

The presence of the recurrent veinlet in the Middle Jurassic Nymphidae (Neuroptera): a unique character condition in Myrmeleontoidea

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Abstract

A well-developed recurrent veinlet is found in the forewing of two species of Nymphidae from the Middle Jurassic locality of Daohugou (Inner Mongolia, China), *Liminymphe makarkini* Ren & Engel and *Daonymphe bisulca* **gen. et sp. n.** This is the first record of this trait in the clade comprised of the superfamilies Myrmeleontoidea and Chrysopoidea. We interpret the recurrent veinlet in these species as a remnant of the condition present more basally in the psychopoid + ithonoid + chrysopoid + myrmeleontoid clade (i.e., as a plesiomorphy). Other venational character states of *D. bisulca* of interest include the configuration of subcosta anterior (ScA), which is very similar to that of extant Nymphidae. We consider the short ScA terminating on ScP to be an autapomorphy of Neuroptera.

Keywords

Neuroptera, Nymphidae, recurrent veinlet, subcosta anterior, Daohugou, Middle Jurassic

Introduction

Understanding the evolution of particular morphological characters during the broad historical development of higher insect taxa is a very interesting and important question. In fact, the phylogeny of a taxon may be realistic only if the evolutionary transformations of all available characters are correctly interpreted (Hennig 1981; Bechly 2000; Kukalová-Peck 2008).

The forewing humeral veinlet (i.e., the proximal-most veinlet of ScP) in all Neuroptera (and generally in all Neoptera) is plesiomorphically a simple, crossvein-like. However, in some families of Neuroptera it is curved, obviously directed towards wing base (i.e., recurrent), and often profusely branched. This condition (the recurrent veinlet for short) is one of the significant informative venational characters found within this order. It is characteristic of several families and subfamilies, the vast majority of which have the costal space basally dilated (see below). However, it was hitherto not found in any of numerous species of the clade comprised the superfamilies Myrmeleontoidea (Nymphidae, Nemopteridae, Ascalaphidae, Myrmeleontidae, Palaeoleontidae and Babinskaiidae) and Chrysopoidea (Chrysopidae, Mesochrysopidae and Ascalochrysidae) (Yang et al. 2012: fig. 32). The costal space in the vast majority of species of this clade is basally narrowed.

Nymphidae are generally accepted to be the most basal family in the superfamilies Myrmeleontoidea, and the only myrmeleontoid family known from the Jurassic. In general, 18 fossil (named) species are known in the family (Krüger 1923; Carpenter 1929; Panfilov 1980; Makarkin 1990a, b; Ponomarenko 1992a; Martins-Neto 2005; Menon et al. 2005; Ren and Engel 2007; Engel and Grimaldi 2008; Archibald et al. 2009; Jepson et al. 2012; Shi et al. in press). Here, we report the occurrence of a recurrent veinlet in the two oldest known specimens of Nymphidae, recovered from the Middle Jurassic Daohugou locality, China: *Liminymphe makarkini* Ren & Engel, 2007; and a new species, described here. Three other nymphid specimens are known from that locality; the recurrent veinlet appears to be absent in one (but its humeral area is poorly preserved), and the basal portion of wings is missing in other two (Shi et al. in press). In this paper, we re-describe *L. makarkini*, describe a new genus and species, and discuss the occurrence of the recurrent veinlet in neuropteran taxa and its possible phylogenetic implications. Also, we discuss the presence of the distinct subcosta anterior in *Daonymphe bisulca* gen. et sp. n. We consider ScA terminating on ScP to be an autapomorphy of Neuroptera.

Material and methods

This paper is based on two specimens collected from the Daohugou locality and housed in the Key Laboratory of Insect Evolution and Environmental Changes, College of Life Sciences, Capital Normal University, Beijing, China (CNUB; Dong Ren,

curator). Daohugou Village is situated in Shantou Township, Ningcheng County, Inner Mongolia, China. The insect-bearing beds of the Daohugou locality are considered to belong to the Jiulongshan Formation, and are dated as Bathonian, Middle Jurassic (Gao and Ren 2006) or Bathonian to Callovian (Middle to late Middle Jurassic) (Yang et al. 2012).

The specimens were examined under a Leica MZ12.5 dissecting microscope; line drawings were prepared with CorelDraw 12 graphics software and Adobe Illustrator CS5 with the aid of Adobe Photoshop CS3; photographed by a Nikon SMZ1000 stereomicroscope; the whole specimens were photographed by Nikon D100 Digital Camera.

Terminology and abbreviations. Wing venation terminology in general follows Kukalová-Peck and Lawrence (2004), except that we treat the median vein as in Yang et al. (2012). Terminology of wing spaces and details of the venation (e.g., subcostal veinlets) follows Oswald (1993).

Venational abbreviations. AA, analis anterior; AP, analis posterior; Cu, cubitus; CuA, cubitus anterior; CuP, cubitus posterior; M, media; MA, media anterior; MP, media posterior; R, radius; RA, radius anterior; RP, radius posterior; RP1, proximal-most branch of RP; rv, recurrent veinlet; ScP, subcosta posterior.

Systematic paleontology

Order Neuroptera Linnaeus, 1758

Family Nymphidae Rambur, 1842

Genus *Daonymphes* gen. n.

<http://zoobank.org/17B6B9EB-D7C9-46A1-A8F9-0F5631FDA7B7>

<http://species-id.net/wiki/Daonymphes>

Type and only species. *Daonymphes bisulca* sp. n.

Diagnosis. Forewing broad proximally [strongly narrowed proximally in *Liminympa*]; vast majority of proximal subcostal veinlets forked [simple in all other Mesozoic genera]; crossveins between branches of MP absent [present in *Nymphites* Haase, 1890, *Mesonymphes* Carpenter, 1929]; CuP space broad, nearly two times as wide as intracubital space [nearly as wide as intracubital space in *Liminympa*].

Etymology. From Daohugou, the locality of the type species, and *Nymphes*, a genus-group name. Gender: feminine.

Remarks. This genus is most closely related to four other Mesozoic genera (*Nymphites*, *Mesonymphes*, *Liminympa* and *Sialium* Westwood, 1854) but clearly distinguished from these as indicated in the diagnosis. The latter genus is only known from single hind wing from the early Berriasian of Purbeck, England. In general, Nymphidae occur very rare in the Jurassic, only six specimens are known. The monotypic genera *Liminympa* (Middle Jurassic [Bathonian/Callovian]) of Dao-

hugou, China) and *Mesonymphes* (Late Jurassic [Tithonian] of Solnhofen, Germany) are represented by almost complete specimens possessing both fore- and hind wings. The type species of *Nymphites* from Solnhofen is represented by only two incomplete hind wings. Two species from Daohugou are assigned to this genus: one species (two specimens) have almost complete fore- and hind wings; the other only hind wings (Shi et al. in press).

***Daonymphes bisulca* sp. n.**

<http://zoobank.org/61D8C637-96AD-4D41-BEF6-270FE5F3A6BA>

http://species-id.net/wiki/Daonymphes_bisulca

Figs 1, 2, 6A

Diagnosis. As for the genus.

Description. Forewing 29 mm long as preserved (estimated complete length about 40 mm), 11.5 mm wide. Costal space relatively broad for entire length, narrowed basally. Humeral veinlet recurrent, with one short branch. Subcostal veinlets somewhat curved, mostly forked once or twice, shallowly, few deeply; several proximal veinlets simple. ScA well developed, terminating on ScP within humeral area. Subcostal space narrow, with several scarce crossveins. RA space relatively narrow, slightly narrowed towards wing apex, with relatively numerous crossveins. RP with nine preserved branches, becoming more closely spaced towards wing apex. Crossveins rather numerous over entire radial space, irregularly spaced. M forked distal of origin of RP. MA incomplete, simple for entire preserved length. MP distally pectinate, with six preserved branches, most of these forked once or twice; no crossveins detected between branches. Cu divided into CuA, CuP rather far from wing base. CuA distally pectinate, with six preserved branches, all forked once or twice; one series of crossveins between branches of CuA, continued CuP ('pseudo-CuP'). CuP long, strongly pectinately branched with nine long branches; of four proximal-most branches, two forked; all distal branches dichotomously forked; no crossveins detected. Eleven crossveins between CuA, CuP rather irregularly spaced. AA3+4 and its posterior branch deeply forked. Basal crossvein between CuP, AA3+4 very short; distal crossvein strongly oblique. AP1+2 deeply forked. AP3+4 not preserved. Membrane around one crossvein between MA, MP near MP and three crossveins between CuA, CuP near CuA broadly heavily shaded; most crossveins between RA, RP apparently broadly shaded, pale fuscous.

Material. Holotype CNU-NEU-NN2011119, deposited in CNUB; an incomplete forewing.

Type locality and horizon. Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China. Jiulongshan Formation, Middle Jurassic.

Etymology. From the Latin *bisulcus*, -a, -um, forked, divided into two parts, in reference to its forked subcostal veinlets.

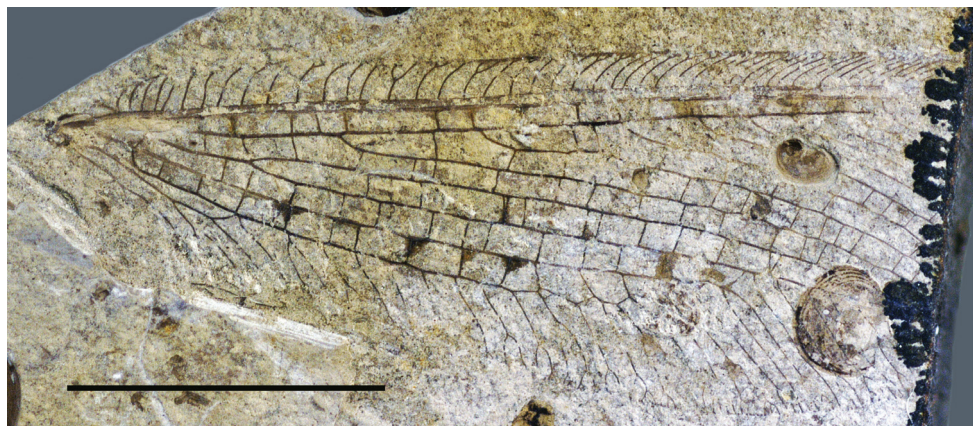


Figure 1. *Daonymphe bisulca* gen. et sp. n. Holotype CNU-NEU-NN2011119 as preserved. Scale bar = 10 mm.

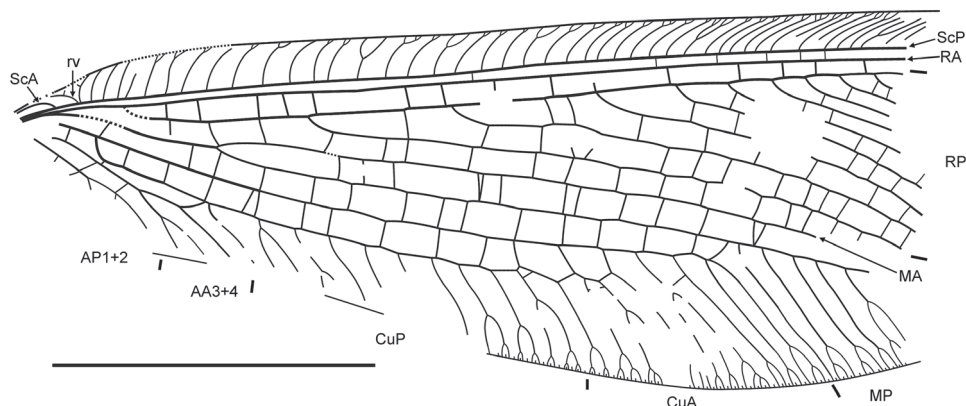


Figure 2. *Daonymphe bisulca* gen. et sp. n. Forewing venation of the holotype CNU-NEU-NN2011119. Scale bar = 10 mm.

Liminymphe Ren & Engel, 2007

<http://species-id.net/wiki/Liminymphe>

Liminymphe Ren & Engel, 2007: 212.

Type and only species. *Liminymphe makarkini* Ren & Engel, 2007, by original designation.

Diagnosis (revised). Forewing strongly narrowed proximally [broad proximally in *Nymphites*, *Daonymphe* gen. n. and *Mesonymphe*]; all veinlets of ScP simple [at least distal veinlets forked once or twice in *Nymphites*, *Daonymphe* gen. n.]; CuP space narrow, nearly as wide as intracubital space [nearly two times as wide as intracubital

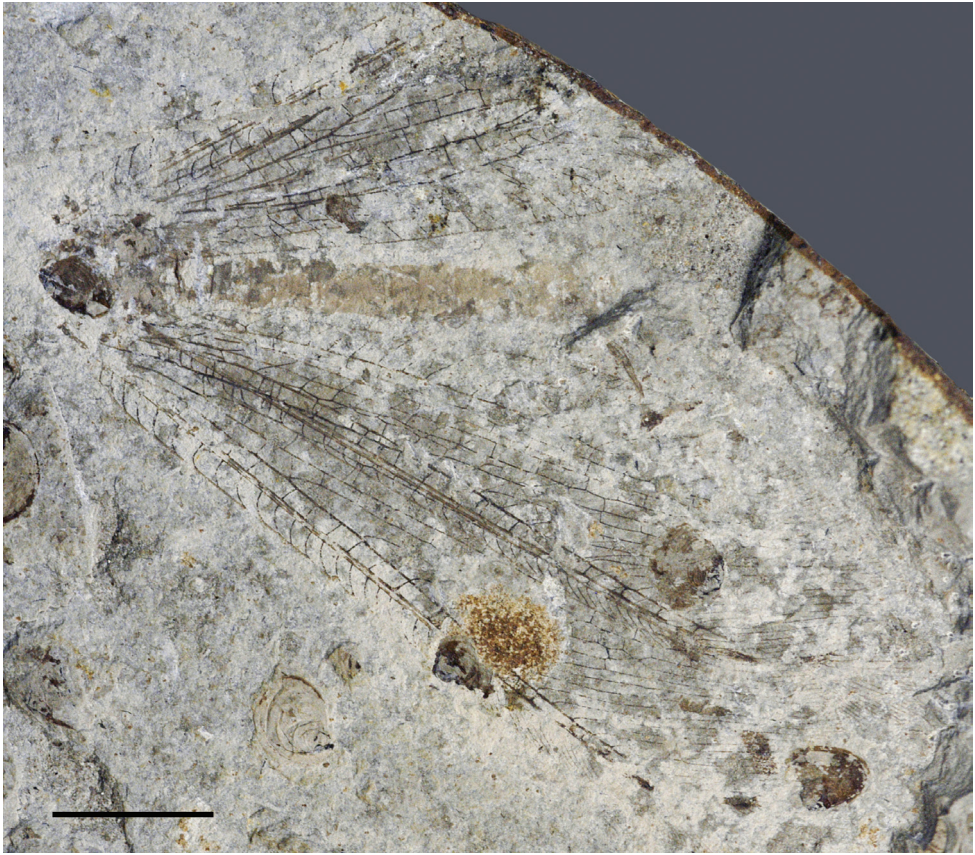


Figure 3. *Liminympa makarkini* Ren & Engel, 2007. Holotype CNU-NEU-NN1999024 (counterpart) as preserved. Scale bar = 5 mm.

space in *Nymphites*, *Daonymphe* gen. n. and *Mesonymphe*]. Hind wing MP with four pectinate branches [eight in *Sialium*]; branches of CuA not connected by crossveins [at least proximal branches of CuA connected by crossveins in *Nymphites*]; anterior branch of CuP simple [deeply forked in *Nymphites* and *Mesonymphe*].

***Liminympa makarkini* Ren & Engel, 2007**

http://species-id.net/wiki/Liminympa_makarkini

Figs 3–5, 6B

Liminympa makarkini Ren & Engel, 2007: 212, figs 1–3; Engel and Grimaldi 2008: 9; Yang et al. 2010: 177.

Redescription. Body (metathorax, abdomen) poorly, fragmentarily preserved. First abdominal tergite rather long; distally with distinct transverse suture, probably heavily

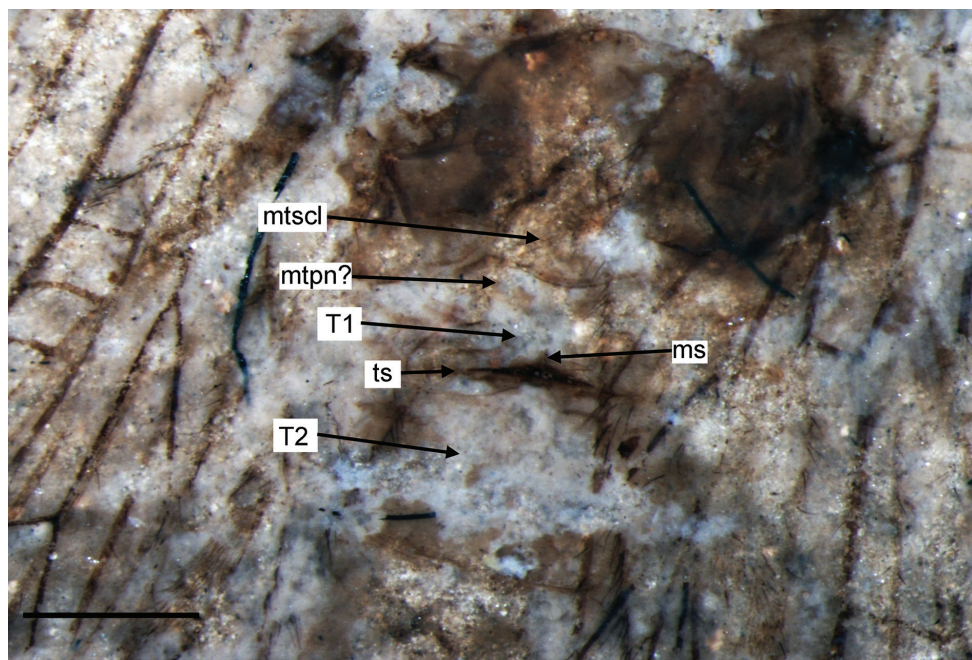


Figure 4. *Liminympa makarkini* Ren & Engel, 2007. Metathorax and the basal part of abdomen of the holotype CNU-NEU-NN1999024 (counterpart). Wetted with ethanol. Abbreviations: **ms**, mediolongitudinal suture of 1st abdominal tergite; **mtpn?**, metapostnotum; **mt scl**, metascutellum; **ts**, transverse suture of 1st abdominal tergite; **T1**, **T2**, 1st, 2nd abdominal tergites. Scale bar = 1 mm.

sclerotized; medially with mediolongitudinal short suture; portion of 1st tergite distal to transverse suture ('Transversalnaht' of Achtelig 1975) very narrow (Fig. 4). Second tergite nearly as wide as long. Other tergites indistinct.

Forewing elongate, narrowed in proximal portion, most dilated at distal 3/4 length; about 30 mm long, 8 mm wide. Costal space narrow, basally narrowed, distally dilated. All preserved subcostal veinlets simple, strongly oblique distally; veinlets of ScP+RA dichotomously branched. Humeral veinlet rather strongly recurrent, branching not detected (Fig. 6B). Subcostal space very narrow; two crossveins in distal part detected, others possible. RA spaces slightly narrower than costal space, narrowed towards apex; crossveins irregularly spaced for entire preserved portion. RP originates rather near wing base, with about 16 branches; RP1 originates far from origin of RP; at least four proximal-most branches widely spaced, more distal branches closely spaced. In right forewing, RP2 terminated at RP1; RP3, RP4 fused for short distance (probably aberrations). Crossveins between branches of RP very scarce, restricted to area between RP1 to RP5. M appears fused with R basally; forked at nearly equal distance from origin of RP, origin of RP1. MA long, slightly arched, distally few-branched. MP long, its anterior trace (stem of MP) nearly straight before terminal branching; with five long distal branches, quite strongly inclined. Crossveins between R/RP and MA, MA and

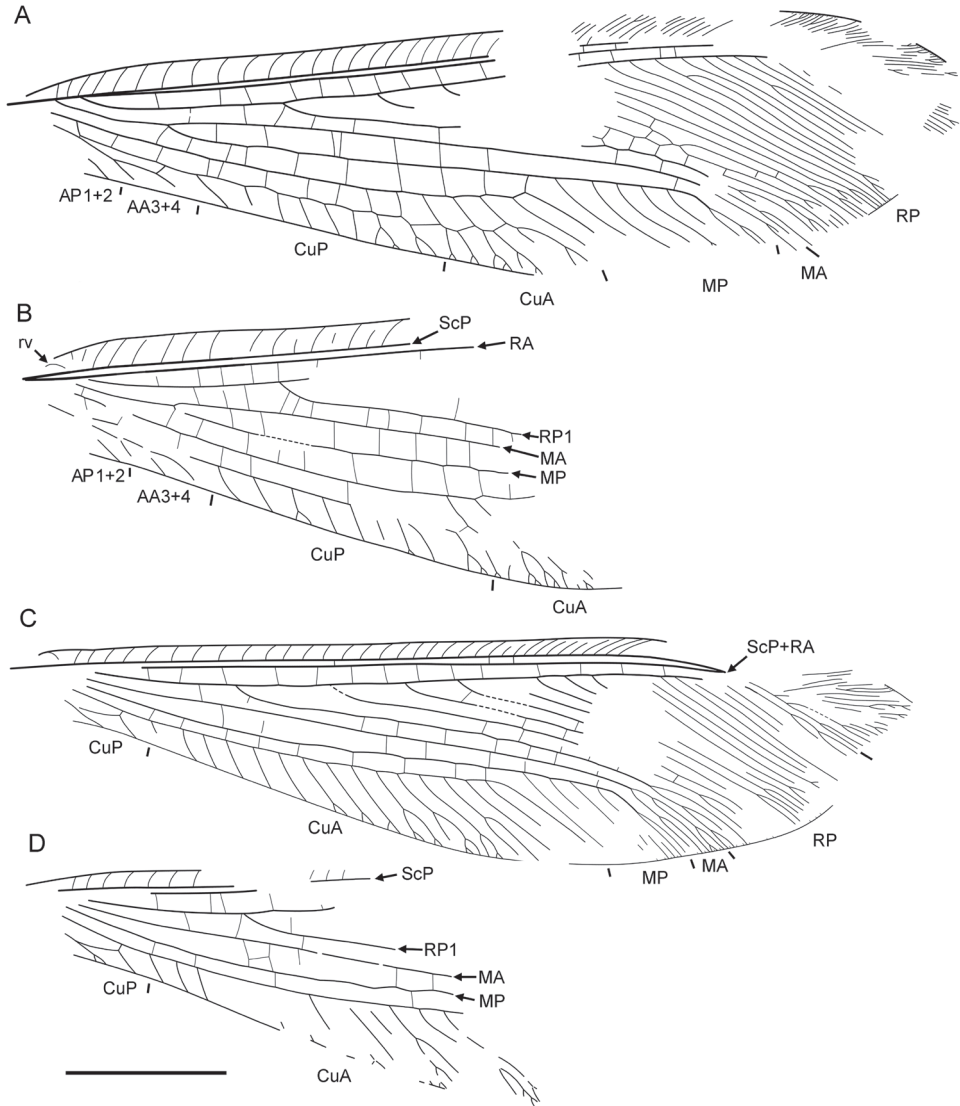


Figure 5. *Liminympa makarkini* Ren & Engel, 2007. Wing venation of the holotype CNU-NEU-NN1999024 **A** right forewing **B** left forewing **C** right hind wing **D** left hind wing. Scale bar = 5 mm (all to scale).

