table 2), suggesting that H. Milne Edwards did not have material of both species available.

Paranaxia serpulifera is found in shallow water in northern Australia, often in seagrass beds and generally not on reefs. Despite its large size and prevalence, little research has been carried out on this species. The only non-taxonomic works have focused on the direct development and brooding of the young (Rathbun 1914, 1924; Morgan 1987).

TABLE 2. Summary of key morphological characters used to differentiate *Paranaxia keesingi* sp. nov. from *P. serpulifera* (Guérin, 1832, in Guérin-Méneville 1829–1837).

	<i>P. serpulifera</i>	<i>P. keesingi</i> sp. nov.
Anterolateral spine placement	Subhepatic region	Pterygostomian region
Cheliped merus posterodistal spine	Low, blunt	Prominent, sharp
Male cheliped/ pereopod 2 length	Up to 1.23	Up to 0.70
Paired sternal cavities	Relatively shallow	Deep, clearly demarcated
Male G1	Evenly curved throughout	Curvature lessening distally

The record from Japan by Sakai (1976) bears the large subhepatic spine characteristic of *P. serpulifera*, but the presence of this species in Japan was considered doubtful by Griffin & Tranter (1986) and no subsequent records exist. The specimens recorded by Rahayu & Ng (2000) are referred to the newly described species (see below) and the authors consider *P. serpulifera* to be endemic to northern and western Australia.

Paranaxia keesingi sp. nov.

(Figs 2, 3E–H, 4E–H)

Paranaxia serpulifera—Rahayu & Ng 2000: 889; non *Paranaxia serpulifera* (Guérin, 1832, in Guérin-Méneville 1829–1837)

Material examined. Holotype: WAM C39266, 1 male, 139.2 × 102.3 mm, off Pelsaert Island, Abrolhos Islands, 28°47.33'S 113°59.13'E, 36–37.5 m, 26 Apr. 2007, A.S. Sampey coll.

Allotype: WAM C41266, 1 ovigerous female, 78.2 × 58.0 mm, Admiralty Gulf, Kimberley, 14°16'S 125°52'E, 1968.

Paratypes: WAM C10971, 1 male, 116.1 × 83.7 mm, 1 female with juveniles, 115.5 × 88.3 mm, Shark Bay, 25°25'S 113°35'E, 174 m, Aug. 1972. WAM C38294, 1 male, 112.7 × 84.3 mm, Point Cloates, 23°39'S 113°11'E, 7 Oct. 1963. WAM C59958, 1 male 84.6 × 62.5 mm, Round Island, Passage Islands, Pilbara, 20°55'49"S 115°51'36"E, 14.6 to 16.2 m, 21 Jun. 2013, E. Morello, G. Fry, M. Miller, D. Thomson, & D. Bearham coll. WAM C66922, 1 female, 33.47 × 17.6 mm, N of Lamarck Island, Kimberley, Stn SOL52/WA045, 14°43.248'S 125°02.378'E, 32.7–32.8 m, Dec. 2015, coll. G.A. Gomez & J.A. Ritchie. QM W9950, 1 female, 99.8 × 77.5 mm, 45 kms NE Cooktown, 15°6'5"S, 145°29'4"E, 34.7 m, Oct. 1979. QM W12653, 1 male, 98.6 × 68.0 mm, SW Yorke Island, Torres Straits, 9°44'S, 143°25'E, 35 m, 23 Feb. 1982.

Other material: WESTERN AUSTRALIA: WAM C11271, 1 female, 71.2 × 49.6 mm, Shark Bay, 25°25'S 113°35'E, Aug. 1965, A. Mackenzie coll. WAM C11274, 1 female, 71.2 × 49.6 mm, Ashburton Area, Onslow, 21°38'S 115°07'E, 1 Oct 1964, W. & W. Poole coll. WAM C13661, 1 male, 88.1 × 68.4 mm, Broome, 17°58'00"S 122°14'00"E, 1965, R. Risbey coll. WAM C13748, 1 male, 85.7 mm, NE Of Montebello Islands, 20°16'00"S 115°47'00"E, 55–57 m, 5 Dec. 1979, S.M. Slack-Smith & L.M. Marsh coll. WAM C13749, 1 male, 121.6 × 88.0 mm, NW Of Shark Bay, 23°34'00"S 113°10'00"E, 151 m, 30 Jun. 1981. WAM C15742, 1 male, 46.2 × 35.7 mm, 1 female, 70.0 × 50.7 mm, Denham, Sep. 1963, FRV *Bluefin*. WAM C39201, 1 female, 86.2 × 62.5 mm, off Pelsaert Island, Abrolhos Islands, 28°44.55'S 113°59'E, 36 m, 26 Apr. 2007, A. Sampey coll. WAM C42080, 1 male, 24.1 × 16.1 mm, north side of Jar Island, Kimberley, 14°08.48'S 126°14.56'E, 0 m, 23 Nov. 1995, J. Short coll. WAM C53543, 1 male, 37.8 × 25.7 mm, east of Lesueur Island, Kimberley, 72 m, 12 Jun. 2013, A.M. Hosie & A. Hara coll. WAM C54862, 1 male, 126.0 × 87.4 mm, Shark Bay, 25°40'S 113°42'E, Jul. 1963, W. & W. Poole coll, FRV *Bluefin*. WAM C54872, 1 male, 84.2 × 66.2 mm, Shark Bay, 25°40'S 113°42'E, Jul. 1963, W. & W. Poole coll, FRV *Bluefin*. WAM C55213, 1 male, 60.4 × 39.3 mm, Exmouth Gulf, 22°07'S 114°17'E, 11 Mar. 2004. WAM C55214, 1 male, 98.8 × 77.3 mm, Denham Sound, 25°46'S 113°15'E, 15 Mar. 2004. WAM C55436, 1 male, 35.6 × 24.2 mm, Shark Bay, 10/03/2004, S. Morrison coll.

