Zootaxa 1064: 39–49 (2005)
www.mapress.com/zootaxa/

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

1064

A new genus of millipede (Diplopoda: Polydesmida: Dalodesmidae) from Tasmania with a pseudo-articulated gonopod telopodite

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Abstract

Ginglymodesmus tasmanianus n. gen., n. sp., *G. penelopae* n. sp. and *G. sumac* n. sp. are described from northwest Tasmania, Australia. The three species have long, slender gonopod telopodites divided into proximal and distal sections, with the distal section pivoting around a hinge-like structure which appears to differ from the typical joint in an arthropod leg.

Key words: Diplopoda, Polydesmida, Dalodesmidae, *Ginglymodesmus*, Tasmania, Australia, gonopod, telopodite

Introduction

The taxonomy of Polydesmida is based largely on the structure of the male gonopods. These first appear after the final moult in place of the anterior leg-pair (leg-pair 8) on segment 7. In the later pre-adult stadia, the gonopods are represented by low, rounded primordia with proximal and distal portions separated by a groove (Filka & Shelley 1980). The two portions are thought to be homologous to the coxa and more distal podomeres, respectively, of a walking leg, and to develop during the final moult into the gonocoxa and telopodite of the gonopod.

No developmental studies to date have related individual components of the gonopod telopodite in any Polydesmida to individual podomeres. Instead, taxonomists have relied on hypotheses of homology to name these components. The most recent hypothesis appears to be that of Jeekel (1956), whose work on paradoxosomatids led him "to the conclusion that the [telopodite] branches arising posteriorly of the course of the spermal channel [prostatic groove] are to be considered as tibiotarsus, and the one which arises anteriorly of this course as a femoral process". The branches to which Jeekel refer arise from the base of the telopodite, which he regarded as homologous to the prefemur. Jeekel (1982) later extended this hypothesis to include all Polydesmida.

Accepted by W. Shear: 19 Sept. 2005; published: 14 Oct. 2005

It is not easy to apply this interpretation to Dalodesmidae, in which "the gonopod is more highly evolved, lacking almost completely any reminiscence to the segmentation of an ambulatory leg" (Jeekel 1982). Difficulties identified by Jeekel (1982) include the following:

(a) the solenomere, i.e. the process on which the prostatic groove terminates, does not arise on the telopodite in a fixed spatial relationship with other processes, as happens in many paradoxosomatids;

(b) the telopodite may be deeply divided into branches in such a way that the femur homologue, as identified by its position relative to the prostatic groove, arises distal to the tibiotarsal homologue;

(c) well-defined subsections of the unbranched portion of the telopodite may or may not represent podomeres. In some dalodesmids the telopodite is swollen and setose at its base, and slender and bare distally. Jeekel (1982) refers to the swelling as "the proximal node of the prefemur" and sees it as "only a somewhat incrassate condyle of the coxal-prefemoral joint." However, in a later paper erecting the dalodesmid genus *Orthorhachis*, Jeekel (1985) identified the setose basal swelling as the prefemur, and its bare extension as "the femorite".

These difficulties can be avoided if no assumptions of homology are made for telopodite components. In this view, development of the telopodite may follow its own rules, producing novel structures developmentally unrelated to the distal podomeres of a walking leg. Alternatively, telopodite development may involve such profound modifications of podomere construction that identification of homologous components by visual inspection is likely to be erroneous.

The genus described here adds an interesting new complexity to the dalodesmid picture. In the three known species of *Ginglymodesmus* n. gen., a pseudo-articulation midway along the telopodite allows a substantial amount of pivoting (described in more detail below) around a hinge-like structure. This structure could be seen as homologous to a prefemur-femur or femur-postfemur articulation. If, on the other hand, the structure is an evolutionary novelty, then its appearance in *Ginglymodesmus* is another reason to question the perhaps conventional view that each telopodite component can be identified by homology with a podomere.

