

New and little-used morphological characters in Polydesmida (Diplopoda)

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Abstract

Polydesmida (Dalodesmidae and Paradoxosomatidae) vary in the structure of spiracles, spinnerets, male leg setae and integument fine sculpture. Although this variation is only clearly seen with scanning electron microscopy, some variations are apparent at low magnification. Spiracle, spinneret and fine sculpture variations are found in both sexes and are thus useful in identifying females. The variations described here are taxonomically useful at the species- and genus-group levels. Their functional significance is unknown.

Keywords: spiracles, spinnerets, leg setae, integument sculpture

1. Introduction

Species of Polydesmida are distinguished primarily on the form of the male gonopods. The extraordinary variety of gonopod shapes, proportions, branchings and adornments makes it possible to identify many species without a multi-character diagnosis. An experienced taxonomist can often compare the gonopod of the specimen in hand with a gonopod illustration and simply ask ‘Do these two structures have the same form, or not?’

However, while gonopod form may be adequate for recognising species, it is less than adequate for classifying them. The gonopods in Polydesmida are often referred to as modified legs, but it might be more correct to call them structures which *replace* legs, namely the eighth pair of legs in mature males. In most species the only leg-like feature of the gonopod is the articulation between the distal telopodite and the basal ‘gonocoxa,’ which unlike all other leg coxae is not attached to a segmental sternite. The phenomenally variable telopodite bears no clear resemblance to any part of a walking leg. The most recent hypothesis of homology (Jeekel 1956, 1982) for components of the telopodite remains speculative more than 50 years after it was first published (Mesibov 2005).

Assignments to genus, subfamily and family in the Polydesmida are therefore often based on non-gonopodal characters (e.g., distinctive shapes of collum, paranota, gonopod aperture or epiproct) or on combinations of gonopodal and non-gonopodal characters – ‘collective attributes of the total animal’ (Hoffman 1980, p. 21). Unfortunately, in groups with numerous very similar genera, such as the hugely speciose Paradoxosomatidae, the more obvious non-gonopodal characters may vary so little that it is often impossible to assign a female or late-juvenile specimen to a genus.

In this paper I discuss some less obvious non-gonopodal characters which have the potential to improve morphological taxonomy below the family level. This is not a systematic review of such characters across the Polydesmida, but a sampling of incidental results in previously published taxonomic studies on Dalodesmidae and Paradoxosomatidae, mainly from Australia. In addition, I present some new observations on paradoxosomatid spiracles.

2. Materials and methods

Specimens figured here are preserved in 80 % ethanol. Isolated body parts were air-dried, sputter-coated with gold and examined with an FEI Quanta 600 ESEM operated in high vacuum mode. Abbreviations: QM = Queensland Museum, Brisbane, Queensland, Australia; QVM = Queen Victoria Museum and Art Gallery, Launceston, Tasmania, Australia. For more information on the undescribed Tasmanian Paradoxosomatidae illustrated in Fig. 2, see the Tasmanian Multipedes website.

<http://www.qvmagtas.gov.au/zoology/multipedes/mulintro.html>.

3. Results

Spiracles. Attems (1937, p. 9) described polydesmidan spiracles as opening on more or less crater-like elevations (‘mehr oder weniger kraterartigen Erhöhungen’). However, the spiracle itself – by which I mean the structure covering the entry to the tracheal system – can take several forms, and may not be confined to the crater.

In most species of Dalodesmidae examined by me the spiracle is recessed and lattice-like (Fig. 1A). In *Dasystigma* Mesibov, 2003 and *Tasmanopeltis* Mesibov, 2006 the spiracle is emergent and consists of a dense packing of hair-like structures resembling the tentacles of sea anemones (Fig. 5 in Mesibov 2003; Fig. 5B in Mesibov 2006a). In these two genera the spiracle craters are larger and have narrower rims than in similar-sized species with recessed spiracles. Further, the posterior spiracle on diplosegments in the more prominently ‘tentacled’ species opens above the anterior leg, close to the anterior spiracle, rather than between the anterior and posterior legs, as is typical for Polydesmida (Figs 1A, 5C).