MP irregularly spaced, arranged differently in right, left wings. Cu dividing into CuA, CuP rather near to wing base. CuA long, smoothly curved anteriorly, pectinate with four long branches, each dichotomously branched. Between branches of CuA at last three crossveins forming gradate series continued CuP ('pseudo-CuP'). CuP long, pectinately branched, with seven-eight rather short branches, most simple. AA3+4 rather

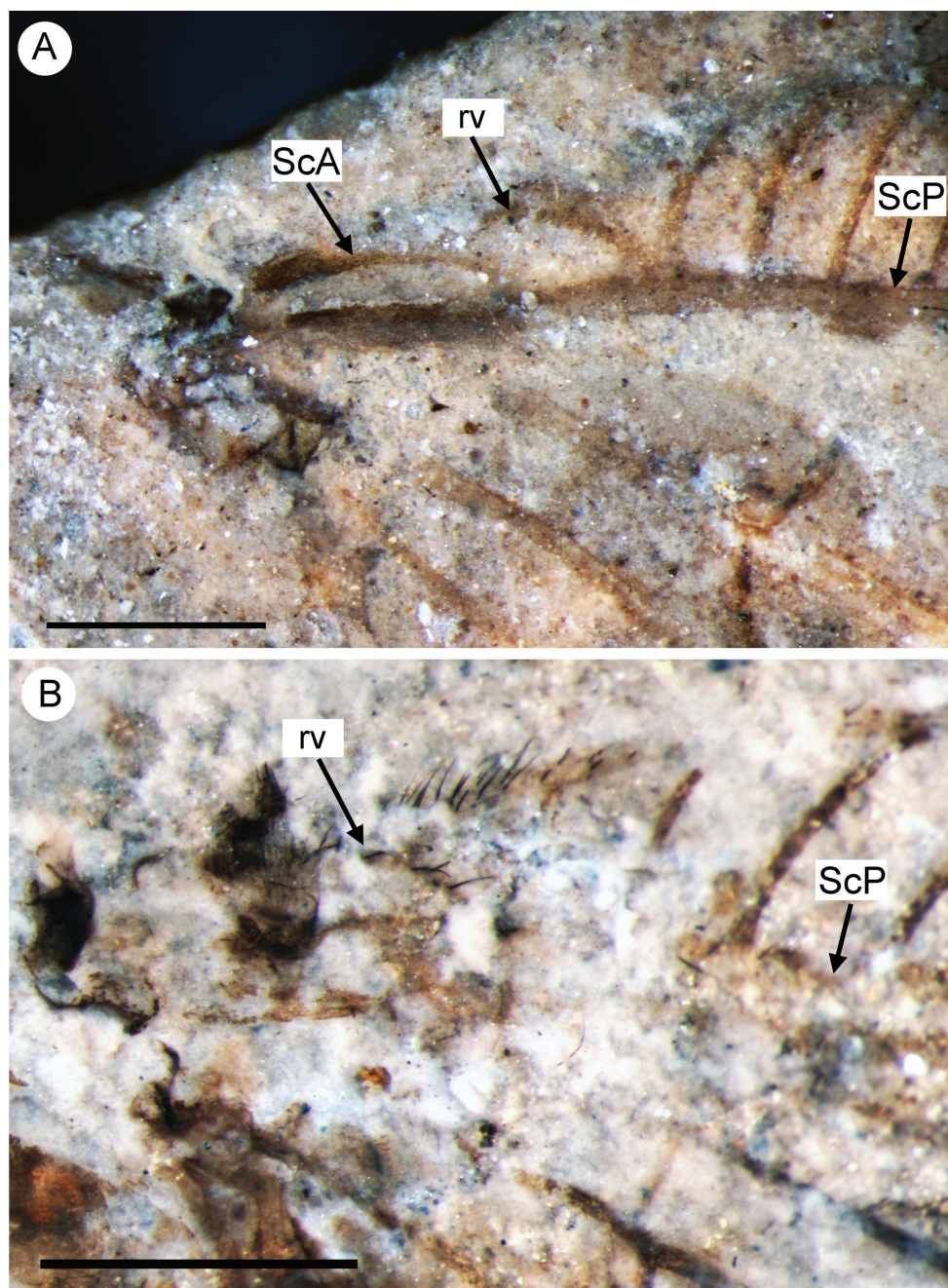


Figure 6. Basal portion of forewings of the Middle Jurassic Nymphidae showing the recurrent veinlet (rv) and the anterior subcosta (ScA) **A** the holotype of *Daonymphes bisulca* gen. et sp. n., CNU-NEU-NN2011119 **B** the holotype of *Liminympha makarkini* Ren & Engel, 2007, CNU-NEU-NN1999024. Both wetted with ethanol. Scale bar = 1 mm.

short; stem simple, with one or two simple branches. AP1+2 incompletely preserved, probably simple. AP3+4 not preserved. One dark rather big spot in distal portion of radial space might be present (apical half of other wing not preserved).

Hind wing similar in shape to forewing, slightly narrower; about 28 mm long, 7 mm wide. Costal space narrow, dilated distally. Subcostal veinlets simple, becoming more oblique, closely spaced, curved towards apex. Humeral veinlet bent to base, nearly straight, not branched. Subcostal space narrow; three crossveins detected, others possible. ScP, RA fused far from wing apex; preserved veinlets of ScP+RA long, dichotomously forked; crossveins between them not detected. RA space basally as wide as costal space, narrowed towards apex; crossveins rather regularly spaced for entire preserved portion (right wing). RP originated near wing base, with about 15 branches; RP1 originated far from origin of RP (but closer to wing base than in forewing); five proximal-most branches widely spaced, other (distal) branches closely spaced. Crossveins between branches of RP very scarce, restricted to area between RP1 to RP4. Origin of M and its fork not preserved. MA long, nearly straight, distally dichotomously branched. MP long, its anterior trace (stem of MP) slightly incurved, with four long distal branches, quite strongly inclined. Origin of Cu and its dividing into CuA, CuP not present. CuA long, pectinate, with 15 branches, which proximally simple, distally once or twice forked. CuP short, deeply forked. Distal crossvein between CuA, CuP rather short connecting CuA, anterior branch of CuP fork. Anal veins not preserved. Crossveins between R/RP and MA, MA and MP, MP and CuA poorly preserved, irregularly spaced, arranged differently in right and left wings; crossveins between branches of MP, CuA absent.

Material. Holotype CNU-NEU-NN1999024 (part, counterpart), deposited in CNUB; an incomplete specimen.

Type locality and horizon. Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China. Jiulongshan Formation, Middle Jurassic.

Remarks. This redescription is only based on the counterpart of the holotype.

Discussion

Recurrent veinlet

The recurrent veinlet is known in the following extant taxa of Neuroptera: all species of Psychopsidae and Ithonidae (including Polystoechotidae and Rapismatidae), the vast majority of Hemerobiidae; rarely in Berothidae (including Rhachiberothinae) and Mantispidae (only Symphrasinae).

The recurrent veinlet has not been detected in any Permian Neuroptera (Permian Ithonidae, Archeosmylidae) and the majority of Triassic taxa represented by these two families, and ‘Mesoberothidae’; however the basal portion of the forewing in any reported specimen of the latter is poorly preserved (e.g., Riek 1955; Lambkin 1988; Vilesov and Novokshonov 1994; Vilesov 1995; Novokshonov 1996; Jell 2004; VM,

pers. obs.). In Triassic Neuroptera, the recurrent veinlet is only found in those taxa that have the costal space strongly dilated basally, i.e., the psychopsoidea (Psychopsidae, Osmolypsychopidae, and broad-winged taxa whose family affinities are not yet clear). These are: (1) several undescribed Osmolypsychopidae from the Ladinian/Carnian Madygen Formation (Kyrgyzstan) (see Shcherbakov 2008: fig. 6); (2) *Triassopsychops superbis* Tillyard, 1922: fig. 89; (3) *Archeopsychops triassicus* Tillyard, 1919: fig. 27; (4) possibly in *Osmolypsychops spillerae* Tillyard, 1923: fig. 93 (however see Lambkin 1992: fig. 2), and (5) *Petropsychops superbis* Riek, 1956: pl. 1, fig. 2 (see also Grimaldi and Engel 2005: fig. 9.15) (all from the Carnian Ipswich Series of Australia). Of these taxa, the recurrent veinlet is most clearly visible in one of the Osmolypsychopidae wings from the Madygen Formation, where it is strongly curved towards the wing base and has eight branches (VM, pers. obs.). In the Australian taxa, the recurrent veinlet is poorly preserved.

Of the Early Jurassic Neuroptera, the recurrent veinlet is detected in all psychopsoidea whose forewing base is well preserved (e.g., Tillyard 1933: fig. 2; Ansoerge 1996; fig. 52) and in Prohemerobiidae. The latter family, however, remains undefined; we treat it as containing only the type genus *Prohemerobius* Handlirsch, 1906 (probably paraphyletic), recorded from the Early Jurassic of Germany and England (Handlirsch 1906–1908, 1939; Bode 1953; Whalley 1988; Ponomarenko 1995) and the Late Jurassic of Mongolia (Khramov 2011). The majority of species in this genus have the basal portion of the forewing costal space missing or poorly preserved. Still, some species (including the type species *Prohemerobius dilaroides* Handlirsch, 1906) possess the recurrent veinlet, configured similarly to that of the Middle Jurassic Nymphidae, i.e., with few (or one) simple branches (J. Ansoerge, VM, pers. obs.). The wings of *Prohemerobius* are not of the psychopsoid type; they are small, relatively narrow with hemerobiid-like venation, and the costal space is narrow compared with those of psychopsoidea. All known Early to Middle Jurassic Parakseneuridae possess a very well developed recurrent veinlet, along with up to 15 dichotomously forked branches (Yang et al. 2012: figs 1, 25, 30). All Jurassic to Cretaceous Osmolypsychopidae and Psychopsidae have the recurrent veinlet (e.g., Peng et al. 2010: fig. 3A; VM, pers. obs.). Some species of the Middle Jurassic to Early Cretaceous family Kalligrammatidae possess the well-developed recurrent veinlet (e.g., Yang et al. 2009: fig. 3, Yang et al. 2011: figs 2, 3A, Ponomarenko 2002: fig. 254); however, this condition is obviously absent in other species, even from the Middle Jurassic (VM, QY, pers. obs.).

The costal space in all numerous undescribed Ithonidae from the Middle Jurassic locality of Daohugou is basally narrowed, and therefore, the recurrent veinlet (where well developed) has short simple branches. Sometimes, the humeral veinlet is not branched and crossvein-like (VM, pers. obs.). Younger Ithonidae (Early Cretaceous to Recent) have the costal space usually broader basally and have a well developed recurrent veinlet (e.g., Archibald and Makarkin 2006: figs 5B, 8D, 9A; Makarkin and Archibald 2009: fig. 3; Makarkin et al. 2012: figs 3D, E). All species of the Middle Jurassic to Early Cretaceous subfamily Mesomantispinae possess a rather well developed recurrent veinlet (Makarkin 1996: fig. 1; Jepson et al. 2013: figs 1C, 2D, 4B).

A similar recurred veinlet is present in the extant subfamily Symphrasinae, the single fossil species of which is known from the middle Eocene of Messel, Germany (Wedmann and Makarkin 2007). Other Mantispidae (both fossil and extant) do not possess the recurred veinlet. All fossil Hemerobiidae, including the oldest known specimens from the Late Jurassic and Early Cretaceous have well-developed recurred veinlet (e.g., Henriksen 1922: fig. 4; Panfilov 1980: fig. 91; Makarkin 1991: fig. 2a; Ponomarenko 1992b: fig. 4). Of the Berothidae, the well-developed recurrent veinlet is detected in the Late Jurassic to Early Cretaceous Mesithoninae (Panfilov 1980: figs 86, 87, 90; Ren and Guo 1996: fig. 6; Makarkin 1999: figs 2a, b, 4), and few other genera (e.g., *Plesiorobius* Klimaszewski & Kevan, 1986: fig. 2). In other berothids, the recurrent veinlet is poorly developed, only slightly recurrent and bearing few branches, or does not develop at all (e.g., Engel and Grimaldi 2008: figs 19, 21, 24, 25).

In the Mesozoic family Brongniartiellidae, the well-developed recurred veinlet with long branches is detected in two species from the Early Cretaceous of the Baissa locality, Transbaikalia (Makarkin 2010: fig. 3). The taxonomic affinities of several Mesozoic genera which bear a well developed recurrent veinlet are uncertain, e.g., *Sibithone* Ponomarenko, 1984: fig. 5a (Early/ Middle Jurassic of Novospasskoe, Siberia); *Osmylogramma* Ponomarenko, 1992b: fig. 5 (Early Cretaceous of Tsagan-Tsab, Mongolia); *Meilingius* Ren et al., 2002: fig. 2 and *Jurapolystoechotes* Ren et al., 2002 (both from Daohugou; pers. obs.).

The presence of the recurrent veinlet was long considered a plesiomorphic condition in Neuroptera (e.g., MacLeod 1970; Oswald 1993; Aspöck and Nemeschkal 1998) because the most ancient, ‘primitive’ extant families possess this condition (e.g., Ithonidae, Psychopsidae), and but it is absent in the youngest, more derived families (e.g., Myrmeleontidae, Ascalaphidae). More recently published phylogenetic analyses of the group place these families in more derived positions and thus the presence of the recurrent veinlet is now considered an apomorphic state evolving independently at least three times (Winterton et al. 2010; Winterton and Makarkin 2010; Yang et al. 2012). The origin of the recurrent veinlet throughout Neuroptera most likely occurred during in the late Permian to earliest Triassic (Figure 7). This condition was secondarily lost at least five times in those families of the clade ‘R’ that lack this condition; and was never possessed in families basal to this clade.

The two species described above from the Middle Jurassic locality of Daohugou are the oldest known record of Nymphidae, indeed, of Myrmeleontoidea. Myrmeleontoidea are believed to belong to the suborder Myrmeleontiformia, which also includes Psychopsidae (Aspöck et al. 2001) or all families of Psychopsoidea (Engel and Grimaldi 2008). According to our phylogeny (Yang et al. 2012: fig. 32), however, the clade comprising Myrmeleontoidea and Chrysopoidea is sister to the ithonoid clade, and that combined clade is sister to the psychopoid clade. Known psychopoid fossils are much older than those of Myrmeleontoidea, and the recurrent veinlet first appears in their Triassic representatives (see above). Therefore, the presence of the recurrent veinlet in the Middle Jurassic Nymphidae may be interpreted as a remnant of ancient condition occurring in the psychopoid + ithonoid + chrysopoid + myrmeleontoid

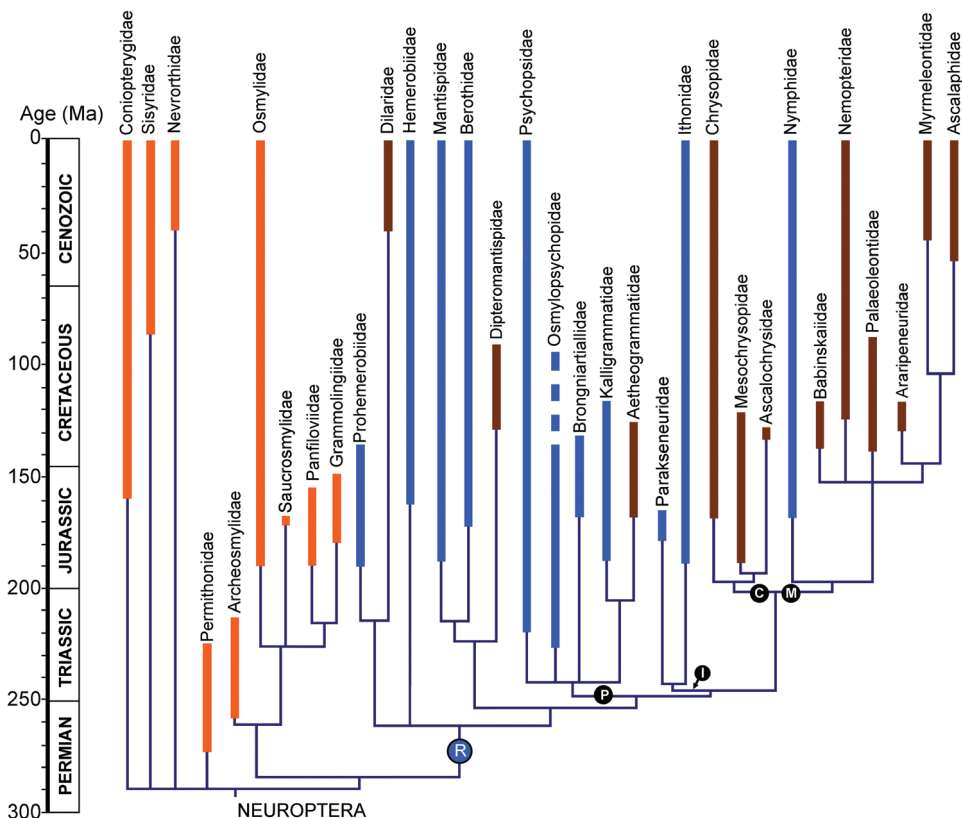


Figure 7. The occurrence of the recurrent veinlet through Neuroptera families. The phylogeny of the order is based on that of Yang et al. (2012), but modified according to the most probable relationships of families as discussed by Yang et al. (2012, 2013) and Makarkin et al. (2013). The families that we propose originally lacked the recurrent veinlet are represented in orange; R, families possessing the recurrent veinlet in blue, and those that we propose lost it secondarily in brown. **I** the ithonoid clade; **C** Chrysopoidea (the chrysopoid clade); **M** Myrmeleontoidea (the myrmeleontoid clade); **P** Psychopoidea (the psychopoid clade).

clade before separation of the clade Myrmeleontoidea + Chrysopoidea. This character condition was lost in other families of Myrmeleontoidea and Chrysopoidea, and in the younger Nymphidae.

The recurrent veinlet is known mainly in species whose costal space is basally dilated. The strong dilation of the basal portion of the costal space is characteristic of Neuroptera. It never occurs in other Holometabola including other Neuropterida orders, although in some taxa, the costal space is markedly dilated at some distance from wing base (e.g., Raphidioptera: Aspöck 1986; the mecopteran family Dinopanorpidae: Archibald 2005: figs 3A–D). The costal space of earlier Neuroptera (basal to the clade ‘R’) is also narrowed basally. The appearance and development of the recurrent veinlets and the strong dilation of the basal costal space are probably functionally and structur-

ally tied. However, in some Mesozoic Neuroptera which possess the recurrent veinlet the costal space is narrowed basally: the two species of the Middle Jurassic Nymphidae described here, and at least some Early Jurassic Prohemerobiidae and the Middle Jurassic Ithonidae. It seems reasonable that these taxa probably retained the recurrent veinlet after the costal space was secondarily narrowed in those lineages.

Subcosta anterior (ScA)

The ScA in all Neuroptera (when present) has a similar configuration: a short vein structure terminating on ScP before the recurrent veinlet. The structure of ScA of *Daonymphe bisulca* gen. et sp. n. is very similar to that found in extant Nymphidae, especially *Nymphes* Leach, 1814 (VM, pers. obs.) and closely related genera (e.g., *Austronymphe* sp.: see Riek 1967: fig. 3D). A similar ScA occurs in most extant Hemerobiidae (e.g., Makarkin 1993: fig. 13). Other extant Neuroptera have no distinct ScA, but a convex sclerotized bulge presented in the humeral area of most other families is considered as the modified ScA (Kukalová-Peck and Lawrence 2004). Of the fossil taxa, the ScA is present in the Mesozoic Kalligrammatidae (e.g., Yang et al. 2011: fig. 2) and Parakseneuridae (Yang et al. 2012: figs 24, 25, 30; QY, VM, pers. obs.). According to the hypothesis of Kukalová-Peck (1983), the ScA of the pterygote wing venation ground plan is a relatively short vein running to the costal margin with a strong subcostal brace connecting ScA and ScP midway (Kukalová-Peck 1983, fig. 15), or by other interpretation the ScA is divided midway into the anterior branch (ScA1+2) running to the costal margin and the posterior branch (ScA3+4) terminating on ScP (Kukalová-Peck 1991: fig. 6.3C). Such a primitive ScA is believed to present in the gigantic Carboniferous Bojophlebiidae (Riek and Kukalová-Peck 1984: fig. 20; Kukalová-Peck 1991: fig. 6.14A), although it appears to be poorly preserved (Prokop et al. 2010). In general, the configuration of ScA in some Paleozoic Palaeoptera is similar to that of Neuroptera in that ScA is terminating on ScP, i.e., in Dictyoneuridae (Palaeodictyoptera; see Kukalová 1970: figs 55, 59, 60, 73) and some families of Ephemeroptera (e.g., Carpenter 1979: figs 1, 8, 11); however, the ScA is branched in the latter order.

The ground-plan Neoptera wing venation is hypothesized to have ScA consisting of two separate veins with no common stem, ScA1+2 and ScA3+4; the former runs to the costal margin, the latter is terminated on ScP (Haas and Kukalová-Peck 2001: fig. 1; Kukalová-Peck 2009: fig. 14). Therefore, the ScA of Neuroptera may be interpreted as the homologue of this hypothesized ScA3+4, i.e., as the ground-plan neopteran ScA lost its anterior branch ScA1+2. ScA in other Neuropterida orders (Megalopectera, Raphidioptera) is configured similarly to most other winged insects, i.e., a vein terminating on the costal margin (Kukalová-Peck 1983: fig. 17A; 1991: fig. 6.16; Liu et al. 2013). Such a configuration of ScA is most developed in Orthoptera (e.g., Béthoux and Nel 2001: fig. 1). This state of ScA may be interpreted as the homologue of the hypothesized ScA1+2, i.e., as the ground-plan Neoptera ScA lost its posterior branch ScA3+4.

The configuration of ScA characteristic of Neuroptera (i.e., short and terminating on ScP) does not occur in other orders of Neoptera, and therefore may be considered as an autapomorphy. On the other hand, the similarities of ScA in Neuroptera and some Paleozoic Palaeoptera (see above) may indicate their homology, and therefore a symplesiomorphy. The latter, however, appears to be less probable than the former.

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A new species of *Peltidium* Philippi, 1839 (Crustacea, Copepoda, Harpacticoida) from the Pacific coast of Mexico

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Abstract

During the analysis of phytal meiobenthic samples collected from a rocky-sandy beach in the state of Nayarit, in the Mexican Pacific, several specimens of harpacticoid copepods were obtained and taxonomically examined. These specimens were found to represent an undescribed species of the peltidiid genus *Peltidium* Philippi, 1839. The new species, *P. nayarit* **sp. n.** is described herein. It resembles *P. nichollsi* Geddes and *P. lernerii* Geddes from Bahamas but also the widespread *P. speciosum* Thompson & Scott and *P. purpureum* Philippi. The new species from the Mexican Pacific differs from its known congeners by its possession of a unique combination of characters, including a modified pectinate seta on the antennary exopod, three terminal setae on the second endopodal segment of leg 1, third exopodal segment of leg 1 with three elements, inner terminal claw twice as long as outer claw, female fifth leg with 5 exopodal setae, exopodal setae I–III stout, spinulose and seta IV being as long as seta V. This is the second species of the family known to be distributed in the Eastern Tropical Pacific and in Mexico. Pending additional data, the distribution of this species appears to be restricted to this area of the Mexican Pacific.

Keywords

Crustacean fauna, marine copepods, phytal meiobenthos, associated copepods, taxonomy

Introduction

Research on phytal meiobenthos has been advancing in many regions, but there are large areas in which this important community has received little attention (Song et al. 2010). Taxonomic study of these communities is a basic step in monitoring their abundance and diversity patterns. Members of the harpacticoid copepod family Peltidiidae Claus are usually recorded from sandy beaches and live associated with algal patches. They have dorso-ventrally flattened bodies adapted to cope with the strong water flow related to their habitat (Hicks 1986). Currently, this family contains 9 genera (Boxshall and Huys 2013) that represent different lineages of which *Peltidium* Philippi and *Parapeltidium* Scott appear to be closest to the ancestral forms (Hicks 1986). The genus *Peltidium* is the most diverse group among peltidiids. It is known to contain 24 species (Boxshall and Halsey 2004, Wells 2007) but the number of species assigned to this taxon has varied depending on the authors criteria. Nicholls (1941) recognized 19 species, Lang (1948) included 15 and Bodin (1997) recognized 14 species. Wells (2007) recognized that several nominal species that have been assigned to this genus still have an uncertain status.

Playa Careyeros (Fig. 1) is a rocky-sandy area on the southern coast of Nayarit, on the Pacific coast of Mexico. It is influenced by the California Current and the North Equatorial current, with high salinity, temperature gradients and local patterns of coastal circulation (Serviere et al. 1993). During a survey of the local phytal meiofauna, har-

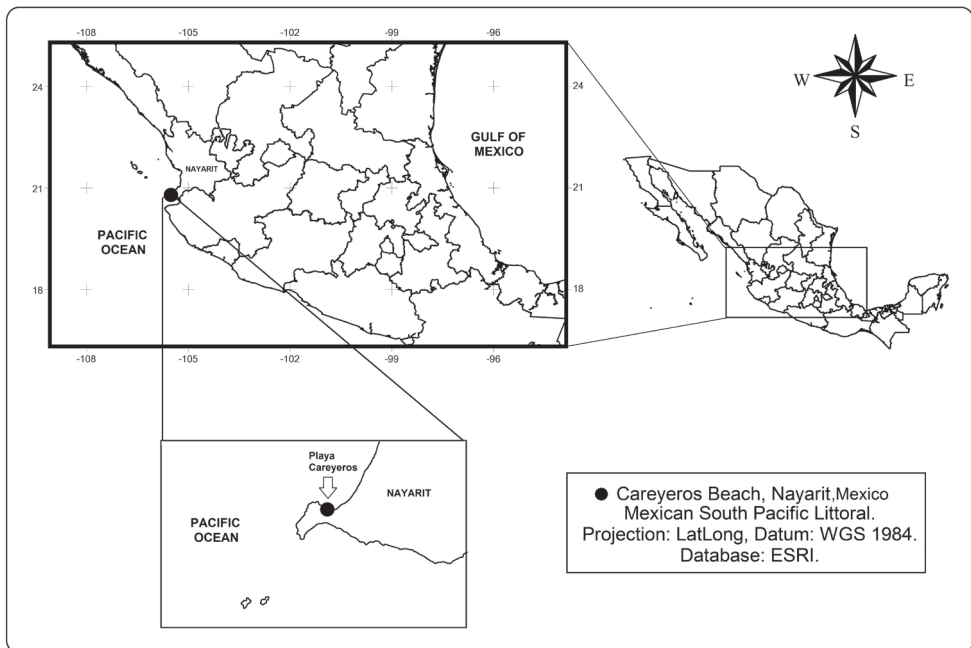


Figure 1. Location of Playa Careyeros, in the State of Nayarit, on the Pacific coast of Mexico, the type locality of *Peltidium nayarit* sp. n.

pacticoid copepods were sorted from samples obtained in algal patches. Several specimens of an harpacticoid copepod that represents a previously undescribed species of the peltidiid genus *Peltidium* Philippi, 1839 were recorded and taxonomically studied. The new species is here described and illustrated; it is compared with its known congeners.