I use the term "pseudo-articulation" because the hinge-like structure in *Ginglymodesmus* (Fig. 2, h) does not appear to be formed from condyles articulating two separate tubular elements, as in a typical arthropod limb. Instead, the distal section of the telopodite appears to be continuous with the proximal section, and to pivot around the "joint" because the cuticle at the junction is less rigid than the adjacent cuticle. The pivoting is largely in a plane parallel to the long axis of the body, and the arc traced in this plane by manipulating the distal section in alcohol-preserved specimens is *ca*. 90°. Pivoting towards the head (extension) appears to be checked by a laminar extension of the anterior surface of the proximal telopodite section (Fig. 2, e), so that most pivoting motion is caudad (flexion). The gonopods in living animals have not yet been manipulated.

The function of the pseudo-articulation in *Ginglymodesmus* is unknown. No pairs have yet been captured *in copula*, and because female *Ginglymodesmus* have not yet been identified, it has not been possible to watch mating in the laboratory. Live males carry their gonopods more or less straight, as shown in Fig. 1, but close to the ventral surface of the body.

Specimens were killed and preserved in 75–80% ethanol. Preliminary drawings on graph paper were made using an eyepiece grid at 160X. Gonopods were cleared and temporarily mounted in 60% lactic acid, while body parts were examined in a glycerine-water mixture. Photomicrographs were taken with an Olympus DP11 digital camera attached to a dissecting microscope. SEM images were acquired digitally using an FEI Quanta 600 operated in high-vacuum mode; preserved specimens were air-dried before sputter-coating with gold.

'Male' in the text refers to stadium VII adults. Locality information is given as a locality name, a UTM grid reference (Australian Map Grid 1966, Grid Zone Designation 55G) and a latitude/longitude (WGS84) calculated from the UTM coordinates. Abbreviations: AM = Australian Museum, Sydney, New South Wales, Australia; AMNH = American Museum of Natural History, New York, New York, USA; NRCP = National Rainforest Conservation Program; QVM = Queen Victoria Museum and Art Gallery, Launceston, Tasmania, Australia.

Taxonomy

Order Polydesmida Leach, 1815
Suborder Dalodesmidea Hoffman, 1980
Family Dalodesmidae Cook, 1896

***Ginglymodesmus* n. gen.**
Type species: *Ginglymodesmus tasmanianus* n. sp.

Diagnosis: Small (5-6 mm long) dalodesmids with a head + 19 segments; high, smooth paranota with rounded corners; reduced tergites 2, 3 and 4; no lateral pit on the underside of segment 2; long, slender gonopod telopodites reaching legpair 3 when retracted, in two sections more or less equal in length, the distal section pivoting around a hinge-like structure.

Etymology: Greek *ginglymos* ("hinge") + *-desmus* (commonly used combining form for Polydesmida), for the hinge-like structure on the gonopod telopodite; masculine.

Remarks: I am currently unable to identify females of any of the *Ginglymodesmus* species, which co-occur with very similar dalodesmids in other genera.

Like dalodesmids in at least four other Tasmanian genera (Mesibov 1997, 2003a, 2003b, 2004), the three known species of *Ginglymodesmus* seem to have a tightly fitted

mosaic distribution (Fig. 5), with *G. penelopae* and *G. tasmanianus* recorded from sites only 10 km apart near the town of Waratah. Documenting the mosaic in detail would be difficult. *Ginglymodesmus* are very hard to find in the field and may be naturally uncommon. The arc-like shape of the *G. tasmanianus* distribution (Fig. 5) is possibly a collecting artifact, as the species may occur further south in the relatively little-sampled central western districts.

***Ginglymodesmus tasmanianus* n. sp.**
Figs. 1, 2A, 3A, 3D, 3E, 4; map Fig. 5

Holotype: Male, Argent River, Tasmania, CP681690 (41°49’06”S 145°24’48”E), 330 m, 21.i.1992, R. Mesibov, QVM 23:46124.