Emergent spiracles are also found in Paradoxosomatidae and are obvious at low magnification (Figs 1B, C; compare Figs 3C, D). At higher magnification, the spiracle in most of the species examined is seen to consist of numerous fine, short, densely packed projections (Figs 2, 3). These may be contained within the crater or extend well beyond it, i.e. ‘recessed’ and ‘emergent’ are arbitrary categories along a continuum of shape. In several genera the projections have multi-pronged tips (Fig. 12 in Rowe and Sierwald 2006; e.g. Fig. 2D here).

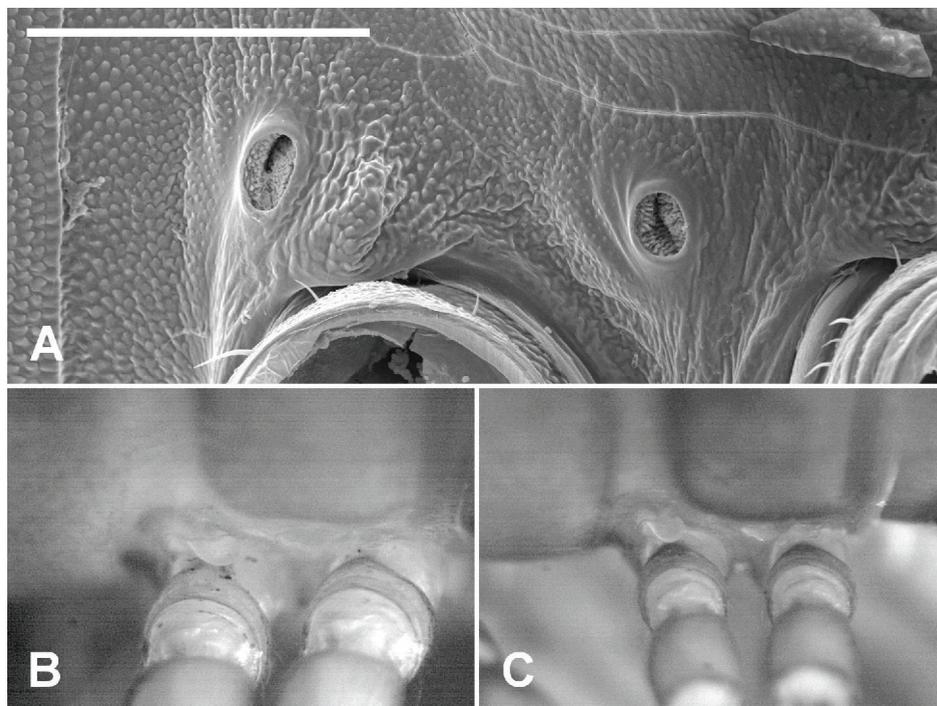


Fig. 1 Left lateral views of spiracles on male midbody rings. A: *Tasmanodesmus hardyi* Chamberlin, 1920 (legs removed), QVM 23:46289, scale bar = 0.5 mm; B: *Somethus mesibovi* Jeekel, 2006, QVM 23:41840; C: *Somethus tasmani* Jeekel, 2006, QVM 23:46238. Original magnification for B and C is 40X; compare Figs 3C and 3D for scale.

Two larger-scale morphological characters in paradoxosomatids are folding of the spiracle surface and shape of the crater. A common pattern of folding is for the dorsal portion of the anterior spiracle on a diplosegment to be convex and the ventral portion concave (Figs 2, 3). Also as shown in Figs 2 and 3, the crater walls, notably of the anterior spiracle, can be simply erect or folded over inwards at the crater rim, and can be extended or reduced in height around a single crater circumference.

Figs 2 and 3 show the anterior spiracle on ring 12 in males of eight paradoxosomatid species. Six are native to Tasmania (Australia), one is an Australian native widely introduced overseas and the last is a pantropical tramp introduced into Australia. Several differences in spiracle structure seem to be taxonomically useful. The fine projections are less dense, individually flatter and with more terminal teeth in the four genera currently assigned to Antichiropodini within Australiosomatinae (Fig. 2) than in the two genera currently assigned to Australiosomatini within Australiosomatinae (Fig. 3 B–D). In all the Australiosomatinae shown here, the anterior spiracle is directed either laterally or posterolaterally, while in *Asiomorpha coarctata* (de Saussure, 1860) (Paradoxosomatinae: Orthomorphini) the anterior spiracle is directed anterolaterally (Fig. 3A; for a larger view see Fig. 5C).

