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Snoqualmia, a new polydesmid milliped genus from the northwestern United States, with a description of two new species (Diplopoda, Polydesmida, Polydesmidae)

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Abstract. Snoqualmia, new genus, is described for two species of polydesmid millipeds from the northwestern United States: Snoqualmia snoqualmie, new species, from Washington State, and S. idaho, new species, from Idaho. Males of S. idaho possess unusually complex gonopods, perhaps the most complex to be found in the Order Polydesmida. Snoqualmia is placed in context with other polydesmid genera known from North America. The polydesmid fauna of North America is discussed, as well as characters of the gonopods of the family.

Keywords: Washington, Idaho, gonopods.

Introduction

Recent work has shown that a poorly understood and sparsely collected fauna of small polydesmid and macrosternodesmid millipeds inhabits western North America (Shear et al., 2009, Shear and Shelley 2007, 2008; Shelley 1993, 1996a, 1996b, 1997, 2003). The putative macrosternodesmids occur for the greater part in the Rocky Mountains, Great Basin and southwestern semideserts, mostly in caves or on forested *inselbergen*. Genera and species that can be assigned with some confidence to Polydesmidae, on the other hand, are found in the Pacific Northwest, mostly west of the crest of the Sierra Nevada and Cascade Mountains from the San Francisco Bay area of California north to Puget Sound, but also in northern Idaho. In the case of these micropolydesmids, at least a score of undescribed species, most of which will be placed in new genera, await description. They are inhabitants of deep, moist litter in temperate forests and require considerable effort and skill for their collection. Their very small size (3-7 mm long) makes them difficult to find.

Among the species so far collected are two with very distinctive, but roughly similar gonopods, and the additional synapomorphy of a knobbed (distally swollen), decurved epiproct. The gonopods of one of these species contrast with those of any previously described North American polydesmidans in their complexity. The two species are described below as **Snoqualmia snoqualmie**, **n. gen., n. sp.** and **S. idaho**, **n. sp**.

Discussion of North American Polydesmida

Polydesmoidea and Trichopolydesmoidea

Unfortunately at the present time the superfamilies Polydesmoidea and Trichopolydesmoidea, and their constituent families, are in a state of flux and confusion. Neither taxon has been unequivocally diagnosed, and both have served as trash bins for families and genera that have either been poorly described originally or have not been studied since their first proposal. In particular the Trichopolydesmoidea and the family Trichopolydesmidae Verhoeff 1910 have been expanded to include many tropical species that probably do not form a monophyletic group with the type genus *Trichopolydesmus* Verhoeff 1898, monotypic, native to Romania, and itself poorly studied. Hoffman's opinion that Trichopolydesmidae are a small family limited to a few species in eastern Europe is probably correct, but this leaves behind more than 50 genera, many monotypic, uncomfortably agglutinated in the family Fuhrmannodesmidae Broleman 1916 (Hoffman 1999). In North America, however, the situation has recently been clarified somewhat by a rediagnosis of the supposedly trichopolydesmoid family

Macrosternodesmidae by Shear and Shelley (2007), though it remains unsettled if this name is or is not a senior synonym of Nearctodesmidae Chamberlin and Hoffman 1950, as proposed by Simonsen (1990).

In the case of the Polydesmoidea, the included families Cryptodesmidae Karsch 1879, Haplodesmidae Cook 1895, Doratodesmidae Cook 1896, and Opisotretidae Hoffman 1999 appear to be well-diagnosed and probably represent monophyletic units. Polydesmidae Leach 1815 has not been so fortunate. It contains at present elements that belong elsewhere, some of them not even to be placed in the same superfamily. For example, Archipolydesmus Attems 1898 is obviously a macrosternodesmid (Abrous-Kherbouche and Mauriès 1996). In various papers on the Antillean fauna, Loomis (*i.e.* 1934) added such diverse genera to Polydesmidae that it became a meaningless wastebasket. Thus I do not agree with the assertion of Simonsen (1990) that Polydesmidae are probably monophyletic. Furthermore, within the polydesmid mélange, genera such as Epanerchodus Attems 1901, with more than 60 species ranged in eight subgenera (most of which have been ignored by systematists recently describing new species in the genus) seems, from a scan of the literature, to be polyphyletic. Even more so is the genus Polydesmus Latrielle 1803, with more than 100 named species in fully 26 subgenera, some of which surely represent full genera. Many of the species have multiple named subspecies and varieties. In North America, where neither genus is indigenous, the situation is simpler by far, but remains potentially daunting because of a substantial number of undescribed taxa.

Polydesmidae and Macrosternodesmidae

Polydesmidae and Macrosternodesmidae in North America are far from distinct, even though the two families are traditionally referred to separate superfamilies (extensive discussion in Shear and Shelley 2007). At this point in time, indigenous North American polydesmids are to be found east of the Central Plains, in the Mississippi Valley and Appalachian Mountains, and in the Pacific Northwest. Macrosternodesmids *sensu strictu* (that is, excluding nearctodesmids) are rare in the Appalachians and Mississippi Valley (but see Lewis 2002) and seem almost to exclude polydesmids in the Southwest and California.