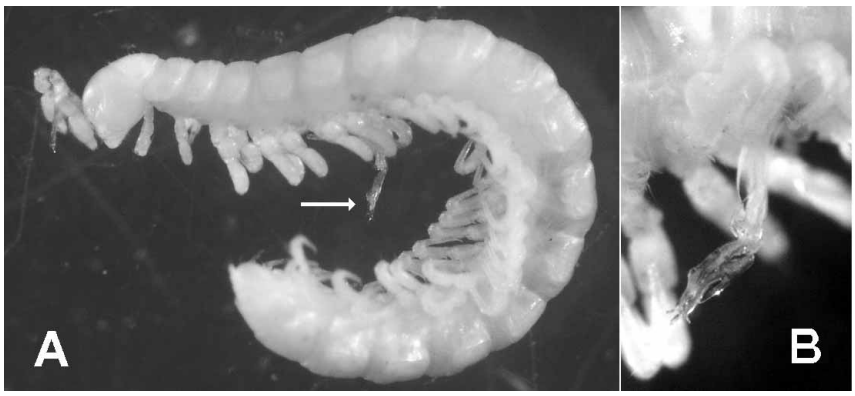

FIGURE 1. *Ginglymodesmus tasmanianus* n. gen., n. sp. (A) Paratype male *ca.* 6 mm long, AM KS92528. Arrow points to gonopod telopodites. (B) Close-up of telopodites of paratype male ex QVM 23:46130.

Paratypes: 2 males, S of Foam Creek, CP255871 (41°38’50”S 144°54’21”E), 10 m, 1.vi.1993, R. Mesibov, QVM 23:46127; male, same details, AM KS92528; 4 males, Library Creek, DQ239419 (41°10’09”S 146°05’39”E), 20 m, 23.iv.1995, R. Mesibov and T. Moule, QVM 23:46130.

Other material examined: 2 males, 5 km S of Renison Bell, approx. CP680670 (41°50’S 145°24’E), 180 m, 1.v.1987, N. Platnick, R. Raven and T. Churchill, AMNH; male, same details, QVM 23:46120; male, Anthony Road, approx. CP854680 (41°50’S 145°37’E), 840 m, 21.iv.1989, NRCP personnel, QVM 23:46121; male, Waratah, CQ806092 (41°27’30”S 145°34’18”E), 630 m, 26.x.1991, R. Mesibov, QVM 23:46122; 3 males, same details but 27.x.1991, QVM 23:46123; male, N of Rocky Creek, CP245920 (41°36’10”S 144°53’43”E), 10 m, 2.v.1993, R. Mesibov, QVM 23:46125; male, Italian River, CQ174058 (41°28’37”S 144°48’52”E), <10 m, 2.v.1993, R. Mesibov, QVM 23:46126; male, N of Pieman Head, CP261860 (41°39’26”S 144°54’46”E), 10 m,

1.vi.1993, R. Mesibov, QVM 23:46128; male, near Dead End Den cave, approx. CP972929 (41°36”S 145°46’E), 330 m, 10.vii.1994, R. Mesibov, QVM 23:46129; 3 males, Black Bog Creek, DP113962 (41°34’46”S 145°56’14”E), 860 m, 3.vii.1997, R. Mesibov, QVM 23:46131; male, Southwell River, CP975922 (41°36’49”S 145°46’16”E), 750 m, pitfall emptied 17.iii.2000, C. Carr, QVM 23:46132.

Diagnosis. Differing from *G. penelopae* and *G. sumac* in bearing a prominent rounded process arising midway along the distal section of the telopodite on the anteromesal surface; from *G. penelopae* in the proximal telopodite section extending laterally on the anterior side of its apex; and from *G. sumac* in bearing a pointed process midway along the distal telopodite section on the posterior rather than anterior side.

Description: Males (Fig. 1A) 5-6 mm long with head and 19 body segments. Well-coloured specimens in alcohol uniformly light tan with white head and legs, sometimes with pinkish tinge to antennomeres.