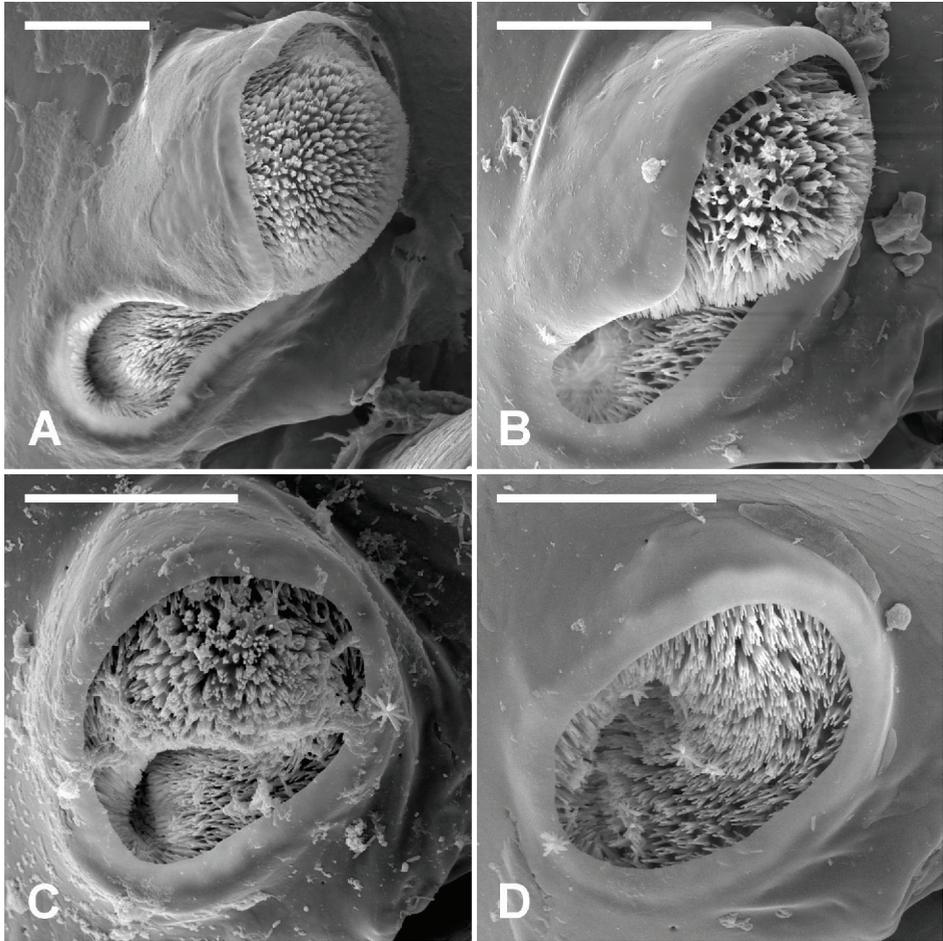


Fig. 2 Left lateral views of anterior spiracle on male ring 12; scale bar = 0.05 mm in all cases. A: *Aethalosoma solum* Jeekel, 2006, QVM 23:45905; B: undescribed *Dicranogonus* sp. from Flinders Island, northeast Tasmania, QVM 23:15170; C: *Notodesmus scotius* Chamberlin, 1920, QVM 23:13871; D: undescribed *Pogonosternum* sp. from northwest Tasmania, QVM 23:15350.

In the three cases in which the spiracle is directed strongly posterolaterally (Figs 2A, 2B, 3C), the crater wall on the anterodorsal side is extended to partly protect the emergent spiracle. There is also a difference between the two illustrated species of *Somethus* Chamberlin, 1920 (Figs 1B, 1C, 3C, 3D), with the anterior spiracle projecting more strongly posterolaterally in *S. mesibovi* Jeekel, 2006 than in *S. tasmani* Jeekel, 2006. The two species are sympatric in northern Tasmania and have previously been distinguishable only as males. If the spiracle difference shown here is consistent between sexes and across the sympatric zone, then it can be used to identify females, even at low magnification (Figs 1B, C).