Methods

A biological survey of the littoral habitats of Playa Careyeros, Nayarit was performed in March 2013. Qualitative samples of algae were taken manually during free diving samplings in the littoral environments of the surveyed area, mainly of algae associated with coral rock at depths not exceeding 3 m. Harpacticoid copepods were extracted by washing the sample through a set of 1.1 and 0.59 mm sieves. Copepods were fixed in 96% ethanol and were then sorted from the original samples and transferred to 70% ethanol with glycerine for long-term preservation. Selected specimens were then placed in glycerol for taxonomical examination and dissection. The dissected appendages were mounted on slides using glycerol as mounting medium and sealed with Entellan®, a fast-drying sealant. Figures were drawn with the aid of a camera lucida. Observations were made with an Olympus BX51 with Nomarski DIC microscope. Morphological terminology follows Huys and Boxshall (1991) and Huys et al. (1996), the systematic arrangement and authority of the family follows Wells (2007). Type specimens were deposited in the Collection of Zooplankton at El Colegio de la Frontera Sur, Chetumal, Mexico (ECO-CHZ) and in the National Museum of Natural History, Smithsonian Institution (NMNH-SI), Washington, D.C.

Results

Order Harpacticoida Sars, 1903

Family Peltidiidae Claus, 1860

Subfamily Peltidiinae Claus, 1860

Genus *Peltidium* Philippi, 1839

Peltidium nayarit sp. n.

<http://zoobank.org/A29D34BE-E213-4840-828D-E39DEEC78E22>

http://species-id.net/wiki/Peltidium_nayarit

Figs 2–4

Type material. Adult female holotype (ECO-CHZ-08979) partially dissected, mounted on glycerine sealed with Entellan®, Playa Careyeros, Nayarit, Mexico, coll. Jani Jarquín-González, Patricia Salazar and Ramiro Gallardo, March 23, 2013, depth=2–3 m, algal patch from coral rock. Paratypes: three adult females, partially dissected, slides, mounted in glycerine sealed with Entellan®, same site, date, and collector (ECO-

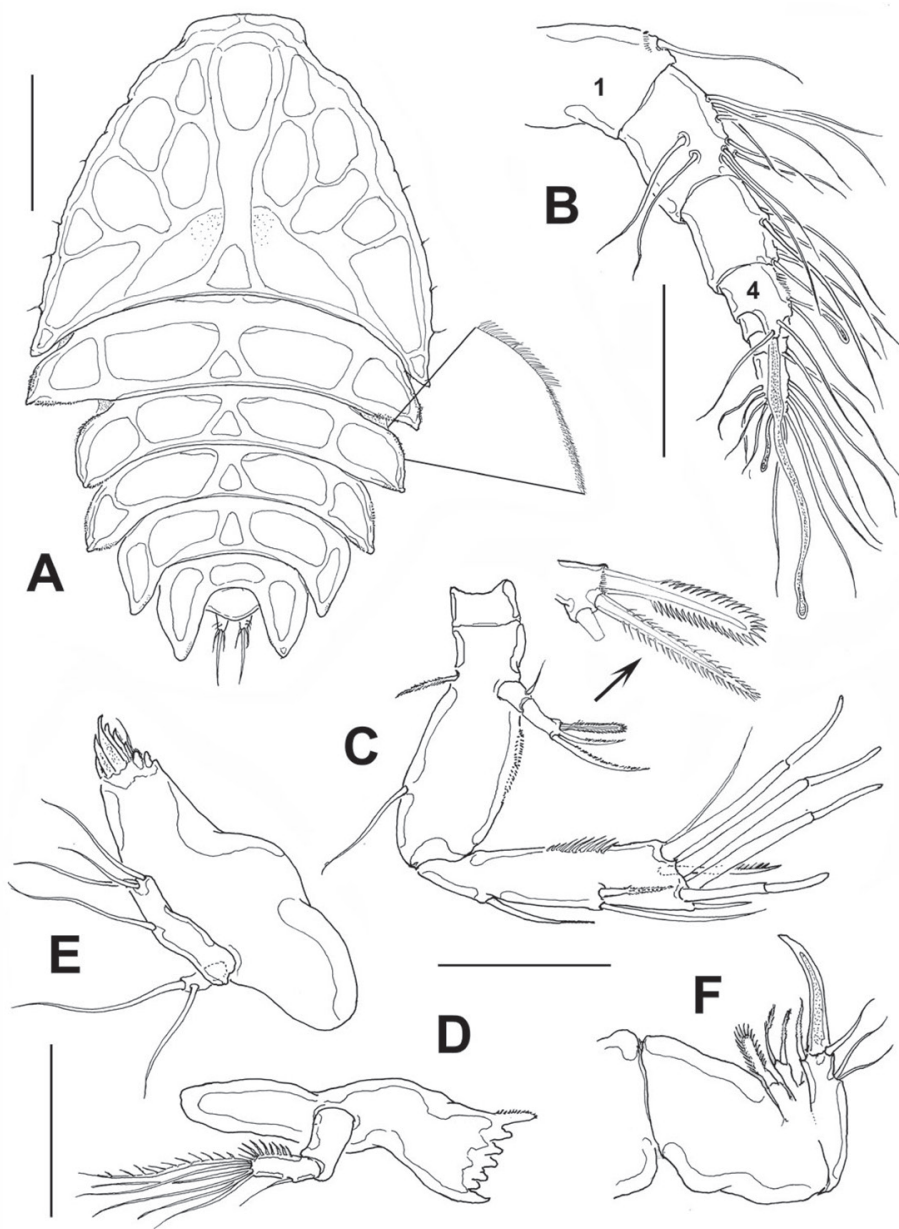


Figure 2. *Peltidium nayarit* sp. n., from Playa Careyerros, Nayarit, Mexican Pacific. **A** adult female, habitus, dorsal view, showing detail of ornamentation of epimeral processes of cephalothorax **B** antennule **C** antenna **D** mandible **E** maxillule **F** maxilla. Scales bars: **A**= 250 μ m, **B–F**=100 μ m.

CHZ-08980), seven undissected adult female specimens preserved in ethanol, vial (ECO-CHZ-08981), same site, date and collector. Two undissected adult females (USNM-1221050), same sampling data.

Type locality. Playa Careyeros (20°46'59.46"N; 105°30'35.48"W), state of Nayarit, central part of the Pacific coast of Mexico.

Etymology. The species is named after the Mexican state of Nayarit, where this species was originally collected. The name of the species is a noun used in apposition.

Descriptions. *Female:* Body (Fig. 2A) broad, dorsoventrally flattened, arched along longitudinal axis. Cephalosome accounting for about half the body length, with its greatest width at first pedigerous somite, behind which the body gradually tapers posteriorly. Epimera of genital somite and preceding somite pointed and backwardly directed. Length of holotype: 1.03 mm measured from tip of rostrum to posterior margin of anal somite. Length range of type females from 0.93 mm to 1.05 mm, average length 0.96 mm, $n=16$. Rostrum fused to cephalosome, broad, downwardly directed.

Cephalosome with a few small, sparsely distributed sensilla on lateral margins (Fig. 2A), posterior margin smooth. Succeeding prosomites, bearing legs 2-4, with flat, laterally expanded subtriangular margins ornamented with a mixed pattern of long and minute spinules (detail in Fig. 2A). First urosomite, bearing leg 5, slightly longer than succeeding genital double-somite; posterior margin of genital double-somite smooth. Anal somite with rounded posterior margin; somite naked in dorsal view, but with a row of long setae along ventral margin (Fig. 3B). Anal area moderately deep, with inner rows of short setules along margin of anal operculum. Caudal rami cylindrical, about twice as long as wide, with 7 setae. Middle caudal apical seta (V) longest. Dorsal seta (VII) about half as long as ramus (Fig. 3C).

Antennule (Fig. 2B) 7-segmented; first segment slightly longer than second, ornamented with distal row of spinules. Armature of antennular segments (s =setae, ae =aesthetasc) as: 1(1), 2(10s), 3(6s), 4(3s+2ae), 5(1s), 6(2s), 7(9s+1ae). Aesthetasc on fourth segment long, about 70% of antennule length.

Antenna (Fig. 2C). Coxa small, Allobasis with short abexopodal seta and longitudinal patch of spinules on outer margin. Exopod two-segmented, elongated, first segment with short slender seta, second segment bearing three setae distally, distal margin with row of short spinules. One exopodal seta modified, with regular pectinate ornamentation along both margins (see detail in Fig. 2C). Free endopodal segment with outer row of long spinules, armed with one spine and two lateral setae plus seven distal setal elements, four of them being articulated stout setae.

Mandible (Fig. 2D) short, tapering distally. Gnathobasis with narrow diastema, armed with 5-6 monocuspidate teeth, plus stout dorsal seta fused to gnathobasis, ornamented with row of short setules. Mandibular palp small, represented by a subrectangular coxa-basis segment and a single-segmented endopod armed with an inner row of spinules, six terminal setae plus a single outer seta.

Maxillule (Fig. 2E). Praecoxal arthrite armed with eight teeth and one distal short seta. Coxa and basis fused, indistinguishable, with three terminal setae. Endopodite represented by one seta. Exopodite one-segmented, with two setae.

Maxilla (Fig. 2F). Syncoxa robust, short, with two endites, the proximal small and bearing one broad seta, distal endite cylindrical, armed with two subequal, pinnate

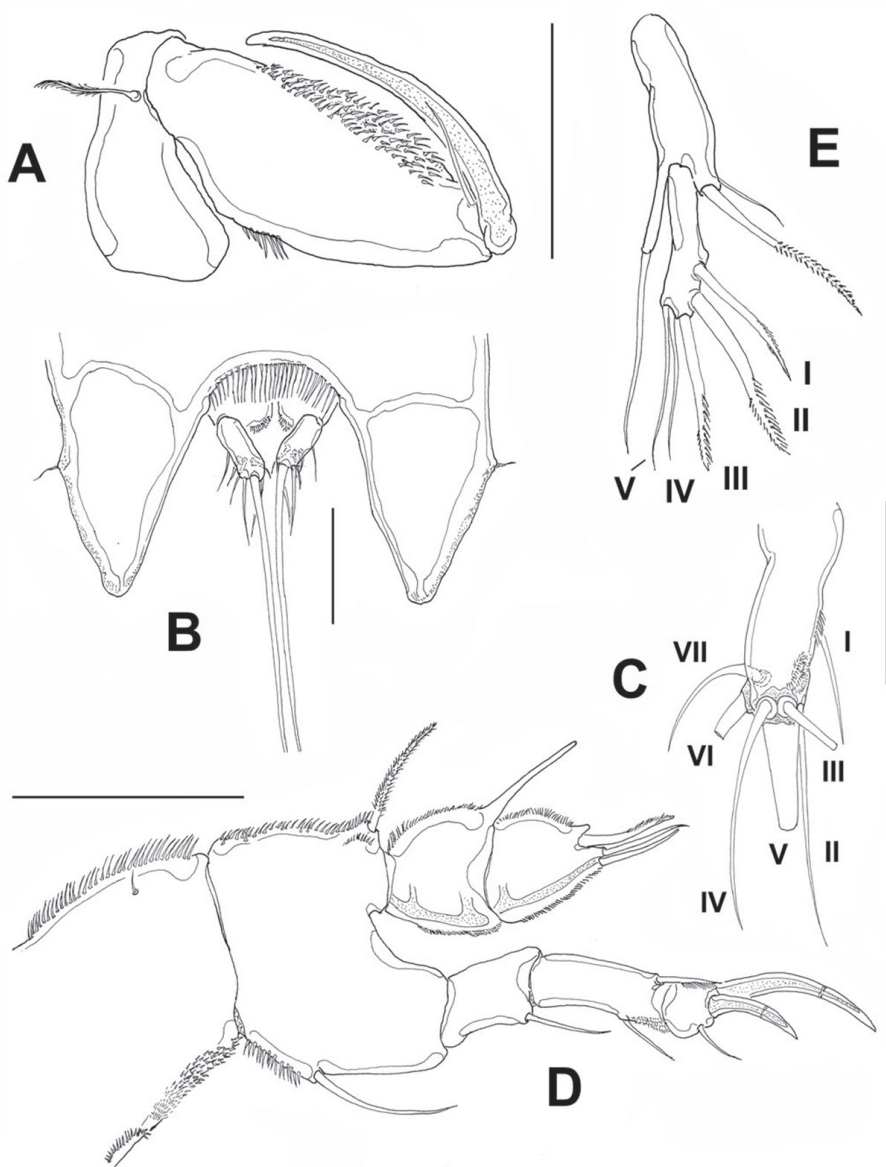


Figure 3. *Peltidium nayarit* sp. n., adult female from Playa Careyeros, Nayarit, Mexican Pacific. **A** maxilliped **B** urosome showing anal somite and caudal rami, ventral view **C** right caudal ramus, ventral view showing setation following nomenclature by Huys et al. (1996) **D** leg 1 **E** leg 5 showing setal nomenclature of exopodal setae following Wells (2007). Scale bars: **A**, **D**, **E**=100 µm, **B**= 50 µm, **C**=20 µm.

setae; allobasis forming a strong terminal claw and with one inner basal seta, one outer basal seta and two subequal outer endopodal setae.

Maxilliped (Fig. 3A) subchelate. Coxa and basis elongate. Basis with smooth surface, bearing a well-developed seta, as depicted. First endopodal segment robust, ornamented

with single row of spinules and large patch of spinules, as shown. Endopodal claw slender, slightly curved, about 1.3 times as long as basis, with single accompanying seta.

Leg 1 (Fig. 3D). Coxa elongate, ornamented with single row of small spinules on inner and outer margins, plus single short seta on inner middle part of segment. Basis wide, inner margin and part of outer margin ornamented with spinules. Inner distal basipodal seta reaching distal margin of first endopodal segment. Outer basipodal seta reaching distal end of basis. Exopod three-segmented, second exopodal segment longest, about 1.5 times as long as first segment, with patch of minute spinules on outer distal margin. Two exopodal claws on distal position of third exopodal segment; outer claw half as long as inner claw. Endopod two-segmented, shorter than exopod. Endopodal segments wide, globose (sensu Wells 2007), ornamented with rows of short setules along the inner and outer margins. Terminal elements include a spine ornamented with distal row of minute spinules and two equally long slender setae.

Leg 2 (Fig. 4A). Coxa small, basis transversely elongated. Basis with outer seta. Endopod three-segmented, longer than exopod, exopod reaching midlength of third endopodal segment. Exopod three-segmented, with spinules on outer margins of third segment and spinules at insertion of spines on first and second segments.

Leg 3 (Fig. 4B). Coxa, basis, and relative length of endopodal and exopodal rami as in leg 2. Endopod and exopod three-segmented.

Leg 4 (Fig. 4C). Coxa and basis as in leg 3. Exopod three-segmented, third segment with 8 setal elements. Insertion points of exopodal spines and outer margins of second and third exopodal segments with rows of spinules. Endopod three-segmented, slightly longer than exopod, outer margins of segments ornamented with rows of short spinules.

Armature of swimming legs 1-4 as in Table 1.

Leg 5 (Fig. 3E) exopod and baseoendopod separated. Baseoendopod bearing single inner seta. External seta long, borne on elongate cylindrical lobe of baseoendopod reaching half the length of exopodal lobe. Exopodite slender, with 5 setal elements (I-V) (sensu Wells 2007), two inserted on inner margin (I, II), three (III-V) distal. Elements I-III represented by stout, distally pinnate setae, elements IV and V represented by equally long slender setae.

Male: Unknown.

Remarks. The available keys to the species of *Peltidium* include those by Nicholls (1941), Lang (1948), and Wells (2007); when following the latter work, our specimens from Nayarit key down to a couplet leading to either *P. nicholli* Geddes, 1968 or *P. lernerii* Geddes, 1968, both from the Bahamas. These species share the following characters with *P. nayarit* sp. n.: female leg 5 with separate exopod and baseoendopod with 5 setae borne on distal and inner edges only; leg 1 with two-segmented endopod, distal endopodal segment with three setal elements; the number of setae on the distal endopodal segment of legs 2-4 is 3:5:4. The new species differs from these two Bahamian species in several characters, as follows. It diverges from *P. nicholli* in having a sharper frontal protuberance of the cephalosome and a longer cephalosome (length/width ratio= 1.26 vs. 1.43 in *P. nayarit* sp. n.). In the new species the outer basipodal seta of leg 1 is slender, inserted on the proximal half of segment, whereas this seta is

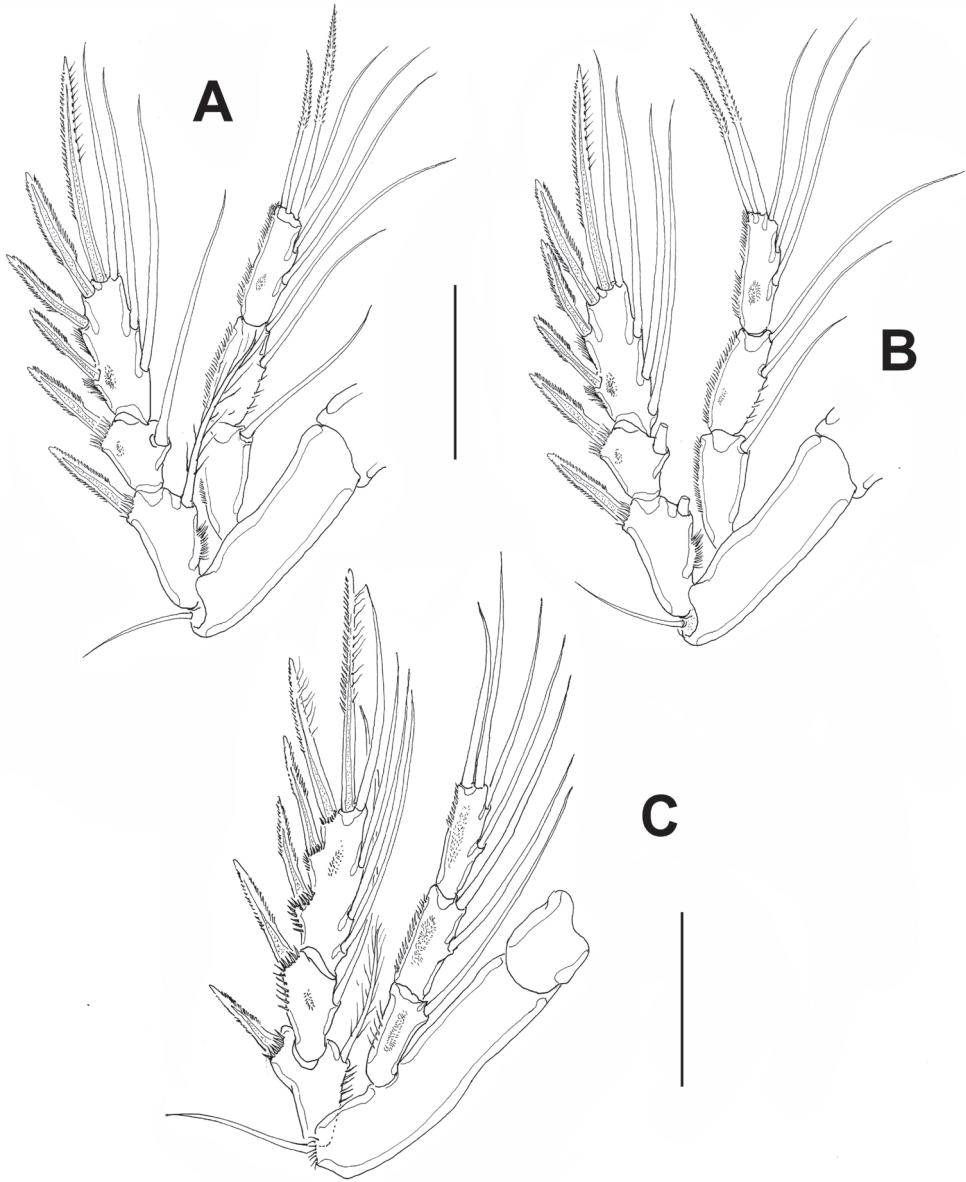


Figure 4. *Peltidium nayarit* sp. n., adult female from Playa Careyeros, Nayarit, Mexican Pacific. **A** leg 2 **B** leg 3 **C** leg 4. Scales bars: A–C=100 μ m.

stouter, shorter, and borne on the distal half of the basipod in *P. nicholksi*. The setal elements of both the exopod and endopod of leg 1 differ in these two species. The third exopodal segment *P. nicholksi* bears two strong, stout subdistal elements in addition to the pair of terminal claws (Geddes 1968, fig. 6B) vs. a single slender seta in *P. nayarit* sp. n. (Fig. 3D) and the terminal claws are equally long in *P. nicholksi*, whereas the in-

Table 1. Armature of swimming legs 1-4 (spines in Roman numerals, setae in Arabic) of *Peltidium nayarit* sp.n. Sequence follows external to internal positions.

	basis	endopod	exopod
leg 1	1-1	0-I; 2,I	1-0;1-1; 1,II
leg 2	1-0	0-1;0-2;II,1,2	I-0;I-1;III,I,1,2
leg 3	1-0	0-1;0-2;II,1,2	I-0;I-1;III,1,2
leg 4	1-0	0-1;0,2;2,2	I-1; I-1; III,I,1,3

ner claw is about twice as long as the outer one in the new species. In *P. nicholli* the three distal elements of the second endopodal segment have different lengths, whereas these elements are equally long in *P. nayarit* sp.n. Both species share the presence of one modified seta on the antennary exopod, but in *P. nicholli* only the tip of the seta is irregularly pectinate (Geddes 1968, fig. 7B), whereas in the new species this seta is regularly pectinate almost its entire length (see detail in Fig. 2C). Another species with a distally pectinate exopodal seta is *P. maldivianum* Sewell, 1940, but it differs in characters of leg 1 and leg 5 from both *P. nicholli* (see Wells 2007) and *P. nayarit* sp.n. The armature of leg 5 is also different between the new species and *P. nicholli*. In the latter, setae I and II are heavily pectinate (Geddes 1968, fig. 7G), they are also clearly shorter than setal elements III and V, and seta IV is shorter than elements III and V. In the new species elements I-III are not heavily pectinate but lightly spinulose (Fig. 3E), element II is longest and seta IV is almost as long as seta V.

The new species can be distinguished from *P. lernerii* by the armature of leg 1. In *P. lernerii* the exopodal claws are subequally long, whereas the inner is twice as long as the outer one in *P. nayarit* sp. n. In addition, the inner spiniform seta of the second endopodal segment is clearly shorter than the other two setae *vs.* an equal length of the three elements in the new species. Also, as indicated by Wells (2007), in *P. lernerii* the shape of the first endopodal segment is quadrate (Geddes 1968, fig. 8C), with straight outer margin and inner margin only slightly convex; this character allows distinction from the globose (i.e. both margins of segment convex) condition present in both *P. nicholli* and *P. nayarit* sp. n. The middle of the three antennary exopodal setae is the longest in *P. lernerii* (Geddes 1968, fig. 9B), but the corresponding seta is the shortest in the new species (Fig. 2C). Most importantly, the female leg 5 is different in these two species. In *P. lernerii* setal element IV is very reduced, about 1/3 as long as adjacent seta V (Geddes 1968, fig. 8G), whereas the same element is as long as seta V in the new species (Fig. 3E). A reduced seta IV is also present in *P. proximum* Nicholls, 1941 (Nicholls 1941). Also, the exopodal lobe is clearly shorter in *P. lernerii* (length/width ratio=1.8) (Geddes 1968, fig. 8G) than it is in *P. nayarit* sp.n., which is an elongate, slender structure (L/W ratio=4.14).

