

## The millipede genus *Gasterogramma* (Diplopoda: Polydesmida: Dalodesmidae) in Tasmania, Australia, with descriptions of seven new species

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### Abstract

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Eight species of *Gasterogramma* (Diplopoda: Polydesmida: Dalodesmidae) occur in Tasmania: *G. austrinum* sp. nov., *G. extremum* sp. nov., *G. imber* sp. nov., *G. plomleyi* sp. nov., *G. psi* Jeekel, 1982, *G. rusticum* sp. nov., *G. tarkinense* sp. nov. and *G. wynyardense* sp. nov. The genus is largely confined to areas with an annual rainfall greater than 1000 mm. *G. psi* is widespread and abundant in the northern and western third of Tasmania, while *G. plomleyi* is restricted to the area of endemism known as Plomleys Island in Tasmania's north-east. *G. plomleyi* and the six other new species form an allopatric/parapatric distribution mosaic in northern, western and southern Tasmania. All eight species are burrowers in soil and deep litter.

### Introduction

C.A.W. Jeekel (1982) established the genus *Gasterogramma* for *Gasterogramma psi* Jeekel, 1982, a peculiar Tasmanian dalodesmid millipede in which the distal portion of the gonopod telopodite appeared to Jeekel to have rotated nearly 180° in development, giving the prostatic groove a spiral path to the solenomerite. Further collections in Tasmania have yielded seven more species of *Gasterogramma*, described here. The new species strongly resemble *G. psi* in general appearance and habits and all have, like *G. psi*, a helical solenomerite, but other features of gonopod structure differ markedly from those in *G. psi*. The generic description is amended accordingly.

Specimens were killed and preserved in 75–80% ethanol. Preliminary drawings on graph paper were made using material cleared in 60% lactic acid and viewed at 100 or 200× magnification through an eyepiece graticule. A Philips Electroscan ESEM 2020 operated in high-vacuum mode was used to examine preserved material which had been air-dried before sputter-coating with gold. SEM images were acquired digitally.

More than 600 *Gasterogramma* samples were examined. To save space in the printed version, full details of localities, dates, collectors, specimens and registration numbers are provided separately on the *Memoirs of Museum Victoria* website, [www.museum.vic.gov.au/memoirs/index.html](http://www.museum.vic.gov.au/memoirs/index.html). The specimen data table is also available from the author and a copy has been deposited at the QVM.

Universal Transverse Mercator (UTM) grid references are the spatial locators used by most field workers to define collecting localities in Tasmania. Collecting sites for all but a few of the specimens examined were estimated in the field to be within particular 100 m UTM grid squares on 1:25000 scale maps published by the State of Tasmania. Grid squares are recorded below in 2-letter, 6-digit form,

e.g. 'EN700712.' The maximum horizontal error in these estimates is likely to be less than 100 m. Latitude/longitude equivalents were calculated using GeoCalc 4.20 (GeoComp Systems, Blackburn, Victoria) and are not as precise as the UTM grid references. LGRSS transect locations (see separate specimen data table) were derived from 1:2000 survey charts made available to the QVM by the Hydro-Electric Commission, Tasmania, in 1994.

Abbreviations are: AM, Australian Museum, Sydney; ANZSES, Australia and New Zealand Scientific Exploration Society; QVM, Queen Victoria Museum and Art Gallery, Launceston. Unless otherwise indicated, male and female refer to stadium 8 adults.

Order **Polydesmida** Leach, 1815

Suborder **Dalodesmidea** Hoffman, 1977

**Dalodesmidae** Cook, 1896

***Gasterogramma*** Jeekel, 1982

*Gasterogramma* Jeekel, 1982: 10.—Shelley et al., 2000: 102.

*Type species.* *Gasterogramma psi* Jeekel, 1982, by original designation.

*Included species.* *G. austrinum* sp. nov., *G. imber* sp. nov., *G. extremum* sp. nov., *G. plomleyi* sp. nov., *G. psi* Jeekel, 1982, *G. rusticum* sp. nov., *G. tarkinense* sp. nov. and *G. wynyardense* sp. nov.

*Remarks.* Jeekel (1982: 10) gave the following diagnosis for somatic features of *Gasterogramma*: "Medium-sized Dalodesmidae with 20 somites and a normal poreformula. Head without particulars; antennae of moderate length, clavate, the 6th antennomere longer than the 5th. Collum without

paranota; the sides almost perpendicular. Somites very weakly constricted, almost cylindrical; the waist broad. Metatergites without sculpture. Paranota weakly developed, ridgelike, only dorsally demarcated by a furrow in which the pores are situated. Sternites much longer than wide, without particular modifications. Legs of moderate length, incrassate in the male and with dense setation of short stiff bristles on ventral side of podomeres 2 to 4 and dense granulation on ventral side of podomeres 5 and 6. Anal somite without particulars." This general description also applies to the seven new species described here but the following generic features should be included: integument well calcified; narrow but clearly distinguishable paranota on second segment, lower on body than the lateral collum margins and the paranotal traces on third segment; gonopod aperture ovoid with long axis transverse, rim not raised in front and variably raised at rear; epiproct blunt, prominent, extending caudad past the anal valves.

Jeekel's diagnosis of the *Gasterogramma* gonopod (1982: 10) is here amended: telopodites elongate, loosely joined medially; solenomerite arising at one-half to two-thirds the length of the telopodite, each solenomerite a small, distally tapering rod twisted in the following sense: a right-handed helix (clockwise turning away from the observer) on the right gonopod, a left-handed helix on the left gonopod.

In an attempt to identify (i.e., homologise) the elements of the *G. psi* gonopod, Jeekel (1982: 11) hypothesised that "the course of the spermal channel [here called "prostatic groove"] is homologous in all polydesmoid millipedes, and that the location of the base of each process in relation to the spermal channel defines its morphological identity." He named the process arising caudad of the prostatic groove the tibiotarsus, and the structure arising cephalad the femoral process. If the distal portion of the *G. psi* gonopod is untwisted, in imagination, then the lateral process with a tip shaped like a bird's head (fig. 6) is identifiable as the femoral process; the anterior, laterally fringed process bearing a rod-like structure is a prolongation of the prefemur; and the rod-like structure is the tibiotarsus. In the notch between the femoral and prefemoral processes arises the solenomerite.

An alternative interpretation is that the distal end of the telopodite is not torqued, and that the 'femoral process' is a growth from the caudomedial side of the gonopod which has displaced the prostatic groove laterally. It is important to note that the course of the prostatic groove in *G. psi* is actually two opposed spirals. From the base of the telopodite of the right gonopod, the groove first runs distally in a left-handed spiral to encircle the "femoral process", then in a right-handed spiral upon entering the solenomerite. The chirality of the spirals on the left gonopod mirrors that on the right. In the three species here assigned to *Gasterogramma* which lack a femoral process (*G. austrinum*, *G. rusticum* and *G. wynyardense*), the basal spiral is missing but the solenomerite spiral persists.

Jeekel's hypothesis sought to make each gonopod process in polydesmoids a homologue of either the prefemur, femur or tibia+tarsus of the millipede leg, and uses a "fixed" solenomerite as a morphological landmark. If the "no torsion"

interpretation of the *Gasterogramma* gonopod is correct, then either the simple notion of homologisation is inadequate, or the solenomerite is not "fixed." Unfortunately, polydesmoid gonopods develop suddenly from unsegmented primordia in the ultimate moult, and there are no visible intermediate stages which would allow us to unambiguously identify individual gonopod processes with prototypical leg segments, in *Gasterogramma* or any other polydesmoid. A correct interpretation of gonopod structure may be possible in future with advances in the developmental genetics of arthropods. For the present, Jeekel's labelling of the gonopod processes in *Gasterogramma* is a useful hypothesis, and is adopted for descriptive purposes in this paper.

*Distribution.* Western and north-eastern Tasmania (fig. 13); not recorded from King I. or the Furneaux Group in Bass Strait.

