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The *Agononida incerta* species complex unravelled (Crustacea: Decapoda: Anomura: Munididae)

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Abstract

Squat lobsters from Australia, east Africa, Taiwan, Philippines and the Norfolk Ridge (southwestern Pacific) previously identified as *Agononida incerta* (Henderson, 1888) are redescribed as four new species in addition to the original: *A. africerta, A. auscerta, A. indocerta* and *A. norfocerta*. *A. rubrizonata* Macpherson & Baba, 2009, also earlier confused with this species, is redescribed. All six species are morphologically distinguishable only on the basis of the shape of the anterolateral lobe of the telson and the shape and setation of the dactyli of pereopods 2–4. The morphological delineation of these species and their taxonomic status are robustly supported by phylogenetic analysis of the partial mitochondrial COI marker. Taken together, subtle morphological differences, geographical distribution patterns and genetic discontinuities have important implications for understanding diversity, systematics and evolution of squat lobsters.

Keywords: Crustacea, Anomura, *Agononida*, new species, Indo-West Pacific, mitochondrial genes

Introduction

The application of molecular data to species differentiation and recognition is increasingly revealing the presence of more species than hitherto acknowledged. Examples can now be found within squat lobsters: four species where previously there was one, *Allogalathea elegans* (Cabezas *et al.* 2011); and three species where only *Uroptychus naso* was recognised previously (Poore & Andreakis 2011). Molecular and morphological data have been combined to reveal numerous new species of *Paramunida* (Cabezas *et al.* 2010). In the case of *Eumunida*, molecular data revealed a cryptic species and the probable synonymy of three others previously separated on morphological grounds (Puillandre *et al.* 2011).

Preliminary DNA analysis of mitochondrial and nuclear genes from a limited number of specimens revealed that munidids collected from the continental slope of Western Australia (McCallum 2011; Poore *et al.* 2008) identified initially as the widespread species *Agononida incerta* (Henderson, 1888) comprised four genealogical lineages. The question arose – which if any of these lineages was *A. incerta* and what do the dozen or so records of this species (see citations in Baba *et al.* 2008 and discussion at end of this paper) from throughout the Indo-West Pacific refer to?

Agononida Baba & de Saint Laurent, 1996 can be distinguished from the other 19 genera of the squat lobster family Munididae Ahyong, Baba, Macpherson & Poore, 2010 by the absence of a process on the mesogastric region, presence of dorsal spines and transverse striae, simple spine-like rostrum and supraocular spines, four (rarely two) spines on the anterior transverse ridge of abdominal somite 4, pereopods 1–3 without epipods, pereopods 2–4 with spinose meri and robust setae along the flexor margin of the dactyli, antennal peduncle articles 1 and 2 each with a distomesial spine, the orbit simple, oblique frontal margin, sternite 7 without lateral seta-like spines, absence of gonopod 1 and presence of gonopod 2 in the male. The genus has been diagnosed most recently by Macpherson & Baba (2011). Baba *et al.* (2008) listed 31 species and Macpherson & Baba one more. *Agononida incerta* is the type species.

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Baba's (2005) key identifies *Agononida incerta* as follows: abdominal segment 4 armed with a spine on its posterior transverse ridge; supraocular spines shorter than the rostral tip; article 1 of antennal peduncle with an extremely long process extending far beyond the end of article 4 at least by the length of articles 2–4 combined; cardiac spines absent; basal article of antennular peduncle with its distomesial spine longer than distolateral one; and carapace with numerous secondary setae. To which can be added from Baba's (2005) diagnosis, two epigastric spines, three (rarely fewer) pairs of postcervical spines, 1–3 spines on the branchiocardiac boundary; no spine on the posterior ridge of the carapace; lateral margin with four spines behind the cervical groove, and abdominal segments 2–4 each with four spines on their anterior ridges. Curiously, Baba (2005) diagnosed pereopods 2–4 with dactyli unarmed and smooth on the flexor margin – the numbers of robust setae along these margins, always present and sometimes numerous, became critical specific characters in this study.

We are not the first to recognise more than one species masquerading as *A. incerta*. Baba (1994) noted individuals from off Central Queensland, Australia, with prominent processes on the anterolateral margin of the telson and different coloration from NW Pacific specimens that he and Macpherson (1994) suspected to be another species. These two authors combined to erect a new species based on this morphotype and colour form, *Agononida rubrizonata* Macpherson & Baba, 2009. *Agononida rubrizonata* occurs in the Western Australia (WA) collections along with *A. incerta* sensu lato.

Suspicion of multiple species in WA lead us to re-examine the type specimen of *Munida incerta* in the Natural History Museum, London (BMNH), and to accumulate as much material as practical from other localities in the Indo-West Pacific. We particularly sought material suitable for molecular analysis. Collections from the entire western coast of Western Australia made during CSIRO'S "Voyages of Discovery" exploratory research program in 2005 and 2007 (McCallum 2011; Poore *et al.* 2008) included over 260 specimens identified as *A. incerta*. These were supplemented by material from eastern Australia in the Australian Museum, (AM), Sydney. Specimens from off Taiwan and the Philippines were obtained from the National Taiwan Ocean University (NTOU), Keelung. The Muséum national d'Histoire naturelle (MNHN), Paris, provided examples from the Mozambique Channel collected as part of the MAINBAZA expedition in 2009 and from the Norfolk Ridge, South Pacific, collected during the BATHUS 3 expedition in 1993 (Richer de Forges & Chevillon 1996). The Zoological Museum, University of Copenhagen (ZMUC) lent specimens collected in the Philippines by Th. Mortensen in 1914. Many thousands of other specimens from the SW Pacific in the collections of the MNHN, some referred to by Macpherson (1994) and others collected later, proved beyond the scope of this study.

DNA extraction, PCR amplification, sequencing and phylogenetic analysis

Following morphometric analysis, three specimens of each species described here were selected from larger samples for direct DNA sequencing of the partial mitochondrial cytochrome oxidase subunit 1 (COI) gene. The rationale was to further support our morphological findings by means of sequence analysis inferred from a barcoding region. A complete phylogeographic survey of this morpho-species complex, based on multiple markers and specimens collected globally is in preparation and will be published elsewhere.

Total genomic DNA was extracted from 50–100 mg ethanol-preserved abdominal tissue or pereopod following the salt-based extraction procedure described by Aljanabi & Martinez (1997) with minor modifications. Quantity and quality of DNA were assessed by means of 1% agarose TAE buffer gel electrophoresis against known standards. The partial mitochondrial cytochrome oxidase subunit 1 (COI) was PCR-amplified using the primer pair LCO1490-HCO2198 described by Folmer *et al.* (1994). Standard PCR reactions were performed in 30 μl of reaction volume containing approximately 10 ng DNA, 1.5 mM MgCl2, 0.2 mM dNTPs, 1 μM of forward and reverse primers each, 1X PCR reaction buffer and 1.25 units of *iTaq* DNA polymerase (Scientifix). Thermal cycling for the partial COI gene included an initial denaturation at 94°C for 4 min followed by 35 cycles of 94°C 1 min, 50°C 1 min and 72°C 1.5 min followed by a final extension cycle at 72°C for 7 min. PCR-products were examined by 1% gel electrophoresis as described above to assess quantity and length of the products. PCR reactions were sent to Macrogen Inc. (Korea, www.macrogen.com) for purification and direct sequencing on both directions. Forward and reverse electropherograms were assembled in Sequencher 4.9 (Gene Codes), imported in Bioedit v7.0.9 (Hall 1999) and aligned manually. Hierarchical Likelihood Ratio Tests (hLRTs) were computed in Modeltest Version 3.7 (Posada & Crandall 1998) to identify the best-fitting parameters (substitution model, gamma

distribution, proportion of invariable sites, transition-transversion ratio) given the data and maximum likelihood analyses (ten random sequence additions and TBR branch swapping) were conducted in PAUP* 4.0b10 version for Windows (Swofford 2002). Bootstrap support for individual clades was calculated on 1000 replicates using the same methods, options and constraints as used in the tree-inferences. *Onconida tropis* (AY351059) and *Onconida alaini* (AY351058) were included in the computation for outgroup comparisons.

Morphological methods

The possibility of multiple species forced a closer examination of morphological features and specific characters were found to support the differentiation of four new species. While the species in the *Agononida incerta* complex are only subtly different, sexual and allometric variation is typical. Males, apparently sexually mature, and ovigerous females are common in collections. Exceptionally large males can sometimes be found with grossly enlarged and expanded chelipeds that are sometimes referred to as 'arched' chelipeds (Thiel & Lovrich 2011) although the arching, at the propodus-dactylus juncture, is slight or non-existent in these species; we refer to these as 'supermales'. Differences between typical males and females are slight but the sexes can be distinguished on the basis of telson shape. Using the DELTA software (Dallwitz *et al.* 1999) principal descriptions are based on individual typical adult males; females and supermales are treated as 'variants.' Variation in counts of spines (between individuals and between left and right sides within individuals) on the carapace and pereopods and of robust setae on the flexor margin of pereopodal dactyli are given under the headings *Variation*. Implicit characters, those true of all species in this complex, are given at the beginning of the taxonomic section.

Conventional characters (spination patterns, proportions) do not serve well to differentiate species in this complex. These data are given as part of the species descriptions but we have little confidence in their value. The male pleopod 2 was dissected and photographed but again, nothing of taxonomic value was apparent. Two new character suites are introduced necessitating explanation of new terms. The *anterolateral margin of the telson* extends from the most anterior lateral corner (close to pereonite 6) to the lateral extent of the first transverse suture. This margin can be viewed as sometimes having three lobes, anterior, middle and posterior, variously developed and distinguished, or two separated by a notch or hiatus. The shape of this margin differs between species and sexes, most spectacularly in *A. rubrizonata*. The lateral shape of the remaining telson between the first and second transverse sutures and beyond varies more with sex and size than with species. The setation along the flexor margin of pereopodal dactyli differs between pereopods 2, 3 and 4, with size, from left to right and randomly, but is species-specific within broad ranges. The counts of these robust articulating setae (not spines as sometimes referred to) beyond the heel of flexor margin are critical. The dactyli of pereopods 2 and 3 are always more setose distally on the extensor margin than on pereopod 4. The shape of the dactyli are also species-specific but only subtly so, except for in *A. auscerta* n. sp. whose dactyli are narrower than all other species.

All measurements were made from photographs and ratios are given to two significant figures (in some cases greater accuracy than appropriate). Carapace length (cl) is measured from the base of the rostrum, the inflection between it and the gastric region, to the midposterior dorsal margin of the carapace. The lengths of the rostrum and the supraocular spines are measured from this datum. The basal width of the supraocular spines is the minimum width (the spines typically diverge beyond this point). Pereopod lengths are measured in situ, from a ventral view, from the proximal end of the coxa to the end of the dactylus. Relative lengths of pereopodal articles are measured along the upper margin. To calculate length:width ratios for the meri width was measured near the most distal marginal spine; for the dactyli, length was measured from the basal lateral ridge fronting the propodus to the tip and the width was measured at its widest basal point near the heel. These dimensions have been measured with the articles planar; they may appear narrower in photographs because meri typically lie oblique to the horizontal plane on intact animals. Telson length is measured along its midline (shorter than most posterior margin) and width is greatest width. None of these measurements and ratios proved taxonomically valuable.

Counts of spines along the margins of pereopodal articles are expressed as 1+x where 1 is the distal spine and x is the number(s) along the margin, flexor or extensor, or upper, mesial or lateral on chelipeds in situ. There is no distal spine on the end of the upper margin of the propodus of the cheliped. These counts were highly variable and proved not to be taxonomically valuable.

Agononida incerta, type species, is dealt with first and the others in alphabetical order.

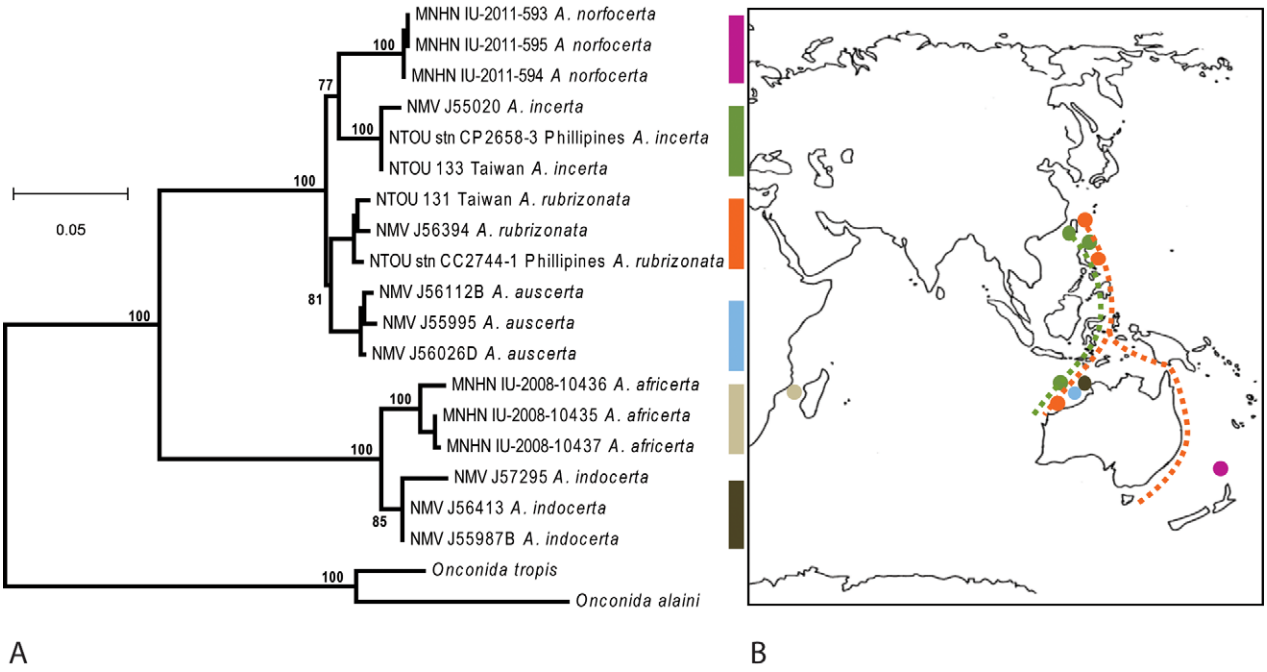

FIGURE 1. A, model-constrained maximum-likelihood phylogeny inferred from the partial COI sequences. Heuristic searches retained one tree (-ln = 2264.2673). Numbers on nodes, indicate bootstrap support for that node. B, geographical distribution of the specimens analysed. Coloured dots correspond with the samples analysed for COI and the dotted lines to the distributions of the only widespread species.

Molecular results

A total of 18 new sequences were obtained from the COI marker (658 bp alignment length; 129 parsimony informative characters); the evolutionary model that best fitted the data was HKY+G (shape parameter α=0.1730; ti/tv ratio = 3.8753; freqA = 0.3456, freqC = 0.1520, freqG = 0.1979, freqT = 0.3045). Taking *Onconida tropis* Baba & de Saint Laurent, 1996 and *O. alaini* Baba & de Saint Laurent, 1996 as outgroups, ML phylogenetic reconstruction corroborated morphological findings confirming six highly differentiated and reciprocally monophyletic genealogical lineages, characterized by strong bootstrap support (see Fig. 1 for phylogenetic reconstruction, geographical distribution and Table 1 for levels of K2P-corrected genetic distances among the six lineages). We discuss the genealogical relationships among pairs of these lineages in each of the species sections to follow.

TABLE 1. Pairwise K2P-corrected evolutionary divergence comparisons among *Agononida* species.

	A rubrizonata	*A incerta*	*A africerta*	*A auscerta*	*A indocerta*	*A norfocerta*
A rubrizonata	–					
A incerta	0.038	–				
A africerta	0.135	0.143	–			
A auscerta	0.028	0.037	0.134	–		
A indocerta	0.124	0.134	0.035	0.123	–	
A norfocerta	0.044	0.043	0.123	0.039	0.112	–

Morphology and systematics

Key to species of the *Agononida incerta* complex

This key relies on only two features: the shape of the anterolateral slope of the telson and the numbers of dactylar robust setae on pereopods 2–4. Both vary between individuals, on the basis of sex, size and randomly. Geography can be helpful but species do co-occur in Western Australia.