The new species shares also some important characters with *P. speciosum* Thompson and Scott, 1903 (see Nicholls 1941), including a leg 5 with a very similar armature and structure except for a relatively robust exopodal segment (length/width ratio= 3.7 *vs.* 4.2 in *P. nayarit* sp. n.) and a shorter outer baseoendopodal seta, reaching to about

half the length of exopodal seta V (Nicholls 1941, fig. 8), thus differing from the new species, in which the same seta almost reaches the distal end of seta V (Fig. 3E). In the new species one of the antennary exopodal setae is modified, as described (Fig. 2C), whereas *P. speciosum* lacks modified setae (Nicholls 1941 fig. 8). Several characters of leg 1 differ in these two species; in *P. speciosum*, the inner basipodal seta is relatively longer than in the new species, it reaches to about half the length of the second endopodal segment (Nicholls 1941, fig. 8), whereas it is clearly shorter in *P. nayarit* sp. n., barely reaching halfway along the first endopodal segment. The shape of the first and second endopodal segments differs in these two species, the first one is subquadrate as in *P. lernerii* (Nicholls 1941, Geddes 1968) and the second is subrectangular, with straight margins, thus diverging from the subtriangular shape present in *P. nayarit* sp. n. (Fig. 3D). Most importantly, in *P. speciosum* there are four setal elements on the second endopodal segment, thus diverging from the new species (and also from *P. lernerii* and *P. nichollii*), with only three such elements. The terminal exopodal claws of leg 1 are subequal in *P. speciosum* and diverge from the pattern described herein for *P. nayarit* sp. n. When Nicholls' (1941) work is followed to identify our specimens from Nayarit, we reach *P. purpureum*, which can be easily separated from the new species by its having 4 setal elements (2 claws, 2 setae) on the third exopodal segment of leg 1 vs. 3 elements (2 claws, 1 seta) in the new species, a different shape of the endopodal segments of leg 1, with narrower segments, and by its having 6 setal elements on the exopodal lobe of leg 5 instead of five found in *P. nayarit* sp. n. Also, *P. purpureum* has 3 maxillar endites (1 proximal, 2 distal) while *P. nayarit* and all other *Peltidium* species mentioned in this paper (except maybe *P. maldivianum*, whose maxilla has not been described) have lost the proximal endite.

Discussion

Peltidium is a very widely distributed genus with records from different regions of the world but it is not very diverse in a given area, for instance only three species are known from the Mediterranean: *P. gracile* (Claus, 1889), *P. purpureum* Philippi, 1839, and *P. robustum* (Claus, 1889) (Todaro and Cecherelli 2010), two species are known to occur in East Asia (Song and Yun 1999), and only five species of *Peltidium* have been known to occur in the Caribbean region (Varela 2005, Suárez-Morales et al. 2006). Records include the recently described *P. proximus* Varela, 2005 from Cuba, which should not be confused with Nicholls' (1941) *P. proximum* from South Australia. The Eastern Pacific region is not an exception, only a few species of Peltidiidae have been recorded and among them there are only some unidentified records of *Peltidium* (Lang 1965, Cordell 2006). Hitherto, there were no previous records of Peltidiidae in Mexican waters of the Atlantic and the Pacific oceans (Suárez-Morales et al. 2000). Recently, Gómez and Varela (2013) described a new species of the peltidiid genus *Alteutha* Baird, 1846 from Sinaloa, southern part of the Gulf of California, northwest Mexico. The finding of the new species *P. nayarit* represents the first species of *Peltidium* described

for Mexico and the second record of Peltidiidae known in this country. Because of the scarce taxonomical surveys of the phytal meiofauna in the Eastern Tropical Pacific, and the record of only one species of *Peltidium* so far, it is assumed that the family and genus diversity remains underestimated in the region.

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New species of *Agathodesmus* Silvestri, 1910 from Australia (Diplopoda, Polydesmida, Haplodesmidae)

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Abstract

The genus *Agathodesmus* Silvestri, 1910 is speciose and widespread in high-rainfall parts of eastern Australia. In addition to the type species *A. steeli* Silvestri, 1910 and *A. johnsi* Mesibov, 2009 from New South Wales and *A. bucculentus* (Jeekel, 1986) from Queensland, the following 18 new species are recognised: *A. adelphus* sp. n., *A. aenigmaticus* sp. n., *A. agnus* sp. n., *A. anici* sp. n., *A. gayundah* sp. n., *A. hahnensis* sp. n., *A. kerensis* sp. n., *A. kirrama* sp. n., *A. millaa* sp. n., *A. parapholeus* sp. n., *A. quintanus* sp. n., *A. sagma* sp. n., *A. summus* sp. n. and *A. yuccabinensis* sp. n. from Queensland; *A. carorum* sp. n. from New South Wales and Victoria; *A. bonang* sp. n. and *A. morwellensis* sp. n. from Victoria; and *A. chandleri* sp. n. from South Australia.

Keywords

Millipede, Diplopoda, Polydesmida, Haplodesmidae, Australia

Introduction

Agathodesmus Silvestri, 1910 was established for a single female of *A. steeli* Silvestri, 1910, a small polydesmidan millipede from New South Wales, Australia. In a recent paper (Mesibov 2009) I redescribed *A. steeli* from freshly collected males and females, and added a second New South Wales species to the genus. The two species share with *Atopogonus baccatus* Carl, 1926 (New Caledonia) and *A. bucculentus* Jeekel, 1986 (Queensland, Australia) a distinctive gonopod conformation: there is no cannula or prostatic

groove, and the telopodite is sharply bent mid-length at a 'knee' topped with a thin tab. In Mesibov (2009) I made *Atopogonus* Carl, 1926 a junior synonym of *Agathodesmus*.

In this paper I describe 18 new species of *Agathodesmus* and add a few observations on *A. bucculentus*. I collected specimens of four of the new species during field trips from 2006 to 2011. The remaining 14 species were found in the Australian National Insect Collection and the Queensland Museum, mainly among arthropods extracted from rainforest litter by the Berlese method.

The late C.A.W. Jeekel wrote of *A. bucculentus*: “With the discovery of a species of *Atopogonus* in what seems to be a perfectly natural habitat in Queensland it becomes likely that the genus is in essence a continental Australian taxon” (Jeekel 1986, p. 46). *Agathodesmus* is now known to be widespread and speciose in parts of eastern Australia with a mean annual rainfall greater than 1000 mm (Fig. 1). *Agathodesmus* is particularly diverse in the Wet Tropics of far north Queensland, which is home to 12 of the 21 known Australian species. The wide gaps in the genus distribution map suggest to me that more species remain to be discovered, especially in the wetter mountain forests of New South Wales, southeast Queensland and Victoria.

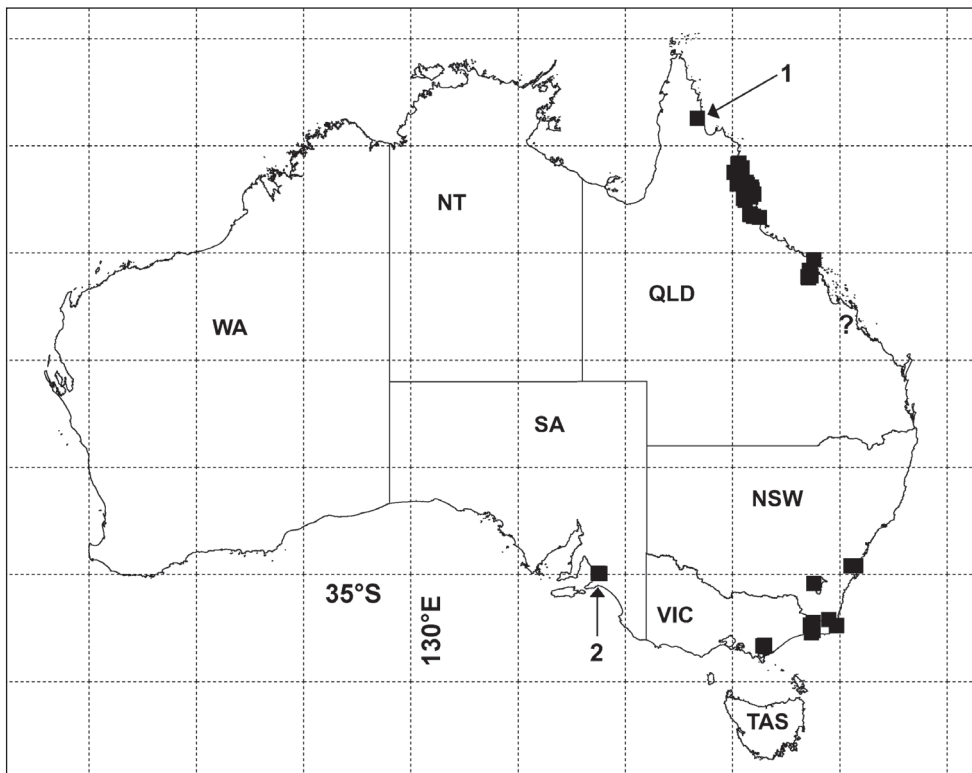


Figure 1. Localities for *Agathodesmus* spp. in Australia (filled black squares) as of July 2012. **1** = only known locality for *A. anici* sp. n. **2** = cluster of 4 localities for *A. chandleri* sp. n., **?** = questionable Cammoo Caves locality for *A. agnus* sp. n.; see Figs 11–13 for other species. Geographic projection, 5° latitude-longitude grid. NSW = New South Wales, NT = Northern Territory, QLD = Queensland, SA = South Australia, TAS = Tasmania, VIC = Victoria, WA = Western Australia.

Methods

'Male' and 'female' in the text refer to adult individuals. All specimens are stored in 75–80% ethanol in their respective repositories.

Gonopods were cleared in 80% lactic acid and temporarily mounted in 60% lactic acid for optical microscopy, while other body parts were temporarily mounted in a 1:1 glycerol:water mixture. Preliminary gonopod drawings were traced from photomicrographs taken at 160× through a binocular microscope. Measurements were made with a Nikon SMZ800 binocular dissecting microscope using an eyepiece scale, and are reported below to the nearest 0.5 mm. SEM images were acquired digitally using a FEI Quanta 600; some specimens were examined after air-drying and sputter-coating with platinum, while others were air-dried, examined and returned to alcohol. Images and drawings were prepared for publication using GIMP 2.8. Maps were generated using ArcView GIS 3.2.

The Appendix tabulates specimen data for all museum lots noted in the text. Locality details are given in all cases with latitude and longitude based on the WGS84 datum. Latitude/longitude data for Queensland Museum specimen localities are mainly taken from the Queensland Museum insect collection database, but some Mt Bellenden Ker data have been corrected following Mesibov (2012b). My estimate of the uncertainty for each locality is the radius of a circle around the stated position, in metres or kilometres.

Abbreviations: AM = Australian Museum, Sydney, NSW; ANIC = Australian National Insect Collection, Canberra, Australian Capital Territory; ANZSES = Australia New Zealand Scientific Exploration Society; NMV = Museum Victoria, Melbourne, Vic; NSW = New South Wales; Qld = Queensland; QM = Queensland Museum, Brisbane, Qld; SA = South Australia; SAM = South Australian Museum, Adelaide, SA; Vic = Victoria.

Taxonomy

Order Polydesmida Pocock, 1887

Suborder Polydesmidea Pocock, 1887

Family Haplodesmidae Cook, 1895

Agathodesmus Silvestri, 1910

<http://species-id.net/wiki/Agathodesmus>

Agathodesmus: Silvestri 1910:362. Attems 1914:282, 1940:487. Brölemann 1916:547, 587. Jeekel 1971:310; 1982:11; 1983:146; 1985:50, 51; 1986:46. Hoffman 1980:184. Simonsen 1990:57. Golovatch et al. 2009:2. Mesibov 2009:92.

Atopogonus: Carl 1926:386. Attems 1940:477. Verhoeff 1941:406. Jeekel 1971:314, 1984:88, 1986:46. Hoffman 1980:186, 1999:480. Simonsen 1990:57. Golovatch et al. 2001:185, 2009:2, 44. Mesibov 2009:92 (synonymised).

Type species. *Agathodesmus steeli* Silvestri, 1910, by original designation; of *Atopogonus*, *A. baccatus* (Carl, 1926), by monotypy.

Other assigned species: *A. adelphus* sp. n., *A. aenigmaticus* sp. n., *A. agnus* sp. n., *A. anici* sp. n., *A. bonang* sp. n., *A. bucculentus* (Jeekel, 1986), *A. carorum* sp. n., *A. chandleri* sp. n., *A. gayundah* sp. n., *A. hahnensis* sp. n., *A. johnsi* Mesibov, 2009, *A. kerensis* sp. n., *A. kirrama* sp. n., *A. millaa* sp. n., *A. morwellensis* sp. n., *A. parapholeus* sp. n., *A. quintanus* sp. n., *A. sagma* sp. n., *A. summus* sp. n., *A. yuccabinensis* sp. n.

Diagnosis. Small Polydesmida with head and 19 or 20 rings; body not curling in spiral; head and telson facing downwards; metatergites with numerous tubercles of varying sizes, sometimes bearing a single seta; ring 2 tergite extended laterally, basally and anteriorly, and edged with large tubercles; no paranota on posterior rings, but 'pseudo-paranota' of metatergal tubercles sometimes present above leg bases; gonopod with neither cannula nor prostatic groove, telopodites separate, each consisting of a more or less cylindrical proximal portion tipped with a thin tab, and a lamellar distal portion arising near the apex of the proximal portion and directed posterobasally or laterobasally.

Remarks. The diagnosis above slightly amends the one given in Mesibov (2009). *Agathodesmus* as a genus is easily recognised by the distinctive structure of the gonopod telopodite (Fig. 2). The proximal portion (**pp**) is typically straight and usually more or less cylindrical, but with the medial and posterior surfaces flattened. The **pp** arises from the distomedial corner of the small, oblong gonocoxa, where its base is partly contained in a small concavity. The telopodite base may extend basally as a short, rounded projection (**be**) to overlap the apex of the gonocoxa in ventral or posterior view. The apex of the **pp** extends distally as a thin tab (**at**), and on or just below the tab on the posterior surface there are three long, closely adjacent, apical setae (**as**) in a row; scattered smaller setae may be present on the posterior surface of the **pp**. Arising just basal to the **as** on the posterodistal surface of the **pp** is the distal portion (**dp**) of the telopodite. Jeekel (1986) used the word 'complicated' three times in his description of the **dp** ('acropodite') in *A. bucculentus*, and while the details of its structure can be very hard to put into words, some generalities are clear and are applicable to all known Australian *Agathodesmus* species. The **dp** is always directed posterobasally or laterobasally, giving the telopodite as a whole the appearance of a leg tightly bent at the knee. The main branch (**mab**) of the **dp** is flattened into a lamella and is usually divided into lobes. The lamella is typically curved so that the surface seen in posterior view is slightly convex, and the distal margin of the **mab** and portions of its inner, concave surface may be thickened or folded. A smaller, medial branch (**meb**) of the **dp** arises near the base of the **dp** on its medial side and usually curves laterally so that its tip is hidden behind the **mab** in ventral view. Portions of the **meb** are sometimes densely covered with fine, hair-like structures.

In this paper I provide posterior or posterolateral gonopod views of all species described here. These views are convenient when examining males with tightly flexed telopodites, and with careful attention to shape and position, a posterior or posterolateral view is diagnostic. However, readers should be aware that important diagnostic details of the telopodites may be hidden in these views, and that in the SEM views published here, thin portions of the **mab** may have been distorted by drying. *Agathodesmus* spp.

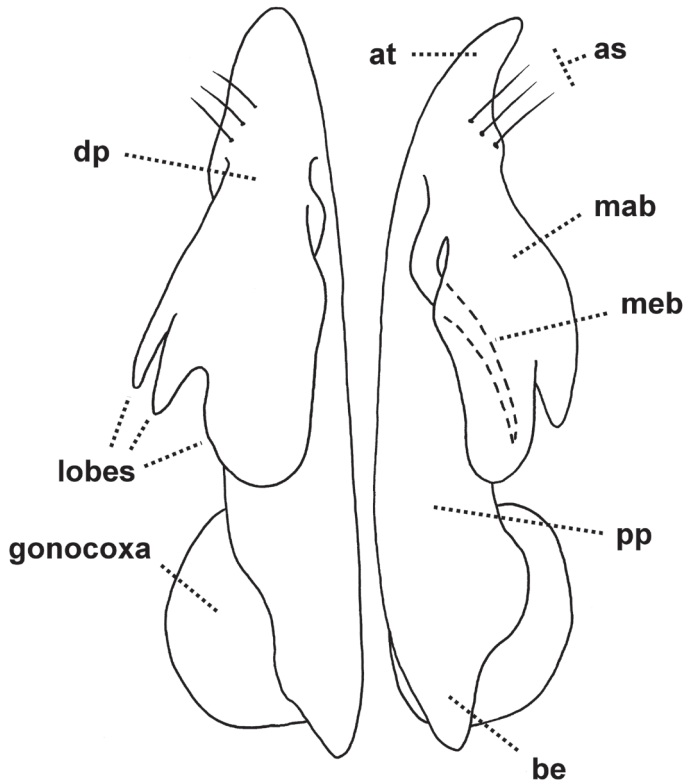


Figure 2. Generalised gonopods of *Agathodesmus* spp., posterior view. **as** = apical setae, **at** = apical tab, **be** = basal extension of telopodite, **dp** = distal portion of telopodite, **mab** = main branch of distal portion of telopodite, **meb** = median branch of distal portion of telopodite, **pp** = proximal portion of telopodite.

are unusual among Australian Polydesmida in their 'hidden' gonopod complexity, and manipulation of the telopodite to partially unbend it and separate the **meb** is often necessary for a positive identification.

When an *Agathodesmus* sp. gonopod is cleared with 80% lactic acid, the telopodite sometimes extends so that the angle between the **pp** and **dp** is greater than 90°. It is easy to imagine that the telopodite extends in this way during mating, and that the apical tab (**at**) serves as a check on the rotation of the telopodite 'knee'. A tab in a similar location is present anterior to the 'joint' in the pseudo-articulated gonopod telopodite of species in the Australian genus *Ginglymodesmus* (Dalodesmidae) (Mesibov 2005). However, I have as yet no evidence to support the idea that the telopodite extends in living males. No *Agathodesmus* have been collected and preserved in copula, and in all of the 430+ *Agathodesmus* males I have examined the uncleared gonopod telopodites are flexed.

Variation in most non-gonopod characters across the genus is minor and the re-description of the type species *A. steeli* in Mesibov (2009) applies to most details in the new species. The 'diagnostic descriptions' given below include only those characters known to vary significantly among Australian *Agathodesmus* spp.

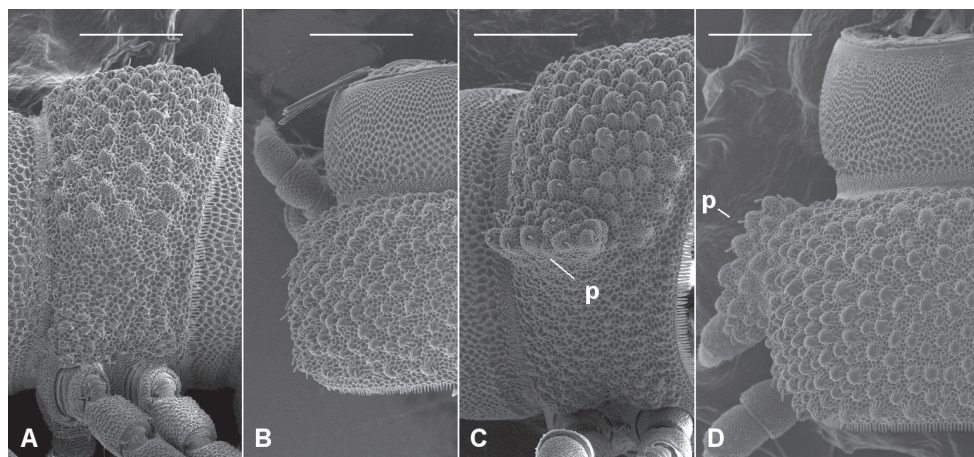


Figure 3. ‘Pseudo-paranotum’ extremes. Lateral (**A**, **C**) and dorsal (**B**, **D**) views of midbody rings of *Agathodesmus bucculentus* (Jeekel, 1986) (**A**, **B**; no pseudo-paranotum; male ex ANIC 64-000332) and *A. gayundah* sp. n. (**C**, **D**; wide pseudo-paranotum, **p**; male paratype ex QM S96038). Scale bars = 0.25 mm; **A** reversed (left-right) for clarity.

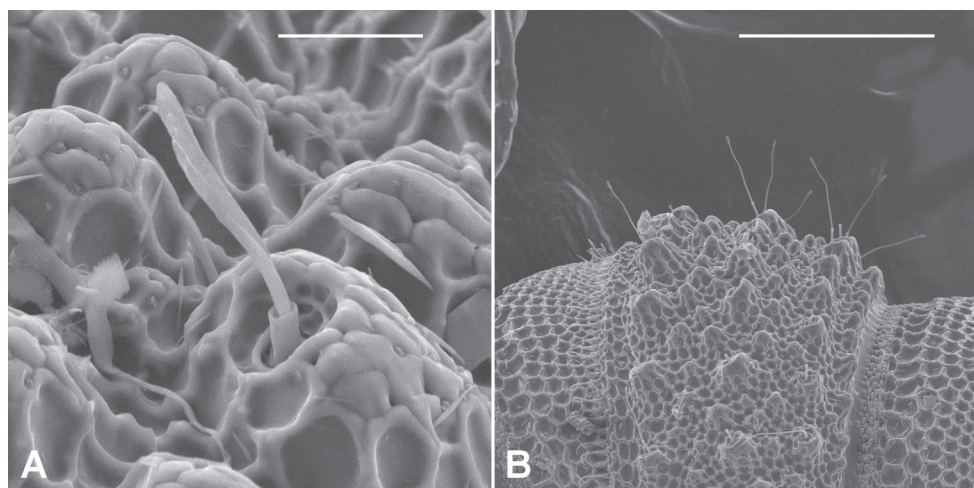


Figure 4. Metatergal setae on midbody rings. **A** *Agathodesmus bucculentus* (Jeekel, 1986), short bipartite seta with slightly flared tip (male ex ANIC 64-000332) **B** *A. quintanus* sp. n., very long bipartite setae with slightly flared tips (male paratype ex QM S96066). Scale bars: **A** = 0.02 mm, **B** = 0.2 mm.

In 12 of the 21 known Australian species, males and females have 19 body rings, in five species 20 rings, and in one species males have 19 rings and females 20; three species known only from males have 19, 19 and 20 rings. The smaller species generally have 19 rings and the larger 20 rings, but the correlation of ring number and body size is loose, and two of the largest Australian species have 19 rings (*A. kirrama* sp. n. and *A. yuccabinensis* sp. n.).

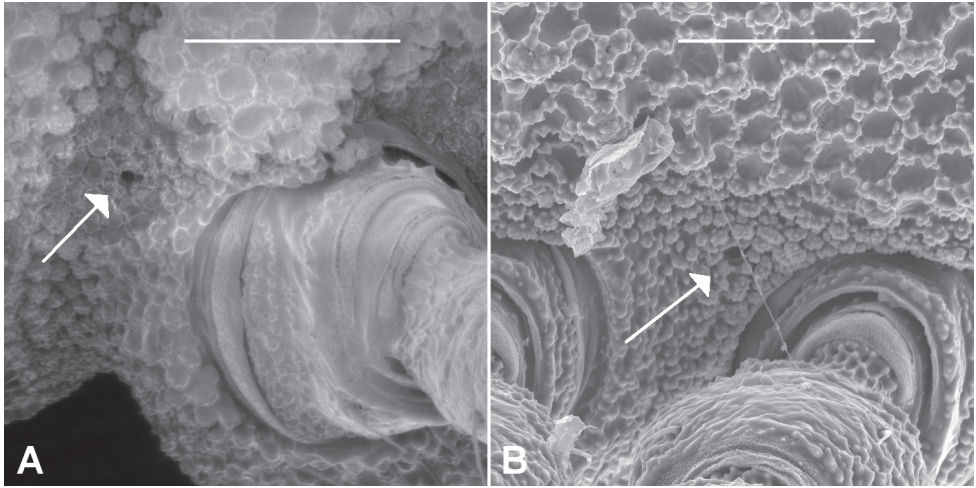


Figure 5. Presumed spiracular openings (arrows) on midbody rings. **A** *Agathodesmus steeli* Silvestri, 1910, AM KS107964, anterior spiracle (anterior to left) **B** *A. chandleri* sp. n., posterior spiracle (anterior to right; male paratype ex series SAM OM-2004-2018). Scale bars = 0.25 mm.

There is also no apparent relationship between body size and the development (or absence) of the 'pseudo-paranota' formed by lateral metatergal tubercles on posterior rings (Fig. 3).

Although the metatergal setae in most Australian *Agathodesmus* spp. are short with slightly flared tips (Fig. 4A), three of the newly described species have very long setae (Fig. 4B) and appear 'hairy' at low magnification.