QUEENSLAND: QM W16108, 1 male, 43.9 × 30.6 mm, near Stephens Island, Torres Strait, 9°24'S 143°24'E, 22m, 28 Sep. 1988. QM W16539, 1 male, 54.2 × 39.3 mm, near Warrior Reefs, Torres Strait. QM W43175, 1 female, 67.5 × 47.7 mm, Great Barrier Reef, site 10614376, 10°36'36"S 143°45'36"E, 10 Jan. 2004. QM W43176, 1 male, 80.6 × 57.6 mm, Great Barrier Reef, site 1968, 10°54'18"S 143°3'18"E, 25m, 26 Sep. 2004. QM W43177, 1 male, 99.9 × 77.7 mm, Great Barrier Reef, site 2479 10°58'30"S 143°15'54"E, 28 m, 26 Sep. 2004. QM W52799,

1 female, 75.8x58.0 mm, Northern Prawn Survey, Stn 98, 13°44'18"S 143°48'E, 18 m, 28 Sep. 1979. QM W52800, 1 female, 28.5 × 19.9 mm, Northern Prawn Survey, Stn 113, 13°26'18"S 143°19'42"E, 18 m, 24 Sep. 1979.

INDONESIA: ZRC 1999.1470, 1 male, 24.5 × 17.2 trawl, Arafura Sea, Papua, 8°37'S 138°18' E, on mud, 10 Dec. 1967.

Diagnosis. Body, ambulatory legs completely covered in dense pubescence, hooked setae present on rostrum, preorbital spines, anterolateral carapace margins, dorsal tubercles, all ambulatory leg articles except dactyls. Male, female rostrum length 0.24–0.50 times CW. Subhepatic region unarmed. Pterygostomian region with sharp spine. Intestinal tubercle produced beyond posterior carapace margin. Sternal cavities prominent, medial cavity on sternite 3, 4 subcircular, posterior margin notched, longitudinally divided; 3 paired cavities on sternites 5. Chelipeds of mature males stout, length up to 0.7 times P2, merus extending to mid-point of rostrum, prominent posterodistal spine acute; propodus length up to 1.09 times CW. Pereiopods 2–5 slender, P2 dactyl 0.55–0.93 times CW.

Description. Holotype male. Carapace pyriform, PCL 1.36 (1.27–1.53) times CW, regions defined, densely covered in short pubescence; hooked setae present on tubercle apices, anterior branchial, hepatic margins. Rostral horns parallel, distally bifid, 0.39 (0.24–0.50) times CW; tufts of hooked setae on lateral, dorsal, mesial surfaces. Orbits closed dorsally, ventrally, preorbital angle produced into large anterodorsally directed spine with hooked setae; postorbital lobe anteriorly cupped; dorsal orbital hiatus as narrow fissure.

Gastric region elevated, slightly higher than other regions; 13 small tubercles distributed in anterior gastric region; apex with 3 larger, blunt tubercles. Hepatic region inflated, unarmed. Pterygostomian region with sharp stout spine directly ventral to subhepatic region, not visible in dorsal view. Branchial region inflated with 2 low mesial tubercles; lateral margin with large laterally directed spine (slightly curved) above pereiopod 3, apex rounded. Cardiac region elevated, apex bluntly rounded. Intestinal tubercle large, apex rounded, protruding beyond posterior margin of carapace.

Eyestalks sparsely setose anteriorly, cornea terminal, retractable into orbit.

Antenna basal article laterally expanded to form suborbital floor; flagellum inserted ventral to rostrum, not visible dorsally.