For the time being, I regard as members of Polydesmidae any species in which the efferent duct of the gonopod debouches through a pulvillus, a pad or region of the gonopod which is set with fine cuticular projections (not setae), and whose telopodites possess a distinct distal zone (*sensu* Shear and Shelley 2007). In addition, most of these species have a loop or at least a curve in the course of the efferent duct just before the pulvillus, and may also have a reservoir distal to the loop. A distinct endomerite may or may not be present. An endomerite is here considered to be a separate branch of the gonopod originating from the basal region of the prefemur on the anteromedial side.

Using developmental studies, Petit (1976) in a little-cited paper, established that the postcoxal part of the polydesmid gonopod develops entirely from the prefemur. Therefore, using the term tibiotarsus for the part of the gonopod extending beyond the pulvillus is misleading. Here I substitute the term distal zone as suggested by Shear and Shelley (2007). Similarly it can no longer be considered accurate to call the region traversed by the efferent duct the femorite because the femur of the walking leg does not form part of the gonopod.

The Family Polydesmidae in North America

Eight endemic genera represent the family Polydesmidae (as characterized above) in North America (Shelley 2003). Several species of the European genus *Polydesmus* Latrielle 1803 have been introduced into disturbed habitats across the continent, and some have subsequently spread into other biotopes, such as secondary deciduous forests. Of the endemic North American genera, *Pseudopolydesmus* Attems 1898 comprises 33 nominal species from the eastern part of the continent and the Mississippi Valley. Hoffman (1999) synonymizes these into 12 species and an unpublished revision by Withrow (1988) reduces the number of species to nine, both these figures doubtless closer to the real number. *Pseudopolydesmus* species are easily distinguished from any of the other genera by their usually larger size [approximately 20-30 mm; smaller, possibly dwarfed individuals have been found in the Central Plains and Florida (R. Shelley, pers. comm.)] and well-marked polygonal areas on their asetose metazonites. In addition, males of *Pseudopolydesmus* species have distinctive modifications of the sterna, at least of

segments 4-7, consisting of paired lobes set with ensiform setae. *Pseudopolydesmus* is the only polydesmid genus whose distribution is limited to eastern North America, but *Pacidesmus* Golovatch 1991 (China, Thailand) is likely a synonym.

Nine species of the genus Scytonotus C. L. Koch 1847occur both in the eastern and western parts of the continent, three in the east and six west of the continental divide [Shelley 1993; a single females-only sample from Alberta, Canada, has been reported (Shelley 2007)]. The genus is distinguished by numerous clavate setae clothing the metazonites, and by gonopods with two subequal branches, including a large and distinct endomerite. Six of the species have males with pronounced modifications of the tibiae of leg pairs 13-22. Generally smaller (about 15 mm long) than species of Pseudopolydesmus, Scytonotus species also have 19 postcephalic segments (collum + 17 + telson), whereas the former genus has 20.

Utadesmus Chamberlin and Hoffman 1958 consists of two species, one from southern Utah and one from central and northern New Mexico (Shelley 1996). These are small (10 mm long), 19-segmented species with unmodified sterna and legs in males, and relatively simple gonopods. The metazonites bear three rows of acute to clavate setae. Calianotus Shelley 1997 was established for three Californian species, 9-10 mm long, and perhaps related to Scytonotus in having a large and distinct endomerite (Shelley 1997). All three species of Calianotus have 19 segments, but only two of the three have modified, lobed sterna on segments 9 and 10, as indicated in the key below. Calianotus sastianus (Causey), the species with unmodified sternites, may not belong in Calianotus, but more must be learned about the California polydesmids before the issue can be settled.

Retrorsia Shelley 2003 is represented by two quite small species (5-6 mm long) of 19-segmented millipeds found along the border between Oregon and Washington. Male sterna are unmodified, but the legaliers anterior to the gonopods are noticeably crassate. The relatively simple gonopods without a large endomerite recall those of *Pseudopolydesmus*.