1. Anterolateral margin of telson of male with a solid thickened tongue-like lobe protruding posterolaterally and dorsally, ornamented with parallel ridges; of female oblique, sinuous, overlapping transverse suture as a thin short projection (Figs 2M, N) . . . . . *A. rubrizonata*
– Anterolateral margin of telson never protruding in this way 2
2. Pereopods 2–4 dactyli with 37, 17, 10 robust setae along flexor margins respectively (median values!); anterolateral margin of telson concave and smooth over anterior 70%, remainder prominent, widest well anterior to transverse suture and narrower adjacent to transverse suture (Figs 2H, I); transverse broad orange bands subdistally on meri of pereopods 1–4, proximally on carpi of pereopods 1–4, subdistally on carpus of pereopod 1, proximally on propodus of pereopod 1, at propodus-dactylus articulation of pereopod 1, and subdistally on propodi of pereopods 2–4 *A. indocerta*
– Pereopods 2–4 dactyli with at most 20, 6, 3 robust setae along flexor margins respectively (rarely more); anterolateral margin of telson not as above; evenly coloured or with bands distal (not subdistal) on pereopodal meri 3
3. Pereopod 2 dactylus with 4 (rarely 2–8) robust setae along flexor margin; pereopodal dactyli 8–9 times as long as basal width . . . . . *A. auscerta*
– Pereopod 2 dactylus with at least 10 (as many as 22) robust setae along flexor margin; pereopodal dactyli 5–6 times as long as basal width. 4
4. Pereopod 2 dactylus with 12 (rarely 10–18) and pereopod 3 dactylus with 1–4 robust setae along flexor margins; anterolateral margin of telson with smooth proximal concavity over anterior 70% that ends at sharp step, remainder truncate-convex, margin oblique anterior to transverse suture, with crenellate margin (Figs 2K, L). . . . . *A. norfocerta*
– Pereopod 2 dactylus with 20 (rarely 4–30) and pereopod 3 dactylus with usually 6 (rarely 1–17) robust setae along flexor margins; anterolateral margin of telson sinuous or with 2 notches 5
5. Anterolateral margin of telson sinusoidal, concave and smooth over anterior 60%, remainder strongly and evenly convex, margin crenellate, rarely with obvious notch (Figs 2D, E) . . . . . *A. africerta*
– Anterolateral margin of telson quasi-3-lobed, middle lobe largest, with sharp edge, deflected dorsally, separated from weak anterior lobe by shallow concavity and from more rounded thicker posterior lobe by deep notch, exaggerated in males, finely crenellate over posterior two-thirds in larger individuals (Figs 2A–C) . . . . . *A. incerta*

Implicit characters

The following are true of all taxa in this complex unless explicitly stated otherwise:

Carapace with numerous short striae and transverse interrupted ridges, with rows of short setae along transverse striae. Gastric region with pair of epigastric spines, without lateral epigastric spines; branchial region with 3 pairs of postcervical spines, first two closer than second and third; posterior border of carapace unarmed. Lateral margins convex, widest at midpoint; anterolateral (first) spine inclined upwards, reaching sinus between rostrum and supraocular spine, second lateral spine about third as long as first, third and fourth spines set obliquely along anterior cervical groove, fifth and sixth lateral spines on branchial region, smaller. Rostrum curving upwards to horizontal distal half; oblique in profile, slightly curved. Abdominal somites 2–4 covered with squamae; each with 2 pairs of spines along anterior transverse ridge; somite 4 with median spine on posterior transverse ridge. Telson with numerous transverse squamae.

Antennule, article 1 with 1 distomesial spine longer than 2 distolateral spines, plus small lateral spine. Antenna article 1 with strong distomesial process overreaching antennular and antennal peduncles; article 2 with strong distomesial spine exceeding article 3, plus small mesial spine, with small distolateral spine; articles 3–4 unarmed. Maxilliped 3 merus with spine on flexor margin and long spine on distal extensor angle.

Pereopod 1 (cheliped) merus trapezoidal in cross-section; carpus subtrapezoidal in cross-section; fixed finger cutting edge with ridge of c. 50 uneven teeth, few more prominent than others, apex bifid. Pereopod 2 propodus with row of robust setae along flexor margin, plus distal pair. Pereopod 3 propodus with row of robust setae along flexor margin, plus distal pair. Pereopod 4 merus without spines proximally on upper face; propodus with row of robust setae along flexor margin, plus distal pair.

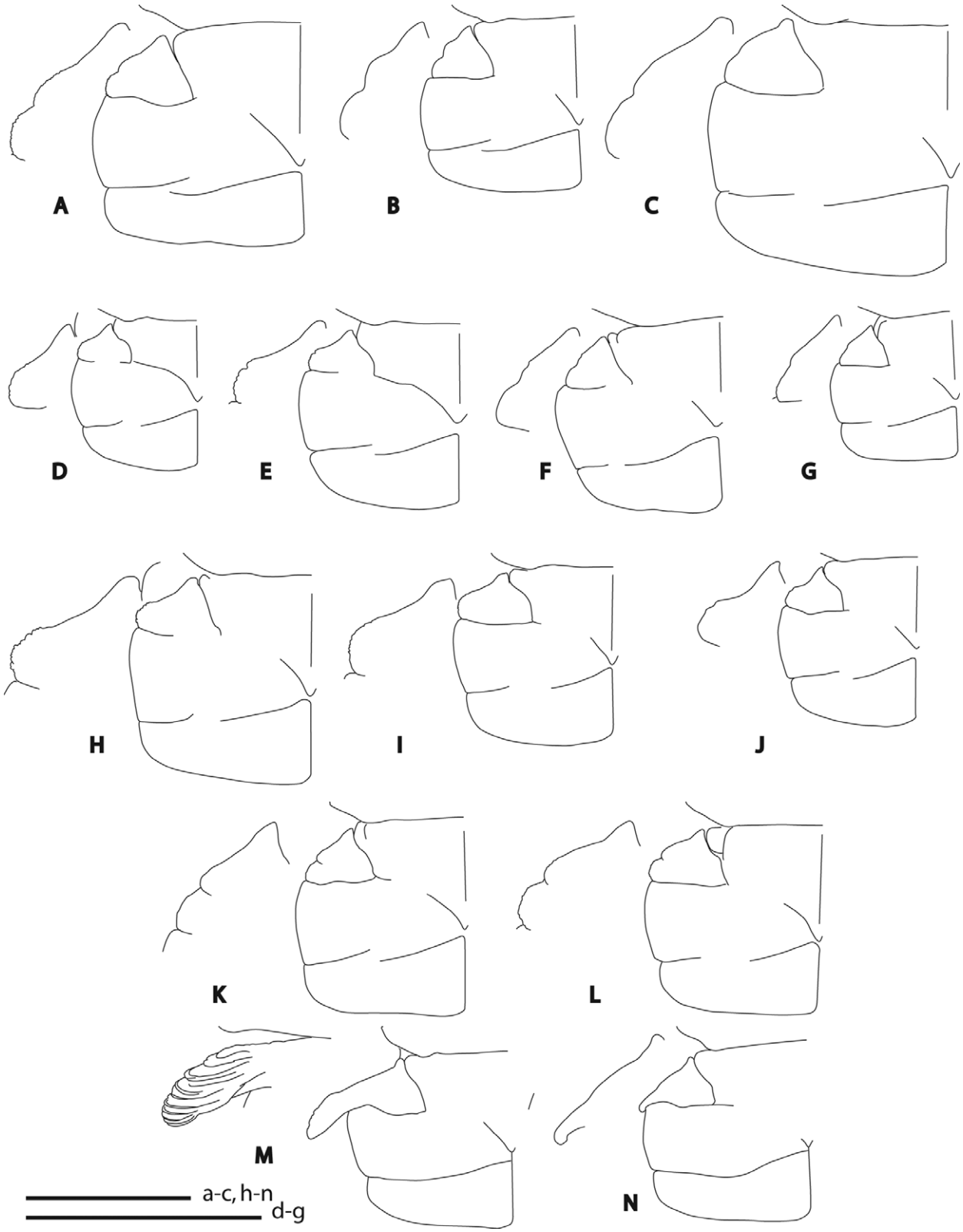

FIGURE 2. Telsons of species of the *Agononida incerta* complex, with details of the anterolateral margin at twice scale . Scale bar = 10 mm. *Agononida incerta*: A, male, cl 32 mm, Western Australia, NMV J56025. B, ovigerous female, cl 24 mm, Western Australia, NMV J55021. C, supermale, cl 38 mm, Philippines, ZMUC CRU11555. *Agononida africerta*: D, male, cl 15.1 mm, MNHN IU-2008-10437. E, female, cl 13.8 mm, MNHN IU-2008-10438. *Agononida auscerta*: F, male, cl 22 mm, NMV J62124. G, ovigerous female, cl 24.3 mm, NMV J55995. *Agononida indocerta*: H, supermale, cl 30.3 mm, NMV J62081. I, male, cl 27 mm, NMV J57295. J, ovigerous female, cl 25 mm, NMV J57295. *Agononida norfocerta*: K, male, cl 30.7 mm, MNHN IU-2011-592. L, female, cl 27 mm, NMV J62814. *Agononida rubrizonata*: M, male, cl 28.2 mm, Western Australia, NMV J57292. N, ovigerous female, Western Australia, cl 25 mm, NMV J57292.

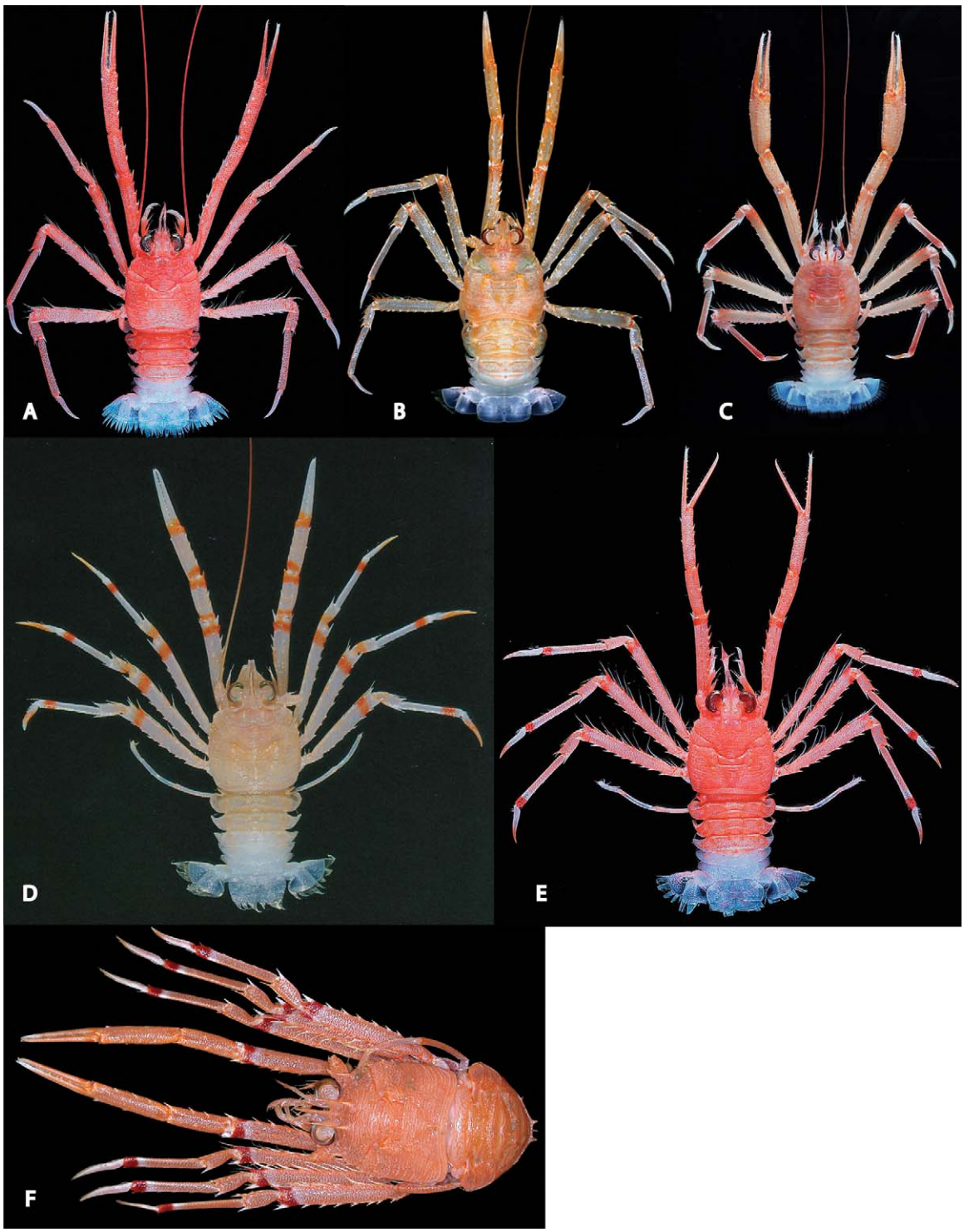

FIGURE 3. Colour photographs of living animals. A, *Agononida incerta*, Nanfang-ao, Taiwan, T.-Y. Chan (from Baba *et al.*, 2009). B, *A. incerta*, NMV J55021, Karen Gowlett-Holmes. C, *A. africerta*, MNHN IU-2008-10192, T.-Y. Chan. D, *A. indocerta*, Western Australia, D. Evans (from Jones & Morgan, 2002). E, *A. rubrizonata*, paratype, Taiwan, T.-Y. Chan. F, *A. rubrizonata*, Western Australia, NMV J55029, Karen Gowlett-Holmes.

Agononida incerta (Henderson, 1888)

(Figs 2A–C, 3A, B, 4–7)

Munida incerta Henderson, 1888: 130, pl. 13, figs 4, 4a.
Agononida incerta.—Baba *et al.* 2009: 76–78, fig. 63.
Agononida sp. aff. *incerta*.—Poore *et al.* 2008: 18 (part).

Material examined. *Holotype*. Celebes Sea, Philippines, off Sibago Island (off Zamboanga), 06°47´N, 122°28´E, 458 m, BMNH 1888:33 (female without chelipeds, pereopods missing or fragmented and unattached, cl 15.8 mm).

Other material. TAIWAN. Su-ao fishing port, 10.03.2005, NTOU M01563 (3 juveniles, cl 9–13 mm); 05.12.1991, NTOU M01564 (2 males, cl 12, 18 mm). Taiwan, 22°11.4'N, 120°22.58′E, 280–452 m, 23.11.2001 (stn CD140), NTOU M01565 (3 ovigerous females, 20–23 mm; 2 males, cl 18, 11 mm).

PHILIPPINES, Celebes Sea, 25 mi E by S of Zamboanga, 06°42'N 122°19′E, 366–293 m, 03.05.1914 (Th. Mortensen colln stn KB555), ZMUC CRU-11555 (4 females, cl 11–21 mm; 2 males, cl 22, 38 mm). 25 mi E of Zamboanga, 06°54'N 122°25′E, 460 m, 04.05.1914 (Th. Mortensen stn KB576), ZMUC CRU-11576 (male, cl 11 mm).

Philippines Sea, E of Luzon, Philippines, 15°59.45'N 121°50.68′E, 422–431 m, 20.05.2007 (stn CP2658), NTOU M01566 (2 females, cl 7.5, 9.5 mm; 2 males cl 7, 11 mm).

AUSTRALIA. Western Australia (all collected by FRV *Southern Surveyor*, 2005–2007). Ashmore L30 transect, 12°31.7′S 123°25.6′E, 401–404 m (stn SS05/2007/192), NMV J56025 (male, cl 32 mm). Ashmore L30 transect, 12°36.1′S 123°25.5′E, 419–403 m (stn SS05/2007/198), NMV J56111 (male, cl 26 mm). Off Barrow Island transect, 21°00.38′S 114°22.86′E, 399–411 m (stn SS10/2005/171), NMV J55054 (2 females, cl 9, 20 mm). Off Barrow Island, 21°00.40′S 114°22.9′E, 399–408 m (stn SS10/2005/172), NMV J59657 (2 males, cl 18. 18 mm). Off Ningaloo North, 21°58.2′S 113°47.5′E, 356–324 m (stn SS10/2005/157), NMV J55025 (males, cl 29 mm). Off Ningaloo North, 21°58.2′S 113°47.4′E, 373–382 m (stn SS10/2005/165), NMV J59659 (male, cl 12 mm); NMV J59658 (male, cl 12 mm). Off Ningaloo South, 22°04.31′S 113°45.3′E, 399–387 m (stn SS10/2005/151), NMV J55020 (male; female, cl 11 mm), NMV J60835 (male, cl 25 mm). Off Point Cloates, 22°50.8′S 113°20.2′E, 420–430 m (stn SS10/2005/137), NMV J55053 (2 males, cl 18, 19 mm). Off Red Bluff, 23°59.1′S 112°32.7′E, 398–402 m (stn SS10/2005/128), NMV J55021 (ovigerous female, cl 24 mm).

