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Zoosystematics and Evolution

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Zoosystematics and Evolution

A Bulletin of Zoology since 1898

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In Focus

The cover picture shows a live male of *Oligodon sublineatus* at Sinharaja Forest Reserve, Sri Lanka (photo: H. Jayasinghe).

See paper of **Amarasinghe A.T.T. et al.** Systematics and ecology of *Oligodon sublineatus* Duméril, Bibron & Duméril, 1854, an endemic snake of Sri Lanka, including the designation of a lectotype

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A review of the scopelocheirid amphipods (Crustacea, Amphipoda, Lysianassoidea), with the description of new taxa from Australian waters

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<http://zoobank.org/CAFFC884-904F-40C2-AACF-12BE3A2F3ECC>

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Abstract

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Key Words

Scopelocheiridae
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Scopelocheirinae
new genus
new species
Austrocallisoma
Tayabasa
Australia.

Scopelocheiridae is a small family of scavenging lysianassoid amphipods. There is a distinct shallow water group (Scopelocheirinae **subfam. n.**) and a distinct deep-sea group (Paracallisominae **subfam. n.**). We catalogue three genera and eight species in the scopelocheirines and move *Scopelocheirus onagawae* Takekawa & Ishimaru, 2000 to the genus *Aroui*. The deep-sea paracallisomines are not often collected and consequently their morphological diversity is not well understood. We catalogue seven genera and 15 species. We provide diagnostic descriptions and a key to all genera in the Scopelocheiridae. We describe two new genera, *Austrocallisoma* **gen. n.** and *Tayabasa* **gen. n.**, and three new species from Australian waters, *Austrocallisoma jerryi* **sp. n.**, *Paracallisoma woolgoolga* **sp. n.** and *P. zivianii* **sp. n.**

Introduction

Scopelocheiridae Lowry & Stoddart, 1997 is a small family of scavenging lysianassoid amphipods which contains two subfamilies, Scopelocheirinae subfam. n. and Paracallisominae subfam. n. The scopelocheirines contain three genera and eight species living in temperate and boreal, mainly shallow, waters of the Mediterranean Sea, the North and South Atlantic, Japan and Australia. They are scavengers feeding on carrion on the sea bottom, with some species reported feeding in the dead tests of spatangoid urchins (Chevreux 1911, Lowry and Stoddart 1989). Paracallisomines are a larger group (seven genera and 15 species) widespread in the deep-

sea of the North and South Pacific, North and South Atlantic, Southern Ocean and Indian Ocean. Paracallisomines are not often collected and consequently their morphological diversity is not well understood. This has made their generic composition difficult to determine. In this paper we describe two new genera, *Austrocallisoma* for *A. jerryi* sp. n., and *Tayabasa* gen. n. for *Eucallisoma barnardi* Lowry & Stoddart, 1983, and provide a key to the world genera. We also describe two new species in the genus *Paracallisoma*, *P. woolgoolga* sp. n., and *P. zivianii* sp. n. (see Suppl. material 1 for specimen data on material examined). All species records from the literature, where found, are catalogued and their distributions and depth ranges noted (see also Suppl. material 2).

Material and methods

The descriptions were generated from a DELTA database (Dallwitz 2010) to the scopelocheirid genera and species of the world. In the diagnostic descriptions, diagnostic characters that distinguish each taxon from all others are denoted in *italic* type. Maxilla 1 setal-tooth arrangements follow the formulae outlined in Lowry and Stoddart (1992, 1995). In describing the telson we define the cleftness as deeply cleft (more than 66%), moderately cleft (33% to 66%), or weakly cleft (less than 33%). We use the term labrum to refer to the epistome and upper lip complex. Material is lodged in the Australian Museum, Sydney (AM); Graduate School of Agricultural Science, Tohoku University (AMTU); Natural History Museum, London (NHM); Muséum National d'Histoire Naturelle, Paris (MNHN); Musée Oceanographique Monaco (MOM); Museo Civico di Storia Naturale, Verona (MSNV); Zoological Museum of Moscow University, Moscow (ZMM); United States National Museum of Natural History, Smithsonian Institution, Washington DC (USNM); Museum für Naturkunde, Berlin (ZMB); Zoological Institute, Russian Academy of Sciences, St. Petersburg (ZIN); Zoological Museum, Hamburg (ZMH). Standard abbreviations used in the figures are: A, antenna; C, coxa; EP, epimeron; G, gnathopod; H, head; IP, inner plate; LM, labrum; MD, mandible; MX, maxilla; MP, maxilliped; OP, outer late; P, pereopod; T, telson; U, uropod; l, left; r, right.

Checklist of the family Scopelocheiridae Lowry & Stoddart, 1997

Scopelocheirinae subfam. n.

- Aroui americana* Lowry & Stoddart, 1997
Aroui hamatopodus Lowry & Stoddart, 1989
Aroui onagawae (Takekawa & Ishimaru, 2000)
Aroui setosus Chevreux, 1911
Paracallisomopsis beljaevi Gurjanova, 1962
Scopelocheirus crenatus Bate, 1857
Scopelocheirus hopei (Costa, 1851)
Scopelocheirus polymedus Bellan-Santini, 1985

Key to Scopelocheirid genera

- | | | |
|---|---|--------------------------|
| 1 | Maxilla 2 outer plate with extremely long distally-barbed slender setae | <i>Aroui</i> |
| – | Maxilla 2 outer plate without long slender distally-barbed setae | 2 |
| 2 | Pereopod 4 coxa with large subquadrate posteroventral lobe | 3 |
| – | Pereopod 4 coxa with subacutely produced posteroventral lobe | 5 |
| 3 | Gnathopod 1 basis swollen, glandular | <i>Eucallisoma</i> |
| – | Gnathopod 1 basis slender, non-glandular | 4 |
| 4 | Gnathopod 1 coxa adze-shaped; pereopod 5 basis wider than long | <i>Scopelocheirus</i> |
| – | Gnathopod 1 coxa subrectangular; pereopod 5 basis longer than wide | <i>Paracallisomopsis</i> |
| 5 | Pereopods 3 and 4 carpus distinctly longer than wide | 6 |
| – | Pereopods 3 and 4 carpus as wide as long or wider than long | 9 |
| 6 | Pereopod 4 coxa posteroventral lobe weakly developed posteriorly | <i>Anisocallisoma</i> |
| – | Pereopod 4 coxa posteroventral lobe well developed posteriorly | 7 |

Paracallisominae subfam. n.

- Anisocallisoma armigera* Hendrycks & Conlan, 2003
Austrocallisoma jerryi gen. n., sp. n.
Bathycallisoma schellenbergi (Birstein & M. Vinogradov, 1958)
Eucallisoma glandulosa J.L. Barnard, 1961
Paracallisoma abyssi (Oldevig, 1959)
Paracallisoma alberti Chevreux, 1903
Paracallisoma coecum (Holmes, 1908)
Paracallisoma platepistomum Andres, 1977
Paracallisoma spinipoda Hendrycks & Conlan, 2003
Paracallisoma woolgoolga sp. n.
Paracallisoma zivianii sp. n.
Scopelocheiropsis abyssalis Schellenberg, 1926
Scopelocheiropsis armata (Ledoyer, 1986)
Scopelocheiropsis sublittoralis G. Vinogradov, 2004
Tayabasa barnardi (Lowry & Stoddart, 1993)

Systematics

Family Scopelocheiridae Lowry & Stoddart, 1997

Scopelocheiridae Lowry & Stoddart, 1997: 122.

Diagnosis. (Modified after Lowry and Stoddart 1997). Head as long as deep, or deeper than long. Labrum, epistome and upper lip separate. Mandible incisors usually symmetrical, sometimes asymmetrical, large with straight or convex margins; left lacinia mobilis a stemmed distally expanded smooth or irregularly cusped blade, a long slender robust seta, or occasionally a cuspidate peg (*Paracallisomopsis*); accessory setal row without distal setal tuft; molar present or absent (*Scopelocheiropsis sublittoralis*), a narrow column with a small triturating surface, or a small non-setose triangular flap when present. Maxilla 1 inner plate usually strongly setose, with more than 2 pappose setae (except *Anisocallisoma*); outer plate broad, with 6–11 setal-teeth in a 7/4 arrangement; palp large, 1- or 2-articulate. Maxilliped outer plate with or without apical slender simple or pappose setae, with or without apical robust setae. Gnathopod 1 simple, dactylus reduced, complex, setose. Pereopods 3–7 usually simple, sometimes prehensile. Telson moderately to deeply cleft.

- 7 Maxilliped palp article 4 well developed. Gnathopod 1 dactylus anterior margin with rows of long slender setae... *Paracallisoma*
 – Maxilliped palp article 4 vestigial. Gnathopod 1 dactylus anterior margin without setae 8
 8 Mandible lacinia mobilis a stemmed, distally expanded blade. Gnathopod 1 coxa reduced *Austrocallisoma*
 – Mandible lacinia mobilis a cuspidate peg. Gnathopod 1 coxa well-developed, almost as large as coxa 2 *Tayabasa*
 9 Mandible lacinia mobilis a long slender robust seta *Bathycallisoma*
 – Mandible lacinia mobilis a distally expanded smooth blade *Scopelocheiropsis*

Subfamily Scopelocheirinae subfam. n.

<http://zoobank.org/3BBA67F9-3DA0-41D4-91C3-FCF000D1B594>

Included genera. The Scopelocheirinae includes three genera: *Aroui* Chevreux, 1911; *Paracallisomopsis* Guranova, 1962; *Scopelocheirus* Bate, 1857.

Diagnosis. Mandible molar a narrow column.

Aroui Chevreux, 1911

Aroui Chevreux, 1911: 169. — J.L. Barnard 1969: 328. — Barnard and Karaman 1991: 434 (key), 467. — Lowry and Stoddart 1989: 112. — Lowry and Stoddart 2003: 249.

Type species. *Aroui setosus* Chevreux, 1911, by monotypy.

Included species. *Aroui* includes four species: *A. americana* Lowry & Stoddart, 1997; *A. hamatopodus* Lowry & Stoddart, 1989; *A. onagawae* (Takekawa & Ishimaru, 2000), comb. n.; *A. setosus* Chevreux, 1911.

Diagnostic description. Mandible lacinia mobilis a stemmed, distally expanded, irregularly cusped blade; palp article 2 broadened. *Maxilla* 2 inner plate longer than outer plate; *outer plate with extremely long distally barbed slender setae*. *Gnathopod* 1 coxa margins diverging distally. Pereopod 5 coxa slightly wider than long; basis greatly expanded posteriorly.

Distribution. Western Atlantic. Mediterranean Sea. Japan. Australia.

Ecology. Found in shallow warm seas. A scavenger, also found in dead spatangoid tests.

Discussion. Previously, the setal fringe on the distal margins of the coxae from gnathopod 1 to pereopod 4 was considered to be a diagnostic character of the genus *Aroui*. Here we exclude that character from the diagnosis of the genus, as the setal fringe is absent in *A. onagawae* (Takekawa & Ishimaru, 2000), comb. n. Instead, we consider the unusual long, distally barbed setae on the outer plate of maxilla 2 to be an autapomorphy that distinguishes *Aroui* from all other genera in the Scopelocheiridae. See *A. onagawae*, below, for further discussion.

Aroui americana Lowry & Stoddart, 1997

Figure 1

Aroui americana Lowry & Stoddart, 1997: 124, figs 60–62.

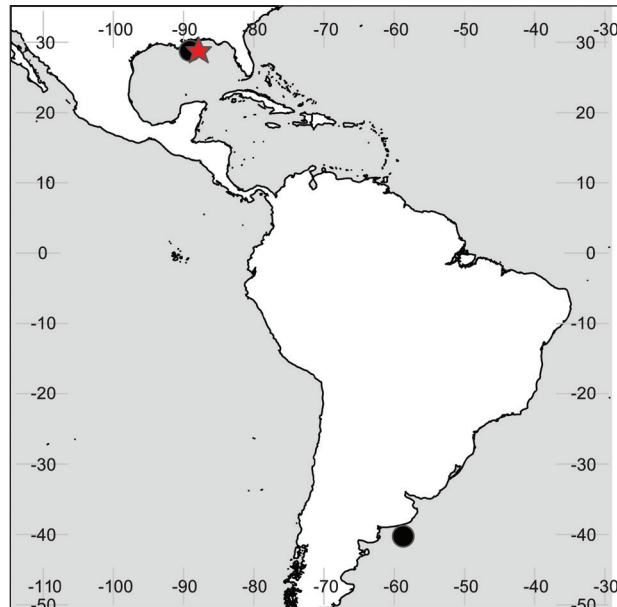


Figure 1. Distribution of *Aroui americana* Lowry & Stoddart, 1997. Star indicates type locality.

— Escobar-Briones and Winfield 2003: 42. — Ortiz et al. 2007: 513. — Martín et al. 2013: 1715 (appendix 1).

Type material. Holotype, female, 5 mm (with oostegite buds), USNM 282716. Paratypes: 1 male, 5.4 mm, USNM 282717; 1 male AM P.45339.

Type locality. Gulf of Mexico, south of Mobile Bay (approximately 29°12'N, 85°07'W), from stomach of a Blackfin grenadier, *Coelorinchus caribbaeus* (Goode & Bean, 1885), 200 m depth.

Depth range. 95–200 m (Lowry and Stoddart 1997). The deeper record represents animals taken from fish stomachs.

Distribution. *Argentina*: east of Bahía Unión (Lowry and Stoddart 1997). *United States*: Gulf of Mexico, south of Mobile Bay and south-east of the Mississippi River Delta (Lowry and Stoddart 1997).

Ecology. Known from sandy bottoms, but also a scavenger by implication (Lowry and Stoddart 1997).

Discussion. This species was described from three specimens: two from fish stomachs in the Gulf of Mexico and in the collections of the USNM, and another specimen taken in a trawl off Argentina by the USS *Albatross* in the collections of the AM. No new material has been recorded in the literature since its description.

***Aroui hamatopodus* Lowry & Stoddart, 1989**

Figure 2

Aroui hamatopodus Lowry & Stoddart, 1989: 114, figs 2–4.
— Springthorpe and Lowry 1994: 18. — Lowry and Stoddart 2003: 249. — Berge et al. 2004: 1719 (table 1).

Type material. Holotype, male, 7.8 mm, AM P.38460. Paratypes: female, 8.0 mm (with oostegites), AMP.38461; 9 specimens, AM P.38462.

Additional Australian material examined. *New South Wales*: 9 specimens, AMP.43490 [NSW-945]; 1 specimen, AM P.44276 [NSW-946]; 1825 specimens, AM P.44256 [NSW-944], off Wollongong (34°31.48'S, 151°13.22'E), 200 m, baited trap, 27–28 March 1994, J.K. Lowry & K. Dempsey, MV *Robin E*; 8 specimens, AM P.44238, off Wollongong (34°31.48'S, 151°13.22'E), 200 m, baited trap, 28–29 March 1994, J.K. Lowry & K. Dempsey, MV *Robin E* [NSW-962]; 1 specimen, AM P.44452, off Wollongong (34°32.25'S, 151°15.16'E), 300 m, baited trap, 6–7 May 1993, P. Freewater, S.J. Keable & W. Vader, MV *Robin E* [NSW-783]; 23 specimens, AM P.44426 [NSW-801]; 2 specimens, AM P.44437 [NSW-802], off Wollongong (34°32.53'S, 151°15.0'E), 300 m, baited trap, 7–8 May 1993, P. Freewater, S.J. Keable & W. Vader, MV *Robin E*; 4 specimens, AM P.47032, off Wollongong (34°32.08'S, 151°12.55'E), 200 m, baited trap, 7–8 May 1993, P. Freewater, S.J. Keable & W. Vader, MV *Robin E* [NSW-797].

Type locality. Australia, New South Wales, from stomach of a jackass morwong (tarakihi), *Nemadactylus macropterus* (Forster, 1801), 73–183 m depth.

Depth range. 73–620 m (Lowry and Stoddart 1989).

Distribution. *Australia*: North-east of Rowley Shoals, Western Australia; Lady Elliot Island, Queensland, to off Wollongong, New South Wales (Lowry and Stoddart 1989, this study).

Ecology. Taken in baited traps (this study). Also recorded feeding on dead spatangoids, *Taimanawa mortenseni* Henderson & Fell, 1969 (Lowry and Stoddart 1989).

***Aroui onagawae* (Takekawa & Ishimaru, 2000), comb. n.**

Figure 3

Scopelocheirus onagawae Takekawa & Ishimaru, 2000: 681, figs 1–6. — Takekawa et al. 2004: 971. — Ide et al. 2005: 725. — Ide et al. 2006a: 194. — Ide et al. 2006b: 1209. — Ide et al. 2007: 71.
? *Scopelocheirus hopei*. — Nagata 1965: 148. — Sekiguchi and Yamaguchi 1983: 10, fig. 6.

Type material. Holotype, male, 10.4 mm, AMTU 110. Paratypes: males, AMTU 101, 102, 104, 105; females AMTU 106, 108, 109; juveniles AMTU 103, 107.

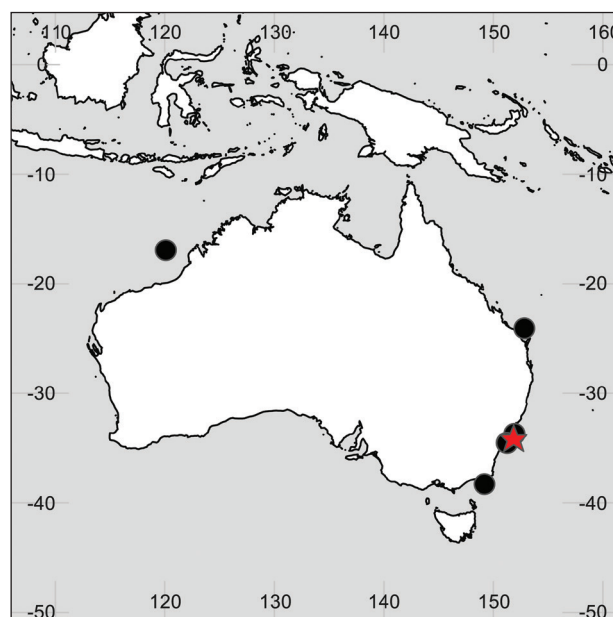


Figure 2. Distribution of *Aroui hamatopodus* Lowry & Stoddart, 1989. Star indicates type locality.

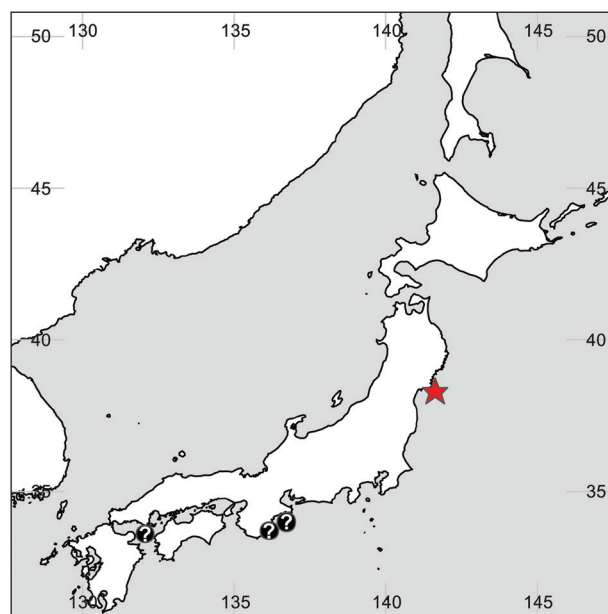


Figure 3. Distribution of *Aroui onagawae* (Takekawa & Ishimaru, 2000). Star indicates type locality, question marks indicate uncertain records.

Type locality. Japan, Miyagi Prefecture, Onagawa Bay (38°25.75'N, 141°32'E), 30 m depth.

Depth range. 30 m (Takekawa and Ishimaru 2000). Possible extension to 519 m (Sekiguchi and Yamaguchi 1983).

Distribution. *Japan*: Onagawa Bay (Takekawa and Ishimaru 2000); Seto Inland Sea? (Nagata 1965) (as *Scopelocheirus hopei*); Enshu- and Kumano-nada? (Sekiguchi and Yamaguchi 1983) (as *Scopelocheirus hopei*).

Ecology. A scavenger, taken in baited traps (Ide et al. 2005), and also known to attack injured flounder juveniles under laboratory conditions (Ide et al. 2006b).

Discussion. Takekawa and Ishimaru (2000) originally placed this species in the genus *Scopelocheirus*, based on the lack of a setal fringe on the coxae of the anterior pereopods. In the present study we have revised the diagnoses for these genera and excluded this character from the diagnosis of *Aroui*. We are therefore removing this species from the genus *Scopelocheirus* to *Aroui* based on maxilla 2, of which the outer plate is shorter than the inner plate and bears long, distally barbed slender setae.

Aroui setosus Chevreux, 1911

Figures 4, 5

Aroui setosus Chevreux, 1911: 170, fig. 3, pl. 7, figs 14–27. — J.L. Barnard 1958: 90 (list). — Belloc 1960: 6. — Thurston and Allen 1969: 356. — Stroobants 1976: 239, figs 1–4, 5B, D, F, H. — Vader 1978: 127. — Diviacco and Ruffo 1989: 476, figs 321, 322. — Lowry and Stoddart 1989: 112, fig. 1. — Barnard and Karaman 1991: 467. — Springthorpe and Lowry 1994: 31. — Stefanidou and Voultsiadou-Koukoura 1995: 602 (table 1), 607. — Bellan-Santini 1998: 874 (table 3). — Bellan-Santini and Ruffo 1998: 900 (table 7). — Berge et al. 2004: 1719 (table 1). — Christodoulou et al. 2013: table 2.

Type material. Lectotype, female, 8 mm, MNHN-Am3985. Paralectotypes: female, 7.6 mm, male, 5.8 mm, AM P.35541; 3 specimens, NHM 1912.4.4:5–7; 93 specimens, MNHN-Am900 and Am901; 3 specimens, MOM.

Type locality. Mediterranean Sea, Algeria, north-east of Cap de Garde (approximately 36°55'N, 7°47'E), 65 m depth, 12 June 1904, *Melita* stn 726.

Depth range. 34–80 m (Stroobants 1976, Stefanidou and Voultsiadou-Koukoura 1995).

Distribution. *Algeria*: off Annaba (Chevreux 1911). *Greece*: near Thasos (Stefanidou and Voultsiadou-Koukoura 1995). *Italy*: Cagliari; and between Capo Ferato and Torre Corallo, Sardinia (Stroobants 1976).

Ecology. Found living on the test of sea urchins (*Spatangus* spp.) (Chevreux 1911, Stroobants 1976). Also collected from the sponge *Suberites* covering a gastropod shell that housed a hermit crab, *Paguristes* sp. (Stroobants 1976).

Discussion. Stroobants (1976) designated a neotype for *Aroui setosus* from material collected from Sardinia. Lowry and Stoddart (1989) subsequently deemed this to be an invalid act, as original syntype material was available, from which these authors selected a lectotype. See Lowry and Stoddart (1989) for a comprehensive synopsis and further discussion.

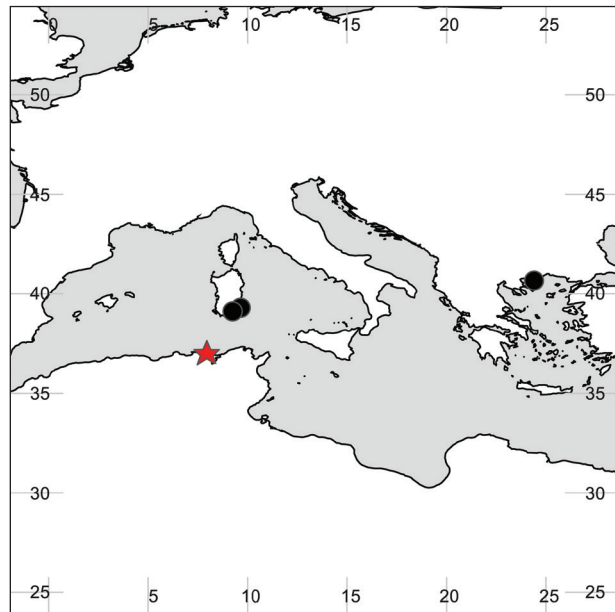


Figure 4. Distribution of *Aroui setosus* Chevreux, 1911. Star indicates type locality.

Paracallisomopsis Gurjanova, 1962

Paracallisomopsis. Gurjanova 1962: 311. — J.L. Barnard 1969: 355. — Barnard and Karaman 1991: 511, fig. 92j.

Type species. *Paracallisomopsis beljaevi* Gurjanova, 1962, by monotypy.

Included species. *Paracallisomopsis* includes one species: *P. beljaevi* Gurjanova, 1962.

Diagnostic description. *Mandible lacinia mobilis* a cuspidate peg; palp article 2 slender. Maxilla 2 inner plate subequal in length to outer plate; outer plate without long distally barbed slender setae. *Gnathopod 1 coxa margins* slightly tapering distally. *Pereopod 5 coxa* slightly wider than long; *basis* linear.

Paracallisomopsis beljaevi Gurjanova, 1962

Figures 6, 7

Paracallisomopsis beljaevi Gurjanova, 1962: 317, fig. 103a–c. — Stroobants 1976: 263, table 3. — Barnard and Karaman 1991: 511, fig. 92j. — Springthorpe and Lowry 1994: 10.

Type material. Syntypes: 1 specimen, sex unknown, 5.5 mm, AM P.35701; 10 specimens, ZIN I-34963.

Type locality. Bering Sea, Russia, Kamchatka, Olyutorsky Bay, 150 m [approximately 60°13'N, 168°23'E].

Depth range. 150 m (Gurjanova 1962).

Distribution. Known only from the type locality, Olyutorsky Bay in the Bering Sea (Gurjanova 1962).

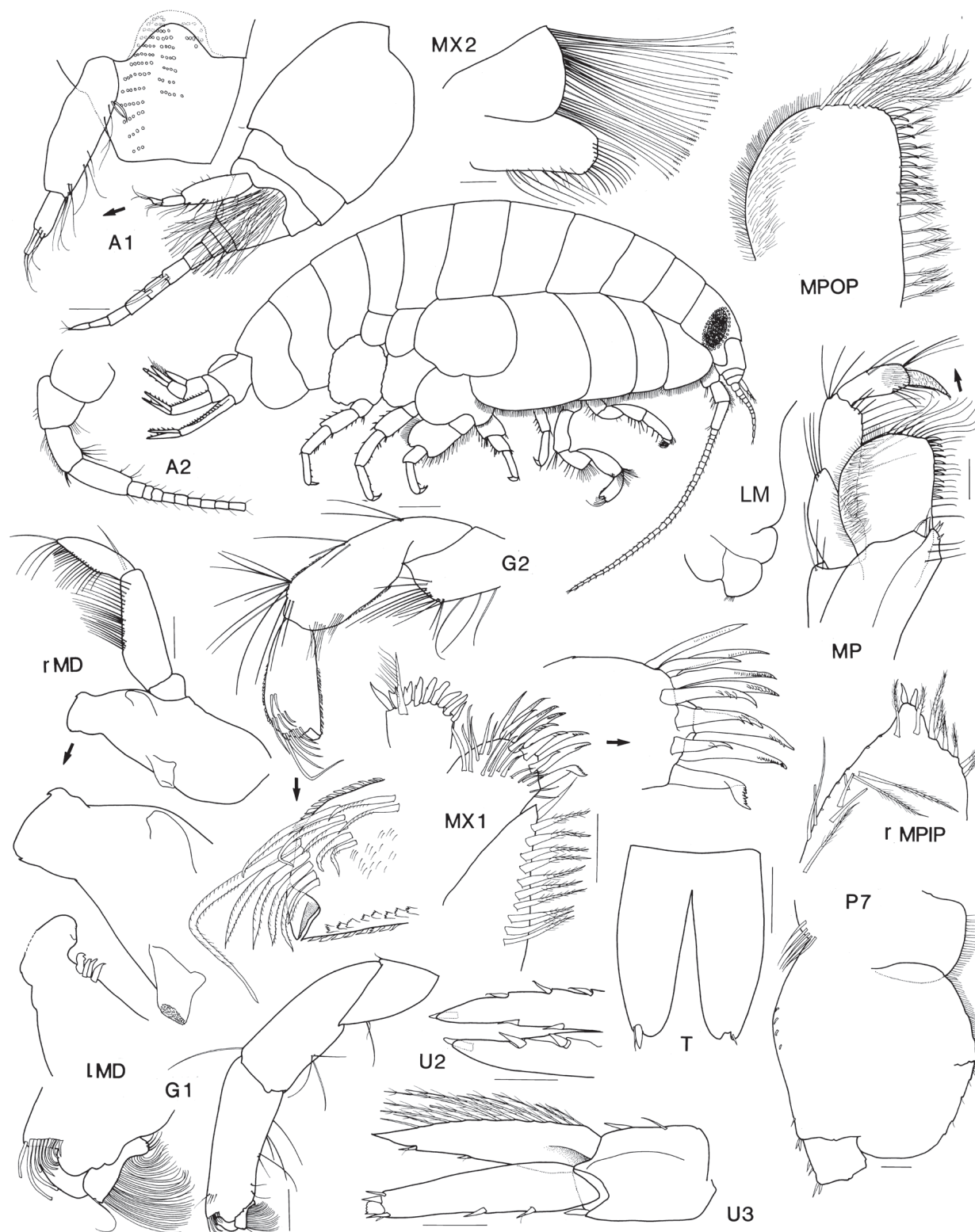


Figure 5. *Aroui setosus* Chevreux, 1911. Lectotype female, 8.0 mm, MNHN-Am3985, off Bône, Mediterranean Sea. Scales represent 0.1 mm.

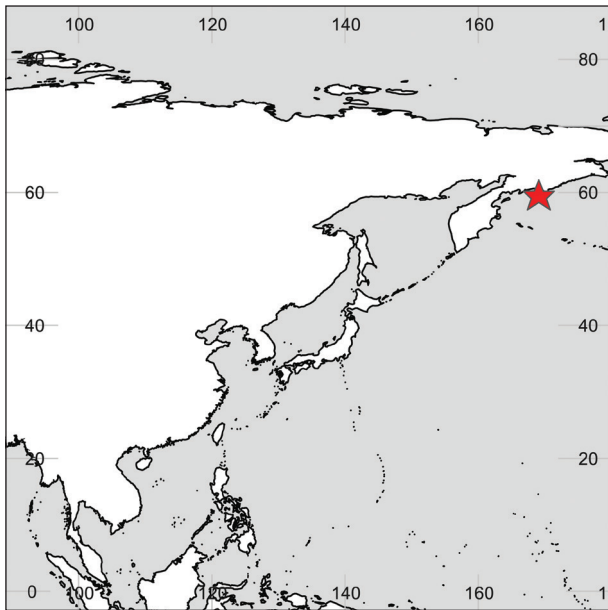


Figure 6. Distribution of *Paracallisomopsis beljaevi* Gurjanova, 1962.

Discussion. Stroobants (1976) considered the possibility that the specimen described by Gurjanova (1962) is a juvenile of *Paracallisoma alberti*. We consider it to be a valid species and placed in the subfamily Scopelocheirinae based on the columnar molar. We examined the syntype in the Australian Museum, but were unable to determine whether the molar has a triturating surface.

Scopelocheirus Bate, 1857

Callisoma O.G. Costa, 1840: 5 (*nomen nudum*). — A. Costa 1851: 1 (homonym, Coleoptera). — Lilljeborg 1865a: 33. — Lilljeborg 1865b: 23. — Heller 1866: 26. — Boeck 1871: 101. — Boeck 1872: 131. — G.O. Sars 1890: 52. — Della Valle 1893: 838.
Scopelocheirus Bate, 1857: 138. — Stebbing 1906: 61. — Chevreux and Fage 1925: 54. — Stephensen 1929: 64. — Schellenberg 1942: 110. — Gurjanova 1951: 241. — J.L. Barnard 1969: 362. — Lincoln 1979: 50. — Diviacco and Ruffo 1989: 542. — Barnard and Karaman 1991: 528, 434 (key), 454 (key).

Type species. *Scopelocheirus crenatus* Bate, 1857 by monotypy.

Included species. *Scopelocheirus* includes three species: *S. crenatus* Bate, 1857; *S. hopei* A. Costa, 1851; *S. polymedus* Bellan-Santini, 1985.

Diagnosis. Mandible lacinia mobilis a stemmed, distally expanded, irregularly cusped blade; palp article 2 broadened. Maxilla 2 inner plate slightly longer than outer; outer plate without long distally barbed slender setae. Gnathopod 1 coxa margins diverging distally. Pereopod 5 slightly wider than long; basis greatly expanded posteriorly.

Ecology. *Scopelocheirus* species are frequently taken in baited traps. They are also reported in the literature as an associate of echinoids.

Discussion. The taxonomic and nomenclatural history of the genus *Scopelocheirus* is highly complex. Della Valle (1893) placed all of the then described species of *Scopelocheirus* (*Callisoma Barthelemyi* Costa, 1853; *Scopelocheirus brevatus* Bate, 1856; *Scopelocheirus crenatus* Bate, 1857; *Anonyx Kröyeri* Bruzelius 1859; *Callisoma Branickii* Wrzesniewski, 1874; and *Tryphosa serra* Meinert 1890) in the synonymy of *Scopelocheirus hopei* (as *Callisoma hopei*). Since then, *S. crenatus* and *S. hopei* have variously been treated as synonyms by some authors, e.g. Lincoln (1979), and as distinct species by others, e.g. Diviacco and Ruffo (1989). As these names have been recorded many times in the literature and appear commonplace in the north-east Atlantic and Mediterranean, the result is a confused synonymy and a distributional record that is beyond the scope of the present study to untangle. In the following catalogue we treat these names separately, and detail what is recorded in the literature without making any assumption on the validity of the taxon concepts in most cases, which would require a much more detailed study of material.

Barnard and Karaman (1991) considered *Bathycallisoma* to be a junior synonym of *Scopelocheirus*, however our re-diagnosis of *Scopelocheirus* excludes *Bathycallisoma* from the Scopelocheirinae on the basis of its flap-like molar. We consider it to be a valid genus, placed in the Paracallisominae.

Scopelocheirus crenatus Bate, 1857

Figures 8, 9

Scopelocheirus brevatus Bate, 1856: 58 (*nomen nudum*)
Scopelocheirus crenatus Bate, 1857: 138. — Stebbing 1906: 62. — Stephensen 1923a: 96. — Stephensen 1923b: 16. — Stephensen 1932: 355. — Chevreux 1935: 41, pl. 7, fig. 3. — Stephensen 1935: 77. — Raitt 1937: 249. — Stephensen 1940: 12. — Stephensen 1942: 472 (table). — Jones 1948: 404, 421. — Enequist 1949: 387 (table). — Jones 1951: 138, 143 (appendix). — Gurjanova 1951: 241 (key), 242 (fig. 107). — J.L. Barnard 1958: 99 (list). — Thurston and Allen 1969: 367. — Laverack and Blackler 1974: 81. — Mattson 1981: 115 (table 1). — Palerud and Vader 1991: 43.
Callisoma crenata. — Bate 1862: 85, pl. 14, fig. 5. — Bate and Westwood 1863: 120, text fig. — Norman 1869: 276. — Boeck 1871: 101. — Boeck 1872: 132, pl. 7, fig. 1. — M'Intosh 1874: 266. — Haddon 1886: 636. — Chevreux 1888: 4. — Robertson 1888: 23. — Pocock 1889: 431. — G.O. Sars 1890: 53, pl. 19, fig. 1. — Meinert 1890: 151. — Walker 1892: 137. — Walker 1895: 291. — Walker 1896: 45. — Scott 1898: 176. — Scott 1900: 180. — Nordgaard 1905: 183. — Nordgaard 1911: 21. — Chumley 1918: [page unknown].

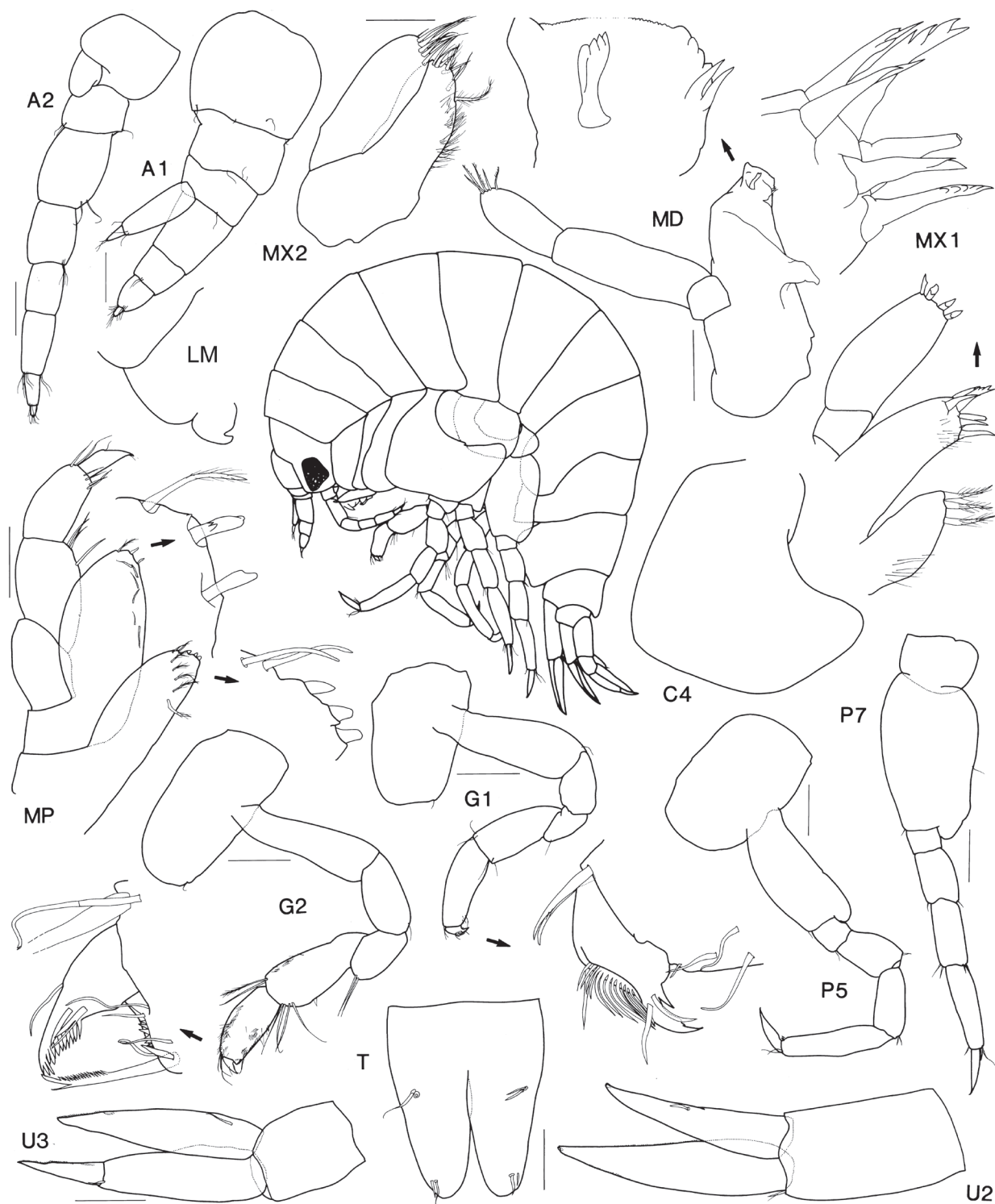


Figure 7. *Paracallisomopsis beljaevi* Gurjanova. Syntype, sex not known, 5.5 mm, AM P.35701, Barents Sea. Scales for gnathopods, pereopods represent 0.2 mm; remainder represents 0.1 mm.

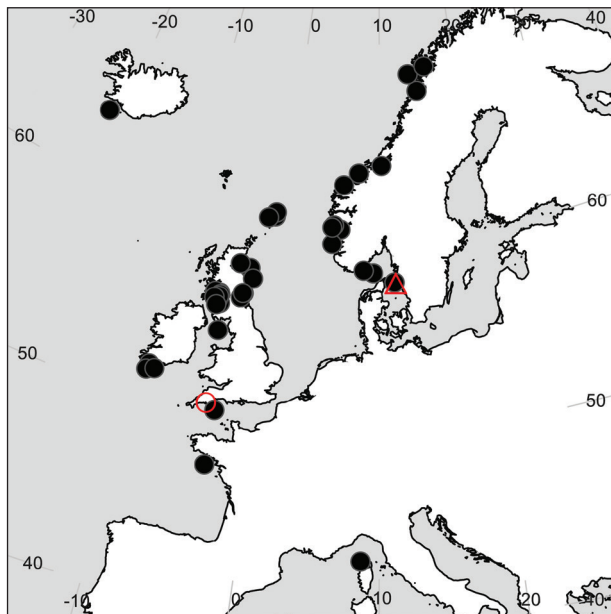


Figure 8. Distribution of *Scopelocheirus crenatus* Bate, 1957, and its synonyms. Circles represent records of *Scopelocheirus crenatus* and its objective synonyms; triangle represents the subjective synonym *Tryphosa serra* Meinert, 1890. Type localities are indicated by the corresponding open symbol.

? *Tryphosa serra* Meinert, 1890: 156, pl. 51, figs 30–38.

Callisoma crenatum. — Chevreux 1898: 476.

Callisoma hopei. — Della Valle 1893: 839 (in part).

Scopelocheirus crenatus. — H.B. Moore 1937: 117.

Scopelocheiropsis crenatus. — Sanderson 1973: 38.

Type material. Syntypes, 26 specimens, NHM 1952:5:7:13.

Type locality. Plymouth Sound, United Kingdom.

Depth range. *Atlantic Ocean*: 3.7–323 m (Laverack and Blackler 1974, Enequist 1949). *Mediterranean Sea*: 2500 m (Chevreux 1935).

Distribution. In the literature, this species name has been widely recorded from the north-east Atlantic Ocean, with a single record from the Mediterranean Sea.

North Atlantic Ocean. *Denmark*: the Skagerrak and the Kattegat (Meinert 1890). *France*: South-west of Belle Île (Chevreux 1898). *Iceland*: South-west coast (Stephensen 1923a). *Ireland*: Bantry Bay (Haddon 1886); off Fastnet Rock (Pocock 1889); off Galley Head (Walker 1895). *North Sea Area*: north-west North Sea (Raitt 1937). *Norway*: Søndfjord; Hardangerfjord; and Hauge-sund (Boeck 1871, 1872); Alesund; Kristiansund (Boeck 1872); Trondheimsfjord (G.O. Sars 1890, Oldevig 1959); Skjerstadfjorden; Herdafjord, Bergen (Nordgaard 1911); Lofotens (Stephensen 1932); the Skagerrak (Enequist 1949); Raunefjorden (Mattson 1981). *United Kingdom*: Plymouth Sound (Bate 1862); Banff (Bate 1862); Mac-duff (Bate 1862); Moray Firth (Bate and Westwood

1863); Shetland Islands (Norman 1869); St. Andrews (from the stomach of a haddock) (M'Intosh 1874, Laverack and Blackler 1974); Loch Fyne (Robertson 1888, Chumley 1918); Loch Goil (Robertson 1888, Chumley 1918); off Garnock Beacon (Robertson 1888); Kilchattan Bay (Robertson 1888); Cumbrae (Robertson 1892); West of Bradda Head, Isle of Man (Walker 1895, 1896); Firth of Forth (Scott 1898); off Aberdeen (Scott 1900); Gare-loch (Chumley 1918); Dunoon Basin (Chumley 1918); Skate Island (Chumley 1918); off Dartmouth, Devon (Chevreux 1935); Clyde (Sanderson 1973).

Mediterranean Sea. *France*: Off Corsica (Chevreux 1935).

Ecology. A scavenger that has been collected in baited traps (Chevreux 1935) and from dead fish on fishermen's lines (Sars 1890).

Discussion. We follow Stebbing (1906) and consider *Tryphosa serra* Meinert, 1890 to be a possible junior subjective synonym of *Scopelocheirus crenatus*. The record of Chevreux (1935) from off Corsica is the only known record of this species from the Mediterranean and is an order of magnitude deeper than all the Atlantic records. It may be a misidentification of *S. polymedus* Bellan-Santini, 1984.

Scopelocheirus hopei (Costa, 1851)

Figure 10

Callisoma Hopei A. Costa, 1851: 5. — A. Costa 1857: 188. — Bate 1862: 86, pl. 14, fig. 6. — Heller 1866: 27, pl. 3, figs 17, 18. Stossich 1880: 247. — Chevreux 1895: 426. — Norman 1895: 480. — Norman 1900: 200. — Chevreux 1903: 84. — Della Valle 1893: 839, pl. 6, fig. 11, pl. 26, figs 1–15 (in part).

? *Callisoma Barthelemyi* Costa, 1853a: 7.

? *Anonyx Kröyeri* Bruzelius, 1859: 45, pl. 2, fig. 7.

? *Callisoma Kröyeri*. — Bate 1862: 371. — Lilljeborg 1865a: 33. — Lilljeborg 1865b: 23. — Boeck 1871: 102. — Boeck 1872: 134. — Metzger 1875: 284 (table). — G.O. Sars 1890: 54, pl. 19, fig. 2. — Norman 1900: 200.

? *Callisoma Branickii* Wrzesniewski, 1874: 15. — Wrzesniewski 1879: 349.

? *Callisoma kröyeri*. — Walker 1898: 166.