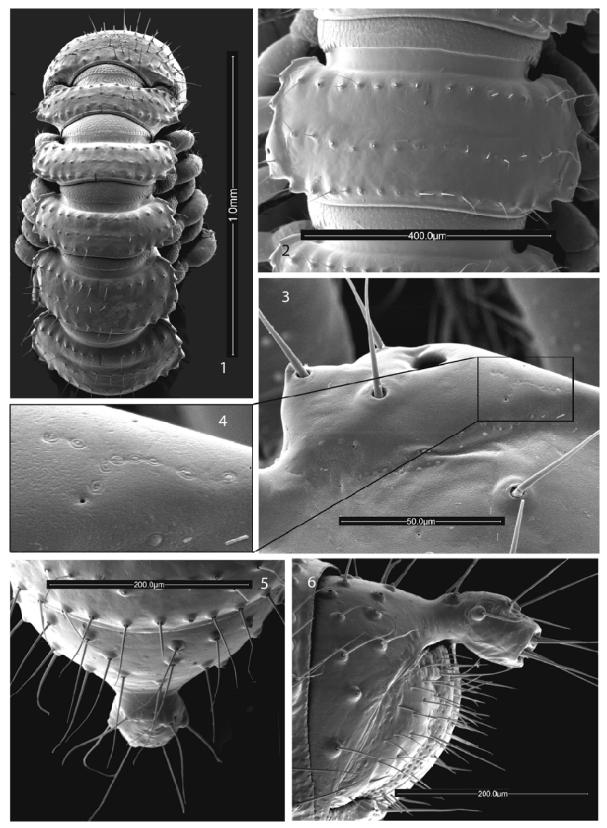
In 1974, I synonymized *Speorthus* Chamberlin 1952 with *Speodesmus* Loomis 1939, which I now see as a mistake, because the Texas species of *Speodesmus* appear to be macrosternodesmids, and *Speorthus tuganbius* Chamberlin 1952 is a polydesmid, with a distinct pulvillus. It is a 20-segmented species which is found in a number of caves in southeastern New Mexico (Shear 1972, Loomis 1960). Parenthetically, *Speodesmus* proper covers two distinct phylogentic lines of millipeds found in caves in Texas that deserve to be recognized at the generic level. The position of *Speodesmus aquiliensis* Shear 1984 and a few more unnamed species occurring in Colorado and Utah caves is currently under study, but they appear to be polydesmids related to *Speorthus*. These possible taxonomic changes need further study and will be the subject of a subsequent paper.

Two named species of *Bidentogon* Buckett and Gardner 1968 occur in coastal California (Shear 1972, Shelley 2003). Both are 19-segmented and about 10 mm in length. The gonopods, however, are atypical for polydesmids and have neither a reservoir or loop in the efferent duct, and appear to lack a pulvillus. There is no endomerite. *Bidentogon* species likewise do not appear to be macrosternodesmids, and after more careful study it may be that a new family will be required to accommodate them. For the time being, I consider them *incertae sedis*.

There seem to be two distinct kinds of gonopod design among indigenous North American polydesmids (this excludes the transplanted species of *Polydesmus*). In one group, a large and distinct endomerite is present. This group includes *Scytonotus*, *Calianotus*, and probably *Speorthus*. In the second group, the endomerite is absent, or possibly so completely fused with the acropodite that it cannot be regarded as a separate gonopod division. In this category fall *Pseudopolydesmus*, *Utadesmus*, *Retrorsia*, and *Snoqualmia*, n. gen.

Gonopods in polydesmidan millipeds range from simple, almost rod-like structures, to highly branched, complicated ones. *Snoqualmia idaho* n. sp., however, seems to reach an entirely new level of complexity in gonopod structure, so much so that establishing homologies with other polydesmid gonopods becomes quite difficult. The complexity extends from the macro- to the micro-level, as revealed by scanning electron micrographs. So far I have found similar micro-level complexity elsewhere only in the gonopods of caseyid and striariid chordeumatidans.

The significance of the tiny details that can be visualized by scanning electron microscopy in gonopods such as these is difficult to understand. Firstly, do these details have any meaning to females? Are they part of an elaborate lock-and-key mechanism to preserve the isolation of the species genome? Recent work (Wojcieszek and Simmons 2011) seems to suggest that for at least some millipeds, this is a viable



Figures 1-6. Snoqualmia snoqualmie, n. sp. 1) Anterior end of male, dorsal view. 2) Poriferous midbody segment, dorsal view. 3) Ozopore, dorsal view. 4) Micropore and possible proprioceptors near ozopore, magnified from Fig. 3. 5) Pygidium, dorsal view. 6) Pygidium, lateral view.



Figures 7-8. Snoqualmia snoqualmie, n. sp., gonopods. 7) Oblique lateral view from right side. 8) Lateral view from left side.

hypothesis. Previous doubts were based on the apparent simplicity of the female genitalia, which did not match the complexity of the male gonopods, but careful analysis using μ CT scanning showed that in fact such complexities exist and that they match those of the gonopods (Wojcieszek et al. 2012). In a widespread analysis of complex male genitalia in animals, Eberhard (1996) hypothesized that such appendages as the gonopods of millipeds represent a kind of internal courtship that allows females to assess not only species identity, but relative fitness of males. Tadler (1996) delimited the functional anatomy of four species of julidan millipeds and arrived at similar conclusions. While there are few detailed observations on milliped courtship and copulation, and none at all on Snoqualmia mating, the fact that in some millipeds the males make many preliminary insertions of the gonopods at least allows for the possibility of female choice by internal courtship. Secondly, these details (in the chordeumatidan species; sample size is too small to be sure in *Snoqualmia*) are repeatable from individual to individual with quite high fidelity, suggesting strong genetic control of their development. How would this work? If there were separate genes for each of the details, it would seem that a substantial part of the animals genome would be coding for the gonopods! How does gonopod development correlate with the genes controlling major factors of body form (homeobox genes)? The fact that even the most complicated gonopods appear only at the last instar makes this final molt in polydesmidans and chordeumatidans nearly the equivalent of insect metamorphosis (Drago et al. 2011); the differences between gonopods and walking legs are so extreme in these two orders (and others) that were it not for their position and that they obviously replace one or two pairs of legs, it would be hard to credit the status of gonopods as modified legs. Clearly this is an area in which very fruitful and illuminating research could be carried out.