Diagnosis. Telson anterolateral margin quasi-3-lobed, middle lobe largest, with sharp edge, deflected dorsally, separated from weak anterior lobe by shallow concavity and from more rounded thicker posterior lobe by deep notch, exaggerated in males, finely crenellate over posterior two-thirds in larger individuals. Pereopodal 2–4 dactyli 5.1–6.6 times as long as greatest basal width; robust setae on dactylus of pereopod 2 number 12–30 (median 17, rarely 4), of pereopod 3, 2–10 (median 6, rarely 1–17), and of pereopod 4, 1–3 (rarely 6). Pereopod 4 merus without spines proximally on upper face.

Descriptions. *Adult male. Based on NMV J56025 (cl 32 mm).* Carapace 0.9 times as long as greatest width. Gastric region with pair of small lateral epigastric spines. Frontal margin inclined posteriorly at 12° from midline. Rostrum spiniform, 0.43 length of carapace (both measured from base of supraocular spines); supraocular spine 0.64 length of rostrum (both measured from base of rostrum). Thoracic sternite 3 0.43 width of sternite 4; midlength of sternal plastron (sternites 4–7) 0.6 width of sternite 7. Telson greatest width twice midlength; anterolateral margin quasi-3-lobed, middle lobe largest, with sharp edge, deflected dorsally, separated from weak anterior lobe by shallow concavity and from more rounded thicker posterior lobe by deep notch, finely crenellate over posterior two-thirds; lateral margin evenly convex.

Eyes with maximum corneal diameter 1.1 basal width of supraocular spines. Maxilliped 3 ischium 0.6 times as long as merus.

Pereopod 1 (cheliped) of typical adult form, covered with flat squamae fringed with short setae; 3.3 times as long as carapace, merus 0.9 times as long as carapace, carpus 0.78 times as long as merus, propodus 1.8 times as long as merus, fingers 0.5 times as long as total propodus length. Pereopod 1 (cheliped) merus with 1+9 spines along upper margin, 4–5 spines along mesial face, 15 spines along lateral face, with distal spine only on lower margin; carpus with 1+3 spines on upper margin, 3 spines on mesial face, 1 spines on lateral face; propodus oval in cross-section, spines with marginal spines, with 3–4 spines on upper margin, with 1+0–1 spines along mesial face, with 1+0 spine on lateral face near base of dactylus, with 1–3 oblique spines along lower margin, without spines on lower lateral face; dactylus cutting edge with ridge of c. 50 uneven teeth, few more prominent than others.

Minor pereopod 1 not differentiated.

Pereopod 2 3.5 times carapace length, merus 1.5 times carapace length, 9.4 times a long as greatest width, carpus 0.25 times as long as merus, propodus 0.6 times as long as merus, dactylus 0.5 times as long as propodus; merus with 1+12 spines along extensor margin, with 1+6 spines along flexor margin; carpus with 1+1 spines along extensor margin; dactylus evenly curved over distal two-thirds, 6.6 times as long as greatest basal width, with row of 18 robust setae distal to heel of flexor margin.

Pereopod 3 3.5 times carapace length, merus 1.5 times carapace length, 8.3 times a long as greatest width, carpus 0.3 times as long as merus, propodus 0.6 times as long as merus, dactylus 0.5 times as long as propodus; merus with 1+15 spines along extensor margin, with 1+6 spines along flexor margin; carpus with 1+2 spines along extensor margin; dactylus evenly curved over distal two-thirds, 6.6 times as long as greatest basal width, with row of 5 robust setae distal to heel of flexor margin.

Pereopod 4 3.3 times carapace length, merus 1.3 times carapace length, 7.2 times a long as greatest width, carpus 0.3 times as long as merus, propodus 0.7 times as long as merus, dactylus 0.5 times as long as propodus; merus with 1+13 spines along extensor margin, with 1+6 spines along flexor margin; carpus with 1+1 spines along extensor margin; dactylus more gently curved than dactyli 2 or 3, distally less setose, 6.5 times as long as greatest basal width, with 5 robust seta(e) distal to heel of flexor margin.

Supermale. Based on ZMUC CRU-11555, cl 38 mm. Carapace as long as greatest width. Rostrum spiniform, 0.4 length of carapace (both measured from base of supraocular spines). Telson anterolateral margin with shallow concavity near anterior curvature of anterior section, almost straight beyond this point, a second shallow concavity 70% along anterolateral margin, separating the anterior section from rounded, lobed, slightly crenellate posterior section; lateral margin almost straight, more curved proximally and distally.

Pereopod 1 (cheliped) of grossly expanded supermale form, slightly asymmetrical, covered with elevated squamae fringed with short setae; 3.7 times as long as carapace, merus 1.1 times as long as carapace, carpus 0.64 times as long as merus, propodus 1.5 times as long as merus. Pereopod 1 (cheliped) merus with 1+5 spines along upper margin, 2 spines along mesial face, 10 spines along lateral face; carpus with 1+2 spines on upper margin, 1 spines on mesial face, 0 spines on lateral face; propodus oval in cross-section, with shallow longitudinal grooves mesially and laterally, palm deeper distally, with 3 spines on upper margin, with 1+0 spines along mesial face, with 1+1 spine on lateral face near base of dactylus, without spines along lower margin or on lower lateral face; dactylus cutting edge with 2 proximal blunt teeth and ridge of c. 50 uneven teeth, few more prominent than others.

Minor pereopod 1 only slightly less developed than other, minor differences in spination.

Pereopod 2 3 times carapace length, merus 1.3 times carapace length, 7.1 times a long as greatest width; merus with 1+11 spines along extensor margin, with 1+4 spines along flexor margin; carpus with 1+0 spines along extensor margin; dactylus 5.1 times as long as greatest basal width, with row of 30 robust setae distal to heel of flexor margin.

Pereopod 3 3 times carapace length, merus 1.3 times carapace length, 6.7 times a long as greatest width; merus with 1+11 spines along extensor margin, merus with 1+4 spines along flexor margin; carpus with 1+1 spines along extensor margin; dactylus 5.2 times as long as greatest basal width, with row of 6 robust setae distal to heel of flexor margin.

Pereopod 4 2.8 times carapace length, merus as long as carapace length; merus with 1+8 spines along extensor margin, merus with 1+4 spines along flexor margin; dactylus 5.3 times as long as greatest basal width, with 1 robust seta distal to heel of flexor margin.

Ovigerous female. Based on NMV J55021 (cl 23 mm). Telson anterolateral margin quasi-3-lobed, middle lobe with rounded edge, not deflected dorsally, separated from weak anterior lobe by shallow concavity and from more rounded thicker posterior lobe by broad notch, finely crenellate over posterior third.

Pereopod 1 (cheliped) merus with 1+5–6 spines along upper margin, 5 spines along mesial face, 11 spines along lateral face. Pereopod 1 (cheliped) carpus with 1+2 spines on upper margin, 2 spines on mesial face. Pereopod 1 (cheliped) propodus with 3 spines on upper margin, with 1+1–3 spines along mesial face, with 1+1 spine on lateral face near base of dactylus.

Colour. Based on WA specimen, NMV J55021 (Figs 3A, B). Unevenly orange over carapace and abdominal somites 1–4, abdominal somites 5, 6 and telson uncoloured; colour highlighted at the bases of abdominal spines and spines on pereopodal meri; narrow transverse orange bands at the ends of meri, carpi and propodi of pereopods 1–4.

Variation. *Agononida incerta* displays both allometric and sexual variation. One supermale captured close to the type locality was identified with thickened chelipeds 12% longer than a typical male. The critical specific character, the anterolateral margin of the telson, always displays a clear deep hiatus between the middle and rounded posterior lobes. The middle lobe is not more prominent than the posterior lobe in females and juveniles, while in adult males, it is larger, with a sharp edge deflected dorsally. The deflection is more subdued in supermales.

Besides this variation is some more at random. Some individuals possess only two postcervical spines on one or both sides (rather than three pairs). Some larger specimens from Western Australia have a minute epigastric spine lateral to the pair of major epigastric spines. While the number of mesial spines on the merus of the cheliped is seven or eight on the male described above, 3–5 is more typical. The numbers of spines on the margins of pereopodal meri may be one or two larger or smaller than the figures given in the descriptions and are not consistent from left to right side. The numbers of robust setae distal to the heel on the flexor margin of the dactyli of pereopods 2–4 vary considerably, more on larger specimens: pereopod 2, 12–30 (median 17; rarely 4); pereopod 3, 2–10 (median 6, rarely 1–17); pereopod 4, 1–3 (rarely 6).

Distribution. Taiwan, Philippines to southern Western Australia; 22°N–24°S; 280–460 m (in Western Australia the species was not taken at stations targeting the 200 m, 800 m or deeper contours).

Remarks. The holotype is a small incomplete female with what few limbs remain detached (Figs 4, 5). Three key features, besides the coincidence of the collecting locality, enable the ZMUC material to be confidently identified. Apart from the supermale, the specimens from this collection were fragmented and limbs mixed. The shape of the anterolateral margin of the telson is consistent across all specimens; the proportions of the dactyli of pereopods 3 and 4 are within the range for this species; and the numbers of robust setae on the flexor margins of these articles, 9 and 1 on the holotype, are consistent with pereopods 3 and 4. The four specimens collected by NTOU in the Philippines are all small with more elongate pereopodal dactyli than typical, fewer robust setae on the dactylus of pereopod 2 (4–5) but the strong hiatus along the anterolateral margin of the telson is typical of *A. incerta*. The material from northwestern Australia could not be distinguished on morphological grounds. A typical male and female from this locality are illustrated.

Agononida incerta is distinguished from other species in the genus by the particularly broad dactyli of pereopods 2–4 in larger specimens, and the high number of robust setae on pereopodal dactyli 2 and 3, up to 30 and 17 respectively (usually around 17 and 6). These numbers are similar to those on *A. indocerta* and *A. africerta*, species that differ in several other ways. As with other species it has its own characteristic shape of the anterolateral margin of telson, notably in adult males the large middle lobe with a sharp edge deflected dorsally, separated from weak anterior lobe by shallow concavity and from more rounded thicker posterior lobe by a deep notch. See remarks under *Agononida auscerta*.

The small holotype has a proportionately longer rostrum and longer telson than the adult male and supermale.

Agononida incerta is genealogically more closely related to *A. norfocerta* found only in Norfolk Ridge (SW Pacific), than to any other species (Fig. 1).

The photograph (Fig. 12A) of a specimen from Nanfang-Ao, Taiwan, and published previously by Baba *et al.* (2009) illustrates narrower pereopods than the large supermale from the same region but is similar to others of the same size.

Agononida africerta n. sp.

(Figs 2D, E, 3C, 8)

?*Munida incerta*.—Kensley 1977: 162.—Baba 1990: 963–964.—Tirmizi 1966: 205, fig. 22.

Material examined. *Holotype*. MOZAMBIQUE. Mozambique Channel. 25°13′S, 35°18′E, 480–503 m, 10.04.2009 (MAINBAZA stn CP3135), MNHN IU-2008-10438 (female, cl 22. 4 mm).

Paratypes. MOZAMBIQUE. Mozambique Channel. 23°31′S, 35°50′E, 446–475 m, 11.04.2009 (MAINBAZA stn CP3142), MNHN IU-2008-10192 (supermale, cl 31 mm); MNHN IU-2008-10440 (female, cl 26 mm); MNHN IU-2008-10441 (female, cl 24 mm); MNHN IU-2008-10442 (male, cl 17 mm). 24°11.71′S, 35°42.3′E, 505–506 m, 15.04.2009 (MAINBAZA stn CC3164), MNHN IU-2008-10435 (female, cl 13.8 mm). 24°11.71′S,35°42.3E, 505–507 m, 15.04.2010 (MAINBAZA stn CC3165), MNHN IU-2008-10436 (male, cl 15.1 mm). 24°11.71′S, 35°42.3′E, 505–508 m, 15.04.2011 (MAINBAZA stn CC3166), MNHN IU-2008-20703. (5, females, cl 6–12 mm; 3 males, cl. 10–17 mm). 25°13′S, 35°18′E, 480–503 m, 10.04.2009 (MAINBAZA stn CP3135), MNHN IU-2008-10191 (female, cl 18 mm); MNHN IU-2008-10437 (male, cl 18.8); MNHN IU-2008-20704 (many juveniles, cl ~18 mm). 25°12′S, 35°17′E, 503–505 m, 10.04.2009 (MAINBAZA stn CP3136), MNHN IU-2008-20705 (3 females, cl 12–24 mm; 2 males, cl 12 mm); MNHN IU-2008-10190 (female, cl 17 mm); MNHN IU-2008-10439 (female).

Other material. MADAGASCAR. 12°44.8′S, 48°10.6′E, 570–563 m, 05.03.1971 (Crosnier stn P1-5), MNHN Ga-685 (3 females; 13 males, cl to 23 mm).

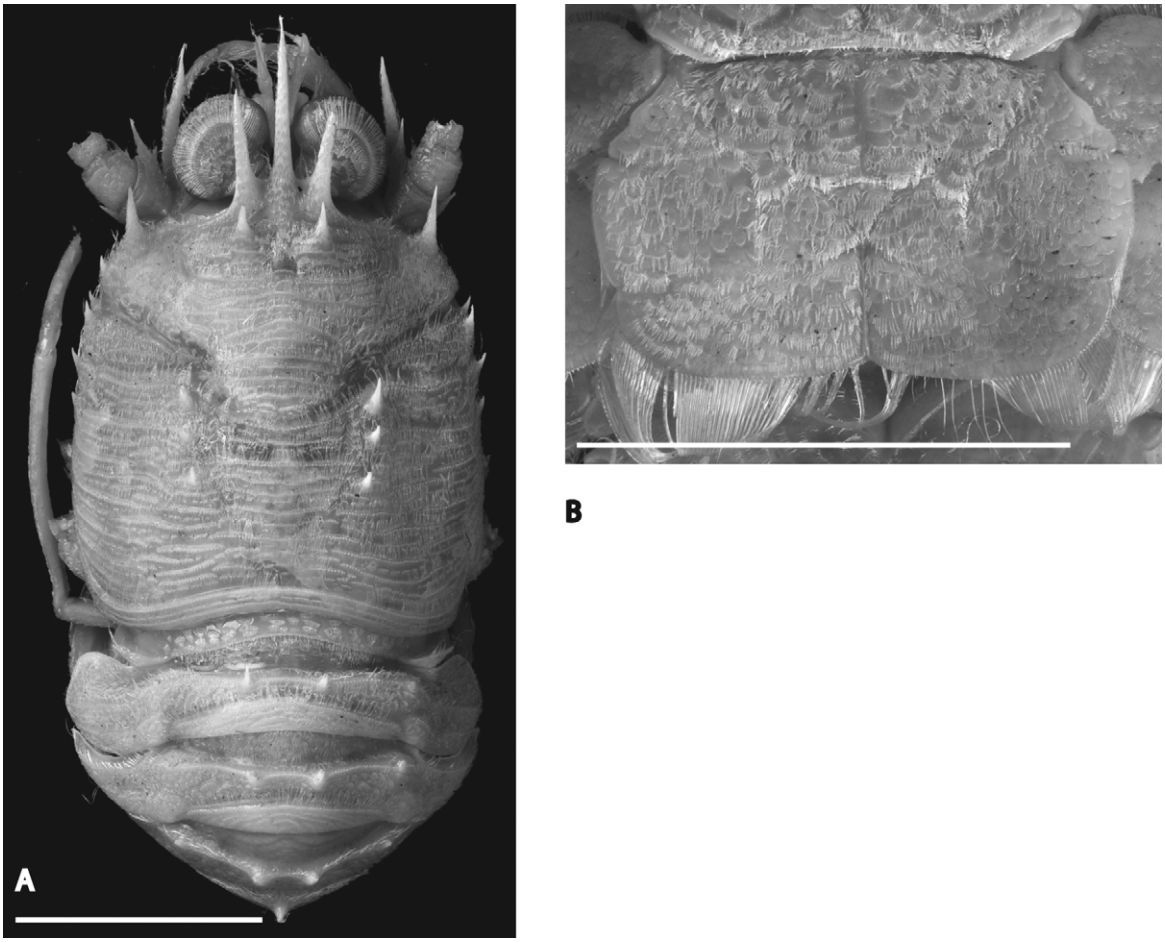

FIGURE 4. *Agononida incerta* (Henderson, 1888) Holotype, juvenile female. A, dorsal view; B, telson. Scale bars = 10 mm.