Scopelocheirus hopei. — Stebbing 1906: 62 (key). — Cecchini 1928: 301. — Marine Biological Association of the UK 1931: 188. — Stephensen 1932: 355. — Stephensen 1935: 76. — Williams 1938: 89. — Schellenberg 1942: 111. — Stephensen 1942: 472 (table). — Enequist 1949: 387, 400 (table). — Gurjanova 1951: 241, fig. 106 (key). — Williams 1954: 77. — Bossanyi 1957: 357. — J.L. Barnard 1958: 99 (list). — Oldevig 1959: 16. — Krapp-Schickel 1974: 321 (list), 339. — Stroobants 1976: 256, figs 6(S)–10(S), tables 1–4. — Ledoyer 1977: 389. — Lincoln 1979: p. 50, fig. 16. — Mattson 1981: 115 (table 1). — P.G. Moore 1984: 36. — Mateus and Mateus 1986: 130. — Dauvin 1988: 420. — Costello et

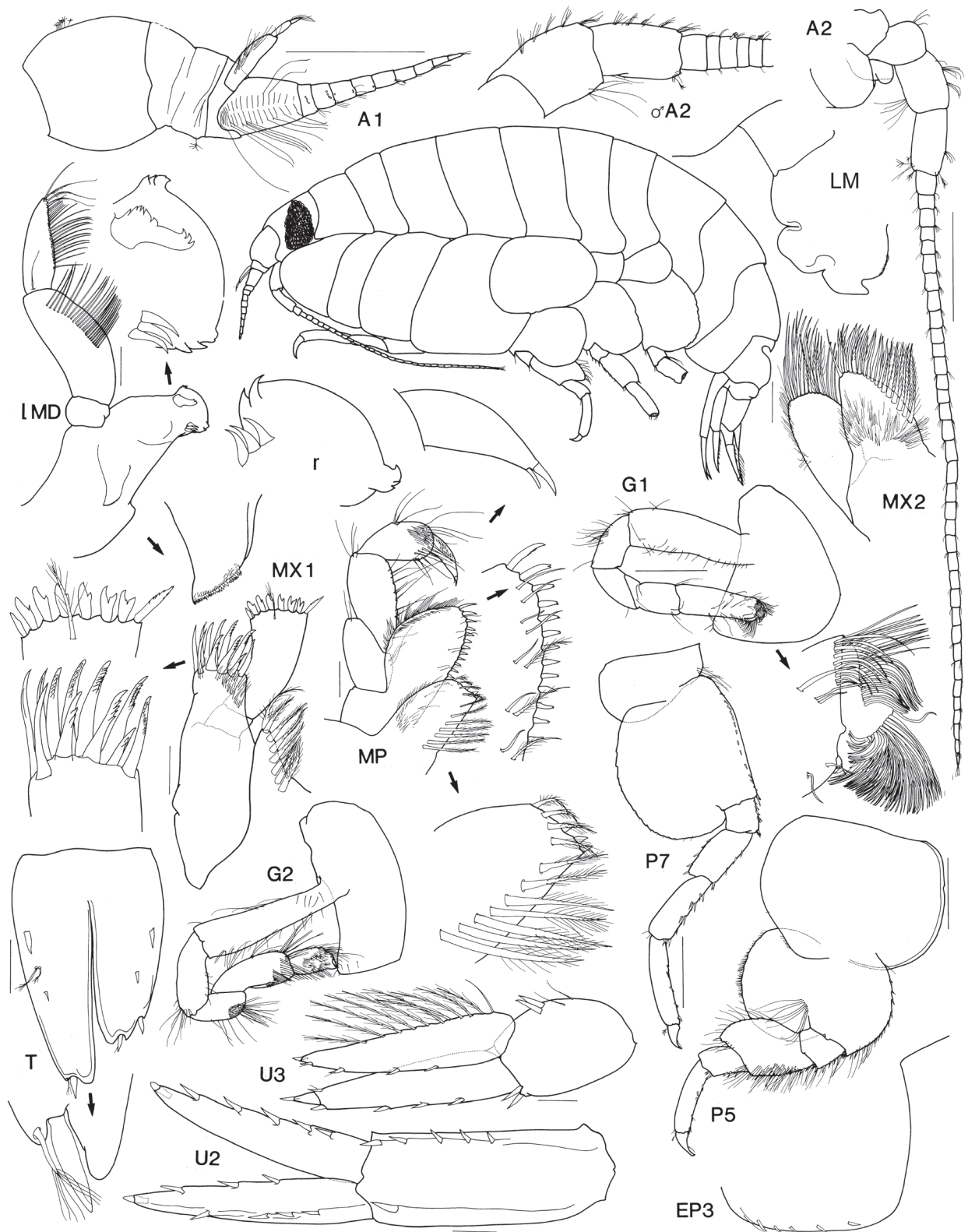


Figure 9. *Scopelocheirus crenatus* Bate. Female, 8.0 mm; male, 7.8 mm; AM P.35895, Skipness Point, Clyde Sea area, Scotland. Scales for antennae, gnathopods, pereopods represent 0.5 mm; remainder represent 0.1 mm.

al. 1989: 35 (in part, part *S. crenatus*). — Diviacco and Ruffo 1989: 542 (key), 544, fig. 372. — Kaartvedt 1989: 191, table 5. — Buhl-Jensen and Fosså 1991: 248, table 2. — Barnard and Karaman 1991: 528. — Nickell and Moore 1991: 368. — Palerud and Vader 1991: 43. — Albertelli et al. 1992: 142, 143, table 2. — Andres et al. 1992: 185, table 1. — Britton and Morton 1993: 369. — Dauvin et al. 1994: 551, table 3. — Ishimaru 1994: 59 (list). — Buhl-Mortensen 1996: 49, appendix 1. — Dauvin and Sorbe 1996: 443, 447, 449 (tables 3–5). — Krapp-Schickel and Zavodnik 1996: 459 (list). — Vallet and Dauvin 1996: 481. — Cunha et al. 1997: 133, appendix 1. — Ramsay et al. 1997: 892, table 6, 894. — Bellan-Santini 1998: 874, table 3. — Bellan-Santini and Ruffo 1998: 900, table 7. — Cartes and Sorbe 1999: 1138, table 1. — Miskov-Nodland et al. 1999: 154, appendix. — Groenewold and Fonds 2000: 1398. — O'Reilly et al. 2001: 36. — Bergmann et al. 2002: 190, figs 6a, 8, appendix 1. — Dauvin and Bellan-Santini 2002: 317, table 1. — Jones et al. 2003: 79, table 3, fig. 3. — Cartes et al. 2003: 748, table 1. — Kaim-Malka 2003: 37, figs 3–13, tables 1–7. — Castro et al. 2005: 442, table 3. — Horton 2006: 19, table 1. — Madurell et al. 2008: 338, table 1, 339, table 2. — Zakhama-Sraieb et al. 2009: 5, table 3. — Danovaro et al. 2010: 6. — Christodoulou et al. 2013: 12, table 2.

Scopelocheirus Hopei. — Chevreux 1911: 169. — Massy 1912: 40, 41. — Monod 1923: 22. — Stephensen 1923b: 15. — Chevreux and Fage 1925: 55, figs 39, 40. — Chevreux 1927: 61. — Stephensen 1929: 64. — Cecchini and Parenzan 1935: 165. — Chevreux 1935: 41. — Macquart-Moulin 1984: 185.

Scopelocheiropsis hopei. — Sanderson 1973: 38.

Not *Scopelocheirus hopei*. — Nagata 1965: 148. — Sekiguchi and Yamaguchi 1983: 10, fig. 6. (Probably = *Aroui onagawae*).

Type material. Probably lost.

Type locality. Naples, Italy, Mediterranean Sea.

Depth range. *Mediterranean Sea*: 34–2500 m (Stroobants 1976, Chevreux 1903). *Atlantic Ocean*: 12–2620 m (Stephensen 1923b, Chevreux 1903). *?Pacific Ocean*: 40–519 m (Nagata 1965, Sekiguchi and Yamaguchi 1983).

Distribution. Widely recorded from the North Atlantic Ocean and Mediterranean Sea. Records from Japan are tentatively referred to *Aroui onagawae* (Sekiguchi & Yamaguchi, 1983).

North Atlantic Ocean. *Denmark*: near Horns Revs Lighthouse (Stephensen 1923b); the eastern Skagerrak (Stephensen 1923b); north of Skagen (Enequist 1949). *France*: Fosse de Capbreton (Norman 1900); Bay of Biscay (Chevreux 1903); off Roscoff (Dauvin 1988, Dauvin et al. 1994); Cap-Ferrat Canyon (Dauvin and Sorbe 1996). *Guinea-Bissau*: (Mateus and Mateus 1986). *Ireland*: Off the Skelligs, Co. Kerry; Ballycotton, Co. Cork

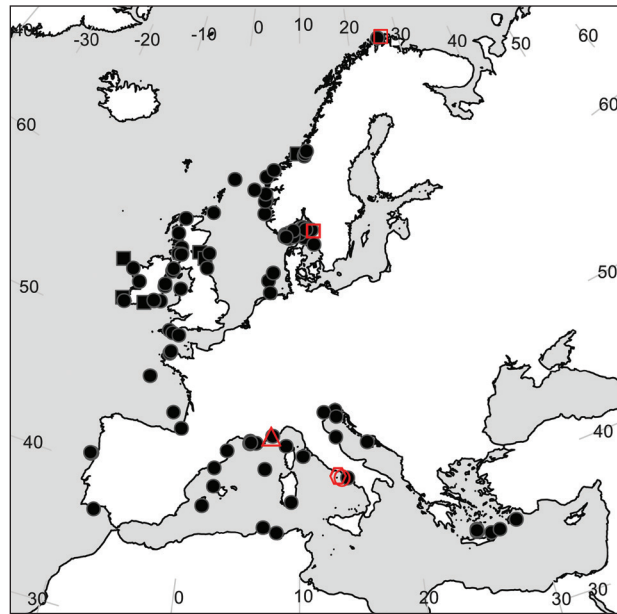


Figure 10. European distribution of *Scopelocheirus hopei* (Costa, 1851) (African distribution excluded). Circles represent records of *Scopelocheirus hopei* and its objective synonyms. Subjective synonyms are represented by the following symbols: (■) *Anonyx Kröyeri* Bruzelius, 1859; (▲) *Callisoma Branickii* Wrzesniewski, 1874; (●) *Callisoma Barthelemyi* Costa, 1853. Type localities are indicated by the corresponding open symbol.

(Walker 1898) (as *Callisoma kröyeri*); off south-west Ireland (Norman 1900); Dundrum-Dublin coast (Massey 1912); Galway Bay (McGrath 1981); Malahide; off Tuskar Rock; Hook Head; off Dunmore East; off Achill Head (Costello et al. 1989). *Norway*: Beian, Trondheimsfjord (G.O. Sars 1890) (as *Callisoma Kröyeri*); Raudeberg, Trondheimsfjord (Norman 1895); Finnmark (Bruzelius 1859) (as *Anonyx Kröyeri*); off the Aas Fjord; Strind Fjord; Gulosen; near Byberget, Trondheim region (Enequist 1949); Ålesund; north-west of Bergen; south-west of Haugesund; Skarnsyndet; Kjelvik (Oldevig 1959); Raunefjorden (Mattson 1981); Masfjorden (Kaartvedt 1989); Norwegian Shelf area (Buhl-Mortensen 1996); the Skagerrak (Miskov-Nodland et al. 1999). *Portugal*: off Aveiro (Andres et al. 1992, Cunha et al. 1997); south of Olhão (Castro et al. 2005). *Sweden*: Bohuslän (Bruzelius 1859) (as *Anonyx Kröyeri*); Gullmar Fjord, Bohuslän (Enequist 1949, Oldevig 1959, Buhl-Jensen and Fosså 1991); west of Hållö (Enequist 1949); Löken, Gåsö Ränn; west of Nidingen (Oldevig 1959). *United Kingdom*: Firth of Forth (Metzger 1875) (as *Callisoma Kröyeri*); Banff; Firth of Clyde; Firth of Forth; Inverary; Northumberland coast; Polperro, Cornwall; Seaham, Co. Durham; Shetland Islands; Sleat Sound (Norman 1900); Devon (Plymouth Marine Fauna 1931); off Dartmouth; east of the Orkney Islands (Chevreux 1935); Strangford Lough, Co. Down; off Donaghadee, Co. Down (Williams 1954); off Blyth, Northumberland (Bossanyi 1957); Clyde Area (Sanderson 1973, Moore 1984, Bergmann et al. 2002); near Assynt (Sanderson 1973); Anglesey (Ramsay et al. 1997).

Mediterranean Sea. *Algeria*: Annaba (Chevreux 1911). *Croatia*: Hvar (Heller 1866); Rovinj (Krapp-Schickel and Zavodnik 1996). *France*: ?Nice (Wrzesniowski 1874) (as *Callisoma branickii*); Calvi, Corsica (Chevreux 1903); Cap d'Ail (Monod 1923); Bonifacio, Corsica (Chevreux 1927); Canyon de Planier (Ledoyer 1977, Kaim-Malka 2003); south-east of Planier, north of Ratonneau; south of Île des Embiez (Ledoyer 1977); Banyuls-sur-Mer (Diviacco and Ruffo 1989); off Marseille (Ledoyer 1977, Kaim-Malka 2003). *Greece*: Cretan Sea; Rhodes Basin (Jones et al. 2003). *Italy*: Gulf of Naples (Costa 1851, 1857, Della Valle 1893, Cecchini 1928, Cecchini and Parenzan 1935); Monte Cristo Island (Chevreux 1895); Cagliari (Stroobants 1976); Ancona; Venice (Diviacco and Ruffo 1989). *Slovenia*: Piran (Heller 1866). *Spain*: Catalan slope (Cartes and Sorbe 1999); Balearic Islands (Cartes et al. 2003; Madurell et al. 2008). *Tunisia*: Between La Galite and Cap Serrat (Chevreux 1911).

Ecology. A known scavenger, taken in baited traps (Chevreux 1895). Also reported as an associate of *Clypeaster* spp. (Wrzesniowski 1874) and *Echinocardium cordatum* (Pennant, 1777) (Metzger 1875, Plymouth Marine Fauna 1931); taken from the back and between the legs of *Maja squinado* (Herbst, 1788) (Plymouth Marine Fauna 1931); taken from the cranial cavity and along the nerve tracts of *Squalus acanthias* Linnaeus, 1758 (Williams 1938).

Discussion. Japanese records of *S. hopei* by Nagata (1965) and Sekiguchi and Yamaguchi (1983) are here considered to be inaccurate on the basis of their distribution, and some morphological inconsistencies with the European form such as the shape of the urosomite 1 (dorsally rounded in the European *S. hopei*, dorsally truncated in the Japanese specimens) and the length of the uropod 3 inner ramus (slightly shorter than and reaching at least to article 2 of outer ramus European specimens, much shorter than outer ramus in the Japanese specimens). It is possible that these records may actually represent *Aroui onagawae*. Unfortunately, the only illustration of Japanese specimens (by Sekiguchi and Yamaguchi (1983)) does not show the setae on the outer plate of maxilla 2 and as such precludes a generic placement in either *Aroui* or *Scopelocheirus*. However, all of the other illustrated characters correspond to the description and illustration of *A. onagawae* by Takekawa and Ishimaru (2000).

Scopelocheirus polymedus Bellan-Santini, 1985

Figure 11

Scopelocheirus polymedus Bellan-Santini, 1985a: 275, figs 1, 2. — Bellan-Santini 1985b: 334. — Diviacco and Ruffo 1989: 542 (key), 544, figs 373, 374. — Bellan-Santini 1998: 874, table 3. — Bellan-Santini and Ruffo 1998: 900, table 7. — Bellan-Santini 1990: 277, 279. — Barnard and Karaman

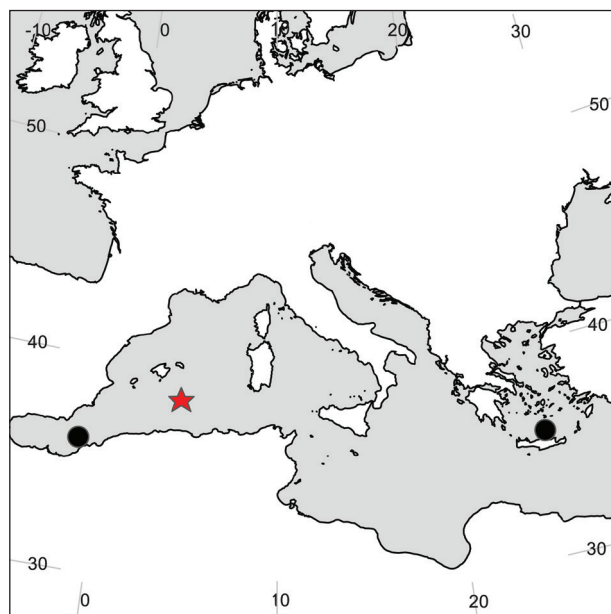


Figure 11. Distribution of *Scopelocheirus polymedus* Bellan-Santini, 1984. Star indicates type locality.

1991: 528. — Jones et al. 2003: 79, table 3, fig. 3. — Danovaro et al. 2010: 6. — Christodoulou et al. 2013: 12, table 2.

Type material. Holotype, female, 9 mm, MSNV 213.

Type locality. South-east of Mallorca, Mediterranean Sea (38°27'N, 04°08'E), 2447 m depth.

Depth range. 1511–2447 m (Jones et al. 2003, Bellan-Santini 1985a).

Distribution. Mediterranean Sea. Western Basin, south-east of Mallorca (Bellan-Santini 1985a). *Algeria*: north-west of Oran (Bellan-Santini 1985a). *Greece*: Cretan Sea (Jones et al. 2003).

Ecology. Taken in baited traps (Jones et al. 2003).

Discussion. Many of the deeper records of *S. hopei*, particularly those from the Mediterranean may actually be misidentifications of *S. polymedus*, and should be re-examined to confirm their identity.

Subfamily Paracallisominae subfam. n.

<http://zoobank.org/015E0211-83B5-4A15-BA80-11E5872DAF2F>

Included genera. The Paracallisominae contains 7 genera: *Anisocallisoma* Hendrycks & Conlan, 2003; *Bathycallisoma* Dahl, 1959; *Eucallisoma* J.L. Barnard, 1961; *Austrocallisoma* gen. n.; *Paracallisoma* Chevreux, 1903; *Scopelocheiropsis* Schellenberg, 1926; *Tayabasa* gen. n.

Diagnosis. Mandible a non-setose flap or occasionally absent (*Scopelocheiropsis sublitoralis*).

Anisocallisoma Hendrycks & Conlan, 2003

Anisocallisoma Hendrycks & Conlan, 2003: 2313.

Type species. *Anisocallisoma armigera* Hendrycks & Conlan, 2003, by monotypy.

Included species. *Anisocallisoma* includes one species: *A. armigera* Hendrycks & Conlan, 2003.

Diagnostic description. *Mandible lacinia mobilis* a long, slender robust seta. *Maxilla 1* inner plate with apical pappose setae only; *palp 1*-articulate. *Maxilla 2* inner and outer plates subequal in width and in length. *Maxilliped* palp article 4 reduced. *Gnathopod 1* coxa reduced, margins tapering distally; basis swollen; dactylus reduced, simple. *Pereopods 3* and *4* carpus short, longer than wide. *Pereopod 4* coxa with weakly-developed, subacutely produced posteroventral lobe.

Discussion. *Anisocallisoma* can be distinguished from all other paracallisomines by the reduction in the number of setae of the *maxilla 1* inner plate. It is most similar to *Eucallisoma* Barnard, 1961, and *Tayabasa* gen. n. They share the following characters: *gnathopod 1* basis swollen, glandular; dactylus reduced, simple. It is also very similar to the new genus *Austrocallisoma*, but it can be distinguished from all of these taxa in lacking the distal tuft of setae on the accessory flagellum, and in having a much more weakly-developed posteroventral lobe on the *pereopod 4* coxa, as well as the reduced setae on the *maxilla 1*.

Anisocallisoma armigera Hendrycks & Conlan, 2003

Figure 12

Anisocallisoma Hendrycks & Conlan, 2003: 2314.

Type material. Holotype, male, 5.5 mm, CMNC 2002-0003. Allotype, female, 3.7 mm, CMNC 2002-0004. Paratypes: 1 male, 4.1 mm, CMNC 2002-0005; 1 male, 5.7 mm, CMNC 2002-0006; 1 male, ZMUC CRU-3722.

Type locality. Station M, 220 km off Point Conception, California, United States (34°47.2'N, 123°03.0'W), 3450 m.

Depth range. 3450–4050 m (Hendrycks and Conlan 2003).

Distribution. *United States*: off Point Conception, California (Hendrycks and Conlan 2003).

Austrocallisoma gen. n.

<http://zoobank.org/13BBD64A-FF5E-40EA-BE98-52946A289F28>

Type species. *Austrocallisoma jerryi* sp. n., by original designation.

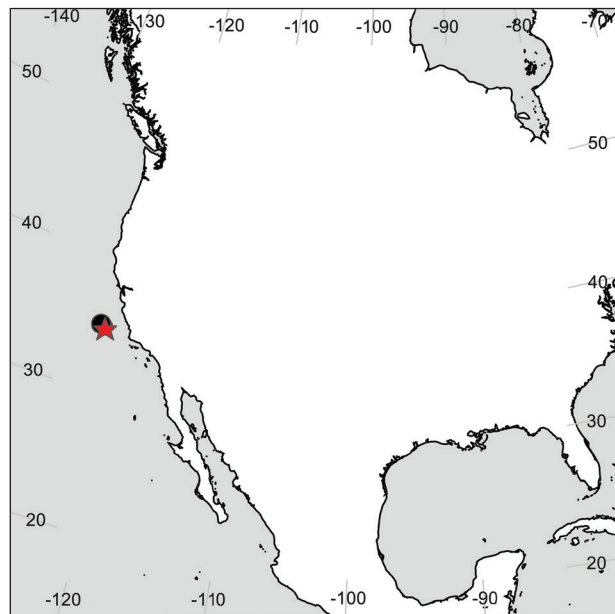


Figure 12. Distribution of *Anisocallisoma armigera* Hendrycks & Conlan, 2003. Star indicates type locality.

Included species. *Austrocallisoma* includes one species: *Austrocallisoma jerryi* sp. n.

Diagnostic description. *Mandible lacinia mobilis* a stemmed distally expanded, irregularly cusped blade. *Maxilla 1* inner plate with pappose setae lining inner margin; *palp 1*-articulate. *Maxilla 2* inner plate broader than outer, inner and outer plates subequal in length. *Maxilliped* palp article 4 vestigial. *Gnathopod 1* coxa reduced, slightly shorter than coxa 2, margins slightly tapering distally; basis swollen, without glandular material; dactylus reduced, simple. *Pereopod 3* carpus short to long, longer than wide. *Pereopod 4* with well-developed, subacute posteroventral lobe.

Etymology. The name is a combination of the prefix *Austro-* from the latin *australis*, meaning southern and referring to the southern hemisphere distribution of the type species, and the suffix *-callisoma* (gender neuter) referring to its placement within the Paracallisominae.

Discussion. *Austrocallisoma* gen. n. is a difficult taxon that has much in common with the monotypic genera *Anisocallisoma*, *Eucallisoma* and *Tayabasa* gen. n. Having four monotypic genera that are highly derived yet clearly closely related is not ideal. However, to maintain consistency of diagnostic characters at a generic level we feel justified in establishing this new genus.

Austrocallisoma can be separated from both *Eucallisoma* and *Anisocallisoma* by the strongly developed and subacute posteroventral lobe on the *pereopod 4* coxa (well-developed and subquadrate in *Eucallisoma*, very weakly-developed and subacute in *Anisocallisoma*). It can be further distinguished from *Anisocallisoma* in having plumose setae lining the inner margin of the inner

plate of maxilla 1, and having a distal tuft of setae on the accessory flagellum. It differs from *Eucallisoma* in having a vestigial maxilliped palp article 4 (well-developed in *Eucallisoma*).

***Austrocallisoma jerryi* sp. n.**

<http://zoobank.org/D2E70936-572C-4DED-BAC7-C465C923AA69>

Figures 13–16

Type material. Holotype, female, 32.0 mm, AMP.69087, east of Sydney, New South Wales, Australia (33°44.5–08.9'S, 152°24.4–09.68'E), 0–1800 m over bottom depth 2994–3828 m, Isaacs-Kidd midwater trawl, 27–28 April 1989, coll. J.R. Paxton, HMAS *Cook* [JP 89-5]. Paratype, 1 immature female with non-setose oostegites, 26.0 mm, AM P.70171, east of Sydney, New South Wales, Australia (33°52.5–53.92'S, 152°39.0–05.9'E), 0–1800 m over bottom depth 1700–4856 m, Isaacs-Kidd midwater trawl, 27 April 1989, coll. J.R. Paxton, HMAS *Cook* [JP 89-3].

Diagnosis. Mandible lacinia mobilis a stemmed distally expanded, irregularly cusped blade. Maxilla 1 palp 1-articulate. Maxilliped palp article 4 absent. Gnathopod 1 coxa reduced, slightly shorter than coxa 2; basis swollen, without glandular material.

Description. Based on holotype female, 32.0 mm, AM P.69087.

Lateral cephalic lobe large, triangular, apically subacute. Rostrum absent. Eyes apparently absent. Antenna 1 short; accessory flagellum long, 2-articulate, forming cap partially covering callynophore; primary flagellum 7-articulate, with strong 2-field callynophore; calceoli absent. Antenna 2 longer than antenna 1; peduncle with strong brush setae, article 1 greatly enlarged, covering article 2; flagellum 30-articulate, calceoli absent.

Labrum, epistome produced, rounded distally; upper lip slightly produced, straight. Mandible incisor with slightly convex margins; lacinia mobilis a stemmed, distally expanded, irregularly cusped blade; molar flap-like; palp attached midway, article 2 slender. Maxilla 1 inner plate with pappose setae lining inner margin; palp 1-articulate. Maxilla 2 inner and outer plates subequal in length; outer plate without long distally barbed slender setae. Maxilliped outer plate small; palp large, 4-articulate; dactylus vestigial, represented by a short, narrow, curving robust seta.

Gnathopods 1–4 coxae without setal fringe along ventral margin. Gnathopod 1 coxa reduced, margins slightly tapering distally; basis broad; ischium long; carpus long, slightly longer than propodus; propodus margins tapering distally, anterodistal margin with row of long, slender setae, with 1 robust seta just above dactylus; dactylus small, simple, well developed, posterior margin without setae, without cusps along posterior margin. Gnathopod 2 minutely subchelate; propo-

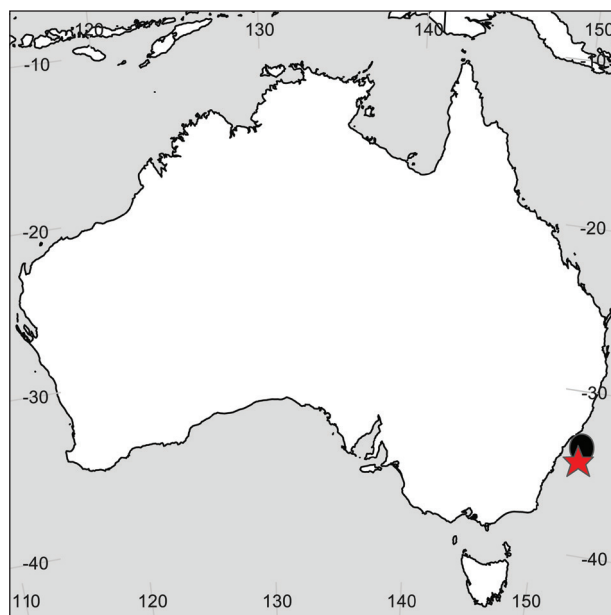


Figure 13. Distribution of *Austrocallisoma jerryi* sp. n. Star indicates type locality.

dus long, palm transverse; dactylus reaching corner of palm. Pereopod 3 simple; propodus with posterodistal locking setae; dactylus short, slender. Pereopod 4 simple; coxa wider than deep, with subacutely produced posteroventral lobe; dactylus short, slender. Pereopod 5 simple; coxa with posterior lobe slightly produced; basis much longer than broad, moderately expanded posteriorly, posterior margin straight, posteroventral lobe moderately broadened, not extending beyond ischium; without row of long slender pappose setae medially; dactylus short, slender. Pereopod 6 basis moderately expanded with straight posterior margin, with rounded, moderately broadened posteroventral lobe, produced into merus; dactylus short, slender. Pereopod 7 basis rounded, expanded posteroproximally, posterior margin almost straight, smooth, forming a posteroventral lobe produced along merus, posteroventral margin rounded; dactylus short, slender.

Epimeron 3 posteroventral corner subquadrate. Urosomite 1 dorsally smooth. Uropod 1 peduncle $2.2 \times$ rami length; rami subequal in length. Uropod inner ramus slightly shorter than outer ramus. Uropod 3 peduncle short; rami lanceolate, subequal in length, outer ramus (?) 2-articulate, with plumose setae. Telson longer than broad, length $2 \times$ breadth, moderately cleft (to 59%).

Etymology. Named in honour of Jerry Barnard, in recognition of his enormous contribution to amphipod taxonomy.

Depth range. 0–1800 m over a bottom depth of 1700–4856 m.

Distribution. *Australia:* east of Sydney, New South Wales.

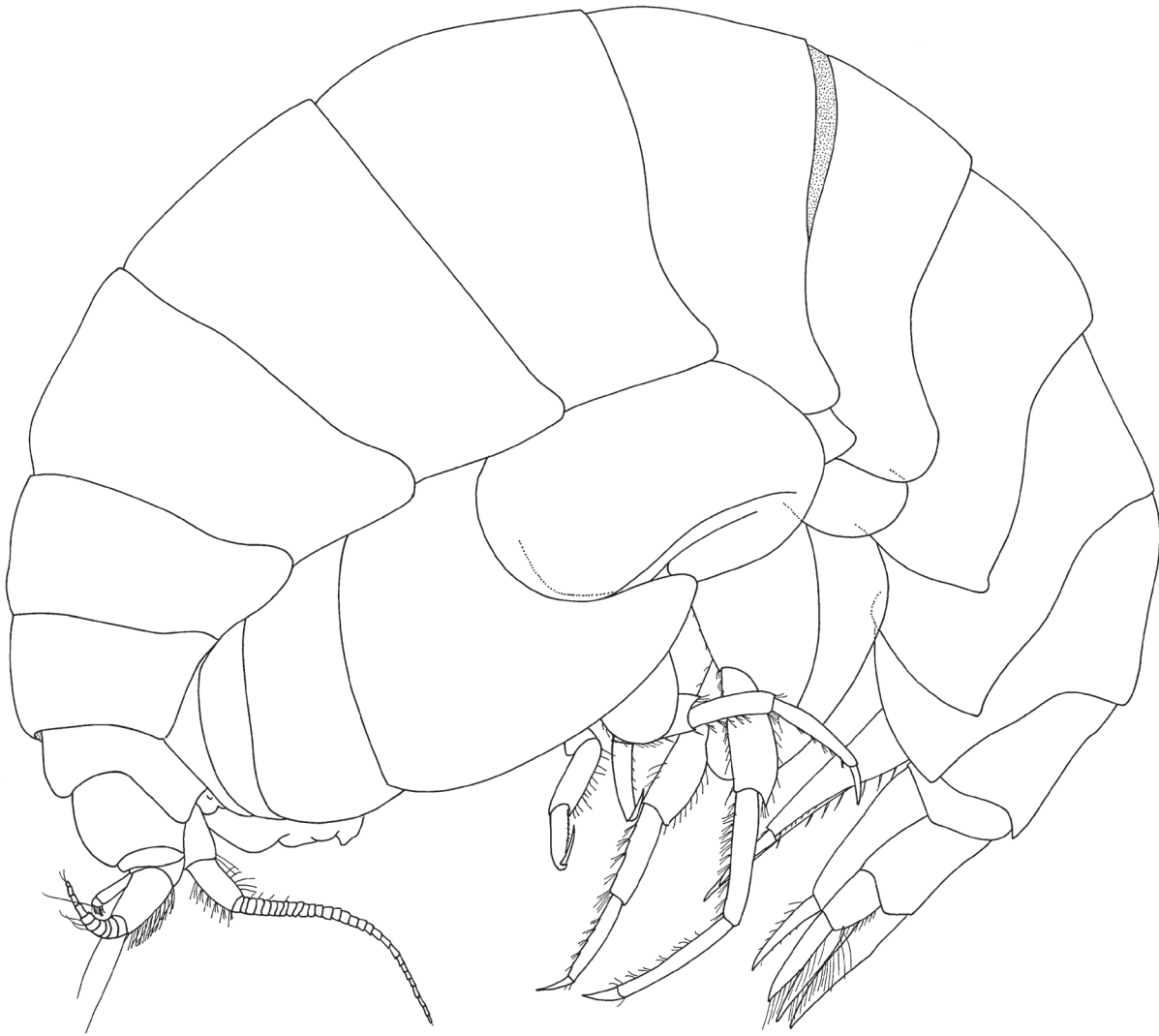


Figure 14. *Austrocallisoma jerryi* sp. n., holotype, female, 32.0 mm, AM P.69087, from east of Sydney, New South Wales, Australia.

Discussion. The tip of the outer ramus on uropod 3 on both sides is damaged in both specimens available for study. Judging from where the damage occurs we suspect that the ramus is 2-articulate, however this is uncertain.

***Bathycallisoma* Dahl, 1959**

Bathycallisoma Dahl, 1959: 220. — Gurjanova 1962: 433.
— J.L. Barnard 1969: 305, key K, 328. — Ledoyer 1986: 733 (in part, part *Scopelocheiropsis*).

Scopelocheirus. — Birstein and Vinogradov 1960: 178 (in part). — Gurjanova 1962: 319 (in part). — Barnard and Karaman 1991: 528 (in part).

Type species. *Bathycallisoma pacifica* Dahl, 1959 by monotypy (= *S. schellenbergi* Birstein & Vinogradov, 1958).

Included species. *Bathycallisoma* includes one species: *Bathycallisoma schellenbergi* (Birstein & Vinogradov, 1958).

Diagnostic description. *Mandible lacinia mobilis* a long, slender robust seta. Maxilla 1 inner plate with pappose setae lining inner margin; palp 2-articulate. Maxilla 2 inner plate broader than outer plate; inner plate slightly shorter than outer plate. Maxilliped palp article 4 well developed. Gnathopod 1 coxa large, margins strongly diverging distally proximally slender, strongly broadened distally; dactylus small, simple, highly modified with blunt apical tip. Pereopod 3 carpus short to compressed, about as long as wide. *Pereopod 4 coxa* with weakly-developed, subacutely produced posteroventral lobe.

Discussion. This monotypic taxon is very similar to *Scopelocheiropsis* Schellenberg, 1926. The main diagnostic character is the form of the lacinia mobilis, which is a long, narrow robust seta in *Bathycallisoma*, compared with a stemmed and distally expanded ‘blade’ in *Scopelocheiropsis*. Aside from this, there is a large difference in body size of these animals, *Bathycallisoma schellenbergi* being an order of magnitude larger than any *Scopelocheiropsis* species.

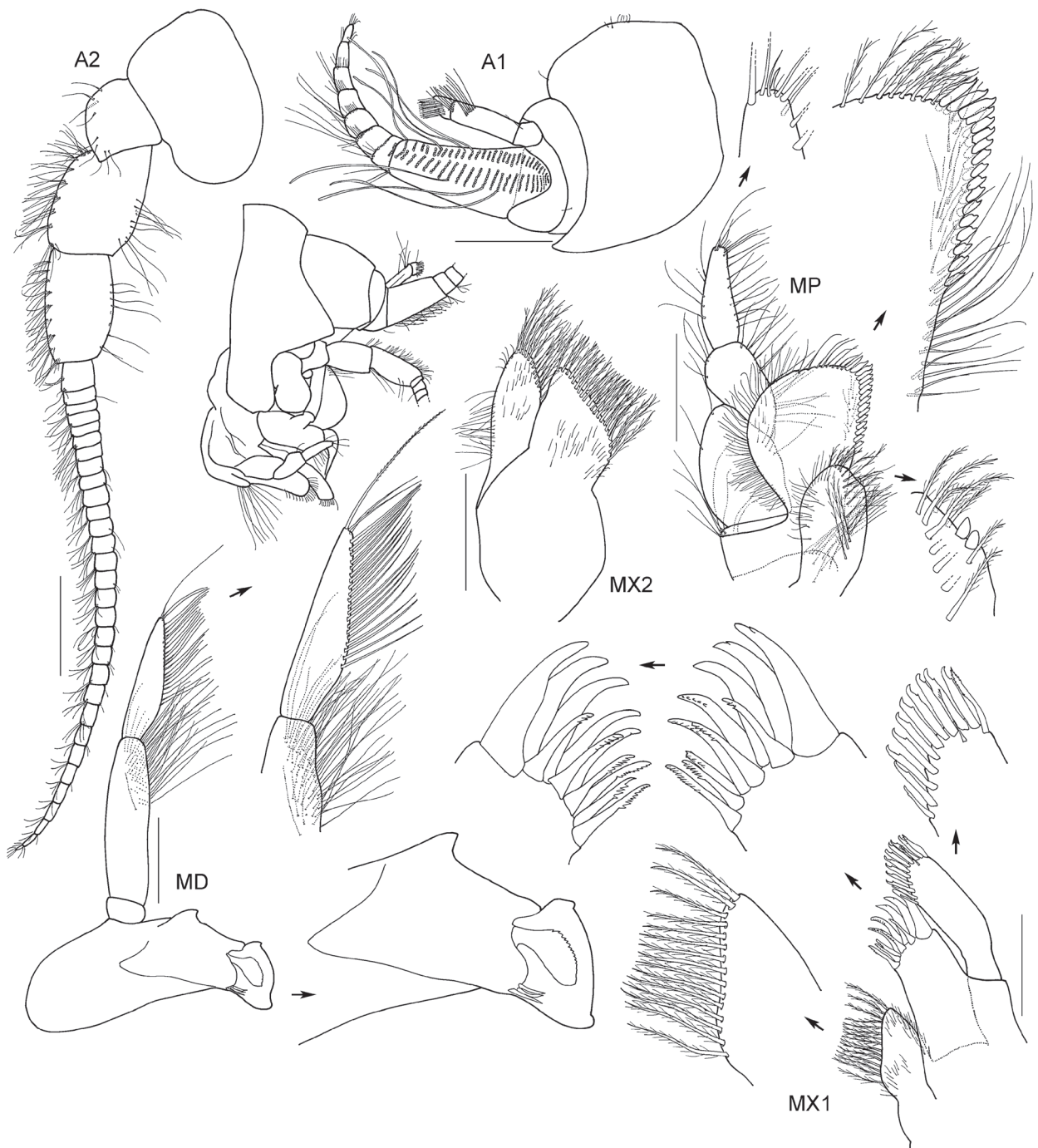


Figure 15. *Austrocallisoma jerryi* sp. n., holotype, female, 32.0 mm, AM P.69087, from east of Sydney, New South Wales, Australia. Scales represent 0.5 mm.

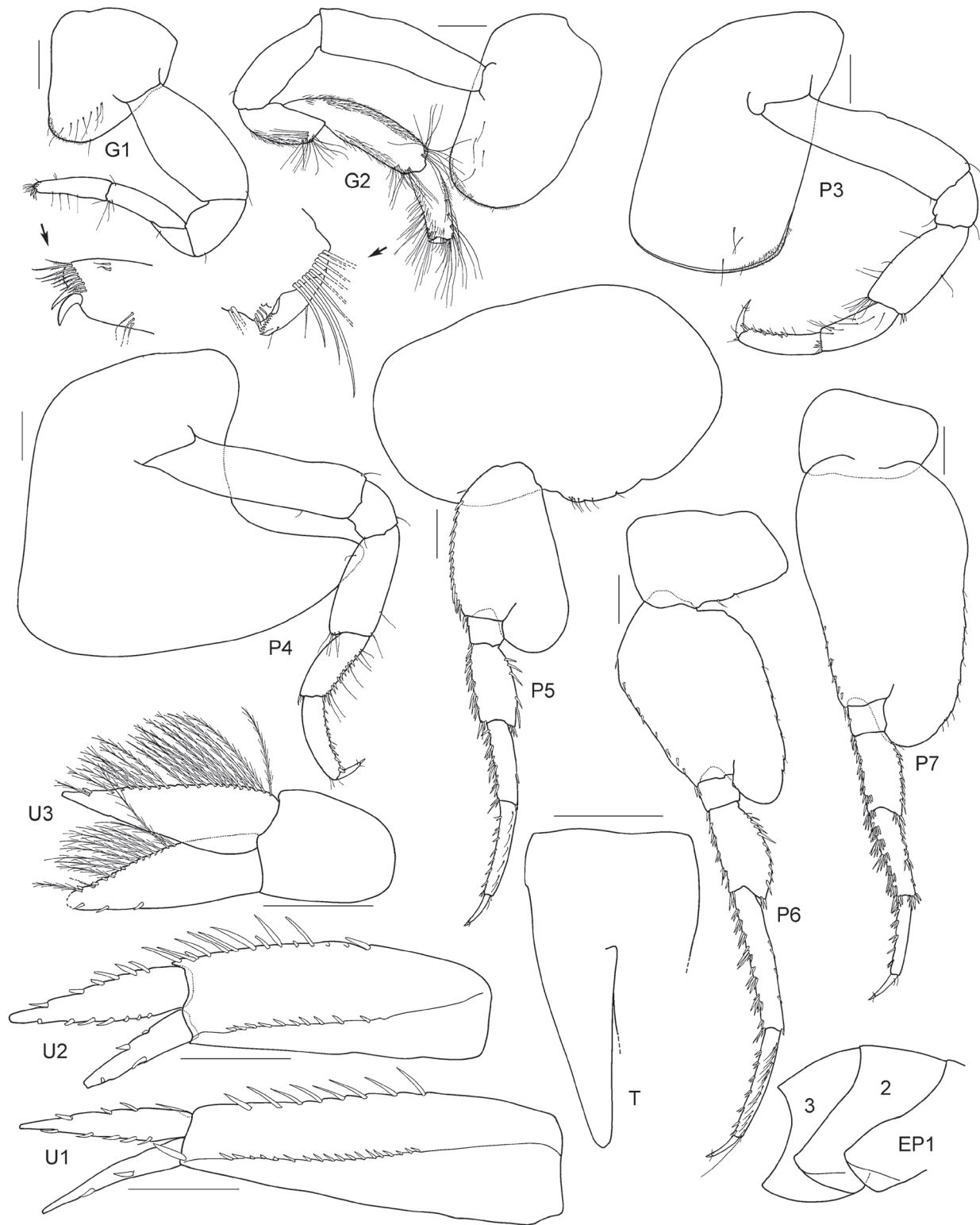


Figure 16. *Austrocallisoma jerryi* sp. n., holotype, female, 32.0 mm, AM P.69087, from east of Sydney, New South Wales, Australia. Scales represent 0.5 mm.

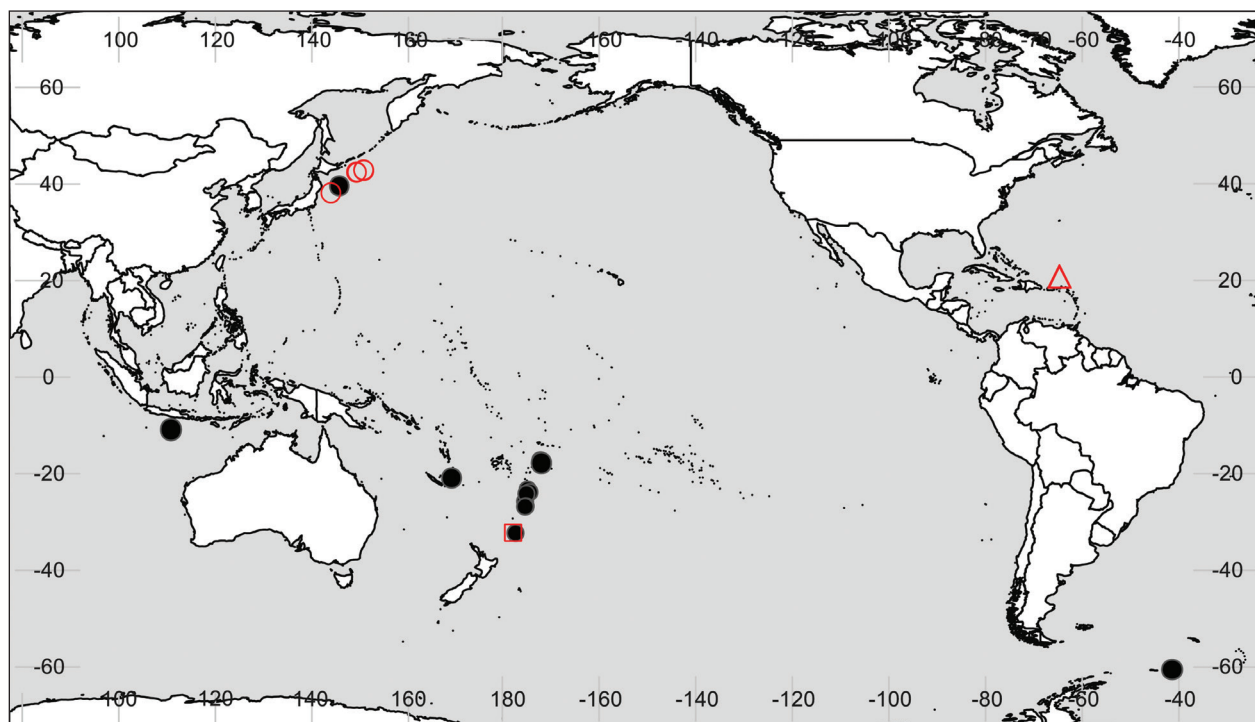


Figure 17. Distribution of *Bathycallisoma schellenbergi* (Birstein & Vinogradov, 1958) and its synonyms. Circles represent *Bathycallisoma schellenbergi* and its objective synonyms. Subjective synonyms are represented by the following symbols: (■) *Bathycallisoma pacifica*, (▲) aff. *Paracallisoma* spec. Type localities are represented by the corresponding open symbol.

***Bathycallisoma schellenbergi* (Birstein & Vinogradov, 1958)**

Figures 17, 18

? aff. *Paracallisoma* spec. Schellenberg, 1955: 185, fig. 1.

Scopelocheirus schellenbergi Birstein & Vinogradov, 1958: 224, figs 3, 4. — Birstein and Vinogradov 1960: 178. — Gurjanova 1962: 321, figs 104a, b. — Birstein and Vinogradov 1964: 161. — J.L. Barnard 1964: 319. — Birstein and Vinogradov 1970: 402, 417 (table 3). — ?Kamenskaya 1981: 42. — Barnard and Karaman 1991: 528. — ?Vinogradov and Vinogradov 1993: 130. — Lörz and Held 2004: 11 (Appendix A). — Blankenship and Yyanos 2005: 892, fig. 2. — Blankenship et al. 2006: 51, 53 (table 2), figs 2, 3. — De Broyer et al. 2007: 159. — Blankenship and Levin 2007: 1685, fig. 1, 1687 (table 1). — Jamieson et al. 2009: 1040. — Jamieson et al. 2011: 54, 55 (table 3), 58 (table 6). — Søreide and Jamieson 2013: 3, fig. 4.

Bathycallisoma pacifica Dahl, 1959: 222, figs 6–8. — Gurjanova 1962: 433. (Holotype, 1 female, about 33 mm, somewhat mutilated, ZMUC CRU-7674; Kermadec Trench, South Pacific Ocean (32°10'S, 177°14'W), brown clay with pumice, 6960–7000 m depth).

Bathycallisoma schellenbergi. — Wolff 1959: 255 (table 1). — Gurjanova 1962: 433. — Nagata 1963: 1. — Ortiz 1979: 19.

Type material. Syntypes, 3 specimens, 26, 27 and 42 mm, ZMM.

Type locality. North Pacific Ocean, Japan Trench (38°03'N, 143°57'E), 0–7000 m over bottom depth 7200 m; Kuril-Kamchatka Trench (43°48'N, 149°55'E), 0–8000 m over bottom depth 9180 m; and Kuril-Kamchatka Trench (44°08'N, 150°22'E), 0–6580 m over bottom depth 8900 m.

Depth range. Approximately 5600–9104 m (current study, Blankenship et al. 2006).

These records represent the shallowest and deepest known certain depths in the literature for *B. schellenbergi*. Records of 0–8129 m over a bottom depth of 10437 m (Birstein and Vinogradov 1960) are excluded as this equates only to length cabled out during mid-water trawls, thus the exact depth of capture is unknown.