Shelley (2003) made reference to a fauna of very small polydesmids (4-7 mm long) living in deep coniferous and deciduous leaf litter in Oregon, Idaho and Washington, two species of which he described in *Retrorsia*. I have been examining these creatures in detail and there seem to be about 20 species that can be ranged in as many as four genera. One of these genera is described below as *Snoqualmia*, new genus.

Taxonomy

Order Polydesmida Leach, 1815

Superfamily Polydesmoidea Leach, 1815

Family Polydesmidae Leach, 1815

Key to genera of indigenous Polydesmidae of North America

1.	Adults with 20 segments
-	Adults with 19 segments
2(1).	Depigmented, less than 10 mm long
3(1).	Length 4 to 7 mm; gonopods lacking endomerite 4 Length more than 7 mm; gonopods with endomerite 5
4(3).	Gonopods relatively simple, distal zone not serrate nor with many acute projections
5(3). -	Metazonites with 3 rows of setae; adults 9 or 10 mm long 6 Metazonites densely set with setae; adults more than 10 mm long Scytonotus C. L. Koch
6(5). -	Ninth and tenth sternites of males with lobes
	Craconta Chamber in and Horman

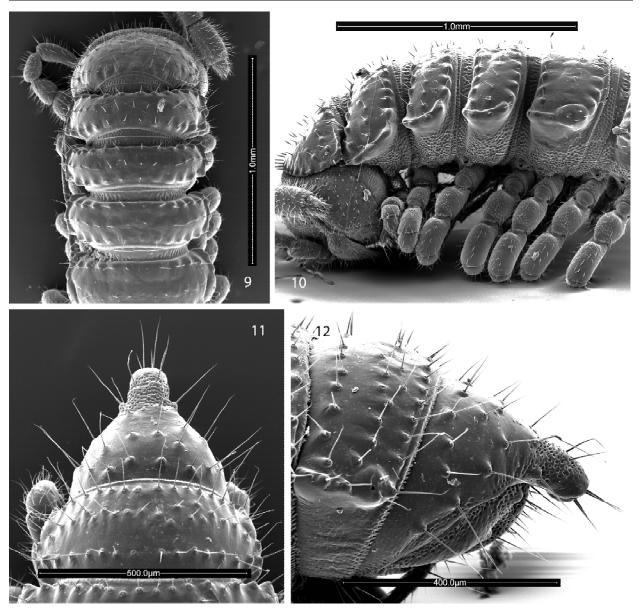
Snoqualmia Shear, new genus

Type species: Snoqualmia snoqualmie Shear, new species.

Etymology. Named for the region of the type locality of the type species, the valley of the Snoqualmie River, Washington, USA. As for the river, Snoqualmie Pass, which carries the major highway I-90 through the Cascade Range at an elevation of 921 m (3,022 ft), is named for the Snoqualmie people, who occupied the valley to the west and used the pass.

Diagnosis. Distinct from any other polydesmid genus due to the complex gonopods with many acute processes, and in the distally swollen, slightly decurved pygidial process.

Description. Small (<7 mm length) polydesmidan millipeds with 19 postcephalic segments (collum + 17 trunk segments + telson), lightly pigmented; metatergites with reduced, toothed paranota, three rows of short, acute setae arising from small pustules, 14-17 in each row. Pygidium (epiproct) short, pygidial process relatively long, decurved, distally swollen, with usual 4 spinnerets, each set in a distinct depression. Males with crassate pregonopodal and postgonopodal legs, lacking modifications of anterior sternites. Gonostome oval, as wide as seventh segment prozonite. Gonopods with large, globular coxae, apparently immovable, filling entire gonostome and sometimes projecting from it, tightly appressed in midline, prefemora sparsely setose, basally transverse, then parallel. Endomerite absent. Gonopod distal zone strongly toothed, serrate, or with many thin, acute branches. Basal part of distal zone with lateral alate process coarsely toothed. Pulvillus sessile (S. snoqualmie) or at tip of long process (S. idaho). Distal zone with acute terminal process.



Figures 9-12. Snoqualmia idaho, n. sp. 9) Anterior end of male, dorsal view. 10) Same, lateral view. 11) Pygidium, dorsal view. 12) Pygidium, lateral view.

Distribution. Northwestern Washington (S. snoqualmie) and central Idaho (S. idaho).

Notes. The unique, almost bizarre appearance of the complex gonopods makes it difficult to relate this genus to any of the other North American genera, and indeed, the gonopods of S. idaho are among the most complex to be found in the entire order Polydesmida. The gonopods of S. snoqualmie are somewhat similar to those of species of the European genus Serradium Verhoeff, 1941 (Enghoff et al. 1997), but even in this case the resemblance is limited to the toothy, sawlike appearance of the distal zone and is probably not indicative of a phylogenetic relationship. Certainly the general appearance of Serradium species, twice the size of Snoqualmia or larger, and with broad, thin paranota, does not suggest kinship. Serradium species are found in northern Italy, Herzegovina, Greece and Crete, and at least one species is a semiaquatic troglobiont (Enghoff et al. 1997). However, stripped of their complexities, Snoqualmia gonopods, lacking an endomerite and with processes on either side of the distal zone, follow the Pseudopolydesmus plan.