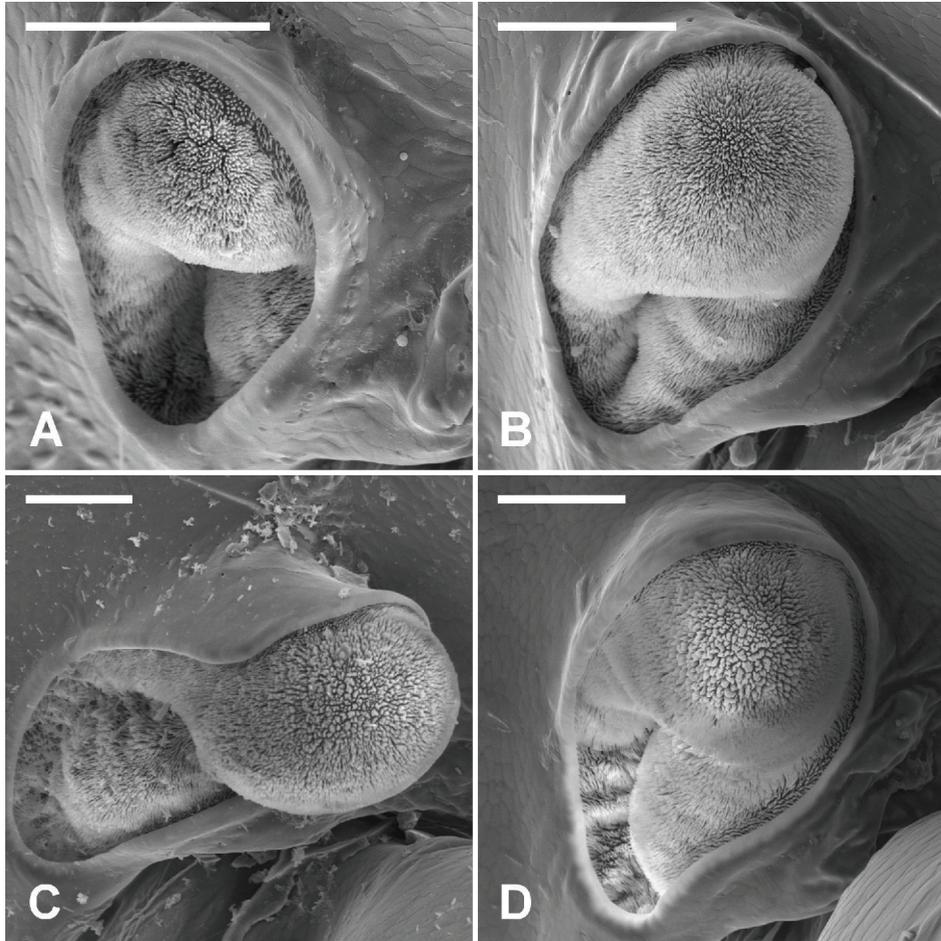


Fig. 3 Left lateral views of anterior spiracle on male ring 12; scale bar = 0.05 mm in all cases. A: *Asiomorpha coarctata* (de Saussure, 1860), QVM specimen from Rapid Creek, Northern Territory, Australia; B: *Akamptogonus novarae* (Humbert & de Saussure, 1869), QVM 23:25732; C: *Somethus mesibovi* Jeekel, 2006, QVM 23:41840; D: *Somethus tasmani* Jeekel, 2006, QVM 23:46238.

I reported another interesting intrageneric difference in spiracle morphology in *Tholerosoma* Mesibov 2006, a paradoxosomatid genus from Queensland, Australia in which the head, legs and metazonites are encrusted with dirt particles. Both of the known species have strongly emergent, non-folded spiracles composed of numerous fine, short projections, but in *T. monteithi* Mesibov, 2006 the spiracle surface is largely covered by minute, irregular plates (compare Figs 6B and 6C in Mesibov 2006b). It is not yet clear whether the plates are produced by the millipede; it is possible they are microbial growths.