Distribution. *Indian Ocean*: Java Trench (Birstein and Vinogradov 1964). *North Pacific Ocean*: Kurile-Kamchatka Trench (Birstein and Vinogradov 1958, Birstein and Vinogradov 1970); Japan Trench (Birstein and Vinogradov 1958, Nagata 1963). *South Pacific Ocean*: Kermadec Trench (Dahl 1959, Blankenship et al. 2006); New Hebrides Trench (Birstein and Vinogradov 1960, current study); Tonga Trench (Birstein and Vinogradov 1960, Blankenship and Levin 2007, Jamieson et al. 2011). ?*North Atlantic Ocean*: Puerto Rico Trench (Schellenberg 1955). ?*South Atlantic Ocean*: Orkney Trench (Vinogradov and Vinogradov 1993).

Ecology. This species has been taken frequently in baited traps (Blankenship et al. 2006, Jamieson et al. 2011),

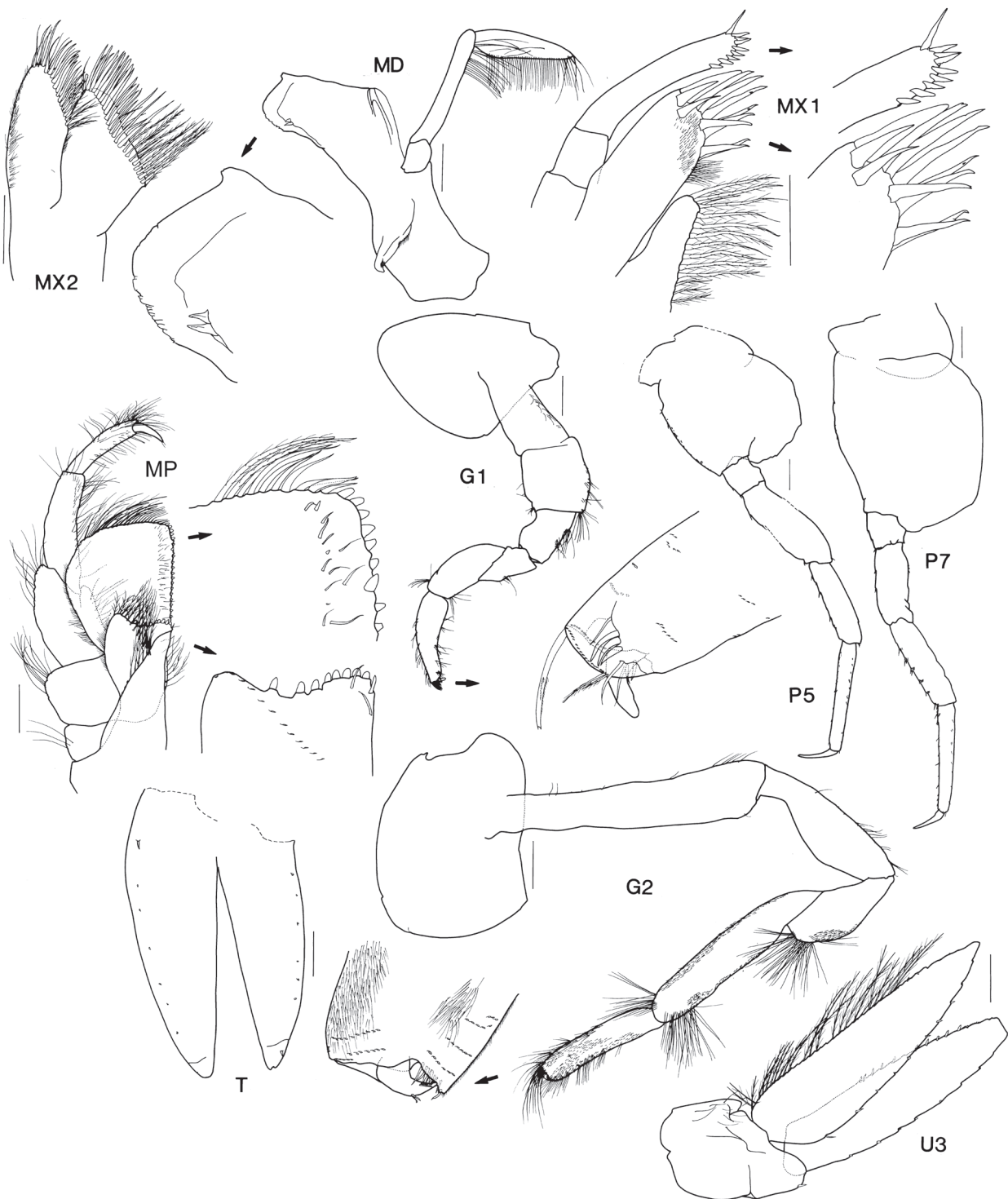


Figure 18. *Bathycallisoma pacifica* Dahl, 1959. Holotype female, 33 mm, ZMUC CRU-7674, Kermadec Trench. Scales for gnathopods, pereopods represent 1.0 mm; remainder represent 0.5 mm.

and seems also to live a semi-pelagic lifestyle as it has been taken in mid-water trawls (e.g. Birstein and Vinogradov 1958). It appears to be a lower abyssal and hadal endemic.

Discussion. Dahl (1959) described the genus *Bathycallisoma* for his new species *B. pacifica* from the Kermadec Trench, placing aff. *Paracallisoma* spec.

Schellenberg 1955 from the Puerto Rico Trench in its synonymy. While Dahl's publication was in press Birstein and Vinogradov (1958) published an account of the amphipods of the north-western Pacific, including a new species, *Scopelocheirus schellenbergi*, also with aff. *Paracallisoma* spec. Schellenberg 1955 in its synonymy. Dahl (1959) consequently included a footnote in his account, stating that Schellenberg's specimen should be

referred to *Scopelocheirus schellenbergi*, which in turn should be recombined as *Bathycallisoma schellenbergi*. He considered his Kermadec specimen to be a separate species from *B. schellenbergi* based on the shape of the first gnathopod and “some other minor characteristics”. We cannot observe these differences and so prefer to retain *B. pacifica* as a junior subjective synonym of *B. schellenbergi*, thereby agreeing with most subsequent authors.

***Eucallisoma* J.L. Barnard, 1961**

Eucallisoma J.L. Barnard, 1961: 32. — J.L. Barnard 1969: 305, key K. — Barnard and Karaman 1991: 454 (key), 484, figs 86C, 92P. — Lowry and Stoddart 1993: 67 (in part).

Type species. *Eucallisoma glandulosa* J.L. Barnard, 1961, original designation.

Included species. *Eucallisoma* includes one species: *E. glandulosa* J.L. Barnard, 1961.

Diagnosis. *Mandible lacinia mobilis* a stemmed, distally expanded, irregularly cusped blade. *Maxilla 1* inner plate with pappose setae along inner margin; *palp 2-articulate*. *Maxilla 2* inner and outer plates subequal in length; inner plate broader than outer plate. *Maxilliped palp article 4* well developed. *Gnathopod 1* coxa large, margins subparallel; *basis* swollen, with glandular material; *dactylus* reduced, simple. *Pereopod 3* carpus compressed to short, about as long as wide. *Pereopod 4* with well-developed, subquadrate posteroventral lobe.

Discussion. The removal of *E. barnardi* Lowry & Stoddart, 1993 to *Tayabasa* gen. n. leaves *Eucallisoma* as a monotypic taxon. Future deep-sea samples will hopefully uncover associated taxa that will provide a clearer picture of the relationships between these animals.

***Eucallisoma glandulosa* J.L. Barnard, 1961**

Figures 19, 20

Eucallisoma glandulosa J.L. Barnard, 1961: 33, fig. 3. — Barnard and Karaman 1991: 484–485. — Lowry and Stoddart 1993: 67, 72. — Hendrycks and Conlan 2003: 232, fig. 7.

Type material. Holotype, ? male, 10 mm, ZMUC CRU-1720.

Type locality. Off Gabon, Africa (4°00'S, 8°25'E), 4020 m depth.

Depth range. 4020 m.

Distribution. *Gabon*: west of Nyanga Province.

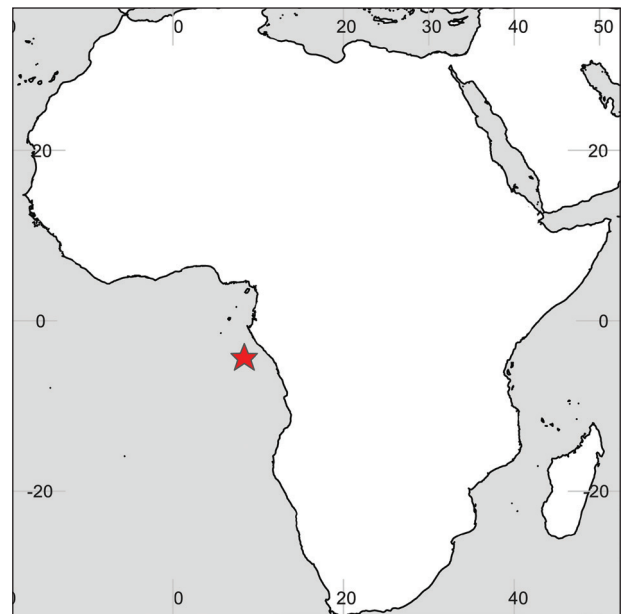


Figure 19. Distribution of *Eucallisoma glandulosa*.

***Paracallisoma* Chevreux, 1903**

Paracallisoma Chevreux, 1903: 84. — Schellenberg 1926: 257. — Chevreux 1935: 39. — Gurjanova 1962: 308. — J.L. Barnard 1969: 305, key K. — Barnard and Karaman 1991: 454 (key), 510.

Scopelocheirus. — Barnard and Karaman 1991: 528 (in part).

Type species. *Paracallisoma alberti* Chevreux, 1903, original designation.

Included species. *Paracallisoma* includes seven species: *P. abyssi* Oldevig, 1959; *P. alberti* Chevreux, 1903; *P. coecum* (Holmes, 1908); *P. platepistomum* Andres, 1977; *P. spinipoda* Hendrycks & Conlan, 2003; *P. woolgoolga* sp. n.; *P. zivianii* sp. n.

Diagnostic description. *Mandible lacinia mobilis* a stemmed, distally expanded, smooth or minutely serrate blade. *Maxilla 1* inner plate with pappose setae lining inner margin; *palp 2-articulate*. *Maxilla 2* inner and outer plates subequal in width or inner plate slightly broader than outer plate, inner plate slightly shorter than or subequal in length to outer plate. *Maxilliped palp article 4* well developed. *Gnathopod 1* coxa large, margins subparallel or diverging distally; *basis* linear; *dactylus* small, simple, highly modified with apical tip. *Pereopod 3* carpus short to long, longer than wide. *Pereopod 4* coxa with strongly-developed, subacutely produced posteroventral lobe.

Discussion. In addition to the two new species described herein, Horton et al. (2013) record an additional five undescribed species of *Paracallisoma* from the North Atlantic Ridge, and Duffy et al. (2012) record two undescribed species from submarine canyons of the Iberian Peninsula. These records indicate that there is still a large knowledge gap in the diversity of deep-sea scopelocheirids.

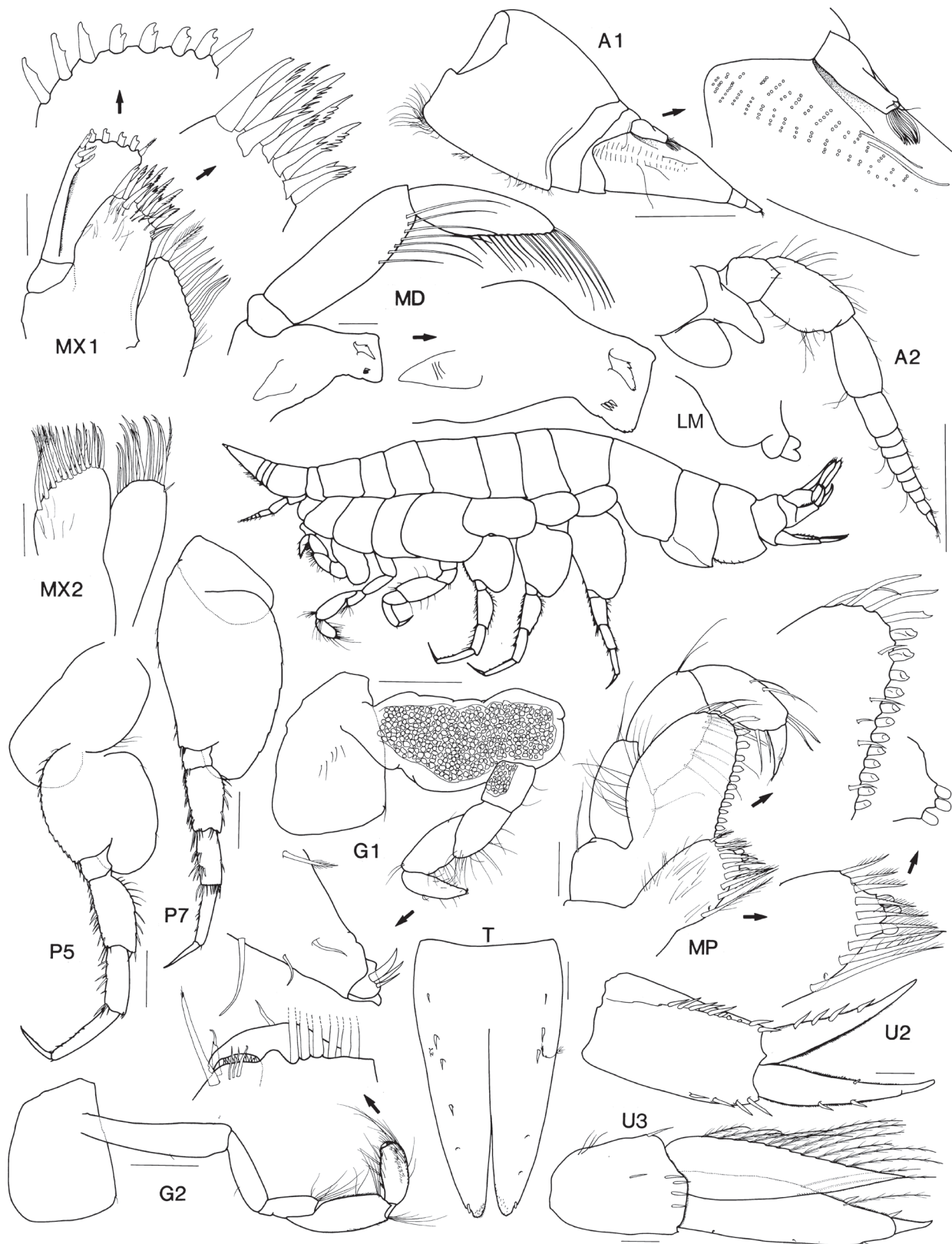


Figure 20. *Eucallisoma glandulosa* J.L. Barnard. Holotype, ?male, 10 mm, ZMUC CRU-1720, off Gabon, east Atlantic Ocean. Scales for antennae, gnathopods, pereopods represent 0.5 mm; remainder represent 0.1 mm.

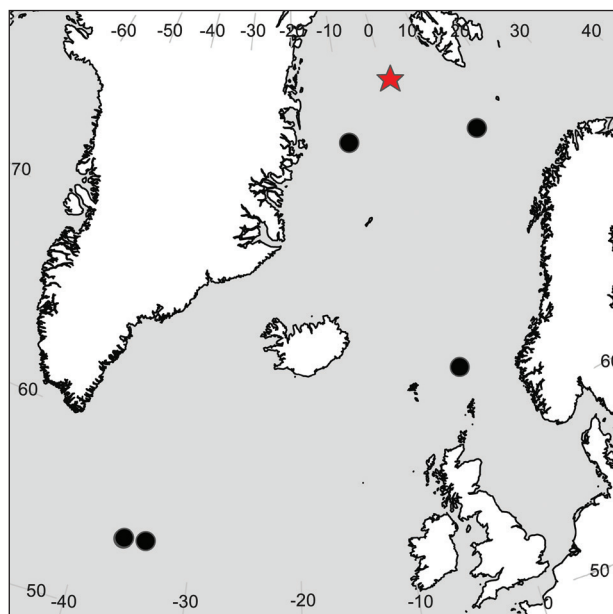


Figure 21. Distribution of *Paracallisoma abyssi* (Oldevig, 1959). Star indicates type locality.

Paracallisoma abyssi (Oldevig, 1959)

Figure 21

Scopelocheirus abyssi Oldevig, 1959: 16, figs 1–3. — Barnard and Karaman 1991: 528. — Vinogradov et al. 1996: 8. — Brandt 1997: 1540 (table 2).

Paracallisoma abyssi. — Horton 2006: 20, table 2. — Horton et al. 2013: 354.

Type material. Syntypes, (24 specimens, maximum length about 15 mm), Stockholm Museum.

Type locality. Swedish Deep (77°39'N, 1°17'E), 3200 m, *Biloculina* ooze, -1.4 °C.

Depth range. 1525–3200 m (Brandt 1997, Oldevig 1959).

Distribution. North Atlantic Ocean. Greenland Sea (Oldevig 1959, Brandt 1997); Norwegian Sea (Vinogradov et al. 1996); Faroe-Shetland Channel (Horton 2006); Mid-Atlantic Ridge (Horton et al. 2013).

Ecology. A scavenger, taken in baited traps (Vinogradov et al. 1996, Horton 2006, Horton et al. 2013).

Discussion. This is a poorly described and little-sampled species that was originally described in the genus *Scopelocheirus*. Horton (2006) removed it to *Paracallisoma*. Horton and Thurston (in prep.) have new material of this species and are in the process of re-describing it.

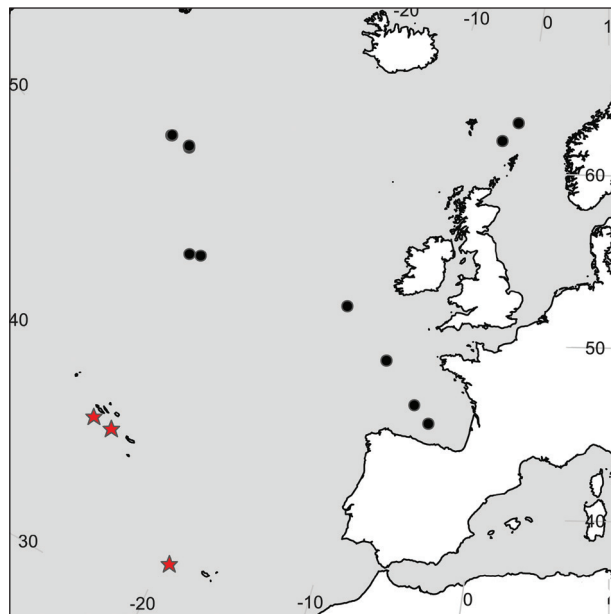


Figure 22. Distribution of *Paracallisoma alberti* Chevreux, 1903. Star indicates type locality.

Paracallisoma alberti Chevreux, 1903

Figures 22, 23

Paracallisoma alberti Chevreux, 1903: 84, figs 2, 3. — Stebbing 1906: 719. — Chevreux 1935: 39, pl. 1, fig. 3, pl. 9, fig. 2, pl. 16, fig. 5. — Birstein and Vinogradov 1955: 223, 279 (in part). — Schellenberg 1955: 191 (in part). — J.L. Barnard 1958: 97 (list). — Belloc 1960: 4. — Lampitt et al. 1983: 76, table 1. — Desbruyères et al. 1985: 236, fig. 1, 237. — Thurston 1990: 266. — Barnard and Karaman 1991: 511. — Pallerud and Vader 1991: 41. — Lopes et al. 1993: 209, table 1. — Dauvin and Bellan-Santini 2002: 316 (table 1). — Horton 2006: 20, table 2. — Horton Thurston and Duffy 2013: 355, table 2.

Not *Paracallisoma alberti*. — Schellenberg 1926a: 258, fig. 11. — Birstein and Vinogradov 1962: 34. — Lowry and Bullock 1976: 102. — De Broyer and Jażdżewski 1993: 73. (= *Paracallisoma* sp. De Broyer et al. 2007).

Not *Paracallisoma alberti*. — Birstein and Vinogradov 1958: 228. — Birstein and Vinogradov 1960: 176, fig. 5, 233, fig. 33. — Gurjanova 1962: 309, fig. 102. — Nagata 1963: 1. — Birstein and Vinogradov 1970: table 1, table 3. — Hatch 1983: 194, 195, table 3. — Nysewander 1983: 328, table 7. — Hatch 2013: 275. (= *P. coecum*).

Not *Paracallisoma alberti*. — Birstein and Vinogradov 1964: 161. (= *Paracallisoma* sp.)

Not *Paracallisoma* aff. *alberti* Treude et al., 2002: 1284, table 2. (= *Paracallisoma* sp.)

Type material. Syntypes: 1 female, 13 mm (stn 532); 3 females (stn 730); 5 males and 9 females (stn 792).

Type locality. Azores region (37°52'N, 24°42.75'W), trap, muddy bottom with *Globigerina*, 2178 m [*Prin-*

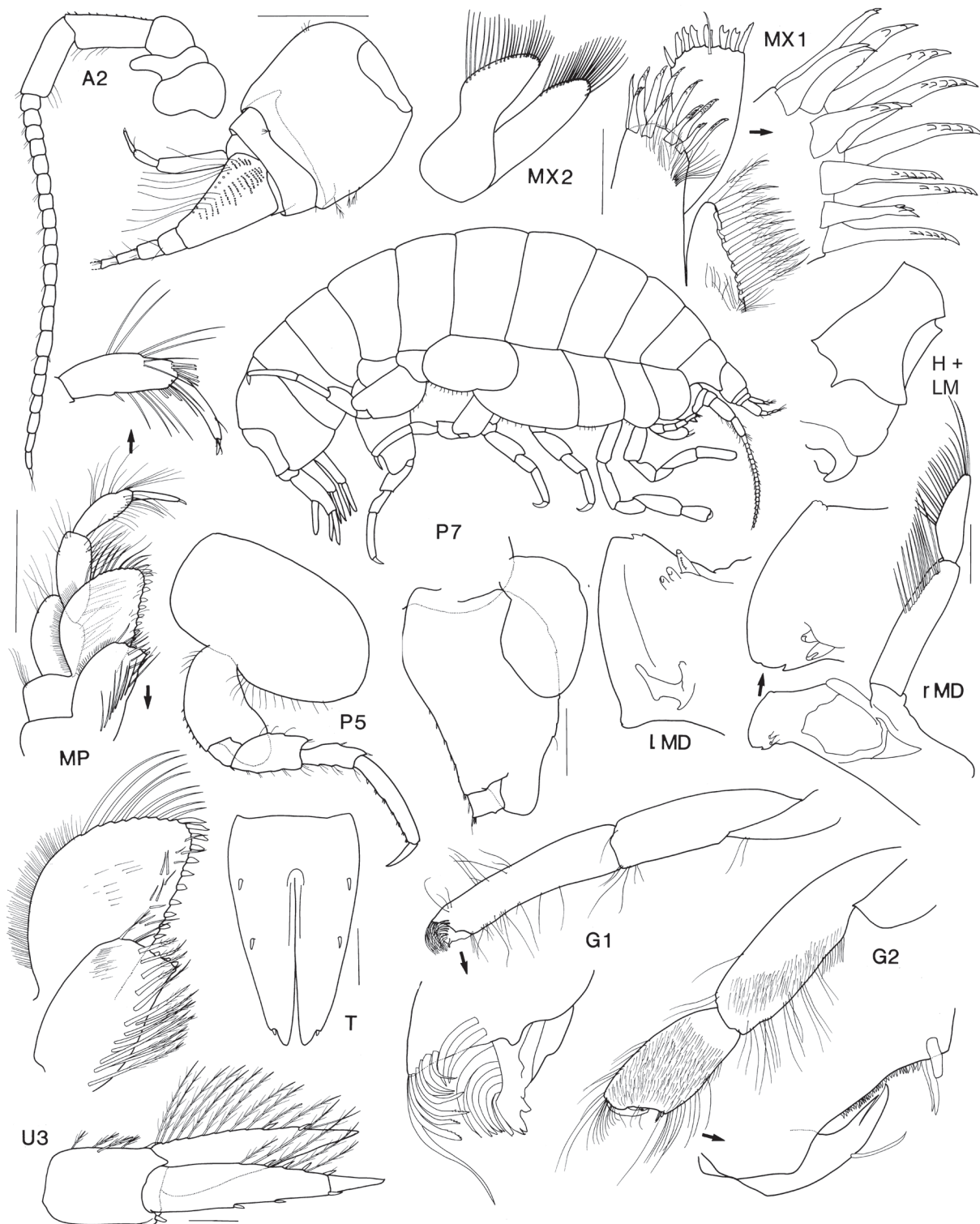


Figure 23. *Paracallisoma alberti* Chevreux, 1903. Syntype female, MOM, near Madeira, North Atlantic Ocean. Whole animal after Chevreux 1903; A2, MX2, P5 after Chevreux 1935. Scales for MD, MX1, U3, T represent 0.2 m; remainder represent 0.5 mm.

cesse-Alice stn 532]; Azores region (37°58'N, 26°13.25'W), trap, muddy sand, 2660 m [*Princesse-Alice* stn 730]; Madeira region (32°32.16'N, 17°04.42'W), trap, bottom of blackish grey mud and fine grained sand, 2480 m [*Princesse-Alice* stn 792]. The co-ordinates given here are based on those reported in Chevreux (1935)

rather than in the original publication (Chevreux 1903), which used the Paris rather than the Greenwich meridian for calculating longitude.

Depth range. 1396–4780 m (Horton 2006, Chevreux 1935).

Distribution. North Atlantic Ocean. Porcupine Seabight (Lampitt et al. 1983); Mid Atlantic Ridge (Horton et al. 2013); Faroe-Shetland Channel (Horton 2006). *Portugal*. Azores and Madeira region (Chevreux 1903). *France*. Bay of Biscay (Chevreux 1935, Desbruyères et al. 1985).

Ecology. A scavenger, frequently taken in baited traps (Chevreux 1903, 1935, Horton 2006, Horton et al. 2013).

Discussion. The distribution of *Paracallisoma alberti* given here (Fig. 22) is much more limited than what has been reported in the literature. This follows Thurston (1990), who concluded that *P. alberti* is restricted to the north-east Atlantic, as material recorded in the literature as *P. alberti* from the Pacific Ocean was confirmed as or presumed to belong to *P. coecum* (Holmes, 1908). The identity of material from the Indian Ocean and Arabian Sea (Birstein and Vinogradov 1964, Treude et al. 2002) is unknown, but it is unlikely to be *P. alberti*. Material from the Southern Ocean appears to be closely related to *P. platepistomum* Andres, 1977 (Thurston 1990).

Paracallisoma coecum (Holmes, 1908)

Figure 24

Scopelocheirus coecus Holmes, 1908: 500, figs 10–12. — Shoemaker 1945: 186 (in part, part ?*P. platepistomum*). — J.L. Barnard 1954: 54, figs 4, 5. — Gurjanova 1951: 241 (key).

Paracallisoma coecum. — Hurley 1963: 61, fig. 18. — Barnard and Karaman 1991: 511. — Thurston 2001: 685 (table 2).

Paracallisoma coecus. — J.L. Barnard 1958: 97 (list). — J.L. Barnard 1964: 319, fig. 3. — Brusca 1967: 384, 385, table 4. — Childress and Nygaard 1974: 228, table 1. — Childress 1975: 788 (table 1a). — Quetin et al. 1980: table 1. — Smith and Baldwin 1982: 292 (table 3). — Austin 1985: 601. — Vermeer and Devito 1988: 65, 67, table 2. — Ikeda 2013: 342 (table 1).

Paracallisoma alberti. — Birstein and Vinogradov 1955: 223, 279 (in part). — Birstein and Vinogradov 1958: 228. — Birstein and Vinogradov 1960: 176, fig. 5, 233, fig. 33. — Gurjanova 1962: 309, fig. 102. — Nagata 1963: 1. — Birstein and Vinogradov 1970: table 1, table 3. — Hatch 1983: 194, 195, table 3. — Nysewander 1983: 328, table 7. — Hatch 2013: 275.

Type material. Holotype, female, 20 mm, USNM 38538.

Type locality. Off San Clemente Island, California, United States, 1196–1287 m depth.

Depth range. 549–4023 m (Shoemaker 1945, Barnard 1964). Some depth records (e.g. 0–9000 m, Birstein and Vinogradov (1958)) are excluded from this range as exact depth of capture is unknown due to the sampling technique.

Distribution. *Pacific Ocean*: off San Clemente Island, California, United States (Holmes 1908); Pacific City, Oregon, United States (from the stomach of a duck) (Shoemaker 1945); San Nicolas Basin and off Santa Barbara Island, California, United States (Barnard 1954); outer Santa Barbara Passage, California, United States (Hurley 1963); off Kamchatka, Russia (Shoemaker 1945, Gurjanova 1962); Gulf of Alaska (Barnard 1964); Kuril-Kamchatka Trench (Birstein and Vinogradov 1958); near the Tenji Seamount, south-south-west of the Aleutian Trench (Birstein and Vinogradov 1958); near the Makarov Seamount (Birstein and Vinogradov 1960); Japan Trench (Nagata 1963).

Discussion. Schellenberg (1926) first considered *Paracallisoma coecum* to be a junior subjective synonym of *P. alberti*, a move that was accepted by many subsequent authors. However, Barnard (1964), and many more recent works (e.g. Thurston 1990, Barnard and Karaman 1991, Thurston et al. 2001) have again treated *P. coecum* as a valid species, a decision with which we agree. *Paracallisoma coecum* can be differentiated from *P. alberti* by following characters: gnathopod 1 coxa much longer than wide, margins slightly tapering distally (coxa slightly longer than wide, margins subparallel in *P. alberti*); gnathopod 1 propodus margins tapering distally (gnathopod 1 propodus margins subparallel in *P. alberti*); gnathopod 2 propodus subovate, palm transverse to slightly acute, dactylus fitting palm (gnathopod 2 propodus diverging distally, palm acute, dactylus shorter than palm in *P. alberti*).

Due to its taxonomic history, many records of *P. coecum* have erroneously been attributed to *P. alberti*. Pacific Ocean material reported as *P. alberti* has now been confirmed as or is presumed to be *P. coecum* (Thurston 1990). According to Thurston (1990), the record of Shoemaker (1945) of *P. coecum* (as *Scopelocheirus coecus*) from Bermuda is referable to *P. platepistomum* Andres, 1977. Indian Ocean material recorded as *P. alberti* is unconfirmed.

Paracallisoma platepistomum Andres, 1977

Figure 25

Paracallisoma platepistomum Andres, 1977: 61, figs 3, 4. — Andres and Lott 1977: 62. — Barnard and Karaman 1991: 511.

Scopelocheirus coecus. — Shoemaker 1945: 186 (in part, part *Paracallisoma coecum*).

Type material. Holotype, female, 28 mm, ZMH K 30455.

Type locality. Iberian deep-sea, *Meteor* Station 3/24 (42°26.8–40.9°N, 14°49.0–49.2°W), 5325 m depth

Depth range. 1463(?)–5325 m (Shoemaker 1945, Andres 1977).

Distribution. *North Atlantic Ocean*: Iberian Basin (Andres 1977); off Bermuda (Shoemaker 1945).

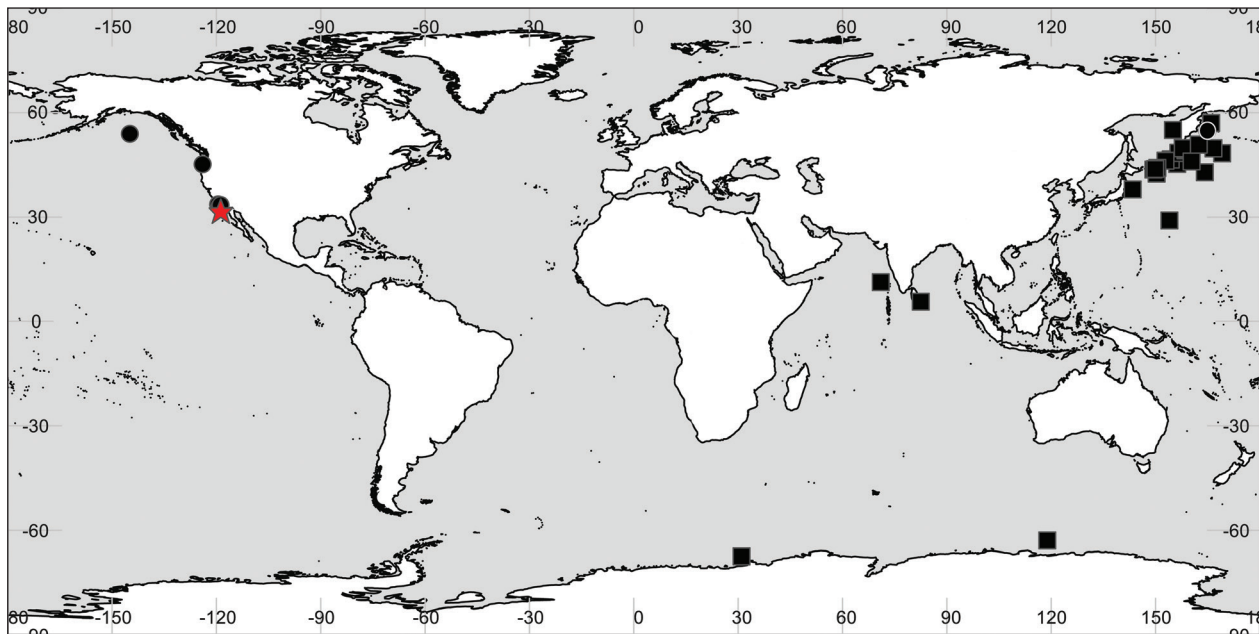


Figure 24. Distribution of *Paracallisoma coecum* (Holmes, 1908). Circles (●) represent records of *Paracallisoma coecum*; squares (■) represent misidentifications of *P. alberti* that may represent *P. coecum* or another species. Star indicates type locality.

***Paracallisoma spinipoda* Hendrycks & Conlan, 2003**

Figure 26

Paracallisoma spinipoda Hendrycks & Conlan, 2003: 2322, figs 8, 9.

Type material. Holotype, male, 10 mm, CMNC 2002-0029. Paratype: juvenile, 5.0 mm, CMNC 2002-0030.

Type locality. North-east Pacific off Point Conception, California, United States (34°47.94'N, 123°03.80'W), 3450 m depth.

Depth range. 3450–4000 m

Distribution. *United States:* North-east Pacific off Point Conception, California (Hendrycks and Conlan 2003).

***Paracallisoma woolgoolga* sp. n.**

<http://zoobank.org/B429CB96-1624-4FF2-AB89-239C9FE45719>
Figures 27–30

Type material. Holotype, female, 10.0 mm, AM P.69088, north-east of Coffs Harbour, New South Wales, Australia (30°10.88'S, 153°32.22'E), 1000 m, baited trap, 12–13 August 1993, coll. P.B. Berents, R.T. Springthorpe & W. Vader, MV *Cheryl Lee* [NSW-877]. Paratypes: 1 male, 7.5 mm, AM P.69089; many specimens, 7.0–9.3 mm, AM P.69090, with same collection details as holotype.

Other Australian material examined. *New South Wales:* 564 specimens, AM P.48095, [NSW-862]; 175 specimens, AM P.48121, [NSW-863], north-east of Coffs

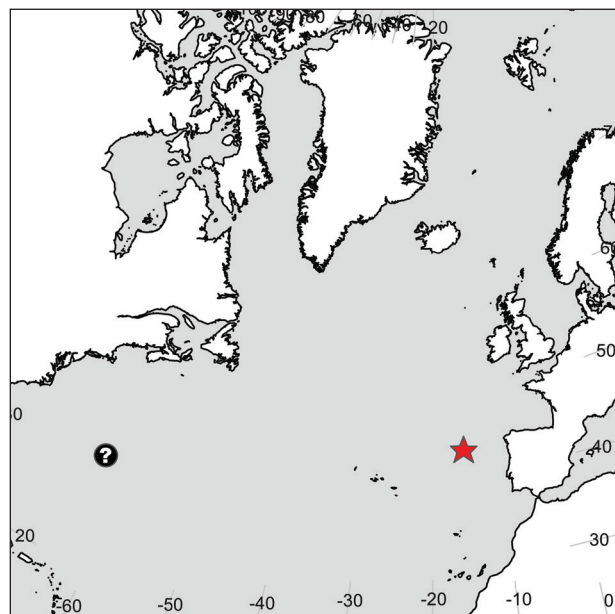


Figure 25. Distribution of *Paracallisoma platepistomum* Andres, 1977. Star indicates type locality, question mark indicates possible misidentification of *Scopelocheirus coecus* by Shoemaker (1945).

Harbour (30°10.93'S, 153°32.26'E), 963 m, baited trap, 11–12 August 1994, coll. P.B. Berents, R.T. Springthorpe & W. Vader, MV *Cheryl Lee*. 6 specimens, AM P.50024, north-east of Coffs Harbour (30°10.93'S, 153°32.26'E), 1000 m, baited trap, 8–9 September 1994, coll. J.K. Lowry & K. Dempsey, MV *Carrie Ann* [NSW-999]. 26 specimens, AM P.50067, [NSW-1021]; 2 specimens, AM P.50082, [NSW-1022], north-east of Coffs Harbour (30°10.93'S, 153°32.26'E), 1000 m, baited trap, 9–10

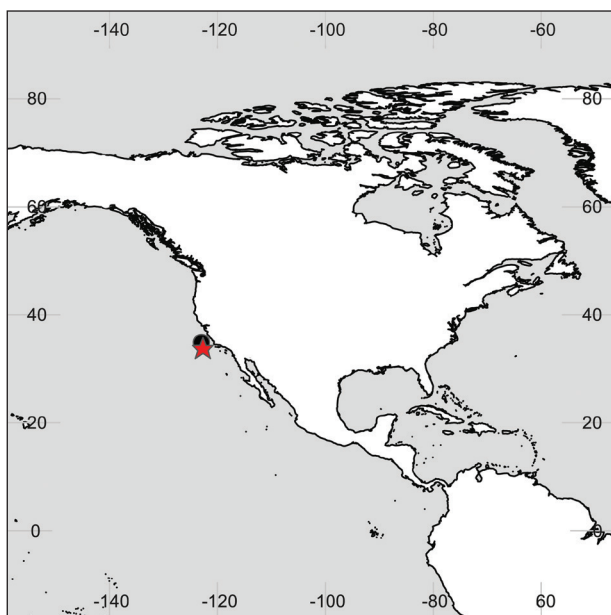


Figure 26. Distribution of *Paracallisoma spinipoda* Hendrycks & Conlan, 2003. Star indicates type locality.

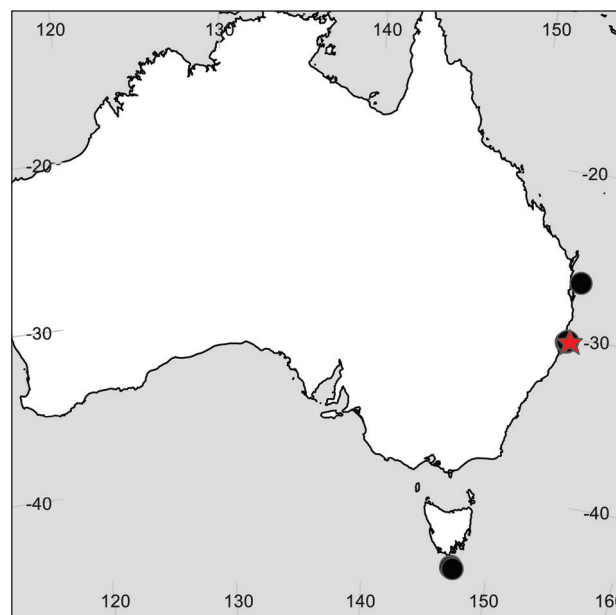


Figure 27. Distribution of *Paracallisoma woolgoolga* sp. n. Star indicates type locality.

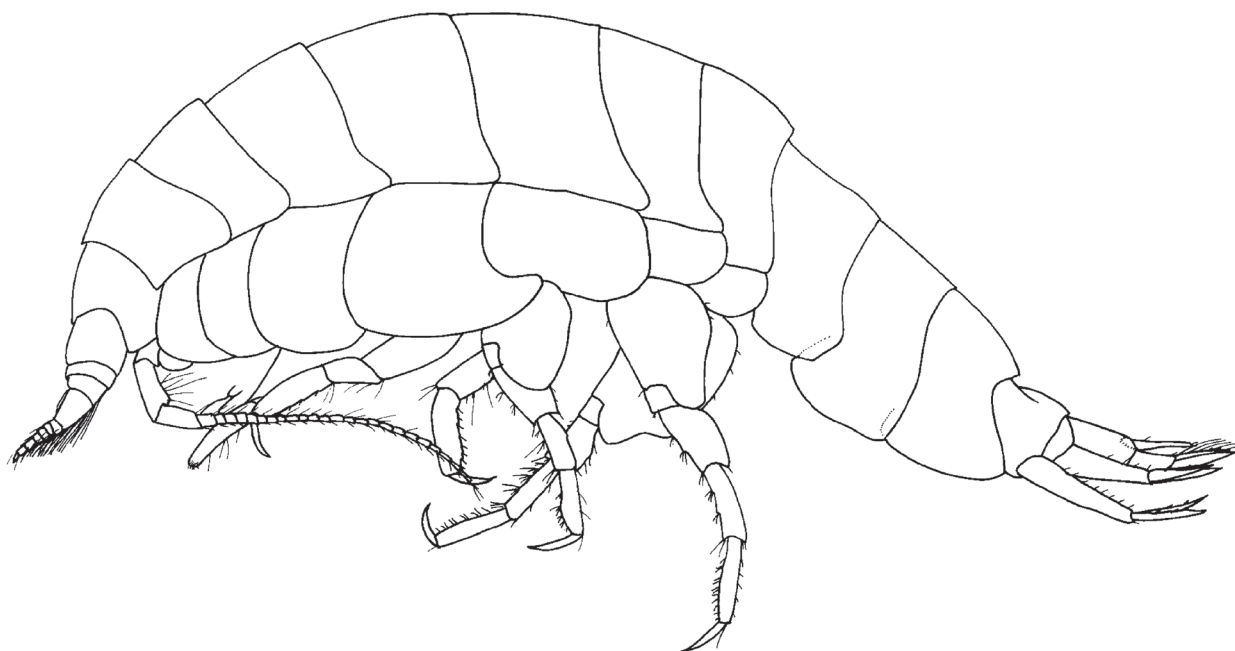


Figure 28. *Paracallisoma woolgoolga* sp. n. Holotype female, 10.0 mm, AM P.69088, from north-east of Coffs Harbour, New South Wales, Australia.

September 1994, coll. J.K. Lowry & K. Dempsey, MV *Carrie Ann*. 1 specimen, AM P.51126, north-east of Coffs Harbour (30°14.83'S, 153°27.55'E), 200 m, baited trap, 11–12 August 1993, coll. P.B. Berents, R.T. Springthorpe & W. Vader, MV *Cheryl Lee* [NSW-869]. 480 specimens, AM P.49808; 237 specimens, AM P.49827; 17 specimens, AM P.52658, north-east of Coffs Harbour (30°10.88'S, 153°32.22'E), 1000 m, baited trap, 12–13 August 1993, coll. P.B. Berents, R.T. Springthorpe & W. Vader, MV *Cheryl Lee* [NSW-876].

Queensland: 3 specimens, AM P.47887, due east of Mooloolaba (26°36.23'S, 153°50.23'E), 1006 m, baited trap, 2–3 August 1994, coll. J.K. Lowry & K. Dempsey, MV *Capricorn I* [QLD-1140].

Tasmania: 20 specimens, AM P.73706, Main Pedra Hill, 76.8 km south-south-east of South East Cape (44°15.6'S, 147°07.8'E), 1312 m, baited trap, 21–24 January 1997, coll. CSIRO party, FRV *Southern Surveyor* [SS01/97/08]. Many specimens, AM P.73707, Hill U, 82.8 km south-south-east of South East Cape

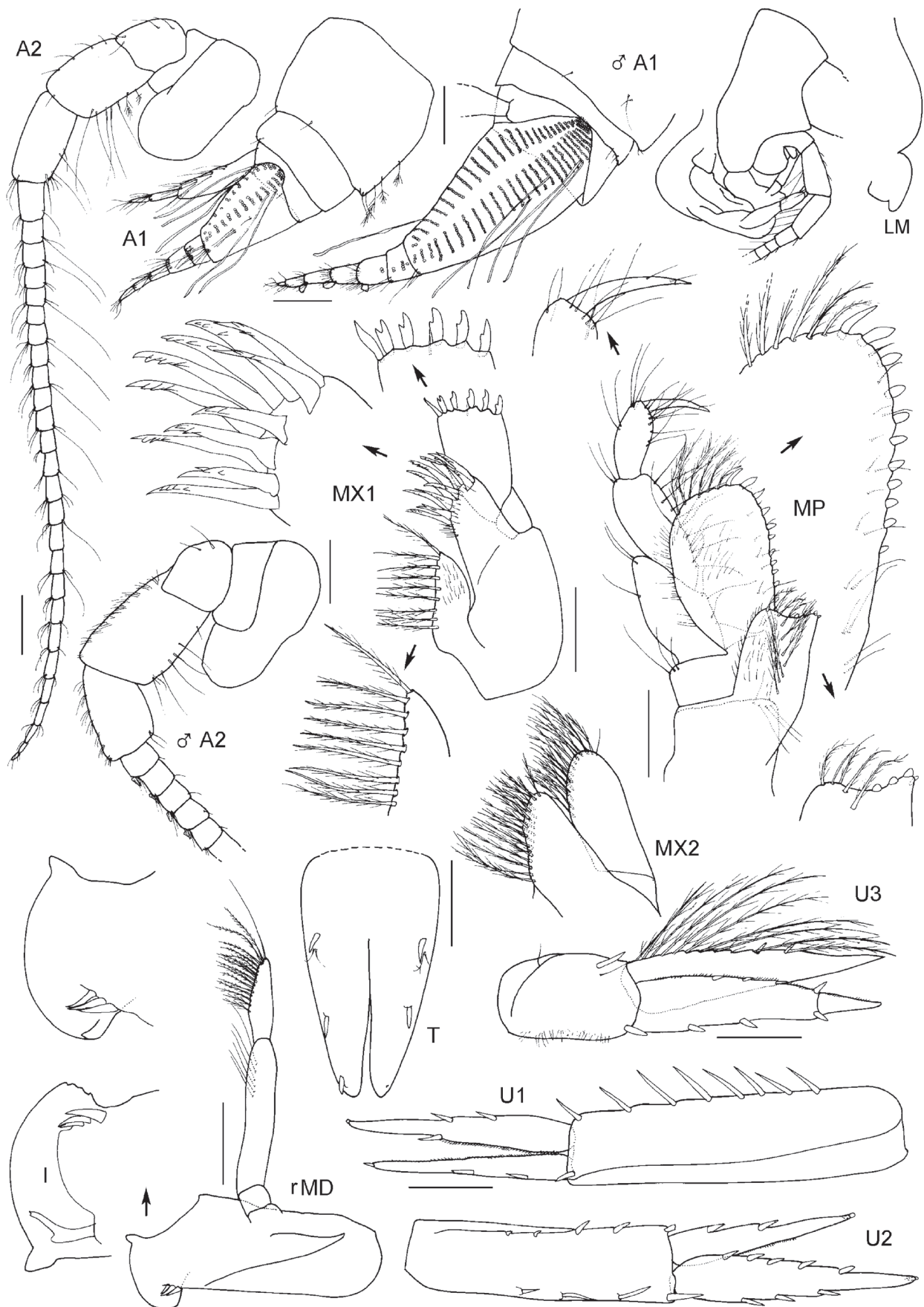


Figure 29. *Paracallisoma woolgoolga* sp. n. Holotype female, 10.0 mm, AM P.69088; paratype male, 7.5 mm, AM P.69089, from north-east of Coffs Harbour, New South Wales, Australia. Scales represent 0.2 mm.