The two species of *Snoqualmia* may be separated by reference to the illustrations given herein.

Snoqualmia snoqualmie Shear, new species (Figures 1-8, 19, 20)

Types: Male holotype and male and female paratypes from Twin Falls/Iron Horse trailhead, highway I-90 at Snoqualmie River, 47°26.651 N, 121°57.217 W, King Co., Washington, collected 25 February 2004 by W. Leonard and C. Richart, deposited in Virginia Museum of Natural History.

Etymology. The species epithet is a noun in apposition, referring to the type locality in the Snoqualmie Valley.

Diagnosis. Individiuals of *Snoqualmia snoqualmie* are a little more than half as long as those of their only known congener, *S. idaho*, which also have far more complex gonopods.

Description. *Male*: Length, 4.0 mm, width 0.45 mm. Antennae short, clavate, sixth antennomere enlarged, with accessory sensory areas distal.

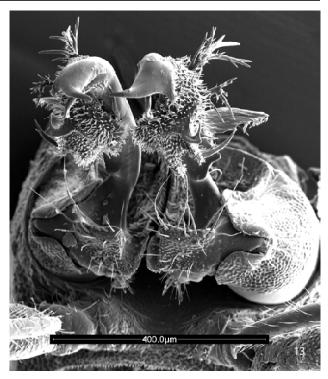


Figure 13. Snoqualmia idaho, n. sp., gonopods, posterioventral view.

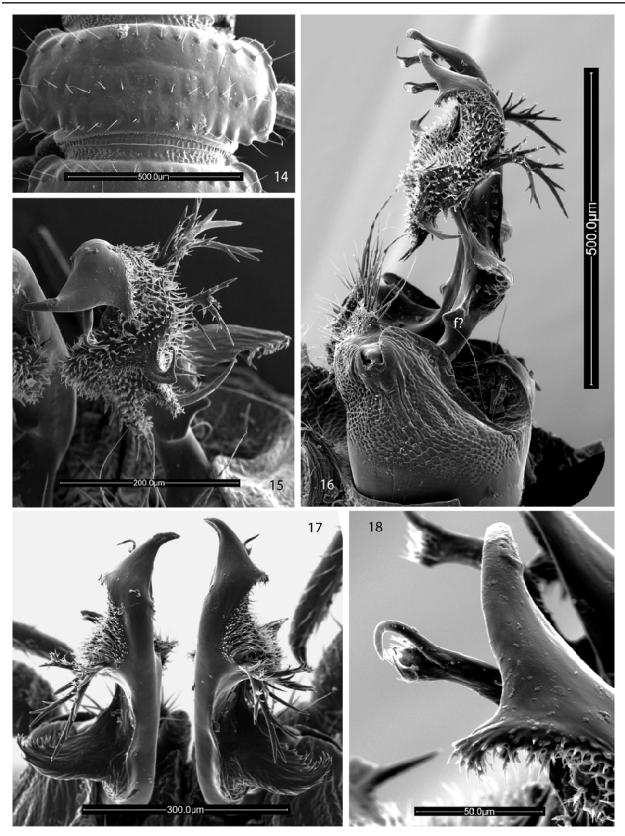
Head and collum subequal in width; collum transversely oval, with anterior marginal row of 18-20 acute setae, additional setae scattered (Fig. 1). Typical midbody segment (Fig. 2) with low, strongly toothed, horizontal paranota slightly extended anteriorly, with 3 rows of acute setae set on low swellings, anterior row with 14-16 setae, middle row with 16-18, posterior row with 14-16; ozopores simple, without rims, directed laterally on paranota (Fig. 3). Pygidium (Fig. 5, 6) rounded, with anterior row of 6 acute setae, 8-10 additional scattered setae; pygidial process prominent, lacking alveolate sculpture, proximally constricted, with 6 long, acute setae and 4 spinnerets, distinctly swollen distally, decurved in lateral view.

All legs markedly more crassate than those of female, femora swollen; pregonopodal legs more so than others (Fig. 1). Gonopods (Fig. 7, 8, 19, 20) with hemispherical coxae filling gonostome and tightly appressed in midline, distinct flaplike portion covers articulation of telopodite. Prefemur large, transversely articulated with coxa, then elongate parallel to body axis; posterior surfaces with many long setae and small cuticular teeth. Attachment of acropodite broad, acute lateral process near origin. Acropodite shaft with broad, curved, toothed lamella, distal zone elongate, with lateral rows of coarse teeth. Pulvillus prominent, sessile, subtended by one small and two large processes; posteriorly at base of distal zone is alate, coarsely toothed process extending anteriorly and laterally.

Female. Length, 4.2 mm, width 0.44 mm, nonsexual characters as in male, but more slender, legs not crassate. Third sternum unmodified.