*Habits.* The eight species of *Gasterogramma* are burrowing millipedes typically found in moist, organic-rich soil, in deep moist leaf litter and in and under wet rotting logs. As noted by Jeekel (1982: 9) for *G. psi*, *Gasterogramma* are "sluggish" and at first sight they resemble "a worm or a dipteran larva rather than a millipede." They are often locally abundant in loose, mixed-age aggregations. All *Gasterogramma* species release a pungent defensive secretion which presumably includes hydrocyanic acid, although this is not the most prominent odour component. The pinkish-purple *Gasterogramma* species have been called "stinky pinkies" by local collectors impressed by the pungency of the secretion. *G. plomleyi* has the strongest smell in the genus, and can be detected by treading heavily through its wet forest habitat and sniffing attentively. Unfortunately, no somatic characters have been so far noted which can reliably be used to distinguish the seven western species (i.e., *Gasterogramma* spp. other than *G. plomleyi*), and at many western sites two *Gasterogramma* species are present. I have not, therefore, assigned non-*plomleyi* females and juveniles to species; these individuals are recorded in the separate specimen data table as "*Gasterogramma* sp." Males and females have been found in copula in all months of the year, but mating is most frequent in the austral spring; the only two pairs so far preserved in copula (*G. psi*, QVM 23:8086 and QVM 23:40560) were collected in late November. Females are often found curled around an egg mass; it is unclear whether such females are in the process of constructing an egg chamber (as expected for Polydesmida) or are brooding their eggs.

*Relationships.* Jeekel (1982: 12) noted that *Gasterogramma* and the Chilean *Semnosoma* Silvestri, 1903 were the only dalodesmid genera in which the prostatic groove had been reported to be helical, and "It seems likely, therefore, that the new genus is closely related to *Semnosoma*. Eventually, the two may form the nucleus of a tribe for which the family-group name Semnosomatidae Brölemann, 1916 is available." The illustrations of *Semnosoma* gonopods in Demange and Silva (1976a, b) show the prostatic groove running first caudally, then laterally, then anteriorly as in *G. psi*. Further, species in the *Semnosoma* group of Chilean dalodesmids (i.e. *Semnosoma*, *Anaulacodesmus* Attems, 1898, *Chilorius* Chamberlin, 1957

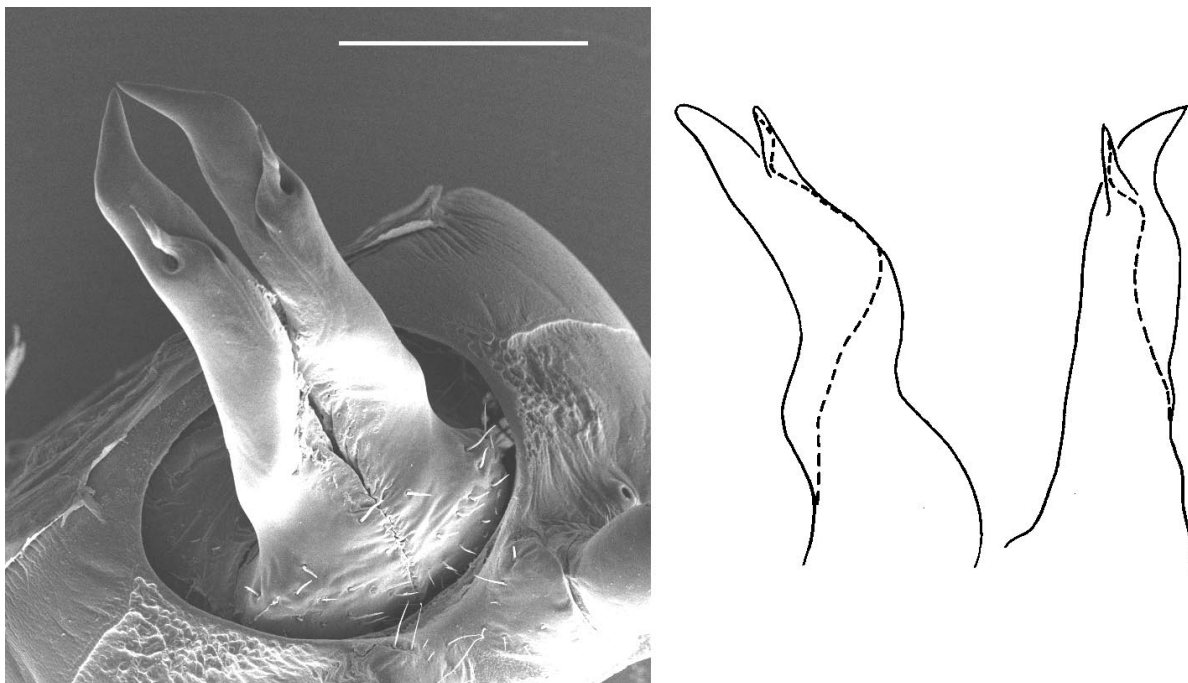


Figure 1. (left) *G. austrinum* sp. nov., Tahune Bridge, southern Tasmania, QVM 23:16195; SEM of gonopods in situ. Scale-bar = 0.5 mm. (right) *G. austrinum* sp. nov., Gold Creek, southern Tasmania, QVM 23:14021; outline sketches of right gonopod showing course of prostatic groove (dashed line): lateral view, left; posterior view, right.

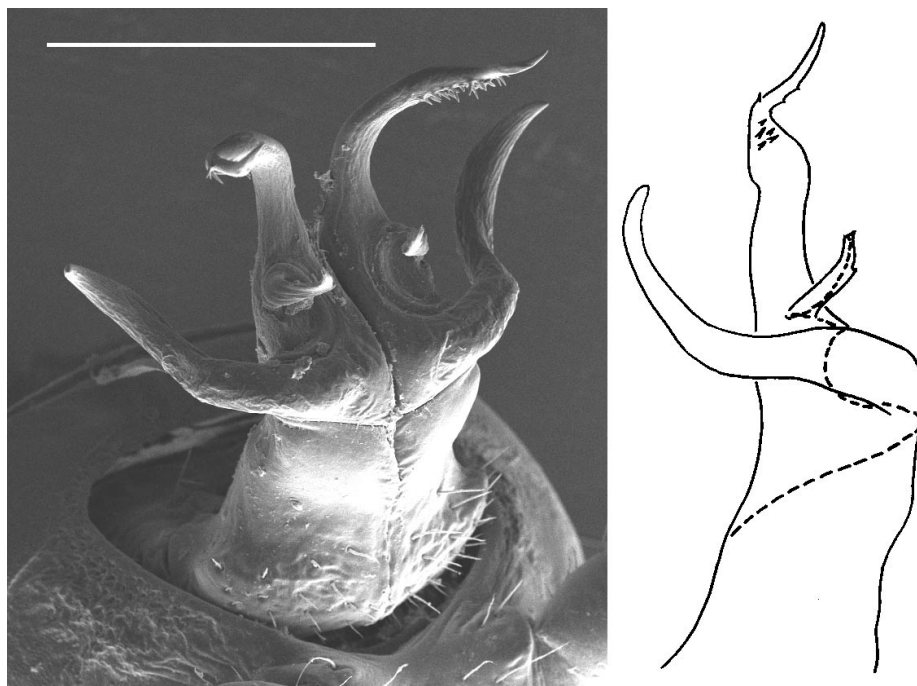


Figure 2. (left) *G. extremum* sp. nov., Lake Sydney, southern Tasmania, QVM 23:14019; SEM of gonopods in situ. Scale-bar = 0.5 mm. (right) *G. extremum* sp. nov., Hastings Caves, southern Tasmania, QVM 23:8059; outline sketch of right gonopod, lateral view, showing course of prostatic groove (dashed line).

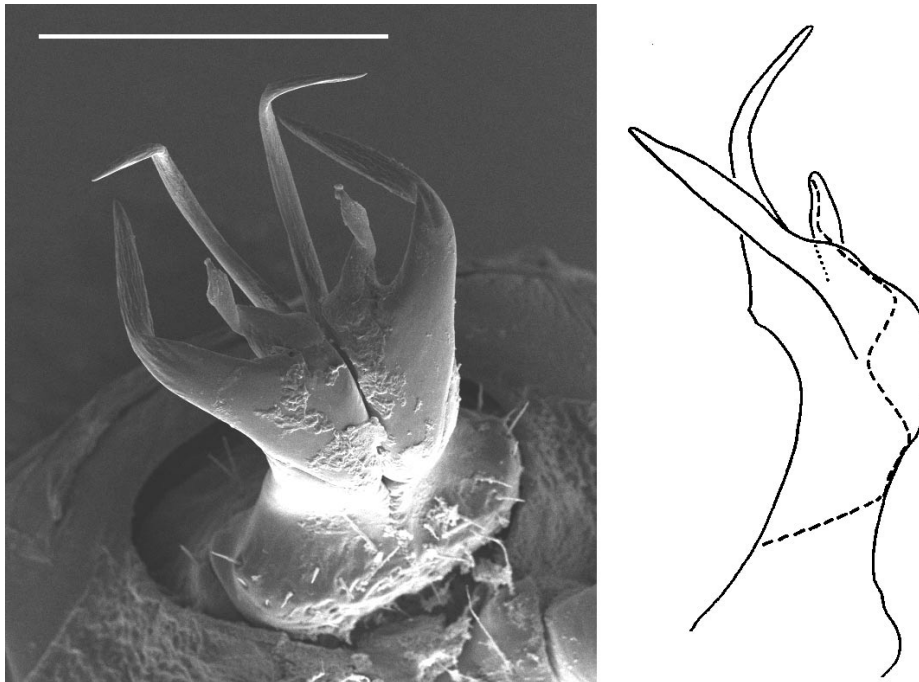


Figure 3. (left) *G. imber* sp. nov., Tarraleah, central Tasmania, QVM 23:8047; SEM of gonopods in situ. Scale-bar = 0.5 mm. Prefemoral processes are parallel in life and in alcohol-preserved material; the divergence seen in this SEM is an artefact of specimen preparation. (right) *G. imber* sp. nov., Argent R., western Tasmania, QVM 23:8051; outline sketch of right gonopod, lateral view, showing course of prostatic groove (dashed line).