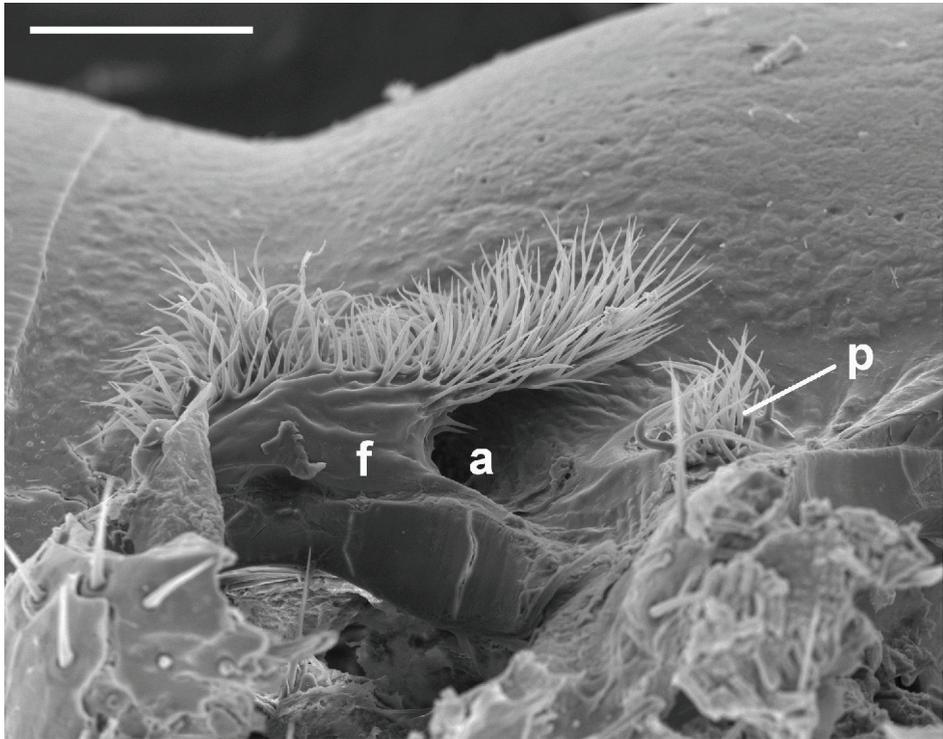


Fig. 4 *Lissodesmus anas* Mesibov, 2006, male, QVM 23:17657. Ventral view of left side of midbody ring. f: 'foxtail' anterior to anterior spiracle; a: space above anterior spiracle; p: posterior spiracle area. For lateral view, see Fig. 5C in Mesibov (2006a). Scale bar = 0.1 mm.

Finally, in an earlier paper (Mesibov 2006a) I described the dalodesmid *Lissodesmus anas* Mesibov, 2006 as having a 'foxtail' of hair-like structures arising just anterior and ventral to the anterior spiracle, curving dorsally and posteriorly to obscure the anterior spiracle and terminating near the posterior spiracle. The form and position of the foxtail are difficult to see in lateral view (Fig. 5C in Mesibov 2006a), but are apparent in ventral view (Fig. 4, this paper). This remarkable structure is an autapomorphy of *L. anas*.

Spinnerets. Just beneath the epiproct in Polydesmida is a group of four prominent setae, called 'Terminalborsten' by Attems (1937, p. 11) and 'a terminal cluster of four setae' by Hoffman (1982, p. 716). Adis et al. (2000) showed that this structure functions as a spinning apparatus in juveniles of two species of Pyrgodesmidae. The setal cluster has subsequently been referred to as 'spinnerets' (e.g., in Mesibov 2006b).

Shear (2008) used scanning electron microscopy to examine the spinnerets in from one to three species in each of 16 families of Polydesmida. He found remarkable variation in structural details:

- the arrangement of spinnerets is typically quadrate, but can be wider than long, longer than wide or trapezoidal narrowing either dorsally or ventrally;
- more than one seta can arise from each setal socket, and each seta can be smooth or spirally grooved, and longer/shorter or thicker/thinner than non-spinneret setae on the epiproct;
- setae usually arise from a sleeve which can be short or long, single or duplex (concentric inner and outer sleeves), with the outer sleeve being smooth or plicate and with a flat or serrate distal margin;
- the four spinnerets may or may not be set within a low-walled depression; the enclosing wall may be continuous or partly open, and may be connected to internal partition walls which separate individual spinnerets.

Mesibov (2008a) showed SEM images of spinnerets in the type species of 10 genera of Dalodesmidae. All four spinnerets are set in a low-walled depression in seven genera, while the dorsal (or posterior) pair are unenclosed in two genera; this suprageneric division is supported by other synapomorphies. However, while low enclosing walls are present in one of the two species examined in the tenth genus, *Orthorhachis* Jeekel, 1985, they are absent in the second species. An unenclosed dorsal (posterior) pair of spinnerets was also found by Shear (2008) in a *Katantodesmus* species (Oniscodesmidae).