Maxilliped 3 with dense pubescence, thicker, longer along borders of articles; ischium narrower than merus, mesial margin dentate, lateral margin approximately 0.7 mesial margin length, outer surface with shallow longitudinal depression; merus subtriangular, anterolateral angle produced.

Chelipeds relatively stout, length 2.08 (1.90–2.08) CW, 0.67 (0.49–0.70) times P2; merus 0.65 (0.62–0.65) CW extending to midway along rostrum, with blunt medial dorsal tubercle, acute posterodistal spine; carpus smooth about as long as dactyl; propodus length 2.42 (2.42–3.95) height, 1.05 (0.56–1.09) times CW; smooth; dactyl with prominent tooth in gape, cutting margins of fingers crenulate.

Ambulatory legs slender, unarmed, covered in dense pubescence except at distal extremities of dactyls; hooked setae present dorsally on all articles except dactyls. P2 3.10 (2.72–3.6) CW; pereiopod 3 2.09 (2.03–2.29) CW; pereiopod 4 1.53 (1.50–1.83) CW; pereiopod 5 1.35 (1.28–1.1.48) CW. Dactyls evenly curved, elongate; P2 dactyl 0.68 (0.62–0.81) CW, unarmed on ventral surface.

Sternum with series of prominent cavities surrounding pleon, each cavity placed across junction sternal segments, cavity on sternite 3, 4 subcircular, deep, longitudinally divided, posterior margin notched; 10 cavities present adjacent to articulation with each pereiopods, sternite 4, 8 cavities smallest; sternite 5–7 cavities transverse, sternite 5 cavity laterally divided into posterior, anterior lobes. Pleonal-locking tubercles prominent, on sternite 5 near suture with sternite 4.

Pleon with 6 free somites plus telson, widest at somites 2, 3, somite 6 lateral margins convex, width 1.45 times wider than long, wider than somite 5; telson triangular, width twice length, apex rounded. Raised ridged running length of pleon, all pleonal somites with transverse ridge, paired lateral cavities present at junctions of each somite.

Gonopod 1 slightly curved laterally, curvature lessening distally tapering distally into acute point, aperture subapical, basally with conspicuously short setae on lateral margins. Gonopod 2 stout, curved laterally, apex inflated spatulate, with scattered stout setae subapically. Penis coxal emerging from P5.

Allotype female. Surface details of carapace and pereiopods 2–5 same as for males. Chelipeds much shorter, more slender than holotype male, length 1.33 CW; merus 0.47 CW, with posterodistal spine; propodus length 3.3 (3.01–3.41) height, 0.43 (0.53–0.83) CW. P2 2.67 (2.46–4.27) times CW, dactyl 0.59 (0.56–0.93) times CW. Sternal cavity on sternite 3, 4 same as male; lacking cavities on sternites 5–8. Pleon covering whole of sternum except sternites 1–3; broadest at segments 5, 6, telson short, broad width 3.0 length. Vulvae subcircular, positioned in anterior half of sternite 6 submedially, blocked internally by chitinous vulvar valve.