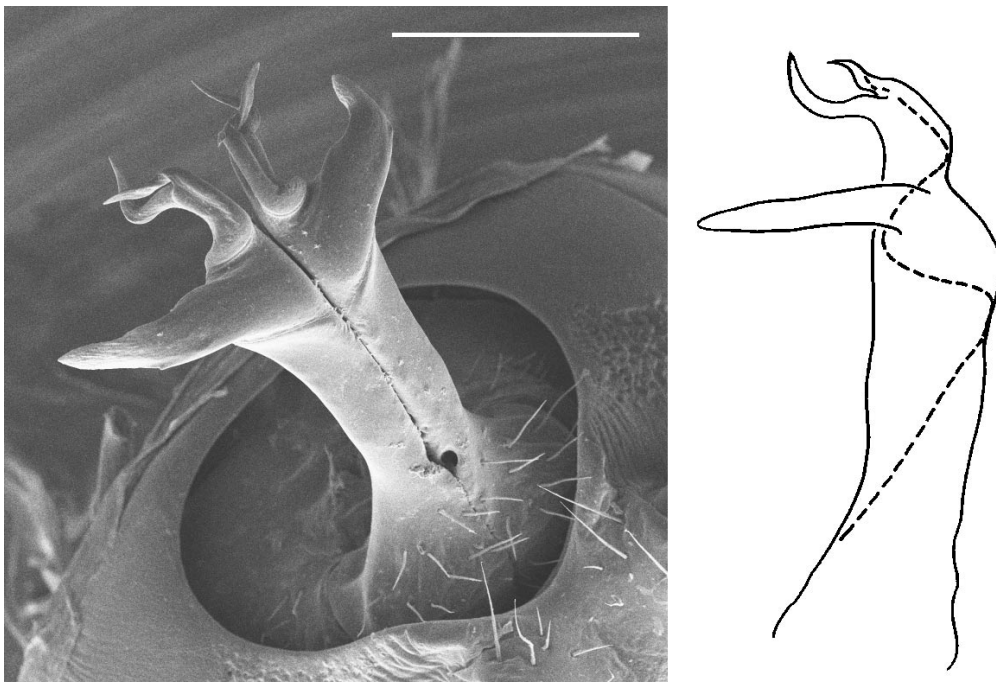


Figure 4. (left) *G. plumleyi* sp. nov., Rattler Hill, north-east Tasmania, QVM 23:8068; SEM of gonopods in situ. Scale-bar = 0.5 mm. (right) *G. plumleyi* sp. nov., Crystal Hill, north-east Tasmania, QVM 23:8069; outline sketch of right gonopod, lateral view, showing course of prostatic groove (dashed line).

and *Tsagonus* Chamberlin, 1957) all have, like *Gasterogramma*, greatly reduced paranota (Chamberlin, 1957: 19). The argument for a Gondwanan dalodesmid lineage including the Chilean and Tasmanian genera thus appears reasonable.

Relationships within *Gasterogramma* are unclear. Grouping phenetically on gonopod form, we might have (*G. extremum* + *G. imber* + *G. plomleyi* + *G. psi* + *G. tarkinense*) with a femoral process and (*G. austrinum* + *G. rusticum* + *G. wynyardense*) without such a process, but relationships within these groups are far from obvious. Both groups are widely dispersed across Tasmania, suggesting that the two might have differentiated independently in the landscape. However (see below) the two groups are not independently distributed: the seven non-*psi* species currently form an allopatric/parapatric mosaic.

### *Gasterogramma austrinum* sp. nov.

Figures 1, 5, 12 (map)

**Material examined.** Holotype. Male. Australia, Tasmania. Huon R. (Arve Rd), DN784273 [43°06'23'' 146°44'04''], 120 m, 2 May 1997, R. Mesibov, plot 3M1, oldgrowth wet eucalypt forest with rainforest understorey, QVM 23:40628.

Paratypes. 3 males, Huon R. (Edwards Rd), DN790284 [43°05'48'' 146°44'31''], 90 m, 23 May 1997, R. Mesibov, plot 3R6, regrowth wet eucalypt forest following clearfelling and burning, QVM 23:40630; 2 males, Edgar Bay area, DN483404 [42°59'13'' 146°21'57''], 350 m, pitfall emptied 16 Nov 2001, D. Driscoll, QVM 23:24802; 4 males, Huon R. (Arve Rd), DN798284 [43°05'48'' 146°45'06''], 200 m, 16 May 1997, R. Mesibov, regrowth wet eucalypt forest following clearfelling and burning, AM KS85097 (formerly QVM 23:40629).

Other material. 19 males from 8 unique localities in southern Tasmania, including Gold Creek, Huon R., Kallista Creek, Picton R., Reuben Falls and Tahune Bridge.

**Diagnosis.** Gonopod with no femoral process or tibiotarsus; telopodite in posterior view ending in broad, mesodistally directed point.

**Description.** Males c. 17–20 mm long and c. 1.8–2.0 mm wide at midbody. Body in both sexes darkly mottled with pink-purple pigmentation. Gonopod telopodites slender in posterior view, lightly joined for about half their length, a few short, coarse setae at their bases, setate area extending just outside aperture (fig. 1). Aperture more or less ovoid, long axis transverse, posterior margin not noticeably raised. Telopodite with a posteromesal concavity near base, somewhat sinuous in lateral view, curving anteriorly, then distally, then anteriorly and slightly tapering, finally tapering mesally to end in blunt, mesodistally pointed tip. Femoral process and tibiotarsus not evident. Solenomerite short, helical, tapering process arising at about four-fifths length of telopodite on its posterior face. Prostatic groove running distally and posteriorly along mesal side of telopodite, then curving laterally before running straight distally to enter solenomerite on its mesal side.

**Distribution.** In rainforest and wet eucalypt forest over at least 750 km<sup>2</sup> in southern Tasmania (fig. 12), at altitudes c. 50–600 m.

**Etymology.** From Latin *austrinus*, southern, adjective. This species is restricted to southern Tasmania.

### *Gasterogramma extremum* sp. nov.

Figures 2, 12 (map)

**Material examined.** Holotype. Male. Australia, Tasmania. Deadmans Bay, DM592802 [43°31'47'' 146°29'42''], <40 m, 26 Jan 1994, R. Mesibov, wet eucalypt forest and rainforest, QVM 23:14018.

Paratypes. Male (dissected), near Hastings Caves, approx. DM870960 [43°23'18'' 146°50'22''], 5 Dec 1952, V.V. Hickman, QVM 23:8059; male (dissected for SEM), Lake Sydney, DN686070 [43°17'20'' 146°36'46''], 690 m, 2 Feb 1994, R. Mesibov, rainforest, QVM 23:14019.

**Diagnosis.** Gonopod without tibiotarsus; femoral process unbranched; prefemoral process curved laterally, then posteriorly, with short, tooth-like projections near tip; solenomerite arising near base of prefemoral process.