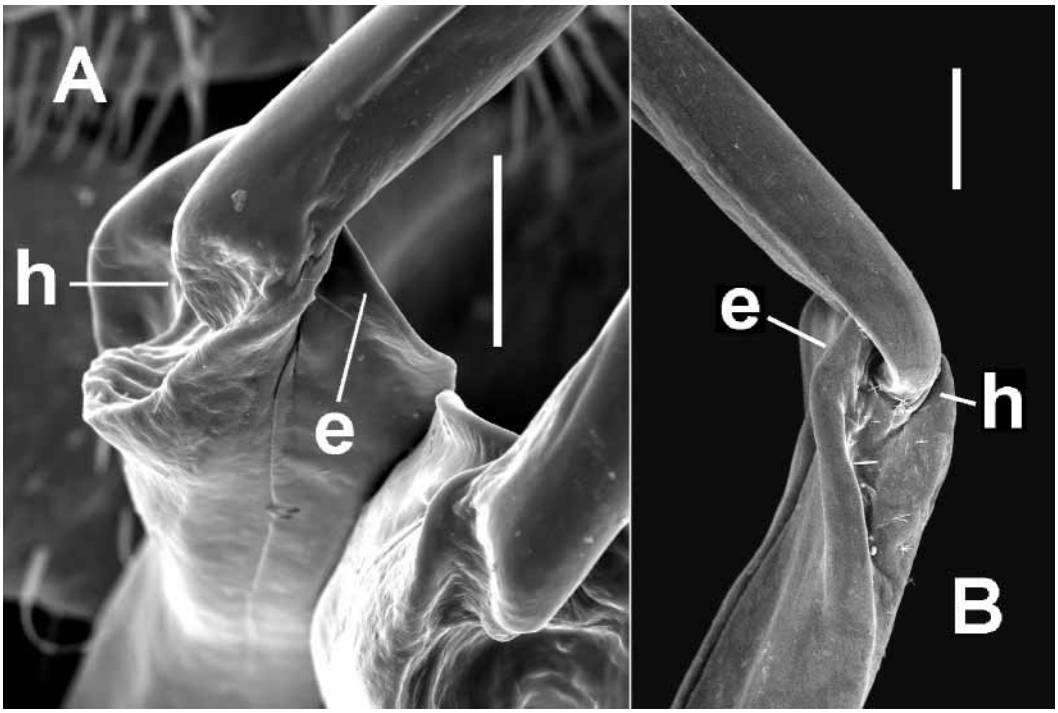

FIGURE 2. SEM views showing hinge-like structure (h) on gonopod telopodite, and laminar extension (e) on anterior side of proximal telopodite section. (A) *Ginglymodesmus tasmanianus* n. gen., n. sp., paratype ex QVM 23:46127. Ventrolateral and slightly posterior view of right gonopod telopodite (centre of image) and left gonopod telopodite (lower right of image). In this preparation the two telopodites are touching; in life and in most preserved specimens, the telopodites are slightly separated. (B) *G. penelopae* n. sp., paratype ex QVM 23:46116. Left lateral view of left gonopod telopodite; head is to left and right gonopod telopodite can just be seen to rear. Scale bars = 0.05 mm.

Head moderately setose with antennal sockets well-impressed laterally and ventrally. Antennae separated by *ca*. 1.25x a socket diameter; antennomere lengths decreasing in the order (2,6), 3, (4,5), 7, antennomere 6 much wider than others (Fig. 3D).

