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Three new genera and eighteen new species of miniature polydesmid millipedes from the northwestern United States (Diplopoda, Polydesmida, Polydesmidae)

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Abstract

Three new genera, ***Retrorsioides***, ***Rowlandesmus*** and ***Benedictesmus***, are described and the polydesmid millipede fauna of North America is briefly reviewed with an emphasis on the genera *Bidentogon* Buckett & Gardner, 1968 and *Retrorsia* Shelley, 2003. Eighteen new species are described: ***Bidentogon buttensis***, ***Bidentogon norcal***, ***Retrorsia leonardi***, ***Retrorsia benedictae***, ***Retrorsia richarti***, ***Retrorsia gracilis***, ***Retrorsia simplicissima***, ***Retrorsioides castellum***, ***Retrorsioides linnensis***, ***Retrorsioides kittitas***, ***Retrorsioides bammerti***, ***Retrorsioides arboramagna***, ***Rowlandesmus millicoma***, ***Rowlandesmus dentogonopus***, ***Benedictesmus aureua***, ***Benedictesmus ellenae***, ***Benedictesmus yaquina*** and ***Benedictesmus timber***. Natural history notes and illustrations are provided of putative commensal fungi, nematodes and a mite found on the millipede specimens.

Key words: New genera, new species, gonopod terminology, commensals, Oregon, Washington, California

Introduction

Polydesmid millipedes in the United States and Canada

The millipede family Polydesmidae Leach, 1815 occurs widely in North America, but is particularly diverse in temperate forest habitats. In the broadleaf forests of the eastern part of the continent, two genera dominate the polydesmid fauna: *Pseudopolydesmus* Attems, 1889 (Sierwald *et al.* 2019) and *Scytonotus* Koch, 1847 (Hoffman 1962, Shelley 1993). Species of *Pseudopolydesmus* are generally common in suitable habitats ranging from Québec to eastern Texas and south and east to the Atlantic Coastal Plain, but are absent from peninsular Florida. They range in size from 7 to 32 mm in length, but most are more than 20 mm long as adults (Sierwald *et al.* 2019). *Scytonotus* species, on the other hand, while occupying about the same range in the east as *Pseudopolydesmus,* are also found in the west, distributed along the Pacific coast from the San Francisco Bay region of California to the Alaska panhandle, and in a separate inland range encompassing parts of the Canadian provinces of British Columbia and Alberta and the U.S. states of Idaho, Montana, Utah and Wyoming (see maps in Shelley 1993). Curiously, neither Hoffman (1962) nor Shelley (1993) provided any specific measurements of length for any of the *Scytonotus* species they discuss, but our own observations are that they are usually smaller than *Pseudopolydesmus* and from 15–22 mm long. Four species of *Polydesmus* Latreille, 1802, and one species of *Brachydesmus* Latzel, 1884, have been introduced to North America from Europe and may be found in disturbed or urban habitats across the continent (Shelley 1996b, Hoffman 1999). All of these introduced species show a range of sizes, from less than 10 mm to as much as 30 mm. Five other native genera (*Bidentogon* Buckett & Gardner, 1968; *Calianotus* Shelley, 1997; *Retrorsia* Shelley, 2003; *Snoqualmia* Shear, 2012; and *Utadesmus* Chamberlin & Hoffman, 1950) have been recorded from coastal and northern California (*Bidentogon* and *Calianotus*), the Cascade Ranges of Oregon and Washington (*Retrorsia* and *Snoqualmia*), and from Utah and New Mexico (*Utadesmus*). These species are also small; most are less than 8 mm long.

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Other polydesmoid genera listed in Hoffman's 1999 *Checklist of the Millipeds of North and Middle America* have either been moved to other families (primarily Macrosternodesmidae; see Shear 2012, Shear & Shelley 2019, and Shear & Reddell 2019 for an extended discussion) or are probably not polydesmids. In addition, numerous genera from the New World tropics, particularly the West Indies, placed in Polydesmidae, ostensibly do not belong to the family but remain unstudied and cannot at this time be assigned to a family. The family Polydesmidae *sensu strictu* seems to be limited to the Northern Hemisphere, including the Oriental Region, despite some introductions of European *Polydesmus* species to temperate regions of the Southern Hemisphere (Sierwald *et al.* 2019).