Diagnosis. Telson anterolateral margin sinusoidal, concave and smooth over anterior 60%, remainder sometimes separated by notch, strongly convex, margin almost longitudinal anterior to transverse suture, with crenellate margin. Pereopodal 2–4 dactyli about 6 times as long as greatest basal width, 15–25 (median about 20, 8 exceptional); pereopod 3, 4–9 (median 6); pereopod 4, 1–3. Pereopod 4 merus with 1–4 spines proximally on upper face.

Descriptions. *Ovigerous female. Based on MNHN IU2008–10438, cl 22.4 mm.* Carapace 0.9 times as long as greatest width. Frontal margin inclined posteriorly at 18° from midline. Rostrum spiniform, 0.45 length of carapace (both measured from base of supraocular spines); supraocular spine 0.65 length of rostrum (both measured from base of rostrum). Thoracic sternite 3 0.48 width of sternite 4; midlength of sternal plastron (sternites 4–7) 0.6 width of sternite 7. Telson greatest width 1.8 times midlength; anterolateral margin sinusoidal, concave and smooth over anterior 60%, remainder separated by notch, strongly convex, margin almost longitudinal anterior to transverse suture, with crenellate margin; lateral margin convex, narrower posteriorly than anteriorly.

Eyes with maximum corneal diameter 0.9 basal width of supraocular spines. Maxilliped 3 ischium 0.6 times as long as merus.

Pereopod 1 (cheliped) of typical adult form, covered with flat squamae fringed with short setae; 3.6 times as long as carapace, merus 0.9 times as long as carapace, carpus 0.7 times as long as merus, propodus 1.9 times as long as merus, fingers 0.5 times as long as total propodus length. Merus with 1+9 spines along upper margin, 4 spines along mesial face, 17 spines along lateral face, with distal spine and 1–3 spine-like squamae on lower margin; propodus spines with marginal spines, with 6 spines on upper margin, with 1+4 spines along mesial face, with 1+3 spine on lateral face near base of dactylus, with 1–3 oblique spines along lower margin plus 1–3 spines on lower lateral face; dactylus cutting edge with ridge of c. 50 denticles.

Minor pereopod 1 with only minor differences.

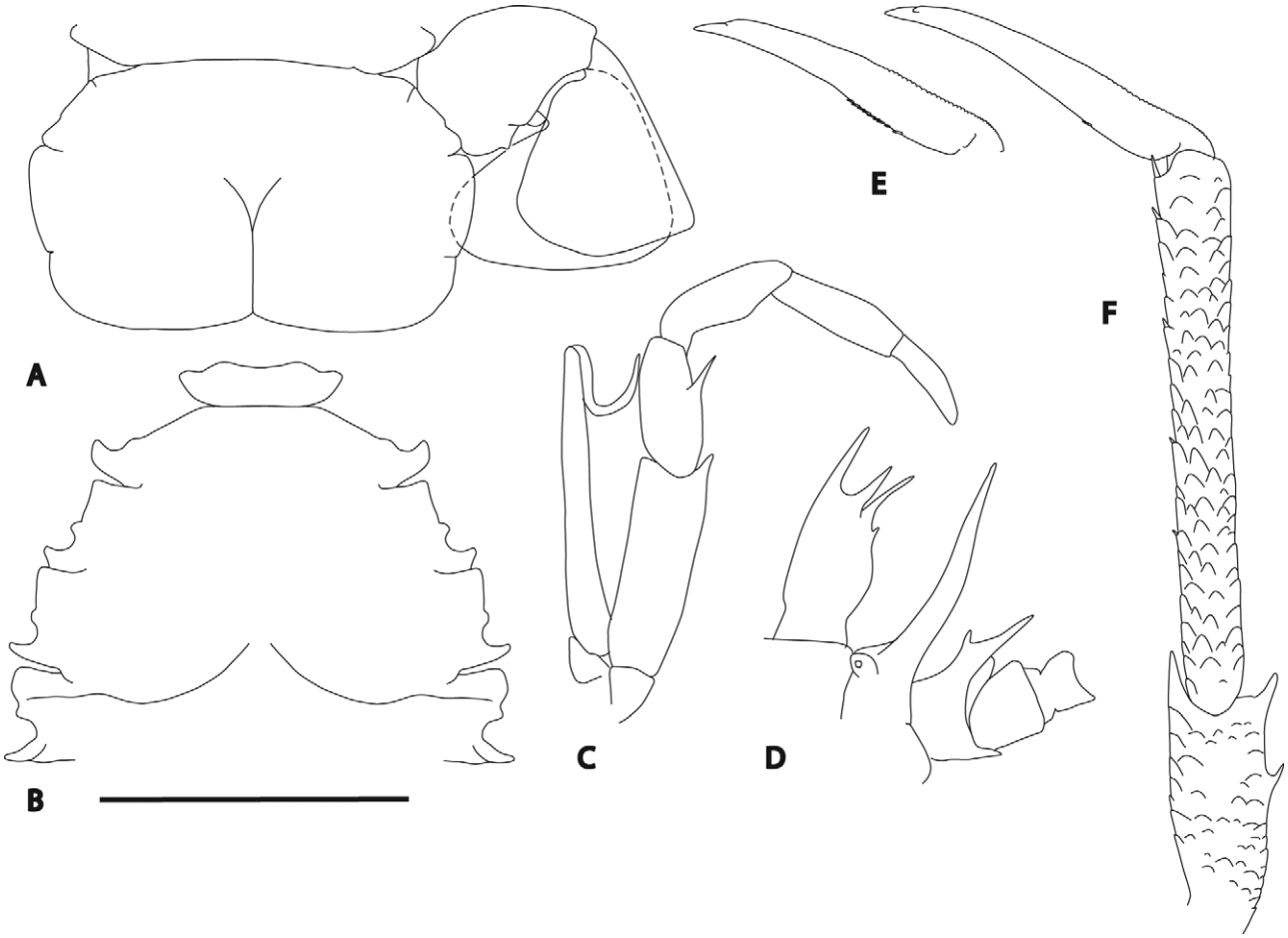

FIGURE 5. *Agononida incerta* (Henderson, 1888) Holotype, juvenile female. A, telson and uropod; B, sternal shield; C, maxilliped 3; C, left antennule and antenna, ventral view; E, free dactylus (probably of pereopod 2, with 9 robust setae); F, carpus–dactylus, pereopod 4 (with 1 robust seta). Scale bar=5 mm.

Pereopod 2 2.9 times carapace length, merus 1.3 times carapace length, 8.8 times a long as greatest width, carpus 0.24 times as long as merus, propodus 0.6 times as long as merus, dactylus 0.6 times as long as propodus; merus with 1+16–20 spines along extensor margin, with 1+8 spines along flexor margin; carpus with 1+1–2 spines along extensor margin; dactylus evenly curved over distal two-thirds, 5.9 times as long as greatest basal width, with row of 20 robust setae distal to heel of flexor margin.

Pereopod 3 2.9 times carapace length, merus 1.3 times carapace length, 7.5 times a long as greatest width, carpus 0.24 times as long as merus, propodus 0.6 times as long as merus, dactylus 0.6 times as long as propodus; merus with 1+16–20 spines along extensor margin, with 1+9–10 spines along flexor margin; carpus with 1+3 spines along extensor margin; dactylus evenly curved over distal two-thirds, 6.1 times as long as greatest basal width, with row of 4 robust setae distal to heel of flexor margin.

Pereopod 4 2.8 times carapace length, merus 1.1 times carapace length, 6.7 times a long as greatest width, carpus 0.3 times as long as merus, propodus 0.7 times as long as merus, dactylus 0.5 times as long as propodus; merus with 1+15–18 spines along extensor margin, with 1+8 spines along flexor margin, merus with 1–4 spines proximally on upper face; carpus with 1+2 spines along extensor margin; dactylus more gently curved than dactyli 2 or 3, distally less setose, 6.1 times as long as greatest basal width, dactylus with 2 robust seta(e) distal to heel of flexor margin.

Male. Based on MNHN IU2008–10437, cl 19.0 mm. Telson anterolateral margin much as in female. Pereopod 1 (cheliped) merus 1.1 times as long as carapace, carpus 0.5 times as long as merus, propodus 1.3 times as long as merus, fingers 0.55 times as long as total propodus length. Merus with 1+8 spines along upper margin, 5–8 spines along mesial face, 14 spines along lateral face.

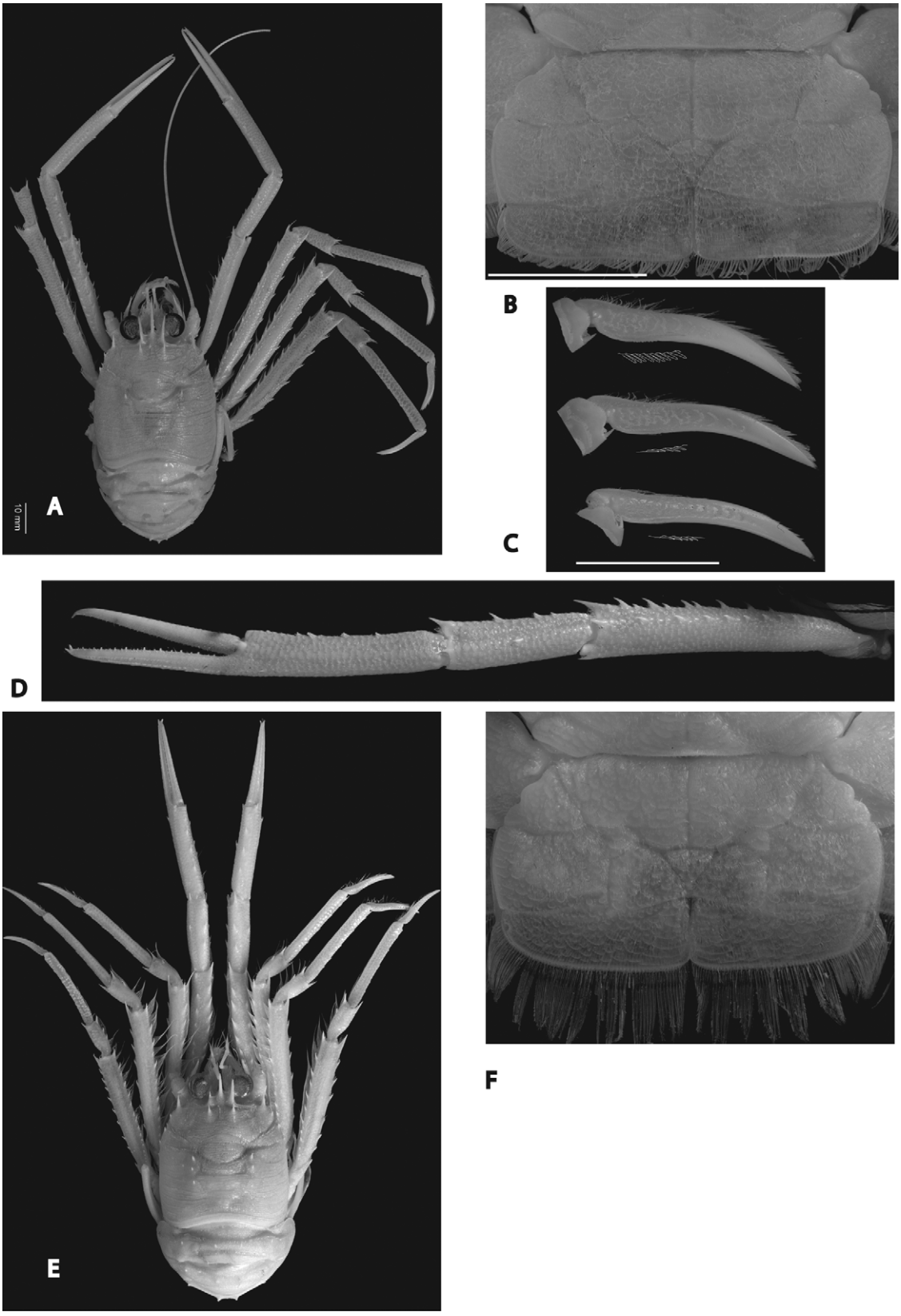

FIGURE 6. *Agononida incerta* (Henderson, 1888) Western Australian specimens. Male, NMV J56025: A, habitus; B, telson; C, dactyli of pereopods 2–4 with detail of robust setae at greater magnification (most broken); D, cheliped in lateral view. Ovigerous female, NMV J55021. **E**, Habitus; **F**, telson. Scale bars = 10 mm.

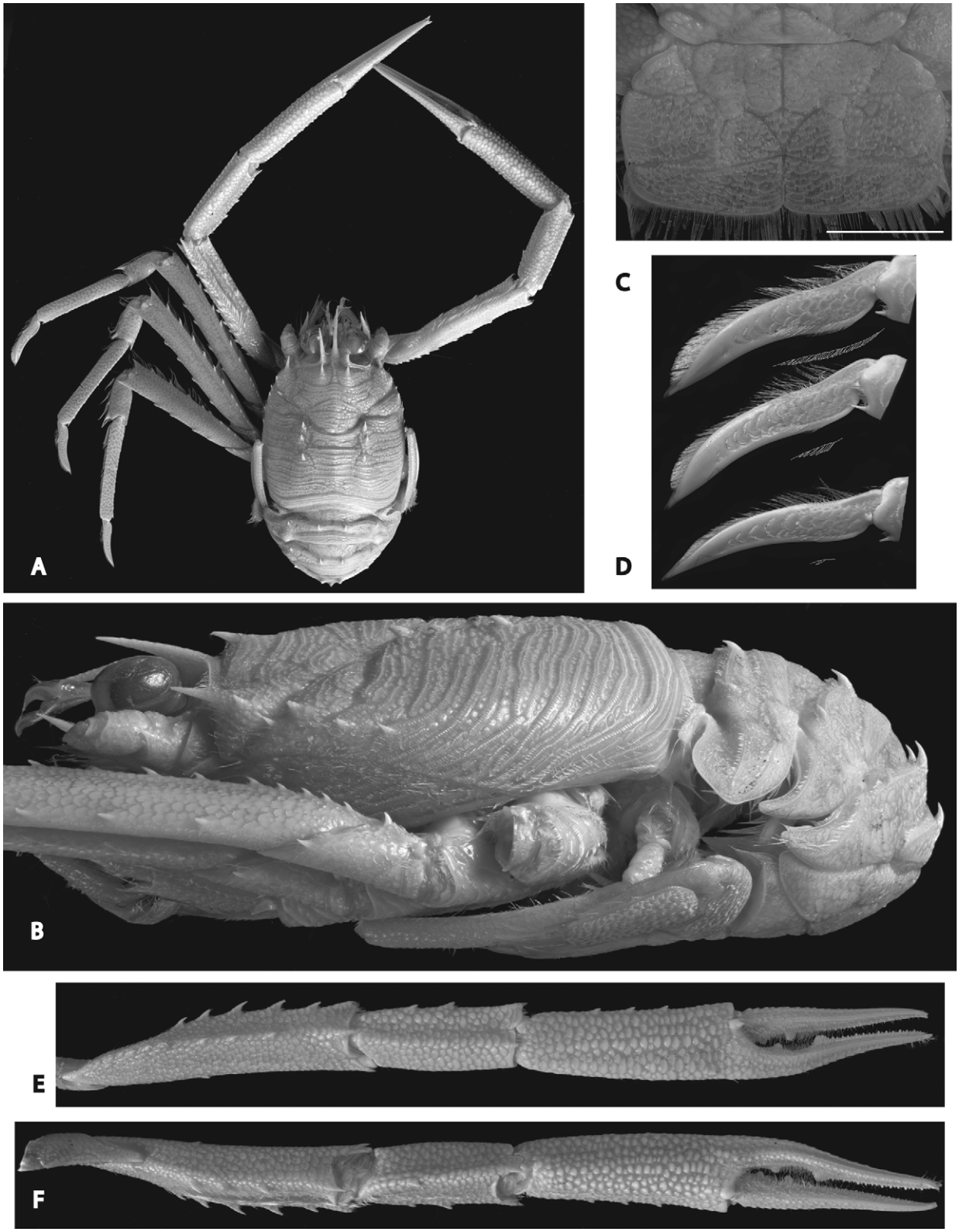

FIGURE 7. *Agononida incerta* (Henderson, 1888) Supermale, ZMUC CRU11555. A, B, habitus in dorsal and lateral views**;** C, telson (scale bar=5 mm); D, left dactyli of pereopods 2–4 with detail of robust setae at greater magnification; E, F, major cheliped in lateral and mesial views.