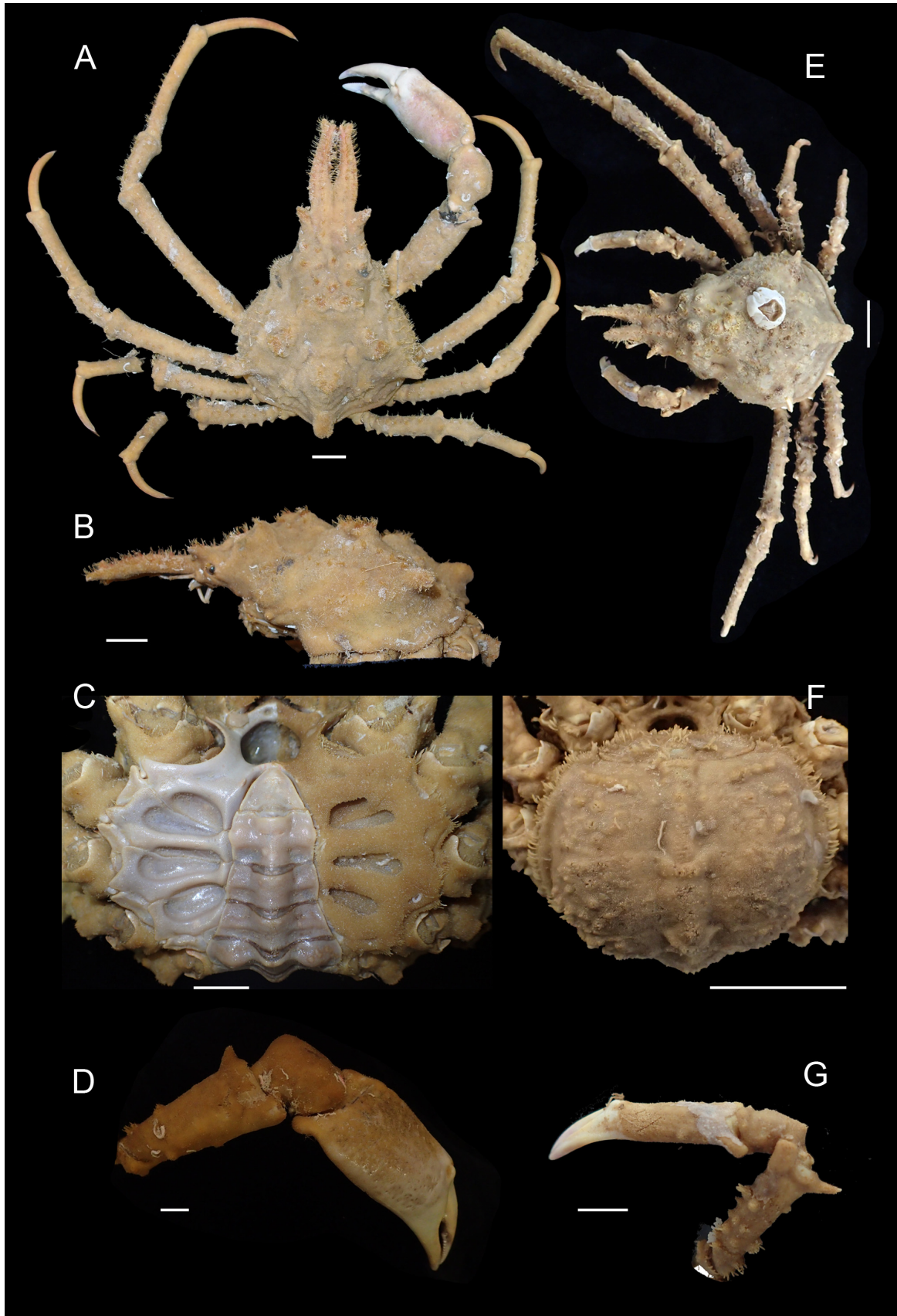


FIGURE 2. *Paranaxia keesingi* sp. nov. A–D, holotype WAM C39266 male; A, whole crab, dorsal view; B, carapace, lateral view; C, sternum and pleon, half denuded; D, male right cheliped, ventral view; E–G, allotype WAM C41266 female, pleon; E, whole crab, dorsal view; F, pleon ventral view; G, left cheliped, ventral view. Scale bars: A–C, E, F, 20 mm; D, G 10 mm.