The families Polydesmidae and Macrosternodesmidae (including Nearctodesminae as a subfamily of the latter) are the only indigenous families of the superfamily Polydesmoidea Pocock, 1887 occurring in North America north of Mexico. A pantropical species of Haplodesmidae, also a polydesmoidean, *Prosopodesmus jacobsoni* Silvestri, 1910 has become established in southern Florida, Louisiana, and Hawaii (Shelley and Golovatch 2000, Mesibov 2012).

Golovatch (2013) placed Macrosternodesmidae in the synonymy of Trichopolydesmidae in the superfamily Trichopolydesmoidea. Shear and Reddell (2017) rejected this synonymy and further asserted that the superfamilies Polydesmoidea and Trichopolydesmoidea could not be distinguished on the basis of Golovatch's diagnoses. Thus, they dispensed with Trichopolydesmoidea as a synonym of Polydesmoidea. The family classification of the suborder Polydesmidea is one of the most fraught and contentious subjects in millipede taxonomy, with an extraordinarily complicated history as the concepts of individual taxonomists evolved and changed. The phylogenomic analysis of Rodriguez *et al*. (2018), showed a ca. 200 mya split between the small-bodied Polydesmidea Pocock, 1887 and the large-bodied Leptodesmidea Brölemann (such as the Xystodesmidae and Platyrhacidae); however, taxon sampling was only limited to about two representatives of each suborder, thereby potentially limiting the scope of inference. At least for North America north of Mexico, we think we have achieved a relatively stable classificatory structure, which will likely be subject to revision as new taxa, primarily from the western half of the continent, are discovered, and more comprehensive phylogenomic analyses of the order are created.

Though the gonopods of some of the new taxa described below resemble the gonopods of previously described *Polydesmus* species, particularly from Europe, the entire group of Pacific Northwest polydesmids is distinguished by an extremely small body size of its members. While species of *Polydesmus* and other established genera of the family are rarely smaller than 8–10 mm in length, some of the new species described below hardly reach 3 mm, and none are longer than 5 mm. Additionally, all have 19 rings in females and the males of some of them only possess 18 rings. The challenges of working with specimens this small are often considerable, since dissections must be carried out with extreme care, and details of both somatic and gonopod characters often simply cannot be seen using even the highest magnifications available on traditional dissecting microscopes (due in large part to the very shallow depth of field at those magnifications). Mounting gonopods temporarily on microscope slides for examination under a compound Nomarski microscope at magnifications of 200 to 400X may result in distortion from the pressure of the cover glass, optical aberration, and the difficulty of getting exactly the same position or view from preparation to preparation. Scanning electron microscopy seems to be an optimal solution, but not one which is practical for everyday identification. In any case, both SEM pictures and drawings (through a compound Nomarski microscope) are presented here in the hope that using the two kinds of presentation in tandem will facilitate the recognition of the taxa.

Genesis of this study

The millipede fauna of the northwestern United States, especially the states of Oregon, Washington and Idaho, has been little explored relative to the region east of the Mississippi River. Collections do exist in many western institutions such as the California Academy of Sciences and the Burke Museum of the University of Washington, but for the most part they remained unstudied; even though the late Rowland Shelley repeatedly visited many of them, partially sorted the collections, and used their material for a few family-level or genus-level revisions.