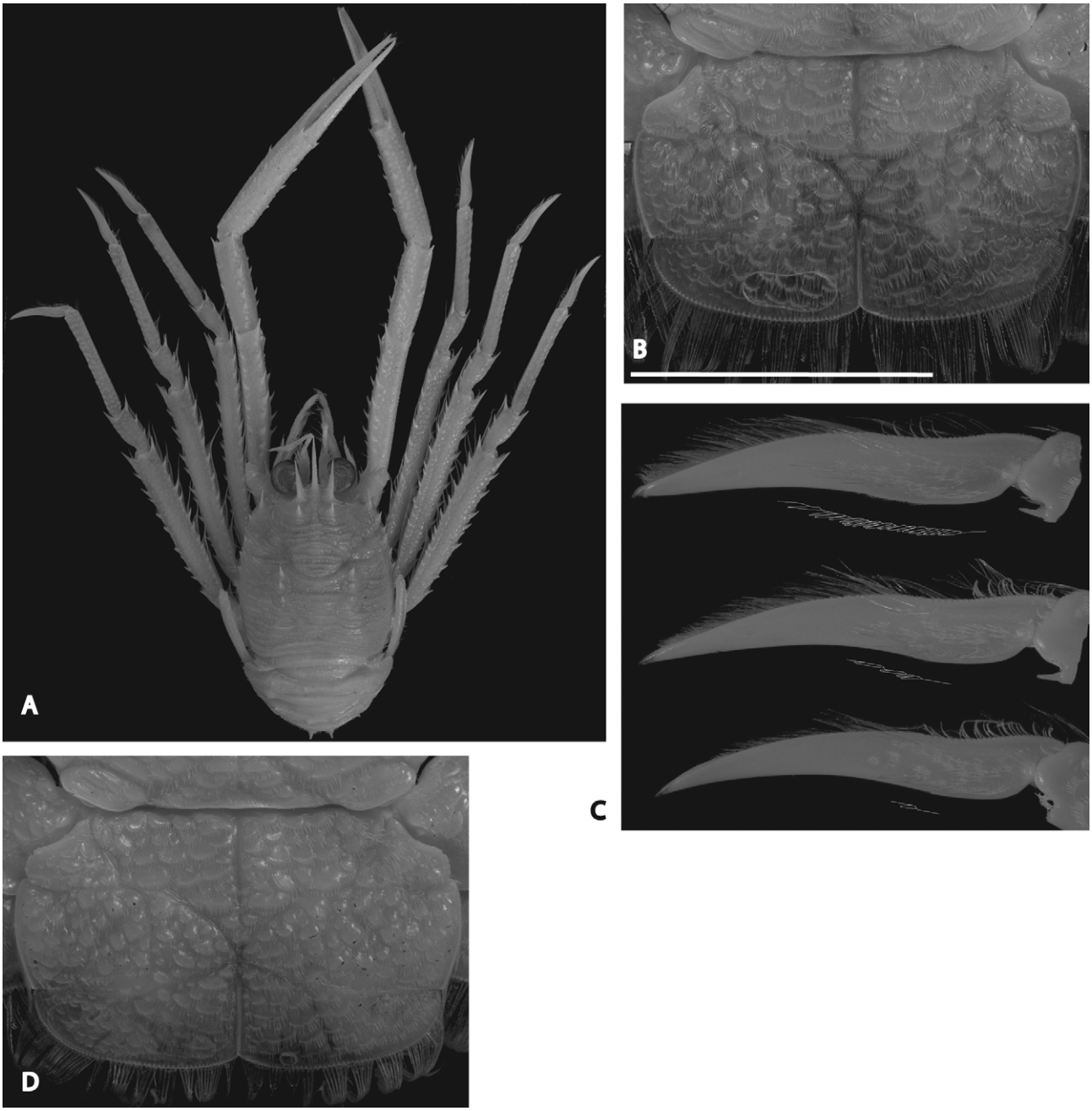

FIGURE 8. *Agononida africerta* n. sp. Holotype, female, MNHN IU-2008-10438. A, habitus; B, telson; C, dactyli of pereopods 2–4 with detail of robust setae at greater magnification. Paratype, male, MNHN IU-2008-10437. D, telson. Scale bar = 10 mm.

Pereopod 2 3.6 times carapace length, carpus 0.23 times as long as merus, dactylus 0.7 times as long as propodus; dactylus with row of 25 robust setae distal to heel of flexor margin.

Pereopod 3 3.1 times carapace length, dactylus 0.7 times as long as propodus; dactylus with row of 4 robust setae distal to heel of flexor margin.

Pereopod 4 3 times carapace length, dactylus 0.6 times as long as propodus; dactylus with 3 robust setae distal to heel of flexor margin.

Colour. From photo by T.Y. Chan (MNHN IU-2008-10192, supermale; Fig. 3C): carapace and abdominal somites 1–4 generally orange, stronger around bases of spines and rostrum. Spines and squamae of pereopods more strongly coloured than elsewhere. Transverse broad orange bands distally on meri of pereopods 1–4, proximally on carpi of pereopods 1–4, subdistally on carpus of pereopod 1, proximally on propodus of pereopod 1, at propodus-dactylus articulation of pereopod 1, and along most length of propodi of pereopods 2–4, stronger distally.

Variation. Five of 40 specimens up to cl 31 mm [plus many juveniles] from MAINBAZA samples at MNHN were examined in greater detail. In these, the numbers of robust setae distal to the heel on the flexor margin of the dactyli of pereopods 2–4 vary, even from one side to the other: pereopod 2, 15–22 (8 exceptional, median about 20); pereopod 3, 4–9 (median 6); pereopod 4, 1–2.

Distribution. Off Madagascar and eastern Mozambique, 13°S–25°S; 446–570 m.

Etymology. *africerta*, a combination from Africa and *incerta*.

Remarks. The telson of *Agononida africerta* differs slightly but consistently from that of the Western Australian species, *A. indocerta* which is resembles. Whereas in the adult male of *A. indocerta* the anterolateral lobe of the telson projects strongly and even tapers posteriorly, that of *A. africerta* is more evenly rounded. The counts of robust setae on the pereopodal dactyli are fewer than in *A. indocerta* (which has median numbers of 35, 17 and 10 on pereopods 2–4 respectively. The dactyli themselves are narrower and more tapering than in *A. indocerta*.

These two are the only species in which 1–4 facial spines are usually (but not always) found on the upper surface of the merus of pereopod 4. Both species also, the propodus of the cheliped has 1–3 spines on the lower lateral face, between the spines on the lateral face near the base of the dactylus and the spines on the lower margin. None of these are present in supermales. The coloration of the fresh specimen of *A. africerta* and the preserved specimens of *A. indocerta* are similar, in as far as this comparison will allow.

Barnard (1925;1950) reported *Munida incerta* from Portuguese East Africa, now Mozambique (25°56´S, 32°52´E), at a depth of 17 m. His description is general and drawing only of the anterior carapace. The occurrence of this species or of *A. africerta* at this shallow depth is improbable. However, Kensley (1977) also reported *M. incerta* from 280–454 m off southern Mozambique and Baba (1990) recorded numerous specimens of the same species from Madagascar at 394–700 m. Tirmizi (1966: 205, fig. 22) provided figures of a specimen off Zanzibar, 421–658 m, but nothing to characterise the species. While none of these been examined by us, it is possible they all referred to *A. africerta*.

Agononida africerta is genealogically most related to *A. indocerta*, known records coming from opposite sides of the Indian Ocean. This relationship is supported by shared morphological characters.

Agononida auscerta n. sp.

(Figs 2F, G, 9)

Agononida sp. aff. *incerta*.—Poore *et al.* 2008: 18 (part).

Material examined. *Holotype*. AUSTRALIA. Western Australia, Imperieuse L23 west transect, 17°31S 118°51.1°E, 406–405 m, 16.06.2007, beam trawl (stn SS05/2007/064), NMV J55995 (ovigerous female, cl 24.3 mm).

Paratypes. AUSTRALIA. Western Australia (all collected by FRV *Southern Surveyor*, 2005–2007). Adele L28 transect, 14°03.68′S 122°37′E, 394–400 m (stn SS05/2007/166), NMV J56126 (male, cl 8 mm). Leveque L27 transect, 14°51.2′S 121°25.8′E, 403–396 m (stn SS05/2007/144), NMV J56026 (5 males, cl 19–23 mm; 4 females, cl 18–25 mm). Broome L25 transect, 16°36.3′S 120°34.4.5′E, 407–414 m (stn SS05/2007/120), NMV J56417 (1 male, cl 10 mm; 3 juvenile females cl 7–12 mm). Imperieuse L23 transect, 17°21.5′S 118°57.3′E, 437–446 m (stn SS05/2007/056), NMV J56110 (2 males, cl 5, 11 mm; female, cl 11 mm). Imperieuse L23 transect, 17°31′S 118°51.1′E, 406–405 m (stn SS05/2007/064), NMV J55992 (6 juveniles). Imperieuse L23 transect, 17°31.7′S 118°50.6′E, 407–403 m (stn SS05/2007/057), NMV J56101 (3 males, cl 18–21 mm; 3 females, cl 19–23 mm). Hedland L22 transect, 18°34.2′S 117°27.8′E, 405–401 m (stn SS05/2007/052), NMV J55275 (3 males, cl 19–22 mm); NMV J62124 (male, cl 22 mm). Hedland L22 transect, 18°34.2′S 117°27.4′E, 407–404 m (stn SS05/2007/049), NMV J56112 (3 males, cl 17–20 mm; female, cl 8 mm). Karratha L21 transect, 18°46.4′S 116°54.7′E, 404–400 m (stn SS05/2007/036), NMV J56106 (female, cl 8 mm). Off Barrow Island, 21°00.4′S 114°22.8′E, 399–408 m (stn SS10/2005/172), NMV J55032 [now in MNHN] (3 males, cl 21 mm); NMV J60648 (male, cl 21 mm). Off Ningaloo North, 21°58.2′S 113°47.4′E, 373–382 m (stn SS10/2005/165), NMV J55022 (male, cl 22 mm).

Diagnosis. Telson anterolateral margin almost straight over anterior three-quarters, posterior quarter separated by shallow hiatus. Pereopodal 2–4 dactyli 8–9 times as long as greatest basal width; robust setae on dactylus of pereopod 2 number 2–6 (median 4; rarely 8), of pereopod 3, 1–4 (median 2) and of pereopod 4, 1–2 (rarely 3). Pereopod 4 merus without spines proximally on upper face.

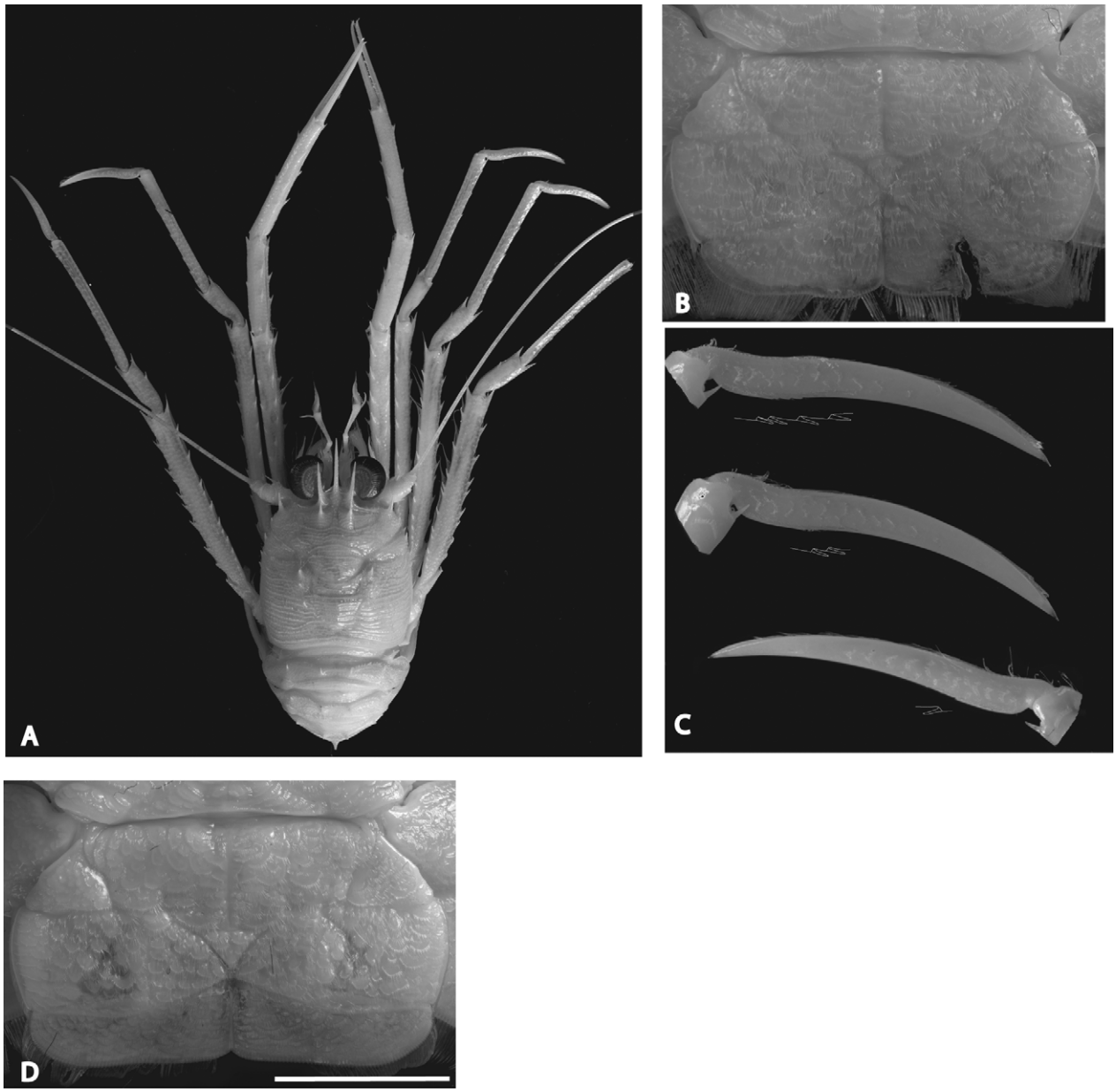

FIGURE 9. *Agononida auscerta* n. sp. Paratype, male, NMV J62124. A, habitus; B, telson; C, dactyli of pereopods 2, 3 (right) and 4 (left) with detail of robust setae at greater magnification. Holotype, ovigerous female, NMV J55995. D, telson. Scale bar = 5 mm.

Descriptions. *Ovigerous female. Based on NMV J55995, cl 24.3 mm.* Carapace 0.9 times as long as greatest width. Frontal margin inclined posteriorly at 11° from midline. Rostrum spiniform, 0.47 length of carapace (both measured from base of supraocular spines); supraocular spine 0.6 length of rostrum (both measured from base of rostrum). Thoracic sternite 3 0.49 width of sternite 4; midlength of sternal plastron (sternites 4–7) 0.6 width of sternite 7. Telson greatest width 1.9 times midlength; anterolateral margin almost straight over anterior three-quarters, posterior quarter separated by shallow hiatus; posterior part with expanded lateral margin then tapering to posterior transverse suture; lateral margin evenly convex.

Eyes with maximum corneal diameter 1.1 basal width of supraocular spines. Maxilliped 3 ischium 0.7 times as long as merus.