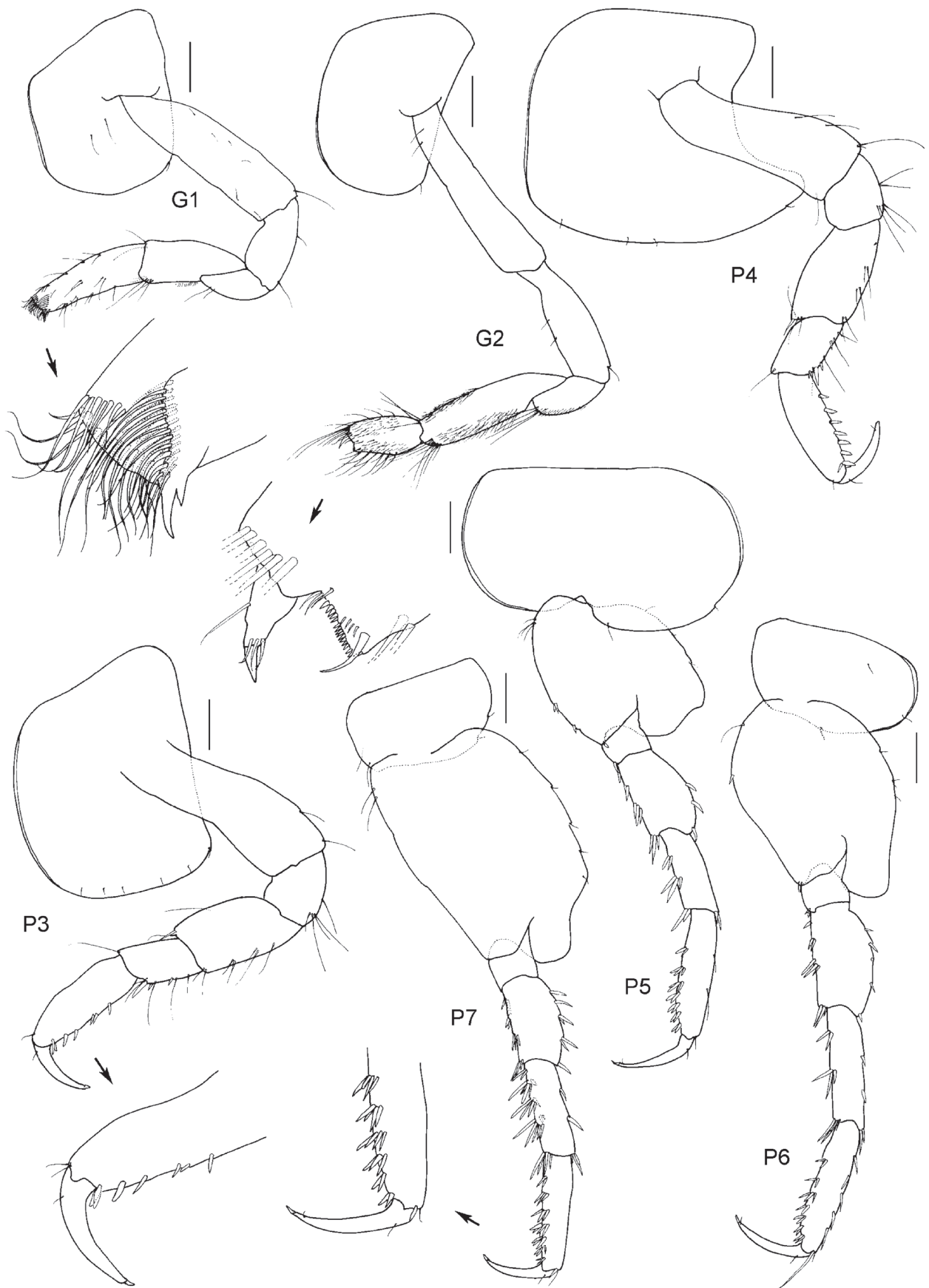


Figure 30. *Paracallisoma woolgoolga* sp. n. Holotype female, 10.0 mm, AM P.69088, from north-east of Coffs Harbour, New South Wales, Australia. Scales represent 0.2 mm.

(44°19.2'S, 147°07.2'E), 1083–1448 m, baited trap, 27–28 January 1997, coll. CSIRO party, FRV *Southern Surveyor* [SS01/97/41]. 132 specimens, AM P.73708, Hill D1, south-south-east of South East Cape (44°23.4'S, 147°16.2'E), 1942 m, baited trap, 31 January 1997, coll. CSIRO party, FRV *Southern Surveyor* [SS01/97/65].

Diagnosis. Gnathopod 1 coxa margins subparallel. Gnathopod 2 propodus palm transverse, with straight, minutely serrate margin; dactylus reaching corner of palm. Pereopod 5 basis as long as broad, broadly expanded posteriorly, slightly excavate posterodistally. Epimeron 3 posteroventral corner narrowly rounded. Telson moderately cleft.

Description. Based on holotype female, 10.0 mm, AM P.69088.

Lateral cephalic lobe large, triangular, apically subacute. Rostrum absent. Eyes apparently absent. Antenna 1 short; accessory flagellum long, 3-articulate, forming cap covering calynophore; primary flagellum 6-articulate, with strong 2-field calynophore; calceoli absent. Antenna 2 longer than antenna 1; peduncle without brush setae, article 1 greatly enlarged, not covering article 2; flagellum 26-articulate, calceoli absent.

Labrum, epistome slightly produced, rounded; upper lip slightly produced, straight. Mandible incisor with slightly convex margins; lacinia mobilis a stemmed, distally expanded, smooth blade; molar flap-like; palp attached midway, article 2 slender. Maxilla 1 palp 2-articulate. Maxilla 2 inner plate shorter than outer plate; outer plate without long, distally barbed slender setae. Maxilliped outer plate small; palp large, 4-articulate.

Gnathopods 1–4 coxae without setal fringe along ventral margin. Gnathopod 1 coxa large, about as long as coxa 2, margins subparallel; basis slender; ischium long, length $2.1 \times$ width; carpus long, length $\times 2.9$ width, subequal in length to propodus; propodus margins slightly tapering distally; anterodistal margin with row of long, slender setae, without robust setae just above dactylus; dactylus small, simple, well developed, posterior margin without setae, with one cusp along posterior margin. Gnathopod 2 minutely subchelate; carpus long, length $3.7 \times$ width; propodus short, length $1.7 \times$ width, palm transverse, with straight, minutely serrate margin; dactylus reaching corner of palm. Pereopod 3 weakly prehensile; propodus without posterodistal locking setae; dactylus short, slender. Pereopod 4 weakly prehensile; coxa wider than deep, with subacutely produced posteroventral lobe; propodus without posterodistal locking setae; dactylus short, slender. Pereopod 5 weakly prehensile; coxa equilobate; basis as long as broad, broadly expanded posteriorly, slightly excavate posterodistally, without row of long pappose setae medially; dactylus short, slender. Pereopod 6 weakly prehensile; basis expanded posteroproximally, posterior margin tapering distally, with very weakly excavate posterodistal margin; dactylus short, slender. Pereopod 7 weakly prehensile; basis expanded

posteriorly, slightly rounded proximally, minutely crenate, posteroventral corner excavate; propodus without anterodistal locking setae; dactylus short, slender.

Epimeron 1 anteroventral corner narrowly rounded. Epimeron 3 posteroventral corner produced, narrowly rounded. Urosomite 1 with anterodorsal notch and rounded boss. Uropod 1 peduncle $1.5 \times$ rami length; rami subequal in length. Uropod 2 rami inner ramus slightly shorter than outer ramus. Uropod 3 peduncle short; rami lanceolate, subequal in length, outer ramus 2-articulate, with plumose setae. Telson longer than broad, length $2.3 \times$ breadth, moderately cleft (to 64%).

Sexually dimorphic characters. Based on paratype male, 7.5 mm, AM P.69089. Antenna 1 flagellum 7-articulate, with strong 2-field calynophore (stronger than in female); calceoli present. Antenna 2 flagellum 35-articulate, calceoli present.

Etymology. Named for Woolgoolga, a town west of the type locality on the coast of New South Wales; used as a noun in apposition.

Distribution. *Australia*: east of Mooloolaba, Queensland, to south of Tasmania.

Ecology. A scavenger taken in baited traps.

Discussion. *Paracallisoma woolgoolga* sp. n. is morphologically very close to *P. spinipoda*. It can be distinguished from that species by the gnathopod 2 palm (slightly concave in *P. spinipoda*, straight in *P. woolgoolga*); the shape of the pereopod 5 basis (evenly rounded in *P. spinipoda*, with a slight excavation along the posteroventral margin in *P. woolgoolga*); and the shape of the epimeron 2 posteroventral corner (producing a small spine in *P. spinipoda*, subquadrate in *P. woolgoolga*). In addition the pereopod 6 basis is much less distinctly excavate posteriorly in *P. woolgoolga* compared with that of *P. spinipoda*.

Paracallisoma zivianii sp. n.

<http://zoobank.org/2DA4860F-478E-4597-B2D6-9E68702B634A>

Figures 31–34

Type material. Holotype, male, 12.0 mm, AM P.69091, east of Flynn Reef, Queensland, Australia (16°37.82'S, 146°23.08'E), 1000 m, baited trap, 7–8 June 1993, coll. J.K. Lowry, P. Freewater & W. Vader, RV *Sunbird* [QLD-950/SEAS]. Paratype, 1 specimen, 0.8 mm, AM P.69092, east of Flynn Reef, Queensland, Australia (16°37.82'S, 146°23.08'E), 1000 m, baited trap, 6–7 June 1993, coll. J.K. Lowry, P. Freewater & W. Vader, RV *Sunbird* [QLD-931/SEAS].

Other Australian material examined. *New South Wales*: 3 specimens, AM P.48103, [NSW-862]; 4 spec-

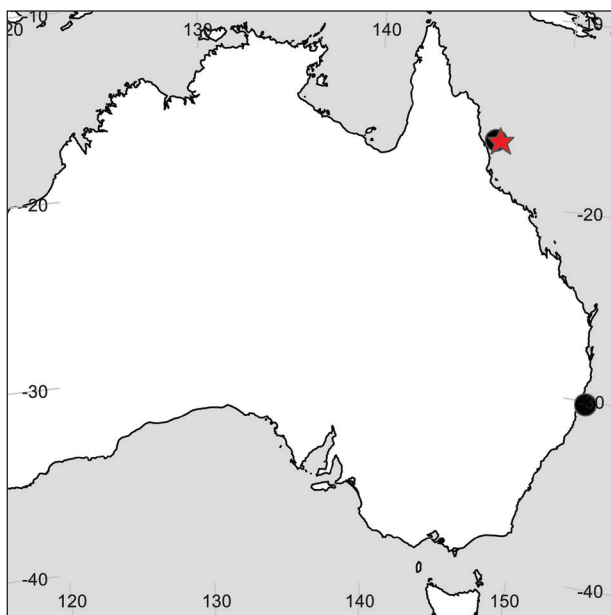


Figure 31. Distribution of *Paracallisoma zivianii* sp. n. Star indicates type locality.

imens, AM P.48127, [NSW-863] north-east of Coffs Harbour ($30^{\circ}10.93'S$, $153^{\circ}32.26'E$), 963 m, baited trap, 11–12 August 1993, coll. P.B. Berents, R.T. Springthorpe & W. Vader, MV *Cheryl Lee*. 1 specimen, AM P.49817, [NSW-876]; 4 specimens, AM P.49831, north-east of Coffs Harbour ($30^{\circ}10.89'S$, $153^{\circ}32.22'E$), 1000 m, baited trap, 12–13 August 1993, coll. P.B. Berents, R.T. Springthorpe & W. Vader, MV *Cheryl Lee* [NSW-877].

Queensland: 6 specimens, AM P.50236, [QLD-931/SEAS]; 3 specimens, AM P.50245, [QLD-932/SEAS] east of Flynn Reef ($16^{\circ}37.82'S$, $146^{\circ}23.08'E$), 1000 m, baited trap, 6–7 June 1993, coll. J.K. Lowry, P. Freewater & W. Vader, RV *Sunbird*.

Diagnosis. Gnathopod 1 coxa margins subparallel. Gnathopod 2 propodus palm transverse, with slightly concave, minutely serrate margin; dactylus reaching corner of palm. Pereopod 5 basis much longer than broad; basis slightly to moderately expanded posteriorly, posterior margin straight. Epimeron 3 posteroventral corner produced into a weak spine. Telson deeply cleft.

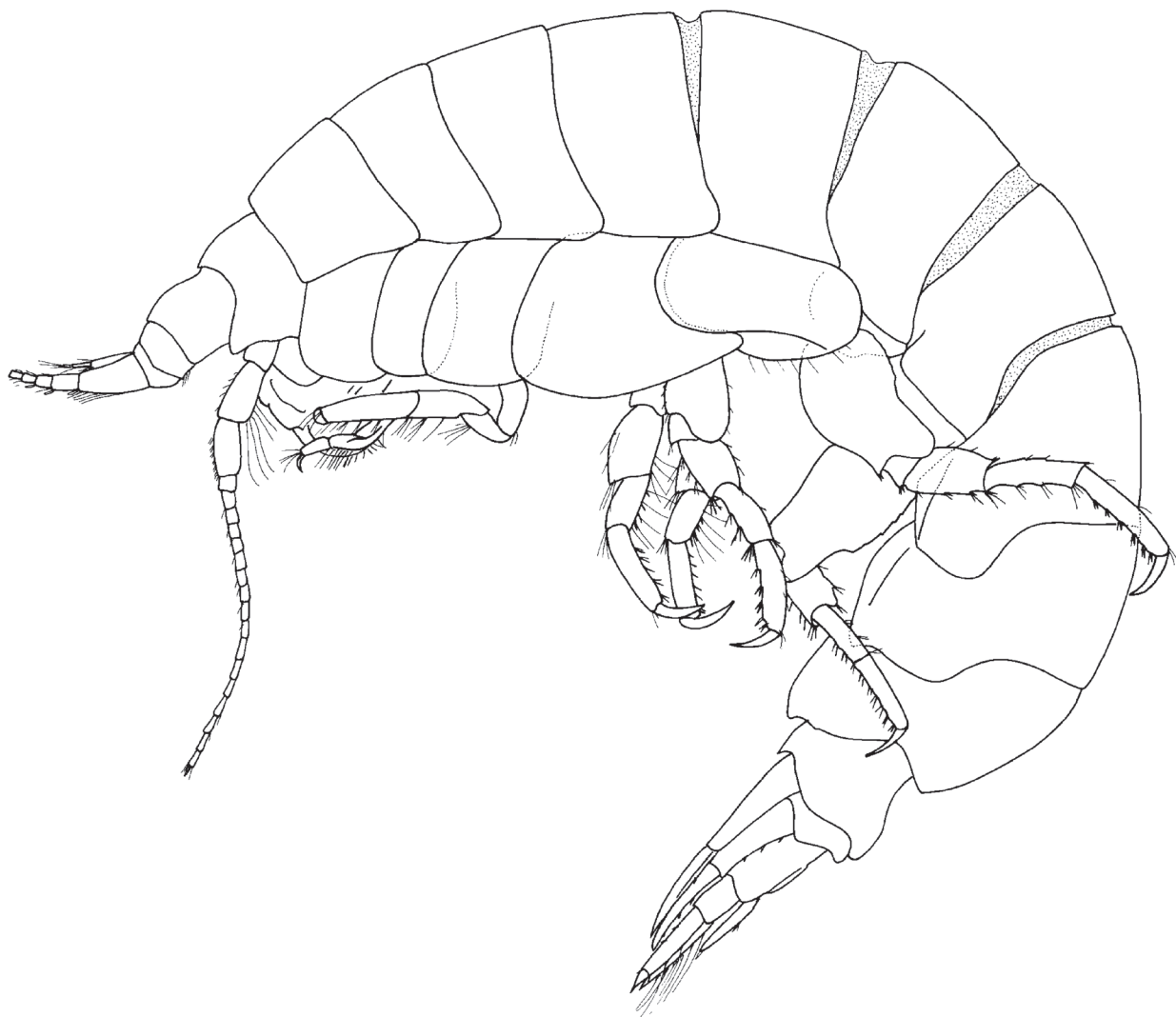


Figure 32. *Paracallisoma zivianii* sp. n. Holotype male, 12.0 mm, AM P.69091, from east of Flynn Reef, Queensland, Australia.

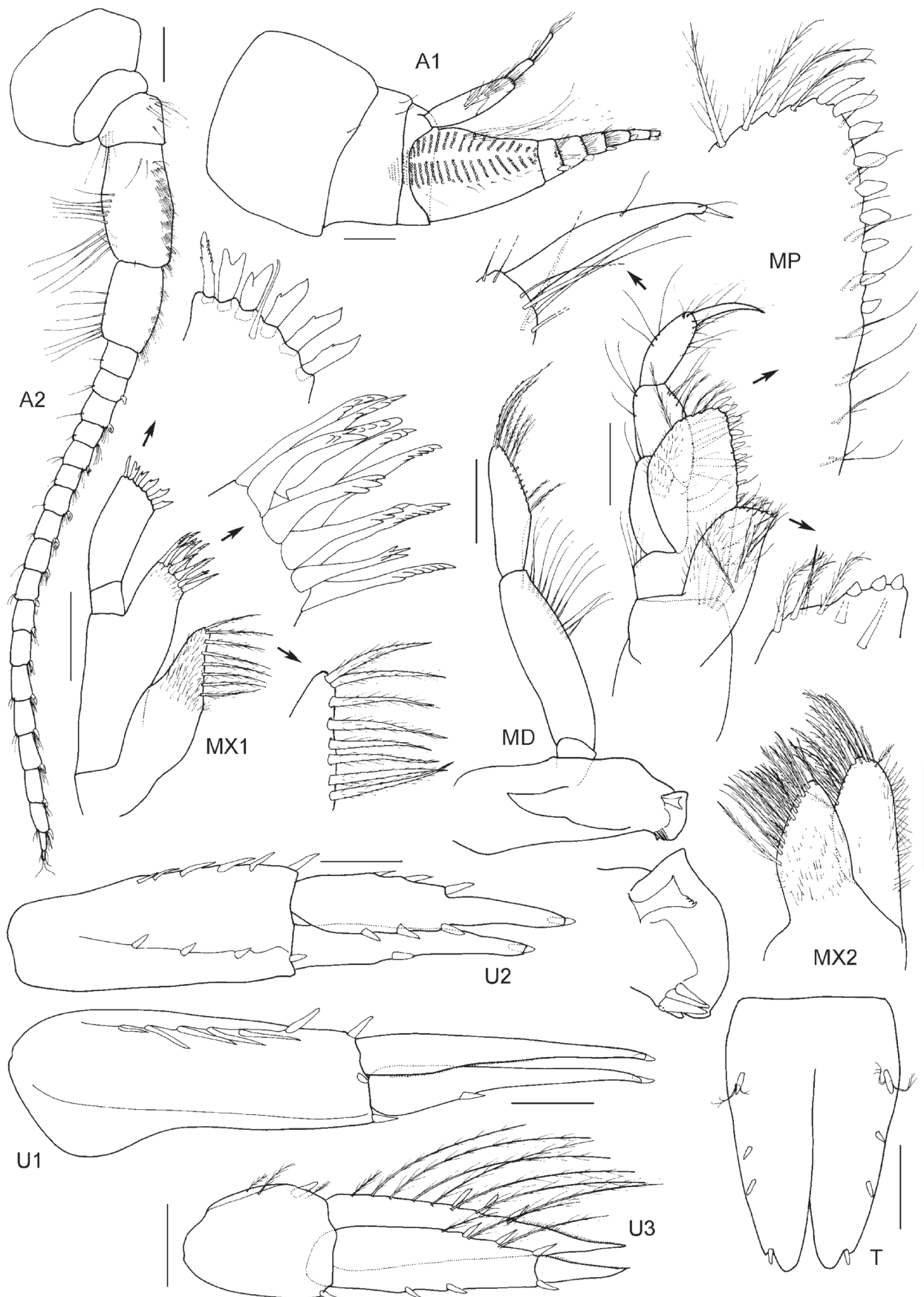


Figure 33. *Paracallisoma zivianii* sp. n. Holotype male, 12.0 mm, AM P.69091, from east of Flynn Reef, Queensland, Australia. Scales represent 0.2 mm.

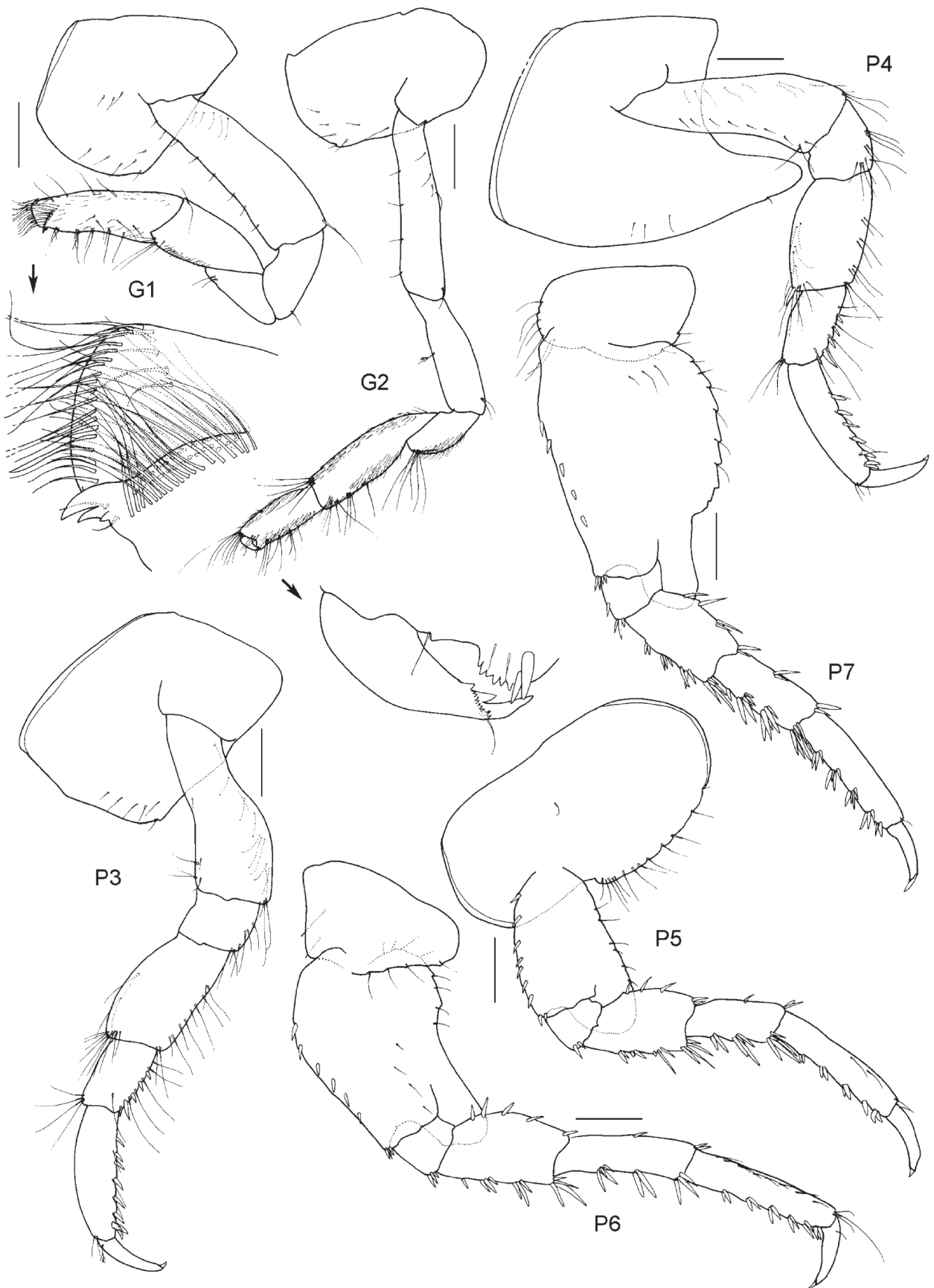


Figure 34. *Paracallisoma zivianii* sp. n. Holotype male, 12.0 mm, AM P.69091, from east of Flynn Reef, Queensland, Australia. Scales represent 0.2 mm.

Description. Based on holotype, male, 12.0 mm, AM P.69091.

Lateral cephalic lobe large, down-turned, narrowly rounded apically. Rostrum absent. Eyes apparently absent. Antenna 1 short; accessory flagellum long, 3-articulate, forming cap covering callynophore; primary flagellum 7-articulate, with strong 2-field callynophore; calceoli present. Antenna 2 longer than antenna 1; peduncle with weak brush setae, article 1 greatly enlarged, not covering article 2; flagellum 19-articulate, calceoli present.

Labrum, epistome slightly produced, rounded; upper lip slightly produced, straight. Mandible incisor with slightly convex margins; lacinia mobilis a stemmed, distally expanded, irregularly cusped blade; molar flap-like; palp attached midway, article 2 slender. Maxilla 1 palp 2-articulate. Maxilla 2 inner plate slightly shorter than outer plate; outer plate without long, distally barbed slender setae. Maxilliped outer plate small; palp large, 4-articulate.

Gnathopods 1–4 coxae without setal fringe along ventral margin. Gnathopod 1 coxa large, about as long as coxa 2, margins subparallel; basis slender; ischium long, length $2.2 \times$ width; carpus long, length $\times 2.0$ width, shorter than propodus; propodus margins slightly tapering distally; anterodistal margin with row of long, slender setae, without robust setae just above dactylus; dactylus small, simple, well developed, posterior margin without setae, with two cusps along posterior margin. Gnathopod 2 minutely subchelate; carpus long, length $3.4 \times$ width; propodus long, length $2.5 \times$ width, palm transverse, with slightly concave, minutely serrate margin; dactylus reaching corner of palm. Pereopod 3 weakly prehensile; propodus without posterodistal locking setae; dactylus short, slender. Pereopod 4 weakly prehensile; coxa wider than deep, with subacutely produced posteroventral lobe; propodus without posterodistal locking setae; dactylus short, slender. Pereopod 5 simple; coxa equilobate; basis much longer than broad; basis slightly to moderately expanded posteriorly, posterior margin straight, posteroventral lobe moderately broadened, extending beyond ischium, without row of long pappose setae medially; dactylus short, slender. Pereopod 6 simple; basis expanded posteroproximally, posterior margin tapering distally, with excavate posteroproximal margin, with rounded, moderately broadened posteroventral lobe, produced into merus; dactylus short, slender. Pereopod 7 simple; basis expanded posteriorly, slightly rounded proximally, minutely crenate, posteroventral corner excavate; propodus without anterodistal locking setae; dactylus short, slender.

Epimeron 1 anteroventral corner rounded. Epimeron 3 posteroventral corner produced into a weak spine. Urosomite 1 with dorsally smooth. Uropod 1 peduncle $1.2 \times$ rami length; rami subequal in length. Uropod 2 rami inner ramus slightly shorter than outer ramus. Uropod 3 peduncle short; rami lanceolate, subequal in length, outer ramus 2-articulate, with plumose setae. Telson longer than broad, length $1.5 \times$ breadth, deeply cleft (to 75%).

Etymology. The species is named for Bert Ziviani, skipper of the RV *Sunbird*.

Distribution. *Australia*: east of Flynn Reef, Queensland, to north-east of Coffs Harbour, New South Wales.

Ecology. A scavenger, taken in baited traps.

Discussion. With its strongly developed pereopod 4 posteroventral lobe and relatively narrow and posterodistally lobate pereopod 5 basis, this species is most similar to *P. alberti*, *P. platepistomum*, and *P. coecum*. It can be differentiated from the latter two species by the shape of the gnathopod 1 coxa, which is short with subparallel margins (longer than broad and tapering distally in *P. platepistomum* and *P. coecum*) and the shape of the pereopod 7 basis (more distinctly excavate posteriorly in *P. zivianii* sp. n.). It differs from *P. alberti* in the shape of the gnathopod 2 palm, which is transverse, and the dactylus, which fits the palm (palm acute, dactylus distinctly shorter than the palm in *P. alberti*).

Scopelocheiropsis Schellenberg, 1926

Scopelocheiropsis Schellenberg, 1926a: 260. — Schellenberg 1942: 110. — J.L. Barnard 1969: 305, key K, 361. — Barnard and Karaman 1991: 527, 434 (key I).

Bathycallisoma. — Ledoyer 1986: 733 (in part, part *Bathycallisoma*).

Type species. *Scopelocheiropsis abyssalis* Schellenberg, 1926, monotypy.

Included species. *Scopelocheiropsis* includes three species: *S. abyssalis* Schellenberg, 1926; *S. armata* (Ledoyer, 1986), comb. n.; *S. sublittoralis* Vinogradov, 2004.

Diagnostic description. *Mandible lacinia mobilis a stemmed, distally expanded, smooth blade.* Maxilla 1 inner plate with pappose setae lining inner margin; palp 2-articulate. Maxilla 2 inner and outer plates subequal in width, inner plate slightly shorter than outer. Maxilliped palp article 4 reduced or well developed. Gnathopod 1 coxa large, margins diverging distally; basis slender, linear; dactylus small, simple, highly modified with apical tip. *Pereopod 3 carpus compressed, wider than long.* Pereopod 4 coxa with weakly-developed, subacutely produced posteroventral lobe.

Discussion. *Scopelocheiropsis* has some variable characters, most importantly the absence of a molar in *S. sublittoralis* (present in the both *S. abyssalis* and *S. armata*), and the blunt, reduced maxilliped palp article 4 in *S. abyssalis* (well-developed in the other two species). Nevertheless, the distinctively compressed carpus of pereopods 3 and 4, as well as the stemmed and distally expanded lacinia mobilis are strong diagnostic characters which separate these taxa from other groups.

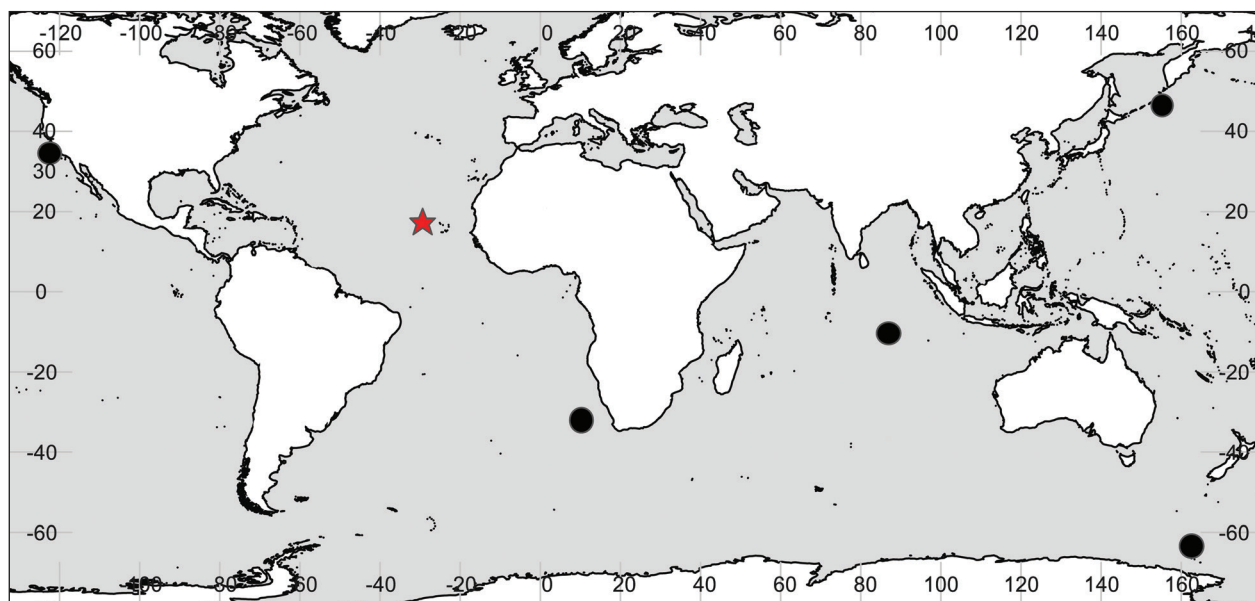


Figure 35. Distribution of *Scopelocheiropsis abyssalis* Schellenberg, 1926. Star indicates type locality.

Scopelocheiropsis abyssalis Schellenberg, 1926

Figures 35, 36

Scopelocheiropsis abyssalis Schellenberg, 1926a: 260, fig. 12. — Schellenberg 1926b: 216, fig. 26b. — J.L. Barnard 1958: 99 (list). — Birstein and Vinogradov 1962: 34, fig. 1. — Birstein and Vinogradov 1964: 162. — Birstein and Vinogradov 1970: 402 (table 1), 417 (table 3). — Lowry and Bullock 1976: 105. — Vader 1983: 140 (table 1). — Barnard and Karaman 1991: 527. — Palerud and Vader 1991: 42. — De Broyer and Jażdżewski 1993: 74. — Thurston 2001: table 2. — Hendrycks and Conlan 2003: 2327, fig. 10. — De Broyer et al. 2007: 159.

Type material. Syntypes, 2 females, 5 mm, ZMB 20319.

Type locality. North Atlantic (17°28'N, 29°42'W), 3000 m.

Depth range. 0–4000 m (Schellenberg 1926a, Hendrycks and Conlan 2003).

Distribution. *Atlantic Ocean:* approximately 650 kms west-north-west of the Cape Verde Islands (Schellenberg 1926a); west of South Africa (Schellenberg 1926b).

Indian Ocean: approximately 1100 kms west-north-west of Cocos (Keeling) Islands (Birstein and Vinogradov 1964).

Pacific Ocean: Kurile-Kamchatka region (Birstein and Vinogradov 1970); United States, west of California (Hendrycks and Conlan 2003).

Southern Ocean: Antarctica, approximately 600 kms north of the Oates Coast (Birstein and Vinogradov 1962).

Discussion. *Scopelocheiropsis abyssalis* was originally described and illustrated as lacking a mandibular molar. Hendrycks and Conlan (2003) described new material and indicated the presence of a small molar. We have re-examined one of the syntypes of this species and can

confirm the presence of a molar on the type material (see Figure 36).

Scopelocheiropsis armata (Ledoyer, 1986)

Figure 37

?*Bathycallisoma armata* Ledoyer, 1986: 733, fig. 282.

?*Scopelocheirus armata*. — Barnard and Karaman 1991: 528.

Type material. Holotype, ?male, 4 mm, MNHN-Am4099.

Type locality. South-east of les Îles Glorieuses (11°31'S, 47°24.1'E), 335–390 m depth.

Depth range. 335–390 m (Ledoyer 1986).

Distribution. *Madagascar:* South-east of les Îles Glorieuses (Ledoyer 1986).

Discussion. Ledoyer (1986) originally described this species, tentatively placing it in the genus *Bathycallisoma* based on the relative length of the gnathopod 1 carpus, which is shorter than the propodus. We do not consider this to be a sound diagnostic character and instead refer to the distally broadened lacinia mobilis (slender robust seta in *Bathycallisoma*).

Scopelocheiropsis sublitoralis G. Vinogradov, 2004

Figure 38

Scopelocheiropsis sublitoralis G. Vinogradov, 2004: 55, fig. 3.

Type material. Holotype, male, 4.5 mm, SAM A40881. Paratype, juvenile, 2.5 mm, P.P. Shirshov Institute of Oceanology of the Russian Academy of Sciences.

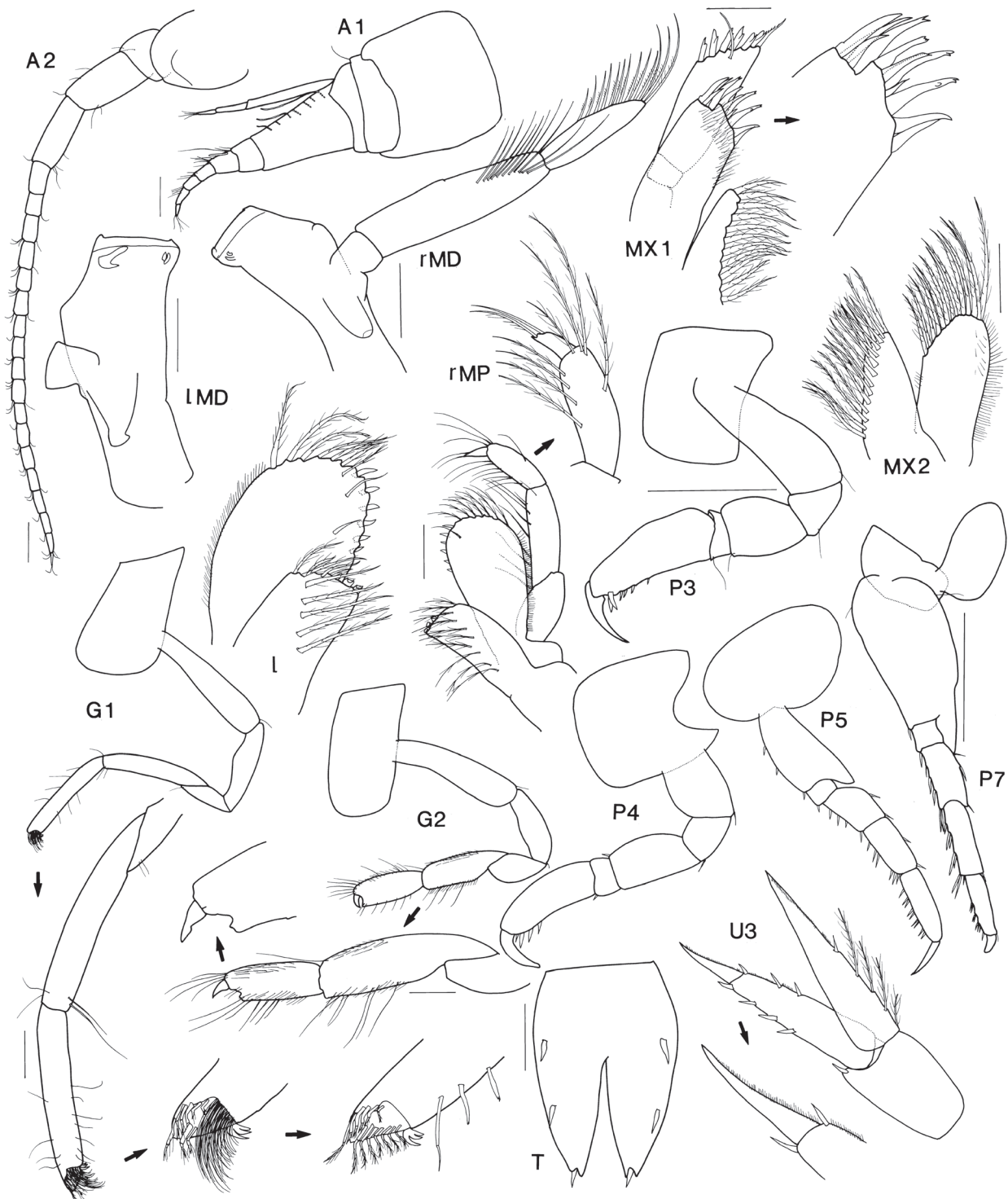


Figure 36. *Scopelocheiropsis abyssalis* Schellenberg, 1926. Syntype female, 5 mm, ZMB 20319, mid Atlantic Ocean. Whole G1, G2, P4, P5 after Schellenberg 1926. Scales for P3, P7 represent 0.5 mm, remainder represent 0.1 mm.

Type locality. Indian Ocean, Madagascar, Mozambique Channel (22°13'S, 43°07'E), 258–300 m (2 meters above the bottom).

Depth range. 258–300 m (Vinogradov 2004).

Distribution. Mozambique Channel, Indian Ocean (Vinogradov 2004).

Ecology. Living over mud with sand.

Discussion. *Scopelocheiropsis sublitoralis* is morphologically close to *S. armata*, both of which have a known distribution that is so far confined to Madagascar. Vinogradov (2004) does not justify his generic placement of the species, but presumably it was due to the absence of a molar, which *S. abyssalis*, the type of the genus, is now

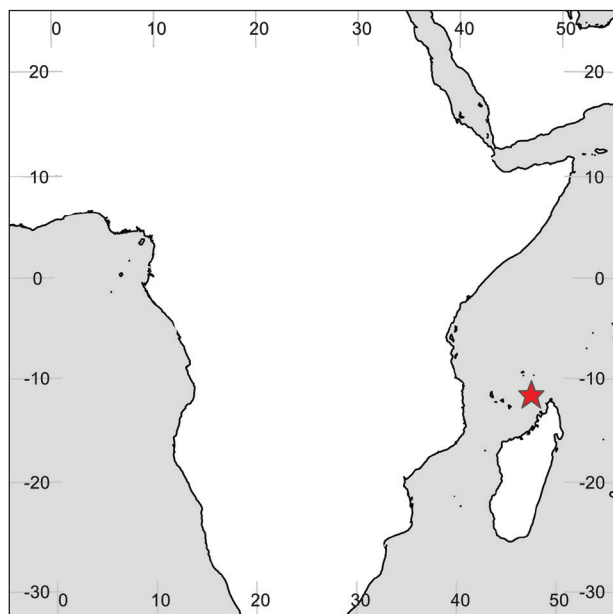


Figure 37. Distribution of *Scopelocheiropsis armata* (Ledoyer, 1986).

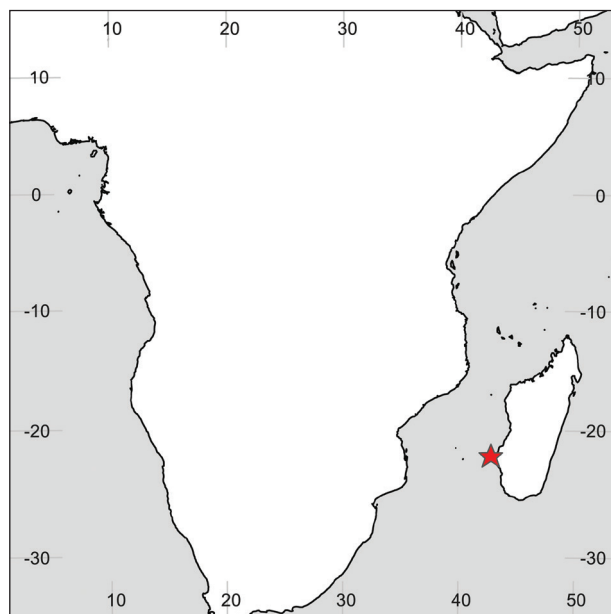


Figure 38. Distribution of *Scopelocheiropsis sublittoralis* Vinogradov, 2004.

known to have. Nonetheless, *S. sublittoralis* exhibits characters which fit within the diagnosis of the genus.

Scopelocheiropsis sublittoralis can be distinguished from *S. armata* by the following characters: molar absent in *S. sublittoralis*, present in *S. armata*; mandible palp broadened medially in *S. sublittoralis*, margins subparallel in *S. armata*; pereopod 5 basis almost linear in *S. sublittoralis*, broadly expanded posteriorly in *S. armata*; uropod 3 rami subequal in length in *S. sublittoralis*, inner ramus distinctly shorter than outer in *S. armata*; telson length $1.5 \times$ width in *S. sublittoralis*, $1.2 \times$ width in *S. armata*.

Scopelocheiropsis sublittoralis can also easily be distinguished from *S. abyssalis* by the absence of a molar (present in *S. sublittoralis*); the shape of gnathopod 1, which is much more elongate and slender in *S. abyssalis*; and the shape of pereopod 7 basis, which has a long, thin posterodistal lobe in *S. sublittoralis* compared to the posteroventrally excavate corner of the pereopod 7 basis in *S. abyssalis*.

Tayabasa gen. n.

<http://zoobank.org/FC8F22E5-8283-4BF4-AF4D-F0C9C7F9CA01>

Eucallisoma. — Lowry and Stoddart 1993: 67 (in part, part *Eucallisoma*).

Type species. *Eucallisoma barnardi* Lowry & Stoddart, 1993, by original designation.

Included species. *Tayabasa* includes one species: *T. barnardi* (Lowry & Stoddart, 1993).

Diagnostic description. Mandible lacinia mobilis a cuspidate peg. Maxilla 1 inner plate with pappose setae

lining inner margin; palp 2-articulate. Maxilla 2 inner plate broader than outer, inner and outer plates subequal in length. Maxilliped palp article 4 vestigial. Gnathopod 1 coxa large, almost as long as coxa 2, margins slightly tapering distally; basis swollen, with glandular material; dactylus reduced, simple. Pereopod 3 carpus short to long, longer than wide. Pereopod 4 with well-developed, subacute posteroventral lobe.

Etymology. The name *Tayabasa* refers to Tayabas Bay, located on the eastern side of Verde Island Passage in the Philippines, close to the type locality of the type species. Gender feminine.

Discussion. *Tayabasa* belongs to a closely related and highly derived complex of genera also comprised of *Anisocallisoma*, *Austrocallisoma* and *Eucallisoma*. See discussion under *Austrocallisoma* for further remarks.

Tayabasa can be separated from *Anisocallisoma* by the 2-articulate maxilla 1 palp and inner plate with setae lining the inner margin (palp 1-articulate and inner plate with apical setae only in *Anisocallisoma*). It differs from *Austrocallisoma* in peg-like lacinia mobilis, the 2-articulate maxilla 1 palp, and the well-developed gnathopod 1 coxa (lacinia mobilis a stemmed, distally expanded blade, maxilla 1 palp 1-articulate, and gnathopod 1 coxa reduced in *Austrocallisoma*). Finally, it can be distinguished from *Eucallisoma* in the peg-like lacinia mobilis, the vestigial maxilliped palp article 4, and the subacute posteroventral lobe of the pereopod 4 coxa (lacinia mobilis a stemmed, distally expanded blade, maxilliped palp article 4 well developed, and pereopod 4 coxa with a subquadrate posteroventral lobe in *Eucallisoma*).