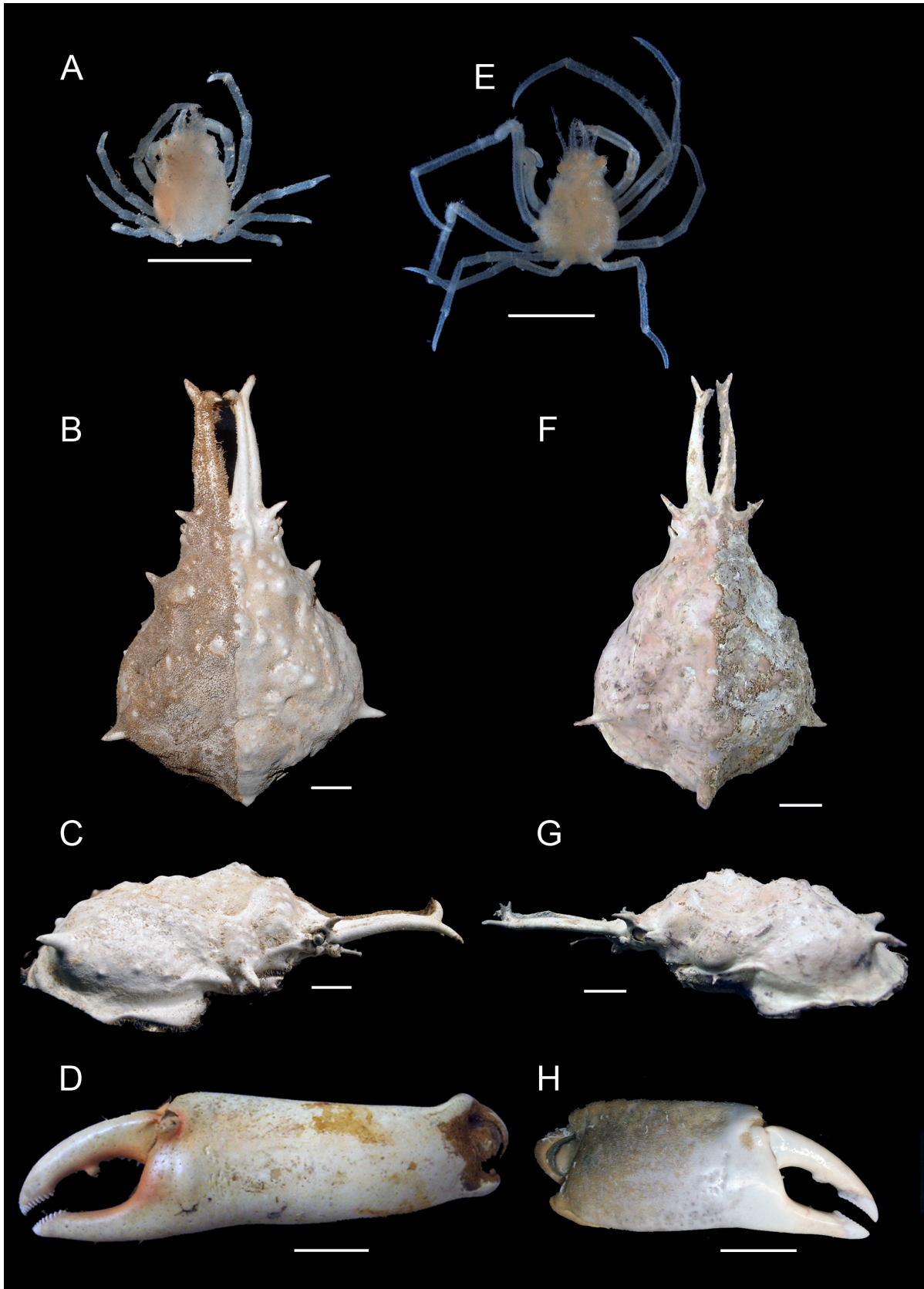


FIGURE 3. A–D, *Paranaxia serpulifera* (Guérin, 1832, in Guérin-Méneville 1829–1837). A, early stage crab, removed from under pleon of WAM C41266; B–D, WAM C56218 male; B, carapace dorsal view; C, carapace, lateral view; D, right chela, lateral view; E–H, *Paranaxia keesingi* **sp. nov.**; E, early stage crab, removed from under pleon of paratype WAM C10971; F–H, paratype WAM C38294 male; F, carapace dorsal view; G, carapace, lateral view; H, right chela, lateral view. Scale bars: A & E, 5 mm; B–D, F–H, 20 mm.

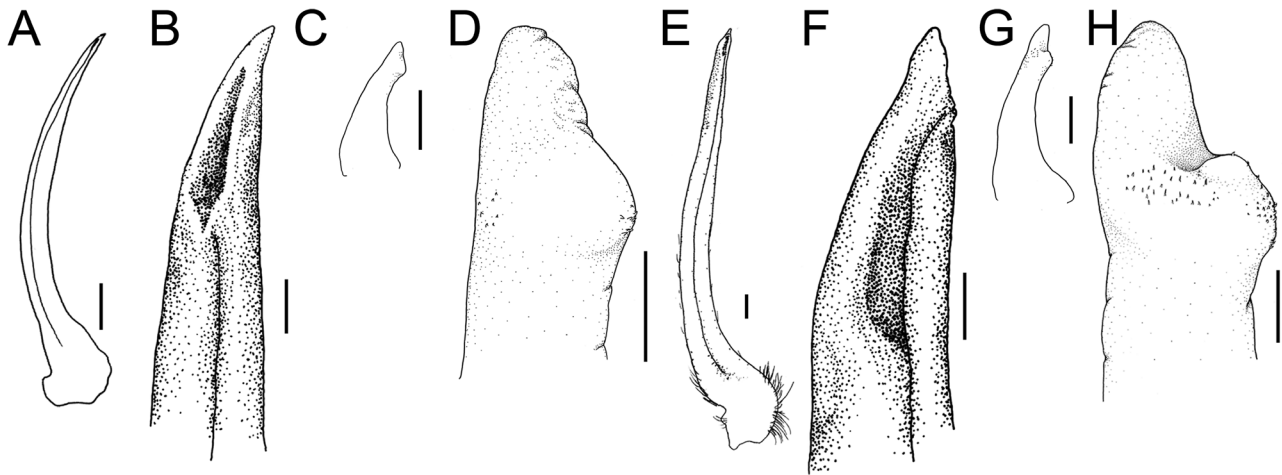


FIGURE 4. Gonopods. A–D, *Paranaxia serpulifera* (Guérin, 1832, in Guérin-Méneville 1829–1837), WAM C55210. A, male right G1, B, right G1 distal portion, C, right G2, D, G2 distal portion. E–H, *Paranaxia keesingi* sp. nov., holotype WAM C39266, E, right G1; F, G1 distal portion; G, right G2; H, G2 distal portion. Scale bars: A, C, E, G, 2 mm; B, D, F, H, 0.5 mm.