While examining the new *Agathodesmus* species I was able to identify what appear to be spiracular openings, something I failed to do earlier (Mesibov 2009). The openings are minute (Fig. 5) and on diplosegments are both located close to the anterior leg base.

Finally, included here as Fig. 10D is a close-up of a typical *Agathodesmus* spp. ozopore, shown at much lower magnification in the *A. steeli* redescription (fig. 4B in Mesibov 2009).

***Agathodesmus adelphus* sp. n.**

<http://zoobank.org/7CDE40B2-0327-40F9-B93D-1679B3824AE4>

http://species-id.net/wiki/Agathodesmus_adelphus

Fig. 6A

Holotype. Male, Mt Bartle Frere, Qld, west slopes, 17°22'57"S, 145°46'45"E ±500m, 800-1000 m a.s.l., 30 December 1989, G. Monteith, QM S96015.

Paratype. 1 female, details as for holotype, QM S96016.

Other material. None.

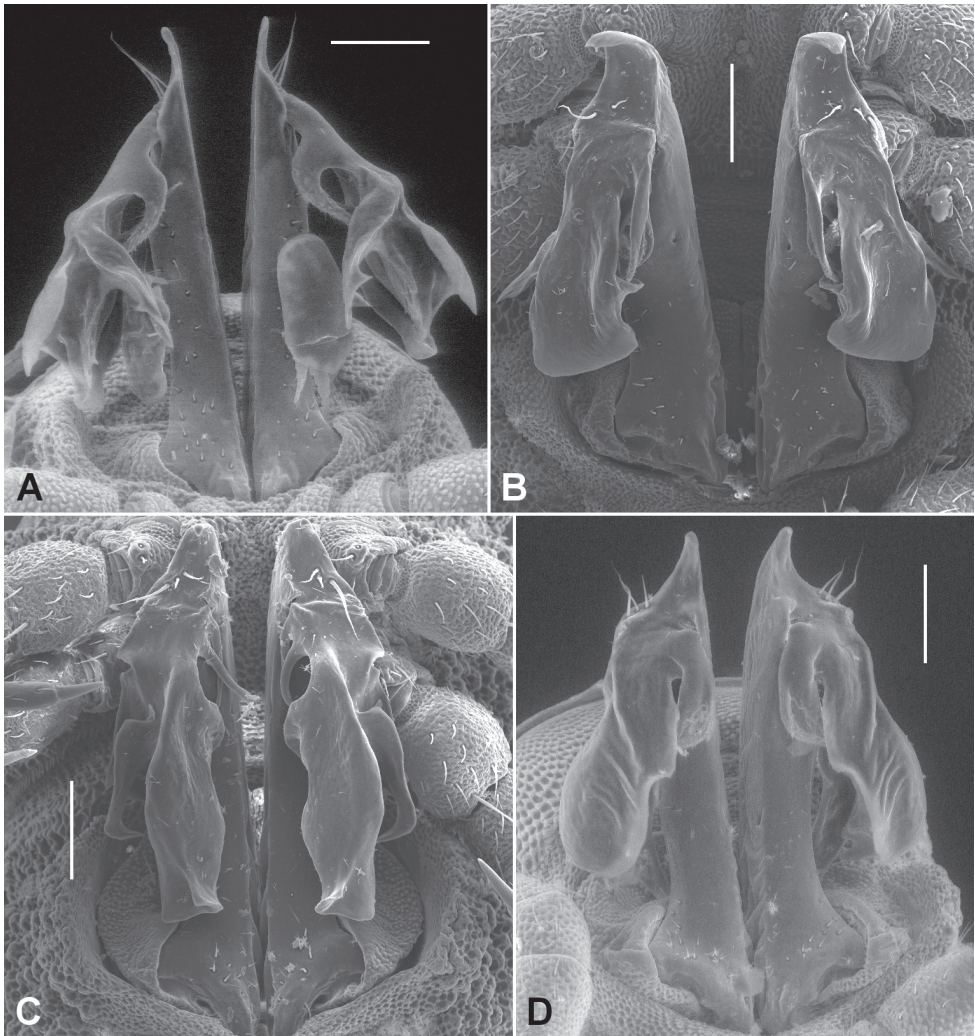


Figure 6. Posterior gonopod views. **A** *Agathodesmus adelphus* sp. n., holotype, QM S96015 **B** *A. aenigmaticus* sp. n., paratype ex QM S96018 **C** *A. agnus* sp. n., paratype ex QM S96021 **D** *A. anici* sp. n., holotype, ANIC 64-000327. **A** and **D** are uncoated specimens; scale bars = 0.1 mm. Note two mites on *A. adelphus* sp. n. telopodites.

Diagnostic description. Male and female with head + 20 rings. Colour in alcohol very faintly reddish. Male/female ca 8.0/8.5 mm long; ring 12 maximum diameter ca 0.6/0.7 mm, maximum width ca 0.85/0.9 mm. Metaternal tubercles in 8-10 irregular transverse rows, mostly without setae; metaternal setae short with slightly flared tips; lateralmost two rows of tubercles not enlarged, together forming narrow pseudo-paranotum with 6 marginal tubercles. Male leg 6 coxa with small, rounded, mediodistal projection. Telopodite (Fig. 6A) with **pp** straight; **at** in longitudinal plane, short and rounded-triangular; **dp** directed laterobasally at base; **mab** concave

medially, deeply divided with smaller medial lobe bent posteriorly, tapering and with sharp subterminal tooth on lateral surface; larger, lateral **mab** lobe widening to thickened, emarginate apex; **meb** curving strongly behind **mab**, divided at ca one-third length into 2 thin processes.

Distribution. Known only from rainforest high on Mt Bartle Frere in tropical north Queensland (Fig. 13A). Possibly co-occurs on Mt Bartle Frere with *A. quintanus* sp. n. and *A. summus* sp. n., although both these species are found at higher elevations on the mountain.

Name. Latin *adelphus*, 'brother', a punning reference to the 'Frere' in the name of the type locality; adjective.

Remarks. Fig. 6A shows two unidentified mites, one on each telopodite. They have not been removed from the holotype.

***Agathodesmus aenigmaticus* sp. n.**

<http://zoobank.org/E912EEC5-BF65-4E3E-8AA0-024389774BFE>

http://species-id.net/wiki/Agathodesmus_aenigmaticus

Fig. 6B

Holotype. Male, Mt Hayward, Qld, 20°19'39"S, 148°45'10"E ±500m, 350 m a.s.l., 20 November 1992, G. Monteith, G. Thompson, D. Cook and H. Janetzki, QM S96017.

Paratypes. 8 males, 3 females, 4 stadium 7 males, 2 stadium 7 females, 4 stadium 6 males, 2 stadium 6 females, details as for holotype, QM S96018.

Other material. 2 males, Bellenden Ker, Centre Peak, Qld, summit, 17°15'40"S, 145°51'25"E ±500m, 1500 m a.s.l., 11 April 1979, G. Monteith, QM berlesate 17, rainforest, sieved litter, QM S96019.

Diagnostic description. Male and female with head + 20 rings. Colour in alcohol pale yellow. Male/female ca 9.0/10 mm long; ring 12 maximum diameter ca 0.75/0.9 mm, maximum width ca 0.9/1.0 mm. Metatergal tubercles in 8-10 irregular transverse rows, larger tubercles mostly with setae; metatergal setae long, bluntly pointed; 5 lateralmost tubercles slightly enlarged, forming very narrow pseudo-paranotum. Male leg 6 coxa with small, rounded, mediodistal projection. Telopodite (Fig. 6B) with **pp** straight; **at** in transverse plane, short, broad and with rounded apex curving posteriorly; **dp** directed posterobasally at base; **mab** slightly expanded apically with rounded distal margin, lateral edge with small, tapering, posterolaterally directed lobe, medial edge with short, curved lobe partly protecting **meb**; **meb** divided near base into 3 thin, subequal processes curving behind **mab**.

Distribution. Known from rainforest at two localities ca 450 km apart in north Queensland (Figs 12, 13A; see Remarks).

Name. Latin *aenigmaticus*, 'puzzling'; adjective (see Remarks).

Remarks. The very wide disjunction between the two known localities is puzzling, and I suspect that the Bellenden Ker locality on the specimen label is incorrect. I have not noticed any differences in gonopod or non-gonopod features between the two populations.

***Agathodesmus agnus* sp. n.**

<http://zoobank.org/33CC8023-FD1A-47D3-8A78-F7590C27F670>

http://species-id.net/wiki/Agathodesmus_agnus

Figs 6C, 10D

Holotype. Male, Lamb Range, 19 km S of Mareeba, Qld, 17°06'39"S, 145°34'04"E ±500 m, 1200 m a.s.l., 3 December 1988, G. Monteith and G. Thompson, QM berlesate 804, rainforest, sieved litter, QM S96020.

Paratypes. 7 males, 10 females, 1 stadium 6 female, details as for holotype, QM S96021.

Other material. QM: 1 male, 3 females, 3 stadium 6 females, North Bell Peak via Gordonvale, Qld, 17°05'19"S, 145°52'44"E ±500 m, 900 m a.s.l., 16 September 1981, G. Monteith and D. Cook, QM berlesate 300, rainforest, sieved litter and moss, S96022; 1 male, 1 female, 22 km SE of Mareeba, Qld, 17°06'39"S, 145°34'04"E ±500 m, 900 m a.s.l., 4 November 1983, D. Yeates and G. Thompson, QM berlesate 615, rainforest, sieved litter, S96023; 1 female, 1 stadium 6 female, North Bell Peak, Qld, 17°05'06"S, 145°52'00"E ±500 m, 600 m a.s.l., 22 November 1990, G. Monteith and G. Thompson, QM berlesate 845, rainforest, sieved litter, S96024; 2 males, 2 females, Mt Haig, Lamb Range, Qld, 17°05'52"S, 145°36'09"E ±500 m, 1000 m a.s.l., 25 February 1997, G. Monteith, QM berlesate 918, rainforest, sieved litter, S37557. **ANIC:** 1 male, near Mt Haig, Qld, 17°10'S, 145°36'E ±1 km, 750 m a.s.l., 30 June 1971, R.W. Taylor and J. Feehan, ANIC berlesate 350, rainforest, 64-000323; 2 males, Mt Haig, Qld, 17°06'S, 145°36'E ±1 km, 1000 m a.s.l., 29 October 1976, R.W. Taylor and T.A. Weir, ANIC berlesate 541, rainforest, 64-000325; 15 males, 9 females, 3 km W by S of Mt Haig, Qld, 17°06'S, 145°34'E ±1 km, 1150 m a.s.l., 3 April 1984, A. Calder and T.A. Weir, ANIC berlesate 952, rainforest, 64-000324; 7 males, 2 females, Cammoo Caves near Rockhampton (? – see Remarks), Qld, 23°10'S, 150°28'E ±1 km, 25 October 1976, R.W. Taylor and T.A. Weir, ANIC berlesate 535, dense low closed forest, ANIC 64-000326.

Diagnostic description. Male and female with head + 19 rings. Colour in alcohol pale yellow. Male/female ca 8.0/8.0 mm long; ring 12 maximum diameter ca 0.65/0.8 mm, maximum width ca 0.7/1.1 mm. Metatergal tubercles in ca 12 irregular transverse rows, mostly without setae; metatergal setae short with slightly flared tips; lateralmost tubercles not enlarged, not forming pseudo-paranotum. Male legs 6 coxa with rounded, mediobasal projection. Telopodite (Fig. 6C) with **pp** straight; **at** in transverse plane, short, triangular and curving posteriorly; **dp** directed posterobasally at base; **mab** deeply divided into large posterior and small posterolateral lobes; posterior lobe of **mab** distally with small folds and with medial edge produced near **mab** base as short, pointed lobe; posterolateral lobe of **mab** folded, the posteriormost fold with apex tooth-like and pointing anteromedially; **meb** divided at base into 2 needle-like processes curving behind **mab**.

Distribution. Rainforest in the Lamb Range and adjacent hills inland from Gordonvale, tropical north Queensland (Fig. 13A). Co-occurs with *A. quintanus* sp. n. on North Bell Peak. There is also a doubtful record from Cammoo Caves in central Queensland (Fig. 1; see Remarks).

Name. Latin *agnus*, 'lamb', for the type locality, the Lamb Range; adjective.

Remarks. Like *A. agnus* sp. n., *Asphalidesmus magnus* Mesibov, 2011 and *Prosopodesmus crater* Mesibov, 2012 were found in ANIC berlesate 535 from Cammoo Caves (Mesibov 2011, 2012a). For all three species, all other specimens are from localities on or near the Lamb Range, ca 800 km to the north of Cammoo Caves. The locality labelling for ANIC berlesate 535 appears to be incorrect (Mesibov 2012a). In March 2013 I searched briefly for millipedes in rainforest in the Cammoo Caves area but found no specimens of *Agathodesmus*, *Asphalidesmus* or *Prosopodesmus*.

***Agathodesmus anici* sp. n.**

<http://zoobank.org/917051E9-2E87-4FB1-830A-4C5B775DAE1E>

http://species-id.net/wiki/Agathodesmus_anici

Fig. 6D

Holotype. Male, 11 km W by N of Bald Hill, McIlwraith Range, Qld, search party campsite, 13°44'S, 143°20'E ±2 km, 520 m a.s.l., 27 June–12 July 1989, T.A. Weir, ANIC berlesate 1111, closed forest, leaf and log litter, in several pieces in genitalia vial, ANIC 64-000327.

Other material. None.

Diagnostic description. Male with head + 20 rings. Colour in alcohol pale white. Male ca 7.5 mm long; ring 12 maximum diameter ca 0.6 mm, maximum width ca 0.75 mm. Metatergal tubercles in 7-8 irregular transverse rows, mainly without setae; metatergal setae long, pointed; 4 lateralmost tubercles not enlarged, forming very narrow pseudo-paranotum. Male leg 6 coxa with prominent mediodistal projection. Telopodite (Fig. 6D) with **pp** straight; **at** in transverse plane, short, narrowly triangular and with tip curving posteriorly; **dp** directed posterobasally and laterally at base; **mab** shallowly divided into narrower anterior and wider posterior lobes; **meb** curving behind **mab** and divided at ca 1/3 length into short, needle-like medial and broader lateral processes, the latter following the curve of the posterior **mab** lobe and nearly as long.

Distribution. Known only from the type locality on the Cape York Peninsula in far north Queensland (Fig. 1).

Name. In honour of ANIC, the Australian National Insect Collection, whose collection of berlesates has yielded many new species of Australian millipedes.

Remarks. The telson of the holotype is damaged and the distal portions of legs 6 are missing.

***Agathodesmus bonang* sp. n.**

<http://zoobank.org/8687C72E-AFF7-4518-AA89-D51D6D03BB10>

http://species-id.net/wiki/Agathodesmus_bonang

Fig. 7A

Holotype. Male, Bonang Road, Vic, 37°23'26"S, 148°35'49"E ±25 m, 320 m a.s.l., 9 April 2011, R. Mesibov, NMV K-11860.

Paratypes. NMV: 9 males (K-11861-11869), 5 females (K-11872-11876), 1 stadium 6 female (K-11871), 1 stadium 5 female (K-11870), details as for holotype; 1 stadium 6 female, same details but 37°15'31"S, 148°44'02"E ±25 m, 620 m a.s.l., K-11878; 1 female, same locality but 37°26'01"S, 148°35'47"E ±25 m, 240 m a.s.l., 8 November 2006, R. Mesibov and T. Moule, K-11877.

Other material. None.

Diagnostic description. Male and female with head + 19 rings. Colour in alcohol pale white. Male/female ca 3.5/4.0 mm long; ring 12 maximum diameter ca 0.3/0.4 mm, maximum width ca 0.4/0.5 mm. Metatergal tubercles in ca 4–5 irregular transverse rows, mostly without setae; metatergal setae short with slightly flared tips; 3 lateralmost tubercles enlarged, forming narrow pseudo-paranotum. Male leg 6 without coxal projection. Telopodite (Fig. 7A) with **pp** straight; **at** in transverse plane, very short, rounded-triangular and bent posteriorly; **dp** directed posterobasally and slightly laterally at base; **mab** deeply and widely divided into 2 subequal lobes with bluntly pointed apices; **meb** not divided, bent first posteriorly, then laterobasally and only very slightly curved, apex behind medial edge of medial lobe of **mab**.

Distribution. Known from wet eucalypt forest in East Gippsland, Victoria, over a linear extent of ca 20 km (Fig. 11).

Name. For the Bonang Highway, a narrow and winding road through the eastern Victorian mountains, type locality of this species; noun in apposition.

Remarks. Like *A. carorum* sp. n., *A. bonang* sp. n. is white in colour when alive, and contrasted well with the wet leaf litter and rotting wood in which I found it.

***Agathodesmus carorum* sp. n.**

<http://zoobank.org/7438443E-DBEF-445A-8E3E-6997A72163A0>

http://species-id.net/wiki/Agathodesmus_carorum

Fig. 7B

Holotype. Male, Imlay Road, NSW, 37°07'40"S, 149°27'28"E ±25 m, 610 m a.s.l., 11 November 2006, C. Car, G. Car, R. Mesibov and T. Moule, NMV K-11879.

Paratypes. NMV: 1 male (K-11882), 1 stadium 6 female (K-11883), Nadgee State Forest, S of Eden, NSW, 37°23'56"S, 149°49'18"E ±25 m, 260 m a.s.l., 12 November 2006, C. Car, G. Car, R. Mesibov and T. Moule; 2 females, same details but 37°24'54"S, 149°48'57"E, 230 m a.s.l., K-11880-11881.

Other material. NMV: 1 male (K-11884), 2 females (K-11885), Dyer Creek, near Murrungowar, Vic, 37°38'26"S, 148°43'24"E ±25 m, 170 m a.s.l., 8 November 2006, R. Mesibov and T. Moule; 1 male, Cabbage Palms Flora Reserve, Vic, 37°44'39"S, 148°38'55"E ±25 m, 30 m a.s.l., 10 April 2011, R. Mesibov, K-11886.

Diagnostic description. Male and female with head + 19 rings. Colour in alcohol pale white. Male/female ca 4.0/4.5 mm long; ring 12 maximum diameter ca 0.4/0.5 mm, maximum width ca 0.5/0.6 mm. Metatergal tubercles in ca 6 irregular transverse rows, mostly without setae; metatergal setae short; 3 lateralmost tubercles enlarged,

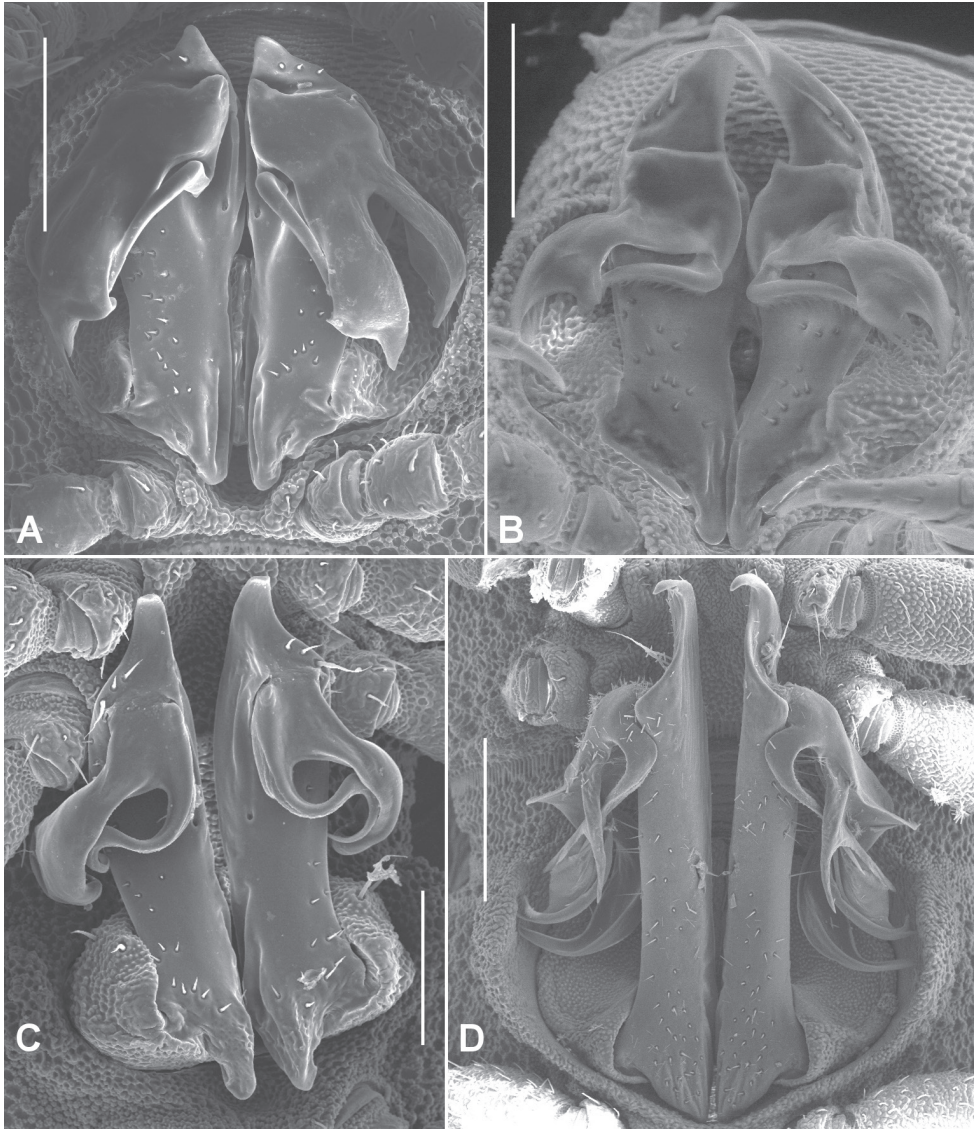


Figure 7. Posterior gonopod views. **A** *Agathodesmus bonang* sp. n., paratype ex series NMV K-11861-11869 **B** *A. carorum* sp. n., NMV K-11884 **C** *A. chandleri* sp. n., paratype ex series SAM OM-2004-2018 **D** *A. halmensis* sp. n., paratype ex QM S38962. **B** is uncoated specimen; scale bars: **A**, **B**, **C** = 0.1 mm, **D** = 0.2 mm.

forming narrow pseudo-paranotum. Male leg 6 without coxal projection. Telopodite (Fig. 7B) with **pp** slightly curved posteriorly, widening distally; **at** in transverse plane, long, tapering to blunt point and curving posteromedially; **dp** directed posterobasally at base; **mab** directed posterolaterally at ca 90° to **pp** axis, then curving basally, the distal margin emarginate in its medial portion; **meb** not divided, bent sharply and directed posterolaterally near base, apex behind medial edge of **mab**.

Distribution. Wet eucalypt forest in far southeastern New South and far eastern Victoria (Fig. 11).

Name. In honour of Catherine and George Car, co-collectors of this species at the holotype and paratype localities; adjective.

Remarks. Like *A. bonang* sp. n., *A. carorum* sp. n. is white in colour when alive.

***Agathodesmus chandleri* sp. n.**

<http://zoobank.org/F1B036CA-96BE-46DA-B0A6-8EFBC9372B3C>

http://species-id.net/wiki/Agathodesmus_chandleri

Figs 5B, 7C

Holotype. Male, Wotton Scrub, Kenneth Stirling Conservation Park, SA, 34°58'58"S, 138°46'39"E ±100 m, 450 m a.s.l., 1 July 2010, R. Mesibov and T. Moule, SAM OM2003.

Paratypes. SAM: 15 males, OM2004-OM2018; 5 females, OM2019-OM2023; 2 stadium 6 males, OM2024, OM2025; details as for holotype.

Other material. SAM: 2 males, Richardsons Road, Uraidla, SA, 34°58'13"S, 138°45'02"E ±25 m, 580 m a.s.l., 21 August 2010, R. Mesibov and T. Moule, OM2026, OM2027; 1 male, Whites Scrub, SA, 34°58'06"S, 138°46'42"E ±25 m, 510 m a.s.l., same date and collectors, OM2028. **ANIC:** 4 males, 1 female, Pill Box Track, Cleland Conservation Park, 16 km SE of Adelaide, SA, 34°58'S, 138°42'E ±1 km, 500 m a.s.l., 25 April 1993, D.S. Chandler, ANIC berlesate 1539, cut dry sclerophyll, Eucalyptus and grass litter, 64-000337.

Diagnostic description. Males and females with head + 19 rings. Colour in alcohol pale yellow. Male/female ca 5.0/5.5 mm long; ring 12 maximum diameter ca 0.45/0.5 mm, maximum width ca 0.55/0.7 mm. Metatergal tubercles in 6-7 irregular transverse rows, mostly without setae; metatergal setae short with slightly flared tips; 5 lateralmost tubercles enlarged, forming very narrow pseudo-paranotum. Male leg 6 without coxal projection. Telopodite (Fig. 7C) with **pp** straight; **at** in transverse plane, short, narrowly triangular with rounded tip curving posteriorly; **dp** directed posterobasally at base; **mab** directed laterobasally and curving anterobasally, narrow and not divided into lobes, distal margin thickened and with small emargination; **meb** curving behind **mab**, then following anterobasal curve of **mab** and terminating with it.