A possible synapomorphy for the dalodesmidean genera *Noteremus* Mesibov, 2009, *Paredrodesmus* Mesibov, 2003 and *Procophorella* Mesibov, 2003 is the spacing of the spinnerets. In all species of all three genera, the ventral spinneret pair are distinctly further apart than the dorsal pair (Mesibov 2009).

With only very preliminary taxon sampling, it is still far from clear which spinneret variations will be useful in Polydesmida taxonomy, and at which taxonomic levels. Another variation to be investigated is functional. In the species studied by Adis et al. (2001), secretion appeared to emerge from the sleeve surrounding the base of each seta. Shear (2008) noted loss or degeneration of the sleeve in several of the species he examined, and suggested that in these forms (at least in adults) the spinning apparatus is vestigial.

Male leg setae. Attems (1937, p. 13) drew attention to two kinds of specialised setae found ventrally on distal podomeres of the legs of mature males. Strongylosomidae (= Paradoxosomatidae) have a dense brush ('Bürste') of simple setae, while Polydesmidae and Sphaerotrichopidae (= Dalodesmidae) have sphaerotrichomes, which are setae each arising from a ball-shaped structure.

Golovatch and Enghoff (1993) found variations on the theme of simple brush setae in the southeast Asian paradoxosomatid genus *Tylopus* Jeekel, 1968. Setae close to the peculiar ventral tubercles characteristic of the genus are short and bend in a curve towards the leg surface in several species, and some species bear dense tarsal brushes of large, apparently textured setae (Golovatch & Enghoff 1993, Fig. 9).

SEM views of the brush setae of several Australian paradoxosomatids were published by Rowe and Sierwald (2006; their Figs 16–18). Brush setae are long and well-separated in *Hoplatessara musgravei* Verhoeff, 1928 and *Gigantowales chisholmi* Verhoeff, 1937, but short and bent into cone-shaped groups in *Cladethosoma trilineatum* (Newport, 1844) (formerly *Cladethosoma clarum* Chamberlin, 1920). The location of brushes, i.e. 'either limited to the pregonopodial legs or occurring on all but the final leg pairs', was said to vary at the species or genus level (Rowe & Sierwald 2006, p. 531).

The Dalodesmidae so far studied show much greater variation in male leg setae than do Paradoxosomatidae. Sphaerotrichomes vary not only in their location (i.e., on which podomeres and on which legs) and their density, but also in their fundamental form, as illustrated in Mesibov (2004). The ball-shaped, concentrically ridged base can be partly enclosed in a socket, or free in a shallow concavity. The setal shaft can arise from the base at a high or low angle, and can taper to a point or end in a slight swelling. The shaft is absent in all eight known species of *Gasterogramma* Jeekel, 1982 (Mesibov 2008a) – sphaerotrichomes without trichomes! This absence is one of several unusual, non-gonopodal synapomorphies in *Gasterogramma*, which shows substantial variation in gonopod form from species to species.

Like Paradoxosomatidae, Dalodesmidae have brush setae on the male legs, but on the more basal podomeres, i.e. the prefemur, femur, and postfemur, and sometimes also the distal end of the coxa/trochanter and the proximal end of the tibia. Four states for the character ‘form of brush seta’ are so far known (Mesibov 2008a, b): unbranched with pointed tip; unbranched with slightly expanded tip; tip divided into two short, finely pointed branches; and bluntly tipped with a short, thick, bluntly tipped branch arising midway along the seta.

Like some of the variations in spiracle morphology, the general patterns of setal form noted above can be seen at relatively low magnification using a light microscope, although details are only clearly visible at much higher magnification.

Fine sculpture of the integument. Many Polydesmida have seta-bearing bumps, bosses or tubercles on the collum and metatergites. These sculptural features have long been used in diagnoses, e.g. as dorsally ‘smooth’ vs. ‘tuberculate’ metatergites (keys in Blower 1985, pp. 189, 210). I recently distinguished two patterns of metatergal tuberculation in two dalodesmid genera (Mesibov 2008a), but a general review of such patterns has apparently never been attempted. Simonsen (1990) used only presence/absence of metatergal tubercles in his cladistic analysis of Polydesmida.

Less attention has been paid by taxonomists to fine sculpturing of the integument. In many polydesmidan taxa the body surface appears smooth under low magnification, and when fine sculpture is apparent it is usually described simply, e.g. as granulate (species of *Desmoxytes* Chamberlin, 1923 in Golovatch & Enghoff 1994).