Etymology. This species is named after Dr. John Keesing of CSIRO Marine and Atmospheric Research, in recognition of his contribution and commitment to the knowledge of Western Australian biodiversity.

Distribution. Australia: Western Australia (south to the Abrolhos Islands), Queensland. Indonesia: Papua (Rahayu & Ng, 2000). Depth: 18–174 m.

Remarks. *Paranaxia keesingi* sp. nov. is clearly related to *P. serpulifera*, having shared characters such as the dense pubescence on the carapace and ambulatory legs, distally bifid rostral spines, structure of the orbits, epibranchial spines, and sternal cavities. Separation of the two species is well supported morphologically and is in congruence with the small molecular dataset presented. Both species grow to roughly the same size and to a minimum carapace length at maturity of approximately 100 mm and 85 mm for males and females, respectively. A comparison of morphological features distinguishing *P. keesingi* sp. nov. from *P. serpulifera* is presented in Table 2 and 3.

One female of *P. keesingi* sp. nov. was found carrying juveniles underneath the pleon, proving that this is also a brooding species. The juveniles showed the characteristic long slender legs of this species (Fig. 4 E) and are easily distinguished from juveniles of *P. serpulifera* (Fig. 4 A).

Photographs of one of the specimens (ZRC 1999.1470) collected by Rahayu and Ng (2000), from near the Papua coast of the Arafura Sea, show distinctive long slender legs and a sub circular sternal cavity and thus this record is herein referred to as belonging to *P. keesingi* sp. nov.

From the examined records it appears that *P. serpulifera* and *P. keesingi* sp. nov. can be found sympatrically, but are typically separated by depth. *Paranaxia serpulifera* is seemingly limited to the intertidal zone down to around 20 m, while *P. keesingi* sp. nov. has been recorded from 18–174 m.

Results and discussion

A total of 80 specimens were examined and the ratios of the articles of the ambulatory legs are given in Table 3. In both species males have relatively longer P2 than females. Even though there was substantial overlap in ratios of some limb articles, overall, *Paranaxia serpulifera* has relatively shorter ambulatory legs than *P. keesingi* sp. nov. (Fig. 5). The range of cheliped propodus length/height ratios between the two species differ only in males with a CW over 80 mm (3.03 and 3.91 in *P. keesingi* sp. nov. and *P. serpulifera* respectively). The small number of large males available precluded a full allometric study.

After aligning and trimming, 391 bp of 12s rDNA were obtained from three and two individuals of *P. serpulifera* and *P. keesingi* sp. nov., respectively. Of these, 234 out of 275 variable sites were parsimony informative. While sequences for *P. keesingi* sp. nov. were identical, evolutionary distances based on p-distance/K2P-distance methods were 0.009/0.009 within *P. serpulifera* and 0.074/0.080 between the two species. This corresponded to 7.4–8.2% sequence divergence between species, which fall within the range of intrageneric

distances of other species within the Majoidea (Table 4). The NJ and ML (tree not shown) methods resulted in similar topologies, but many branches have very low bootstrap support owing to the use of a single locus (Fig. 6). The two putative species, *P. serpulifera* and *P. keesingi* **sp. nov.** form a well-supported monophyletic clade in both analyses. This clade is genetically allied with genera of Epialtidae Macleay, 1838, but the arrangement lacked bootstrap support.

TABLE 3. Comparison of the ratio of the articles of pereopods. Abbreviations: ChL, cheliped propodus length; ChH, cheliped propodus height; CW, carapace width; P2, pereopod 2; d, dactyl; p, propodus; c, carpus; m, merus.

	<i>P. serpulifera</i>		<i>P. keesingi</i> sp. nov.	
	male	female	male	female
ChL/CW	0.5–1.32	0.17–0.57	0.61–1.09	0.53–0.83
ChL/ChH	2.62–3.91	2.39–3.64	2.42–4.19	3.01–3.95
P2/CW	1.44–2.62	1.30–2.05	2.72–3.61	2.36–4.27
P2d/CW	0.28–0.48	0.18–0.40	0.62–0.81	0.56–0.93
P2p/CW	0.28–0.57	0.26–0.49	0.76–1.04	0.57–1.27
P2c/CW	0.29–0.48	0.25–0.43	0.46–0.58	0.47–0.70
P2m/CW	0.62–1.04	0.49–0.73	0.9–1.18	0.79–1.38