**Description.** Males c. 15–17 mm long and c. 1.6–1.8 mm wide at midbody. Body in both sexes ivory-coloured with faint pink-purple mottling. Gonopod telopodites massive at base (fig. 2), lightly joined mesally for most of their length, with a few short, coarse basal setae, setate area extending just outside aperture. Aperture more or less ovoid, long axis transverse, posterior margin not noticeably raised. Telopodite axis more or less straight. Telopodite base ending abruptly at about one-half length of telopodite, with a relatively slender, anterioposteriorly flattened prefemoral process arising from anteromesal corner of top of base. Prefemoral process tapering gradually to a fine point, bending first laterally, then posteriorly, and bearing set of 10–20 short, simple or bifid teeth on posterolateral surface just proximal to tip. Tibiotarsus not evident. Femoral process massive, tapering gradually to a fine point, arising from posteromesal corner of top of telopodite base and curving laterally, then anteriorly, then distally and slightly laterally. Solenomerite a short, helical, somewhat flattened process arising at base of prefemoral process on its posterior face. Prostatic groove running first posteriorly and distally across mesal face of telopodite base to its posterior surface, then curving laterally, distally and mesally around base of femoral process, then extending distally to enter solenomerite base on its mesal side.

**Distribution.** Rainforest and wet eucalypt forest at 3 locations in far southern Tasmania (fig. 12) from near sea level to 690 m, with maximum linear range of c. 30 km. Likely to be more widespread in this little-sampled part of Tasmania.

**Etymology.** From Latin *extremus*, farthest, adjective. This species extends to the southern-most part of mainland Tasmania.

### *Gasterogramma imber* sp. nov.

Figure 3, 12 (map)

**Material examined.** Holotype. Male. Australia, Tasmania. Little Florentine R., DN525683 [42°44'10'' 146°25'10''], 440 m, pitfall emptied 10 Apr 1986, R. Bashford, QVM 23:24958.

Paratypes. Male, details as for holotype, QVM 23:40586; male, Tarraleah, DP473196 [42°16'25'' 146°21'39''], 750 m, 4 May 1992, R. Mesibov, oldgrowth wet eucalypt forest with rainforest understorey, QVM 23:8048; male, Needles Picnic Ground, DN512656 [42°45'37'' 146°24'12''], 470 m, 23 Feb 1994, R. Mesibov, oldgrowth wet eucalypt forest with rainforest understorey, QVM 23:13840; 5 males,

Tarraleah, DP473197 [42°16'22" 146°21'39"], 780 m, 5 May 1992, R. Mesibov, oldgrowth wet eucalypt forest with rainforest understorey, AM KS85098 (formerly QVM 23:8045).

Other material. 49 males from 26 unique localities in central, south-western and western Tasmania, including Argent R., Boyd R., Denison R., Franklin R., Frenchmans Cap, Gordon R., Humboldt Divide, Huon R., Kallista Creek, Little Florentine R., Mossy Marsh Creek, Queenstown, Scotts Peak Dam, Taffys Creek, Tarraleah, Trappes Inlet, Wedge Inlet and Wedge R..

**Diagnosis.** Gonopod without tibiotarsus; femoral process unbranched; prefemoral process slender, straight, without tooth-like projections, flexed sharply at tip; solenomerite rising near base of prefemoral process.

**Description.** Males c. 17–20 mm long and c. 1.8–2.0 mm wide at midbody. Body in both sexes darkly mottled with pink-purple pigmentation. Gonopod telopodites massive at base (fig. 3), lightly joined mesally for about half their length, a few short, coarse basal setae, setate area extending just outside aperture. Aperture more or less ovoid, long axis transverse, posterior margin not noticeably raised. Telopodite narrowing near its base, bending slightly in anterior direction at about half telopodite length, narrowing greatly and abruptly at bend and extending from anteromesal corner of top of base as a spear-like, sharply pointed prefemoral process flexed sharply posteriolaterally at about three-quarters of its length. (In life and in alcohol preservative, axis of prefemoral process parallels that of telopodite; prefemoral processes in SEM image in fig. 3 bend laterally at their bases as a result of drying-out during specimen preservation) Tibiotarsus not evident. Femoral process massive, arising from posterior face of telopodite base and directed laterally and distally, bending sharply anteriorly and distally at about two-thirds its length and tapering to a blunt point. Solenomerite a short, helical, tapering, somewhat flattened process arising between bases of femoral and prefemoral processes. Prostatic groove running first posteriorly and distally across mesal face of telopodite base to its posterior surface, then curving laterally, distally and mesally around base of femoral process, then extending distally to enter solenomerite base on its mesal side.

**Distribution.** In rainforest and wet eucalypt forest over at least 6000 km<sup>2</sup> in western Tasmania (fig. 12), at altitudes c. 50–800 m. Syntopic with *G. psi* at various locations through its range.

**Etymology.** Latin *imber*, shower, noun in apposition. This species occurs in the highest rainfall zone in Tasmania.

### *Gasterogramma plomleyi* sp. nov.

Figures 4, 5, 12 (map)

**Material examined.** Holotype. Male. Australia, Tasmania. Rattler Hill, EQ744353 [41°13'48" 147°53'15"], 650 m, 29 Aug 1990, R. Mesibov, oldgrowth rainforest, QVM 23:24960.

Paratypes. 2 males (1 dissected for SEM), details as for holotype, QVM 23:8068; 2 females, details as for holotype, QVM 23:8307; 3 males, Forest Lodge, EQ786296 [41°16'51" 147°56'18"], 410 m, 13 Jan 1993, R. Mesibov, wet eucalypt forest, QVM 23:8066; 1 male, Pecks Hill, EQ282251 [41°19'29" 147°20'13"], 450 m, 14 Jan 1993, R. Mesibov, wet eucalypt forest, QVM 23:8061; 3 males, Williams

Hill, EQ558548 [41°03'21" 147°39'50"], 300 m, 10 Mar 1993, R. Mesibov, wet eucalypt forest, QVM 23:16477; 3 males, Mathinna Plains, EQ616221 [41°21'00" 147°44'10"], 800 m, 12 Jan 1993, R. Mesibov, AM KS85099 (formerly QVM 23:8063).

Other material. 26 males, 40 females and 52 juveniles from 33 unique localities in north-east Tasmania, including Carters Creek, Chinaman Corner, Crystal Hill, Cuckoo, Forest Lodge, Golconda, Hogarth Rivulet, Joseph Creek, Lisle, Mathinna Plains, Milly Brook, Mt Arthur, Mt Michael, Mt Victoria, Northallerton Valley, Patersonia Rivulet, Pecks Hill, Peddles Hill, Rattler Hill, Rayners Hill, Sideling Range, South Springfield, Tombstone Creek, Weldborough and Williams Hill.

**Diagnosis.** Epiproct unusually broad, with bumpy appearance (fig. 5B). Gonopod without tibiotarsus; femoral process unbranched; prefemoral process short, without tooth-like projections, bent anteriorly, then distally and mesally; solenomerite seemingly fused with prefemoral process for half length of latter.

**Description.** Males c. 20–23 mm long and c. 2.0–2.4 mm wide at midbody, females somewhat larger. Body in both sexes fairly uniformly ivory-coloured. Epiproct (fig. 5B) enlarged relative to other *Gasterogramma* (fig. 5A), lateral and terminal setae on prominent bumps (fig. 5C). Gonopod telopodites (fig. 4) fairly straight and slender, lightly joined mesally for most of their length, a few long setae at their bases just inside aperture. Aperture more or less ovoid, long axis transverse, posterior margin very slightly raised and broadly, medially notched. Femoral process massive, arising on posteromesal face of telopodite at about two-thirds its length, directed laterally and slightly distally before turning abruptly anteriorly at about half length of process and tapering to a blunt point. Telopodite extending from femoral process base as a short, slender prefemoral process which bends anteriorly, then curves distally and mesally to terminate in a fine point. Tibiotarsus not evident. Solenomerite about as long as prefemoral process, arising near base of prefemoral process on its posterior face and apparently fused with it to point where prefemoral process bends anteriorly, from this point helical and slightly flattened. Prostatic groove running distally and posteriorly across mesal surface of telopodite, then curving laterally, distally and mesodistally around femoral process before entering solenomerite on its mesal side. Cyphopods not examined.

**Distribution.** In rainforest and wet eucalypt forest over c. 1700 km<sup>2</sup> in high-rainfall parts of north-east Tasmania (fig. 12), at altitudes 150–850 m.

**Etymology.** In honour of Brian Plomley (1912–1994), Tasmanian scientist and scholar who encouraged biological research in north-east Tasmania.

### *Gasterogramma psi* Jeekel, 1982

Figures 6, 7, 11 (map)

*Gasterogramma psi* Jeekel, 1982: 12.—Shelley et al., 2000: 102.

Holotype. Male. Australia, Tasmania. "Sta. 100, Hellyer Gorge, 32 km SSW Somerset, 25.XI.1980 (temperate rain-forest (*Nothofagus*, *Eucalyptus*, *Dicksonia*) along the Hellyer R., under logs)" (Jeekel, 1982: 12). Holotype probably in Zoological Museum, Amsterdam; not examined.