Beginning around 2003, mollusk researcher William Leonard, along with Casey Richart and other associates, began collecting millipedes—incidental to work on terrestrial mollusks—and sent specimens to Shelley and WAS. By 2015, these collections had become quite large and had revealed heretofore unrecognized diversity of millipedes at taxonomic levels from species to family in the Pacific Northwest. Since most of the material consisted of groups of interest to WAS, Shelley forwarded to him what he had received. WAS added this material to specimens sorted during the 1970s from Berlese samples taken in Oregon and Washington by the late Ellen Benedict, a pseudoscorpion specialist, as well as Berlese residues from the region deposited in the Field Museum of Natural History, Chicago. One striking result was the appearance of many species of tiny polydesmids, all less than 5 mm in length, and some as small or smaller than 3 mm. Shelley (2003) described two of these species, *Retrorsia benedictae* and *Retrorsia leonardi,* in honor of the two collectors, but the material we have accumulated since is much more diverse, and is described below.

Methods

As we and others have noted in previous studies, millipedes, and probably soil and litter fauna in general, are active, mature and seeking mates during the cool, wet winter months in the Pacific Northwest. It will be obvious from a quick scan of the "Records" sections for the species described below that nearly all collections were made in a time span from November of one year to March of the next. These collections contained mature males and females, and not infrequently, mated pairs. Collections made during the dry, warm summer months yielded few mature specimens and mostly juveniles. This collecting bias helps to explain why so little of the millipede fauna of the Pacific Northwest has been described—most collecting prior to the efforts of Benedict, Leonard and Richart took place at a time of the year when most of these millipedes would probably be lurking deep in the soil.

Specimens were field-preserved in 70–85% ethanol. Morphological studies were accomplished using an Olympus SZH stereomicroscope and an Olympus BX-50 compound microscope equipped with Nomarski optics. Gonopods were temporarily mounted on microscope slides in glycerine for detailed study up to 400X magnification. Drawings were made at 400X from the temporary slide mounts using an Olympus U-DA drawing tube fitted to the BX-50. These preparations were crucial in that they allowed for the tracing of the course of the seminal canal. Specimens used in scanning electron microscopy (SEM) were first cleaned in a Branson 200 ultrasonic cleaner to remove debris (some older, long preserved specimens were too delicate for this treatment or had coatings from the preservative that could not be removed). Specimens were mounted on 12.7 mm diameter aluminum SEM stubs affixed with double-sided carbon conductive tape and air-dried. These were sputter coated with a 40 nm thick layer of platinum and palladium metals using a Leica EM ACE600 high vacuum sputter coater. Scanning electron micrographs were taken with a FEI Quanta 600 FEG environmental SEM. Photographs and drawings were edited and refined using GIMP and plates were composed in Inkscape. Scales on scanning electron micrographs were relied on for measurements of width and length of selected specimens.

Geographical coordinate data, expressed in degrees, minutes and seconds, were converted to decimal degrees using an online converter at https://www.latlong.net/degrees-minutes-seconds-to-decimal-degrees. Original locality descriptions without coordinate data were georeferenced using GoogleEarthPro. Converted geographical coordinate values were rounded to four significant figures, which is approximately 10 meters of horizontal distance. Maps were created in Simplemappr. In locality descriptions, **SR** means State Route, **FR** means Forest Service Road, **US** means United States Federal Highway, **Co.** means county, and **I** means Interstate. Standard abbreviations for compass directions and states of the United States apply.

Unless stated otherwise, all type specimens and others are deposited in the California Academy of Sciences (**CAS**), San Francisco, California, USA. Other repositories are Florida State Collection of Arthropods (**FSCA**), Gainesville, Florida, USA, and Field Museum of Natural History (**FMNH**), Chicago, Illinois, USA. In a few cases where only a single male specimen was available, the specimen was left mounted on the SEM stub; the dried specimens are virtually impossible to remove from the stubs without their crumbling into many bits. These stubs and other material were deposited in the designated collections.