Distribution. Washington: King Co.: 1.5 mi. N of Hobart, Issaquah Exit on Rt. 18, N47°27.135, W121°57.217, 25 February 2004, W. Leonard, C. Richart, female presumably this species; I-90 Exit #37, N47°26.613, W121°40.061, 1300 asl, 21 January 2005, W. Leonard, C. Richart, male; I-90 Exit #38, near Olallie State Park, N47°26.651, W121°40.081 25 February 2004, W. Leonard, C. Richart, male.

Notes. The known localities for this species are tightly clustered in the Snoqualmie Valley east of Seattle, as can be seen from the coordinates given.



Figures 14-18. Snoqualmia idaho, n. sp. **14**) Nonporiferous midbody segment, dorsal view. **15**) Gonopods, lateral view from left side. **16**) Left gonopod, posterioventral view. **17**) Gonopods, anterior view. **18**) Gonopod pulvillus, lateral view.

Near the ozopores are some minute cuticular structures that may be proprioceptors of some kind (Fig. 4). They closely resemble the objects called intercalary microscutes described by Akkari and Enghoff (2011) from several polydesmidan species.

Despite the much greater complexity of the gonopods of S. idaho, it is possible to suggest potential homologies in the processes of the gonopods of the two species (see Fig. 19-22 as labeled). The distal zone is indicated by \mathbf{b} , and is more strongly developed in S. snoqualmie, with rows of teeth. Process \mathbf{a} is the most likely candidate for homology, being similarly alate and toothed in both species, extending anteriorly and laterally. Process \mathbf{c} subtends the pulvillus (\mathbf{p}); something similar occurs in nearly all polydesmids. In S. snoqualmie, processes \mathbf{c} and \mathbf{f} appear not to have correspondants in S. idaho, but see (\mathbf{f} ?) as labeled on Figure 15. Process \mathbf{d} is at least positionally similar in the two species, but far larger in S. Idaho, and divided into two distinct parts ($\mathbf{d}\mathbf{1}$, $\mathbf{d}\mathbf{2}$).

While the habitat in which the specimens were collected is dominated by coniferous trees such as western hemlock and western redcedar, the material was all taken from deciduous leaf litter derived from red alder, poplar, and deer fern (W. Leonard and C. Richart, pers. comm.).

Snoqualmia idaho Shear, new species

(Figures 9-18, 21, 22)

Types: Male holotype and female paratype from OHara Bar Campground, Nez Perce National Forest, along Selway River Road, 7 mi SE of State Route 12, 7 mi S of Lowell, Idaho Co., Idaho, collected 16 April 2004 by W. Leonard, deposited in Virginia Museum of Natural History.

Diagnosis. Adults are about twice as long as those of *S. snoqualmie*, with far more complex gonopods.

Etymology. The species epithet is a noun in apposition, referring to the state of Idaho.

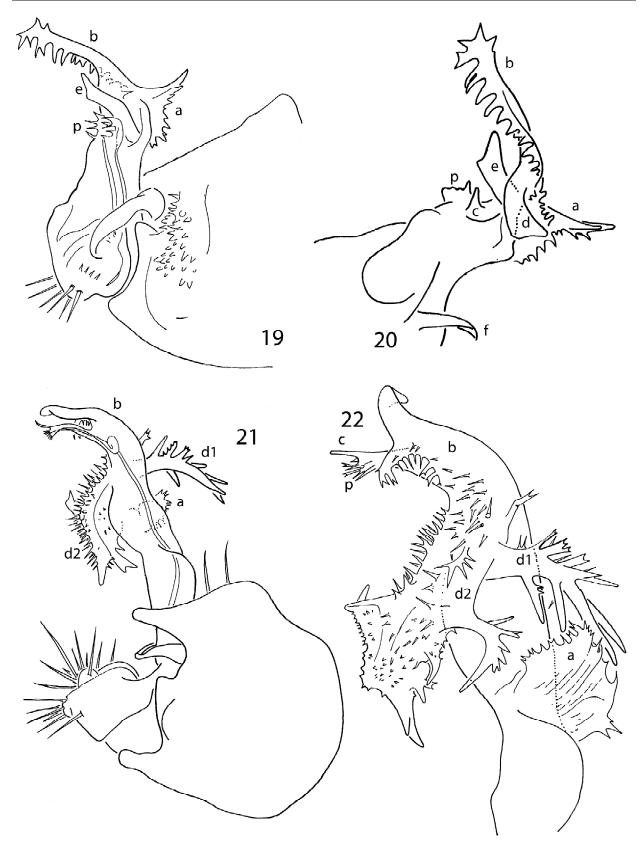
Description. *Male.* Length, 7.5 mm, width 0.78 mm. Antennae short, clavate, sixth segment enlarged, with accessory sensory areas distal. Head and collum (Fig. 9) subequal in width, proximal part of cranium with alveolate sculpture; collum transversely oval, with anterior marginal row of 18-20 acute setae, additional setae scattered. Typical midbody segment (Fig. 14) with low, toothed, horizontal paranota slightly extended anteriorly, with 3 rows of acute setae set on low swellings, anterior row with 14-16 setae, middle row with 16-18, posterior row with 14-16. Pygidium (Fig. 11, 12) rounded, with about 16 scattered acute setae, pygidial process prominent, with alveolate sculpture and four spinnerets, slightly swollen distally, somewhat decurved in lateral view.