Distribution. Wet and dry eucalypt forest in the Adelaide Hills east of Adelaide, South Australia (Fig. 1).

Name. In honour of the American entomologist Don Chandler, who collected the first known specimens of this species while on a field trip to Australia; adjective.

Remarks. At the type locality I found an isolated aggregation of individuals of this species in very wet, friable material inside a rotting eucalypt log (<http://www.polydesmida.info/polydesmida/thanks.html>). Other specimens were in wet litter close to rotting wood.

As with *Agathodesmus* spp. localities elsewhere in eastern Australia, the four *A. chandleri* sp. n. localities in the Adelaide Hills all have mean annual rainfalls of at least

1000 mm. This species is likely to be a wet-forest relict surviving on a high-rainfall 'island' in an otherwise dry region of the Australian continent. Nevertheless, *A. chandleri* sp. n. appears to be locally abundant in the Adelaide Hills, and occurs in habitats much disturbed by burning and (formerly) stock grazing.

***Agathodesmus gayundah* sp. n.**

<http://zoobank.org/5390D7BE-197E-46ED-8B07-774D5EFFFFD52>

http://species-id.net/wiki/Agathodesmus_gayundah

Figs 3C, 3D, 8A, 8B

Holotype. Male, Gayundah Creek, Hinchinbrook Island, Qld, 18°21'59"S, 146°13'09"E ±500 m, 10 m a.s.l., 11 November 1984, V. Davies, G. Thompson and J. Gallon, QM berlesate 664, rainforest sieved litter, QM S96029.

Paratypes. QM: 4 males, 2 females, details as for holotype, S96035; 1 male, 2 females, 3 stadium 7 males, 1 stadium 7 female, 3 stadium 6 males, 4 stadium 6 females, 1 stadium 5 male, 1 stadium 4 male, same details but 9 November 1984, QM berlesate 663, S96033; 1 male, same details but 10 November 1984, QM berlesate 666, S96031; 2 males, 1 female, same details but QM berlesate 668, S96034; 1 male, 1 female, same details but 8 November 1984, G. Monteith, V. Davies, G. Thompson and J. Gallon, QM berlesate 667, S96032; 1 male, same details but QM berlesate 665, S96030; 3 males, same locality, 7–14 November 1984, V. Davies and J. Gallon, S96038; 3 males, 3 females, 2 stadium 7 females, 1 stadium 6 male, same locality, 7–15 November 1984, G. Monteith, G. Thompson and D. Cook, S96039; 3 males, 4 females, 2 stadium 7 males, 4 stadium 7 females, 1 stadium 6 male, 1 stadium 6 female, same locality but 18°21'36"S, 146°13'33"E ±500 m, 80 m a.s.l., 12 November 1984, G. Monteith, V. Davies, G. Thompson and J. Gallon, QM berlesate 669, S96036; 1 female, 2 stadium 7 females, same details but G. Monteith and G. Thompson, S96037.

Other material. None.

Diagnostic description. Male and female with head + 20 rings. Colour in alcohol very pale yellow. Male/female ca 10.5/10.5 mm long; ring 12 maximum diameter ca 0.9/1.1 mm, maximum width ca 1.25/1.3 mm. Metatergal tubercles in 10–12 irregular transverse rows, mainly without setae; metatergal setae short with slightly flared tips; lateralmost row of tubercles enlarged, together with more medial 1–2 rows forming wide pseudo-paranotum with 5–6 marginal tubercles (Figs 3C, 3D). Male leg 6 coxa with small, rounded, mediobasal projection. Telopodite (Figs 8A, 8B) with **pp** slightly flattened mediolaterally, slightly curved posteriorly; **at** in oblique plane (facing posterolaterally), short, narrowly triangular, curving posteriorly; **dp** directed laterobasally at base; **mab** directed basally and a little anteriorly, widening distally and divided into 2 lobes; longer anterior **mab** lobe medially concave with interior folds; shorter posterior **mab** lobe concave medially with flat, spike-like, basally directed process at medial edge; **meb** curving behind **mab**, divided at about one-third length into 2 paral-

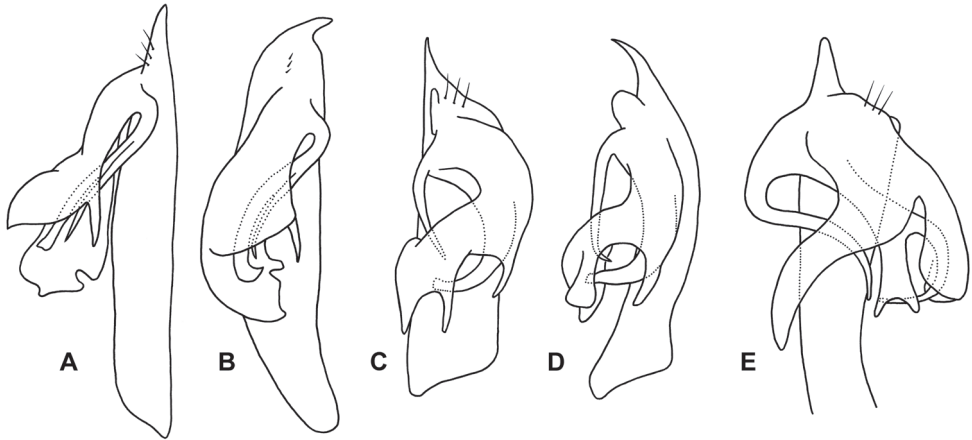


Figure 8. *Agathodesmus* spp. gonopod telopodites, not to same scale. **A, B** *A. gayundah* sp. n., paratype ex QM S96039, right gonopod, posterior (**A**) and lateral (**B**) views **C, D** *A. millaa* sp. n., paratype ex QM S96055, left gonopod, posterior (**C**) and lateral (**D**) views, **as** not shown in lateral view **E** *A. quintanus* sp. n., paratype ex QM S96074, left gonopod, posterior and slightly basal view.

lel processes, the shorter posteromedial process needle-like, the longer, wider antero-lateral process terminating in triangular tooth.

Distribution. Known only from rainforest on Hinchinbrook Island, east of Cardwell in tropical north Queensland (Fig. 13A).

Name. For the type locality, Gayundah Creek; noun in apposition.

***Agathodesmus hahnensis* sp. n.**

<http://zoobank.org/DA20F497-5F24-402A-AB92-ED2C01361DF3>

http://species-id.net/wiki/Agathodesmus_hahnensis

Fig. 7D

Holotype. Male, Hahn Tableland, N end, Qld, 16°48'35"S, 145°10'53"E ±500 m, 950–1000 m a.s.l., 11–14 December 1995, G. Monteith, G. Thompson and D. Cook, rainforest, QM S96040 (ex S38962).

Paratypes. 9 males, 6 females, details as for holotype, QM S38962.

Other material. QM: 1 male, Mt Finnigan, 37 km S of Cooktown, Qld, 15°48'53"S, 145°16'28"E ±500 m, 850–1100 m a.s.l., 22 April 1982, G. Monteith, D. Yeates and D. Cook, rainforest, S96044; 1 male, Mossman Bluff track, 9 km W of Mossman, Qld, 16°27'52"S, 145°17'12"E ±500 m, 1000 m a.s.l., 22–24 December 1989, G. Monteith and G. Thompson, pitfall trap, S96042; 1 male, 1 stadium 7 female, 10 km N of Mt Lewis, Qld, 16°29'29"S, 145°15'10"E ±500 m, 1100 m a.s.l., 25 November 1990, G. Monteith, G. Thompson, D. Cook, R. Sheridan and H. Janetzki, S96043; 1 male, 1 female, Mt Misery road, Qld, 15°52'39"S, 145°12'58"E ±500 m, 730 m a.s.l., 2 January 1991, ANZSES personnel, S37591; 1 female, Graham

Range, Qld, 17°16'24"S, 145°57'58"E ±500 m, 550 m a.s.l., 1 November 1995, G. Monteith, pyrethrum, trees and logs, S96041; 2 males, same details but 8-9 December 1995, G. Monteith, G. Thompson and D. Cook, S38960. **ANIC:** 1 male, Windsor Tableland, 1.2 km past barracks, Qld, 16°15'10"S, 145°02'30"E ±500 m, 1060 m a.s.l., 8 February 1998, G. Monteith and D. Cook, ANIC berlesate 1831, 64-000338.

Diagnostic description. Male and female with head + 20 rings. Colour in alcohol very pale yellow. Male/female ca 9.0/10.0 mm long; ring 12 maximum diameter ca 0.8/1.0 mm, maximum width ca 0.9/1.2 mm. Metatergal tubercles in 10-12 irregular transverse rows, mainly without setae; metatergal setae short with slightly flared tips; lateralmost row of tubercles enlarged, together with more medial 1-2 rows forming prominent pseudo-paranotum with 6 marginal tubercles. Male leg 6 coxa with small, rounded, mediobasal projection. Telopodite (Fig. 7D) with **pp** straight, slightly flattened mediolaterally; **at** in oblique plane (facing posterolaterally), short, narrowly triangular, curving posteriorly; **dp** directed laterobasally at base; **mab** deeply divided into 3 lobes: 2 anterolateral lobes curving anteriorly, then posterolaterally, narrowing and with upturned apices, and a basally directed posteromedial lobe widely divaricate at mid-length; **meb** curving behind **mab**, divided at ca one-third length into 2 closely appressed, needle-like processes, terminating between divaricate posteromedial and curved anterolateral lobes of **mab**.

Distribution. Rainforest in tropical north Queensland from Mt Finnigan near Cooktown south to the Graham Range, a linear extent of ca 180 km (Fig. 13A). Co-occurs with *A. quintanus* sp. n. in the Graham Range.

Name. For the type locality, the Hahn Plateau; adjective.

***Agathodesmus kerensis* sp. n.**

<http://zoobank.org/92DA65F0-C022-4642-99AD-BE9835F8EE72>

http://species-id.net/wiki/Agathodesmus_kerensis

Fig. 9A

Holotype. Male, Bellenden Ker Range, Qld, summit TV station, 17°15'50"S, 145°51'14"E ±100m, 1550 m a.s.l., 25-31 October 1981, Queensland Museum and Earthwatch personnel, QM S96045.

Paratypes. **QM:** 2 males, 1 stadium 6 female, details as for holotype, S96046; 3 males, same details but 1-7 November 1981, S96047; 2 males, same details but 1-7 November 1981, QM berlesate 338, rainforest, sieved litter, S96048.

Other material. None.

Diagnostic description. Male with head + 19 rings. Colour in alcohol brownish yellow. Male ca 8.0 mm long; ring 12 maximum diameter ca 0.6 mm, maximum width ca 0.65 mm. Metatergal tubercles in ca 10 irregular transverse rows, mainly without setae; metatergal setae short with slightly flared tips; lateralmost row of tubercles not enlarged, not forming pseudo-paranotum. Male leg 6 coxa with small, rounded, mediobasal projection. Telopodite (Fig. 9A) with **pp** curving anteriorly, then distally at

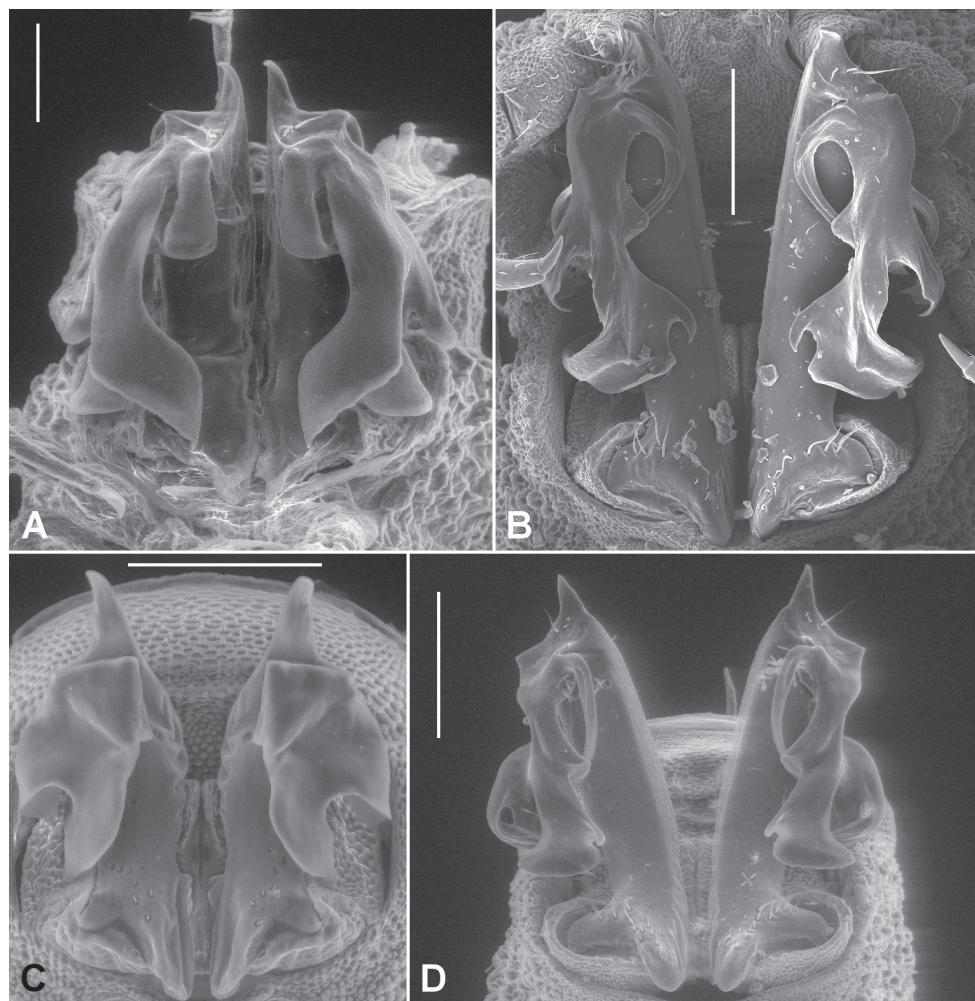


Figure 9. Posterior gonopod views. **A** *Agathodesmus kerensis* sp. n., paratype ex QM S96046 **B** *A. kirrama* sp. n., paratype ex QM S96051 **C** *A. morwellensis* sp. n., paratype, NMV K-11889 **D** *A. parapholeus* sp. n., paratype ex QM S96057. **A, C, D** are uncoated specimens; scale bars: **A, C** = 0.1 mm, **B, D** = 0.2 mm.

base, slightly flattened anteroposteriorly; **at** in oblique plane (facing posterolaterally), short, narrowly triangular, arising abruptly from medial side of truncate **pp** apex, curving slightly posterolaterally; **dp** directed posterobasally at base; **mab** divided into 2 distally notched lobes, the posterior lobe curving medially and terminating in a basally directed point; **meb** broad, not divided, curving behind **mab**, apex slightly expanded.

Distribution. Known only from rainforest on the summit of Mt Bellenden Ker in tropical north Queensland (Fig. 13A). *A. quintanus* sp. n. occurs lower down on the same mountain.

Name. For the type locality, Mt Bellenden Ker; adjective.

Remarks. Latitude/longitude data corrected following Mesibov (2012b).

***Agathodesmus kirrama* sp. n.**

<http://zoobank.org/2D19A715-D908-40DD-80C4-4DA9EAC3A65F>

http://species-id.net/wiki/Agathodesmus_kirrama

Fig. 9B

Holotype. Male, Mt Pershouse, Kirrama Range, Qld, 18°13'30"S, 145°47'42"E ±500m, 12 December 1986, G. Monteith and G. Thompson, QM berlesate 734, rainforest, sieved litter, QM S96049.

Paratypes. QM: 4 males, 1 female, 1 stadium 6 male, details as for holotype, S96051; 2 males, 2 females, same details but QM berlesate 735, S96050.

Other material. QM: 1 male, 2 females, Mt Hosie, Kirrama Range Qld, 18°12'29"S, 145°46'41"E ±500m, 800 m a.s.l., 10 December 1986, G. Monteith and G. Thompson, S96052; 2 males, same details but 930 m a.s.l., 11 December 1986, QM berlesate 733, rainforest, sieved litter, S96053.

Diagnostic description. Male and female with head + 19 rings. Colour in alcohol pale yellow. Male/female ca 10.0/10.5 mm long; ring 12 maximum diameter ca 0.75/0.8 mm, maximum width ca 0.8/0.9 mm. Metatergal tubercles in 12-16 irregular transverse rows, mainly without setae; metatergal setae short with slightly flared tips; lateralmost row of tubercles not enlarged, not forming pseudo-paranotum. Legs 6 and 7 coxae with long mediobasal projections (shorter on leg 7) with rounded tips. Telopodite (Fig. 9B) with **pp** straight; **at** in transverse plane, short and narrowly triangular, tip not curving posteriorly (curve in Fig. 9B is artefact of drying); **dp** directed posterobasally and laterally at base; **mab** divided into 3 lobes increasing in width and length from anterior to posterior, with anterior lobe curving medially and pointed, middle lobe distally truncate, posterior lobe distally expanded, the distal margin curving cup-like anteriorly and with small notch near medial edge; **meb** curving behind **mab**, divided at ca one-quarter length into 2 subequal, closely appressed, needle-like processes.

Distribution. Known only from rainforest on Mt Hosie and Mt Pershouse, ca 3 km apart in tropical north Queensland (Fig. 13A). Co-occurs with *A. yuccabinensis* sp. n. on Mt Hosie.

Name. For the Kirrama Range; noun in apposition.

***Agathodesmus millaa* sp. n.**

<http://zoobank.org/6D607416-62E9-4A33-8687-1A390D172A19>

http://species-id.net/wiki/Agathodesmus_millaa

Figs 8C, 8D

Holotype. Male, Mt Fisher, 7 km SW of Millaa Millaa, Qld, Whiteing Road, 17°33'56"S, 145°33'47"E ±500m, 1200 m a.s.l., 5 May 1983, G. Monteith and D. Yeates, QM berlesate 583, moss on rocks and logs; in 3 pieces in genitalia vial, QM S96054.

Paratypes. 1 male, 1 stadium 5 male, details as for holotype, QM S96055.

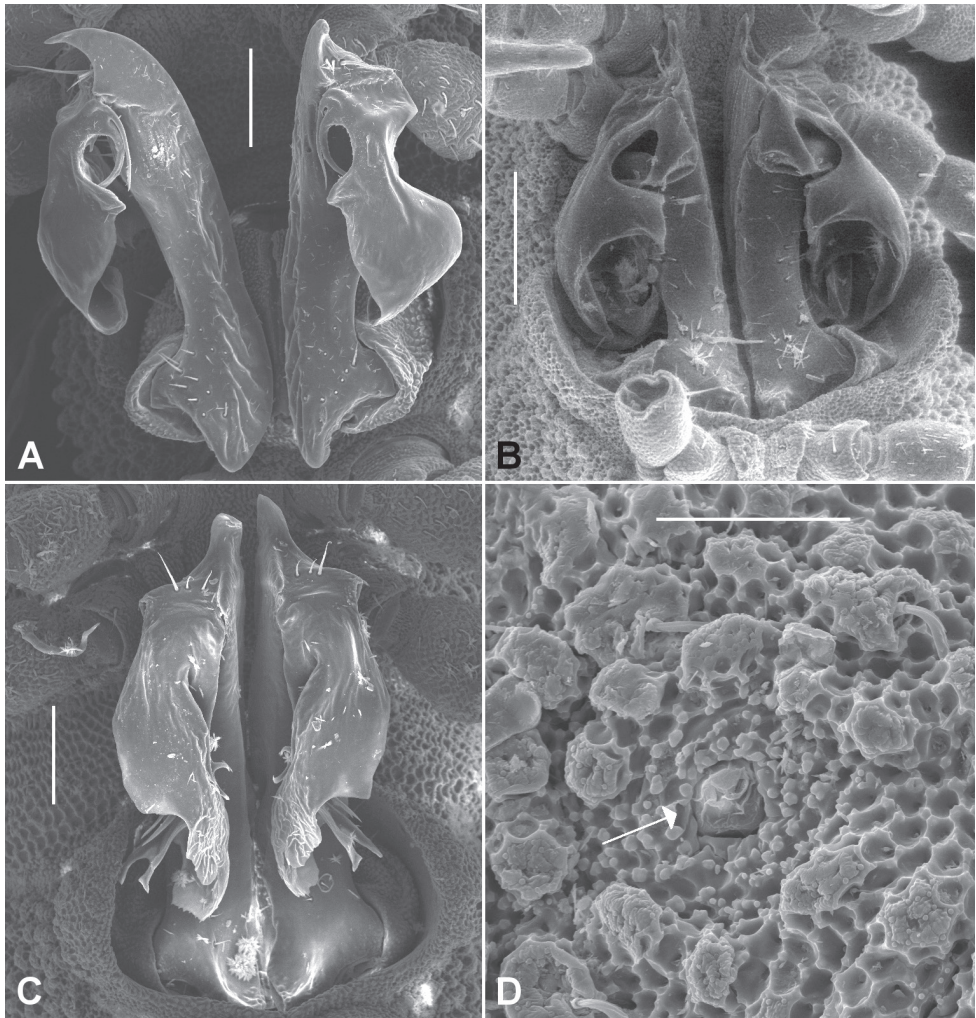


Figure 10. A–C, posterior gonopod views. **A** *Agathodesmus sagma* sp. n., paratype ex QM S96076 **B** *A. summus* sp. n., paratype ex QM S96091 **C** *A. yuccabinensis* sp. n., paratype ex QM S96094 **D** Midbody ozopore (arrow) of *A. agnus* sp. n., male paratype ex QM S96021. **B** is uncoated specimen; scale bars: **A**, **C** = 0.1 mm, **B** = 0.2 mm, **D** = 0.05 mm.

Other material. None.

Diagnostic description. Male with head + 19 rings. Colour in alcohol pale yellow. Male ca 7.5 mm long; ring 12 maximum diameter ca 0.5 mm, maximum width ca 0.6 mm. Metatergal tubercles in ca 10–12 irregular transverse rows, mainly without setae; metatergal setae short with slightly flared tips; lateralmost row of tubercles not enlarged, not forming pseudo-paranotum. Male leg 6 without coxal projection. Telopodite (Figs 8C, 8D) with **pp** curving posteriorly, anteroposte-

riorly flattened (wider in posterior view than lateral); **at** in oblique plane (facing posterolaterally), short, narrowly triangular, curving posterolaterally; **dp** directed posterobasally and laterally at base, a small, rounded, mediolaterally flattened tab arising on posterior surface just above (basal to) **mab** origin; **mab** divided into 2 lobes; lateral **mab** lobe terminating in basomedially curving, finger-like process; medial **mab** lobe curving medially, divided into broad medial and narrow, distally expanded lateral process with truncate distal margin; **meb** curving behind **mab**, divided near base into needle-like, basally directed medial process and long, broad lateral process curving medially and terminating in short, broad hook behind medial lobe of **mab**.

Distribution. Known only from rainforest at the type locality on the Atherton Tableland in tropical north Queensland (Fig. 13A).

Name. For the type locality, Millaa Millaa; noun in apposition.

***Agathodesmus morwellensis* sp. n.**

<http://zoobank.org/71AF8186-F2FF-483F-AA02-F76DA644A211>

http://species-id.net/wiki/Agathodesmus_morwellensis

Fig. 9C

Holotype. Male, Fosters Gully, Morwell National Park, Vic, 38°21'41"S, 146°23'20"E ±25 m, 170 m a.s.l., 31 July 2006, R. Mesibov, in pieces in genitalia vial, NMV K-11887.

Paratypes. NMV: 1 female, details as for holotype, K-11888; 1 male (K-11889), 1 female (K-11890), E of Churchill, Vic, 38°19'39"S, 146°27'59"E ±25 m, 190 m a.s.l., same date and collector.

Other material. None.

Diagnostic description. Male and female with head + 19 rings. Colour in alcohol pale white. Male/female ca 4.5/5.0 mm long; ring 12 maximum diameter ca 0.4/0.5 mm, maximum width ca 0.5/0.6 mm. Metatergal tubercles in ca 5 irregular transverse rows, mainly without setae; metatergal setae very short; 4 lateralmost tubercles enlarged, forming narrow pseudo-paranotum. Male leg 6 without coxal projection. Telopodite (Fig. 9C) with **pp** gently curving posteriorly, somewhat fusiform; **at** in transverse plane, short, narrowly triangular, curving posteriorly; **dp** directed posterobasally at base; **mab** folded outwards at base, shallowly divided into 2 lobes; **meb** short, broad, pointed, bent behind **mab**, not visible in posterior view.