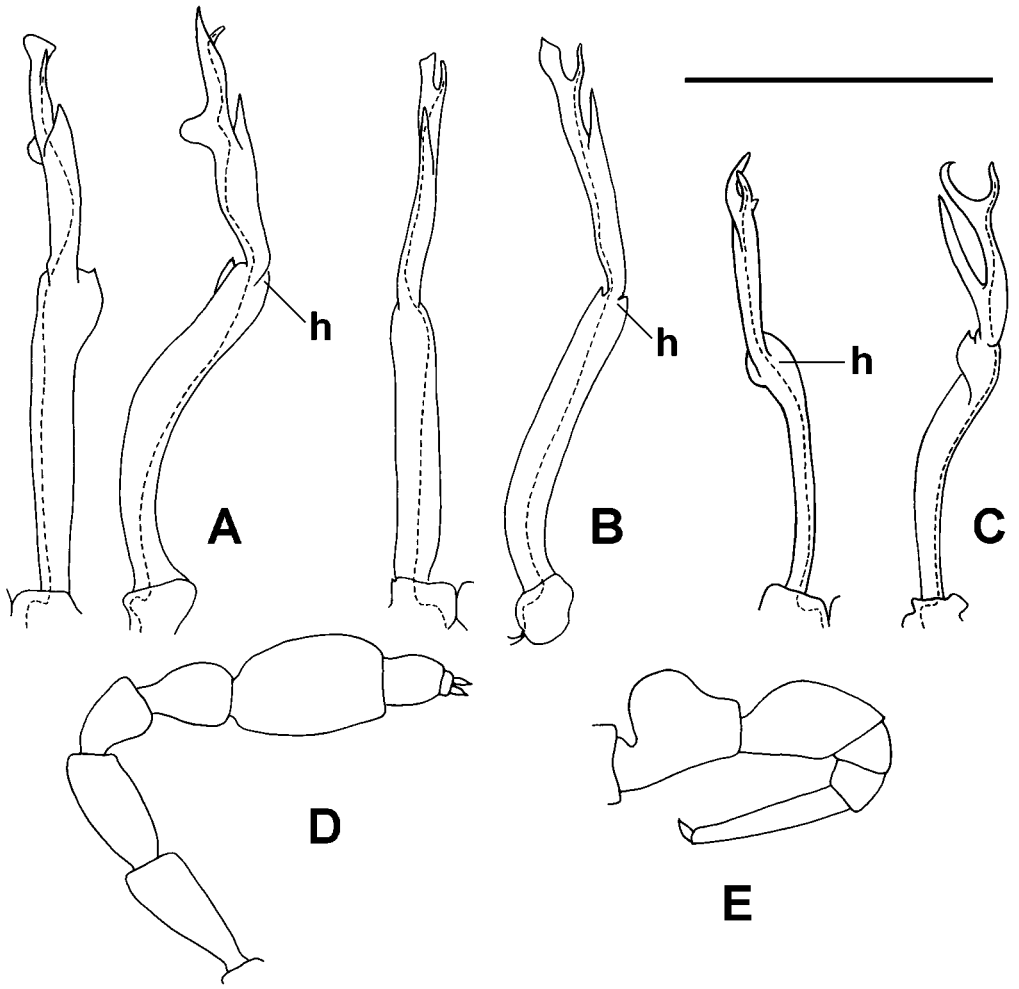

FIGURE 3. Gonopod telopodites, antenna and leg. (A) *Ginglymodesmus tasmanianus* n. gen., n. sp., QVM 23:46123; posterior and mesal views of left telopodite. (B) *G. penelopae* n. sp., paratype ex QVM 23:46116; posterior and lateral views of right telopodite. (C) *G. sumac* n. sp., paratype QVM 23:46112; posterior and lateral views of right telopodite. In A, B and C, dashed lines indicate course of prostatic groove and h = hinge-like structure. (D) and (E) *Ginglymodesmus tasmanianus* n. gen., n. sp., QVM 23:46130; (D) antenna, (E) leg 6. Setae not shown; scale bar = 0.5 mm.