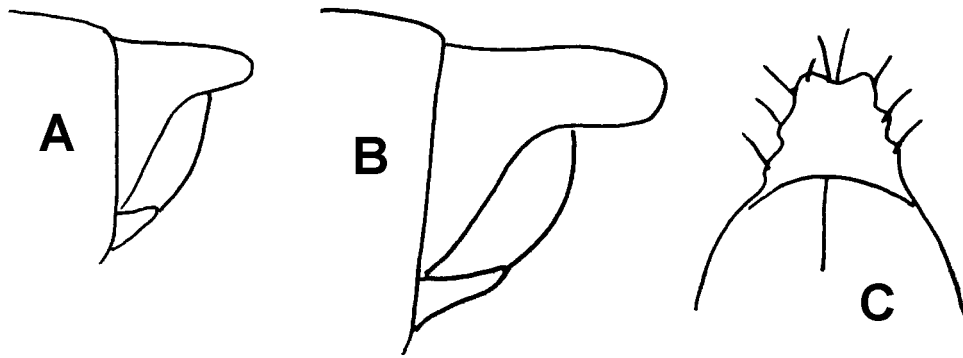


Figure 5. Sketches of epiproct form. A, Typical form in *Gasterogramma*; *G. austrinum* paratype, QVM 23:40629; lateral view. B, *G. plumleyi*, male paratype, QVM 23:8068, lateral view. C, same specimen as B, ventral view.

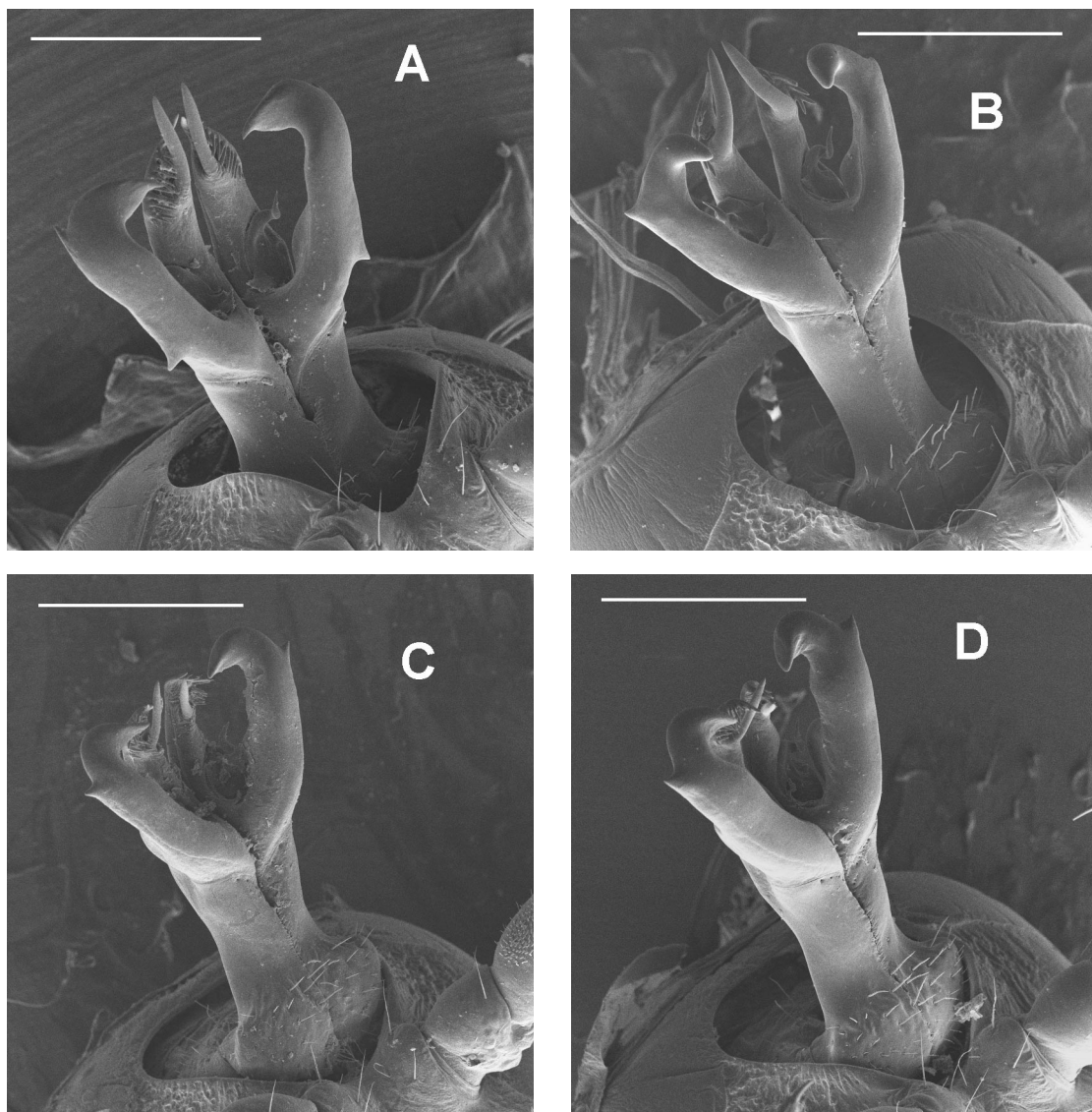


Figure 6. A–D, *G. psi* gonopod variations, seen in situ; see fig. 11 for locations. A, Washpond Forest, north-west Tasmania, QVM 23:8085. B, Notley Gorge, north-central Tasmania, QVM 23:8139. C, Coles Creek, central Tasmania, QVM 23:24797. D, Henty R., western Tasmania, QVM 23:8143. Scale-bar in all cases = 0.5 mm.



Figure 7. A–C, body pattern variations in *G. psi*. A, almost uniformly pale; Cam R., north-west Tasmania. B, dark-spotted; Dial Range, north-west Tasmania. C, dark with faint mottling; Florentine R., south-west Tasmania.

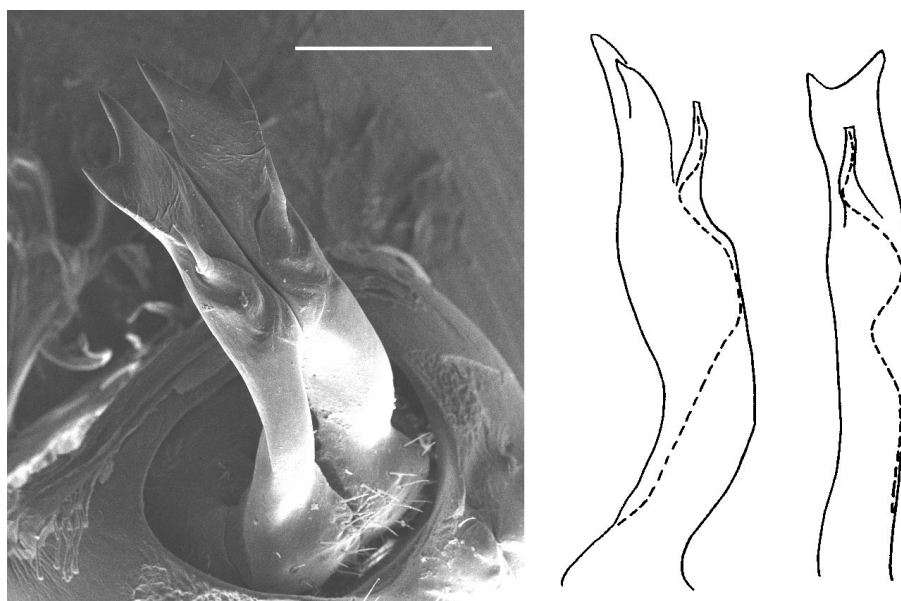


Figure 8. (left) *G. rusticum* sp. nov., Don Reserve, north-central Tasmania, QVM 23:16199; SEM of gonopods in situ. Scale-bar = 0.5 mm. (right) *G. rusticum* sp. nov., Gog Range, north-central Tasmania, QVM 23:8053; outline sketches of right gonopod showing course of prostatic groove (dashed line): lateral view, left; posterior view, right.





Figure 9. (left) *G. tarkinense* sp. nov., The Clump, north-west Tasmania, QVM 23:8056; SEM of gonopods in situ. Scale-bar = 0.5 mm. (right) *G. tarkinense* sp. nov., Wombat Hill, north-west Tasmania, QVM 23:8057; outline sketch of right gonopod showing course of prostatic groove (dashed line).