At high magnification, the integument in all species I have examined is covered with tightly fitted polygonal elements. These may be flat, as in a parquet or mosaic floor, or with one side of each element elevated and overlapping the adjacent element, like scales on a fish skin, or both flat and slightly overlapping in a small area of integument (Fig. 5 in Rowe & Sierwald 2006). In *Lissodesmus hamatus* Mesibov, 2006, the overlapping edge of elements on the prozonite, close to the limbus of the adjacent ring, is finely toothed (Fig. 6B in Mesibov 2006a).

In some species, portions of the integument are distinctly cellular, i.e. divided into minute, shallow cells by raised partition walls (Fig. 5A). Cellular integument is confined to the prozonite anterior to the waist in *Desmoxytoides hasenpuschorum* Mesibov, 2006 (Fig. 1A in Mesibov 2006b), and apparently to the metazonite posterior to the waist in *Tholerosoma monteithi* Mesibov, 2006 (Fig. 3E in Mesibov 2006b); both species are paradoxosomatids. Several species in the dalodesmid genus *Orthorhachis* have areas of cellular integument. It is found on both the prozonite and the metazonite in *O. kerewong* Mesibov, 2008 and *O. weiri* Mesibov, 2008 (Figs 7B and 7C, respectively, in Mesibov 2008a).

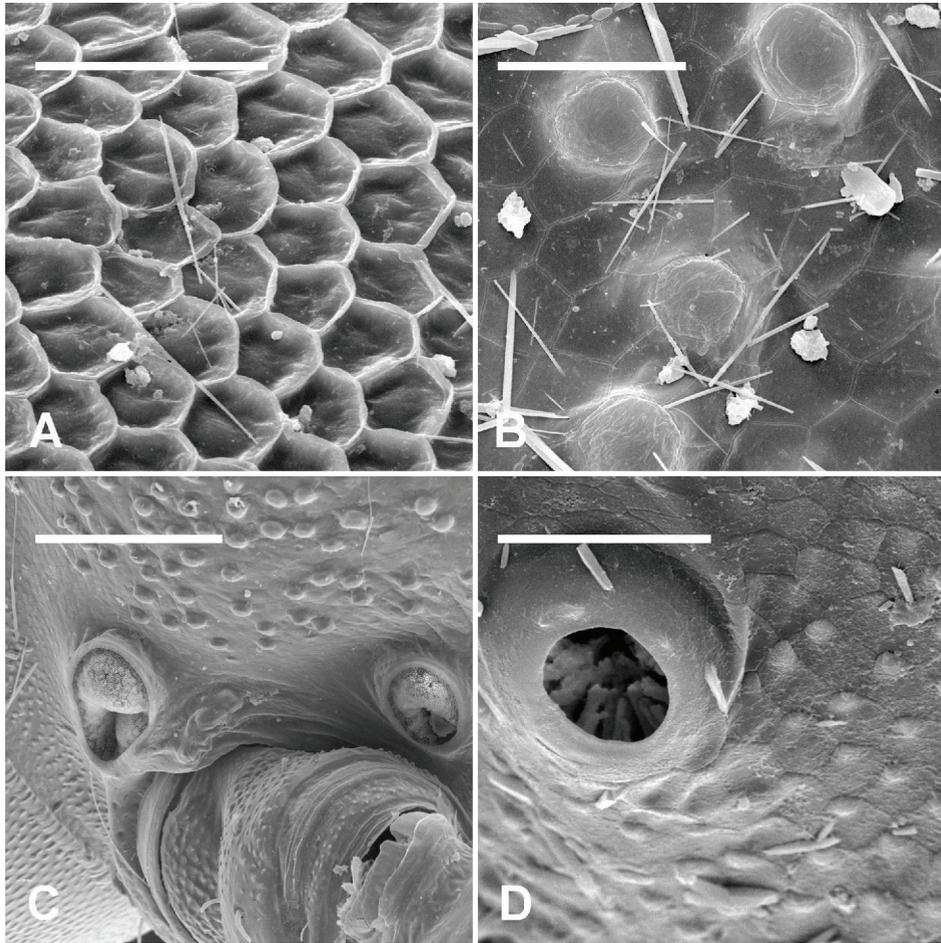


Fig. 5 *Desmoxytoides hasenpuschorum* Mesibov, 2006, male, QM S73968. A: Left lateral view of cellular prozonite sculpture on midbody ring; B: Left lateral view of microtubercles on midbody ring (enlargement of image cropped as Fig. 1E in Mesibov 2006b); C: *Asiomorpha coarctata* (de Saussure, 1860), male, QVM specimen from Rapid Creek, Northern Territory, Australia. Left lateral view of spiracles area on ring 12; D: *Paurodesmus sjoestedti* (Verhoeff, 1924), male, QM S51455. Left lateral view of posterior spiracle on ring 11 (enlargement of image cropped as Fig. 4B in Mesibov 2008b). Scale bar = 0.1 mm in C, others = 0.025 mm.