Collum moderately setose, semicircular in dorsal outline, narrower than head and tergite 2. Tergite 2 with lateral margin much lower than collum corner, somewhat lower than tergite 3 margin (Fig. 1A); anterior margin projecting slightly forward; no pit on underside. Widths of tergites 2 and 4 about equal, tergite 3 narrower and shorter. Paranota

placed high on body (Fig. 1A), with rounded anterior "shoulders", well-defined margins and no posterior projections (Fig. 4A). Tergites smooth with three transverse rows of small setae and a few small setae on lateral and posterior margins (Fig. 4A). Limbus (Fig. 4B) composed of tab-like, irregularly toothed elements. Sternites longer than wide with transverse impression somewhat deeper than longitudinal impression. Preanal segment moderately setose; epiproct with rounded tip, extending slightly past anal valves; hypoproct trapezoidal.

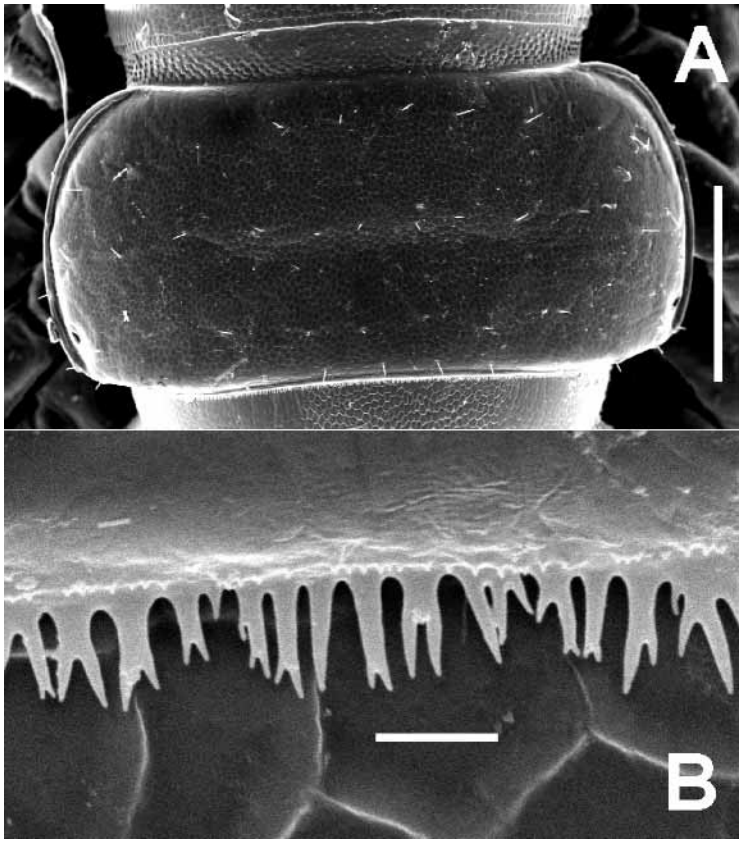

FIGURE 4. *Ginglymodesmus tasmanianus* n. gen., n. sp., paratype ex QVM 23:46127. (A) Dorsal view of midbody segment; scale bar = 0.25 mm. (B) Limbus on same segment; scale bar = 0.005 mm.

Anterior legs (Fig. 3E) with dorsally much-swollen prefemur, slightly swollen femur; tarsus straight, podomere lengths decreasing in the order tarsus, (prefemur, femur), (postfemur, tibia). Sphaerotrichomes on tarsus and tibia, one or two on postfemur; sphaerotrichome shafts tapering to points. Dense "brush" setae on prefemur and femur, tapering to points. Gonopore opening in small conical projection distomedially on leg 2 coxa.

Ozopores on segments 5, 7, 9, 10, 12, 13, 15-18, opening laterally near rear of paranota above margin (Fig. 4A). Spiracles simple pits, on diplosegments opening just above anterior leg and above and slightly forward of posterior leg.

Gonopod aperture between one-third and one-half the width of the segment 7 prozonite; aperture slightly reniform (concave anteriorly), the posterior margin extended towards each of the leg 9 bases to form small "embayments" in the aperture, and the posterolateral margin extending ventrally on either side as a bluntly pointed process.