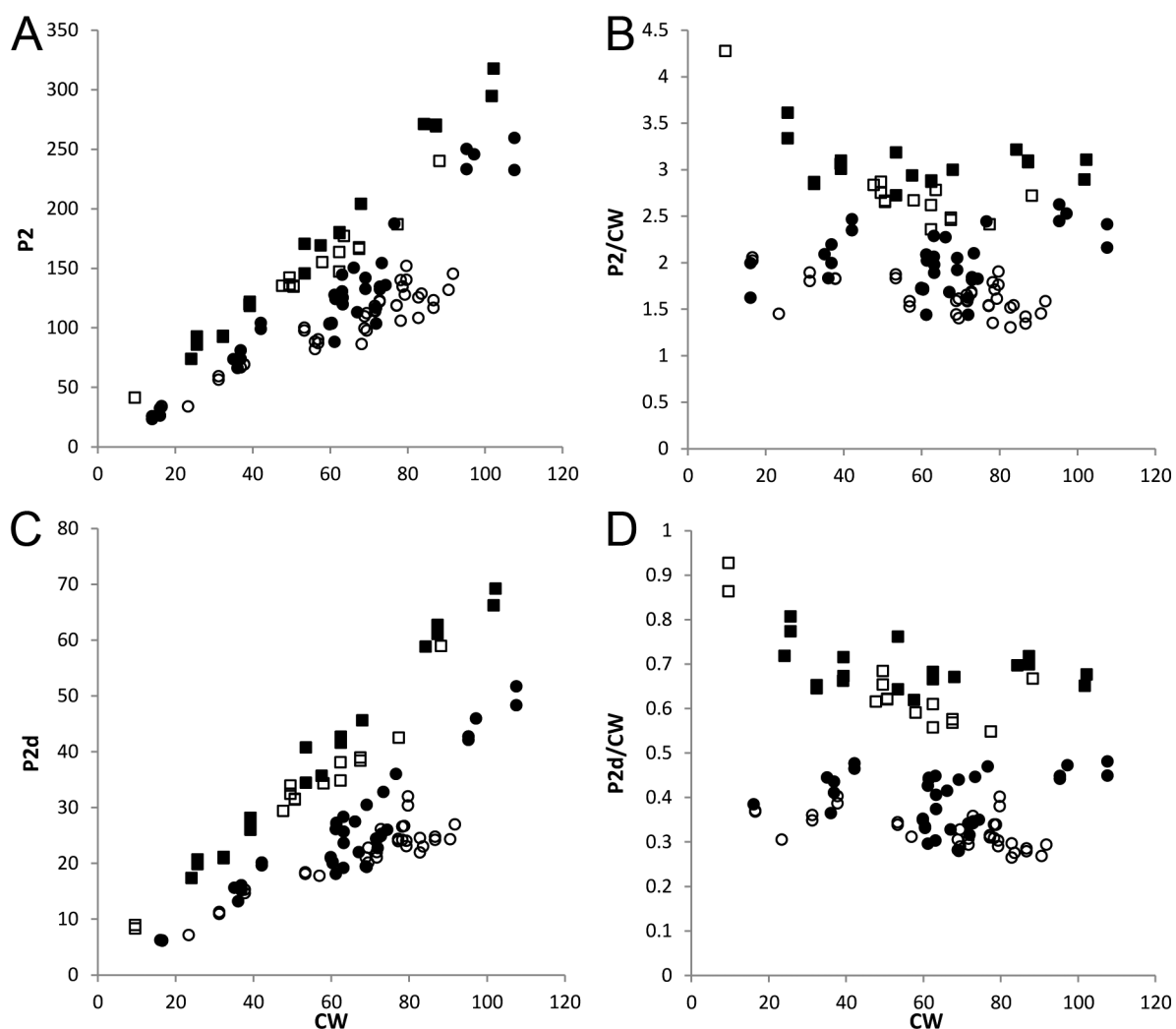


FIGURE 5. Comparison of *Paranaxia keesingi* **sp. nov.** (males ■; females □) and *P. serpulifera* (Guérin, 1832, in Guérin-Ménéville 1829–37) (males ●; females ○). Morphometric relationships between carapace width (CW) and length of A, pereopod 2 (P2); B, ratio of P2/CW; C, P2 dactyl (P2d); D, ratio of P2d/CW.