Pereopod 1 (cheliped) of typical adult form, covered with flat squamae fringed with short setae; 3.5 times as long as carapace, merus 1.3 times as long as carapace, carpus 0.54 times as long as merus, propodus 1.3 times as long as merus, fingers 0.43 times as long as total propodus length. Merus with 1+7–8 spines along upper margin,

3–4 spines along mesial face, 10–12 spines along lateral face, with distal spine and 1–3 spine-like squamae on lower margin; carpus with 1+2 spines on upper margin, 2–3 spines on mesial face, 0–1 spines on lateral face; propodus oval in cross-section, spines with marginal spines, with 3–4 spines on upper margin, with 1+1–3 spines along mesial face, with 1+1–2 spine on lateral face near base of dactylus, with 1–3 oblique spines along lower margin, without spines on lower lateral face; dactylus cutting edge with ridge of c. 20 uneven teeth, few more prominent than others.

Minor pereopod 1 not differentiated (except in numbers of spines).

Pereopod 2 3.4 times carapace length, merus 1.3 times carapace length, 8.5 times a long as greatest width, carpus 0.25 times as long as merus, propodus 0.7 times as long as merus, dactylus 0.7 times as long as propodus; merus with 1+11 spines along extensor margin, with 1+7 spines along flexor margin; carpus with 1+0 spines along extensor margin; dactylus evenly curved over distal two-thirds, 9 times as long as greatest basal width, with row of 4 robust setae distal to heel of flexor margin.

Pereopod 3 3.5 times carapace length, merus 1.3 times carapace length, 8.5 times a long as greatest width, carpus 0.3 times as long as merus, propodus 0.7 times as long as merus, dactylus 0.6 times as long as propodus; merus with 1+15 spines along extensor margin, with 1+9 spines along flexor margin; carpus with 1+1 spines along extensor margin; dactylus evenly curved over distal two-thirds, 8.1 times as long as greatest basal width, dactylus with 2 robust setae distal to heel of flexor margin.

Pereopod 4 3.5 times carapace length, merus 1.3 times carapace length, 7.1 times a long as greatest width, carpus 0.3 times as long as merus, propodus 0.7 times as long as merus, dactylus 0.5 times as long as propodus; merus with 1+11 spines along extensor margin, with 1+8 spines along flexor margin; carpus with 1+1 spines along extensor margin; dactylus of similar curvature to dactyli 2 and 3, distally less setose, 8.6 times as long as greatest basal width, dactylus with 1 robust seta(e) distal to heel of flexor margin.

Male. Based on NMV J62124, cl 22 mm. Telson anterolateral margin almost straight over anterior half, posterior half with irregular anterior margin and convex posterior lobe; lateral margin convex, narrower posteriorly than anteriorly.

Variation. No supermale is known. Males and ovigerous females of similar sizes differ only slightly, the anterolateral margin of the telson being slightly more irregular in males than females; the chelipeds do not differ between sexes. The numbers of spines on the margins of pereopodal meri may be one or two larger or smaller than the figures given in the descriptions and are not consistent from left to right side. The numbers of robust setae distal to the heel on the flexor margin of the dactyli of pereopods 2–4 vary considerably: pereopod 2, 2–6 (median 4; rarely 8); pereopod 3, 1–4 (median 2); pereopod 4, 1–2 (rarely 3).

Distribution. Western Australia, 14°S–22°S; 373–446 m (the species was not taken at stations targeting the 200 m, 800 m or deeper contours).

Etymology. *auscerta*, a combination from Australia and *incerta*.

Remarks. *Agononida auscerta* is morphologically similar to *A. incerta*, differing in its characteristic telson, more elongate dactyli of pereopods 2–4, and in the numbers of robust setae along their flexor margins. The anterolateral margin on the telson has only a slight indentation in the male (almost none in the female), the anterior three-quarters being only slightly concave if at all and the posterior quarter barely convex (*A. incerta* always has a clear notch separating these two sections). The pereopodal dactyli are narrower than those of all other species. The numbers of robust setae on pereopodal dactyli are fewer, usually 2–6 on pereopod 2 (12–30, median 17, in *A. incerta*) and 1–4 on pereopod 3 (2–10, median 6, in *A. incerta*). Both have 1–3 on pereopod 4. *Agononida auscerta* differs from *A. indocerta* with which it also co-occurs in WA in having the telson anterolateral margin almost straight over anterior three-quarters (concave and smooth over anterior 70% in *A. indocerta*) and lacking the prominent posterior lobe with a crenellate margin, and in having usually 2–6 robust setae on the dactylus of pereopod 2 (25–50,median about 35 in *A. indocerta*), and 1–4 on pereopod 3 (6–31, median about 17 in *A. indocerta*).

Our mitochondrial phylogenetic reconstruction placed *Agononida auscerta* as sister taxon to *A. rubrizonata*. The latter species shows a wider geographical distribution, encompassing the former, and can be distinguished from the former on the basis of telson shape, even as females.

***Agononida indocerta* n. sp.**
(Figs 2H–J, 3D, 10)

?*Munida incerta*.—Tirmizi & Javed 1993: 100, figs 43, 44.
Munida sp.—Jones & Morgan 1994: 135, fig.
Agononida sp. cf. *squamosa*.—Jones & Morgan 2002: 135, fig.
Agononida sp. aff. *incerta*—Poore *et al.* 2008: 18 (part).

Material examined. *Holotype*. AUSTRALIA. Western Australia. Ashmore L30 transect, 12°36.1′S 123°25.5′E, 419-403 m, 07.07.2007 (stn SS05/2007/198), NMV J62081 (male, cl 30.2 mm).

Paratypes. AUSTRALIA. Western Australia (all collected by FRV *Southern Surveyor*, 2005–2007). Collected with holotype (stn SS05/2007/198), NMV J57295 (5 males, cl 19–27 mm; 5 ovigerous females, cl 19–24 mm; 2 juveniles females, cl 17 mm). Ashmore L30 transect, 12°28.8′S 123°25′E, 397–405 m (stn SS05/2007/189), NMV J55987 [now in MNHN] (male, cl 18 mm; ovigerous female, cl 23 mm); NMV J57257 (5 juveniles, cl 7 mm). Kulumburu L29 transect, 13°15.9′S 123°22.4′E, 394–390 m (stn SS05/2007/180), NMV J55988 (3 males, cl 20–24 mm; 2 ovigerous females, cl 22, 25 mm; 2 juvenile females 22, 23 mm; 1 with bopyrid parasite and 2 with *Peltagaster* parasite). Adele L28 transect, 14°03.7′S 122°37.0′E, 394–400 m (stn SS05/2007/166), NMV J55985 (ovigerous female, cl 24 mm). Adele L28 transect, 14°03.8′S 122°36.2′E, 397–393 m (stn SS05/2007/167), NMV J55989 (male, cl 7 mm; 2 ovigerous females, cl 20, 24 mm; juvenile female, cl 11 mm). Lacepede L26 transect, 15°36.6′S 120°48.4′E, 399 m (stn SS05/2007/130), NMV J57293 (17 juveniles). Broome L25 transect, 16°36.3′S 120°34.4′E, 407–414 m (stn SS05/2007/120), NMV J55986 (2 males, cl 24 27 mm; ovigerous female, cl 21 mm). Mermaid L24 north transect, 17°01.1′S 119°35.4′E, 451–440 m (stn SS05/2007/080), NMV J55983 (27 juveniles, cl 7 mm). Mermaid L24 south transect, 17°11.8′S 119°34.8′E, 435–438 m (stn SS05/2007/079), NMV J56022 (female, cl 10 mm). Mermaid L24 east transect, 17°02.8′S 119°39.6′E, 424–456 m (stn SS05/2007/077), NMV J56413 (male, cl 32 mm). Imperieuse L23 transect, 17°21.5′S 118°57.3′E, 437–446 m (stn SS05/2007/056), NMV J62811 (2 supermales, cl 29, 33 mm, 1 male; 4 juvenile females, 3 ovigerous females). off Point Cloates, 22°50.8′S 113°20.2′E, 420–430 m (stn SS10/2005/137), NMV J60796 (ovigerous female, cl 28 mm). Perth Canyon, 31°59.5′S 115°10.9′E, 508–478 m (stn SS10/2005/068), NMV J55031 (3 males, cl 17–22; 3 ovigerous females, cl 21–23 mm; 1 juvenile female cl 10 mm).

Other material. Northwestern Australia no further data (stn SS05/2007/unknown), NMV J57294 (17 specimens). 220 km N of Port Hedland, 17°59′S 118°17′E, 768 m, (stn S02/82/17), AM P67303 (male, cl 26.6 mm; ovigerous female, cl 25.8 mm).

Diagnosis. Telson anterolateral margin concave and smooth over anterior 70%, remainder prominent, widest well anterior to transverse suture and narrower adjacent to transverse suture, with crenellate margin. Pereopodal 2–4 dactyli 5.1–5.77 times as long as greatest basal width; robust setae on dactylus of pereopod 2 number 25–50 (median about 35), of pereopod 3, 6–31 (median about 17) and of pereopod 4, 2–19 (median about 10). Pereopod 4 merus usually with spines proximally on upper face.

Descriptions. *Supermale. Based on NMV J62081, cl 30.2 mm.* Frontal margin inclined posteriorly at 18° from midline. Rostrum spiniform, 0.44 length of carapace (both measured from base of supraocular spines); supraocular spine 0.56 length of rostrum (both measured from base of rostrum). Thoracic sternite 3 0.48 width of sternite 4. Telson greatest width 1.9 times midlength; anterolateral margin concave and smooth over anterior 70%, remainder prominent, widest well anterior to transverse suture and narrower adjacent to transverse suture, with crenellate margin; lateral margin almost straight, more curved proximally and distally.

Eyes with maximum corneal diameter 1 basal width of supraocular spines. Maxilliped 3 ischium 0.6 times as long as merus.

Pereopod 1 (cheliped) of grossly expanded supermale form, slightly asymmetrical, covered with elevated squamae fringed with short setae; 4.6 times as long as carapace, carpus 0.6 times as long as merus, propodus 1.6 times as long as merus, fingers 0.53 times as long as total propodus length. Merus with 1+7 spines along upper margin, 4 spines along mesial face, 14 spines along lateral face, with distal spine only on lower margin; carpus with 1+0 spines on upper margin (modified squamae only), 0 spines on mesial face, 0 spines on lateral face; propodus oval in cross-section, with shallow longitudinal grooves mesially and laterally, palm deeper distally, spines with spines at base of dactylus only, propodus without spines along lower margin or on lower lateral face; dactylus cutting edge with 2 proximal blunt teeth and ridge of c. 50 uneven teeth, few more prominent than others.

Minor pereopod 1 with only minor differences.

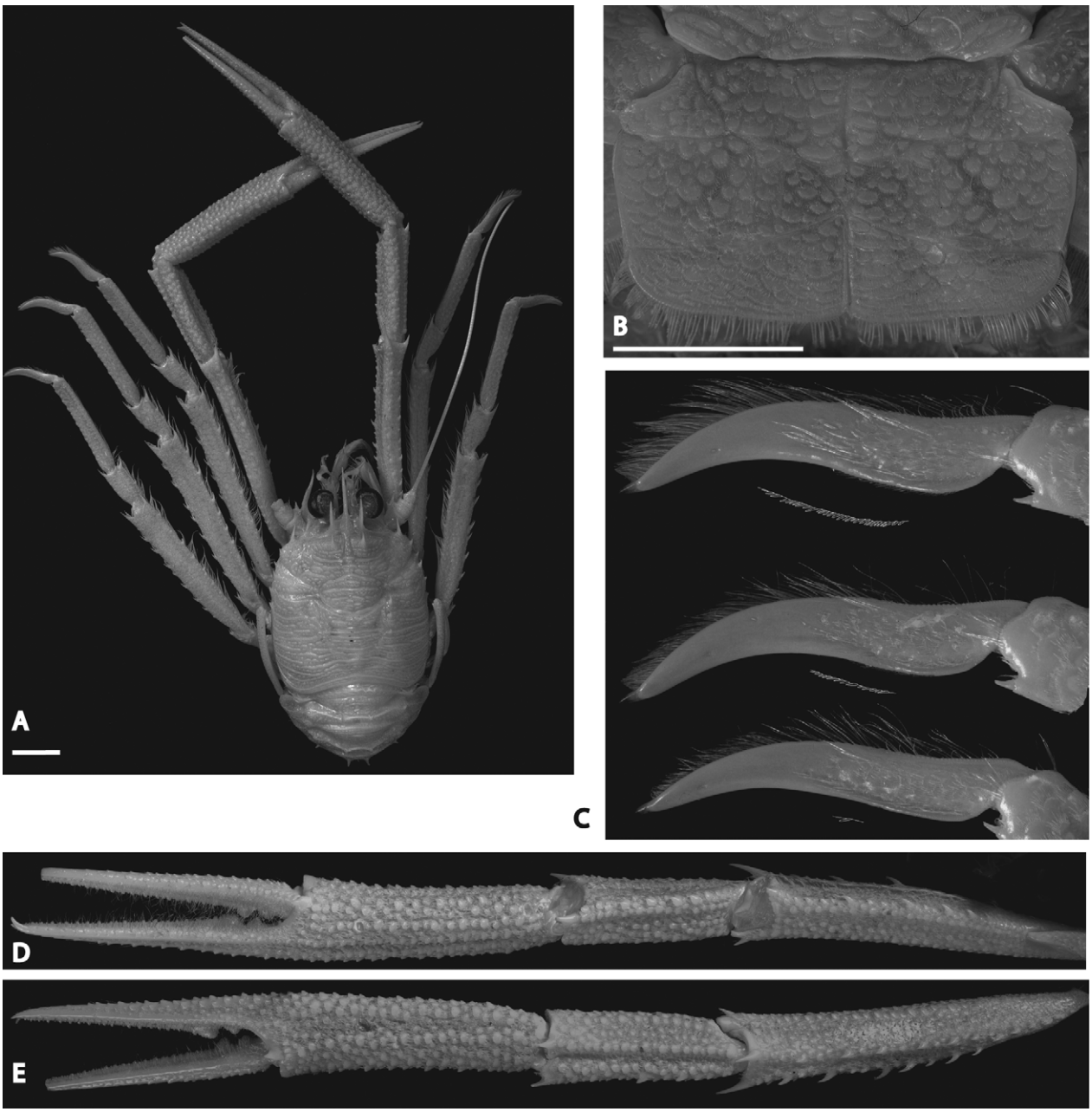

FIGURE 10. *Agononida indocerta* n. sp. Holotype, male, NMV J62081. A, habitus; B, telson; C, dactyli of pereopods 2–4 with detail of robust setae at greater magnification; D, E, cheliped in lateral and mesial views. Scale bar = 10 mm.

Pereopod 2 3.2 times carapace length, 8.3 times a long as greatest width, carpus 0.22 times as long as merus, propodus 0.5 times as long as merus, dactylus 0.6 times as long as propodus; merus with 1+12–14 spines along extensor margin, with 1+3–4 spines along flexor margin; carpus with 1+3–4 spines along extensor margin; dactylus strongly curved over distal half, 5.7 times as long as greatest basal width, with row of 36 robust setae distal to heel of flexor margin.

Pereopod 3 3.2 times carapace length, 7.2 times a long as greatest width, carpus 0.23 times as long as merus, propodus 0.6 times as long as merus, dactylus 0.5 times as long as propodus; merus with 1+11 spines along extensor margin, with 1+8 spines along flexor margin; carpus with 1+2 spines along extensor margin; dactylus 5.4 times as long as greatest basal width, with row of 20 robust setae distal to heel of flexor margin.

Pereopod 4 3 times carapace length, merus 1.1 times carapace length, 6.6 times a long as greatest width; merus with 1+12–13 spines along extensor margin, with 1+7–8 spines along flexor margin; carpus with 1+1–2 spines along extensor margin; dactylus more gently curved than dactyli 2 or 3, distally less setose, 5.1 times as long as greatest basal width, with 2–14 robust setae distal to heel of flexor margin.

Ovigerous female. Based on NMV J57295, cl 24.6 mm. Rostrum spiniform, 0.4 length of carapace (both measured from base of supraocular spines); supraocular spine 0.61 length of rostrum (both measured from base of rostrum). Telson greatest width 1.7 times midlength; anterolateral margin sinusoidal, concave and smooth over anterior 60%, remainder convex, widest adjacent to transverse suture, with crenellate margin.

Pereopod 1 (cheliped) 3.4 times as long as carapace, merus as long as carapace, carpus 0.6 times as long as merus, propodus 1.5 times as long as merus, fingers 0.5 times as long as total propodus length. Merus with 1+5 spines along upper margin, 3 spines along mesial face, 10 spines along lateral face, with distal spine only on lower margin; carpus with 1+2 spines on mesial face, 0 spines on lateral face; propodus with 4 spines on upper margin, with 1+1 spines along mesial face, with 1+1 spine on lateral face near base of dactylus, with 1–3 oblique spines along lower margin plus 1–3 spines on lower lateral face; dactylus cutting edge with ridge of c. 50 denticles.