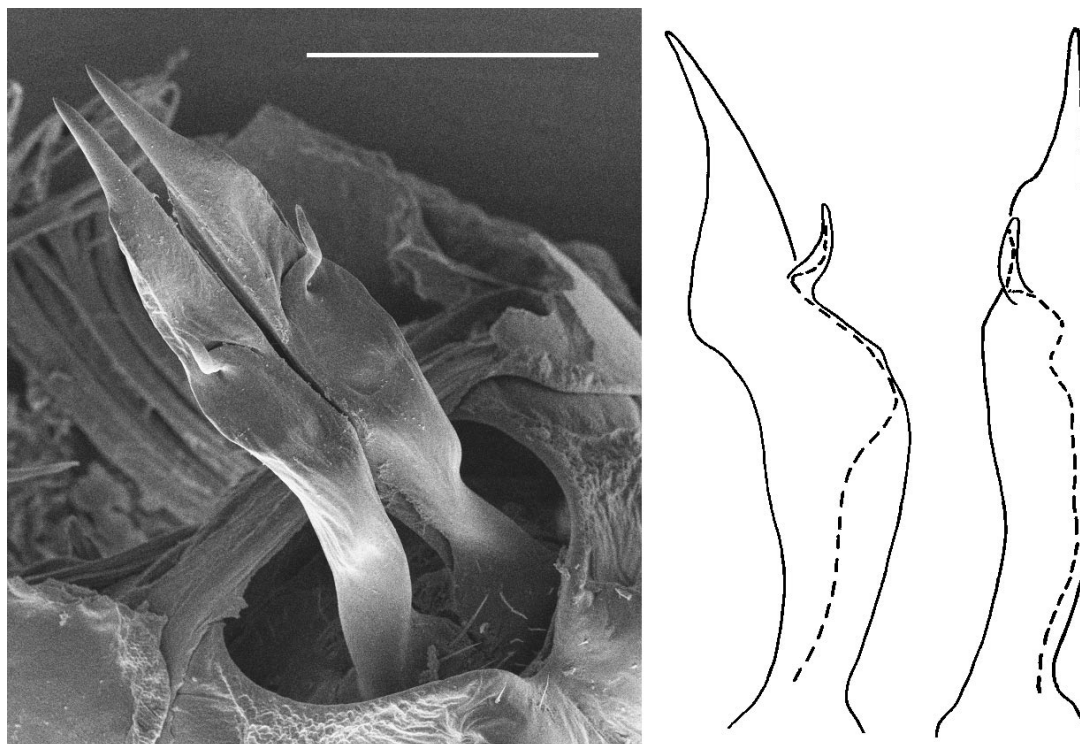


Figure 10. (left) *G. wynyardense* sp. nov., Inglis R., north-west Tasmania, QVM 23:41909; SEM of gonopods in situ. Scale-bar = 0.5 mm. (right) *G. wynyardense* sp. nov., Seabrook Creek, north-west Tasmania, QVM 23:40632; outline sketches of right gonopod showing course of prostatic groove (dashed line): lateral view, left; posterior view, right.

**Material examined.** Paratypes. 10 males, 12 females, 3 stadium VII males, 3 stadium VI males, collection details as for holotype; locations unknown.

Other material. 393 males from 190 unique localities in northern and western Tasmania, including Allen Creek, Animal Creek, Arthur R., Balfour, Bellana Creek, Big Creek, Black Bog Creek, Black R., Blackfish Creek, Bond Tier, Bonneys Tier, Borradale Creek, Branchs Creek, Broadsword cave (Gunns Plains), Brooks Creek, Bubs Hill, Burnie Park, Burning Down the House cave (June–Florentine), Cam R., Cann Creek, Central Castra, Chester Creek, Christmas Hill, Christmas Hills, Coles Creek, Companion Hill, Companion Rd, Crayfish Creek, Dalgath Forest Reserve, Dark Creek, Dawson R., Dead End Den cave (Mt Cripps), Dee Lagoon, Deep Creek Bay, Denison R., Dip R., Don R., Duck Creek, Dundas R., East Ridgley, Emu R., Fisher R., Florentine R., Flowerdale, Gawler R., Gibson Creek, Goderich Rd, Gordon R., Guildford Rd, Hardwood R., Heemskirk Rd, Henty R., Hermit Hill, Holwell Gorge, Inglis R., Interview R., Jessie Rd, Jones Creek, Julius R., Kelcey Tier, Kenzies Hill, Lake Chisholm, Lake Lea, Lake Mackenzie, Laughing Jack Lagoon, Lawson Plains, Library Creek, Little Claytons Rivulet, Loongana cave L9, Maggs Mountain, Mahoneys Creek, Marine Creek, Maxwell R., Mersey R., Meunna, Meunna Hills, Milkshakes, Montagu Swamp, Mossy Marsh Creek, Mostyn Hardy cave (Loongana), Mt Oakleigh, Mt Sprent, Newall Creek, Nietta Creek, No Mans Creek, Nook, Notley Gorge, Olga R., Orange R., Ordance Point, Parrawe Creek, Pelion Valley, Pencil Pine Creek, Philrod cave (Mt Cripps), Poppys Lagoon, Punchs Terror, Richardsons Flats, Roger R., Roger R. West, Rosebery, Salmon R., Sassafras Creek, Savage R., Saxons Creek, Scopus, Seabrook Creek, Serpentine Dam, Shadow Lake, Sisters Creek, Smithton, Somerset, Sterling R., Stony Rises, Sundown Point, Table Cape, Tarraleah, Three Hummock I., Trowutta Caves, Tunnel, Upper Natone, Wakefield Creek, Wandle R., Washpond Forest, Weaning Paddock Creek, Welcome Heath, West Montagu, Whisky Creek, Wild Wave R., Williamsford, Wilsons Creek and Wombat Hill.

**Diagnosis.** Gonopod with femoral process terminating in a mesally directed tip with shape of bird's head; prefemoral process fringed with tooth-like projections; tibiotarsus prominent, distally or distally and mesally directed; solenomerite arising near base of prefemoral process.

**Descriptive notes.** For a very detailed description of this species, see Jeekel (1982: 12–14). Variations in gonopod structure and body colour pattern (see below) occur across the range of *G. psi*, but I am reluctant to divide *G. psi* into subspecies.

**Gonopod:** The form described by Jeekel (1982) from north-west Tasmania (site "TL" in fig. 11) extends with little variation to central Tasmania. In the latter area ("C" in fig. 11), the tip of the prefemoral process is shortened and bent slightly posteriorly (fig. 6C). In the central west ("D" in fig. 11), the tip of the prefemoral process is further flexed and lies lateral to the tibiotarsus, which is directed posteriomesally (fig. 6D) rather than standing more or less "upright" as in north-west forms. In the far north-west ("A" in fig. 11), the tibiotarsus extends well distal of the prefemoral process, and a second small, lateral tooth is present towards the base of the femoral process (fig. 6A). In the north-east of the *G. psi* range ("B" in fig. 11), the tibiotarsus is enlarged and directed slightly mesally, and the tips of the femoral process turn slightly posteriorly (fig. 6B).

**Colour:** Over much of the western and north-western portion of its range, *G. psi* is pale with very faint, brownish gray markings (fig. 7A). In the north of the range almost all

specimens have a striking pattern of dark lateral spots on the segments with ozopores (5, 7, 9, 10, 12, 13, 15–18; fig. 7B), while specimens from the south and central portions of the *G. psi* range are dark with faint mottling (fig. 7C).

**Distribution.** From sea level to c. 1250 m over c. 25 000 km<sup>2</sup> in northern and western Tasmania, including Three Hummock Island in Bass Strait (fig. 11). In coastal, subalpine and riparian scrubs; in swamp forest, wet eucalypt forest and rainforest; in exotic tree plantations; and occasionally in caves. Syntopic with *G. imber*, *G. rusticum*, *G. tarkinense*, and *G. wynyardense* over parts of its range.

**Remarks.** *Gasterogramma psi* is the most ecologically tolerant species of the genus in north-west Tasmania, and is generally more abundant than co-occurring *G. rusticum*, *G. tarkinense* or *G. wynyardense*.

### *Gasterogramma rusticum* sp. nov.

Figures 8, 12 (map)

**Material examined.** Holotype. Male. Australia, Tasmania. Christmas Hill, DQ697095, 340 m, 10 Nov 1993, R. Mesibov, wet eucalypt forest, QVM 23:16476.