Very small, rounded tubercles are scattered across portions of the integument in some paradoxosomatids, e.g. *Asiomorpha coarctata* (Fig 5C), giving a ‘granular’ appearance at low magnification. In *D. hasenpuschorum* the microtubercles are seen to arise between polygonal elements (Fig. 5B). However, in the dalodesmid *Paurodesmus sjoestedti* (Verhoeff, 1924) each microtubercular swelling seems to arise as an expansion of one corner of an element (Fig. 5D).

5. Discussion

Fine-scale, non-gonopodal characters have so far been used very little in Polydesmida classification. Simonsen (1990) made use of limbus differences in distinguishing suborders, and suggested (his Fig. 27) some evolutionary trends in this character. Rowe and Sierwald (2006) published a number of scanning electron micrographs of selected characters in Australian Paradoxosomatidae as supplementary data for a genus revision, commenting ‘To date, millipede morphology remains poorly described’ (p. 530).

The morphological character set used for Polydesmida in recent taxonomic publications differs little from the one used early last century by specialists such as Attems, Brolemann, Silvestri and Verhoeff. It consists largely of non-gonopodal characters which are visible at low magnification without dissection. Many character states seem to be reported principally for use in confirming identifications, e.g. ‘lateral margin of paranotum slightly convex’ and ‘hypoproct subtrapezoidal’, or for the sake of consistency within the long tradition of describing Polydesmida. The diagnostic value of some reported character states, such as ‘sternites lightly setose’ and ‘vertigial sulcus lightly impressed’, is limited, either because they are nearly universal or because they refer to inadequately defined categories on a continuum of variation. Over the years the published record of these non-gonopodal character states has become a catalogue of the mundane. Against this background, a small number of exceptional character states can be shown to be useful in diagnoses, e.g. the antler-like paranota of dragon millipedes (Golovatch & Enghoff 1994). Most reported character states, however, remain in a kind of limbo. They have neither been tested for their practical value in generating classifications, nor investigated for clues to their evolutionary origins (symplesiomorphy or convergence).

Perhaps the most obvious reason for this lack of focus on non-gonopodal characters is that Polydesmida are morphologically conservative. Taxonomists interested in distinguishing species within a single genus, or genera within a small clade in a single family, may not be able to find any clear diagnostic differences away from the gonopod. (For an exception, see the key to *Tylopus* species in Golovatch and Enghoff 1993). Further, describers often have only a single male on which to base a new species, and simply do not know whether the more subtle non-gonopodal character states seen in the type are intraspecifically variable.

In this paper I point to the unexpectedly large variability found in some little-studied, non-gonopodal character sets. I urge Polydesmida specialists to routinely examine these character sets and to look for others using scanning electron microscopy. As shown above, fine-scale features have considerable potential for use in genus- and species-level taxonomy. Diagnostic differences in spiracles, spinnerets and integument fine sculpture are likely to be present in females as well as males, and will help in the assignment of females to species and genera. Since these three character sets are present in all Polydesmida, they are likely to be useful in family-group taxonomic studies as well.

SEM studies may also clarify questions of homology, and assist comparative studies of function. It is a remarkable fact that after more than a century of close study of Polydesmida we still know very little about the functional significance of the structures described in this paper. The finding that the spinnerets are a spinning apparatus in juvenile pyrgodesmids is only about 10 years old. All we can currently say about spiracles is that millipedes breathe through them, but the remarkable variation now recognised in spiracles suggests that there is much more to be learned about how they work.

6. Acknowledgements

I thank Bill Shear for sharing with me his results on spinnerets, Karsten Goemann (University of Tasmania) for acquiring the SEM images, and Henrik Enghoff and an anonymous reviewer for excellent suggestions on improving this paper.

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Accepted 05 May 2009