All legs markedly more crassate than those of female, femora swollen; pregonopodal legs more so than others (Fig. 10). Gonopods (Fig. 13, 15-18, 21, 22) with hemispherical coxae filling gonostome and tightly appressed in midline, extending from gonostome. Prefemur relatively small, transversely articulated with coxa, then parallel to body axis. Attachment of acropodite narrowed, low triangular process near origin. Acropodite shaft with broad, curved, toothed lamella, distal to this, split into strongly decurved alate process and distal zone, alate process with both coarse and fine marginal teeth. Distal zone extremely complex with many acute processes and branched cuticular setulae. Pulvillus at end of elongate process, subtended at tip of process by long, curved spine, tip of distal zone acute, curved mesally.

Female. Length, 7.0 mm, width 0.72 mm, nonsexual characters as in male, but more slender, legs not crassate. Third sternum with bifurcate medial knob.

Distribution. Known definitively only from the type locality.

Notes. This species was first detected by Withrow and named in his unpublished 1988 thesis as Idahodesmus dentatus, the type locality of which was given as U. S. Forest Service Campground, 1.5 mi E of Harvard, Latah Co., Idaho. A holotype was supposedly deposited in the United States National Museum of Natural History (USNM), and two male paratypes in the North Carolina Museum of Natural History (NCSM). Neither museum ever received these specimens. Simonsen (1990) and Golovatch



Figures 19-22. Snoqualmia sp. gonopods. 19, 20) S. snoqualmie. 19) Mesal view. 20) Telopodite, lateral view. 21, 22) S. idaho. 21) Mesal view. 22) Telopodite, lateral view.

(1991) cited this taxon as if it had actually been published, but Shelley (1996b) pointed out that it clearly had not been. Later, Shelley (1997) attempted to solve a persistant polydesmid puzzle, the identity of Brachydesmus hastingsus (Chamberlin) 1941, an enigmatic species described from the Hastings Reservation in Monterey Co., California. The type vial (USNM) of B. hastingsus contained three males, whereas Chamberlin (1941) had clearly stated that the holotype male was the only specimen. Two of the males in the vial were specimens we now know are referable to Snoqualmia idaho, the other probably the actual holotype of B. hastingsus, but according to Shelley, bearing little or no resemblance to the gonopod drawing provided by Chamberlin (1941). Not knowing anything about the range of Idahodesmus dentatus or possible relatives, Shelley was reluctant to decide which if any specimen was actually B. hastingsus. He concluded that a previous worker carelessly mixed specimens and destroyed the integrity of the type sample and that it was now impossible to determine the identity of *B. hastingsus* from the holotype. It seems reasonable to conclude that the previous worker was Withrow, who in studying North American polydesmids would have borrowed the type material of B. hastingsus, though he does not refer to it in his thesis. I would speculate that the two males of S. idaho that are now in the type vial of B. hastingsus were those destined for the North Carolina Museum of Natural History as paratypes of Idahodesmus dentatus, and that they were placed in the wrong vial. In any case, the record cited in the thesis provides a second locality for the species.

As with *S. snoqualmie*, the specimens were collected from deciduous leaf litter (red alder, bigleaf maple, deer fern) in a forest dominated by western redcedar and Douglas fir.

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Literature cited

- **Abrous-Kherbouche, O., and J.-P. Mauriès. 1996.** Découverte du genre *Archipolydesmus* en Algérie: description de trois espèces nouvelles (Diplopoda, Polydesmida, Polydesmidae). Bulletin du Muséum national d'Histoire naturelle, 4° série 18: 571-587.
- **Akkari, N., and H. Enghoff. 2011.** On some surface structures of potential taxonomic importance in families of the suborders Polydesmidea and Dalodesmidea (Polydesmida, Diplopoda). ZooKeys 156: 1-24.
- **Chamberlin, R. V. 1941.** New western millipedes. Bulletin of the University of Utah, Biological Series 31·1-23
- **Drago, L., F. Fusco, E. Garollo, and A. Minelli. 2011.** Structural aspects of leg-to-gonopod metamorphosis in male helminthomorph millipedes (Diplopoda). Frontiers in Zoology 8: 19-26.
- **Eberhard, W. G. 1996.** Female Control: sexual selection by cryptic female choice. Monographs in Behavior and Ecology, Princeton University Press; Princeton, NJ. 472 p.
- Enghoff, H., G. Caoduro, J. Adis, and B. Messner. 1997. A new cavernicolous, semiaquatic species of *Serradium* (Diplopoda, Polydesmida) and its terrestrial, sympatric congener, with notes on the genus *Serradium*. Zoologica Scripta 3: 279-290.
- **Golovatch, S. I. 1991.** The millipede family Polydesmidae in Southeast Asia, with notes on phylogeny (Diplopoda: Polydesmida). Steenstrupia 17:141-159.
- **Hoffman, R. L.** 1999. Checklist of the millipeds of North and Middle America. Virginia Museum of Natural History Special Publication 8: 1-584.
- **Lewis, J. J. 2002.** Chaetaspis aleyorum, a new species of milliped from Tumbling Creek Cave, Missouri, with a synopsis of the cavernicolous species of *Chaetaspis* (Diplopoda, Polydesmida). Myriapodologica 7: 101-111.