Paratypes. 2 males, Little Claytons Rivulet, DQ321385 [41°12'06'' 146°11'24''], 80 m, 31 Oct 1996, R. Mesibov, wet eucalypt forest, QVM 23:40594; 2 males, Elizabeth Town, DQ633091 [41°28'07'' 146°33'37''], 210 m, 17 Sep 1997, R. Mesibov, wet eucalypt forest, QVM 23:40600; 5 males, Gawler R., DQ277347 [41°14'08'' 146°08'14''], 150 m, 29 Apr 1999, K. Bonham, site 6b, blackwood forest, AM KS 85100 (formerly QVM 23:41901).

Other material. 31 males from 21 unique localities in northern Tasmania, including Caroline Creek, Christmas Hill, Dalgath Forest Reserve, Dasher R., Don Reserve, Dulverton, Dysodile Hills, East Gawler R., Gog Range, Kelcey Tier, Latrobe, Lobster Rivulet, Long Hill, Marine Creek, Mersey R., Nook, Staggs Hill, Stella Glen, Warners Sugarloaf and Winter Brook.

**Diagnosis.** Gonopod with no femoral process or tibiotarsus; telopodite in posterior view with broadly notched tip, i.e. with 2 well-separated terminal teeth.

**Description.** Males c. 17–20 mm long and c. 1.8–2.0 mm wide at midbody. Body in both sexes lightly mottled with brownish-pink pigmentation. Gonopod telopodites slender, more or less straight, lightly joined for about middle third of their length, a few short, coarse setae near bases just inside aperture (fig. 8). Aperture more or less ovoid, long axis transverse, posterior margin not noticeably raised. Telopodite slightly sinuous in lateral view, curving first anteriorly, then distally, then anteriorly, anterioposteriorly flattened towards its end and bending slightly laterally, broadly notched at its terminus to form two subequal teeth. No evidence of femoral process or tibiotarsus. Solenomerite short, helical, tapering process arising at about three-quarters of length of telopodite on its posterior face. Prostatic groove running distally and posteriorly on mesal side of telopodite, then bending first laterally, then mesally on posterior telopodite surface before running distally to enter solenomerite on its mesal side.

**Distribution.** In rainforest and wet eucalypt forest over c. 2300 km<sup>2</sup> in north-central Tasmania (fig. 12), from sea level to

c. 700 m. Syntopic with *G. psi* at various locations through its range.

**Etymology.** From Latin *rusticus*, rural, adjective. Much of the range of this species is now an intensively farmed landscape.

***Gasterogramma tarkinense* sp. nov.**

Figures 9, 12 (map)

**Material examined.** Holotype. Male. Australia, Tasmania. The Clump, CQ213361 [41°12'23'' 144°52'06''], 190 m, 6 Feb 1992, R. Mesibov, wet eucalypt forest, QVM 23:8058.

Paratypes. 3 males (1 dissected for SEM), details as for holotype but 17 Sep 1989, QVM 23:8056; 1 male, Little Donaldson R. area, CQ552256 [41°18'28'' 145°16'12''], 500 m, 7 Jan 1997, ANZSES personnel, rainforest, AM KS85101 (formerly QVM 23:40584).

Other material. One male each from Newdegate Creek and Waratah in north-west Tasmania.

**Diagnosis.** Gonopod with branched femoral process; tibiotarsus prominent, directed mesally and posteriorly from prefemoral process fringed with tooth-like projections; solenomerite arising near base of prefemoral process.

**Description.** Males c. 17–20 mm long and c. 1.8–2.0 mm wide at midbody. Body in both sexes ivory-coloured with traces of pink-purple pigmentation middorsally and anteriorly on each segment. Gonopod telopodites slender, narrowing somewhat near base, lightly joined mesally for about two-thirds their length, at which point they bend slightly anteriorly (fig. 9). A projection like a shark's dorsal fin, pointed distally, on anterior surface of telopodite at about one-third its length. A few short, coarse setae at telopodite bases, setate area extending just outside aperture. Aperture more or less ovoid, long axis transverse, posterior margin not noticeably raised. Telopodite flattened anterioposteriorly past bend and tapering laterally, with a lateral and terminal fringe of c. 20 short teeth, simple and bifid, directed posteriorly on tapered portion. Tibiotarsus about as long as tapered portion of prefemoral process, a straight, pointed rod arising on mesal side of prefemoral process at about halfway along tapered portion and directed mesally and posteriorly. Femoral process beginning as a bulge on posterior surface of telopodite just proximal to bend, extending laterally in two diverging, rod-like branches. Distal branch straight, directed distally and laterally and terminating abruptly in a finely pointed, posteriorly directed hook. Proximal branch about one-third length of distal branch, directed proximally and laterally and curving posteriorly at its blunt tip. Solenomerite a short, helical, tapering process arising near base of prefemoral process on its posterior face. Prostatic groove running distally and posteriorly on mesal side of telopodite, then curving laterally, then distally, then mesally around femoral process before running distally to enter solenomerite on its mesal side.

**Distribution.** Rainforest and wet eucalypt forest at four sites in north-west Tasmania (fig. 12), at altitudes c. 200–900 m, with an estimated minimum range of c. 2300 km<sup>2</sup>. Syntopic with *G. psi* on Wombat Hill, near Waratah.

**Etymology.** Adjectival form of Tarkine, a popular name for the area between the Arthur and Pieman Rivers where the range of this species is centred.

***Gasterogramma wynyardense* sp. nov.**

Figures 10, 12 (map)

**Material examined.** Holotype. Male. Australia, Tasmania. Inglis R., CQ850382 [41°11'57'' 145°37'42''], 390 m, 27 May 1999, K. Bonham, site 35b, wet eucalypt forest, QVM 23:41910.

Paratypes. 2 males, details as for holotype, QVM 23:41910; 1 male, Meryanna, CQ388491 [41°05'35'' 145°04'50''], 190 m, 10 Apr 1999, R. Mesibov, rainforest, QVM 23:41044.

Other material. 9 males from 8 unique localities in north-west Tasmania: Arthur R., Blackfish Creek, Cam R., Inglis R., Julius R., Oonah, Seabrook Creek and Sumac Rivulet.

**Diagnosis.** Gonopod with no femoral process or tibiotarsus; telopodite in posterior view ending in a narrow, distally directed point

**Description.** Males c. 15–17 mm long and c. 1.6–1.8 mm wide at midbody. Body in both sexes lightly mottled with brownish-pink pigmentation. Gonopod telopodites slender (fig. 10), arising from syncoxite well-separated, but lightly joined from about one-third their length, a few short, coarse setae at telopodite bases within aperture. Aperture more or less ovoid, long axis transverse, posterior margin slightly raised and narrowly, medially notched. Each telopodite bends anteriorly at about half its length, bears a narrow, smoothly curved ridge on its anterior surface at about three-quarters of its length, and tapers mesally to blunt point. Solenomerite short, helical process arising from flattened area on posterior side of telopodite just distal to its bend, solenomerite cradled at its base in a shallow depression in telopodite. Prostatic groove running distally on mesal side of telopodite to vicinity of bend, then curving to posterior side of telopodite, entering base of solenomerite on a slightly sinuous, distal course. No indication of a femoral process or a tibiotarsus.

**Distribution.** Rainforest and closed wet eucalypt forest (and exotic tree plantations) over at least 900 km<sup>2</sup> in north-west Tasmania (fig. 12), from near sea level to c. 500 m. Syntopic with *G. psi* at various locations through its range.

**Etymology.** Adjectival form of Wynyard, a Tasmanian town close to which this species is abundant.

***Gasterogramma* sp.**

**Material.** 2 males. Australia, Tasmania. Cam R. area, DQ019512 [41°05'03'' 145°49'55''], 140 m, 30 Jul 1997, R. Mesibov and R. van Riet, QVM 23:40634.

**Remarks.** These specimens were found at the extreme eastern end of the *G. wynyardense* range, close to a locality for that species. However, they seem closest to *G. rusticum*: the prefemoral prolongation has a wide terminal notch, the prostatic groove has an "S-bend" as it crosses the posterior face of the telopodite, and the body is larger and more deeply pigmented than it is in *G. wynyardense*. They differ from *G. rusticum* in having a mesodistally directed, spike-like process arising on the mesoposterior face of the telopodite at about the level of the solenomerite. One interpretation is that the specimens represent a disjunct *G. rusticum* population (the nearest known *G. rusticum* locality is 30 km to the east) which

has long been separated from the main population and is somewhat differentiated. It is curious that the specimens were collected at the edge of the *wynyardense/rusticum* distribution gap, in which only *G. psi* has so far been found. Genetic studies of *Gasterogramma* populations in the area may help to clarify the taxonomic situation.