Gonocoxae ovoid, partly fused along midline, bearing a few setae and entirely contained within gonopod cavity. In specimens with extended gonopods (Fig. 1), the lower portion of the telopodite also hidden in cavity.

Telopodite (Figs. 1, 2A, 3A) reaching leg 3 when retracted, divided into base, proximal section and distal section with approximate relative lengths 1:5:4; distal section pivoting anteroposteriorly around tip of proximal section. Base more or less oblong, wider than long with rounded corners, lightly joined medially to contralateral base, a few long, coarse setae on posterodistal surface and numerous fine setae on posterobasal surface. Proximal telopodite section extending from lateral and distal surface of base, gently curved posteriorly, free of setae, extending anterolaterally at its end as a lamina and terminating distally in a small tooth. Distal telopodite section continuous basally with a shallow cuticular "basin" on the posterior surface of the proximal section (Fig. 2A), the two structures resembling a disarticulated ball-and-socket joint. Distal section more or less straight and coaxial with proximal section, free of setae, divided at about three-quarters its length into a slender posterior branch (solenomere) curving posteriorly and bearing the prostatic groove, and a slightly longer anterior branch with a somewhat obovate, anteroposteriorly flattened tip. Distal section also bearing large, tooth-like, distally pointing process arising at about half the section length on posterolateral surface, terminating proximal to solenomere base, and a rounded, mesolaterally flattened structure arising just distal to base of tooth-like process on opposite (anteromesal) surface of distal section. Prostatic groove entering base on mesal side, turning abruptly laterally then distally to run without interruption along proximal and distal sections and terminating at tip of solenomere.

Distribution and habitat: In coastal scrub, wet eucalypt forest and cool temperate rainforest over ca. 3500 km^2 in northwest Tasmania (Fig. 5), from sea level to at least 860 m.

Etymology: For Tasmania, to which *Ginglymodesmus* appears to be endemic.

Remarks: Across the range of this species there is a little variation in the shape of the rounded extension on the anteromesal surface of the distal telopodite section, and in the shape of the tip of the anterior terminal branch.

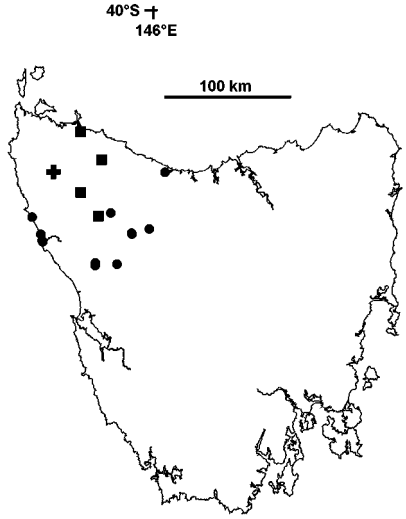

FIGURE 5. Localities for *Ginglymodesmus penelopae* n. sp. (filled squares), *G. sumac* n. sp. (cross) and *G. tasmanianus* n. gen., n. sp. (filled circles).

***Ginglymodesmus penelopae* n. sp.**
Figs. 2B, 3B; map Fig. 5

Holotype: Male, Savage River Pipeline Road, Tasmania, approx. CQ560255 (41°18'S 145°17'E), 500 m, 21.iv.1989, NRCP personnel, QVM 23:46133.

Paratypes: male, details as for holotype but 19.iv.1989, QVM 23:46114; 2 males, details as for holotype but 20.iv.1989, QVM 23:46115; 4 males, details as for holotype, QVM 23:46116; male, Wombat Hill, CQ703065 (41°28'52"S 145°26'52"E), 670 m, 26.ix.1990, R. Mesibov, plot NW2, QVM 23:46117; male, Black River, CQ561743 (40°52'05"S 145°17'37"E), 10 m, 12.xi.1991, R. Mesibov, QVM 23:46118; male, Meunna, CQ728519 (41°04'21"S 145°29'14"E), 240 m, 11.v.1999, K. Bonham, QVM 23: 46119.