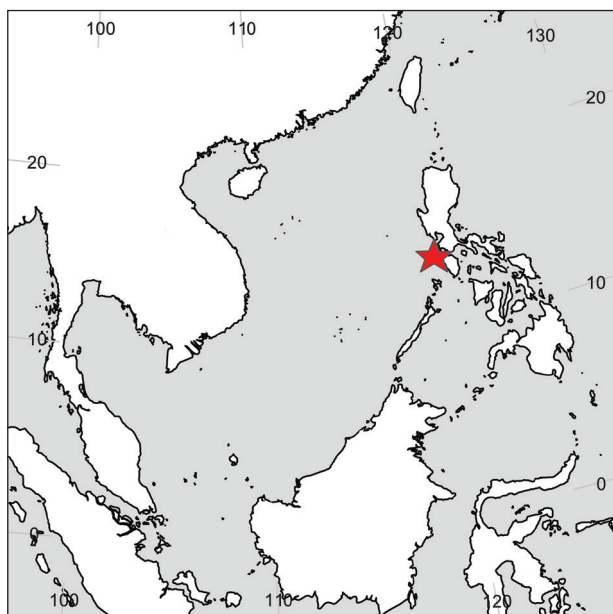


Figure 39. Distribution of *Tayabasa barnardi* (Lowry & Stoddart, 1993).

Tayabasa barnardi (Lowry & Stoddart, 1993)

Figure 39

Eucallisoma barnardi Lowry & Stoddart, 1993: 68, figs 8–10. — Lowry 2000: 323 (list).

Type material. Holotype, female, 40 mm, MNHN-Am4449.

Type locality. Eastern entrance to Verde Island Passage, Philippines (13°36.7–38.11'N, 120°33.7–32.3'E), 810–820 m depth.

Depth range. 810–820 m.

Distribution. *Philippines*: Verde Island Passage.

Discussion. *Eucallisoma barnardi* is here transferred to its own genus, *Tayabasa* gen. n., on the basis of the cuspidate peg form of the lacinia mobilis, the vestigial maxilliped palp article 4, and the subacute posteroventral lobe on the pereopod 4 coxa.

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Supplementary material 1

Collection data for new species of Scopelocheiridae described

Authors: Niamh M. Kilgallen, James K. Lowry

Data type: species data

Explanation note: Collection data and registration information for new taxa described in this paper.

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Supplementary material 2

Distribution data for Scopelocheiridae species

Authors: Niamh M. Kilgallen, James K. Lowry

Data type: distribution data

Explanation note: Collection data of scopelocheirid specimens as recorded in the literature. This information is taken from the literature referenced within and includes as much information as available, including locality, depth, habitat, sampling method, museum registration details and the name as originally recorded.

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The shallow-water chitons (Mollusca, Polyplacophora) of Caldera, Region of Atacama, northern Chile

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Southeastern Pacific

intertidal

The Molluscan species of the northern littoral of Chile have been sparsely studied. This work reviews for the first time the diversity of polyplacophoran molluscs around the port of Caldera, in the Region of Atacama (26°45'49"S; 70°45'17"W to 27°20'23"S; 70°56'46"W), northern Chile. Eleven species were found in this study: *Acanthopleura echinata* (Barnes, 1824); *Callistochiton pulchellus* (Gray, 1828); *Calloplax vivipara* (Plate, 1899), *Chaetopleura peruviana* (Lamarck, 1819); *Chiton cumingsii* Frembly, 1827; *Chiton granosus* Frembly, 1827; *Chiton magnificus* Deshayes, 1827; *Enoplochiton niger* (Barnes, 1824), *Radsia barnesii* (Gray, 1828), *Tonicia atrata* (G. B. Sowerby II, 1840) and *Tonicia chilensis* (Frembly, 1827). All of the species occurring in the area have distributions in the southeastern Pacific Ocean, from Ecuador to central Chile, and three of them are species endemic to the Chilean coasts (*Calloplax vivipara*, *Radsia barnesii*, and *Tonicia atrata*). This diversity of species is comparable to that of better surveyed faunas of central and southern Chile or Patagonia. Of the eleven species recorded, the geographic distribution records for *Callistochiton pulchellus*, *Radsia barnesii* and *Tonicia atrata* are extended, and *Calloplax vivipara* is found alive again after 40 years, filling a gap in its known distribution. Illustrations of living specimens in their habitat, distribution records and a taxonomic key for all the studied taxa are also provided.

Introduction

Research on marine molluscs of northern Chile began with the descriptions of some species by Sowerby (1832), d'Orbigny (1847), Hupé (1854) and Philippi (1860) in the late 19th century. Further works include the studies done by Dall (1909), mostly in deep water areas along the Chilean and Peruvian coasts; Gigoux (1934), which listed the species found in the Region of Atacama, Marincovich (1973), describing the intertidal molluscs of Iquique; Acuña (1977), Bretos (1980), Bretos et al. (1983) and McLean (1984) dealing with fissurellid limpets and, more recently, the works of Guzmán et al. (1998) which studied

the molluscan fauna of Antofagasta; Véliz and Vásquez (2000) reviewing the Trochidae species from northern Chile, and a few works, among others, describing new Calyptraeidae (Brown and Olivares 1996, Véliz et al. 2012), Limidae (Campusano et al. 2012) or Buccinidae species (Araya 2013).

Regarding the Chilean Polyplacophora — apart from the early works of Frembly (1827), Rochebrune and Mabilie (1885), Rochebrune (1889), Pilsbry (1893), Plate (1901, 1902), Thiele (1906, 1911) or Melvill and Standen (1912) among others — it was the work of Leloup (1956) which produced the most detailed study dealing with this molluscan class in the country; encompassing

material from between Iquique (20°S) in northern Chile to Punta Arenas (53°S) in the extreme south of the country. Most of the subsequent works dealing with chitons have been focused on species from central and southern Chile (Castellanos 1948, 1951, Stuardo 1959, Osorio and Reid 2004, Schwabe and Sellanes 2004, 2010, Sirenko 2006), with a few works including shallow water species (Schwabe et al. 2006, Sirenko 2007). Further recent works including species from the Region of Atacama or northern Chile in particular only include the Kaas and Van Belle monograph series (Kaas and Van Belle 1985a, 1985b, 1987, 1990, 1994) which studied the worldwide chitons and, among them, Chilean species.

This molluscan class is often overlooked in Chile, as their species are mostly small and hard to collect and to preserve, however, three of the large species of Chilean

chitons (*Acanthopleura echinata* (Barnes, 1824), *Chiton* (*Chiton*) *magnificus* Deshayes, 1827 and *Chiton* (*Chiton*) *granosus* (Frembly, 1827)) are collected with gastronomic purposes (Osorio 2002), and some species are used in traditional medicine in northern Chile. Chitons play a role in controlling the green algal cover in mid-intertidal exposed rocky-shores of central Chile (Aguilera and Navarrete 2007) eating encrusting corallines (Camus et al. 2012), newly settled barnacles (Aguilera 2005) and other sessile and mobile invertebrates (Camus et al. 2008), and thus they have a direct impact on the intertidal ecosystem.

The coast of the Region of Atacama consists of rocky formations of volcanic origin with a few sandy beaches. The intertidal area of most of the coast, with the exception of a few scattered bays, is narrow (up to 20 m) and presents a diverse geography including cliffs, rocky plat-

Table 1. Sampling sites, arranged from north to south.

Locality	Habitat type/Macroalgae	Coordinates	Species present
Obispito	Rocky coast with tidal pools, crustose coralline algae.	26°45'49"S; 70°45'17"W	<i>Calloplax vivipara</i> , <i>Chiton cumingsii</i> .
Aguas Verdes	Rocky coast with tidal pools, large phaeophyta algae (<i>Lessonia</i> sp.).	26°52'20"S; 70°49'25"W	<i>Chiton cumingsii</i> , <i>Chiton magnificus</i> , <i>Tonicia chilensis</i> .
Playa Granito Orbicular	Pebble beach, minor algae covering.	26°58'22"S; 70°47'43"W	<i>Chiton cumingsii</i> .
Playa Rodillo	Exposed rocky coast and pebble beach.	26°59'48"S; 70°47'27"W	<i>Enoplochiton niger</i> .
Sur de Playa Ramada	Rocky coast with tidal pools and rock intrusions in sandy beach. Great diversity of algae.	27°00'37"S; 70°48'04"W	<i>Callistochiton pulchellus</i> , <i>Calloplax vivipara</i> , <i>Chaetopleura peruviana</i> , <i>Chiton cumingsii</i> , <i>Chiton magnificus</i> , <i>Radsia barnesii</i> , <i>Tonicia chilensis</i> .
Islote Playa Ramada	Rocky coast, big boulders. Holdfasts of <i>Lessonia nigrescens</i> .	27°00'41"S; 70°48'23"W	<i>Chaetopleura peruviana</i> , <i>Chiton cumingsii</i> , <i>Enoplochiton niger</i> .
Playa El Pulpito	Pebble beach, rock formation. Several algae.	27°01'22"S; 70°48'30"W	<i>Chaetopleura peruviana</i> , <i>Callistochiton pulchellus</i> , <i>Chiton cumingsii</i> , <i>Enoplochiton niger</i> .
Playa El Pulpo	Rocky coast with protected sandy beach. Great diversity of algae.	27°01'37"S; 70°48'39"W	<i>Chaetopleura peruviana</i> , <i>Callistochiton pulchellus</i> , <i>Chiton cumingsii</i> , <i>Chiton granosus</i> , <i>Radsia barnesii</i> .
Norte Bahía de Caldera	Rocky coast, rock slabs and pockets of sand. Encrusting algae, <i>Ulva lactuca</i> , etc.	27°03'01"S; 70°48'30"W	<i>Acanthopleura echinata</i> , <i>Chaetopleura peruviana</i> , <i>Chiton granosus</i> , <i>Enoplochiton niger</i> .
Sur de Playa Negra	Sandy beach with rock formation. Minor algal covering.	27°03'38"S; 70°48'51"W	<i>Chaetopleura peruviana</i> , <i>Chiton cumingsii</i> .
Sur de Playa Brava	Rock formation among sandy beaches, <i>Ulva lactuca</i> and red algae.	27°03'50"S; 70°49'13"W	<i>Chaetopleura peruviana</i> , <i>Chiton cumingsii</i> .
Playa Mansa	Limestone slabs on sandy beach. Small algae covering, encrusting algae.	27°03'58"S; 70°49'36"W	<i>Acanthopleura echinata</i> , <i>Chaetopleura peruviana</i> , <i>Chiton cumingsii</i> , <i>Chiton granosus</i> , <i>Tonicia atrata</i> , <i>Tonicia chilensis</i> .
Sur Bahía de Caldera	Rock slabs, pebble beach. Encrusting algae.	27°03'33"S; 70°49'55"W	<i>Chaetopleura peruviana</i> , <i>Chiton cumingsii</i> , <i>Chiton granosus</i> , <i>Tonicia chilensis</i> .
Calderilla	Loose boulders on sandy beach, <i>Gracilaria</i> algae.	27°05'30"S; 70°50'56"W	<i>Chaetopleura peruviana</i> , <i>Chiton cumingsii</i> , <i>Tonicia chilensis</i> .
Peninsula Calderilla	Rocky coast with small pebble beach, <i>Ulva lactuca</i> and red algae.	27°05'15"S; 70°51'27"W	<i>Calloplax vivipara</i> , <i>Chaetopleura peruviana</i> , <i>Chiton cumingsii</i> , <i>Radsia barnesii</i> .
Norte Bahía Inglesa	Rocky beach, scattered sandy pockets.	27°05'14"S; 70°51'49"W	<i>Chaetopleura peruviana</i> , <i>Chiton cumingsii</i> .
Sur Playa Rocas Negras	Rocky formation on sandy beach. Encrusting corallines.	27°07'39"S; 70°54'53"W	<i>Chaetopleura peruviana</i> , <i>Chiton cumingsii</i> .
Playa Chorrillos	Rocky coast with scattered pebble beaches. Large algae holdfasts (<i>Lessonia nigrescens</i> , <i>Lessonia trabeculata</i>)	27°12'44"S; 70°57'05"W	<i>Chaetopleura peruviana</i> , <i>Chiton cumingsii</i> , <i>Chiton magnificus</i> .
Bahía Cisne	Sandy beach with rock platforms. Filamentous algae.	27°14'57"S; 70°57'42"W	<i>Chiton cumingsii</i> .
Puerto Viejo	Sandy beach with limestone rocks intrusions. Minor algae communities.	27°20'23"S; 70°56'46"W	<i>Chiton cumingsii</i> .

forms, intertidal pools, and boulder fields. The exposed side of rocks and boulders are exposed to strong surf, with just a few sheltered areas, particularly in the area of the Bay of Caldera, Obispito and Calderilla (Table 1).

This work presents an overview, with distributions and illustrations, of all the species of Polyplacophora found in the Region of Atacama, northern Chile. The distribution range and a taxonomic key to all the studied species is also provided. The aim of this preliminary paper is thus to contribute on the knowledge of the molluscan fauna, in particular of northern Chile.

Material and methods

The material considered in this study was mostly obtained by sampling in the rocky coastal areas around the port of Caldera (27°04'S; 70°50'W), between Calenta Obispito (26°45'49"S; 70°45'17"W) and Puerto Viejo (27°20'23"S; 70°56'46"W), and in specific localities along the coasts of the Region of Atacama, northern Chile, during the summers of 2011 to 2012 and in August–December 2012. A synopsis of all the stations is given in Table 1. The surveys used a similar approach to the work of García-Ríos et al. (2011). The terminology of shell morphology is based upon Schwabe (2010). Original descriptions of all species were carefully reviewed and voucher specimens, unless indicated, are deposited under accession number 3072014 in the collections of the Museo Paleontológico de Caldera, Caldera, Chile (MP-CCL). Abbreviations used are: LACM, Natural History Museum of Los Angeles County, Los Angeles, USA; SBMNH, Santa Barbara Museum of Natural History, Santa Barbara, USA; NHMUK, National History Museum, London, United Kingdom.

Systematic taxonomy

Class Polyplacophora Gray, 1821

Subclass Neoloricata Bergenhayn, 1955

Order Chitonida Thiele, 1909

Suborder Chitonina Thiele, 1909

Superfamily Chitonoidea Rafinesque, 1815

Family Callistoplacidae Pilsbry, 1893

Genus *Callistochiton* Carpenter MS, Dall, 1879

Type species. *Callistochiton palmulatus* Carpenter MS, Dall, 1879, by monotypy.

***Callistochiton pulchellus* (Gray, 1828)**

Plate 1, Fig. 2; Table 2

Chiton pulchellus Gray, 1828: 6, pl. 3, fig. 9. *Chiton bicostatus* d'Orbigny, 1847: 486, pl. 81, figs 7–9. *Callistochiton shuttleworthianus*: Bergenhayn 1937: 284, figs

3f–g (non *Callistochiton shuttleworthianus* Pilsbry, 1893). *Callistochiton carmenae* Smith & Ferreira, 1977: 87, figs 10–11. *Callistochiton pulchellus*: Ferreira 1979: 460, figs 25–26; Aguilera 2005a: 207, fig. 1. Detailed bibliography and synonymy in Kaas and Van Belle (1994: 161).

Description. Animal of small size, up to 11.5 mm in examined specimens, elongate oval, moderately elevated, color of tegmentum creamy white or bright white. Head valve semicircular, sculpture with 10–15 low rounded, equally spaced, nodulose, annulate, radial ribs, becoming obsolete towards the apex, the posterior ribs being strongest and more nodulose. Intermediate valves rectangular, lateral areas well defined, sculptured with two strong radial ribs. Central area with two series of equally spaced, diagonal lirae, forming rounded depressions in the interspaces. Tail valve semi-oval, slightly less wide than head valve, sculptured like head valve, with 8–11 weaker radial ribs. Girdle rather wide, yellowish white, dorsally covered with small, oval, imbricating scales (After Kaas and Van Belle 1994).

Material examined. Specimens found under sunken rocks in tidal pools in Playa El Pulpito (SBMNH 452240, 1 specimen), Sur de Playa Ramada and Playa El Pulpito (Table 1).

Distribution. This species has records from Islay (17°03'S; 72°06'W), Peru to Chanavayita cove, 54 km south of Iquique, Chile (20°42'S; 70°09'W), with records also in the Galápagos Islands (01°40'N; 92°01'W), Ecuador (Aguilera 2005a). The present record (at 27°S) is now the southernmost record for this species.

Remarks. This is a small (under 12 mm) chiton, easily overlooked but for its bright whitish color. It is a fairly rare species; they were not abundant and were found only in two of the studied locations (Table 1), under rocks sunken in tidal pools, associated to small communities of *Acar pusilla* Sowerby, 1832, *Liotia cancellata* Gray, 1842, *Rissoina inca* Sowerby, 1832, encrusting algae and sponges. It has been reported that this species feeds on sponges, bryozoa and diatoms (Aguilera 2005). This species can be mistaken for *Calloplax vivipara* (Plate, 1902), differing from this species in having a less elongate body shape, with a much finer and subtle sculpture (especially noticeable on the terminal valves), it differs from *C. vivipara* in having rounded depressions in the central-lateral areas of the valves, especially in the middle valves.

Genus *Calloplax* Thiele, 1909

Type species. *Chiton janeirensis* Gray, 1828, by monotypy.

***Calloplax vivipara* (Plate, 1899)**

Plate 1, Fig. 3; Table 2

Callistochiton viviparus Plate, 1899: 154, pl. 9, figs 267–281; Dall 1909: 246; Gigoux 1934: 281; Boudet 1945: 134; Leloup 1956: 46; Stuardo 1959: 144; Smith 1966: 436, 437, 441, 442. *Chiton janeirensis*, Var.?: Gray 1828: 5; Sowerby 1840: 6, sp. no. 78 (spelled *janierensis*). *Calloplax viviparus*: Ferreira 1978: 60, figs 2 & 5.

Description. Animal of small size, up to 12 mm in examined specimens, elongate oval, moderately elevated, color of tegmentum tan or creamy white. Head valve semicircular, sculpture with about nine equally spaced, nodulose, annulate and well defined radial ribs. Intermediate valves rectangular, lateral areas well defined, sculptured with two strong radial ribs. Central area with about eight longitudinal riblets per side, well-marked in the pleural areas but becoming obsolete at the jugum. The riblets tend to converge anteriorly and are not latticed. Posterior valve semi-oval, elevated at the central mucro, with nine well defined radial ribs. Girdle yellowish white, dorsally covered with small scales (After Ferreira 1978).

Material examined. Specimens found under rocks in a tidal pool at Obispito (MPCCL 3072014B, 1 specimen), Sur de Playa Ramada and under rock slabs sunken under boulders in Peninsula Calderilla (SBMNH 452241, 1 specimen).

Distribution. Plate (1899) described this species for Isla Pacharos (=Pájaros), near Coquimbo, Chile (29°58'S; 71°21'W). Ferreira (1978) additionally recorded this species from the intertidal of Pozo Toyo, South of Iquique, Tarapacá Province (20°25'S; 70°10.5'W) and mainland East of Isla Santa María, North of Antofagasta, Antofagasta Province (23°25'S; 70°36'W) from specimens housed at the LACM. A specimen labelled *Chiton janeirensis* (NHMUK 197742) identified by Ferreira (1978) as *C. viviparus* extended the southern distribution of this species at Valparaíso (33°02'S; 71°38'W). This is the first time this species is recorded, in the field, since its description and the present record fills a gap in the distribution in Chile of this rare species.

Remarks. This is a rare species, found in only two of the locations under study; in both places this species was found under rocks sunken in tidal pools, associated to encrusting sponges and to communities of the small mussel *Brachidontes granulata* (Hanley, 1843). According to Plate (1899) this species is ovoviviparous; that cited author found about 15 embryos, some with seven shell valves, in the ovary of a single specimen. In fact, this is the only chiton species ever reported to be ovoviviparous (Pearse 1979). This species is somewhat similar to *Callistochiton pulchellus* (Gray, 1828), differing in the coarse sculpture (especially in the anterior valve, with fewer and stronger ribs), the presence of longitudinal riblets in the central areas, and the more yellowish body color.

Family Chaetopleuridae Plate, 1899**Subfamily Chaetopleurinae Plate, 1899****Genus *Chaetopleura* Shuttleworth, 1853**

Type species. *Chiton peruvianus* Lamarck, 1819, by subsequent designation.

***Chaetopleura (Chaetopleura) peruviana* (Lamarck, 1819)**

Plate 1, Fig. 4; Table 2

Chiton peruvianus Lamarck, 1819: 321; Barnes 1824: 70, pl. 3, fig. 2. *Chaetopleura peruviana*: Plate 1902: 182, pl. 2, figs 141–142, pl. 10, figs 294–301, pl. 11, figs 302–303; Dall 1909: 244; Marincovich 1973: 44, fig. 101; Aldea and Valdovinos 2005: 383, fig. 5C. *Chaetopleura (Chaetopleura) peruviana*: Kaas and Van Belle 1987: 62, fig. 27; Reid and Osorio 2000: 113, fig. 2A.

Description. Animal of medium to large size, up to 45 mm long in examined specimens. Oval to elongate oval, slightly depressed, color of tegmentum greenish-brown to dark brown. Head valve semicircular, front slope straight, posterior margin V-shaped. Intermediate valves broadly rectangular. Tail valve less than semicircular, almost as wide as head valve. Girdle profusely beset with very long (up to 10 mm) thick, coarse, corneous hairs, not only interspersed throughout girdle but in girdle bridges, protruding at sutures and extending over valves. Tegmentum pustulose sculptured with minute and neatly separated pustules, on the end valves the pustules are arranged in radiating rows. Body width/length, mean 0.66; height/length, mean 0.22 (After Ferreira 1983).

Material examined. Specimens found in almost all locations, with the exception of Bahía Cisne, Puerto Viejo and Playa Rodillo up to Obispito (Table 1). Calderilla (MPCCL 3072014C, 1 specimen).

Distribution. Kaas and Van Belle (1987) cited this species along the western coast of South America, between Cape San Lorenzo (1°4'0"S; 80°55'60"W), Ecuador to the Chonos Archipelago (45°0'0"S; 74°0'0"W), southern Chile. This species lives in the intertidal zone down to a depth of 40 m (Kaas and Van Belle 1987).

Remarks. This species is easily distinguished from all other chitons in the region by the presence of hairs covering the valves and sutures. A similar species, *Chaetopleura (Chaetopleura) benaventei* Plate, 1899 is slightly smaller in size and differs in the overall coloration and in the absence of the corneous bristles. *Chaetopleura hennahi* (Gray, 1828) found between El Callao, Peru and Arica, Chile (Kaas and Van Belle 1987) has a wine-red to reddish brown tegmentum and lacks the blackish corneous hairs which protrude at the sutures in *Chaetopleura peruviana*.

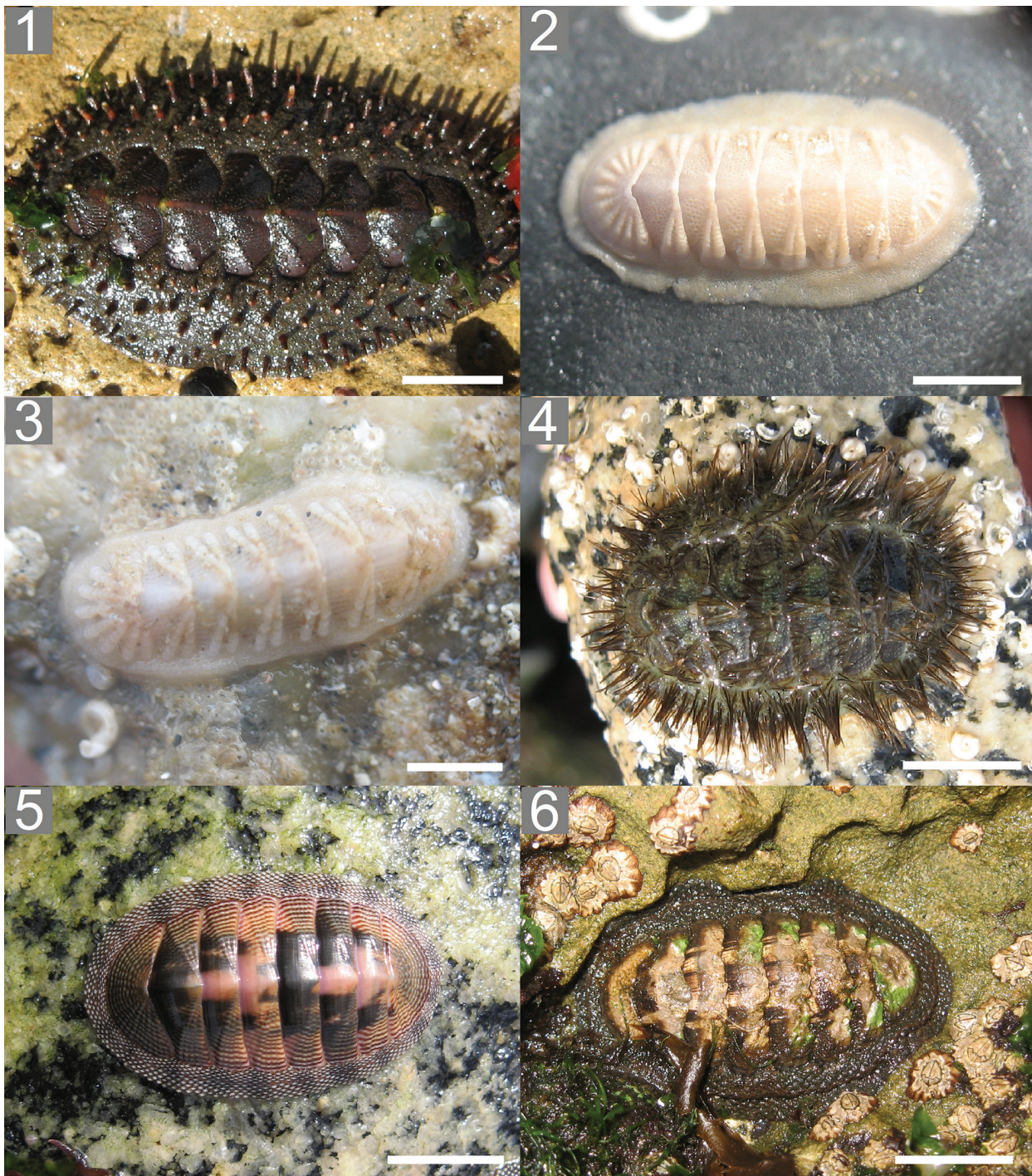


Plate 1. *Chiton* species photographed in situ; **1.** *Acanthopleura echinata*, Playa Mansa; **2.** *Callistochiton pulchellus*, Playa El Pulpo; **3.** *Calloplax vivipara*, Peninsula Calderilla; **4.** *Chaetopleura peruviana*, Sur Playa Ramada; **5.** *Chiton cumingsii*, Playa El Pulpo; **6.** *Chiton granosus*, Playa Mansa. Scale bars are: 2 cm for **1, 2, 3** and 1 cm for **4, 5, 6**.

Family Chitonidae Rafinesque, 1815
Subfamily Acanthopleurinae Dall, 1889

Genus *Acanthopleura* Guilding, 1829

Type species. *Chiton spinosus* Bruguière, 1792, by subsequent designation.

***Acanthopleura echinata* (Barnes, 1824)**

Plate 1, Fig. 1; Table 2

Chiton echinatus Barnes, 1824: 71, pl. 3, figs 4a, b. *Chiton spiniferus* Frembly, 1827: 196, suppl. pl. 16, fig. 6; Sowerby 1833, pl. 1, fig. 47. *Acanthopleura echinata*: Dall

Table 2. Distribution range of taxa considered in this work.

Species	Distribution	References
<i>Acanthopleura echinata</i> (Barnes, 1824)	Talara, Peru (04°34'S; 81°16'W) to Punta Tumbes, Bahía de Concepción, Chile (36°49'S; 73°03'W).	Ferreira 1986
<i>Callistochiton pulchellus</i> (Gray, 1828)	Islay (17°03'S; 72°06'W), Peru to Ramada Beach, Caldera (26°56'S; 70°47'W).	Aguilera 2005a and this study.
<i>Calloplax vivipara</i> (Plate, 1902)	Pozo Toyo, South of Iquique (20°25'S; 70°10.5'W) to Valparaíso (33°02'S; 71°38'W), Chile.	Plate 1902; Ferreira 1978 and this work
<i>Chaetopleura</i> (<i>Chaetopleura</i>) <i>peruviana</i> (Lamarck, 1819)	Cape San Lorenzo, Ecuador (01°04'S; 80°55'60"W) to the Chonos Archipelago, Chile (45°00'S; 74°00'W).	Kaas and Van Belle (1983)
<i>Chiton</i> (<i>Chiton</i>) <i>cummingsii</i> Frembly, 1827	Paita, Peru (05°05'34"S; 81°06'07"W) to Puerto Montt (41°28'S; 72°56'W), Chile.	Marincovich (1973).
<i>Chiton</i> (<i>Chiton</i>) <i>granosus</i> Frembly, 1827	Paita, Peru (05°05'34"S; 81°06'07"W) to Boca de Guafo (43°39'S; 74°00'W), Region of Aysén, Chile.	Marincovich (1973) and Osorio et al. (2005).
<i>Chiton</i> (<i>Chiton</i>) <i>magnificus</i> Deshayes, 1827	San Lorenzo Island, Peru (12°05'23"S; 77°13'26"W) south to Bahía Tictoc, Chiloé Province, Chile. (43°36'40"S; 72°57'15"W).	Bullock (1988)
<i>Enoplochiton niger</i> (Barnes, 1824)	Talara, Peru (04°34'S; 81°16'W) to Coquimbo Bay, Chile (29°58'S; 71°21'W).	Ferreira 1986
<i>Radsia barnesii</i> (Gray, 1828)	Ramada Beach, Caldera (26°56'S; 70°47'W) to the Chonos Archipelago (45°0'0"S; 74°0'0"W), Chile.	Bullock (1988) and this study
<i>Tonicia atrata</i> (Sowerby II, 1840)	Playa Mansa, Caldera (27°03'58"S; 70°49'36"W) to Tierra del Fuego (54°S), Chile.	Reid and Osorio (2000) and this study
<i>Tonicia chilensis</i> (Frembly, 1827)	Peru (12°S) to Chile (54°S).	Reid and Osorio (2000).

1909: 180, 248, pl. 23, fig. 6; Marincovich 1973: 44, fig. 100; Osorio 2002: 52.

Description. Animal of very large size, up to 158 mm in examined specimens. Tegmentum smooth to shiny (but often eroded), dark reddish-brown, with occasional small blue spots. Lateral areas hardly raised, smooth except for two radial rows, one of 5–9 round granules indenting sutural edge. Anterior valve with some 10 radial rows of round granules; space between rows smooth. Central areas with raised, well-defined, smooth jugal band bordered by shallow, longitudinal grooves with short, wavy, longitudinally oriented riblets on pleural areas. Girdle upper surface with erect, strong, spike-like spines, round in cross section, up to 8 mm long in large specimens (longer if not broken), often encrusted. Girdle bridges empty (After Ferreira 1986). According to Osorio (2002) this is a dioecious species, which can reach a maximum length of 200 mm.

Material examined. Specimens found in two locations; Norte Bahía de Caldera (MPCCL 3072014A, 1 specimen) and in Playa Mansa, in subtidal areas in exposed rocks and in rocks associated with the giant kelp *Lessonia nigrescens* Bory de Saint-Vincent, 1826.

Distribution. According to Ferreira (1986) this species is found from Talara, Peru (04°34'S; 81°16'W) to Punta Tumbes, Bahía de Concepción, Chile (36°49'S; 73°03'W), and is limited to the intertidal zone and shallow subtidal, 0–4 m depth, on rocks often exposed to heavy surf.

Remarks. This is one of the largest polyplacophoran in Chile, differing from the also large *Enoplochiton niger* in having conspicuous spines in the girdle, not sparse scales

as in *E. niger*. This species prefers the subtidal zone and wave-exposed shores, and it is often covered with algae and epibionts (*Scurria* species, *Mytilus* species, etc) which allow this species to blend in with its surroundings. The spines are often covered with encrusting algae in older specimens. This is a commercially important species (Osorio 2002).

Genus *Enoplochiton* Gray, 1827

Type species. *Chiton niger* Barnes, 1824, by monotypy.

Enoplochiton niger (Barnes, 1824)

Plate 2, Fig. 1; Table 2

Chiton niger Barnes, 1824: 71, pl. 3, fig. 3. *Enoplochiton niger*: Pilsbry 1893: 14: 252, pl. 52, figs 22–29; Marincovich 1973: 43, fig 99. *Acanthopleura nigra*: Ferreira 1986: 266, figs 106–111 and 113–N.

Description. Animal very large in size, up to 190 mm in examined specimens. Tegmentum dark chocolate-brown, shiny, but easily eroded. Anterior valve with 4–6 concentric, zig-zagged furrows. Lateral areas elevated, well defined by strong round rib at diagonal line, with zig-zagged furrows as on anterior valve. Central areas well defined, smooth jugum bordered by narrow, depressed area with irregular, short, oblique furrows; para-jugal area smooth; pleural area with longitudinal, parallel furrows, not usually reaching anterior border of valve. Girdle thick, muscular; dorsal surface dark brown, conspicuously dotted with light brown scales, scales irregular in size (larger in middle

1/3 of girdle), up to 1.5–2 mm long in specimens 50 mm long (larger in larger specimens), vaguely striate, usually eroded at upper edge, clearly separated from each other by area as wide as scale; on outer 1/5 of girdle, scales much smaller, shorter, dark brown, erect, spine-like; girdle surface completely covered otherwise with minute, dark brown, lanceolate spicules, up to 100 µm long, 25 µm thick. Girdle bridges, empty in middle third, but crowded with small, dark brown spiculoid elements (akin to those on girdle proper) in outer thirds (After Ferreira 1986).

Material examined. Specimens found exposed on large boulders in the surf-zone, in Playa Rodillo, Playa El Pulpito (MPCCL 3072014E, 1 specimen) and in Norte Bahía de Caldera.

Distribution. This species is confined to the western temperate coast of South America, from Talara, Peru (04°34'S; 81°16'W) to Coquimbo Bay, Chile (29°57'S; 71°20'W). Its bathymetric range is limited to the intertidal zone (Ferreira 1986).

Remarks. With sizes up to 200 mm (Sanhueza et al. 2008), this is one of the largest polyplacophoran species in the country. It lives almost exclusively in exposed rocks or in the surf zone. Although this species is mostly herbivore, it has been described also as a generalist polyphagous consumer, and a potential omnivorous, (Sanhueza et al. 2008). A brown-colored variety of the limpet species, *Scurria variabilis* (Sowerby, 1839), lives on the valves of this species, having been found in all the specimens examined in this study. An unidentified barnacle was also observed on the valves of a few specimens. In some places (Rodillo beach, Obispito bay; Table 1) juvenile specimens can be found among crevices of large boulders. It was observed that this species is preyed by the common gull, *Larus dominicanus* (Lichtenstein, 1823), an omnivore species that also preys on the intertidal large keyhole limpets of the genus *Fissurella* (Bahamondes & Castilla, 1986).

Family Chitonidae Rafinesque, 1815

Subfamily Chitoninae Rafinesque, 1815

Genus *Chiton* Linnaeus, 1758

Type species. *Chiton tuberculatus* Linnaeus, 1758, by subsequent designation.

Chiton (Chiton) cumingsii Frembly, 1827

Plate 1, Fig. 5; Table 2

Chiton cumingsii Frembly, 1827: 198, suppl. pl. 16, fig. 3;

Dall 1909: 247. *Chiton cumingsii*: Reeve, 1847, pl. 1, figs 2a, b; Plate 1902: 46, pl. 3, figs 179–184, pl. 4. *Chiton cumingi*: Pilsbry 1893: 164, pl. 30, figs 29–31. *Chiton (Amaurochiton) cumingsii*: Bullock 1988: 166, figs 59–63, 69, 74 and 77.

Description. Animal of large size, reaching almost 60 mm in length in examined specimens. Anterior valve straight; post-mucronal slope of posterior valve slightly concave. Shell color yellowish white with concentric brown bands crossing lateral triangle longitudinally, then proceeding antero-medially over ribs of central area. Girdle light olive green or pinkish-brown. Interior of shell white with some dull green in posterior depression (After Bullock 1988).

Material examined. Specimens found in all the rocky shore stations (except Playa Rodillo and Norte Bahía de Caldera). Collected under rocks and rock slabs, Sur de Playa Brava (MZUC 39613, 1 specimen).

Distribution. Marincovich (1973) cites this species from Paita (05°05'S; 81°06'W), Peru to Puerto Montt (41°28'S; 72°56'W), Chile.

Remarks. This colorful species is the most common and abundant chiton distributed in the zone; found in almost all the locations. It is commonly found in accumulations of several individuals on the underside of rocks at low tide, crawling quickly to the dark if exposed to sunlight. Among the examined specimens, some of them had a pink/orange coloration when juveniles with some adult specimens retaining a uniform pink coloration. This species has been cited as an introduced species in Las Palmas Port, Canary Islands (28°06'N, 15°25'W), being one of the few alien polyplacophoran found in European waters (Arias and Anadón 2013).

Chiton (Chiton) granosus Frembly, 1827

Plate 1, Fig. 6; Table 2

Chiton granosus Frembly, 1827: 200, suppl. pl. 17, fig. 1; Plate 1902: 56, pl. 4, fig. 190; Pilsbry 1893: 167, pl. 30, figs 27, 28; Dall 1909: 247. *Chiton (Chiton) granosus*: Marincovich 1973: 43, fig. 98. *Chiton (Chondroplax) granosus*: Bullock 1988: 185, figs 96, 97, 103, 140, 141, 143, and 144; Osorio 2002: 56.

Description. Animal of large size, up to 45 mm in examined specimens. Intermediate valves often eroded and rather flat. Anterior valve convex, post-mucronal slope straight. Mucro moderately blunt; centrally located on posterior valve. Jugal tract smooth, central areas with somewhat beaded longitudinal ribs. Lateral triangle barely raised; low, broad, nodular rib extends along diagonal line. Often a few other radiating rows of nodules appear

on lateral triangle. Terminal areas with 10–12 radiating rows of widely spaced nodules. Color of tegmentum nearly totally dark brown to greenish brown, with occasional streaks of cream white on jugal and central areas. Girdle black. Interior of valves white with dull blue muscle scars and reddish brown on posterior slope of callus (After Bullock 1988). According to Osorio (2002) this species is gonochoric, like almost all other chiton species that have been studied. It can reach a maximum length of 80 mm.

Material examined. Specimens found in Playa El Pulpo, Norte de Bahía de Caldera, Playa Mansa and Sur de Bahía de Caldera, in crevices in large rocks, often in surf zone in large colonies. Playa el Pulpo (MPCCL 3072014D, 1 specimen).

Distribution. Marinovich (1973) gives the northernmost distribution for this species at Paita (05°05'34"S; 81°06'07"W), Peru. Osorio et al. (2005) records the southernmost record of this species at Boca del Guafo (43°39'S; 74°00'W), Region of Aysén, southern Chile.

Remarks. This species is somewhat uncommon in shallower waters; it is found mostly in crevices and in rocky outcrops, mostly in clustered distributions. Juvenile specimens are somewhat similar to the juvenile specimens of *Chiton cumingsii* differing in the paler coloration (of various shades of green), the granulation on the valves and in the overall wider body. It has been reported that this species feeds on barnacle cyprids (Moreno and Jaramillo 1983, Aguilera 2005) and is preyed on by the common gull *Larus dominicanus* (Lichtenstein, 1823). It was observed also that some specimens had barnacles on the valves. This species is a physiological omnivore, having the digestive flexibility and enzymatic capacity to digest and assimilate animal preys (Camus et al. 2009) and it is also a commercially important species (Osorio 2002).

Chiton (Chiton) magnificus Deshayes, 1827

Table 2

Chiton (Chiton) magnificus Deshayes, 1827: 454. *Chiton magnificus*: Pilsbry 1893: 160, pl. 30, figs 23, 24; *Chiton (Amaurochiton) magnificus magnificus*: Bullock 1988: 163, figs 52–54, 57, 58, 64, 65, 68, 72, 73 and 76. *Chiton magnificus*: Schwabe et al. 2006: 9, figs 7, 8 and 15. A more detailed bibliography and synonymy can be found in Bullock (1988: 163).

Description. Animal of large size, reaching 115 mm in examined specimens. Body dark bluish-grey, broad-oval, slightly carinated, rather flat. Valves flattened to moderately carinated. Anterior valve slightly convex, semicircular, with wide V-shaped to straight posterior margin unnotched in middle, with numerous radially arranged, shallow ribs; intermediate valves rectangular with slight-

ly concave posterior margin at both sides of faintly protruding apex, lateral areas slightly elevated, sculptured with up to 5 radial ribs between a wider diagonal ridge and a very wide posterior rib; tail valve semicircular with an anterior mucro; post-mucronal area with same sculpture as head valve and lateral areas (After Schwabe et al. 2006). According to Osorio (2002), this species can reach a maximum length of 174 mm.

Material examined. Specimens found in Aguas Verdes, Sur de Playa Ramada and in Playa Chorrillos, in subtidal areas attached to large boulders.

Distribution. Bullock (1988) gives a distribution for this species from Isla San Lorenzo, Peru south to Bahía Tictoc (43°36'40"S; 72°57'15"W), Chiloé Province, southern Chile. This species can be found in rock pools and boulder fields with strong water exchange, from the intertidal down to a maximum of 30.5 m depth at the Comau Fjord (42°23'S; 72°27'W), Region of Aysén (Schwabe et al. 2006). Smith and Ferreira (1977) considered the records of this species from Galapagos Islands as erroneous.

Remarks. A shiny, large and conspicuous chiton, this species has been overlooked in recent molluscan literature, being cited by Valdovinos (1999) as *Chiton latus* and by Osorio (2002) as *Chiton magnificus boweni*. It seems to be an uncommon species, restricted to specific localities along the coast of Chile. Juvenile specimens may be misidentified as *Chiton cumingsii*, differing from this species in having a wider and flatter body, with smoother sculpture and with bright blue spots on the valves, which are cream white to greenish yellow in color. Apparently, in northern Chile this species is found only in subtidal areas. This is a commercially important species (Osorio 2002).

Genus *Radsia* Gray, 1847

Type species. *Chiton barnesii* Gray, 1893 by monotypy.

Radsia barnesii (Gray, 1828)

Plate 1, Fig. 2; Table 2

Chiton barnesii Gray, 1828: 5; Reeve 1847: pl. 1, sp. 1. *Chiton (Radsia) barnesii*: Pilsbry 1893: 190, pl. 29, figs 10–12; Dall 1909: 247. *Chiton barnesii*: Plate 1899: 59, pl. 4, fig. 191; Leloup 1956: 46. *Radsia barnesii*: Bullock 1988: 282, figs 2,4,6,7, 11–13, 15, 31, 32. A more complete synonymy in Bullock (1988: 282)

Description. Animal of medium size, reaching a length of 28 mm in the examined specimens. Anterior valve straight; post-mucronal slope of posterior valve straight to slightly concave. Valves quite flat. Jugal region smooth;

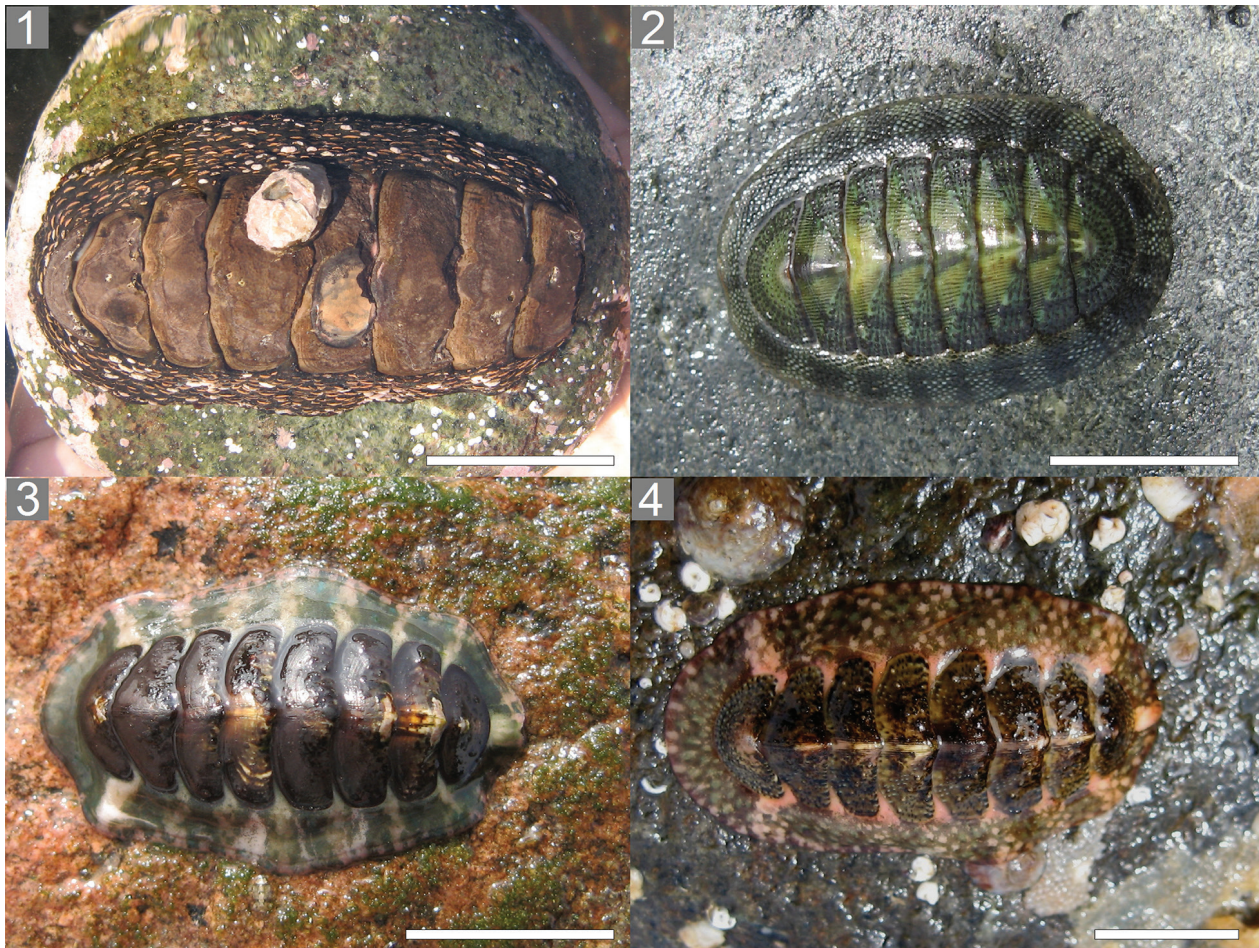


Plate 2. *Chiton* species photographed in situ; **1.** *Enoplochiton niger*, Isla Playa Ramada, 123 mm; **2.** *Radsia barnesii*, Sur Playa Ramada, 22 mm; **3.** *Tonicia atrata*, Sur de Playa Brava, 30 mm; **4.** *Tonicia chilensis*, Playa Mansa, 32 mm. Scale bars are: 1 cm for 2 and 4, 2 cm for 3 and 4 cm for 1.

central area with numerous uneven longitudinal ribs. Lateral triangle barely raised, with 5–7 irregular nodules. Shell color cream white with reddish brown splotches on central areas, irregular longitudinal dark reddish brown bands on lateral triangles, and occasional dark reddish brown on jugum. Girdle light greenish brown with faint trace of alternating lighter bands in some specimens. Interior of valves white (After Bullock 1988).