Minor pereopod 1 not differentiated.

Pereopod 2 2.8 times carapace length, merus 1.3 times as long as carapace; merus with 1+13 spines along extensor margin, with 1+6 spines along flexor margin; carpus with 1+1 spines along extensor margin; dactylus strongly curved over distal half, with row of 27–30 robust setae distal to heel of flexor margin.

Pereopod 3 3 times carapace length, merus 1.2 times carapace length; merus with 1+13 spines along extensor margin, with 1+7 spines along flexor margin; carpus with 1+2 spines along extensor margin; dactylus with row of 6–15 robust setae distal to heel of flexor margin.

Pereopod 4 2.9 times carapace length, merus as long as carapace; merus with 1+15 spines along extensor margin, without spines or with 1–4 spines proximally on upper face (usual); carpus with 1+2 spines along extensor margin; dactylus unknown on this specimen.

Colour. (from specimens fixed in formalin and stored in alcohol, NMV J55031 and J62811, probably somewhat faded, and Fig. 3D). Carapace colour not known. Transverse broad orange bands subdistally on meri of pereopods 1–4, proximally on carpi of pereopods 1–4, subdistally on carpus of pereopod 1, proximally on propodus of pereopod 1, at propodus-dactylus articulation of pereopod 1, and subdistally on propodi of pereopods 2–4.

Variation. The numbers of spines on the margins of pereopodal meri may be one or two larger or smaller than the figures given in the descriptions and are not consistent from left to right side. The numbers of robust setae distal to the heel on the flexor margin of the dactyli of pereopods 2–4 vary considerably, even from one side to the other: pereopod 2, 25–50 (median about 35); pereopod 3, 6–31 (median about 17); pereopod 4, 2–19 (median about 10).

Although the largest males of *Agononida indocerta* have somewhat expanded chelipeds none possesses opposing teeth on the cutting edges of the fingers. Chelipeds in these individuals are 3.6 times carapace length and exceed pereopods 2–4 when held laterally. In ovigerous females chelipeds can be longer than pereopods 2 and 3 but not necessarily so.

Distribution. Western Australia, 12.5°S–32°S; 394–508 m (the species was not taken at stations targeting the 200 m, 800 m or deeper contours). The southern outlying sample at 32°S was taken deeper than others further north.

Etymology. *indocerta*, a combination from Indian Ocean and *incerta*.

Remarks. *Agononida indocerta* is notable for the prominent semicircular lobes at the posterolateral corner of the anterolateral margin of the telson, more prominent in males. The pereopodal dactyli possess more robust setae on the flexor margin than any other species, usually around 35 and 17 on pereopods 2 and 3 respectively. Few species have more than 1 or 2 robust setae on the dactylus of pereopod 4; *A. indocerta* has usually around ten. Most specimens (not all and not always on both sides) possess 1–3 spines at the proximal end of the upper face of the merus of pereopod 4, quite distinct from the rows of marginal spines, a feature shared with *A. africerta*. Further similarities and differences are discussed above with this species.

The species has a characteristic colour pattern, notable for the transverse bands on the pereopods *not* being at the distal ends of the articles. The colour patterns on the two lots of preserved material is consistent with that displayed in a published colour photograph of a live animal labelled "*Munida* sp." in Jones & Morgan (1994) and "*Agononida* sp. cf. *squamosa*" in Jones & Morgan (2002). Ahyong & Poore (2004) suspected that these photographs may be of their form-a of *A. incerta*, a form later described as *A. rubrizonata*. Macpherson & Baba (2009) realised the error. The photographed specimen can not now be found.

The drawing of the telson of a male identified as *M. incerta* from the Bay of Bengal (Tirmizi & Javed 1993) suggests the western Australian *A. indocerta* which would extend its distribution northwards.

The mitochondrial phylogeny places *A. indocerta* and *A. africerta* as sister taxa and the two as sister clade to all other species.

***Agononida norfocerta* n. sp.**
(Figs 2K, L, 11)

Agononida incerta. —Machordom & Macpherson, 2004: 261.

Material examined. *Holotype*. SOUTHWESTERN PACIFIC, Norfolk Ridge. 23°22.76′S 168°51.6′E, 980–1000 m, 29.11.1993 (BATHUS 3 stn CP823), MNHN IU-2011-592 (male , cl 30.7 mm).

Paratypes. SOUTHWESTERN PACIFIC, Norfolk Ridge. 23°19.32′S 168°0.31′E, 601–608 m, 29.11.1993 (BATHUS 3 stn DW824), MNHN IU-2008-20706(2 specimens, 16S sequences AY351066–7 and COI sequences AF283888–9 det. by E. Macpherson, 2004 as *A. incerta*); MNHN IU-2011-593 (male, cl 23 mm); MNHN IU-2011-594 (female, cl 29 mm); MNHN IU-2011-595 (female, cl 23 mm); IU-2011-596 (female, cl 20 mm); MNHN IU-2011-597 (female, cl 21 mm); MNHN IU-2011-598 [now NMV J62814] (female, cl 27 mm).

Diagnosis. Telson anterolateral margin with smooth proximal concavity over anterior 70% that ends at sharp step, remainder truncate-convex, margin oblique anterior to transverse suture, with crenellate margin. Pereopodal 2–4 dactyli 5.9–6.2 times as long as greatest basal width, robust setae on dactylus of pereopod 2 number 10–18 (5 exceptional, median 12), of pereopod 3, 1–4 (median 3), and of pereopod 4, 0–3 (median 2). Pereopod 4 merus without spines proximally on upper face.

Descriptions. *Supermale. Based on MNHN IU2011-592, male cl 30.7 mm.* Carapace as long as greatest width. Frontal margin inclined posteriorly at 16° from midline. Rostrum spiniform, 0.38 length of carapace (both measured from base of supraocular spines); supraocular spine 0.67 length of rostrum (both measured from base of rostrum). Thoracic sternite 3 0.47 width of sternite 4; midlength of sternal plastron (sternites 4–7) 0.6 width of sternite 7. Telson greatest width 1.6 times midlength; anterolateral margin smooth proximal concavity over anterior 70% that ends at sharp step, remainder truncate-convex, margin oblique anterior to transverse suture, with crenellate margin; lateral margin almost straight, more curved proximally and distally.

Eyes with maximum corneal diameter 0.9 basal width of supraocular spines. Maxilliped 3 ischium 0.6 times as long as merus.

Pereopod 1 (cheliped) of grossly expanded supermale form, slightly asymmetrical, covered with elevated squamae fringed with short setae; 4.7 times as long as carapace, merus 1.4 times as long as carapace, carpus 0.8 times as long as merus, propodus 2.2 times as long as merus, fingers 0.46 times as long as total propodus length. Pereopod 1 (cheliped) merus with 1+6–8 spines along upper margin, with 1+4–6 spines along mesial face, with 1+11–13 spines along lateral face, with distal spine only on lower margin; with 1+2–3 spines on upper margin, with 1+2–5 spines on mesial face, with 1+0–1 spines on lateral face; propodus oval in cross-section, with shallow longitudinal grooves mesially and laterally, palm deeper distally, spines with marginal spines, with 4 spines on upper margin, with 1+2 spines along mesial face, with 1+0 spine on lateral face near base of dactylus, propodus with 1–3 oblique spines along lower margin, without spines on lower lateral face; fixed finger cutting edge with blunt proximal tooth, second tooth proximal to ridge of c. 50 uneven teeth, few more prominent than others, apex bifid; dactylus cutting edge with 2 proximal blunt teeth and ridge of c. 50 uneven teeth, few more prominent than others.

Minor pereopod 1 not differentiated.

Pereopod 2 3.4 times carapace length, merus 1.4 times carapace length, 9.2 times a long as greatest width, carpus 0.22 times as long as merus, propodus 0.5 times as long as merus, dactylus 0.5 times as long as propodus; merus with 1+13–15 spines along extensor margin, with 1+6–7 spines along flexor margin; carpus with 1+2 spines along extensor margin; dactylus evenly curved over distal two-thirds, 5.9 times as long as greatest basal width, dactylus with row of 10 robust setae distal to heel of flexor margin.

Pereopod 3 3.4 times carapace length, merus 1.3 times carapace length, 8.2 times a long as greatest width, carpus 0.26 times as long as merus, propodus 0.6 times as long as merus, dactylus 0.5 times as long as propodus; merus with 1+14–16 spines along extensor margin, with 1+6–8 spines along flexor margin; carpus with 1+1–2 spines along extensor margin; dactylus evenly curved over distal two-thirds, 6.2 times as long as greatest basal width, dactylus with row of 2–3 robust setae distal to heel of flexor margin.

Pereopod 4 3.1 times carapace length, merus 1.1 times carapace length, 6.9 times a long as greatest width, carpus 0.3 times as long as merus, propodus 0.7 times as long as merus, dactylus 0.5 times as long as propodus; merus with 1+11–12 spines along extensor margin, with 1+5–7 spines along flexor margin, merus without spines proximally on upper face; carpus with 1+1–2 spines along extensor margin; dactylus of similar curvature to dactyli

2 and 3, distally less setose, 6.3 times as long as greatest basal width, dactylus with 2–3 robust setae distal to heel of flexor margin.

Female. Based on NMV J62814; 3.5 times as long as carapace.

Pereopod 2 3 times carapace length; merus with 1+15 spines along extensor margin, with 1+5 spines along flexor margin; dactylus with row of 10–12 robust setae distal to heel of flexor margin.

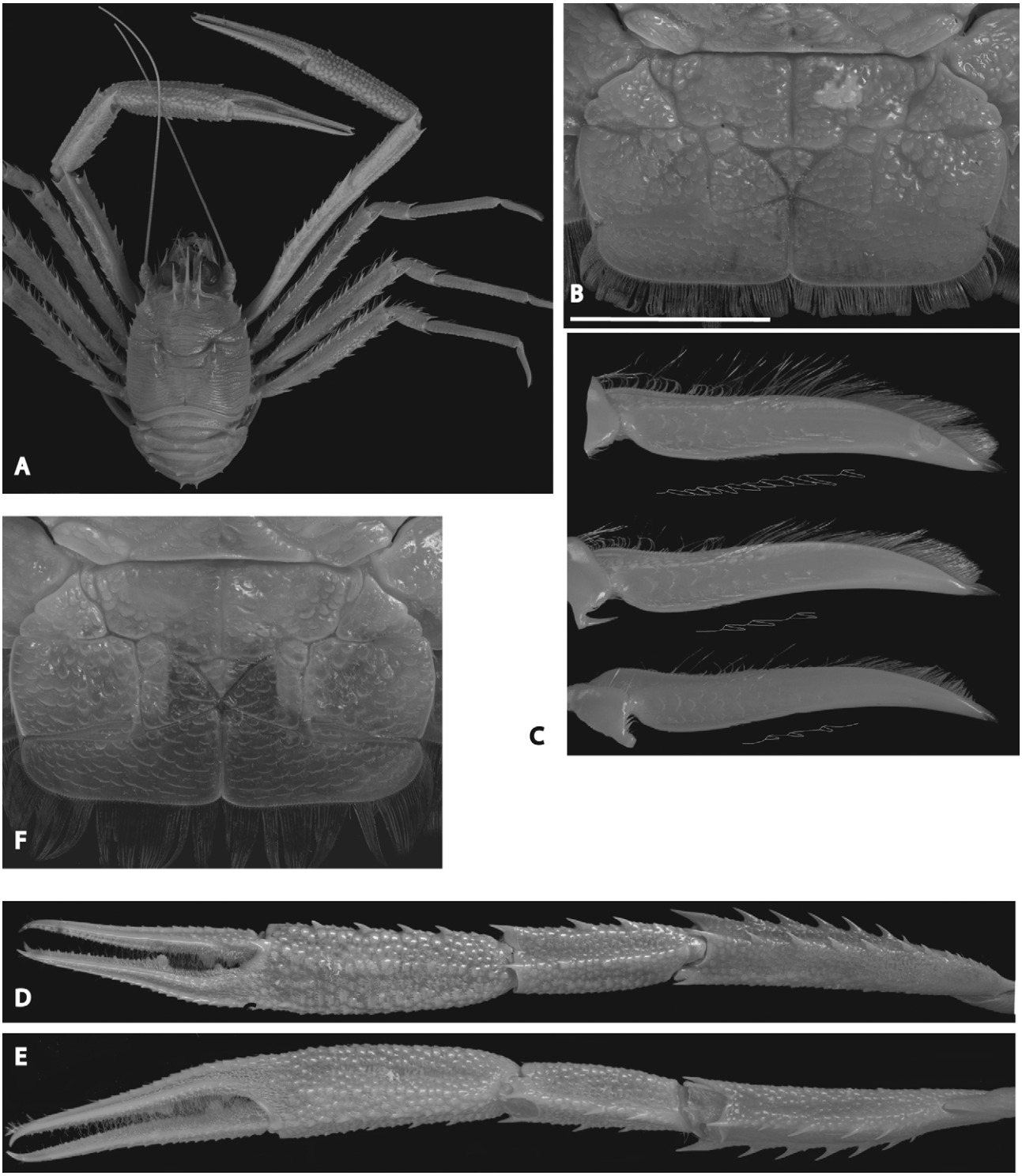

FIGURE 11. *Agononida norfocerta* n. sp. Holotype, male, MNHN IU-2011-592. A, habitus; B, telson; C, dactyli of pereopods 2–4 with detail of robust setae at greater magnification. D, E, cheliped in lateral and mesial views. Paratype, female, MNHN IU-2011-598. F, telson. Scale bar = 10 mm.

Pereopod 3 3.1 times carapace length; merus with 1+12–14 spines along extensor margin, with 1+5 spines along flexor margin; carpus with 1+2 spines along extensor margin; dactylus with row of 1–4 robust setae distal to heel of flexor margin.

Pereopod 4 2.9 times carapace length; merus with 1+10 spines along extensor margin, with 1+6 spines along flexor margin; carpus with 1+3 spines along extensor margin.

Variation. Among the six specimens examined the numbers of robust setae distal to the heel on the flexor margin of the dactyli of pereopods 2–4 vary, even from one side to the other: pereopod 2, 10–18 (5 exceptional, median 12); pereopod 3, 1–4 (median 3); pereopod 4, 0–3 (median 2).

Distribution. South Western Pacific Ocean, Norfolk Ridge, 23°S, 168°E; 600 m.

Etymology. *norfocerta*, a combination from Norfolk Ridge and *incerta.*

Remarks. Six specimens from the one station on the Norfolk Ridge were examined. Two others from the same station were included among the types on the basis of concordant genetic COI and 16S sequences. Abundant material from other south-western Pacific localities identified as *A. incerta* by Macpherson (1994) has not been examined in detail. He noted geographic variation in cheliped structure, colour and the telson but did not investigate further.

The telson of the male and female are scarcely differentiated in this species. The strong step about two-thirds the way along the anterolateral margin is characteristic

The numbers of dactylar robust setae are variable as in all species but the number on pereopod 2 overlaps the lower numbers of only *A. incerta* and *A. africerta*. The anterolateral lobe of the telson of *A. incerta* has two more or less well defined lobes while *A. norfocerta* has a single step two-thirds along. The telson of *A. africerta* has a more longitudinal, rather than oblique, margin on the section anterior to the transverse groove and usually lacks the step. Mitochondrial phylogenies recovered *A. norfocerta* and *A. incerta* as sister taxa and genealogically closely related to the *A. auscerta* + A. *rubrizonata* subclade.

Agononida rubrizonata Macpherson & Baba, 2009

(Figs 2M, N, 3E, F, 12)

?*Munida incerta*. — Baba 1994: 12.
Munida incerta form-a. — Ahyong & Poore 2004: 8.
Agononida sp. aff. *incerta*. — Poore *et al.* 2008: 18.
Agononida rubrizonata Macpherson & Baba, 2009: 60–63, figs 2F, 3, 4.

Material examined. TAIWAN, Su-ao, 09.03.2005, NTOU M01567 (male paratype, cl 15 mm); 10.03.2005 NTOU M01570 (6 male paratypes, cl 15–17 mm, 3 female paratypes, 2 ovigerous females, cl 17 mm).