Distribution. Known from eucalypt forest in the Latrobe River valley in West Gippsland, Victoria, at two sites ca 7 km apart (Fig. 11). Non-male specimens (in NMV) only tentatively assigned to *Agathodesmus* have been found in the mountains northwest of the type locality.

Name. For the type locality, Morwell National Park; adjective.

***Agathodesmus parapholeus* sp. n.**

<http://zoobank.org/F6965A14-A93B-4EB9-9F09-B201AF32BAFA>

http://species-id.net/wiki/Agathodesmus_parapholeus

Fig. 9D

Holotype. Male, Tower near The Crater, Qld, 17°27'23"S, 145°29'12"E ±500 m, 1230 m a.s.l., 23 November 1994, G. Monteith, QM berlesate 878, rainforest, sieved litter, QM S96056 (ex QM S46994).

Paratypes. QM: 12 males, 4 females, 1 stadium 6 male, 1 stadium 6 female, details as for holotype, S96057; 1 male, 2 females, same details but 16 May 1995, QM berlesate 886, rainforest, stick brushing, S96058.

Other material. QM: 1 female, 21 km S of Atherton, Qld, 17°26'41"S, 145°28'35"E ±500 m, 1000 m a.s.l., 5 November 1983, D. Yeates and G. Thompson, QM berlesate 616, rainforest, sieved litter, S96059; 3 males, 1 female, same details but QM berlesate 617, S96060; 1 male, 1 female, Kjellberg Road, Mt Fisher, Qld, 17°32'34"S, 145°33'31"E ±500 m, 1100 m a.s.l., 18 May 1995, G. Monteith, QM berlesate 892, rainforest, sieved litter, S96061; 16 males, 5 females, 2 stadium 6 females, 2 stadium 5 females, Mt Murray Prior, Qld, 16°55'59"S, 145°50'59"E ±500 m, 770 m a.s.l., 30 October 1995, G. Monteith, QM berlesate 894, rainforest, sieved litter, QM S96062. **ANIC:** Longlands Gap Road, 27 km S of Atherton, Qld, 17°28'S, 145°29'E ±2 km, 11 November 1969, J.G. Brooks, ANIC berlesate 169, leaf mould, rainforest, 64-000339.

Diagnostic description. Male and female with head + 19 rings. Colour in alcohol pale yellow. Male/female ca 8.0/9.0 mm long; ring 12 maximum diameter ca 0.75/0.85 mm, maximum width ca 0.75/0.85 mm. Metatergal tubercles in ca 12 irregular transverse rows, mainly without setae; metatergal setae short with slightly flared tips; lateralmost tubercles not enlarged, not forming pseudo-paranotum. Male leg 6 coxa with prominent mediodistal projection. Telopodite (Fig. 9D) with **pp** straight; **at** in transverse plane, short, rounded-triangular, tip not curving posteriorly; **dp** directed posterobasally and laterally at base; **mab** deeply divided into 2 lobes; anterior **mab** lobe subdivided, its posterior portion curving medially; posterior **mab** lobe with cup-like partial fold at midlength, the distal margin bent into narrow shelf and with small notch near medial edge; **meb** curving behind **mab**, divided at base into 2 subequal, closely appressed, needle-like processes.

Distribution. Known from rainforest on the Atherton Tableland and the coastal range just southeast of Cairns in tropical north Queensland (Fig. 13B); the two areas are ca 70 km apart. Co-occurs with *A. quintanus* sp. n. on the Atherton Tableland.

Name. Greek *para*, 'near', and *pholeos*, 'hole'; adjective. The type locality is close to Mt Hypipamee Crater, a vertical volcanic pipe.

Remarks. *A. parapholeus* sp. n. is very similar to *A. kirrama* sp. n. (compare Figs 9B and 9D). I am separating them on the number of **mab** lobes (three in *kirrama* sp. n. vs two in *parapholeus* sp. n.) and the development of long mediodistal projections on the leg 6 coxae in *kirrama* sp. n. These differences may be clinal, and further collecting would be useful in the ca 70 km-wide gap between closest known occurrences of the two species.

***Agathodesmus quintanus* sp. n.**

<http://zoobank.org/71796952-F691-4A75-B90F-B564EA88E414>

http://species-id.net/wiki/Agathodesmus_quintanus

Figs 4B, 8E

Holotype. Male, Bellenden Ker Range, Qld, cable tower 5, 17°16'04"S, 145°53'00"E ±100 m, 500 m a.s.l., 17-24 October 1981, Queensland Museum and Earthwatch personnel, QM S96063.

Paratypes. QM: 4 males, 4 females, details as for holotype, S96064; 2 males, same locality but cableway base station, 17°16'06"S, 145°53'54"E ±100 m, 110 m a.s.l., 25-31 October 1981, same collectors, S96067; 2 males, 1 female, same details but QM berlesate 309, rainforest, stick brushings, S96073; 1 male, 1 female, 1 stadium 6 female, same locality but 1 km S of cable tower 6, 17°16'33"S, 145°53'15"E ±100 m, 500 m a.s.l., 17-24 October 1981, same collectors, QM berlesate 319, rainforest, sieved litter, S96074; 1 male, 1 female, 1 stadium 6 male, 1 stadium 6 female, 1 stadium 5 male, same details but 25-31 October 1981, QM berlesate 321, rainforest, sieved litter, S96068; 3 males, same locality but cable tower 3, 17°16'02"S, 145°52'12"E ±100 m, 1020 m a.s.l., 17-24 October 1981, same collectors, S96066.

Other material. QM: 1 male, 2 females, 1 stadium 6 female, North Bell Peak via Gordonvale, Qld, 17°05'19"S, 145°52'44"E ±500 m, 900 m a.s.l., 16 September 1981, G. Monteith and D. Cook, QM berlesate 300, rainforest, sieved litter and moss, QM S96065; 1 male, Massey Range, Qld, 17°15'45"S, 145°49'06"E ±500 m, 1250 m a.s.l., 10 October 1991, G. Monteith and H. Janetzki, QM berlesate 853, rainforest, sieved litter, S96069; 1 male, 2 females, Tower near The Crater, Qld, 17°27'23"S, 145°29'12"E ±500 m, 1230 m a.s.l., 23 November 1994, G. Monteith, QM berlesate 878, rainforest, sieved litter, ex S46994, S96070; 2 males, 1 female, Kjellberg Road, Mt Fisher, Qld, 17°32'34"S, 145°33'31"E ±500 m, 1100 m a.s.l., 18 May 1995, G. Monteith, QM berlesate 892, rainforest, sieved litter, S96071; 2 males, Graham Range, Qld, 17°16'24"S, 145°57'58"E ±500 m, 550 m a.s.l., 1 November 1995, G. Monteith, QM berlesate 895, rainforest, sieved litter, S96072. **ANIC:** 1 male, Bartle Frere Track, 17 km E of Malanda, Qld 17°22'57"S, 145°46'45"E ±500 m, 1200 m a.s.l., 8 December 1988, G. Monteith and G. Thompson, QM berlesate 815, rainforest, sieved litter, 64-000340 [handwritten ANIC label incorrectly gives '17 km W' and '1989']

Diagnostic description. Male and female with head + 19 rings. Colour in alcohol very pale yellow. Male/female ca 5.5/6.0 mm long; ring 12 maximum diameter ca 0.6/0.65 mm, maximum width ca 0.8/0.85 mm. Metaternal tubercles in 4-5 irregular transverse rows, larger tubercles mainly with setae; metaternal setae long with slightly flared tips (Fig. 4B); 3 lateralmost tubercles enlarged, forming narrow pseudo-paranotum. Male leg 6 coxa with small, rounded, mediodistal projection. Telopodite (Fig. 8E) with **pp** curving gently posteriorly; **at** in transverse plane, short, rounded-triangular, curving posteriorly; **dp** directed posterobasally at base; **mab** greatly widening distally, divided into 2 lobes; lateral **mab** lobe directed anterobasally, distally spoon-shaped, concave medially; medial **mab** lobe produced basomedially with roundly pointed tip;

meb large and complex, divided into 2 lobes; medial **meb** lobe curving widely mediobasally at base, then laterobasally, then basally, tapering to blunt point, the curve at base often overlapping the initial curve of the contralateral medial **meb** lobe; lateral **meb** lobe directed basolaterally, divided at about midlength into flat, basally directed, distally deeply emarginate tab, and long, needle-like process curving first posteriorly, then anterobasally, terminating anterior to **pp**.

Distribution. Rainforest southwest of Babinda in tropical north Queensland, with a known east-west extent of ca 50 km (Fig. 13B). Co-occurs with *A. hahnensis* sp. n. in the Graham Range and with *A. parapholeus* sp. n. near Mt Hypipamee Crater. Possibly co-occurs on Mt Bartle Frere with *A. adelphus* sp. n.

Name. Latin *quintanus*, 'of the fifth'; adjective. The type locality was recorded as the fifth tower supporting the cableway to the top of Mt Bellenden Ker. This tower has since been renumbered '4' (Mesibov 2012b)

Remarks. *A. quintanus* sp. n. has a particularly complicated gonopod telopodite and I am not certain that I have clearly seen all its details. The species is distinguished by the wide initial curve of the medial **meb** lobe and the basomedially directed, roundly pointed medial **mab** lobe.

Specimens from North Bell Peak are larger than those from the type locality and have more prominent dorsal tubercles. Latitude/longitude data for the types have been corrected following Mesibov (2012b).

***Agathodesmus sagma* sp. n.**

<http://zoobank.org/6C431D39-25DB-4C23-BF3D-97860D5C331C>

http://species-id.net/wiki/Agathodesmus_sagma

Fig. 10A

Holotype. Male, Saddle Mountain, Qld, summit, 16°49'11"S, 145°39'42"E ±500 m, 650 m a.s.l., 21 November 1994, G. Monteith, QM berlesate 877, rainforest, sieved litter, QM S96075.

Paratypes. 6 males, 1 female, 1 stadium 6 female, details as for holotype, QM S96076.

Other material. QM: 1 male, Mt Demi, 7.0 km S of Mossman, Qld, 16°29'54"S, 145°19'13"E ±500 m, 900–1000 m a.s.l., 26 April 1983, G. Monteith and D. Yeates, QM berlesate 546, rainforest, litter, S96085; 1 male, 2.5 km N of Mt Lewis via Jullatten, Qld, 16°33'49"S, 145°15'51"E ±500 m, 1040 m a.s.l., 3 November 1983, D. Yeates and G. Thompson, QM berlesate 611, rainforest, sieved litter, S96077; 1 male, 1 female, 1 stadium 5 male, 2 km SE of Mt Spurgeon via Mt Carbine, Qld, 16°27'17"S, 145°12'26"E ±500 m, 1100 m a.s.l., 20 December 1988, G. Monteith and G. Thompson, QM berlesate 825, rainforest, sieved litter, S96078; 1 male, Lambs Head, 10 km W of Edmonton, Qld, campsite, 17°01'23"S, 145°38'33"E ±500 m, 1200 m a.s.l., 12 December 1989, G. Monteith, G. Thompson and H. Janetzki, QM berlesate 835, rainforest, litter, S96086; 1 male, 1 female, same details but 10 De-

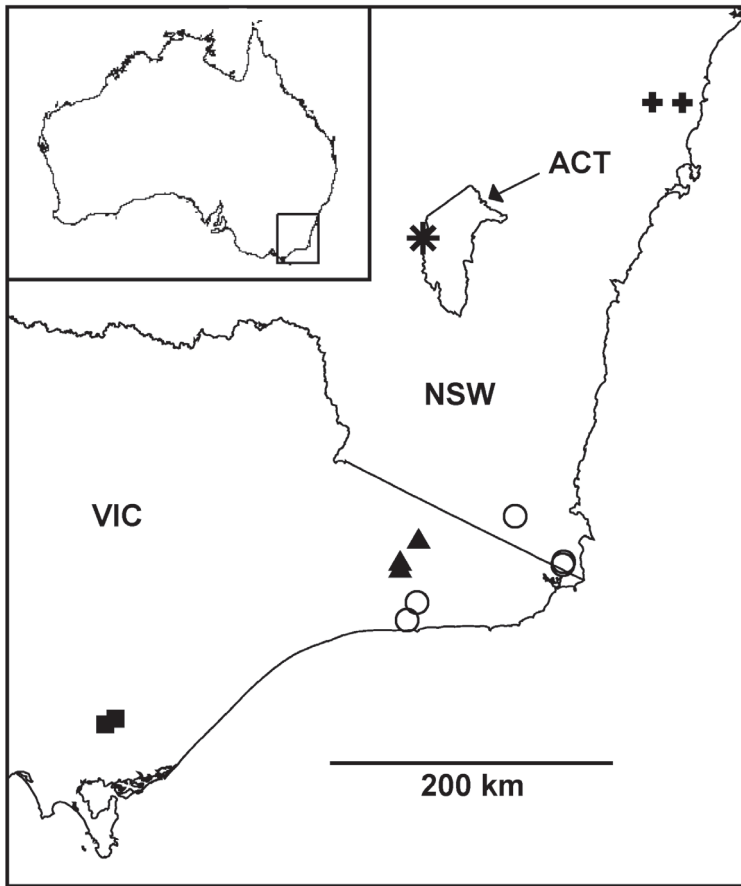


Figure 11. Localities for *Agathodesmus bonang* sp. n. (filled triangles), *A. carorum* sp. n. (open circles), *A. johnsi* Mesibov, 2009 (star), *A. morwellensis* sp. n. (filled squares) and *A. steeli* Silvestri, 1910 (crosses). Mercator projection; ACT = Australian Capital Territory, NSW = New South Wales, VIC = Victoria. Inset shows location of main map.

cember 1989 to 8 January 1990, rainforest pitfalls, S96087; 4 males, 1 female, Davies Creek Road, Qld, 17°02'33"S, 145°36'51"E ±500 m, 750 m a.s.l., 17 December 1989, G. Monteith and G. Thompson, QM berlesate 836, rainforest, sieved litter, S96079; 2 males, 2 females, same details but QM berlesate 841, S96080; 1 male, 6 females, 1 stadium 6 male, Mt Formartine South, Qld, 16°43'48"S, 145°36'45"E ±500 m, 700 m a.s.l., 24 November 1990, G. Monteith and G. Thompson, QM berlesate 848, rainforest, sieved litter, S96081; 1 male, same details but 23–24 November 1990, pitfall traps, S96084; 6 males, 4 females, Mt Halcyon, Qld, 16°03'16"S, 145°25'16"E ±500 m, 870 m a.s.l., 24 November 1993, G. Monteith and H. Janetzki, QM berlesate 864, rainforest, sieved litter, S96082; 5 males, 1 female, Isley Hills, Qld, 17°02'52"S, 145°41'25"E ±500 m, 1050 m a.s.l., 1 December 1993, G. Monteith and H. Janetzki, QM berlesate 866, rainforest, sieved litter and moss, S96083; 1 male, 1 female, 2 sta-

dium 6 males, Mt Spurgeon, Qld, summit, 16°26'22"S, 145°12'00"E ±500 m, 1300 m a.s.l., 22 November 1997, G. Monteith, QM berlesate 956, rainforest, sieved litter, S46128; 1 male, 3 km S of Mt Spurgeon, Qld, 16°27'59"S, 145°12'02"E ±500 m, 1140 m a.s.l., 19–23 November 1997, G. Monteith, D. Cook and C. Burwell, sclerophyll forest, S35882. **ANIC:** 1 male, Mt Lewis, Qld, 16°35'S, 145°17'E ±1 km, 960 m a.s.l., 30 October 1976, R.W. Taylor and T.A. Weir, ANIC berlesate 545, rainforest, 64-000341; 5 males, 2 km N by E of Mt Tiptree, Qld, 17°03'S, 145°37'E ±1 km, 1 April 1984, A. Calder and T.A. Weir, ANIC berlesate 950, rainforest, 64-000343; 4 males, Mt Tiptree, Qld, 17°03'S, 145°37'E ±1 km, 13 July 1984, B. Halliday, ANIC berlesate 1006, rainforest, leaf litter, 64-000342.

Diagnostic description. Male and female with head + 19 rings. Colour in alcohol very pale yellow. Male/female ca 8.0/8.0 mm long; ring 12 maximum diameter ca 0.7/0.8 mm, maximum width ca 0.7/0.85 mm. Metatergal tubercles in 10–12 irregular transverse rows, mainly without setae; metatergal setae short with slightly flared tips; lateralmost tubercles not enlarged, not forming pseudo-paranotum. Male leg 6 coxa with small, rounded, mediiodistal projection. Telopodite (Fig. 11A) with **pp** straight; **at** in oblique plane (facing posterolaterally), short, rounded-triangular, curving posterolaterally; **dp** directed posterobasally and laterally at base; **mab** somewhat expanded distally, divided into 2 lobes with large anterior fold; **meb** divided at base into 2 needle-like processes, the smaller medial process directed basally, the longer medial process curving behind **mab**.

Distribution. Wet forest in tropical north Queensland from the Cape tribulation area south to the Atherton Tableland, a north-south extent of ca 120 km (Fig. 13B).

Name. Latin *sagma*, 'saddle'; noun in apposition. For the type locality, Saddle Mountain.

***Agathodesmus summus* sp. n.**

<http://zoobank.org/0FFE6498-73F7-4CBD-9C82-24473D6FF6A7>

http://species-id.net/wiki/Agathodesmus_summus

Fig. 10B

Holotype. Male, Mt Bartle Frere, Qld, centre peak ridge, 17°23'27"S, 145°48'33"E ±500 m, 1400–1500 m a.s.l., 7–8 November 1981, Queensland Museum and Earth-watch personnel, QM berlesate 358, rainforest, sieved litter, QM S96088.

Paratypes. **QM:** 2 males, 2 females, 1 stadium 7 female, details as for holotype, S96091; 2 males, same locality and collectors but S peak summit, 17°24'03"S, 145°49'00"E ±500 m, 1620 m a.s.l., 6–8 November 1981, QM berlesate 359, rainforest, sieved litter, S96090; 1 female, same details but QM berlesate 354, S96089; 2 females, same locality but top camp, 17°23'47"S, 145°48'53"E ±500 m, 1500 m a.s.l., 29 November 1998, G. Monteith, pyrethrum knockdown, S96092.

Other material. None.

Diagnostic description. Male with head + 19 rings, female with head + 20. Colour in alcohol very pale yellow. Male/female ca 9.0/9.5 mm long; ring 12 maximum diameter ca 0.75/0.9 mm, maximum width ca 0.8/1.0 mm. Metatergal tubercles in 10–12 irregular transverse rows, mainly without setae; metatergal setae short with slightly flared tips; lateralmost tubercles not enlarged, not forming pseudo-paranotum. Male leg 6 without coxal projection. Telopodite (Fig. 11B) with **pp** slightly curving posteriorly; **at** in oblique plane (facing posterolaterally), short, narrowly triangular, curving posterolaterally; **dp** directed laterobasally and slightly posteriorly at base; **mab** expanded distally, divided into 2 distally rounded lobes, the medial lobe with truncate medial projection at ca midlength; **meb** curving behind **mab** and nearly as long, divided at ca midlength into shorter, needle-like lateral process and broad medial process terminating in upturned hook.

Distribution. Known only from rainforest at the type locality in tropical north Queensland (Fig. 13B). Possibly co-occurs on Mt Bartle Frere with *A. adelphus* sp. n. and *A. quintanus* sp. n.

Name. Latin *summus*, 'highest'; adjective. This species was found at the top of Queensland's highest mountain, Mt Bartle Frere.

Remarks. The Bartle Frere females were assigned to this species rather than to the co-occurring *A. adelphus* sp. n. and *A. quintanus* sp. n. because the females lack the narrow pseudo-paranota found in the other two species.

***Agathodesmus yuccabinensis* sp. n.**

<http://zoobank.org/024140B1-5299-4539-9873-898BD7CC8D55>

http://species-id.net/wiki/Agathodesmus_yuccabinensis

Fig. 10C

Holotype. Male, near Yuccabine Creek, Kirrama Range, Qld, 18°12'21"S, 145°45'47"E ±500 m, 700 m a.s.l., 10 December 1986, G. Monteith and G. Thompson, QM berlesate 732, rainforest, sieved litter, QM S96093.

Paratypes. 3 males, 7 females, 1 stadium 6 female, details as for holotype, QM S96094.

Other material. QM: 2 males, 1 female, Kirrama Range, Qld, 18°12'57"S, 145°47'15"E ±500 m, 700 m a.s.l., G. Monteith and G. Thompson, QM berlesate 730, rainforest, sieved litter, S96095; 3 males, Mt Hosie, Kirrama Range, Qld, 18°12'29"S, 145°46'41"E ±500 m, 930 m a.s.l., 11 December 1986, same collectors and method but QM berlesate 733, S96096; 3 males, 2 females, Mt Macalister, Cardwell Range, Qld, 18°18'16"S, 145°56'32"E ±500 m, 1000 m a.s.l., 20 December 1986, same collectors and method but QM berlesate 739, S96098; 1 male, 1 stadium 6 male, 1 stadium 6 female, same details but 700 m a.s.l., QM berlesate 741, moss on trees and rocks, S96097; 1 female, same locality but 900 m a.s.l., 15 January 1987, S. Hamlet, QM berlesate 757, rainforest, sieved litter, S96099.

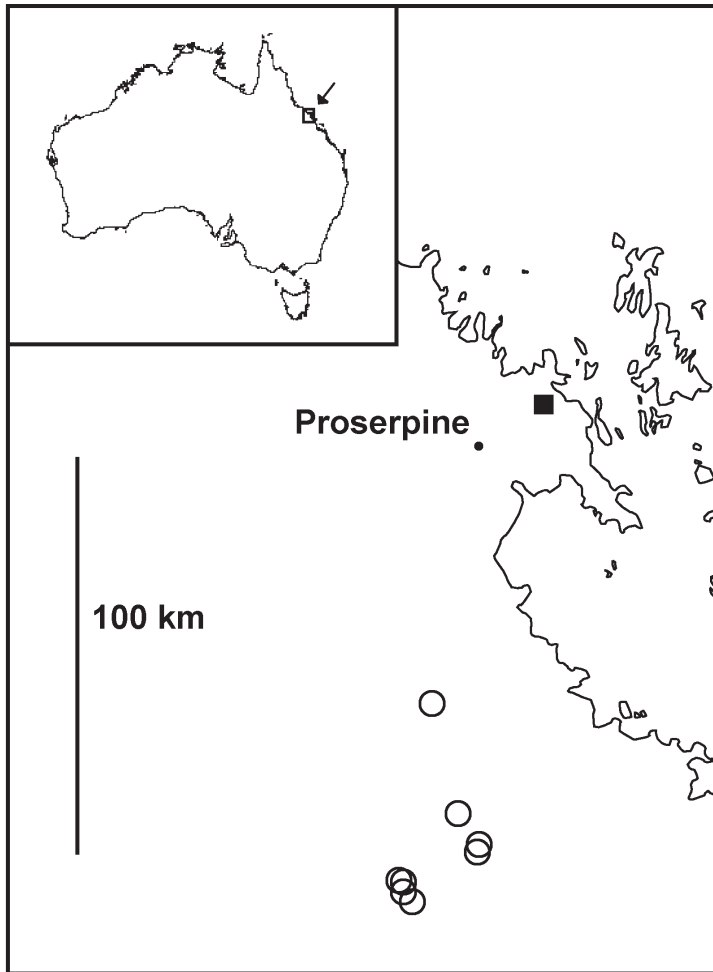


Figure 12. Localities for *Agathodesmus aenigmaticus* sp. n. (filled square) and *A. bucculentus* (Jeekel, 1986) (open circles) in central coastal Queensland. Mercator projection; inset shows location of main map.

Diagnostic description. Male and female with head + 19 rings. Colour in alcohol pale yellow. Male/female ca 9.0/9.5 mm long; ring 12 maximum diameter ca 0.7/0.85 mm, maximum width ca 0.8/0.9 mm. Metatergal tubercles in 10–12 irregular transverse rows, mainly without setae; metatergal setae short with slightly flared tips; lateralmost tubercles not enlarged, not forming pseudo-paranotum. Male leg 6 without coxal projection. Telopodite (Fig. 11C) with **pp** straight; **at** in transverse plane, short, rounded-triangular, tip curving very slightly posteriorly; **dp** directed posterobasally at base; **mab** curving medially, then basally, the apex divided into truncate lobe with fine marginal teeth, and apically forked lobe; **meb** broad, curving behind **mab** and nearly as long, divided at midlength into short, rounded lateral lobe and 2 slender, subequal, pointed posterior processes reaching almost to **mab** apex.