Material examined. Specimens found in three locations; Peninsula Calderilla, Sur de Playa Ramada and in Playa El Pulpo Beach (Table 1). Collected under rocks and rock slabs, Peninsula Calderilla (MZUC 39614, 1 specimen).

Distribution. Bullock (1988) cites this species from Coquimbo (29°58'S; 71°21'W), to the Chonos Archipelago (45°0'0"S; 74°0'0"W), Chile. The present record (at 27°S) is now the northernmost record for this species.

Remarks. This species was uncommon in the zone under study; only a few specimens were found in the undersides of rocks at low tide. This species is clearly identified from the other species found in this work by having a wide, flat shell, with narrower valves and a pattern of clear and

darker alternating bands in the girdle. It can be misidentified as *Chiton granosus*; differing from this species in the smaller size, the much smaller girdle scales, a much weak valve sculpture and in the alternating bands of the perinotum, absent in *Chiton granosus*.

Family Chitonidae

Subfamily Toniciinae Pilsbry, 1893

Genus *Tonicia* Gray, 1827

Type species. *Chiton chilensis* Fremby, 1827, non De Blainville 1825 (= *Chiton chilensis* Fremby, 1827), by subsequent designation (Gray 1847: 168).

Tonicia atrata (G.B. Sowerby II, 1840)

Plate 2, Fig. 3; Table 2

Chiton atratus G.B. Sowerby II, 1840: 294. *Tonicia atrata* Aldea & Valdovinos, 2005: 368, Table 1, fig.

5I; Schwabe et al. 2006: 12, figs 9, 18; Gordillo and Schwabe 2009: 267, fig. 2D. A more detailed synonymy can be found in Kaas and Van Belle (1998: 25).

Description. Animal of medium to large size, reaching 51 mm in examined specimens. Shell elongate-oval, moderately elevated, subcarinated dorsum. Color reddish brown to blackish purple. Head valve semicircular, with straight posterior valve margin unnotched in middle; intermediate valves broadly rectangular, with distinct protruding apex and concave posterior valve margins. Lateral area hardly elevated, but clearly indicated by faint depression in front of diagonal ridge. Jugal area weakly developed, but showing partly a more or less distinct keel, especially in the more posterior intermediate valves. Tail valve with centrally situated, forward-directed, and slightly elevated mucro, straight antemucronal area and rather steep, straight postmucronal slope. Jugal area of tail valve extending towards anterior. Tegmentum without sculpture, except for growth marks and faint radial striations on terminal valves and lateral areas. Perinotum wide and fleshy (After Schwabe et al. 2006).

Material examined. Specimens collected in a single location; Playa Mansa, in submerged rocky platform (Table 1), MPCCL 011928A, 1 specimen.

Distribution. According to Reid and Osorio (2000), this species distributes in Chile between 40°S and 54°S, at Tierra del Fuego and around the Falkland Islands. The species ranges in depth from the low eulittoral to a depth of 36 m (Schwabe et al. 2006). The record presented here (at 27°S) is now the northernmost record for this species.

Remarks. Two specimens of this species were found in a single location; among a community of *Tonicia chilensis*, from which it distinguishes in attaining larger sizes and in having a darker body and almost smooth valves with minute granulation at the sides. It is interesting to note also that the valves of the examined specimens were widely separated, almost as in *Tonicia disjuncta* (Frembly, 1827). The presence of this species extends considerably the northernmost record of this species in about 1040 km (from 40°S to 27°S).

Tonicia chilensis (Frembly, 1827)

Plate 2, Fig. 4; Table 2

Chiton chilensis Frembly, 1827: 203, pl. 17, fig. 6; Reeve 1847: pl. 4, f. 19. *Tonicia elegans* Subspecies *chilensis*: Pilsbry 1893: 196, pl. 41, figs 22–24, pl. 42, figs 31–35. *Tonicia chilensis*: Gordillo and Schwabe 2009: 269, fig. 2E, F. A more complete synonymy can be found at Kaas and Van Belle (1998: 45).

Description. Animal of medium to large size, reaching 43 mm in examined specimens. Shell elongate-oval, not

much elevated, the dorsal ridge rounded, side-slopes straightened. Color umber-brown at the sides, becoming chestnut in the middle, delicately and peculiarly speckled and blotched and streaked with buff or buff-white. Lateral areas hardly raised, but separated from the central areas by an obtuse diagonal ridge bearing a series of low tubercles, sometimes subobsolete; sculptured with subradiating rows of small granules, and showing a band of irregularly placed black eyes on the forward part. Central area of second valve having in the middle, a keel or a group of lirae; central areas of the other valves having a narrow smooth dorsal band with several longitudinal furrows on each side of it; and at the sides there are longitudinal diverging delicate rows of granules. End valves radially sub-granulate, and crowded with eye-spots subradially arranged (After Pilsbry 1893).

Material examined. Specimens found on rocks at low tide in Aguas Verdes, Sur de Playa Ramada, Playa Mansa (MPCCL 3072014F, 1 specimen), Sur Bahía de Caldera and in Calderilla.

Distribution. According to Reid and Osorio (2000) this species distributes in Chile and Peru between latitudes 12° and 54°S. It has a bathymetric range from 0–28 m (Schwabe et al. 2006).

Remarks. This species has large and colorful mantles and plates of variable shades, which are similar to the encrusting calcareous algae commonly found in the rocky coasts. Due to the high diversity of forms, several synonyms have been described (see Kaas and Van Belle 1998), and this species needs a complete revision according to Schwabe et al. (2006). This species was found only in the lower intertidal to the subtidal areas, especially in protected locations.

Discussion

Schwabe and Sellanes (2010) reported 41 species of chitons from Chilean waters. Our results from the Region of Atacama, with eleven species found, accounts for 27 % of those reported species. All of the species occurring in the area have distributions in the southeastern Pacific Ocean, from Peru to southern Chile, with *Calloplax vivipara*, *Radsia barnesii* and *Tonicia atrata* as the only species endemic to the Chilean coast. The polyplacophoran diversity of the Region of Atacama is thus comparable to that described for southern areas of Chile, including central Chile (Aldea and Valdovinos 2005), the Comau fjord (Schwabe et al. 2006) and the Estero Elefantes and Laguna San Rafael areas (Osorio and Reid 2004), from where a similar diversity of this molluscan class has been recorded (with eleven, nine and nine species, respectively). With the exception of *Callistochiton pulchellus*, all of the species found in the Region of Atacama also occur in central and southern Chile.

All of the studied species can be classified in two main groups according to their habitat; species with a higher relative frequency on exposed areas include the very large species *Acanthopleura echinata* and *Enoplochiton niger*. The other group includes species associated with protected intertidal areas: *Callistochiton pulchellus*, *Calloplax vivipara*, *Chiton cumingsii*, *Chiton granosus* (mostly found in rock fissures and crevices) and *Radsia barnesii*. *Chiton magnificus* was found in the Region of Atacama only in subtidal areas, always near large boulders in hold-fast communities of the giant kelp *Lessonia nigrescens*. *Chiton magnificus*, however, is much more common in central and southern Chile, being found mostly in intertidal areas (Osorio 2002). The small-bodied species, *Callistochiton pulchellus* and *Calloplax vivipara*, were always restricted to submerged rocks in the bottom of tidal pools. This last habitat may explain the feeding behaviour of these small species, living over encrusting sponges and calcareous algae. Regarding feeding preferences; most of the large species of chitons from the Region of Atacama should have generalist diets, however it is possible that the smaller species have more specific diets, for example feeding in sponges, algal species, diatoms or barnacles.

The new distribution records of *Callistochiton pulchellus*, *Radsia barnesii* and *Tonicia atrata* and the new record of *Calloplax vivipara* may reflect the lack of sampling in the Atacama region or in northern Chile in general, where the scientific studies on invertebrates are still lacking. In particular, *Callistochiton pulchellus* and *Calloplax vivipara* may be more widespread in the country; however their particular habitat (and small adult size) may prevent their sampling by traditional methods. Some of these species may have also been overlooked or misidentified as juvenile specimens of other chiton spe-

cies (for example *Radsia barnesii* as *Chiton granosus*). The considerable new range extension of *Tonicia atrata* found in this study may reflect the current complicated, unresolved status of the genus *Tonicia* in Chile; the revision of some particular species or species-groups is thus imperative, considering the great diversity in the valve and mantle morphology, which has derived in a large synonymy for some species, for instance for *Tonicia chilensis* (Schwabe et al. 2006).

The absence of other species, for example those cited by Valdovinos (1999) in the last complete revision of the Chilean mollusks (which have been traditionally considered as having distribution records in northern Chile), including *Acanthochitona hirudiniformis* (Sowerby, 1832), *Acanthopleura granulata* (Gmelin, 1791), *Chaetopleura benaventei* Plate, 1902, *Chaetopleura hennahi* (Gray, 1828), *Ischnochiton imitator* (Smith, 1881), *Ischnochiton (Ischnochiton) punctulatissimus* (Sowerby in Broderip & Sowerby, 1832) or *Ischnochiton pusio* (Sowerby, 1832) may be explained because the sampling activities in the Region of Atacama were restricted to, at most, sublittoral areas (2 m depth). Deep water areas must definitely harbor more unrecorded or undescribed species, as is the case with other invertebrate groups like sponges (Reiswig and Araya 2014) or stony corals (Araya et al. in prep.). It is, then, very probable that the number of chitons known from the Region of Atacama, or northern Chile in general, will increase with larger collecting efforts, including additional sampling methods such as dredges and samples from greater depths, even subtidal waters (incorporating also the bycatch of the commercial deep water fisheries). Like other zones of Chile, the deep water areas off Caldera (or off northern Chile in general) have not been investigated in detail and could yield interesting results.

Identification key

This key is primarily macroscopic (intended for identification of adult specimens) including external characters as shell features and general girdle features.

- | | | |
|----|--|---|
| 1 | Whitish or cream colored chiton, of small size (up to 14 mm)..... | 2 |
| 1a | Animal of green, brown, pink or black coloration..... | 3 |
| 2 | Animal bright whitish in color, with 10–16 radial ribs on head valve, with rounded depressions on the lateral areas of the valves | <i>Callistochiton pulchellus</i> (Gray, 1828) |
| 2a | Animal whitish-cream in color, with about nine radial ribs on head valve, with longitudinal riblets in the lateral areas... | <i>Calloplax vivipara</i> (Plate, 1902) |
| 3 | Girdle naked or covered with small scales or by blunt spines | 4 |
| 3a | Girdle covered by hairs, which can be also found between the valves, fleshy girdle | <i>Chaetopleura peruviana</i> (Lamarck, 1819) |
| 4 | Girdle covered by visible round scales, in neat rows..... | 5 |
| 4a | Girdle fleshy, naked or with sparse spines | 8 |
| 5 | Valves visible granulose, often eroded and rather flat, with two white fringes on the central areas of the valves, terminal areas with 10–12 radiating rows of widely spaced nodules, girdle black | <i>Chiton granosus</i> Frembly, 1827 |
| 5a | Valves striated in the middle, central valves narrow | 6 |
| 6 | Valves carinate, of green, light brown or pink-yellowish color, girdle with alternating bands of color..... | <i>Chiton cumingsii</i> Frembly, 1827 |
| 6a | Valves rather flat, olive green to black | 7 |

- 7 Girdle with alternating pale and dark bands, central valves with uneven longitudinal ribs, color olive green, size small (up to 35 mm) and rather flat..... *Radsia barnesii* (Lesson, 1828)
- 7a Girdle black, valves flattened with central areas with fine longitudinal lirae, color dark green to nearly black, with tiny blue points, size up to 174 mm..... *Chiton magnificus* Deshayes, 1827
- 8 Girdle naked, ample, decorated with green and pink spots, plaques with variegated colouration..... 10
- 8a Girdle muscular, covered by blunt spines or lanceolate spicules..... 9
- 9 Girdle covered by blunt spines, anterior valve with some ten radial rows of rounded granules, valves usually encrusted with algae *Acanthopleura echinata* (Barnes, 1824)
- 9a Girdle covered with irregularly-sized scales, anterior valve with 4-6 concentric, zig-zagged furrows, valves often eroded *Enoplochiton niger* (Barnes, 1824)
- 10 Valves sculptured with minute granulation, central areas with a narrow smooth dorsal band or a group of lirae, with an obtuse diagonal ridge bearing a series of low tubercles..... *Tonicia chilensis* (Frembly, 1827)
- 10a Valves almost smooth; only sculptured by growth marks and faint radial striations on terminal valves and lateral areas *Tonicia atrata* (G. B. Sowerby II, 1840)

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First record of *Pareiasmopus setiger* Chevreux, 1901 from Singapore, including synonymization of *Pareiasmopus siamensis* Wongkamhaeng, Coleman & Pholpunthin, 2013 with *Pareiasmopus setiger* (Crustacea, Amphipoda, Maeridae)

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Abstract

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Key Words

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Pareiasmopus setiger has been widely described from tropical to subtropical regions from Philippine Islands, Sulu Sea, Indonesia, Australia, north Indian Ocean and the Seychelles by several authors. The present study provides detailed descriptions of *Pareiasmopus setiger* Chevreux, 1901 (Crustacea: Amphipoda) based on newly collected specimens from Pulau Hantu, Singapore. Morphological characters of the specimens closely resemble those of *Pareiasmopus setiger* and *Pareiasmopus siamensis* Wongkamhaeng, Coleman & Pholpunthin, 2013. The specimens of both the species were quite similar to the Singapore specimens, although the shapes of appendages vary with growth and locality; therefore, *P. siamensis* is synonymized with *P. setiger*. The following species characteristics for *P. setiger* are indicated: 1) antenna 1 peduncle with 2 setae; 2) male gnathopod 2 propodus palm transverse; 3) Pereopods 5 to 7 posterior margins with long slender setae; and 4) dorsal carina pattern for pereonite 7 and pleonites 1 to 3.

Introduction

Few works have been published on amphipods from Singapore and most are a century old. These works include Stebbing (1887), Mayer (1903) and Tattersall (1922). The genus *Pareiasmopus* Stebbing, 1888 belongs to the family Maeridae Krapp-Schickel, 2008, with species typically occurring in the Indo-West Pacific (Hughes 2009). To date only three species, *Pareiasmopus suluensis* (Dana, 1853), *P. setiger* Chevreux, 1901 and *P. dancaui* Ortiz & Lalana (1997) are recognized with certainty from the Southeast Asian waters. Australia and the adjacent waters have the largest number of recorded taxa within this genus with seven species altogether namely, *Pareiasmopus*

aumogo Hughes, 2011, *P. cymatilis* Lowry & Hughes, 2009, *P. echo* Barnard, 1972, *P. poorei* Hughes, 2009, *P. sowpigiensis* Lowry & Springthorpe, 2005, *P. suensis* (Haswell, 1879), and *P. ya* Barnard, 1972.

Materials and methods

This study was based on material collected in July 2013, from the shallow-water coral reef habitats of Pulau Hantu, Singapore (Fig. 1). Samples were collected using artificial substrates (mesh bath netting) that were laid amongst corals and were then carefully transferred into plastic containers. Material was fixed in 10% buffered formalin. In the labo-

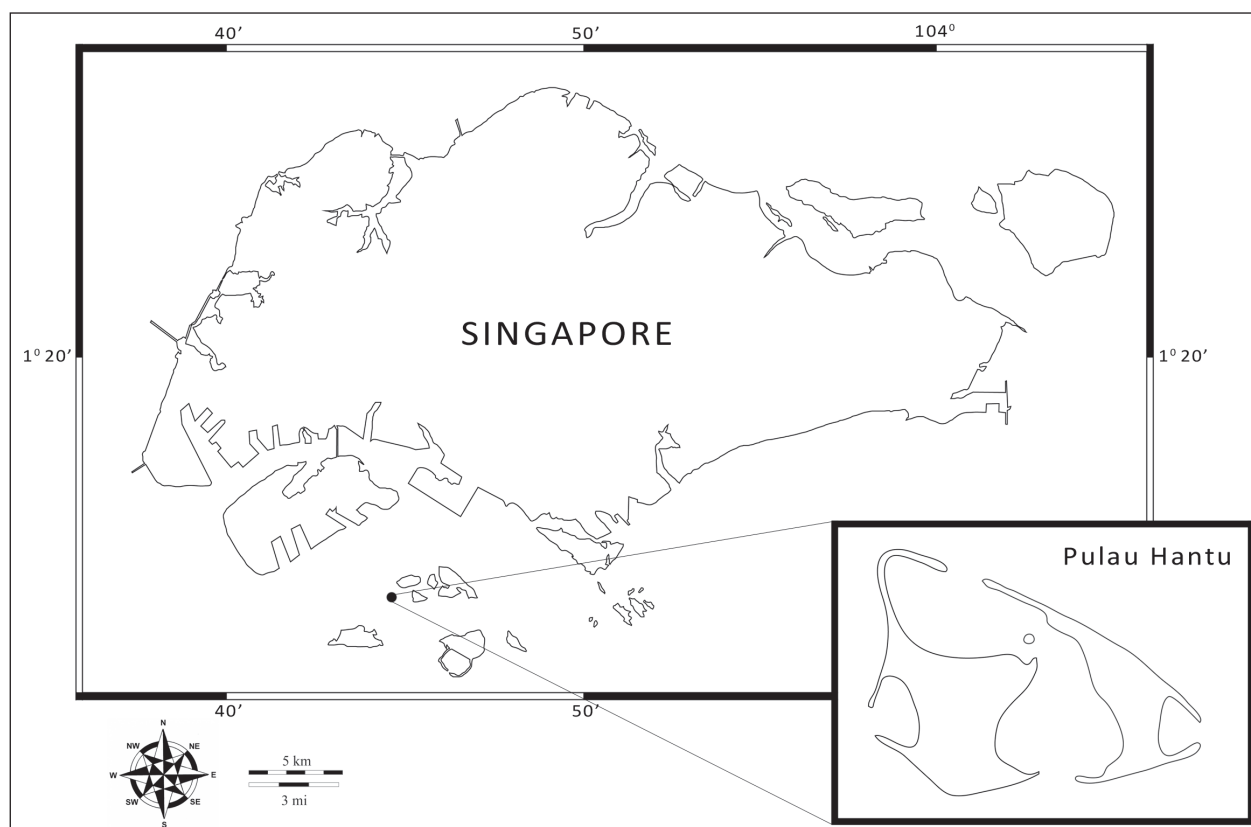


Figure 1. Pulau Hantu, Singapore.

ratory, amphipod specimens were sorted and preserved in 70% alcohol. The specimens were examined under a compound microscope and later selected for dissection. Specimens were introduced into increasing concentrations of glycerol before dissection was carried out in an excavated glass block with glycerol as a medium. Dissected parts were then permanently mounted in 100% glycerol. Dissections and mounting of specimens were carried out in glycerol. The appendages of the dissected specimens were examined using an Olympus SZ30 and figures were produced using an Olympus CH20 Leica light microscope with a camera lucida. All illustrations were digitally 'inked' following Coleman (2003). Setae and mouthparts are classified following Watling (1989). The following abbreviations are used: A, antenna; G, gnathopod; HD, head; LL, lower lip; MD, mandible; MX, maxilla; MP, maxilliped; P, pereopod; EP, epimeron; T, telson; U, uropod; UR, urosome; UL, upper lip; R, right; L, left; ♂, male; ♀, female. All material is lodged with the Universiti Kebangsaan Malaysia Muzium Zoologi (UKMMZ).

Systematics

Suborder Senticauda Lowry & Myers, 2013
Maeridae Krapp-Schickel, 2008

***Parelasmpus* Stebbing, 1888**

Type species. *Megamoera suensis* (Haswell, 1879).

Diagnosis. *Head* with notch on cheek. *Mandible* mandibular palp 3-articulate, article 2 much shorter than article 1, article 3 straight, not setiferopectinate. *Urosomite 1* with pair of dorsal carinae. *Uropod 3* rami length subequal to peduncle; *Epimeron 3* posteriorly serrate on lower margin. (After Hughes 2011)

Species composition. *Parelasmpus* includes 13 species: *P. albidus* (Dana, 1853); *P. aumogo* Hughes, 2011; *P. cymatilis* Lowry & Hughes, 2009; *P. echo* J.L. Barnard, 1972a; *P. dancaui* Ortiz & Lalana, 1997; *P. mallacootaformis* Ledoyer, 1984; *P. poorei* Hughes 2009; *P. setiger* Chevreux, 1901; *P. sowpigensis* Lowry & Springthorpe, 2005; *P. suensis* (Haswell, 1879); *P. suluensis* (Dana, 1852); *P. ya* J.L. Barnard, 1972 and *P. zelei* Ledoyer, 1983.

***Parelasmpus setiger* Chevreux, 1901**

Figures 2–9

?*Megamoera suensis* Haswell, 1880c: 335–336, pl. 21: fig. 5.

Megamoera suensis. – Miers 1884: 317–318.

Megamoera haswelli Miers, 1884: 318 [name in text].

Not *Megamoera suensis*. – Haswell 1885: 103–104, pl. 15: figs 1–4 [= *Maera hamigera* (Haswell) fide Stebbing, 1906, but see Stebbing, 1910a: 600].

Elasmpus suensis. – Stebbing 1906: 442–443.

Parelasmpus setiger Chevreux, 1901: 412–418, fig. 32–39.

Parelasmpus suluensis. – Chilton 1922: 7–8, fig. 3 [not Dana].

?*Parelasmpus suluensis*. – Walker 1904: 278, pl. 6: fig. 3 [?not Dana]

Parelasmpus siamensis Wongkamhaeng, Coleman & Pholpunthin, 2013: 525–532, figs 19–24.

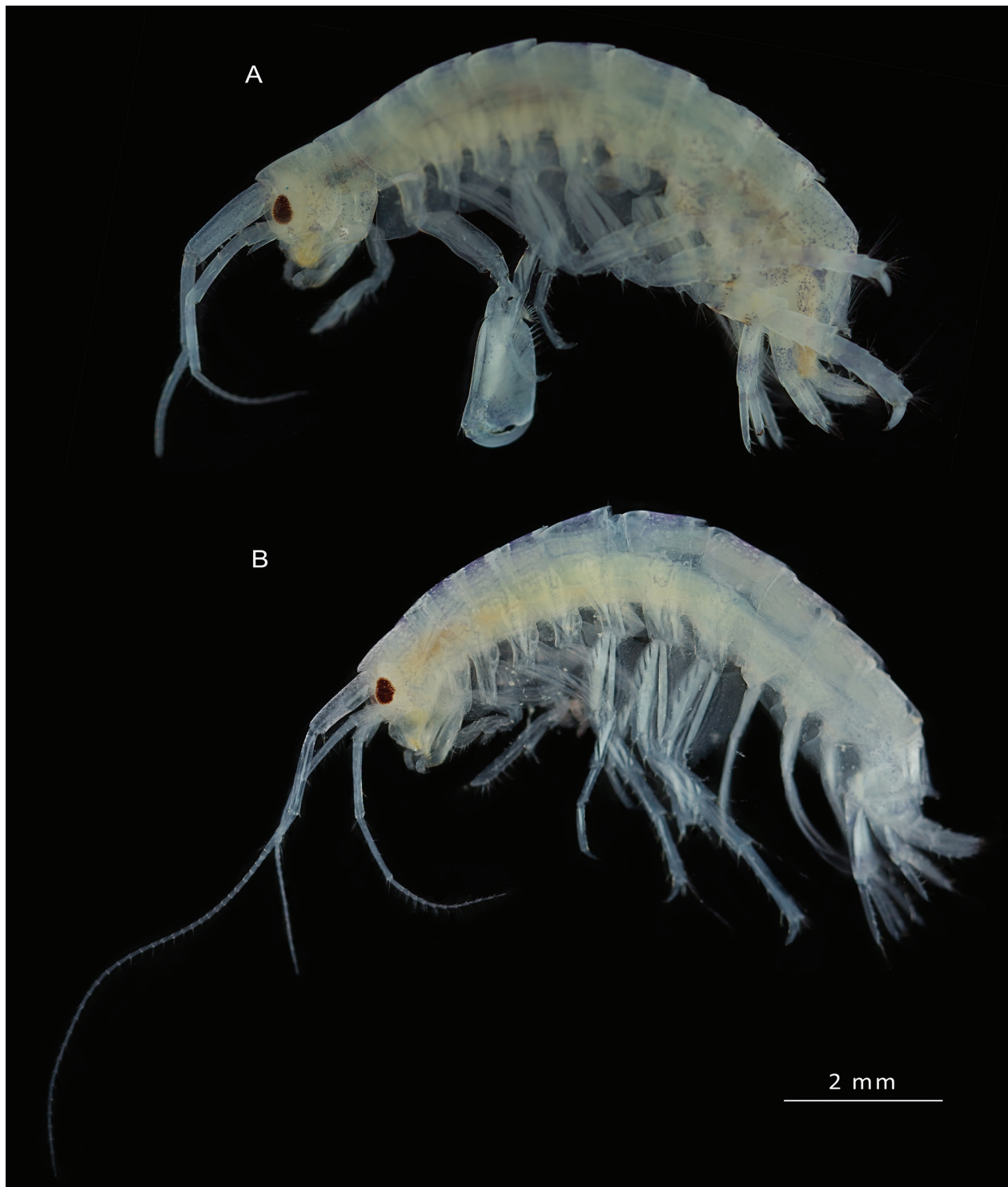


Figure 2. *Parelasmopus setiger* Chevreux, 1901, **A.** male, 10.3 mm, UKMMZ-1527; **B.** female, 9.8 mm, UKMMZ-1528. Pulau Hantu, Singapore. Scale 2 mm.

Material examined. – 1 male, 10.3 mm, UKMMZ-1527, shallow water coral habitat of Pulau Hantu, Singapore, 1°13'37.9"N, 103°44'27.6"E, mesh bath netting, 5 m, coll. E.A. Ali, Tan, Y.K. and Lee, A.C., 26 November 2013: 3 males; 1 female; 2 juveniles, UKMMZ-1529, same station data.

Type locality. Port Of Victoria, Mahé, Seychelles.

Description. Based on male, 10.3 mm, UKMMZ-1527.

Head. Head slightly longer than pereonites 1–2 combined; rostrum small; lateral cephalic lobe broad, moderately produced, anteroventral margin with notch/slit; eyes well developed, ovate. *Urosomite 1–3* serrated dorsally. *Antenna 1* longer than antenna 2; peduncular article 1 subequal to article 2, with 2 robust setae along posterior margin, ventrodistal margin with 1 group of robust setae

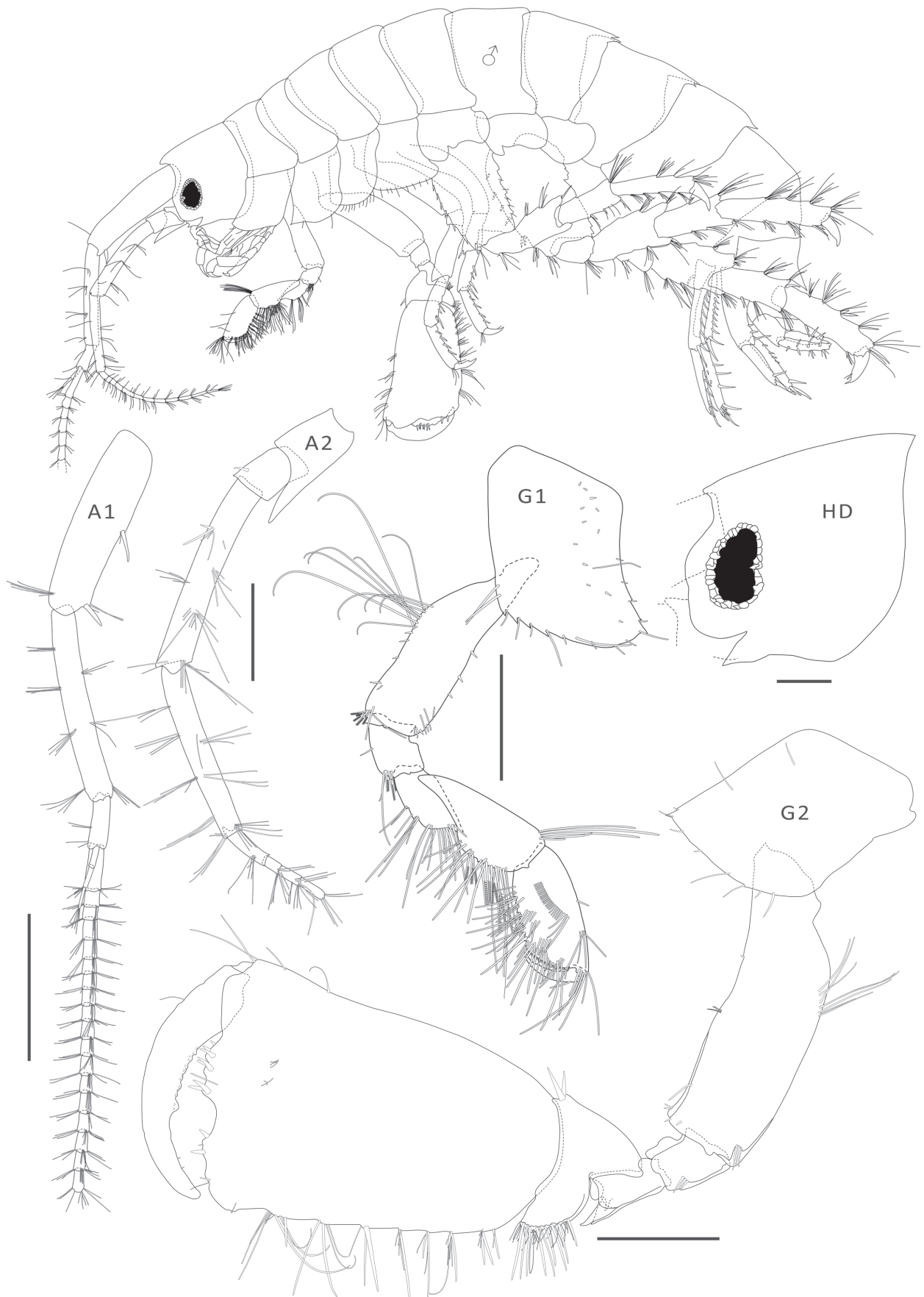


Figure 3. *Pareiasmopus setiger* Chevreux, 1901, male, (UKMMZ-1527), 10.3 mm. Pulau Hantu, Singapore. Scale for **A1** = 0.01 mm; **A2** = 0.005 mm; **HD** = 0.5 mm; **G1** = 0.05 mm; **G2** = 0.005 mm.

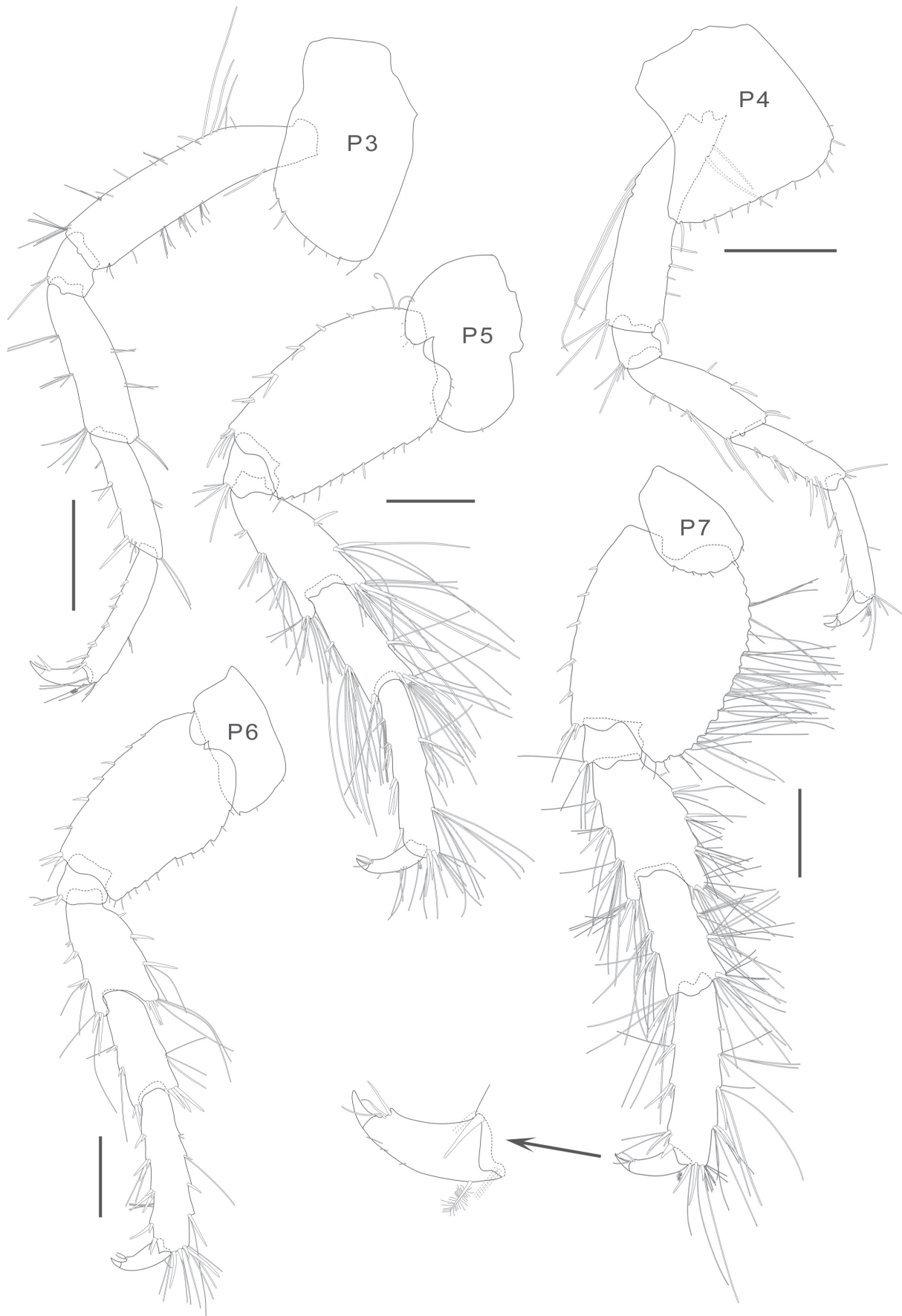


Figure 4. *Parelasmopus setiger* Chevreux, 1901, male, (UKMMZ-1527), 10.3 mm. Pulau Hantu, Singapore. Scale for **P3** = 0.005 mm; **P4** = 0.5 mm; **P5** = 0.5 mm; **P6** = 0.5 mm; **P7** = 0.005 mm.

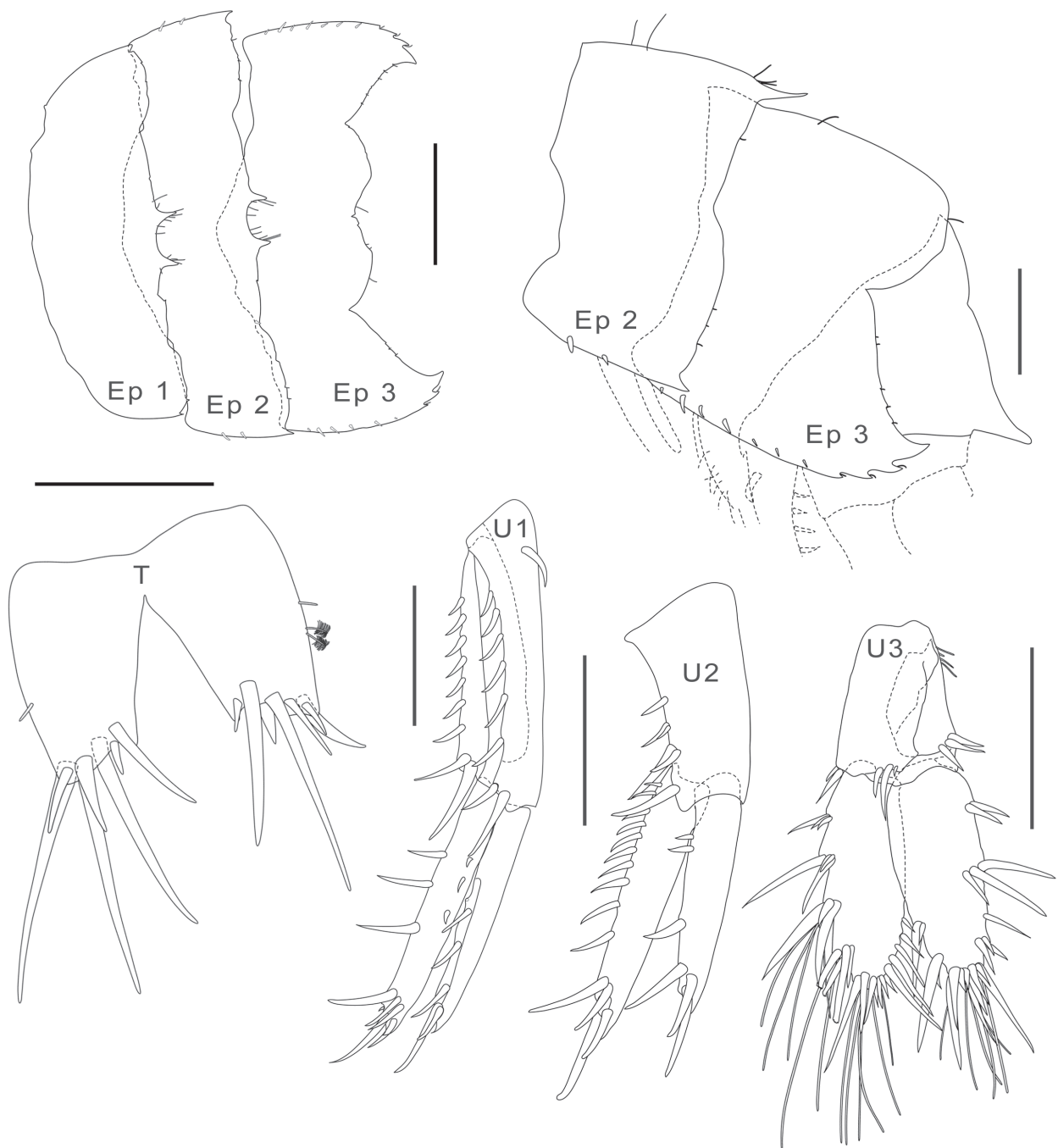


Figure 5. *Parelasmpopus setiger* Chevreux, 1901, male, (UKMMZ-1527), 10.3 mm. Pulau Hantu, Singapore. Scale for EP = 1 mm; U1 = 0.5 mm; U2 = 0.5 mm; U3 = 0.5 mm; T = 0.025 mm.

and 2 fine setae; article 2 with several fine setae along both margins; flagellum articles broader than long, with 18+ articles (broken); accessory flagellum minute, with 3 plus one rudimentary article. *Antenna 2* peduncular article 2 cone gland reaching beyond peduncular article 3; article 4 longer than article 5; flagellum with 11 articles. *Upper lip* semicircular, pubescent. *Lower lip* outer lobes with two pairs of ducts, mandibular lobes apically subacute. *Maxilla 1* inner plate subtriangular, with 2 apical plumose setae; outer plate armed with 6 serrate robust setae, facial side with row of 5 serrate robust setae; palp biarticulate, article 1 shorter than article 2, article 2 with

6 thick setae terminally. *Maxilla 2* outer plate slightly broader than inner plate; inner plate armed with 13 mostly long setae from distal end to inner half margin; outer plate with 10 setae only on apex. *Mandible* (left), incisor armed with 4 teeth; lacinia mobilis serrate apically; accessory setal row well developed and composed of 4 setae and 1 broad plate; molar process well developed, tritritative, provided with 2 plumose setae and 1 stout seta; mandibular condyle well developed; palp triarticulate, article 1 distally swollen, article 2 short almost 2.5 times as long as article 3, article 3 and apically provided with 1 couple of long setae.

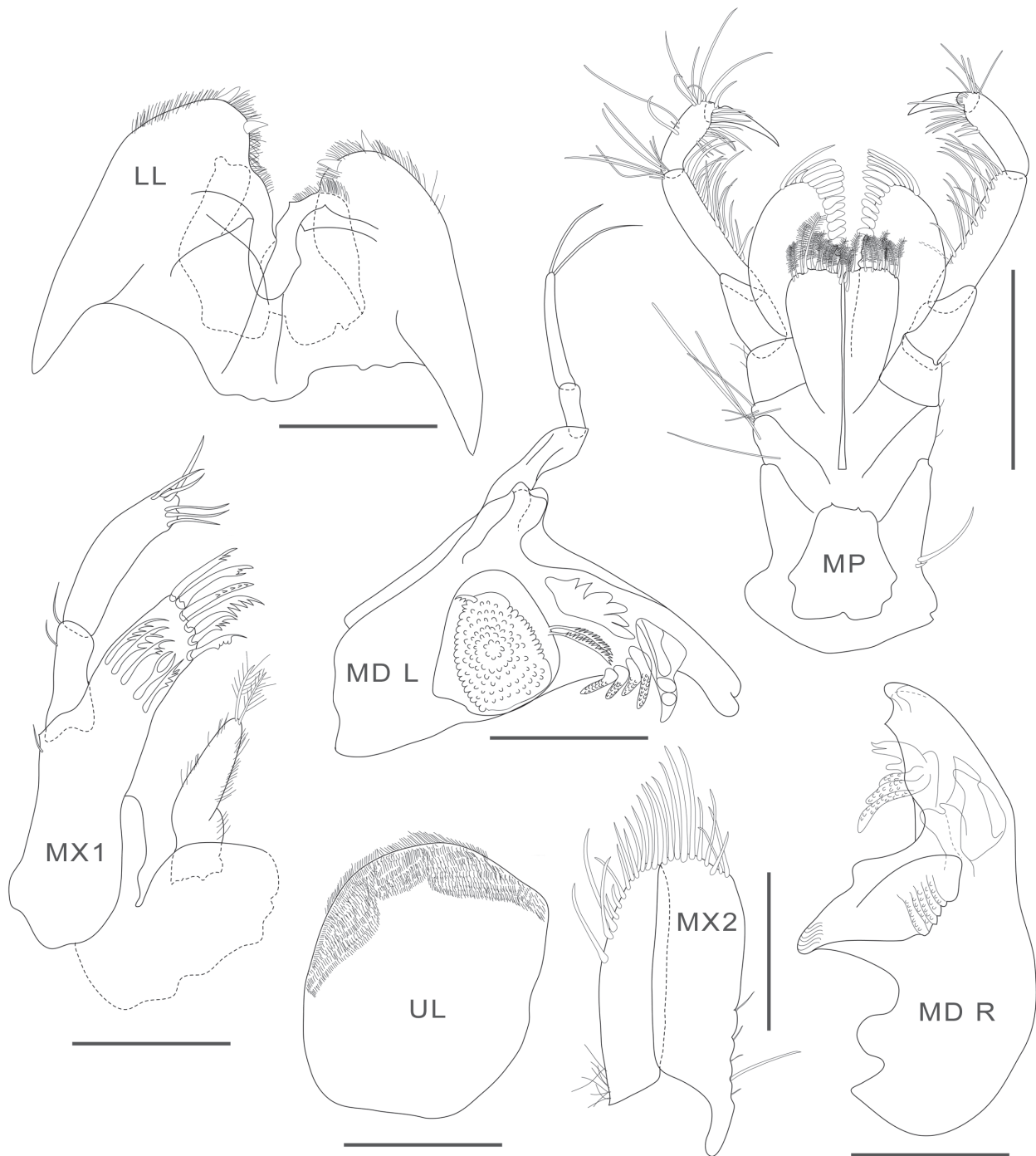


Figure 6. *Parelasmopus setiger* Chevreux, 1901, male, (UKMMZ-1527), 10.3 mm. Pulau Hantu, Singapore. Scale for UL, LL, MX1, MX2, MD(R), MD(L), = 0.25 mm; MP = 0.5 mm.

Pereon. *Gnathopod 1* smaller than gnathopod 2; coxa 1 anterior margin concave, produced forward anteroventrally, posteroventral corner notched; basis anterior margin straight with 3 short robust setae along the margin, posterodistally provided with several plumose setae, posterior margin with several long setae on mid length; ischium subcylindrical, about 33% as long as basis, posterodistally provided by 3 plumose and 2 medium length setae; merus slightly longer than ischium with a row of short and long setae on distal half; carpus as long

as propodus, anterodistally with 3 long and 2 short setae, medial surface with rows of pectinate setae; propodus medial surface with comb, palm convex defined by 1 pronounced spine, marginally provided with about 7 bifid small spines and many minute setae; dactylus falcate, overlapping palm.

Gnathopod 2 coxa 2 subquadrate, posteroventral corner notched; basis slender with slight excavation along anterior margin, anterodistal corner subquadrate, posterior margin with medium length setae on mid length;

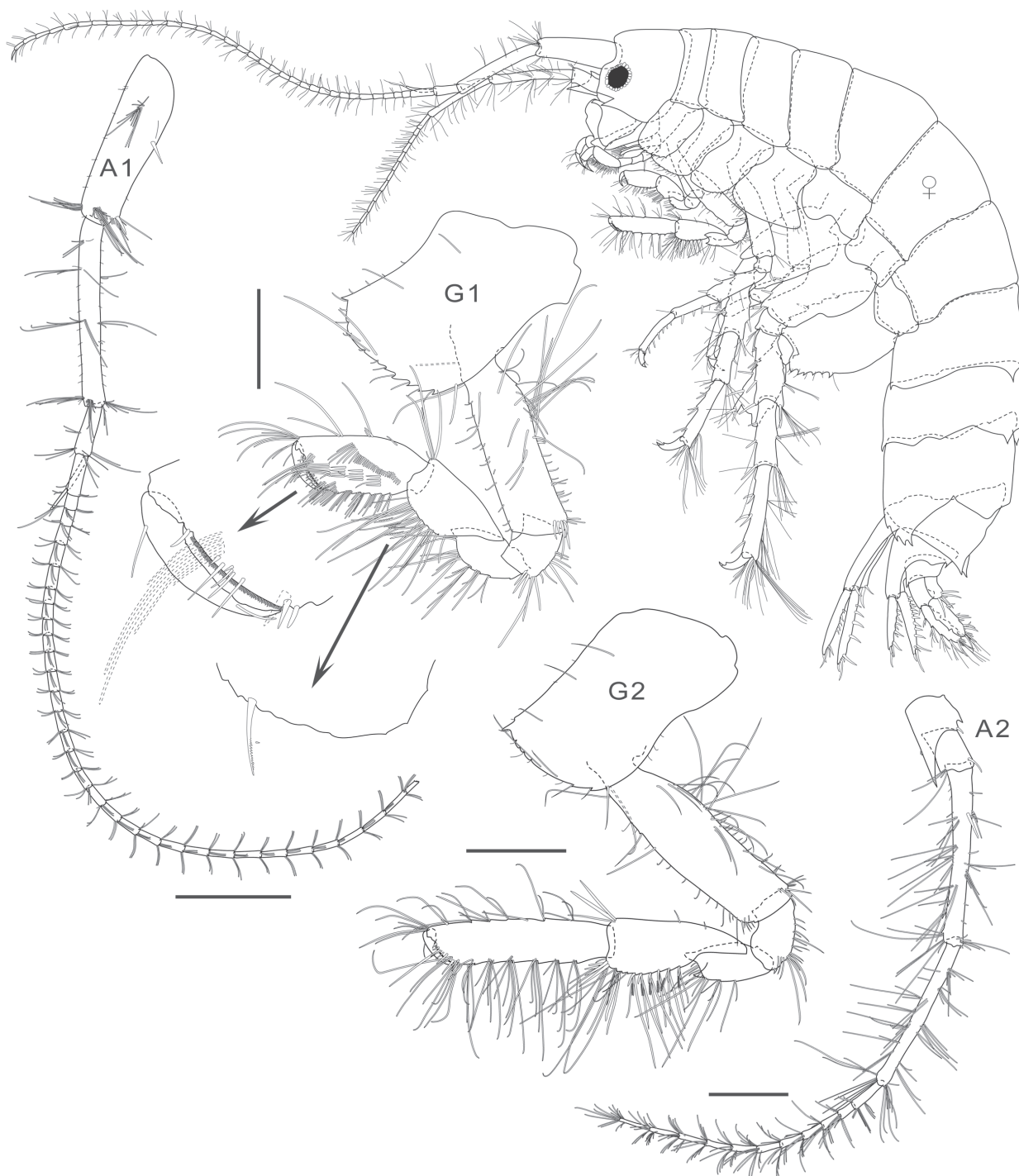


Figure 7. *Pareiasmopus setiger* Chevreux, 1901, female, (UKMMZ-1528), 9.8 mm. Pulau Hantu, Singapore. Scale for **A1** = 1 mm; **A2**, **G1**, **G2** = 0.5 mm.

merus acutely produced distoventrally; carpus compressed, subtriangular, posterior expansion densely setaceous in rows, anterodistally with 2 stout setae; propodus expanded and subrectangular, posterior margin with thick setae, palm transverse, defined by 9 robust setae along the palmar margin, deeply concave medially; dactylus falcate, with crenulated posteroproximal shelf.