Diagnosis: Differing from *G. tasmanianus* in lacking a rounded process on the anteromesal surface midway along the distal section of the telopodite; from *G. sumac* and *G. tasmanianus* in the proximal section not extending laterally at its apex; and from *G. sumac* in bearing a pointed process midway along the distal telopodite section on the posterior rather than anterior side.

Description: As for *G. tasmanianus*, but differing in gonopod details. Telopodite (Figs. 2B, 3B) with proximal section not expanded apically, the end bearing a small posterolateral tooth and with a thickened loop of cuticle on the posterior surface (Fig. 2B) surrounding the base of the distal section. Distal section of telopodite more or less coaxial

with proximal section, divided at slightly more than three-quarters of its length into a slender posteromesal branch (solenomere) bearing the prostatic groove and a slightly longer, flattened, anterolateral branch with a rhomboid tip. Spine-like process arising at about two-thirds the length of the distal telopodite section on the posterior surface, terminating at about the level of the solenomere base.

Distribution and habitat: In wet eucalypt forest and cool temperate rainforest over ca. 1500 km^2 in northwest Tasmania (Fig. 5), from sea level to at least 670 m.

Etymology: For Penelope Greenslade, who organised the National Rainforest Conservation Program invertebrate survey in Tasmania in the late 1980s. *G. penelopae* and many other forest invertebrates were first collected by NRCP personnel.

***Ginglymodesmus sumac* n. sp.**
Fig. 3C; map Fig. 5

Holotype: Male, Julius River, Tasmania, CQ344421 (41°09'14"S 145°01'41"E), 150 m, 26.viii.2005, R. Mesibov, QVM 23:46113.

Paratype: Male, Julius River, CQ343422 (41°09'11"S 145°01'36"E), 150 m, pitfall emptied 10.xi.2000, C. Carr, QVM 23:46112.

Diagnosis: Differing from *G. tasmanianus* and *G. penelopae* in bearing a subterminal pointed process on the distal section of the telopodite arising on the anterior rather than posterior side, and in the distal telopodite section dividing apically into a solenomere and a branch with a pointed rather than flattened tip.

Description: As for *G. tasmanianus*, but differing in gonopod details. Telopodite (Fig. 3C) with long axis of distal section lateral to long axis of proximal section; distal section broadly divided at about two-thirds its length into curved, opposing, subequal, anterolateral and posteromesal branches, the posteromesal branch (solenomere) bearing the prostatic groove and a small, mesally pointing tooth near its base. Spine-like process arising at about one-quarter the length of the distal telopodite section on its anterolateral surface, terminating just distal to the level of the solenomere base.

Distribution and habitat: Known only from two neighbouring sites in cool temperate rainforest near the Julius River in northwest Tasmania (Fig. 5). The holotype was collected under moss on a rotting log of myrtle beech, *Nothofagus cunninghamii*.

Etymology: "Sumac", proper name, noun in apposition. Named for a rivulet which rises in the area, "the Sumac" is a large block of wet eucalypt forest and cool temperate rainforest in northwest Tasmania. The Sumac was wilderness until accessed for logging in the early 1970s; it now contains a 9860 ha reserve (Sumac Forest Reserve) of undisturbed rainforest. I have collected forest litter invertebrates on many occasions in the Sumac since 1976 but did not find *G. sumac* until 2005, when I returned to the area to search for a second specimen, now the holotype.

Remarks: The hinge-like structure in *G. sumac* has not yet been examined using scanning electron microscopy.

Acknowledgments

This study was assisted by a grant from the Plomley Foundation. I thank Jim Hutton (University of Tasmania) for acquiring the SEM images, and Bill Shear and two anonymous reviewers for helpful comments on a draft of this paper.

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