- **Loomis, H. F. 1934.** Millipedes of the West Indies and Guyana collected by the Allison V. Armour Expedition in 1932. Smithsonian Miscellaneous Collections 89: 1-69.
- **Loomis, H. F. 1960.** Millipedes of the order Polydesmida from the western states and Baja California. Journal of the Kansas Entomological Society 33: 57-68.
- **Petit, G. 1976.** Développements comparés des appendices copulateurs (gonopodes) chez *Polydesmus angustus* Latzel et *Brachydesmus superus* Latzel (Diplopodes: Polydesmidae). International Journal of Insect Morphology & Embryology 5: 261-272.
- **Shear, W. A.** 1972. The milliped genus *Bidentogon* (Diplopoda, Polydesmida, Trichopolydesmidae). Proceedings of the Biological Society of Washington 42: 489-492.
- **Shear, W. A. 1974.** North American cave millipeds. II. An unusual new species from California (Dorypetalidae), and new records of *Speodesmus tuganbius* (Trichopolydesmidae) from New Mexico. Occasional Papers of the California Academy of Sciences 112: 1-9.
- **Shear, W. A., and R. M. Shelley. 2007.** The milliped genus *Tidesmus* Chamberlin, 1943 (Polydesmida, Macrosternodesmidae). Zootaxa 1656: 51-68.
- **Shear, W. A., and R. M. Shelley. 2008.** Cave millipeds of the United States . VI. *Sequoiadesmus krejcae*, n. gen., n. sp., from Sequoia and Kings Canyon National Parks, California, USA (Diplopoda, Polydesmida, Polydesmidea, Macrosternodesmidae). Zootaxa 1693: 41-48.
- **Shear, W. A., S. J. Taylor, J. J. Wynne, and J. K. Krejca. 2009.** Cave millipeds of the United States. VIII. New genera and species of polydesmidan millipeds from caves in the southwestern United States (Diplopoda, Polydesmida, Macrosternodesmidae). Zootaxa 2151: 47-65.
- **Shelley, R. M. 1994 (1993).** Revision of the milliped genus *Scytonotus* Koch (Polydesmida: Polydesmidae). Brimleyana 19: 1-60.
- **Shelley, R. M. 1996a.** The milliped genus *Utadesmus* Chamberlin & Hoffman (Polydesmida: Polydesmidae). Myriapodologica 4: 9-16.
- **Shelley, R. M. 1996b.** The identity of *Alpertia lunatifrons* Loomis, with records of introduced polydesmids from northwestern North America, deletion of *Polydesmus racovitzai* Brolemann, and identification of invalid taxa (Polydesmida: Polydesmidae). Myriapodologica 4: 17-20.
- **Shelley, R. M. 1997.** The identity of *Polydesmus sastianus* Chamberlin, proposal of a new milliped genus, and remarks on the identity of *Phreatodesmus hastingsus* (Chamberlin) (Polydesmida: Polydesmidae). Myriapodologica 4: 59-67.
- **Shelley, R. M. 2003.** A new polydesmid milliped genus and two new species from Oregon and Washington, U. S. A., with a review of *Bidentogon* Buckett & Gardner, 1968, and a summary of the family in western North America (Polydesmida: Polydesmidae). Zootaxa 296: 1-12.
- **Shelley, R. M. 2007.** Occurrence of the milliped genus *Scytonotus* C. L. Koch (1847) (Polydesmida: Polydesmidae) in Alberta, Canada. Entomological News 118: 319-320.
- **Simonsen, A. 1990.** Phylogeny and biogeography of the millipede order Polydesmida, with special emphasis on the suborder Polydesmidea. Zoological Museum of the University of Bergen; Bergen. 114 p.
- **Tadler, A. 1996.** Functional morphology of genitalia of four species of julidan millipedes (Diplopoda: Nemasomatidae; Julidae). Zoological Journal of the Linnean Society 118: 83-97.
- **Withrow, C. 1988.** Revision of the genus *Pseudopolydesmus* Attems 1898 and its relationships to the North American genera of the family Polydesmidae Leach 1915. Unpublished PhD. Thesis, Ohio State University; Columbus, OH. 298 p.
- **Wojcieszek, J. M., and L. W. Simmons. 2011**. Male genital morphology influences paternity success in the millipede *Antichiropus variabilis*. Behavioral Ecology and Sociobiology 65: 1843-1856.
- Wojcieszek, J. M., Austin, P., Harvey, M. S., and L. W. Simmons. 2012. Micro-CT scanning provides insight into the functional morphology of millipede genitalia. Journal of Zoology 2012: 1-5.

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