Pereopods 3–4 *coxa 3* produced forward on ventral half part of anterior margin. *coxa 4* broader than deep,

posteroventral lobe well developed, with subrectangular posteromedial corner. *Pereopods 3–4* similar except for pereopod 3 shorter; carpus posterodistally provided with 2 or more prominent robust setae; propodus posteriorly provided with row of short robust setae. *Pereopods 5–7* *coxae* concave, both anterodistally and posterodistally, basis slightly expanded, posterior margin crenulate, without long slender setae, except for pereopod 7; merus and carpus not broadened; carpus and propodus with,

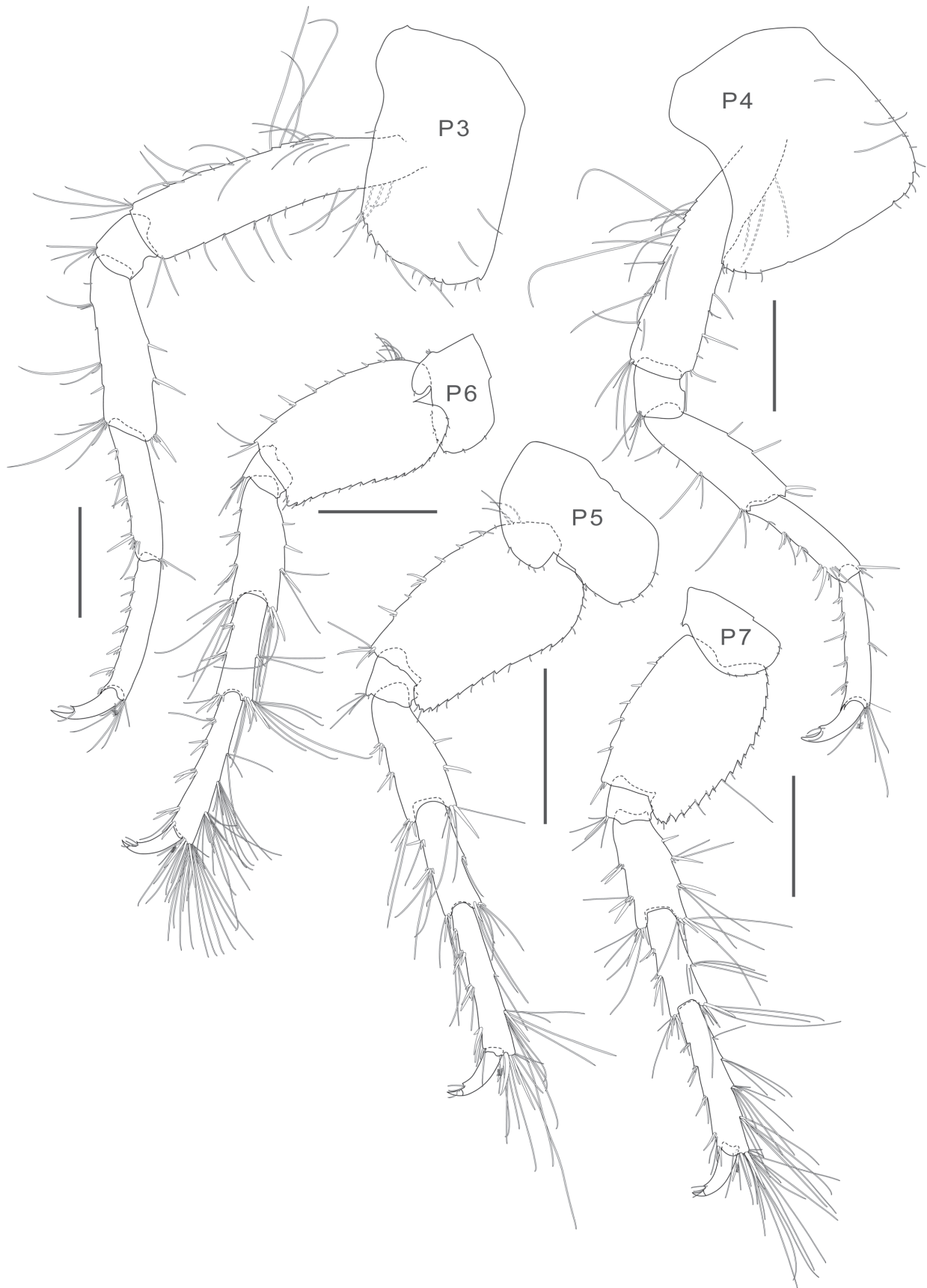


Figure 8. *Parelasmopus setiger* Chevreux, 1901, female, (UKMMZ-1528), 9.8 mm. Pulau Hantu, Singapore. Scale for **P3**, **P4** = 0.5 mm; **P5**, **P6**, **P7** = 1 mm.

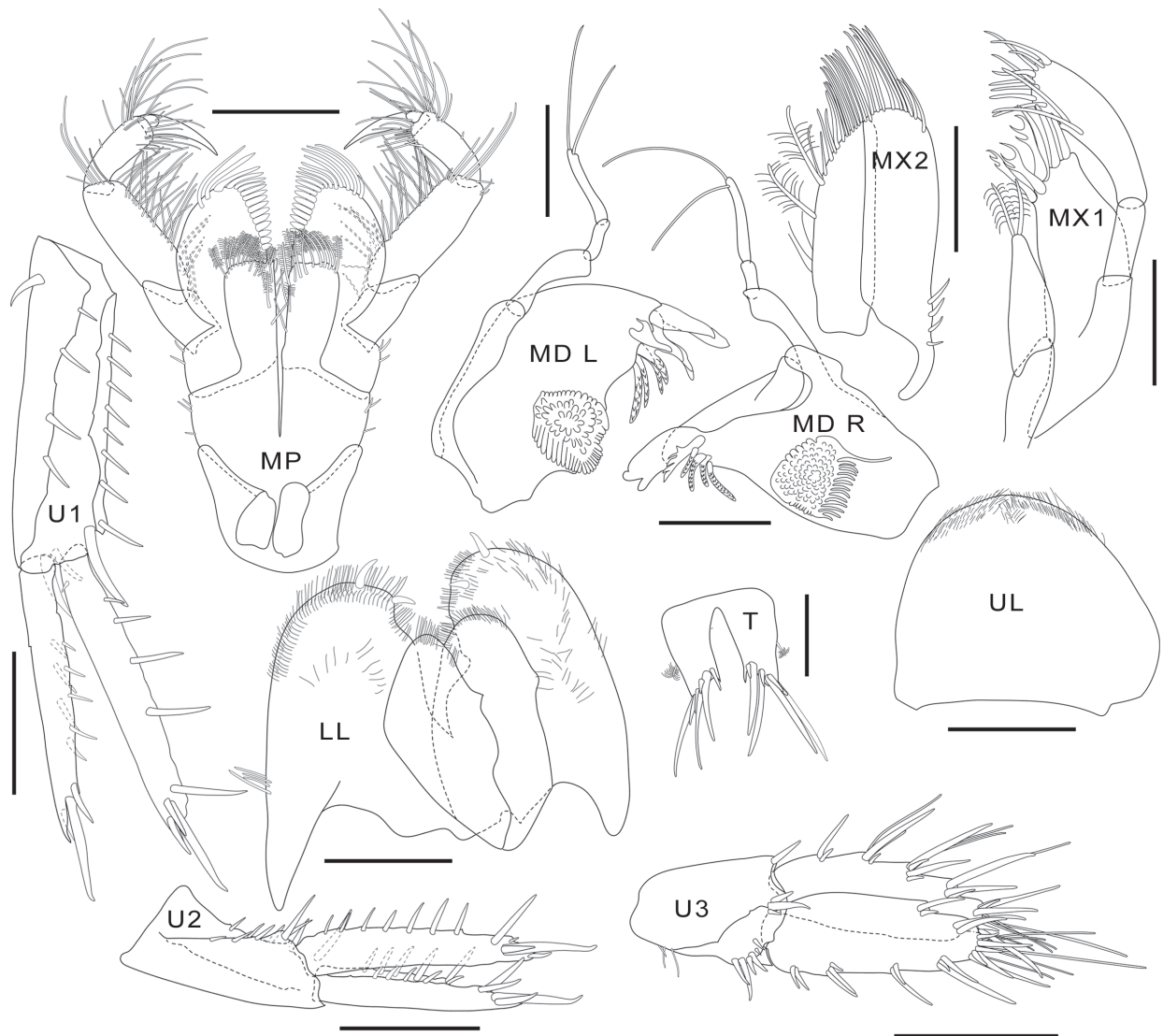


Figure 9. *Pareiasmopus setiger* Chevreux, 1901, female, (UKMMZ-1528), 9.8 mm. Pulau Hantu, Singapore. Scale for UL, LL, MX1, MX2, MD(R), MD(L), MP, T = 0.25 mm; U1, U2, U3 = 0.5 mm.

slender setae along posterior margin; propodus not expanded posterodistally; dactylar ungues simple.

Urosome. *Urosomite 1–3* dorsally bicarinate. *Epimeron 1–3* posteroventral corner with small acute spine. *Epimeron 3* ventral margin serrate distally, posteroventral margin serrate below posteroventral corner, posteroventral corner with strongly produced acute spine. *Uropod 1* extending beyond peduncle of uropod 3; peduncle longer than rami, outer-ventrodistally provided with 1 robust seta, upper margin with 8 inner and 9 outer robust setae; rami subequal, truncate, apically provided with 1 pronounced and 2 robust setae, outer ramus with 3 outer robust setae, inner ramus with 4 outer small setae and 3 inner median robust setae. *Uropod 2* not extending beyond peduncle of uropod 3; peduncle shorter than rami, upper-marginally provided with 5 median robust setae, 1 inner-distal robust seta; rami subequal, truncate, outer ramus provided with 4 median robust setae, 1 distal robust seta and 1 apical robust seta, inner ramus provided

with 10 inner median and 3 inner distal robust seta, and 1 apical robust seta. *Uropod 3* peduncle 33% as long as outer ramus, provided with 2 outer, 3 inner and 2 distal robust setae; rami foliaceous, both rami distally truncated to subacute, with long and short apical robust setae. *Telson* broader than long, small, 5/6 cleft, each lobe with slight ridges on central line, with 7 distal robust setae.

Female (dimorphic characters). Based on female, 9.8 mm, UKMMZ-1528.

Gnathopod 2 carpus relatively long about, 1.5 times as long as wide, slightly lobate; propodus linear, almost five times as long as broad, without distomedial shelf; dactylus apically subacute.

Remarks. Chevreux (1901) described *Pareiasmopus setiger* from Port of Victoria, Mahé, Seychelles. His description was based on a male of 7 mm body length, with figures of a lateral view, mandible, maxilliped, accessory flagellum of antenna 1, gnathopods 1 and 2, uropod 3

and telson. In Barnard (1972), he recorded the occurrence of *P. setiger* from the Philippine Islands and discussed the possible occurrence of *P. setiger* that include tropical Australia, Indonesia and the northern Indian Ocean. He also pointed out the difficulty in working with the Indo-Pacific *Parelasomus*, due to growth stage and historic identification being mixed. Barnard identifies *P. albidus*, *P. setiger*, *P. suluensis* and *P. suensis* in particular as requiring revision before further progress can be made. Hughes (2011) identification of *P. cf. suensis* restates this problem (p77).

Both Chevreux's (1901) and Barnard's (1972) figures of the species are similar to ours, antenna 1 peduncle with 2 setae, male gnathopod 2 propodus palm transverse with posteroproximal elevation with 6 robust setae, pereopods 5 to 7 posterior margins with long slender setae and the dorsal carina pattern for pereonite 7 and pleonites 1 to 3. Thus, our male specimen agrees well with the original description of Chevreux (1901), except for a few minor differences, such as the serrated robust setae on the inner surface of the outer plate of maxilla 1. However, this could possibly be the next developing stage of the new growth (internal growth of next instar) of a maxilla 1. Additionally, our female specimens are observed without paired dorsal carina in pereonite 7.

The recently described *P. siamensis* Wongkamhaeng et al. (2013) has close resemblance to our specimens. As both *P. siamensis* and our specimen is considered to be in their terminal adult stage, they share the same form of the gnathopod 2 palmar margin with posteroproximal elevation with 6–7 robust setae, the midposterior toothed dactylus and the serration on coxa 1–3. Therefore *P. siamensis* Wongkamhaeng et al (2013) is here synonymized with *Parelasomus setiger* Chevreux (1901). Until now the species was recorded from Seychelles, Philippine Islands, Sulu Sea, Indonesia, Australia, north Indian Ocean, Gulf of Thailand and Singapore. The present records confirm this distribution.

The present comparison suggests that further taxonomic studies on this species group are necessary. Detailed drawings and descriptions provided in this study could aid in eliminating further confusion within the *P. setiger* complex, including and thus establish its definitive characteristics.

Distribution. Seychelles, Philippine Islands, Sulu Sea, Indonesia, Gulf of Thailand, Australia, north Indian Ocean and Singapore (current study).

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Systematics and ecology of *Oligodon sublineatus* Duméril, Bibron & Duméril, 1854, an endemic snake of Sri Lanka, including the designation of a lectotype

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Abstract

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The description of *Oligodon sublineatus* Duméril, Bibron & Duméril, 1854 was based on two syntypes located at Paris Natural History Museum (MNHN). The larger specimen (SVL 254 mm) was described in detail, but erroneously labelled as originating from the Philippines, the second specimen (SVL 150 mm) was labelled as originating from ‘Ceylan’ (=Sri Lanka). The smaller specimen, up to this point, has always been considered as the holotype by monotypy. Since recognising the larger specimen in the collection of MNHN as a syntype, we hereby designate it as the lectotype of *Oligodon sublineatus* and redescribe comprehensively both syntypes. *Oligodon sublineatus* (SVL 152–310 mm) has 130–161 ventral scales, 23–42 divided subcaudals, a divided anal plate, a loreal, seven supralabials, and 1+2 temporals. Furthermore, we provide a detailed account of the distribution and natural history of this widely distributed Sri Lankan endemic snake.

Introduction

The colubrid genus *Oligodon* Fitzinger, 1826 is currently known to include 75 valid species (Uetz and Hallermann 2014, 1st September 2014). Only four species have been recorded from Sri Lanka: *Oligodon calamarius* (Linnaeus, 1758); *Oligodon arnensis* (Shaw, 1802); *Oligodon taeniolatus* (Jerdon, 1853); and *Oligodon sublineatus* Duméril, Bibron & Duméril, 1854. Following the description of *Oligodon sublineatus* in 1854, this species has since been recorded from various locations in Sri Lanka (Boulenger 1890, 1894; Wall 1921; Smith 1943;

Deraniyagala 1955; Taylor 1953; De Silva 1980; de Silva 1990; Das and de Silva 2005; Somaweera 2006; Green 2010; Green et al. 2010; David and Vogel 2012; Deepak and Harikrishnan 2013; Pyron et al. 2013). The original description of *O. sublineatus* was clearly based on two syntypes, the first and larger of the two having no collector details associated with it, and labelled as coming from the Philippines, obviously in error. The second syntype came from Ceylan (= Ceylon) and was collected by Leschenault according to the original description. The larger specimen (MNHN 3238) has been correctly identified as *O. sublineatus* in the MNHN collections but,

until now, was not recognized as a syntype. However the smaller specimen (MNHN 3239) has been mistakenly considered as the holotype by Wallach et al. (2014). We have identified the large specimen as being one of the syntypes, so we hereby designate it as a lectotype, and redescribe it in detail in order to stabilize that name with a recognised type specimen.

Methods

Museum acronyms follow Sabaj Pérez (2014). Specimens were examined in the collections of the British Museum of Natural History, UK (BMNH); Muséum national d'Histoire naturelle, France (MNHN); Naturhistorisches Museum Basel, Switzerland (NMB); and National Museum of Sri Lanka (NMSL). Morphometric and meristic data for species comparisons were obtained from examined specimens (see Appendix 1). We checked the external morphology of specimens with a Wild M3Z stereomicroscope and photographed them with a Canon EOS 7D SLR digital camera. The map was constructed based on Cooray (1967). The conservation status of the species was evaluated using Red List Categories and Criteria in IUCN Standards and Petitions Subcommittee (2013: version 10.1) to assess their risk of extinction. Sex was determined by ventral tail incision of adult specimens followed by the checking for the presence or absence of hemipenes. All the natural history data were taken from our own field observation notes made during the last ten years.

The following characters were measured with a digital caliper (± 0.1 mm) on the left side of the body for symmetrical characters: eye diameter (ED, horizontal diameter of eye); eye–nostril length (EN, distance between anterior most point of eye and middle of nostril); snout length (ES, distance between anterior most point of eye and snout); nostril diameter (ND, horizontal diameter of nostril); internarial distance (IN, least distance between nostrils); mandible–posterior eye distance (MPE, distance between posterior edge of mandible and posterior most edge of eye); interorbital width (IO, least distance between upper margins of orbits); head length (HL, distance between posterior edge of mandible and tip of snout); head width (HW, maximum width of head); snout–vent length (SVL, measured from tip of snout to anterior margin of vent); tail length (TAL, measured from anterior margin of vent to tail tip). Meristic characters were taken as follows: supralabials and infralabials (SUP and INF, first labial scale to last labial scale bordering gape); costal scales (COS, counted around the body from one side of ventrals to the other in three positions, on one head length behind neck, at mid body and at one ventral scale prior to preanal); when counting the number of ventral scales (MVS), we scored specimens according to method described by Dowling (1951). We counted subcaudal scales (SUB) from first postcloacal scale to the scale before the tip of the tail.

Results

Oligodon sublineatus Duméril, Bibron & Duméril, 1854

Figs 1–3; Tables 1, 2

Remarks. Standard morphometric and meristic data of the two syntypes are presented in Table 1. We hereby recognise two syntypes: the larger specimen (MNHN 3238) and the smaller specimen (MNHN 3239). Uncertainties still exist in *Oligodon* taxonomy and *O. sublineatus* may represent a cryptic species complex in Sri Lanka (see table 2 showing the wide range of subcaudal and ventral counts within *O. sublineatus*), therefore it is necessary to stabilize the name with a recognised lectotype. There are two main reasons for selecting MNHN 3238 as the lectotype: (1) it was used in the original description and its morphometric data has been provided and (2) it is a fully grown, well-developed and well preserved adult specimen in good shape.

Lectotype (here designated). MNHN 3238, adult female collected from the Philippines (mistakenly so in the original description) [from Java (also in error) according to the museum registry] by an unknown collector [by Bosc (in error) according to the museum registry].

Paralectotype. MNHN 3239, sub adult male collected at ‘Ceylan’ [= Sri Lanka] by Leschenault. This specimen was previously erroneously considered as the holotype by Wallach et al. (2014).

Diagnosis. *Oligodon sublineatus* shows sexual dimorphism in scalation (Table 2) and is distinguished from all congeners by the following characters: SVL 152–310 mm; TAL 20.0–42.0 mm; 130–161 ventrals; 23–42 subcaudals (divided); anal plate divided; loreal present; seven supralabials; temporals 1+2; ventral side with three series of dark brown points forming almost continuous stripes, with the middle series of points absent on the tail; dorsal coloration (live or in alcohol) greyish brown, speckled with small elongated spots irregularly placed; posterior part of the jaws has a large, oblique spot extending along the neck posteriorly; dorsally a “^” shaped marking between the eyes, which continues laterally across them; an irregular, brown, transverse band from the frontal to the post-parietal region.

English translation of the original French description in Duméril, Bibron & Duméril (1854: 57). Characters. Ventral side with three series of points forming stripes.

This species is mostly characteristic, as its specific name, by having three black stripes along the ventral side, which are made up of a series of points, meeting together. The two stripes outside the ventral plates form a continuous line up to the ventral surface of the tail, but the central one is made up of distinct points in the centre of the ventral plates. These points are quite large, round and wide posteriorly, and are as notched at the front; the median stripe does not prolongate onto the ventral side of the tail.



Figure 1. A live male of *Oligodon sublineatus* (not collected) at Sinharaja Forest Reserve, Sri Lanka (photo: H. Jayasinghe).

Table 1. Morphometric and meristic characters of *Oligodon sublineatus* lectotype (MNHN 3238) and paralectotype (MNHN 3239).

Character	MNHN 3238 Lectotype (female)	MNHN 3239 Paralectotype (male)
snout–vent length (SVL)	254.0	150.0
tail length (TAL)	35.0	27.0
head length (HL)	10.8	8.1
head width (HW)	4.7	4.1
internarial distance (IN)	2.1	1.5
interorbital width (IO)	3.7	3.3
eye–nostril length (EN)	1.9	1.7
eye–snout length (ES)	3.4	2.7
mandible–posterior eye distance (MPE)	5.8	4.1
nostril diameter (ND)	0.3	0.4
eye diameter (ED)	1.7	1.4
costals (COS)	17·15·15	17·15·15
subcaudals (SUB)	28	36
ventrals (MVS)	150	138
supralabials (SUP)	7 (3, 4 touch eye)	7 (3, 4 touch eye)
infralabials (INF)	8	8

Dorsal coloration grey, speckled with lines or with small elongated spots irregularly placed; however, around the anterior third of the body and laterally, three of those spots appear enlarged with increased width, having a circular border. The spots are constricted central-

ly and have white borders. The posterior section of the jaws has a large, oblique patch along the neck posteriorly where it forms a tip pointing in the opposite direction to the characteristic collar of the first species [note from the translator: *Oligodon sub-quadratum*].

Dorsal scales are very smooth, and are close to each other; they are slightly overlapping, like roof tiles, mostly around the tail area, and in this respect, very skink-like in appearance.

Rostral plate is notched, and crescent shaped; other plates covering the head are large and clearly distinct as in colubrids.

We were only able to examine one well preserved specimen, having no clues as to the origin of the specimen [the Philippines] and the name '*Oligodon torquatus*' appears along with the letter "R" on the jar.

Another specimen, younger and obviously added much later, had a median stripe made up of numerous spots which were less distinct, was collected from Ceylan by Mr. Leschenault. This specimen bears all the characters previously described: the large, brown, post-maxillary mark set posteriorly on the neck forming a croissant shape; with a laterally set, black mark extending onto the anterior third of the body.

We counted 15 scale rows on that specimen, 155 ventrals and 25 subcaudals.

Total length was 180 cm [sic]; among them 155 for SVL and 25 for the tail.

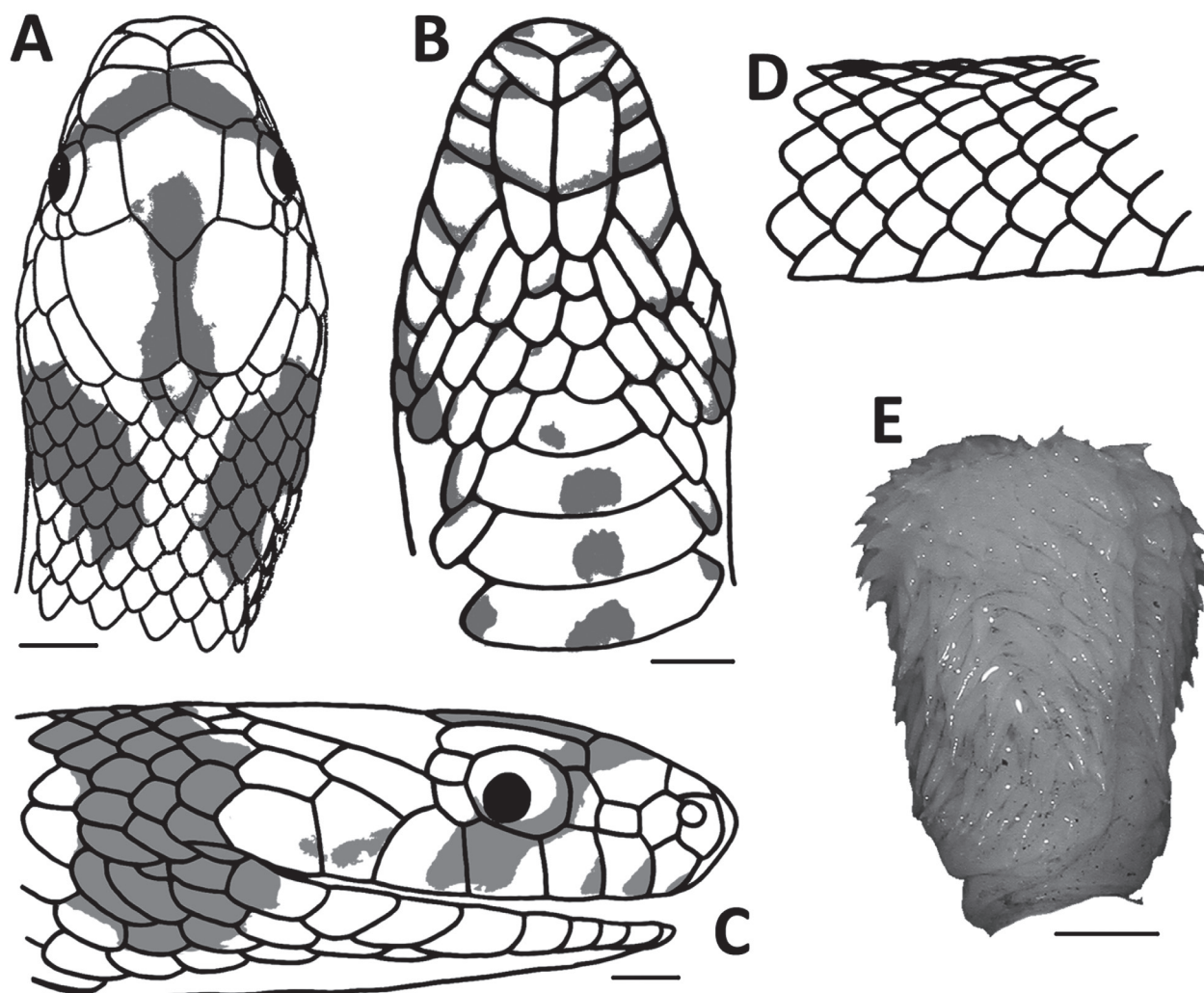


Figure 2. *Oligodon sublineatus* male, NMSL 5161 collected from Nuwara Eliya (1600 m a.s.l.), Sri Lanka: **A** dorsal aspect of head **B** ventral aspect of head **C** lateral aspect of head **D** lateral aspect of midbody **E** dorso-lateral aspect of right hemipenis (scale = 1 mm).

Table 2. Some sexual dimorphic characters of *Oligodon sublineatus* based on examined material. See Methods for abbreviations.

sex	SVL (mm)	TAL (mm)	VEN	SUB
male	152.0–227.0 (n=12)	25.0–38.0 (n=12)	135–151 (n=18)	30–42 (n=18)
female	156.5–295.0 (n=17)	20.0–42.0 (n=17)	145–159 (n=21)	24–29 (n=21)

Description of the designated lectotype, MNHN 3238.

Adult female, SVL 254 mm; tail length 35 mm; head elongate (HL 4.3% of SVL), twice as long as wide (HW 43.5% of HL), slightly flattened, distinct from neck; snout elongate (ES 31.5% of HL), moderate, blunt in dorsal view, rounded in lateral profile, forming an oval shape, rather depressed.

Rostral shield large, hemispherical, distinctly visible from above, pointed posteriorly; interorbital width broad (IO 78.7% of HW); internasals semicircular; nostrils rather large; nasals completely divided by nostrils into two scales unequal in size; anterior nasal larger, in anterior contact with rostral, internasal dorsally, 1st SUP ventrally; posterior nasal in contact with internasal and prefrontal

dorsally, loreal posteriorly, 1st and 2nd SUP ventrally; prefrontal rather large, broader than long, and subhexagonal; frontal large, subhexagonal, elongate posteriorly and longer than its width; supraoculars narrow, elongated, subrectangular, posteriorly wider; parietals large, butterfly wing-like in shape, bordered by supraoculars, frontal, upper postoculars anteriorly, anterior and upper posterior temporals, and six dorso-nuchal scales posteriorly; loreal large, slightly elongated, subrectangular, in contact with prefrontal dorsally and preoculars posteriorly, ventrally only touching the 2nd SUP; one preocular (both sides), vertically elongated, subrectangular, in contact with prefrontal and loreal anteriorly, supraocular dorsally, and 3rd SUP ventrally; eye moderate (ED 15.7% of HL), ellip-

tical, nearly a half of the size of snout length (ED 50% of ES), pupil rounded; two postoculars, upper postocular smaller, quadrangular, contact with supraocular and parietal broad, in narrow contact with anterior temporal; lower postocular crescent in contact with 4th and 5th SUP ventrally, anterior temporal posteriorly; temporals 1+2, elongated, hexagonal; anterior temporal larger and longer than posterior temporals, in contact with parietal dorsally, 5th and 6th SUP ventrally; posterior temporals smaller, lower one in contact with 6th and 7th supralabials ventrally.

Supralabials 7 (on both sides), 4th–7th larger in size; 1st SUP in contact with rostral anteriorly, nasals dorsally, 2nd supralabial with posterior nasal and loreal dorsally, 3rd SUP with preocular and orbit dorsally, 4th SUP with orbit and the lower postocular dorsally, 5th SUP with lower postocular and anterior temporal dorsally, 6th supralabial with anterior temporal and lower posterior temporal dorsally, and 7th SUP with lower posterior temporal dorsally and body scales posteriorly.

Mental of moderate size, triangular; first infralabial pair larger than mental plate and in broad contact with each other, in contact with anterior chin shield posteriorly; eight infralabials, 1st–5th in contact with first chin shield, 5th infralabial largest in size in narrow contact with the anterior chin shield and in broader contact with the posterior chin shield; 6th–8th infralabials in contact with gular scales; two larger anterior chin shields, and two smaller posterior chinshields all in broad contact; posterior chin shield bordered posteriorly by six gular scales.

Body robust, elongate and sub cylindrical; costal scales in 17–15–15 rows, all smooth and bluntly pointed; 150 ventral scales; anal plate divided. Tail comparatively short (TL 13.8% of SVL), robust and thick; subcaudals 28, divided.

Description of the paralectotype, MNHN 3239, and an additional specimen, NMSL 5161. The values of NMSL 5161 (when different) included within parenthesis. Sub adult male (adult male), SVL 150.0 (183.3) mm; head elongate, HL 5.4 (5.6)% of SVL, twice as long as wide, HW 50.6 (53.9)% of HL, slightly flattened, distinct from neck; snout elongate, ES 31.4 (33.3)% of HL, moderate, blunt in dorsal view, rounded in lateral profile, forming an oval shape, rather depressed.

Rostral shield large, hemispherical, distinctly visible from above, pointed posteriorly; interorbital width broader, IO 80.5% of HW; internasals semicircular; nostrils rather large; nasals divided into two scales unequal in size; anterior nasal larger, in contact with the rostral plate anteriorly, internasal dorsally, 1st SUP ventrally; posterior nasal in contact with internasal and prefrontal dorsally, loreal posteriorly, 1st and 2nd SUP ventrally; prefrontal rather large, broad, and subhexagonal; frontal large, subhexagonal, elongate posteriorly and longer than its width; supraoculars narrow, elongated, subrectangular, posteriorly wider; parietals large, butterfly-like in shape, bordered by supraoculars, frontal, upper postoculars anteriorly, anterior and upper posterior temporals, and six

dorso-nuchal scales posteriorly; loreal large, slightly elongated, subrectangular, in contact with prefrontal dorsally, preoculars posteriorly, posterior nasal anteriorly, ventrally just meets the 2nd SUP; one preocular in both sides, vertically elongated, subrectangular, in contact with prefrontal and loreal anteriorly, supraocular dorsally, and 3rd SUP ventrally; eye moderate, ED 17.3 (17.6)% of HL, elliptical, nearly a quarter of the snout length, ED 51.9 (56.2)% of ES, pupil rounded; two postoculars, upper postocular smaller, quadrangular, in contact with supraocular and parietal broad, in narrow contact with anterior temporal; lower postocular crescent in contact with 4th and 5th SUP ventrally, anterior temporal posteriorly; temporals 1+2, elongated, hexagonal; anterior temporal larger and longer than posterior temporals, in contact with parietal dorsally, 5th and 6th SUP ventrally; posterior temporals smaller, lower one in contact with 6th and 7th SUP ventrally.

Supralabials 7 on both sides, 4th–7th larger in size; 1st SUP in contact with rostral anteriorly, nasals dorsally, 2nd SUP with posterior nasal and loreal dorsally, 3rd SUP with preocular and orbit dorsally, 4th SUP with orbit and the lower postocular dorsally, 5th SUP with lower postocular and anterior temporal dorsally, 6th SUP with anterior temporal and lower posterior temporal, and 7th SUP with lower posterior temporal dorsally and body scales posteriorly.

Mental moderate, triangular; first infralabial pair larger than mental and contact with each other broad, in contact with anterior chin shield posteriorly; eight infralabials, 1st–5th in contact with first chin shield, 5th infralabial largest in size in narrow contact with anterior chin shield and contact with posterior chin shield broad; 6th–8th infralabials in contact with gular scales; two larger anterior chin shields, and two smaller posterior chinshields all in broad contact; posterior chin shield bordered posteriorly by six gular scales.

Body robust, elongate and sub cylindrical; costal scales in 17–15–15 rows, all smooth and bluntly pointed; 138 (142) ventral scales; anal plate divided. NMSL 5161 has an everted hemipenis covered by lobes, non-bifurcated, slightly clavate; base naked; *sulcus spermaticus* single and deep; spinous ornamentation present on each lobe, shorter spines at the apex; apex not divided into segments (Fig. 2E); tail comparatively short, TL 18.0 (20.5)% of SVL, robust and thick; subcaudals 36 in both specimens, divided.

Distribution. This species has never been recorded outside of Sri Lanka, hence we here restrict *terra-typica* to Sri Lanka. Wall (1921), Smith (1943), Deraniyagala (1955), De Silva (1980), de Silva (1990), Das and de Silva (2005), Somaweera (2006), Karunarathna and Amarasinghe (2010, 2011, 2012), Botejue and Wattavidanage (2012), and Karunarathna et al. (2010, 2013) recorded this species from Bellanwila–Attidiya, Beraliya, Colombo, Galle, Gammaduwa (Knuckles), Kitulgala, Kotmale, Kukulugala, Matugama, Nilgala, Peradeniya, Ratnapura, Veyangoda, Welimada, and Yatiyantota (Fig. 3). In addition to the above locations, during our

fieldwork operations of the last decade we have recorded (not collected) *O. sublineatus* from a 10–1600 m altitude range, including all vegetational zones of Sri Lanka: Ambalangoda (6°14'42.35"N, 80°03'44.56"E), Anuradhapura (8°20'46.43"N, 80°25'43.77"E), Atwel-tota (6°31'33.87"N, 80°18'12.02"E), Baduraliya (6°30'53.70"N, 80°13'41.81"E), Bibile (7°10'58.02"N, 81°13'43.61"E), Chilaw (7°35'11.49"N, 79°49'16.54"E), Deniyaya (6°20'11.54"N, 80°34'10.44"E), El-pitiya (6°17'39.31"N, 80°08'44.78"E), Eluwankulama (6°20'11.54"N, 80°34'10.44"E), Gampaha (7°05'03.68"N, 79°58'25.66"E), Habarana (8°11'12.43"N, 80°50'17.89"E), Horana (6°42'24.74"N, 80°03'02.77"E), Illukkumbura (Knuckles) (7°35'46.09"N, 80°46'14.10"E), Kalutara (6°35'13.29"N, 80°58'21.49"E), Kaneliya (6°12'37.49"N, 80°24'04.60"E), Kegalle (7°14'10.26"N, 80°19'57.27"E), Kottawa-Homagama (6°47'07.00"N, 79°57'52.17"E), Kurunegala (7°30'25.80"N, 80°23'46.95"E), Kuruwita (6°46'29.02"N, 80°22'35.50"E), Maharagama (6°50'52.54"N, 79°55'45.54"E), Mahiyanganaya (7°20'06.03"N, 81°00'34.51"E), Matara (5°57'08.63"N, 80°31'59.74"E), Monaragala (6°52'40.25"N, 80°20'27.39"E), Naula (7°44'18.42"N, 80°43'38.22"E), Nugegoda (6°51'35.26"N, 79°53'08.19"E), Panadura (6°42'42.76"N, 79°54'24.44"E), Pidurutalagala (7°01'08.11"N, 80°47'23.47"E), Polonnaruwa (7°56'15.64"N, 81°01'15.38"E), Puttalam (8°02'42.88"N, 79°51'38.84"E), Rakwana (6°28'03.23"N, 80°36'32.84"E), Ritigala (8°12'35.71"N, 80°35'02.78"E), Sinharaja (6°24'59.18"N, 80°24'28.33"E), Tanamalwila (6°27'00.66"N, 81°09'07.66"E), Tissamaharamaya (6°16'52.45"N, 81°16'41.40"E), Trincomalee (8°35'57.38"N, 81°10'15.73"E), Udawalawe (6°26'48.46"N, 80°52'26.25"E), Wasgomuwa (7°43'23.36"N, 80°58'06.01"E), Wilpattu (8°30'51.13"N, 79°57'44.67"E), Yagirala (6°22'47.13"N, 80°10'23.93"E) (see Fig. 3 for the distribution map).

The result of the application of the IUCN (2013) B2 a, b (iii) Red List criteria shows that *O. sublineatus* as Least Concern (LC): recorded from an altitude range of 10–1600 m in all vegetation zones of Sri Lanka. Its area of occupancy is 6,000 km², and its extent of occurrence is 40,000 km².

Natural history. A nocturnal snake, sometimes active during day time. Temperature, humidity, and light intensities for daytime activity were respectively measured at 24.8–27.2 °C, 67–82%, and 38–365 lux, based on 50 observations in dense forested areas. It usually does not bite, but if this does occur then it will lead to soreness, pain and temporary bleeding in the victim. Biting has been occasionally observed during touching or handling attempts by the victim. When frightened, the snake either coils up and hides its head within its coiled up body; or it quickly tries to escape to a safe hiding place inside the leaf litter.

When the snake coils, it enlarges its body and displays its vivid skin colours (white, pink and brown), which is visible between the scales around the mid body. We observed, on a number of occasions, the snake practicing thanatosis (death mimicry) for up to 10–15 minutes after carrying out our own handling attempts. Once the snake had noticed that threat had disappeared, it quickly escaped and hid itself in the leaf litter. We have observed this species living in sympatry with other snakes of several families such as *Aspidura guentheri* Ferguson, 1876 (Natricidae); *Hypnale zara* (Gray, 1849) (Viperidae); and *Sibynophis subpunctatus* (Duméril, Bibron & Duméril, 1854) (Colubridae).

Based on our observations, its diet consists mostly of lizards (saurophagy) and small snakes eggs (oophagy), small spiders, beetles, other insects and the larvae of other invertebrates. More specifically, we observed the snake feeding on ground dwelling skinks (*Lankascincus* sp.) and geckos (*Hemidactylus frenatus* and *Cnemaspis* sp.). If the prey is large, the snake wraps itself around it and squeezes it until it suffocates. In captivity, it was fed with jumping spiders, small wild cockroaches, annelid worms, meal-worms, small frogs, and the freshly detached tail tips of geckos.

During the breeding season (May–June) 3–5 individuals can be observed close by and we observed several copulations in the evenings just after dark (18.0–19.0 hrs). The species lays 3–5 eggs at a time on dry, cool, loose soil or under decaying logs on the ground (soil temperature 26.2–27.9 °C; humidity 58–73%; light intensity 0–27 lux, based on observations of 10 ovipositions). Eggs are cream in colour and oval in shape (12–14 mm long and 4–5 mm wide, $n = 40$). The lectotype MNHN 3238 is a gravid female with three eggs in its genital tract. The incubation period is 38–45 days (based on observations of 10 incubating clutches). We did not see the parents close by during the incubation nor shortly afterwards, indicating the lack of parental care of the eggs or hatchlings. The new born juveniles were 4–5 cm in total length and their body colour varied from dark brown to black. We noticed that ants were their main egg predators on about ten occasions. We also observed on several occasions, this snake attempting to avoid ant-nests when moving or resting.

We have found this species inside termite mounds on many occasions, an observation also made by Smith (1943). This may indicate either a strategy used by the snake to avoid ants (because we never observed ant nests in or around termite mounds) or a neat way for the snake to have instant access to food (may be feeding on termite eggs). Further studies on habitat ecology would be interesting. Even though this is a ground dwelling species, we observed it climbing on rock boulders which have crevices, indicating that this snake may be searching for geckos or their eggs for food. During floods, the snake is usually found off the floor, in trees at 1–2 m above ground level. It is also found deep inside forests, and has been observed under old coconut harnesses, decaying logs on the ground, and inside termite mounds (as mentioned earlier) set in well maintained home gardens.

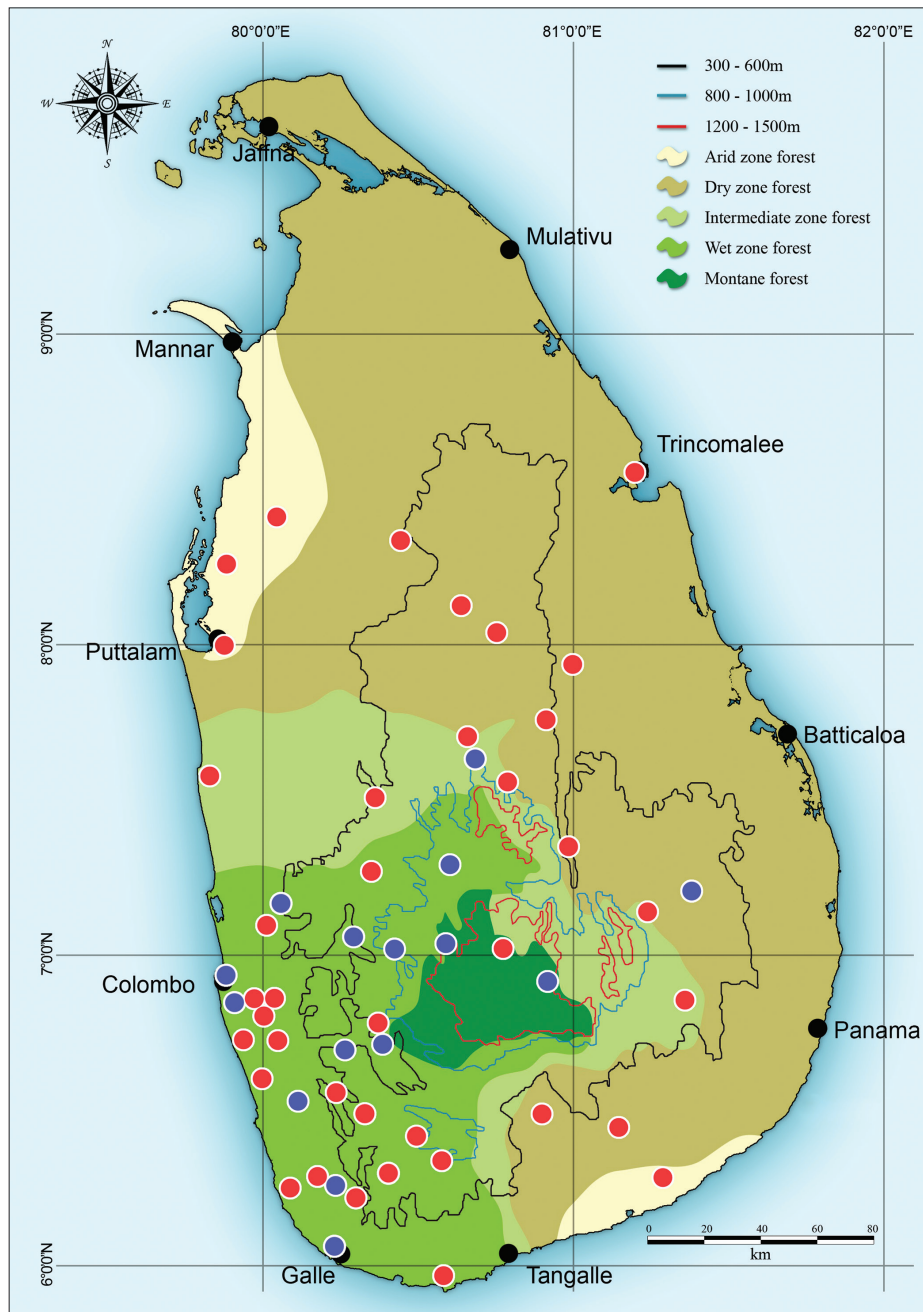


Figure 3. Distribution pattern of *Oligodon sublineatus*: blue dots, previous records and red dots, our observations; major towns are displayed on the map (map source: Cooray 1967).