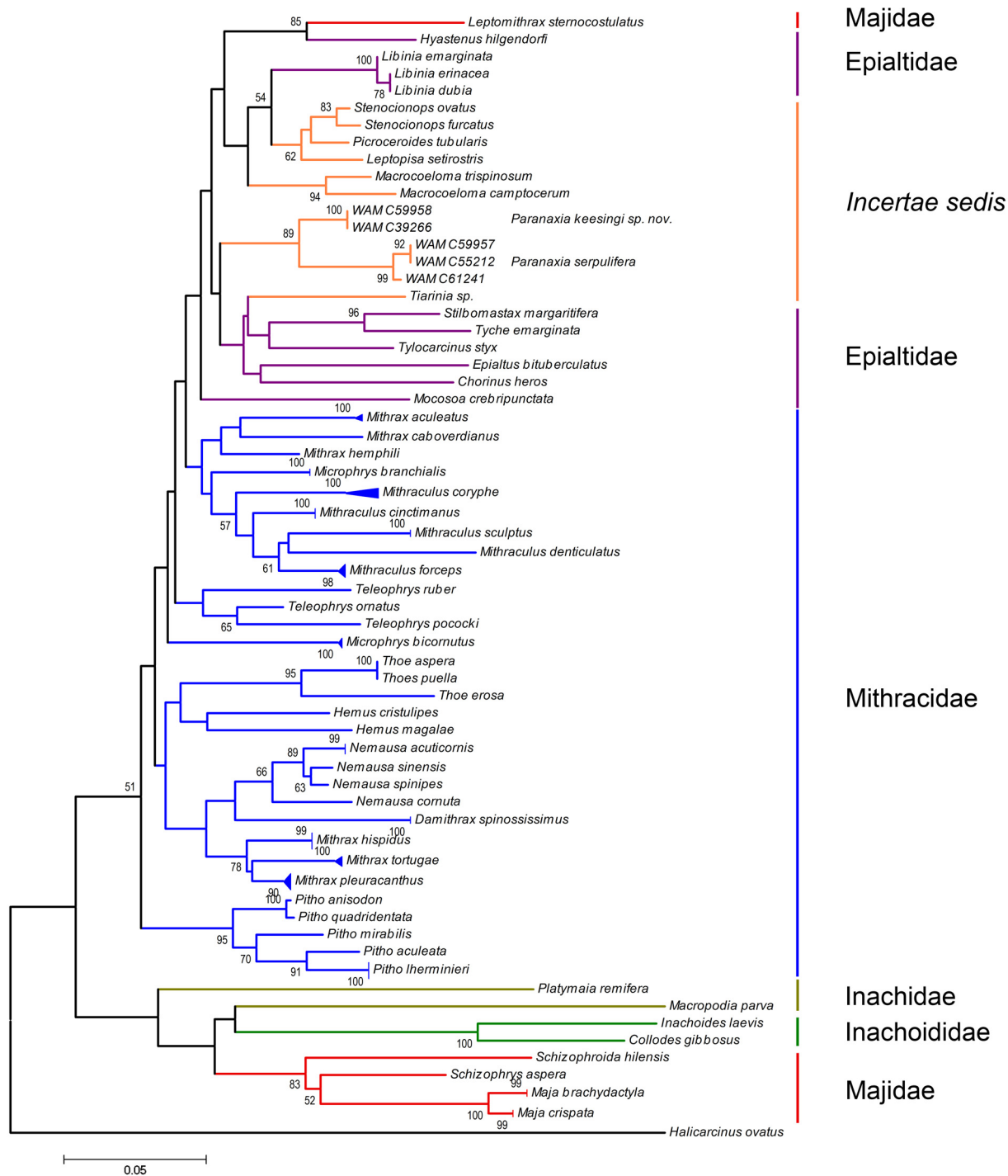


FIGURE 6. Phylogenetic tree of aligned 12s sequence data. Numbers at branches are bootstrap support values for Neighbour Joining method (1000 replicates), values <50% not shown.

The primary aim of using 12s sequences was to delimit the two species of *Paranaxia* and, as can be expected from using only 12s, has resulted in very little statistical support for many of the clades in the phylogenetic tree above genus level (Fig. 6). Windsor & Felder (2014) excluded *Paranaxia* from Mithracidae Macleay, 1838, despite not having sequences from this genus. The present results support their decision to exclude *Paranaxia* by placing it in a clade alongside the other Indo-West Pacific genera that were also removed from Mithracidae, as well as all the sequenced genera belonging to Epialtidae and one genus of Majidae (*Leptomithrax* Miers, 1876). This suggests *Paranaxia* is more closely related to members of Epialtidae than those of Majidae. Without additional loci to help provide statistical support for the molecular analysis, or a thorough morphological review of the family, the result

is inconclusive and reassigning *Paranaxia* would be premature. Therefore, we have followed Windsor & Felder (2014) by leaving *Paranaxia incertae sedis*.

TABLE 4. Comparison of evolutionary distances between species of selected genera of Majoidea using p-distance and K2P-distance methods. See Windsor & Felder (2014: table 1.) for species used and Genbank accession numbers.

Genus	Number of species compared	P-distance	K2P-distance
Paranaxia	2	0.074	0.080
Maja	2	0.028	0.029
Mithraculus	5	0.081–0.123	0.087–0.139
Mithrax	6	0.048–0.144	0.051–0.166
Nemausa	4	0.019–0.077	0.020–0.083

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