PHILIPPINES. 15°59.45′N 121°50.68′E, 422–431 m, 20.05.2007 (stn CP2658), NTOU M01568 (10 males, 18 females). 15°58.75′N 121°50.36′E, 418–456 m, 02.06.2007 (stn CP2744), NTOU M01569 (2 males, cl 17 mm, 7 juveniles).

AUSTRALIA. Western Australia. Ashmore L30 transect, stn SS05/2007/189, 12°28.8′S 123°25′E, 397–405 m, NMV J60836 (3); stn SS05/2007/192, 12°31.7′S, 123°25.6′E, 401–404 m, NMV J56083 (8). North West Shelf, 240 km NW of Port Hedland, 18°06′S, 117°45′E, 500 m, 07 Apr 1982 (stn SO2/82/31), AM P.67305 (5). 250 km NW of Port Hedland, 18°40′S 116°42′E, 600 m, 04 Apr 1982 (stn SO2/82/19-20), AM P.67302 (1). Dampier L20 transect, stn SS05/2007/028, 19°43.5′S 115°20.6′E, 428–415 m, NMV J56407 (4); stn SS05/2007/028, 19°43.5′S 115°20.6′E, 428–415 m, NMV J60839 (4); stn SS05/2007/034, 19°43.7′S 115°21.2′E, 389–423 m, NMV J57292 (6 males, cl 17–28 mm, 3 females, cl 23–26 mm, 6 ovigerous females, 20-23 mm). Onslow L19 transect, stn SS05/2007/015, 20°7.96′S 114°58.7′E, 415–470 m, NMV J56394 (2). off Ningaloo North, stn SS10/2005/165, 21°58.2′S 113°47.4′E, 373–382 m, NMV J55028 (1). off Ningaloo South, stn SS10/2005/149, 22°0.23′S 113°40.7′E, 658–754 m, NMV J55026 (1); stn SS10/2005/151, 22°4.31′S, 113°45.3′E, 399–387 m, NMV J55030 (6), NMV J55144 (11); stn SS10/2005/148, 22°4.36′S 113°45.3′E, 396–391 m, NMV J55027 (1). off Point Cloates, stn SS10/2005/137, 22°50.8′S 113°20.2′E, 420–430 m, NMV J55029 (5).

New South Wales, NE of North Solitary Island, 29°32′S 153°48′E, 412 m, 02 Aug 1978 (stn K78-16-03), AM P.31496 (1). SE of Yamba, 29°37′S 153°47′E, 476, 07 Nov 1978 (stn K78-23-15), AM P.31495 (5). SE of Clarence River, 29°41′S, 29°32′S 153°45′E, 153°47′E, 406–414 m, 10 Oct 1975 (stn K75-09-04), AM P.21690 (1), AM

P.21761 (1). NE of North Solitary Island, 29°47′S 153°44′E, 439 m, 02 Aug 1978 (stn K78-16-07), AM P.31427 (1). E of Wooli, 29°52′S 153°43′E, 512 m, 23 Aug 1977 (stn K77-13-10), AM P.67306 (1). NE of Sugarloaf Point, 32°15′S 153°02′E, 457 m, 05 Apr 1978 (stn K78-03-04), AM P.42274 (1). Approx. 65km E of Sydney, 33°50′S 151°55′E, 457 m, 17 Feb 1997, AM P.49277 (1). E of Batemans Bay, 35°44′S 35°46′S, 150°37′E, 150°35′E, 275 m, 27 Apr 1977 (stn K77-03-04), AM P.31486 (1).

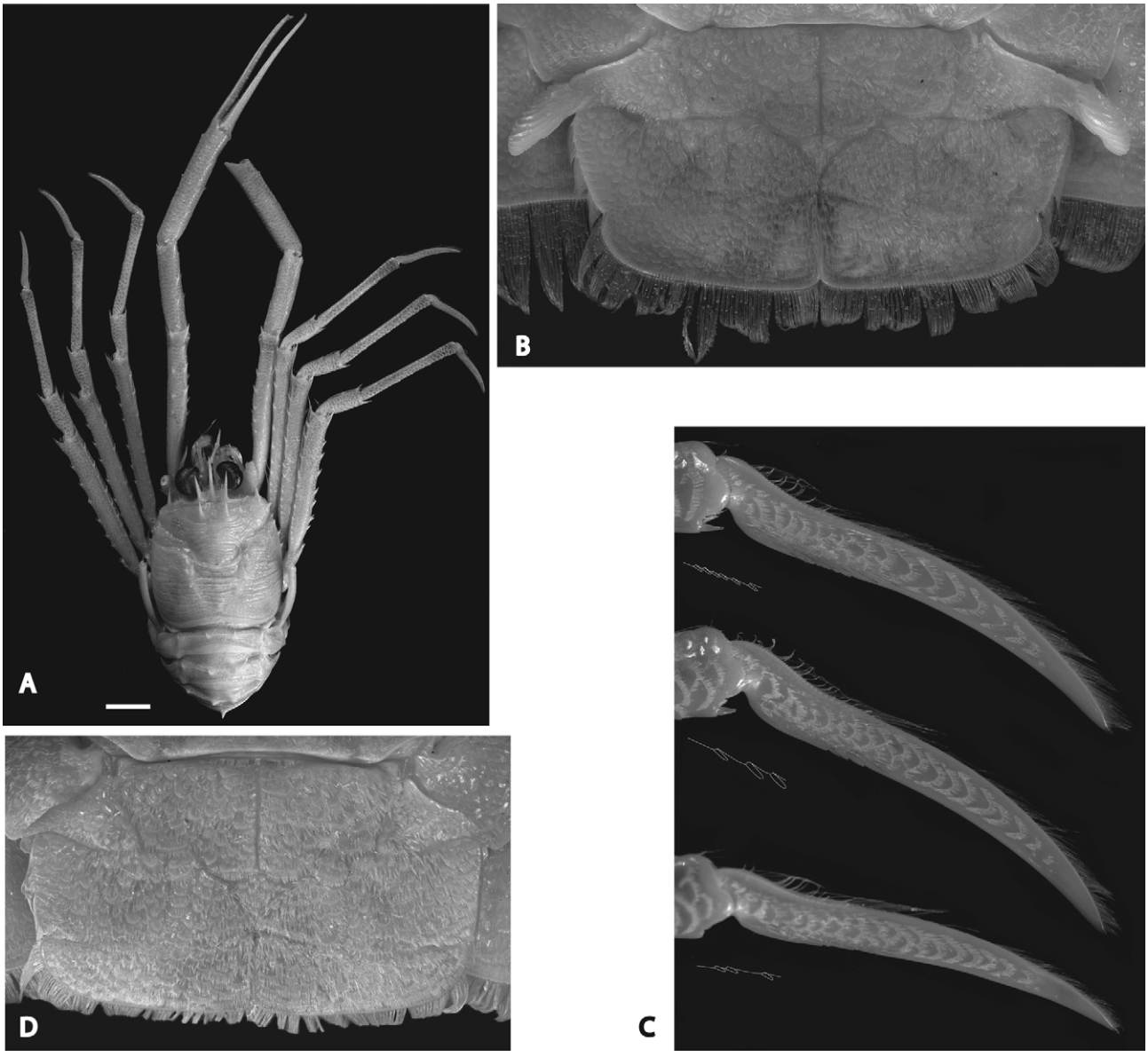

FIGURE 12. *Agononida rubrizonata* Baba & Macpherson, 2009. Male, NMV J57292. A, habitus; B, telson; C, dactyli of pereopods 2–4 with detail of robust setae at greater magnification. Female, NMV J57292. D, telson. Scale bar = 10 mm.

Tasmania, 42°07′S, 148°04′E, 450 m, 30 Jun 1984, stn S03/84/12), AM P.67304 (9).

Diagnosis. Telson anterolateral margin in male extending broadly to a small notch, with a solid thickened tongue-like lobe protruding posterolaterally and dorsally, ornamented with parallel ridges. Pereopodal 2–4 dactyli 7.0–7.6 times as long as greatest basal width; robust setae on dactylus of pereopod 2 number 3–13 (low numbers exceptional, median 10); pereopod 3, 1–6 (median 3); pereopod 4, 1–3 (median 1). Pereopod 4 merus without spines proximally on upper face.

Descriptions. *Male. Based on NMV J57292 (cl 27.6 mm).* Carapace 0.9 times as long as greatest width. Frontal margin inclined posteriorly at 12 degrees from midline. Rostrum spiniform, 0.38 length of carapace (both measured from base of supraocular spines); supraocular spine 0.62 length of rostrum (both measured from base of rostrum). Thoracic sternite 3 0.46 width of sternite 4; midlength of sternal plastron (sternites 4–7) 0.6 width of sternite 7.

Eyes with maximum corneal diameter 1 basal width of supraocular spines. Maxilliped 3 ischium 0.6 times as long as merus.

Pereopod 1 (cheliped) of typical adult form, covered with flat squamae fringed with short setae; 4.6 times as long as carapace, merus 1.3 times as long as carapace, carpus 0.6 times as long as merus, propodus 1.7 times as long as merus, fingers 0.54 times as long as total propodus length. Pereopod 1 (cheliped) merus with 1+5 spines along upper margin, with 1+3 spines along mesial face, with 1+12 spines along lateral face, with distal spine only on lower margin; with 1+2 spines on upper margin, with 1+2 spines on mesial face, with 1+0 spines on lateral face; propodus oval in cross-section, spines with marginal spines, with 3 spines on upper margin, with 1+1 spines along mesial face, with 1+0 spine on lateral face near base of dactylus, propodus with 1–3 oblique spines along lower margin plus 1–3 spines on lower lateral face; dactylus cutting edge with ridge of c. 50 uneven teeth, few more prominent than others.

Minor pereopod 1 not differentiated.

Pereopod 2 3.4 times carapace length, merus 1.4 times carapace length, 8.5 times a long as greatest width, carpus 0.25 times as long as merus, propodus 0.6 times as long as merus, dactylus 0.6 times as long as propodus; merus with 1+9 spines along extensor margin, with 1+6 spines along flexor margin; carpus with 1+0 spines along extensor margin; dactylus evenly curved over distal two-thirds, 7 times as long as greatest basal width, dactylus with row of 4–6 robust setae distal to heel of flexor margin.

Pereopod 3 3.4 times carapace length, merus 1.3 times carapace length, 8 times a long as greatest width, carpus 0.28 times as long as merus, propodus 0.7 times as long as merus, dactylus 0.6 times as long as propodus; merus with 1+14 spines along extensor margin, with 1+7 spines along flexor margin; carpus with 1+1 spines along extensor margin; dactylus evenly curved over distal two-thirds, 7.6 times as long as greatest basal width, dactylus with row of 1–3 robust setae distal to heel of flexor margin.

Pereopod 4 3.3 times carapace length, merus 1.2 times carapace length, 7.4 times a long as greatest width, carpus 0.3 times as long as merus, propodus 0.7 times as long as merus, dactylus 0.5 times as long as propodus; merus with 1+13 spines along extensor margin, with 1+7 spines along flexor margin, merus without spines proximally on upper face; carpus with 1+1 spines along extensor margin; dactylus of similar curvature to dactyli 2 and 3, distally less setose, 7.4 times as long as greatest basal width, dactylus with 1–3 robust setae distal to heel of flexor margin.

Ovigerous female. Based on NMV J57292 (cl 26.8 mm). Telson anterolateral margin sinuous, overlapping transverse suture as a thin short projection; lateral margin evenly convex.

Pereopod 1 (cheliped) 3.3 times as long as carapace, merus 0.9 times as long as carapace.

Pereopod 2 dactylus with row of 8 robust setae distal to heel of flexor margin.

Pereopod 3 6.3 times as long as greatest basal width, dactylus with row of 1 robust setae distal to heel of flexor margin.

Pereopod 4 5.6 times as long as greatest basal width, dactylus with 1 robust seta(e) distal to heel of flexor margin.

Colour. Carapace and abdominal somites 1–4 generally orange; pereopods pale orange with adjacent transverse white and bright red bands distally on meri of pereopods 1–4 and distally on propodi of pereopods 2–4.

Variation. Among the ten specimens examined the numbers of robust setae distal to the heel on the flexor margin of the dactyli of pereopods 2–4 vary, even from one side to the other: pereopod 2, 3–13 (low numbers exceptional, median 10); pereopod 3, 1–6 (median 3); and pereopod 4, 1–3 (median 1).

Distribution. Taiwan, Vanuatu, New Caledonia, Loyalty Islands, eastern (to 42°S) and western margins (to 23°S) of Australia; 275–754 m.

Remarks. *Agononida rubrizonata* is the most easily recognised of this species complex. The dominant lobes on the anterolateral margin of the telson of males are obvious but even in the smallest females and juveniles this margin ends posteriorly in an acute overlapping projection unlike in any other species. The differences in the male telson and colour patterns between this species and *A. incerta* were first noted by Baba (1994) in a collection from around 500 m off northern Queensland and later by Ahyong & Poore (2004) in more southern Australian samples. Macpherson & Baba (2009) described the species in detail but many of the features they dealt with are typical of all species of this complex. They gave ranges for many ratios that encompass the data given above; differences may be attributable to the way measurements were made. They noted red bands distally on the merus and proximally on the propodus and fingers of pereopod 1. These are not especially apparent on Fig. 3E of a specimen from the type

locality, Taiwan, reproduced here. These bands are not visible in the Western Australian material (Fig 3F but otherwise colour bands on the meri and propodi are comparable. Macpherson & Baba (2009) did not remark on the white bands, more obvious in the Australian than Taiwanese specimens.

Agononida rubrizonata would appear to be sister species to *A. auscerta* on the basis of the COI data. Genetic differences were not detected among specimens from material from Taiwan, Philippines and Western Australia.

Discussion

Several collections, besides those previously referred to, have been previously identified as *Agononida incerta* (Baba *et al.* 2008). None are convincingly *A. incerta* and most remain unidentifiable. The illustrations of Yanagita (1943: 15, figs 1, 2) of a specimen collected off Miya, Aichi Prefecture, or Kumanonada at 360 m show considerably more elongate pereopodal dactyli than in *A. incerta*. The colour plates of specimens from Kumanonada, Japan, 200–300 m (Miyake 1982: 146, colour pl. 49 fig. 5), and Okinawa Trough and Tosa Bay, 325–440 m (Baba in Baba *et al.* 1986: 171, 290, colour fig. 121) show even carapace colouring and denser colour at the base of meral spines and at the end of pereopodal articles. This pattern is consistent with *A. incerta* from Western Australia but not as dense as that from Taiwan (Baba *et al.*, 2009: fig. 63; Fig. 3A). Wu *et al.* (1998 (1997)) drew a small specimen from Taiwan (p. 114 fig. 23) with only two pairs of postcervical spines and supplementary gastric spines (unusual but not inconsistent with *A. incerta*). Their colour figs 26D and 26E are of two different species but neither is clear enough to identify. *Agononida incerta* is the only species known from the NE Pacific.

Macpherson (1994: 478, fig. 74) recorded material from several new localities from the South Pacific, Kiribati, New Caledonia, Loyalty Islands, Chesterfield Islands at 170–720 m. His colour photo of a specimen from the Loyalty Islands shows three transverse orange bands on the meri of pereopods 1–4, and bands on the carpi and propodi of these limbs. This may be *A. norfocerta*.

Records from the Moluccas, off the W coast of Halmahera, Sulu Archipelago, off NE Borneo, off N Mindanao, and the South China Sea, off Luzon, at 70–558 m (Baba 1988) and from the SW Pacific (Wallis Islands, Tuscaroa Bank, Waterwitch Bank, Field Bank and Bayonnaise Bank) at 105–600 m (Macpherson 1996) provided no data by which the specimens could be identified.

Agononida incerta is not the only species in this genus to have been widely recorded throughout the Indo-West Pacific. Others are *A. eminens* (Baba, 1988), *A. normani* (Henderson, 1885), *A. pilosimanus* (Baba, 1969), *A. similis* (Baba, 1988) and *A. squamosa* (Henderson, 1885) (see records in Baba *et al.* 2008). Any of the aforementioned species may also embody cryptic speciation events. Furthermore, the geographical patterns of the cryptic species may represent a standard distribution trend suggesting that biogeographic boundaries are more effective than is presently imagined for bathyal depths in this region (Poore & Andreakis 2011). Given the biogeographic importance of the region, we believe the same question deserves to be asked with several other supposedly widespread species in other squat lobster genera and families.

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