Road kills are identified as a major growing threat in addition to forest fragmentation and habitat loss. People are also a threat, killing the snake out of fear, believing that it to be venomous, especially because as it displays such vivid head and body colours. We observed natural predators including birds: the yellow-billed babbler [*Turdoides affinis* (Jerdon, 1845)], southern coucal (*Centropus parroti* Stresemann, 1913), common mynah [*Acridotheres tristis* (Linnaeus, 1766)], white-throated kingfisher [*Halcyon smyrnensis* (Linnaeus, 1758)], and the Sri Lankan grey hornbill (*Ocyrceros gingalensis* Shaw, 1811); ophiophagous snakes including: two elapids, the Sri Lankan krait (*Bungarus ceylonicus* Gün-

ther, 1864), and the Indian krait (*Bungarus caeruleus* Schneider, 1801); and amphibians including forest toads (*Duttaphrynus* sp.). In addition, Karunarathna and Asela (2007), and Karunarathna (2009) have observed the common rat snake (*Ptyas mucosus* Linnaeus, 1758) feeding on *Oligodon sublineatus* and *Oligodon calamarius* (Linnaeus, 1758) in Sri Lanka

Discussion

In the description of *Oligodon sublineatus*, Duméril et al. (1854) clearly states the following “We only have ob-

served one specimen well preserved”, they further stated “We counted 15 scale rows on that specimen, 155 ventrals and 25 subcaudals”. Those counts are in accordance with MNHN 3238 (respectively 150 and 28) hence; we hereby designate it as the lectotype. However, the measurements given in the last line “Total length was 180 cm; among them 155 for SVL and 25 for the tail.” is a mistake; we believe that the wrong units of measurements were chosen in error; it should have been in millimeters and not centimeters! In addition, the newly recognized syntype (MNHN 3238) had a total length of about 289 mm with 254 mm SVL and 35 mm for the tail. Again we are making the assumption that Duméril et al. (1854) must have mistakenly typed the total length as “180cm” instead of ~280 mm and “SVL 155cm” instead of ~255 mm (typing a ‘1’ instead of a ‘2’). Interestingly, the syntype MNHN 3239 (now paralectotype) measured 177 mm total length with SVL 150 mm but its ventral and subcaudal counts do not match those of the original description (respectively 138 and 36 [typical of a male] versus 155 and 25 in the description [typical of a female]). However, the most probable explanation of this is that they mistyped, rather than used (which may seem the obvious explanation here) the measurement of the second specimen, because Duméril et al. (1854) clearly stated that they had examined only one specimen (the largest of both syntypes), even though they compared the colour patterns of both specimens, thus both are here considered as syntypes. Furthermore, the scale counts in the smaller specimen (MNHN 3239) do not match the original scale description of Duméril et al. (1854), and the spots of the larger specimen (MNHN 3238) are much more narrowed towards the middle of the body compared to the spots of the smaller specimen (MNHN 3239), which is in accordance with the details of the examined specimen in the original description. Thus Duméril et al. (1854) made a mistake when describing characteristics of the examined specimens and their ventral and subcaudal counts also reflect the classical mistake often seen when one single, old and very small specimen is examined by many different researchers over time. We have no doubt that MNHN 3238 is the Philippines (in error) specimen of the original description and MNHN 3239 the Ceylan specimen of Leschenault as reported in the original description, both being the only two syntypes of *O. sublineatus*.

To be sure that there are no other specimens which could possibly be a syntype, we examined all the available *Oligodon sublineatus* specimens and all the specimens of *Oligodon* collected from Sri Lanka and the Philippines which were registered on or before 1864 in the MNHN collection (1864 is the date of the oldest handwritten register available for the MNHN herpetological collections). Among the available specimens (except MNHN 3238–39), MNHN 0611, 3537, 5768, 1900.0381–385, and 1900.0381, 1900.0381A–B are *O. ancorus* from the Philippines, MNHN 1012 is *O. modestus* from the Philippines and MNHN 6129 is *O. calamarius* from Sri Lanka. In the 1864 unpublished catalogue, there were five specimens of

O. sublineatus registered. However out of the three other available specimens of *O. sublineatus* (MNHN 1747, 4234, and 4234A) two do not match the original description. The third specimen MNHN 4234 closely matches the original description, however we believe that it does not qualify as the larger syntype based on the following statement from the original description: “Another specimen, obviously younger,” which clearly means that the former specimen is considerably larger (being older by inference, or fully grown), than the latter. The specimen MNHN 4234 is slightly smaller, than the younger specimen (MNHN 3239) of Leschenault. It also has a definite collector’s name (Janssen), and a definite locality (Sri Lanka) associated with it. Therefore, we can confidently reject this specimen MNHN 4234 as a syntype and can confirm MNHN 3238–39 as the syntypes of *O. sublineatus*. The location “Philippine” was never included in any of the MNHN registers for *O. sublineatus*, not even in the 1864 register, so it could be that subsequent curators have corrected the error adding “Java, collector Bosc” in the register (which is also wrong). These were probably changed sometime between 1854 and 1864. Therefore, here we correct the locality of the designated lectotype as “Sri Lanka”.

Louis-Augustin-Guillaume Bosc (1759–1828) was a French botanist, zoologist, and politician during the Revolution, who described many amphibians and reptiles of eastern North America. He also described the Savanna Monitor (*Varanus exanthematicus* Bosc, 1792) from Senegal in West Africa (Adler et al. 2012). Bosc never visited Sri Lanka. As MNHN 3238 belongs to an endemic Sri Lankan species with incorrect collection locality details (Philippines or even Java), we also agree that the collectors name, Bosc, is a mistake and we follow Duméril et al. (1854) and believe that the collector details for this specimen is not known.

Duméril et al. (1854), in the original description states that “on the jar there was no other indication that the [data] one on its origin, Philippines and the name *Oligodon torquatus* with the letter “R””; no such indication was found on any jar that we examined in MNHN collections. It is strange that *O. torquatus* was mentioned in the original description, a species which was described by Boulenger in 1888, 34 years after *O. sublineatus*. However, based on the characters mentioned in the original description of *O. sublineatus*, we can be sure that both examined syntypes of Duméril et al. (1854) belong to the same endemic species of Sri Lanka, *O. sublineatus*, and neither match any of the species from the Philippines (see Leviton 1963). This is also confirmed by the existence of ventral scales having a series of dark brown spots arranged in three lines in the syntypes of *O. sublineatus* [vs. uniform in *O. ancorus* (Girard, 1858) and *O. notospilus* Günther, 1873], and 25 subcaudals in our lectotype [vs. 28–49 in *O. meyerinkii* (Steindachner, 1891); 52–54 in *O. maculatus* (Taylor, 1918); 27–44 in *O. modestus* Günther, 1864; 48–60 in *O. octolineatus* (Schneider, 1801), and 34–45 in *O. perkinsi* (Taylor, 1925); scale counts

after Leviton (1963)]. Furthermore, based on the description, it can also be easily distinguished from *O. torquatus* (Boulenger, 1888) by having ventrals with a series of dark brown spots in three lines (vs. uniform).

Boulenger (1894) recorded *Oligodon sublineatus* from Nicobar Island. Deepak and Harikrishnan (2013) observed a couple of specimens (ZSI 8899 and 8900) of *O. sublineatus* deposited at ZSI-Kolkata, which were labelled as “Camorta, Nicobars”. They confirmed that both the collection locality and the identity were wrong. The species is definitively absent from Nicobar Islands, as originally stated by Wall (1921) and has to be considered as a species strictly endemic to Sri Lanka, but widespread over the forested areas of the country.

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Appendix 1

Other materials examined

- O. ancorus***: Philippines: MNHN 0611, 3537, 5768, 1900.0381–385, 1900.0381A–B.
- O. calamarius***: Sri Lanka: MNHN 6129.
- O. modestus***: Philippines: MNHN 1012, BMNH 1946.1.5.54 (type).
- O. sublineatus***: Java (in error): MNHN 1747; Sri Lanka: MNHN 4234, 4234A; NMB 21366–7, 1595–9, 10775, 21364–5; BMNH 1841.1.7.12, 1858.10.19.29, 1858.10.19.37–38, 1852.9.13.41, 1845.8.7.6, 1846.12.2, 1853.3.30.53, 1852.2.19.90, 1852.2.19.95, 1969.2769–2771, 1890.11.8.21–22, 1895.7.23.29, 1897.10.20.14, 1915.5.3.6, 1920.5.6.3, 1951.1.8.36, 1955.1.9.81–82, 1862.8.14.31, 1968.875.
- Oligodon torquatus***: Burma: BMNH 1946.1.4.21–22 (syntypes).

The legacy of the Crusaders: Complex history of colonization and anthropochory in the land snails *Levantina* (Gastropoda, Pulmonata) in the Eastern Mediterranean

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Abstract

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The Eastern Mediterranean land snails *Levantina* display a disjunct distribution spanning the Middle East (Levant), Cyprus, few locations along the Aegean Turkish coast between Bodrum and Datça and on the islands of Rhodes, Karpathos and a few surrounding islets (Dodecanese). These land snails are strictly bound to limestone; shell variability is noticeable with a pair of umbilicate and non-umbilicate forms parapatrically distributed in the Levant and along the Aegean Turkish coast; they overlap on the Dodecanese islands. We sequenced fragments of two mitochondrial genes (Cytochrome Oxidase I and 16S rRNA) from the historical *Levantina* materials available at the Museums of Hamburg and Berlin. The aim of the study is to explain the current distribution of *Levantina* in the Eastern Mediterranean in light of an earlier hypothesis suggesting anthropochory due to the movements of Crusaders across the area. The deeper nodes in our phylogeny indicate that *Levantina* reached the Dodecanese from continental Turkey during the Pliocene exploiting continuity of landmasses. In five circumstances the same haplotype co-occurs on two different islands; one haplotype is shared between one island (Rhodes) and the Levant. We suggest that the movements of Crusaders likely explain the current distribution of haplotypes. In particular, the Knights Hospitaller of St. John occupied Cyprus, the Dodecanese and the facing Turkish coasts for more than two centuries (1306–1522) after they withdrew from Jerusalem in 1187 and from the Levant in 1291. Snails could have been introduced as an item of food or transported with other material including limestone used for building.

Introduction

In a study that appeared in the journal “Nature” on the 6th of April 1882, just a few days before his death, Charles Darwin returned to his lifelong fascination with mechanisms of passive long-distance dispersal in mollusks (Darwin 1882). Ever since Darwin’s pioneer work, land snails occurring on islands have puzzled evolutionary biologists; it is indeed challenging to explain how these fragile and slow moving creatures could travel long distances across unsuitable ecological areas if not by passive

transport. The advent of molecular tools in biogeography has proved Darwin’s intuition right. Recently, various studies convincingly demonstrated that passive dispersal by birds and humans is the most likely explanation for the current distribution of insular genetic lineages in land snails of the genera *Balea* and *Cepaea* (Gittenberger et al. 2006; Grindon and Davison 2013).

In the Eastern Mediterranean area, *Levantina* shows notable morphological shell variation and a geographic distribution that has been baffling biogeographers for decades (Glaubrecht 1993a, 1993b, 1995 and reference

therein). This helicid genus includes rather large edible land snails strictly bound to limestone and displays a disjunct range, represented by two species each in the Middle East (Levant), on Cyprus, in a few locations along the Aegean Turkish coast between Bodrum and Datça and on Rhodes, Karpathos, and a few surrounding islets of the Dodecanese (see Glaubrecht 1993a for further details). Shell variability resides in the lack or presence of an umbilical opening in the adults (Glaubrecht 1993a, 1993b, 1995). In the Levant the two species differentiated by their shell form are distributed parapatrically (the non-umbilicate *L. caesareana* in the north and the umbilicate *L. hierosolyma* in the south) (Heller 1979). Heller (1979) identified a narrow hybrid zone between the two species. A similar pattern of parapatric distribution (but with no areas of hybridization identified thus far) is observed over a much-reduced geographic scale along the Turkish coasts. On the Dodecanese islands the umbilicate *spiriplana* is replaced in places by the non-umbilicate *malziana*, but this is not always the case. On Rhodes, the *malziana* type is widespread while the *spiriplana* type is restricted to a few places, among them the fortress of the Knights Hospitaller of St. John on the northern tip of the island (Glaubrecht 1993a), while the two species are distributed parapatrically on Karpathos and form mixed populations on Symi and surrounding islets (Glaubrecht 1993a).

Based on the above geographic occurrence of shell forms and on field observations, two alternative scenarios have been hypothesized to explain such a peculiar insular distribution (Glaubrecht 1993a, 1993b). Following the paleogeographic history of the area, the Dodecanese could have been colonized during one of the multiple changes in sea level that created transitory land bridges between the islands and the continent from the late Miocene to the middle Pliocene. Similar scenarios have been validated on molecular grounds in a variety of scarcely vagile groups, including land snails (Ketmaier et al. 2006; Jesse et al. 2011; Kotsakiozi et al. 2012 and references therein). An alternative scenario argues for an historical, anthropogenic introduction of *Levantina spiriplana* on the Dodecanese islands. This hypothesis relies on the observation that most of the locations where the taxon is found – and in particular where the two shell forms co-occur – are actually historical human settlements, i.e. the castles of the Knights Hospitaller of St. John on Rhodes and in Bodrum (Turkey). It was suggested that the movements of Crusaders in the area could explain this distribution pattern (Glaubrecht 1993a, 1993b). Following their withdrawal from the Levant in 1291 after the fall of Acre (Israel), Crusaders conquered Rhodes in 1306 and kept the area under their control until the fall of the Rhodes Grand Master's Palace in 1522 (for the history of the crusaders, see e.g. Mayer 2005; Murray 2006). For more than two centuries the Dodecanese – and in particular the island of Rhodes with the headquarter of the Knights Hospitaller of St. John – became a key area of occupation and activities, with frequent passages of ships sailing between the

islands and the Turkish mainland, transporting Crusaders, the goods they traded and materials used for building.

Here we tested these two alternative scenarios by using sequences of two mitochondrial DNA (mtDNA) genes and the *Levantina* material available in the collections of the Zoological Museum Hamburg and the Museum für Naturkunde Berlin (Germany); this material was collected about two decades ago in a first attempt to verify the above biogeographical hypotheses (Glaubrecht 1993a, 1993b, 1995). The predictions for the above alternative hypotheses in terms of patterns of genetic structuring are the following. The paleogeographic scenario would translate into discrete amount of genetic divergence and the identification of allopatric haplogroups. In contrast, if the Crusades scenario were true, given the short (in evolutionary terms) time elapsed since the alleged translocation event(s) we would find very little (if any) genetic divergence between currently allopatric haplotypes.

Materials and methods

The study is based on material collected by MG in April 1989 and May 1990 (Glaubrecht 1993a, 1993b); samples were preserved in 70%–95% ethanol and vouchers deposited in the Zoological Museum Hamburg (ZMH) with some additional material in the Museum für Naturkunde Berlin (ZMB). Details on sampling localities are given in Table 1. Fragments of the mitochondrial Cytochrome Oxidase I (COI) and 16S rRNA (16S) genes were amplified by Polymerase Chain Reaction (PCR) and directly sequenced as detailed in Ketmaier et al. (2006, 2010); given the age of the samples for about 50% of them we were unable to amplify directly the whole PCR fragments due to DNA degradation. For these samples, we used a nested PCR approach with internal primers designed anew for this study. Precautions were taken to avoid any cross-contamination of samples as detailed in Ketmaier et al. (2006). The first round of PCR amplification was followed by a second round of PCR cycling, using as template the undiluted PCR products from the first PCR amplification. PCR primers used for this second round were designed on the basis of *Levantina* sequences obtained in the first (not nested) PCR rounds. The primer pair for the nested PCR of the COI gene is (COI-Lev-for: 5'-TTGTAACWGICY-CATGCATTG-3' and COI-Lev-rev: 5'-AACTWATTC-CAGGAGATCGYA-3'). The primer pair for the nested PCR of the 16S gene is (16S-Lev-for: 5'-CCCTGACTGTGCAAAGGTAGC-3' and 16S-Lev-rev: 5'-GGC-CCTAATCCAACATCGAGGTC-3'). Nested PCR cycling conditions were as in Ketmaier et al. (2006, 2010).

Sequences were edited and aligned in SEQUENCHER 4.1 (Gene Code Corporation, Ann Arbor, MI, USA); the alignment was further checked by eye. We included a selection of *Codringtonia* sequences from (Kotsakiozi et al. 2012) for the molecular clock analyses and *Cornu aspersum* to root the phylogenetic searches (Table 1). Phylogenetic searches were carried out by Maximum

Table 1. Taxa included in the study and their geographic origin. For each individual we detail the presence (O)/absence (C) of the umbilicus in the shell, the voucher number in the collections of the Zoological Museum Hamburg (ZMH) and the Museum für Naturkunde Berlin (ZMB) and the composite COI/16S haplotype identifier number.

Taxon	Umbilicus (O/C)	Location	Specimen voucher	mtDNA Haplotype
<i>Levantina malziana</i>	C	Greece, Karpathos, Mertonas, E Arhangells	ZMH.1555b	1
<i>Levantina malziana</i>	C	Greece, Karpathos, Mertonas, E Arhangells	ZMH.1555c	2
<i>Levantina malziana</i>	C	Greece, Karpathos, Mertonas, E Arhangells	ZMH.1555d	2
<i>Levantina malziana</i>	C	Greece, Karpathos, Mertonas, E Arhangells	ZMH.1555e	3
<i>Levantina malziana</i>	C	Greece, Karpathos, Mertonas, E Arhangells	ZMH.1555f	4
<i>Levantina malziana</i>	C	Greece, Karpathos, Mertonas, E Arhangells	ZMH.1555g	5
<i>Levantina malziana</i>	C	Greece, Karpathos, Mertonas, E Arhangells	ZMH.1555i/ j	3
<i>Levantina malziana</i>	C	Greece, Rhodes, Moni Amos, Kap Ladiko	ZMH.1557a	6
<i>Levantina malziana</i>	C	Greece, Rhodes, Moni Amos, Kap Ladiko	ZMH.1557b	7
<i>Levantina malziana</i>	C	Greece, Rhodes, Moni Amos, Kap Ladiko	ZMH.1557d	8
<i>Levantina malziana</i>	C	Greece, Rhodes, Charaki, Feraklos	ZMH.1557e	9
<i>Levantina malziana</i>	C	Greece, Rhodes, Kamiros Castle	ZMH.1557f	2
<i>Levantina malziana</i>	C	Greece, Rhodes, Kamiros Castle	ZMH.1557h	3
<i>Levantina malziana</i>	C	Greece, Rhodes, Kamiros Castle	ZMH.1557i	6
<i>Levantina malziana</i>	C	Greece, Rhodes, Profitis Ilias (900m)	ZMH.1557j	1
<i>Levantina malziana</i>	C	Greece, Rhodes, Profitis Ilias (900m)	ZMH.1557k	6
<i>Levantina malziana</i>	C	Greece, Rhodes, Monolithos Castle	ZMH.1557n	10
<i>Levantina malziana</i>	C	Greece, Rhodes, Monolithos Castle	ZMH.1557o	11
<i>Levantina malziana</i>	C	Greece, Symi, northern slope Vigala	ZMH.1558a	5
<i>Levantina malziana</i>	C	Greece, Symi, NW Hariani harbor, Th. Sikidi	ZMH.1558c	12
<i>Levantina malziana</i>	C	Greece, Symi, NW Hariani harbor, Th. Sikidi	ZMH.1558d	13
<i>Levantina malziana</i>	C	Greece, Symi, NW Hariani harbor, Th. Sikidi	ZMH.1558e	14
<i>Levantina malziana</i>	C	Greece, Symi, NW Hariani harbor, Th. Sikidi	ZMH.1558f	13
<i>Levantina malziana</i>	C	Greece, Symi, NW Hariani harbor, Th. Sikidi	ZMH.1558g	14
<i>Levantina malziana</i>	C	Greece, Symi, Panormitis, N monastery	ZMH.1561a	24
<i>Levantina malziana</i>	C	Greece, Nimos	ZMH.1556a	15
<i>Levantina malziana</i>	C	Turkey, Karaova, near Bodrum	ZMH. 1565	16
<i>Levantina spiriplana</i>	O	Greece, Karpathos, Larniotisa, near Kap Volakas	ZMH.1559a	17
<i>Levantina spiriplana</i>	O	Greece, Karpathos, Pigadia, Patella mountain	ZMH.1559d	17
<i>Levantina spiriplana</i>	O	Greece, Karpathos, Pigadia, Patella mountain	ZMH.1559e	17
<i>Levantina spiriplana</i>	O	Greece, Karpathos, Pigadia, Patella mountain	ZMH.1559f	18
<i>Levantina spiriplana</i>	O	Greece, Karpathos, Profitis Ilias, SE Aperi	ZMH.1559g	19
<i>Levantina spiriplana</i>	O	Greece, Karpathos, E Mentis	ZMH.1559i	20
<i>Levantina spiriplana</i>	O	Greece, Karpathos, E Mentis	ZMH.1559j	20
<i>Levantina spiriplana</i>	O	Greece, Rhodes, Rampart d'Ambosie gate	ZMH.1560a	21
<i>Levantina spiriplana</i>	O	Greece, Rhodes, Rampart d'Ambosie gate	ZMH.1560b	21
<i>Levantina spiriplana</i>	O	Greece, Rhodes, Rampart d'Ambosie gate	ZMH.1560c	21
<i>Levantina spiriplana</i>	O	Greece, Rhodes, Rampart d'Ambosie gate	ZMH.1560d	22
<i>Levantina spiriplana</i>	O	Greece, Rhodes, Filerimos	ZMH.1560e	23
<i>Levantina spiriplana</i>	O	Greece, SW Symi, Xisos	ZMH.1561b	25
<i>Levantina spiriplana</i>	O	Greece, SW Symi, Xisos	ZMH.1561c	23
<i>Levantina spiriplana</i>	O	Greece, SW Symi, Xisos	ZMH.1561d	23
<i>Levantina spiriplana</i>	O	Greece, Symi, Skourmisa Bay, Kefala	ZMH.1561e	23
<i>Levantina spiriplana</i>	O	Greece, Rhodes, Rampart d'Ambosie gate	ZMB 127533	27
<i>Levantina spiriplana</i>	O	Turkey, Datça	ZMH.1564	30
<i>Levantina hierosolyma</i>	O	Jerusalem	ZMB.74072	27
<i>Levantina hierosolyma</i>	O	Jerusalem	ZMB.9126	27

Taxon	Umbilicus (O/C)	Location	Specimen voucher	mtDNA Haplotype
<i>Levantina hierosolyma</i>	O	Jerusalem, Givat Ram Campus, Hebrew Univ.	ZMH.1562	27
<i>Levantina hierosolyma</i>	O	Jerusalem, Givat Ram Campus, Hebrew Univ.	ZMH.1563a	27
<i>Levantina hierosolyma</i>	O	Jerusalem, Givat Ram Campus, Hebrew Univ.	ZMH.1563b	29
<i>Levantina caesareana</i>	C	Arbell Cliff, Lake Tiberias	ZMH.1568	27
<i>Levantina caesareana</i>	C	Arbell Cliff, Lake Tiberias	ZMH.1569d	31
<i>Levantina caesareana</i>	O	Arbell Cliff, Lake Tiberias	ZMH.1569e	27
<i>Levantina caesareana</i>	C	Arbell Cliff, Lake Tiberias	ZMH.1569g	32
<i>Levantina caesareana</i>	C	Arbell Cliff, Lake Tiberias	ZMH.1569h/i	33
<i>Codringtonia codringtonii</i>	-	Greece, Peloponnese, Marathopolis village, Messina	ZMB 107155	N/A
<i>Codringtonia codringtonii</i>	-	-	Kotsakiozi et al. 2012	N/A
<i>Codringtonia eucineta</i>	-	-	Kotsakiozi et al. 2012	N/A
<i>Codringtonia intusplacata</i>	-	-	Kotsakiozi et al. 2012	N/A
<i>Codringtonia helenae</i>	-	-	Kotsakiozi et al. 2012	N/A
<i>Assyriella guttata</i>	C	Turkey, Harput near Elazig	ZMB 127531	26
<i>Assyriella mardinensis</i>	C	Turkey, Anatolia, 3 km SE Mardin	ZMB 127532	28
<i>Gyrostomella leachii</i>	-	Lybia, Tripoli, Djebel Garim	ZMB 86612-1	N/A
<i>Gyrostomella leachii</i>	-	Lybia, Tripoli,	ZMB 86612-2	N/A
<i>Cornu aspersum</i>	-	-	Regnier et al. 2011 Guiller and Madec 2010	N/A N/A

Likelihood (ML) (run online on the Mobyle portal with the phym1 option) and by Bayesian analyses (MrBAYES 3.2) (Ronquist et al. 2011). For both analyses the most appropriate model of sequence evolution was selected using JMODELTEST 2 (Darriba et al. 2012). JMODELTEST 2 returned the HKY+I+G as the best model fitting the concatenated dataset (proportion of invariable sites I=0.575; Gamma distribution shape parameter = 0.576). These settings were then adopted in the Maximum Likelihood, Bayesian and Beast searches.

The robustness of the ML hypothesis was tested by 1,000 bootstrap replicates; MrBAYES was run two times independently for 2,000,000 generations with a sampling frequency of 100 generations. We ran one cold and three heated Markov chains and two independent runs. To establish if the Markov chains had reached stationarity, we plotted the likelihood scores of the sampled trees against generation time. Trees generated before stationarity were discarded as burn-in (first 10% of the sampled trees) and posterior probability values for each node were calculated on the basis of the remaining 90% of sampled trees. We applied coalescence as implemented in the BEAST 1.7.2 package (Drummond and Rambaut 2007) to estimate divergence times in million years (Myr) for the supported clades found by the phylogenetic analyses. BEAST was used to estimate node ages to the most common recent ancestor (TMCRA) of the splits and substitution rates using an uncorrelated lognormal relaxed clock with a Yule or 'pure birth' prior process to model speciation. The output of each independent run was visualized using TRACER v1.4. Samples from both independent runs were then pooled after removing the first 10% as

burn-in using LogCombiner 1.4.8. After an optimization step during which parameters were calculated to reach an optimum performance and achieve a reasonable effective sampling size (ESS, number of independent samples of the posterior distribution) for the parameters of interest, we carried out two independent runs of 30 million generations each, using a Yule tree prior and the default options for all other prior and operator settings. The age of the basal split in the geographically and phylogenetically closely related genus *Codringtonia*, estimated at 4.4 Myr in Kotsakiozi et al. (2012), was used to calibrate the tree with a normal distribution for the prior. Finally, we conducted a Bayesian binary MCMC dispersal-vicariance analysis in RASP (Yu et al. 2011). Analyses were run with the maximum units of areas allowed in ancestral nodes equal to three; other parameters were kept at the default settings.

Results

The final alignment including all samples amplified by nested PCR was 482 base pair (bp) long, with 281 bp for COI and 201 for 16S and defined a total of 33 unique haplotypes (GenBank accession numbers KR080942-KR081055; additional sequences used for the phylogenetic searches are JQ239955, JQ239934, JQ239967, JQ239977, JQ240123, JQ240103, JQ240134, JQ240145, HQ203051 and EU912763). These haplotypes are robustly clustered in a monophyletic clade in all phylogenetic searches (Fig. 1). The two *Assyriella* taxa, viz. *guttata* and *mardinensis*, and the *Levantina* clade were found not

to be reciprocally monophyletic and the placement of *Assyriella* is not supported statistically.

Levantina hierosolyma, *L. caesareana* and the two *L. spiriplana* forms from the Dodecanese traditionally considered as subspecies (i.e. *spiriplana spiriplana* and *spiriplana malziana*) (Glaubrecht 1993a, 1993b) were not retrieved as separate clades. This claims for a revision of the systematics of the group, which is outside the scopes of this study and would require a denser sampling in terms of taxa, geographic coverage and molecular markers. Such a larger study would also allow alternative hypotheses such as incomplete lineage sorting and introgression to be tested in details. We found strong support for three main haplogroups, in spite of the short mtDNA fragments we were able to amplify and sequence. Haplotypes 12, 16, 31 and 33 are from non-umbilicate shelled populations distributed in Turkey, Israel as well as on Symi and their last common ancestor is not older than about 3 Myr old. A large group not older than 3 Myr clusters populations with umbilicate shells distributed over a broad geographic area from Israel, Turkey and the Dodecanese (Karthos, Rhodes and Symi Islands); haplotypes 23 and 27 are present on Rhodes and Symi Islands and on Rhodes and in Israel, respectively. The remaining haplotypes are gathered in a clade with non-umbilicate shells only; this cluster is limited to the Dodecanese and dates back to about 2.6 Myr ago. Within this clade, in three circumstances the same haplotype is shared between two islands. The RASP analysis (Fig. 2) postulates an origin of the *Levantina* / *Assyriella* clade in Turkey (node I; occurrence of this range 92.2%; 80% marginal probability) followed by two dispersal events to the Dodecanese (node II) and the Levant (node IV), respectively. Node V grouping umbilicate populations implies a back dispersal from the Levant to the island of Rhodes followed by multiple dispersal events across Rhodes, Karpathos and Symi. The distribution of haplotypes 19, 27 and 30 supports a close association of umbilicate forms in the Levant, continental Turkey and Rhodes where the umbilicate form (*spiriplana*) exclusively occurs in the vicinity of the Crusaders' fortresses (node VII; 82% marginal probability). The lineage with a covered umbilicus (*malziana*) originated on Rhodes (node VIII; occurrence of this range 93.7%; 79% marginal probability) and progressively spread and diversified across Rhodes, Karpathos and Symi. Haplotypes found on Symi and on the neighboring islet of Nimos (haplotypes 13, 14, 24 and 15) reached the islands via two independent dispersal events from Rhodes (nodes XI and XIII).

Discussion

We could not retrieve two reciprocally monophyletic clades for *Levantina* and *Assyriella*. The validity of the distinction between *Assyriella* and *Levantina* was already questioned (Glaubrecht 1995); this is an issue in need of further work based on a taxonomically more exhaustive

sampling. Our results do not fully embrace neither the paleogeographic nor the Crusaders hypothesis but rather suggest that both played a role in shaping the observed mtDNA diversity in *Levantina*. The umbilicate and non-umbilicate shell forms, although clearly distinguishable morphologically (Glaubrecht 1993b, 1995), do not cluster in two reciprocally monophyletic lineages. The umbilicate populations are restricted to a single and highly supported monophyletic clade whereas the non-umbilicate shell is displaced as a paraphyletic trait in the tree of Fig. 1. It is also worth emphasizing that in our phylogeny only the non-umbilicate shell form is associated to both basal and terminal branches.

The biogeographic reconstruction presented in Fig. 2 supports multiple long-distance and over-sea dispersal events; some of these events are phylogenetically very recent (Figs 1 and 2). The scenario we detail here requires particular caution in its interpretation for the following reasons. First, inferences are based on mtDNA only, a single genetic locus and hence do not give any indication on the geographic origin of the rest of the genome. Second, the uncertainty of the tree topology is not taken into account. Nonetheless, in our opinion it represents a likely scenario given the phylogenetic and geographic information available and the ecology of the group. The origin of the whole *Levantina* clade, with the inclusion of one of the "*Assyriella*" taxa, should be sought in continental Turkey (node I; Fig. 2). Nodes V and VIII are roughly coeval (Fig. 2; 3.03 – 2.64 Myr, ages in bold in Fig. 1) and group only insular non-umbilicate populations (*malziana*) on one hand and almost exclusively insular umbilicate populations (*spiriplana*) on the other. The exceptions to insularity in the umbilicate clade will be discussed later on; we anticipate that these are, in our opinion, due to anthropogenic translocations. The above time estimates perfectly overlap with the last connection of Karpathos and Rhodes to the mainland, which dates back to 3.5 – 2.8 Myr ago (Beerli et al. 1996); this suggests that *Levantina* reached the Dodecanese exploiting continuity of landmasses. This, however, did not happen via a single colonization event but rather through a two-fold process, which brought on Rhodes two immigrant lineages of independent origin. The reconstruction of Fig. 2 identifies a first dispersal event from continental Turkey to Rhodes (nodes II), which resulted in the insular non-umbilicate clade widespread there (*malziana*). A second wave of colonization arrived on Rhodes following an earlier dispersal from Turkey to the Levant (nodes IV and V); this clade had the latter as the most likely area of origin and marked the appearance of the umbilicate shell type (*spiriplana*). Subsequently, both lineages colonized Karpathos and Symi (nodes VI–XIII); the non-umbilicate lineage realized more across-island movements (nodes VIII–XIII) than the umbilicate lineage (nodes VI–VII). How and when *Levantina* dispersed from Turkey to the Levant and why the umbilicate shell type is mostly insular are questions that remain to be answered. Recent evidence suggests that shell shape diversification in Mediter-

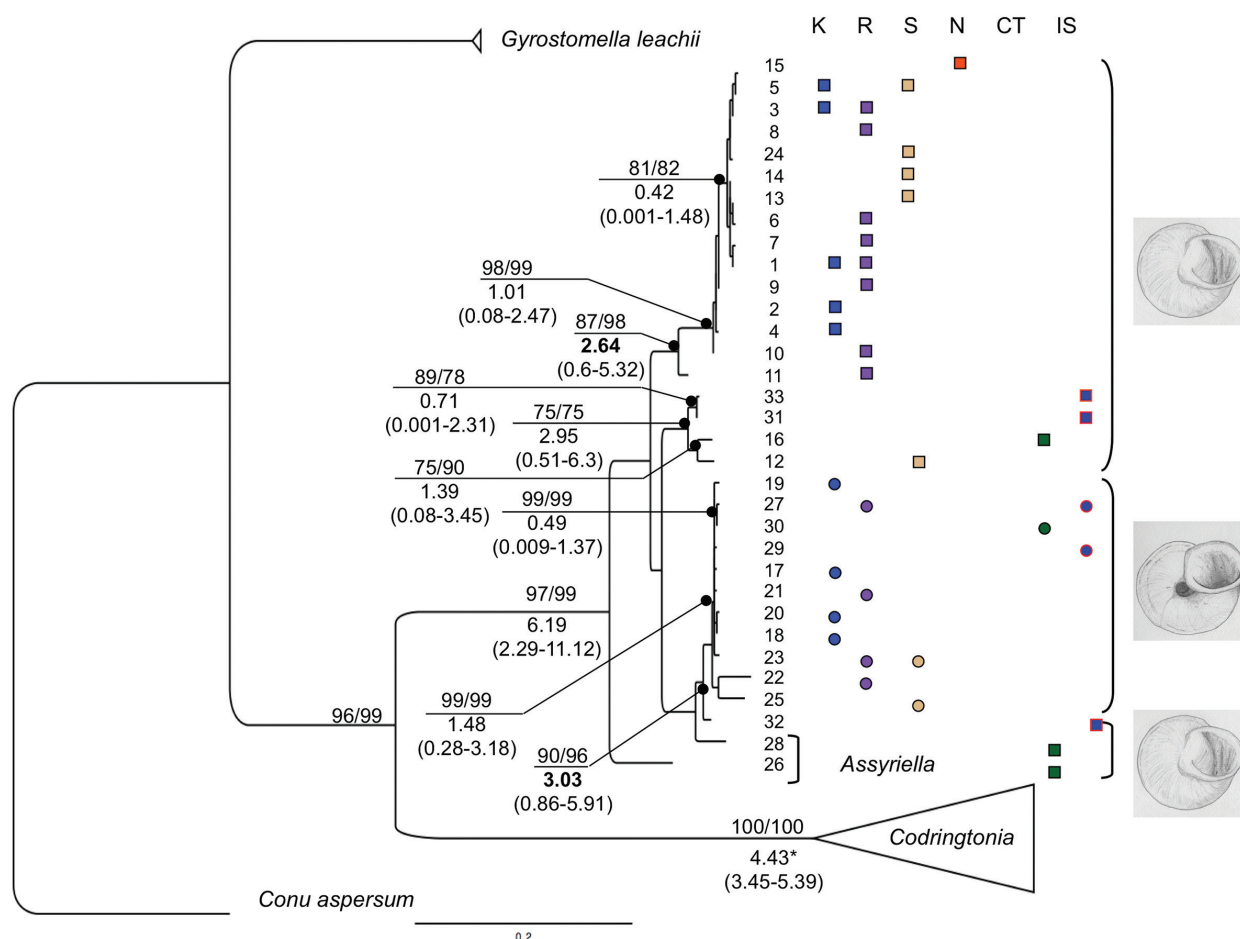


Figure 1. Evolutionary relationships in *Levantina*. Numbers at nodes are statistical support for the ML and Bayesian searches (first and second value above branches). Numbers below branches are age estimates in millions of years with the 95% highest posterior density (HPD) credibility interval in parentheses. Age estimates in bold are discussed in details in the text. Haplotype numbering is as in Table 1. The distribution of each haplotype and the relative shell shape is summarized in the column to the right of the haplotype identifiers (K = Karpathos Is.; R = Rhodes Is.; S = Symi Is.; N = Nimos Is.; CT = Continental Turkey; IS = Israel). Pictures illustrate how shell variability (closed or open umbilicus; squares and circles, respectively) is distributed in *Levantina* and *Assyriella*.

anean land snails might be due to the interplay between historical and ecological factors (Fiorentino et al. 2013). The positioning of haplotypes from the Levant at the base and within the otherwise poorly differentiated umbilicate clade suggests that the occurrences of this form in the Dodecanese and in southwestern Turkey is probably the result of (anthropogenic?) introductions. Such a shallow level of differentiation in the umbilicate clade is not mirrored in the non-umbilicate clade.

Even though the hypothesis of the non-umbilicate clade being of insular origin is appealing from an evolutionary perspective, we should not overlook the fact that this result could be an artifact due our limited sampling. In particular, we cannot completely rule out the hypothesis that the non-umbilicate clade originated in the Levant and subsequently reached the Dodecanese. We indeed identified a non-umbilicate clade grouping haplotypes from both the Levant and the Dodecanese (haplotypes 12, 16, 31, and 33). The non-umbilicate samples from the Levant are genetically close to a few samples from Symi. The other

non-umbilicate individuals from that island are spread in the upper part of the tree of Fig. 1, scattered among haplotypes found on other islands. In order to test this hypothesis adequately we would have needed a better survey of the genetic variation in *Levantina* from the Levant that is, on the contrary, too limited to address the issue.

Rhodes, the largest island of the Dodecanese and the closest to the mainland, is identified as the first colonized by the two *Levantina* lineages (nodes V and VIII). The non-umbilicate form is widespread across the island while umbilicate-shelled individuals are restricted to the fortress of the Knights Hospitaller of St. John in the northern part of island (city of Rhodes) (Glaubrecht 1993b, 1995). This has been taken as an indication that humans introduced this shell type on the island (Glaubrecht 1993b, 1995). Our molecular time estimates reject this hypothesis, at least for the basal haplotypes involved in the event (haplotypes 11 and 22). In our phylogeny, however, we found five cases of haplotypes shared between islands or between islands and distant locations. These distri-

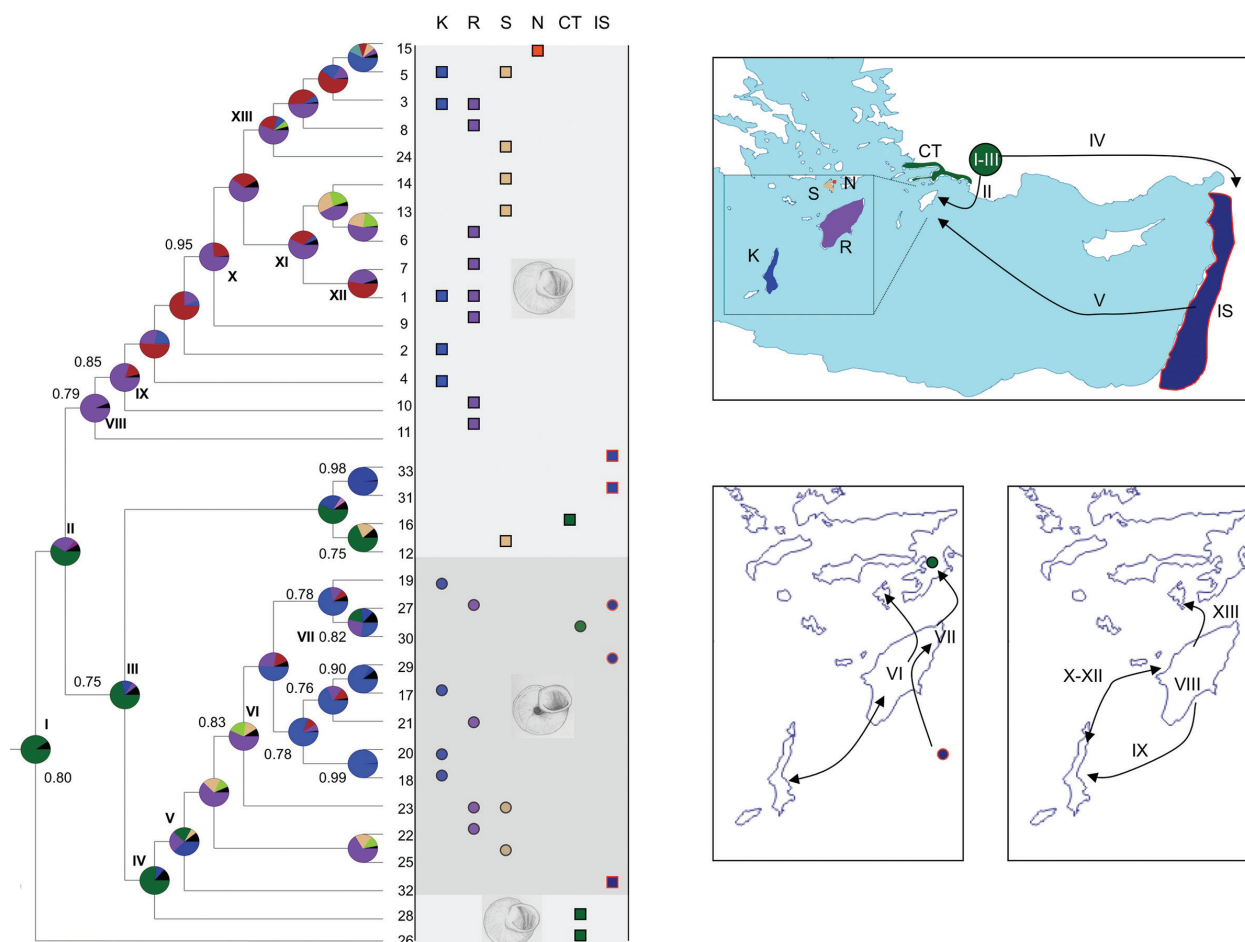


Figure 2. Historical biogeography in *Levantina*. On the left is the cladogram (as in Fig. 1 but pruned of the outgroup taxa) summarizing the Bayesian dispersal – vicariance analysis. The distribution of each haplotype and the relative shell shape is summarized in the column to the right of the haplotype identifiers (K = Karpathos Is.; R = Rhodes Is.; S = Symi Is.; N = Nimos Is.; CT = Continental Turkey; IS = Israel). Pie charts and numbers next to them indicate marginal probabilities of alternative ancestral ranges; colors identify the different geographic areas considered and match those in Fig. 1. Roman numbers identify events discussed in the text. On the right is the schematic of the proposed biogeographic history of *Levantina*. Arrows indicate the direction of the dispersal events inferred by the Bayesian dispersal – vicariance analysis and discussed in the text; roman numbers are the same as in the cladogram shown on the left. The bottom left panel details events within the umbilicate clade (circles), the bottom right panel those within the insular non-umbilicate clade (squares).

butions are difficult to justify on natural bases; the lack of any genetic differentiation indicates very recent dispersal in spite of the intervening marine barriers. Within the umbilicate clade, node VII suggests a recent dispersal event across Rhodes, continental Turkey and Levant; the same haplotype 27 co-occurs on Rhodes and in the Levant. Similarly, haplotype 23 is present on Rhodes and Symi. Haplotypes 1, 2, 3 and 5 (all non-umbilicate) are shared between two islands (alternatively Karpathos and Rhodes or Karpathos and Symi); most interestingly, on Rhodes these haplotypes are confined to human settlements (Table 1). How could we explain the allopatric occurrence of the same (or slightly diverging) haplotypes currently separated by geographic barriers theoretically insurmountable by land snails? Over-sea passive dispersal through i.e. hitchhiking on birds and/or surviving the passage through birds' gut has been documented in land

snails (Gittenberger et al. 2006; Miura et al. 2012). It should also be considered that large helicids are edible and they have been found associated with human settlements in many Mediterranean archeological sites (Grindon and Davison 2013); furthermore, the limestone they dwell upon had been used for a long time as a building material and transported in large blocks along historical trading routes across the Mediterranean Sea (Fiorentino et al. 2008). The geographic distributions of haplotypes 27 and 30 (Rhodes, Israel and continental Turkey) and that of the closely related haplotypes 17 (Karpathos) and 29 (Israel) are particularly striking and advocates for bringing the Knights Hospitaller of St. John back into the play. After the rising power of Islam expelled in 1291 the Knights from Jerusalem (where haplotypes 27 and 29 are found), they conquered Rhodes (where we found haplotype 27), the neighboring islands (i.e. Karpathos with haplotype

17) and the coast of Anatolia (haplotype 30). The Knights kept the Dodecanese and the Anatolian ports facing it under their control for 200 years before being defeated in 1522 by Sultan Suleiman the Magnificent and forced to withdraw to Malta (Mayer 2005; Murray 2006). During this period of time, they built anew or fortified with huge walls the already existing castles. In particular, they fortified the city of Rhodes with the Palace of the Grand Master where one of the two only umbilicate (*spiriplan*) populations of the island are found (Glaubrecht 1993a, 1993b); haplotype 27 (co-occurring on the island and Israel) is indeed carried by land snails collected on the rampart of one of the city gates (D'Amboise gate; Table 1). It is thus not difficult to envision these historical events as being responsible for the unusual geographic distribution of some of the mtDNA haplotypes we identified in the study (Figs 1 and 2). It would be interesting to expand this study to include samples of *Levantina* from Cyprus; the island was never connected to the Anatolian mainland but served as the first stronghold or retreat of the Crusaders after they had to leave the Levant following the fall of Acre in 1291.

We are aware that the scenario presented in here – although fascinating – is not the only possible one. Due to the sub-optimal quality of most of the samples at our disposal, we were able to sequence short gene fragments. This implies that we could have easily missed out on rare genetic variants. In addition, Örstan (2004) already suggested that three disjunctive records of *L. spiriplana* in western Turkey, just north of the region considered of this present study, could be due to introduction by humans during the Ionian period, perhaps on ballast rocks. Similarly, Welter-Schultes (1998) suggested that some *Albinaria* species that are found aestivating on rocks in Crete might have been carried to places outside their natural ranges on rocks used for construction or as ballast in ships. More recently, the same author (Welter-Schultes 2008) provided direct evidence that land snails have been carried on ships for more than 3,000 years in the Mediterranean area by describing shells discovered in the underwater archaeological excavations of a Late Bronze Age (3,300 years BP) shipwreck at a Southern Turkey location. Däumer et al (2012 and references therein) revealed a complex scenario in the invasive land snail *Theba pisana* suggesting that primarily human activities rather than natural processes have shaped (and still are) the distribution of the taxon. The authors also suggested that different lineages identified on genetic bases only could have different adaptive and invasive potentials, unveiling a complex scenario where different forces at different levels (from the ecological to the genomic one) could come into play.

The data presented in here, along with the similar evidence existing for the area mentioned in the previous paragraph, suggest that two different layers of complexity (natural colonization vs. historical human activities) should be considered when addressing puzzling distributions in an area interested by intense human activi-

ties since historical times. Also, this study represents a starting point for further investigations based on a more extensive sampling in terms of geographic and taxon coverage as well as molecular markers.

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