### Biogeography and conservation

*Gasterogramma* is largely restricted to areas with an annual rainfall greater than 1000 mm (fig. 13), i.e. to areas which at least potentially carry wet forest habitat. The distributions of individual species, however, are not as simply explained. *Gasterogramma psi* occupies the north-western third of Tasmania (fig. 11) from sea level to nearly 1300 m, and is sympatric with *G. imber*, *G. rusticum*, *G. tarkinense* and *G. wynyardense*. There is no obvious ecological reason why *G. psi* could not extend into the ranges of *G. austrinum* and *G. extremum* in the south, or into the *G. plomleyi* range in the north-east (the closest known approach to the latter is only 12 km through formerly forested country).

The seven newly described species in the genus form an allopatric/parapatric spatial mosaic (fig. 12). In north-east Tasmania, the *G. plomleyi* range is closely congruent with that of the land snail *Anoglypta launcestonensis* (Reeve, 1853). These two distributions partly define the area of endemism known as Plomleys Island (Mesibov, 1994), which is also characterised by the presence of a number of other narrow-range endemic invertebrates and by the absence of some wide-ranging species. On the north coast, the 30-km-wide gap between the ranges of *G. wynyardense* and *G. rusticum* is now largely farmland. A search of forest remnants in the gap has so far yielded only *G. psi*, so it is not known whether *G. wynyardense* met *G. rusticum* in parapatry before forests in the gap were cleared for agriculture. Parapatric boundaries may yet be found between *G. wynyardense* and *G. tarkinense* and between *G. tarkinense* and *G. imber* in the relatively inaccessible forests of the Arthur-Pieman area in north-west Tasmania, and between *G. austrinum* and *G. extremum* in the wilderness forests of the upper Picton R. catchment. The Gordon River Rd in south-west Tasmania crosses the *G. imber/G. austrinum* parapatric zone and the easy access afforded by this road has facilitated preliminary fine-scale mapping of the two species. As with parapatric millipedes in north-east Tasmania (Mesibov, 1997), the two ranges overlap in a zone less than 1 km wide, and a site has been found along the road where *G. austrinum* and *G. imber* co-occur in litter at the base of a single large tree (see separate specimen table). Possible historical explanations for the mosaic distribution pattern seen in *Gasterogramma* will be discussed elsewhere.

Where rotting logs and deep, well-drained forest soils are available as refuges, the four northern *Gasterogramma* species (*G. plomleyi*, *G. psi*, *G. rusticum* and *G. wynyardense*) and the southern *G. austrinum* appear to tolerate burning, logging and

partial clearing of their wet forest habitat. *G. psi* and *G. wynyardense* are also known to tolerate replacement of native forest by exotic tree plantation. A survey of litter invertebrates in north-west Tasmania (Bonham et al., 2002) found these two species to be equally abundant in forest plantations (mainly *Pinus radiata*) and nearby native forest. Remarkably, *G. psi* has been collected in tiny (<0.25 ha) degraded remnants of riparian eucalypt forest on farms, having evidently persisted in the litter under a few surviving eucalypt trees for many years.

Although *G. rusticum* and *G. wynyardense* have lost substantial portions of their ranges to agriculture on the more fertile soils of northern Tasmania, all eight *Gasterogramma* species can be regarded as well conserved. All are known to occur (or are likely to occur) in formal, forested reserves within their respective ranges, and all seem likely to persist indefinitely outside reserves under land management regimes which perpetuate closed forest cover, i.e. logging and regeneration of native forest, and plantation forestry.

### Acknowledgments

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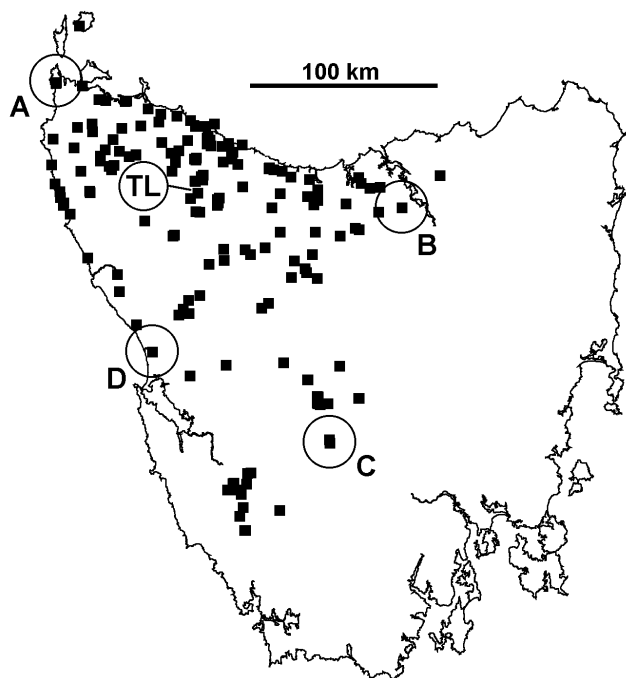


Figure 11. Localities (squares) for *G. psi* males. Circled and labelled localities correspond to the four sites noted in fig. 6: A, Washpond Forest, B, Notley Gorge, C, Coles Creek, D, Henty R. "TL" points to the type locality, Hellyer Gorge.

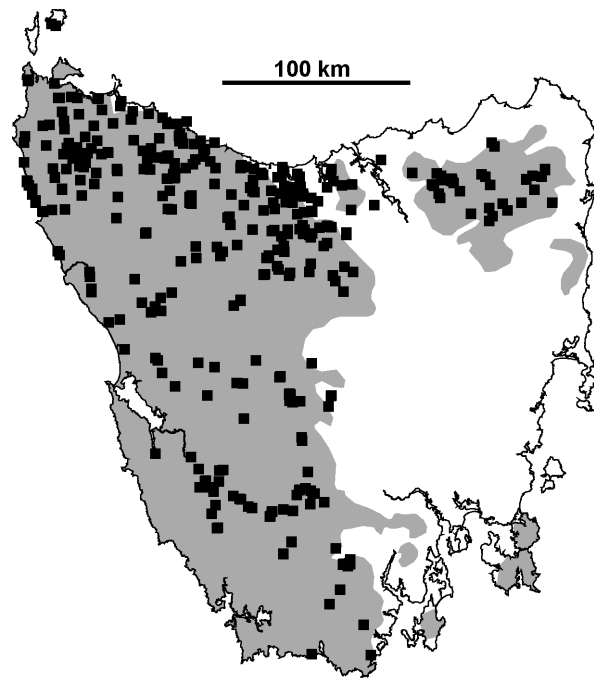


Figure 13. All known localities for *Gasterogramma* spp. (■). Shaded areas have annual rainfall of at least 1000 mm.

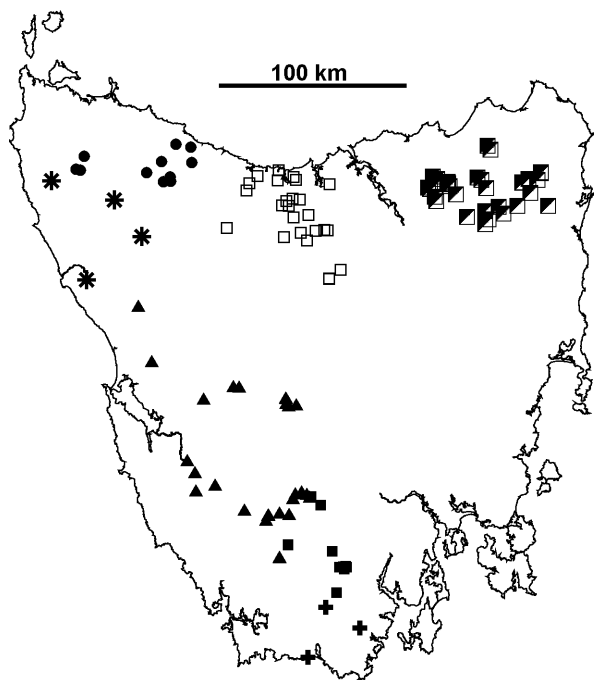


Figure 12. Localities for males of *G. austrinum* sp. nov. (■ south), *G. extremum* sp. nov. (+, far south), *G. imber* sp. nov. (▲, west and south-west), *G. rusticum* sp. nov. (□ north-central), *G. tarkinense* sp. nov. (\*, north-west) and *G. wynyardense* sp. nov. (•, north-west), and for all specimens of *G. plomleyi* sp. nov. (half-filled squares, north-east).