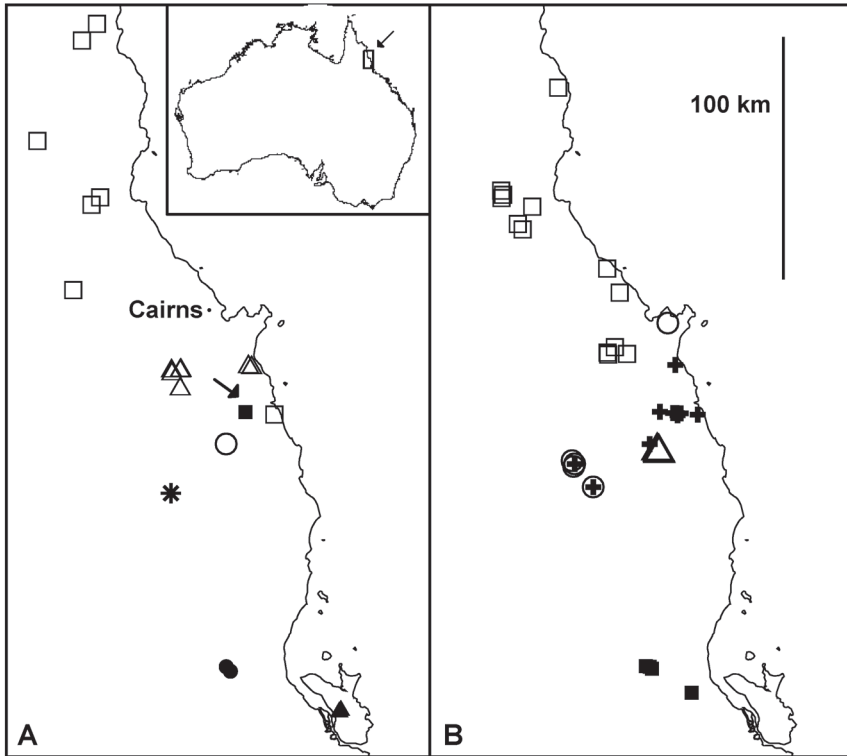


Figure 13. Localities in far north Queensland for **A** *Agathodesmus adelphus* sp. n. (open circle), *A. agnus* sp. n. (open triangles), *A. gayundah* sp. n. (filled triangle), *A. hahnensis* sp. n. (open squares), *A. kerensis* sp. n. (filled square), *A. kirrama* sp. n. (filled circles), *A. millaa* sp. n. (star) and **B** *A. paropholeus* sp. n. (open circles), *A. quintanus* sp. n. (crosses), *A. sagma* sp. n. (open squares), *A. summus* sp. n. (open triangles), and *A. yuccabinensis* sp. n. (filled squares). Arrow in **A** indicates questionable, disjunct locality for *A. aenigmaticus* sp. n. Mercator projections; inset shows location of main maps.

Distribution. Rainforest in the Cardwell Range (includes Kirrama Range), inland between Tully and Ingham in tropical north Queensland (Fig. 13B). The linear extent of the known range is ca 20 km. Co-occurs with *A. kirrama* sp. n. on Mt Hosie.

Name. For Yuccabine Creek, the type locality; adjective.

Agathodesmus bucculentus (Jeekel, 1986)

http://species-id.net/wiki/Agathodesmus_bucculentus

Figs 3A, 3B, 4A

Note. This species was described from three specimens collected by Dr and Mrs Jeekel in 1980, under logs in rainforest along the 'Broken Hill' [probably 'Broken River'] track in Eungella National Park (Jeekel 1986). Another 183 specimens from the same general area are in Australian collections (see below), and the *A. bucculentus*

range in central coastal Queensland is now known to have a north-south extent of ca 50 km (Fig. 12).

Material examined. ANIC: 35 males, 17 females, 1 stadium 7 female, Eungella National Park, Qld, 21°09'S, 148°30'E ±1 km, 760 m a.s.l., 10 November 1976, R.W. Taylor and T.A. Weir, ANIC berlesate 562, rainforest, 64-000332; 16 males, same details but ANIC berlesate 563, 64-000329; 27 males, same details but ANIC berlesate 564, 64-000333; 4 males, Finch Hatton Gorge, Qld, 21°05'S, 148°38'E ±1 km, 200 m a.s.l., 11 November 1976, R.W. same collectors, ANIC berlesate 565, rainforest, 64-000334; 6 males, 4 females, 2 stadium 7 males, 5 stadium 7 females, Broken River, Eungella National Park, Qld, 21°10'S, 148°31'E ±1 km, 700 m a.s.l., 10-12 November 1976, same collectors, ANIC berlesate 559, rainforest, 64-000331; 3 males, 1 female, same details but ANIC berlesate 560, 64-000330; 17 males, 1 female, 1 stadium 7 female, same details but ANIC berlesate 561, 64-000335; 7 males, 1 female, 1 stadium 7 female, same details but ANIC berlesate 568, 64-000328; 18 males, 2 females, same details but ANIC berlesate 570, 64-000336. **QM:** 1 male, 2 females, Mt William, Eungella National Park, Qld, 21°01'05"S, 148°35'57"E ±500 m, 1240 m a.s.l., 19 April 1979, G. Monteith, QM berlesate 41, rainforest, sieved litter, S96025; 2 males, 1 stadium 7 female, Eungella, Qld, schoolhouse, 21°07'51"S, 148°29'32"E ±2 km, 13 February 1986, J. Gallon and R. Raven, QM berlesate 709, rainforest, S96026; 1 male, Finch Hatton Gorge, Qld, 21°04'13"S, 148°38'11"E ±500 m, 300 m a.s.l., 18 November 1992, G. Monteith, G. Thompson, D. Cook and H. Janetzki, S96027; 3 males, 4 females, Mt Macartney, Qld, 20°49'57"S, 148°33'07"E ±500 m, 950 m a.s.l., 19 November 1992, same collectors, S96028.

Remarks. There is little to add to the excellent description and illustrations of Jeekel (1986), except to confirm that the short metatergal setae noted by Jeekel are bipartite with slightly flared tips (Fig. 4A) as in most other *Agathodesmus*, and that the **dp** in *A. bucculentus* is indeed 'complicated'. Fig. 16 in Jeekel (1986) clearly shows the **meb**: it is divided near its base into a curving, needle-like medial process and a more or less parallel, broader, distally expanded and lamellar lateral process. However, the **meb** in *A. bucculentus* is not 'on caudal side' (Jeekel 1986, p. 49), but lies between the **mab** and the **pp**, as in other *Agathodesmus* spp.

Acknowledgements

I thank Beth Mantle, Robyn Meier and Cate Lemann (ANIC), Peter Lillywhite (NMV) and Owen Seeman (QM) for assistance, registrations and the loan of specimens, and Kate Sparks (SAM) for registrations. SEM images were acquired with the help of Karsten Goemann (Central Science Laboratory, University of Tasmania). Robert and Jenni Henzell very kindly provided access to their private forest at Uraidla, SA. Valuable suggestions for improvement were made by reviewers Sergei Golovatch and Nguyen Duc Anh. Field trips and laboratory studies were funded by the author.

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Appendix

Specimen records of Australian *Agathodesmus* species. (doi: 10.3897/zookeys.325.5932.app) File format: Comma Separated Value File (csv).

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Citation: Mesibov R (2013) New species of *Agathodesmus* Silvestri, 1910 from Australia (Diplopoda, Polydesmida, Haplodesmidae). ZooKeys 325: 33–64. doi: 10.3897/zookeys.325.5932 Specimen records of Australian *Agathodesmus* species. doi: 10.3897/zookeys.325.5932.app

Fossil echinoid (Echinoidea, Echinodermata) diversity of the Early Cretaceous (Hauterivian) in the Paris Basin (France)

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Resource citation: Thomas Saucède (2013) Fossil echinoid (Echinoidea, Echinodermata) diversity of the Early Cretaceous (Hauterivian) in the Paris Basin (France). Online at http://ipt.pensoft.net/ipt/resource.do?r=hauterivian_echinoids_of_the_paris_basin, Version 2.0 (last updated on 2013-08-16), GBIF key: <http://gbirds.gbif.org/browse/agent?uuid=98442b0b-9f7b-4924-9289-5b793946ca01>. Data Paper ID: doi: 10.3897/zookeys.325.5085

Abstract

This dataset inventories occurrence records of fossil echinoid specimens collected in the Calcaires à Spatangues Formation (CSF) that crops out in the southeast of the Paris Basin (France), and is dated from the *Acanthodiscus radiatus* chronozone (*ca.* 132 Ma, early Hauterivian, Early Cretaceous). Fossil richness and abundance of the CSF has attracted the attention of palaeontologists since the middle of the nineteenth century. This dataset compiles occurrence data (referenced by locality names and geographic coordinates with decimal numbers) of fossil echinoids both collated from the literature published over a century and a half, and completed by data from collection specimens. The dataset also gives information on taxonomy (from species to order and higher taxonomic levels), which has been checked for reliability and consistency. It compiles a total of 628 georeferenced occurrence data of 26 echinoid species represented by 22 genera, 14 families, and 9 orders.

Keywords

Echinoids, Hauterivian, Early Cretaceous, Paris Basin, France, Calcaires à Spatangues Formation

Introduction

The Calcaires à Spatangues Formation (CSF) consists of shallow marine sediments deposited in the southeast of the Paris Basin (France) during the very Early Cretaceous (early Hauterivian, *Acanthodiscus radiatus* chronozone) about 132 million years ago, at the maximum of a second order sea level rise (Bulot et al. 2000; Courtinat et al. 2006; Bodin et al. 2009). Preserved deposits of near-shore and shallow marine environments are not common in Western Europe for that time-interval where deep-sea basin and deep shelf sediments predominated (Canérot and Cugny 1982; Rat et al. 1987; Schootbrugge et al. 2000). Deposits of the CSF yield a diversified, speciose and locally abundant fossil fauna, essentially composed of benthic invertebrates among which echinoids are common and locally very abundant (Cornuel 1841; Rat et al. 1987; Courtinat et al. 2006). In that respect, the CSF is a window on the little known benthic communities that thrived in shallow marine environments in the Early Cretaceous.

Fossil richness of the CSF has attracted the attention of palaeontologists since the middle of the nineteenth century (Cotteau 1857–1878, 1862–1867; Valette 1908; Corroy 1925; Rat et al. 1987; Walter 1996; Saucède et al. 2012). Fifty-four echinoid species were described in the CSF in all, half of them (26 species) based on type specimens collected in the CSF. However, many nominal species are geographically restricted and morphologically little differentiated. Of the 54 echinoid species ever described, Saucède et al. (2012) recognized only 26 species that belong to 16 different families, among which regular (13 species) and irregular (13 species) echinoids are represented in equal proportion. This still represents a high level of fossil echinoid diversity for that time-period, which can be explained by a putative high beta-diversity due to the numerous microhabitats present in shallow marine environments at that time and by the richness of cassiduloid echinoids, the group being particularly well-diversified in coarse sediment environments in the Early Cretaceous (Kier 1962).

Project details

Project title: Inventory of the fossil echinoid diversity of the Early Cretaceous (Hauterivian) in the Paris Basin (France).

Personnel: Sophie Benetti (data manager, data publisher), Thomas Saucède (collection identifier, data collector, data manager, data publisher), Bruno David (data collector, data manager)

Funding sources: BioME team, UMR CNRS 6282 Biogéosciences, Université de Bourgogne.

Study area description. This dataset inventories occurrence records of fossil echinoid specimens collected in the Calcaires à Spatangues Formation (CSF) that crops out in the southeast of the Paris Basin (France), from the town of Bar-le-Duc in the northeast to Sancerre in the southwest (Fig. 1A). The CSF is dated from the *Acanthodiscus radiatus* chronozone (*ca.* 132 Ma, early Hauterivian, Early Cretaceous) accord-

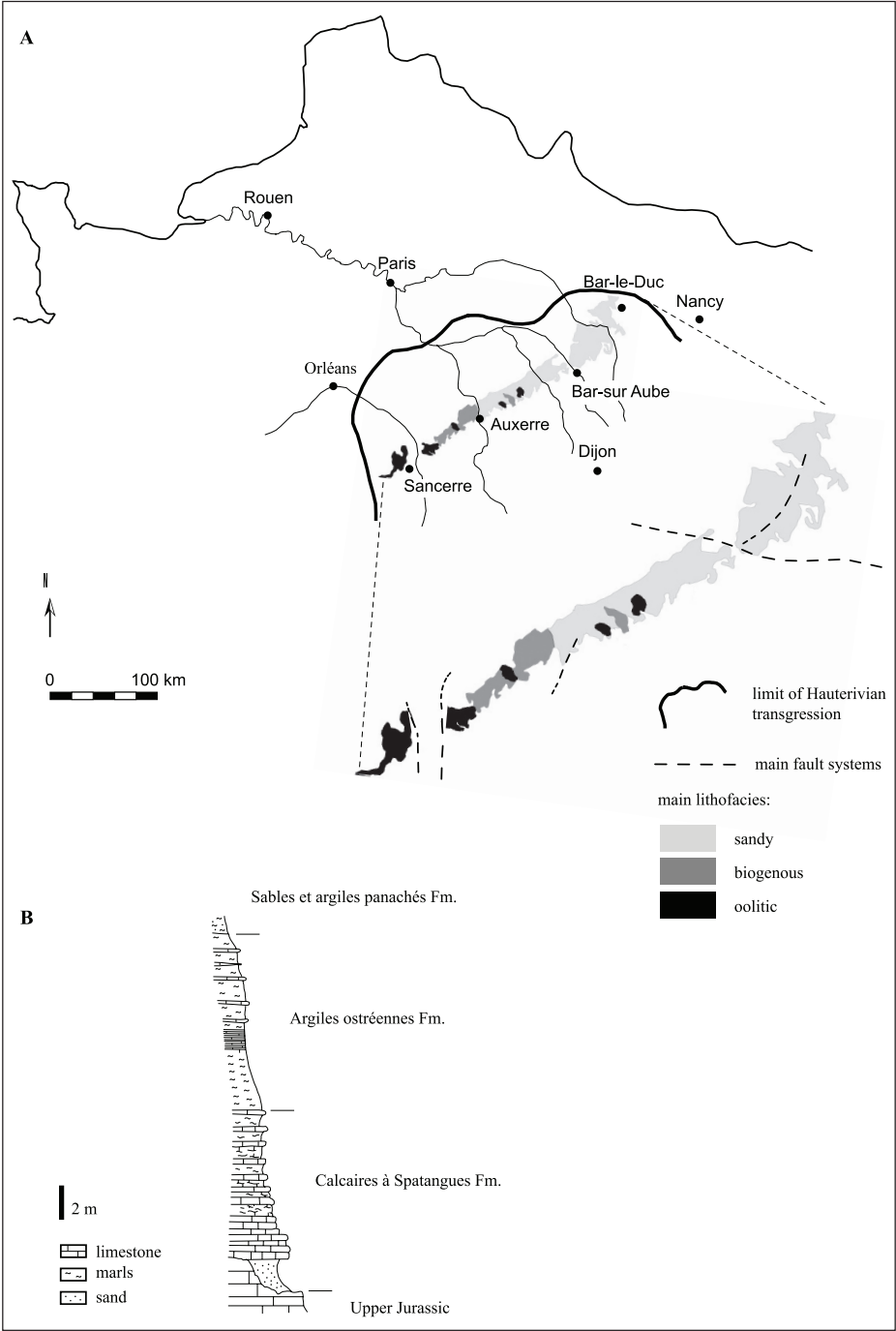


Figure 1. Geographic, geologic, and stratigraphic settings. A. Map showing the area of the Paris Basin (France) where the Calcaires à Spatangues Fm. crops out (modified after Courtinat et al. 2006 and Saucède et al. 2012). Distribution of main lithofacies as defined by Rat et al. (1987). B. Calcaires à Spatangues Fm. section at Lantages 48°08'N; 4°24'E (modified after Rat et al. 1987).

ing to the cephalopods collected: *Acanthodiscus radiatus* (Bruguière, 1789), *Leopoldia leopoldina* group (d'Orbigny, 1841), and *Cymatoceras pseudoelegans* (d'Orbigny, 1840) (Cornuel 1841; Mégnien and Mégnien 1980; Magniez-Jannin 1984; Rat et al. 1987; Reboulet et al. 2009). The CSF is composed of limestone and clay deposits (Fig. 1B), only a few meter thick (*ca.* 0.5 to 8 m) with dominant bioclastic lithofacies (Rat et al. 1987). The average palaeo-depth was moderate (approximately few meters to *ca.* 20–30 m) based on dinoflagellates, foraminifer and bryozoan assemblages, and the overall sedimentation rate was low as suggested by the abundance of worn ferruginous bioclasts and ooliths (Rat et al. 1987; Walter 1996; Courtinat et al. 2006).

Design description. This dataset compiles occurrence data (all data are referenced by locality names and georeferenced WGS1984) of fossil echinoids collated from the literature published over a century and a half, from 1857 to 2012, by Cotteau (1857–1878; 1862–1867), Valette (1908), Corroy (1925), Rat et al. (1987), and Saucède et al. (2012). The dataset was completed by data from collection specimens housed at the department of Geology of Université de Bourgogne (Dijon, France), specimens sampled in the field by J Houdard, A Valette, B David, and P Robert, at the Muséum national d'Histoire naturelle (Paris, France), specimens sampled by J Lambert, and at the department of Geosciences of Université de Rennes 1 (Rennes, France), specimens sampled by P Courville. The dataset also gives information on taxonomy (from species to order and higher taxonomic levels). Systematics was reviewed and homogenized by T Saucède for taxonomic relevance (Saucède et al. 2012).

Taxonomic coverage

General taxonomic coverage description: fossil regular and irregular echinoids (Echinodermata: Echinoidea) of the Calcaires à Spatangues Formation represented by 26 species, 22 genera, 14 families, and 9 orders.

Taxonomic ranks

Kingdom: Animalia

Phylum: Echinodermata

Class: Echinoidea Leske, 1778

Orders: Arbacioida Gregory, 1900; Cassiduloida L. Agassiz & Desor, 1847; Cidaroida Claus, 1880; Holasteroida Durham & Melville, 1957; Holecypoida Duncan, 1889; Pedinoida Mortensen, 1939; Phymosomatoida Mortensen, 1904; Salenioidea Delage & Herouard, 1903; Spatangoida L. Agassiz, 1840.

Families: Cidaridae Gray, 1825; Hemicydaridae Wright, 1857; Emiratiidae Ali, 1990; Stomechinidae Pomel, 1883; Acropeltidae Lambert & Thiéry, 1914; Arbaciidae Gray, 1855; Saleniidae L. Agassiz, 1838; Pedinidae Pomel, 1883; Holecypidae Lambert, 1899; Conulidae Lambert, 1911; Clypeidae Lambert,

1898; Pygaulidae Lambert, 1905; Nucleolitidae Agassiz & Desor, 1847; Toxasteridae Lambert, 1920.

Genera: *Goniopygus* Agassiz, 1838; *Codiopsis* Agassiz, 1840; *Disaster* Agassiz, 1836; *Pseudocidaris* Etallon, 1859; *Pygurus* Agassiz, 1839; *Clypeopygus* d'Orbigny, 1856; *Nucleolites* Lamarck, 1801; *Phyllobrissus* Cotteau, 1859; *Pygorhynchus* Agassiz, 1839; *Plagiochasma* Pomel, 1883; *Plegiocidaris* Pomel, 1883; *Salvaster* Saucède, Dudicourt & Courville, 2012; *Pseudholaster* Pomel, 1883; *Globator* Agassiz, 1840; *Coenholectypus* Pomel, 1883; *Pygolampas* Saucède, Dudicourt & Courville, 2012; *Hemipedina* Wright, 1855; *Loriolia* Neumayr, 1881; *Tetragramma* Agassiz, 1840; *Stomechinus* Desor, 1856; *Hyposalenia* Desor, 1856; *Toxaster* Agassiz, 1840.

Species: *Plegiocidaris salviensis* (Cotteau, 1851); *Plegiocidaris lardyi* (Desor, 1855); *Plegiocidaris friburgensis* (de Loriol, 1873); *Plegiocidaris muricata* (Roemer, 1836); *Pseudocidaris clunifera* (Agassiz, 1836); *Loriolia rotularis* (Agassiz, 1836); *Loriolia bourgueti* (Agassiz, 1840); *Tetragramma autissiodorensis* (Cotteau, 1851); *Stomechinus fallax* (Agassiz, 1840); *Goniopygus peltatus* (Agassiz, 1836); *Codiopsis lorini* Cotteau, 1851; *Hyposalenia stellulata* (Agassiz, 1838); *Hemipedina minima* (Cotteau, 1851); *Coenholectypus macropygus* (Agassiz, 1836); *Globator incisa* (Agassiz, in Desor 1842); *Pygurus montmollini* (Agassiz, 1836); *Plagiochasma olfersii* (Agassiz, 1836); *Pygorhynchus obovatus* (Agassiz, 1836); *Nucleolites salviensis* Cotteau, 1851; *Phyllobrissus gresslyi* (Agassiz, 1839); *Clypeopygus paultrei* (Cotteau, 1851); *Pygolampas edita* Saucède, Dudicourt & Courville 2012; *Disaster subelongatus* (d'Orbigny, 1853); *Salvaster roberti* Saucède, Dudicourt & Courville 2012; *Pseudholaster intermedius* (Goldfuss, 1829); *Toxaster retusus* (Lamarck, 1816).

Spatial coverage

General spatial coverage

The sampling area focuses on the Calcaires à Spatangues Formation that crops out in the southeast of the Paris Basin (France) (Fig. 1A). The study area extends over the six following French departments: Cher, Nièvre, Yonne, Aube, Haute-Marne, and Meuse.

Coordinates

47°33.00'N and 48°73.00'N Latitude; 2°75.00'E and 5°12.00'E Longitude.

Temporal coverage

1851–1995.

Collection description

Collection names: J Houdard, A Valette, B David, and P Robert collections housed at Université de Bourgogne (Dijon, France); P Courville collection housed at Université de Rennes 1 (Rennes, Dijon); J Lambert collection housed at Muséum national d'Histoire naturelle (Paris, France).

Curatorial unit: Géosciences, Université de Rennes 1 (Rennes, France), Geology department, Université de Bourgogne (Dijon, France), Muséum national d'Histoire Naturelle (Paris, France).

Collection identifiers: B David, T Saucède.

Method

Method step description. Specimens were both collected in the field and consulted in public collections of Université de Rennes 1 (Rennes, France), Université de Bourgogne (Dijon, France), and Muséum national d'Histoire Naturelle (Paris, France). Identification of specimens was performed at species level based on descriptions by G Cotteau (1857–1878; 1862–1867), A Valette (1908), G Corroy (1925), P Rat et al. (1987), and T Saucède et al. (2012). Taxonomy was updated when it proved necessary following Kier (1962), Durham et al. (1966), Smith (1984), and Kroh and Smith (2010). Though paraphyletic, some family names have been used for convenience (Nucleolitidae Agassiz & Desor, 1847; Toxasteridae Lambert, 1920). The accuracy and geographic coordinates of localities where collection specimens came from was checked based on geological grounds (BRGM sources). Dubious localities were discarded.

Study extent description. The Calcaires à Spatangues Formation consists of shallow marine sediments that were deposited in the southeast of the Paris Basin (France) during the early Hauterivian (*Acanthodiscus radiatus* zone). These deposits are rich and diversified in a benthic fauna among which echinoids predominate. The systematic status of echinoids of the Calcaires à Spatangues Fm. was revised so as to update the list of echinoid species reported in the Formation and better assess its remarkable diversity. Of the 54 echinoid species ever described, 26 species are recognized that belong to 16 different families, among which regular (13 species) and irregular (13 species) echinoids are represented in equal proportion.

Data resources: the data underpinning analyses of the paper are deposited at GBIF, the Global Biodiversity Information Facility, http://ipt.pensoft.net/ipt/archive.do?r=hauterivian_echinoids_of_the_paris_basin

Dataset

Citation identifier: http://ipt.pensoft.net/ipt/resource.do?r=hauterivian_echinoids_of_the_paris_basin

Dataset description: see design description

Object name: Darwin Core Archive hauterivian_echinoids_of_the_paris_basin

Character encoding: UTF-8

Format name: Darwin Core Archive format

Format version: 1.0

Distribution: http://ipt.pensoft.net/ipt/archive.do?r=hauterivian_echinoids_of_the_paris_basin

Publication date of data: 2013-08-13

Language: English

Metadata language: English

Date of metadata creation: 2013-08-13

Hierarchy level: Dataset

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Appendix

Occurrence records of Hauterivian echinoids of the Paris basin. (doi: 10.3897/zookeys.325.5085.app) File format: Microsoft Excel document (xls).

Explanation note: Table with occurrence data (referenced by locality names and geographic coordinates with decimal numbers) of fossil echinoids both collated from the literature and completed by data from collection specimens. The table also gives information on taxonomy (from species to order and higher taxonomic levels), which has been checked for reliability and consistency. It compiles a total of 628 georeferenced occurrence data of 26 echinoid species represented by 22 genera, 14 families, and 9 orders.

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