Gonopod terminology

Somatic characters differentiating species and even genera can be difficult to find in the Diplopoda. Generations of millipede taxonomists have therefore relied heavily on secondary sexual characters of the males, especially the gonopods, modified legs on the seventh ring which are used to transfer seminal fluid or spermatophores to the females. We encourage researchers publishing on polydesmidan millipedes to include explicit accounts of their terminology, as, for example done by Sierwald *et al*. (2019) for *Pseudopolydesmus* and by Olsen *et al*. (2020) for Gomphodesmidae.

Without delving too deeply into the tortuous history of terms applied to the gonopods of members of Polydesmidae, it is worth observing that this terminology seems to be becoming more uniform; although different authors still use dissimilar terminologies or apply the same term to radically different structures. While the earliest terminology applied to polydesmid gonopods (Attems 1894, 1940) assumed that the gonopod, a modified leg, was divisible into discrete units each homologous to a podomere of an unmodified walking leg, the developmental studies of Petit (1976) challenged that view, showing that the telopodite of the gonopod (gonopod distal to the coxa) was entirely derived from the prefemur—thus such terms as "femorite" and "tibiotarsus" were quite inaccurate in their implications. Simonsen (1990) summarized these findings, and his remarks were accepted and amplified by Shear & Shelley (2007) in a study of the closely related family Macrosternodesmidae. More recently, Sierwald *et al.* (2019) presented a discussion specifically addressing gonopod terminology in the North American genus *Pseudopolydesmus,* which also contained many useful observations applicable to the family as a whole. While we can now dispense, at least in Polydesmidae, with most of the inaccurate homology-based terms of the past, it is not possible to replace them with terms that might reflect their function, because little is known exactly how to homologize gonopod structures with those structures of the unmodified walking leg—at least in Polydesmidae (but see articles on functional morphology of the gonopod by Wojcieszek *et al*. [2012] in Paradoxosomatidae and of Tanabe & Sota [2008] on Xystodesmidae). In this paper, the following terms for parts of the polydesmid gonopod will be used, largely following Djursvoll (2019). We advise the reader to carefully examine the figures provided here that include various labelled parts.

The ***coxa*** is the most basal segment of the gonopod, a cylindrical, hemispherical or D-shaped podomere with a strong apodeme, to which are attached muscles originating from the pleurotergal and sternal regions of the seventh ring. The presence of this apodeme, derived from a tracheal trunk, suggests that the coxae might actually incorporate parts of the gonopod sternum, of which there is no other evidence in most polydesmids. The coxa is either asetose or sparsely setose in North American species, with 1–4 ventral macrosetae; some Asian polydesmids have densely setose coxae. In species of Polydesmidae (and other related families in the suborder), the coxae are tightly appressed to one another in the midline, attached to the posterior margin of the gonopod arperture, and apparently only slightly movable. However, the coxae are not fused, as Golovatch (*i.e.,* 2013, 2014) has asserted; they separate easily into complete podomeres during dissection. The anterior mesal surface of the coxa has a deep depression that receives the more distal parts of the gonopod at rest; this cavity has been referred to as a ***gonocoel***. The ***cannula*** is a movable process originating mesally on the coxa in a notch or socket; it is C-shaped or sigmoid and inserts in a fossa at the base of the gonopod telopodite. The ***telopodite*** is the distal division of the gonopod, movably articulating with the coxa and presumably (Petit 1976) homologous to the prefemur of a walking leg. The telopodite is hinged to the coxa in such a way that it can move only parallel to the body axis—perhaps by the knob-like lateral extension of the telopodite that articulates with the coxa and acts like a hinge joint (ginglymus). Movement is also limited in some species by a lateral apophysis from the coxa. The basal portion of the telopodite is usually densely setose and has been called the "prefemur" in the past, but the term ***prefemorite*** seems to us to be preferable, since the whole telopodite of the gonopod is of prefemoral origin. Further distal is a long, generally asetose and frequently complex extension called the ***acropodite***. In many polydesmids (*i.e.,* all *Scytonotus* and many *Polydesmus* species) a strong process that parallels the acropodite is developed from the distal or basal prefemorite. This is termed the ***exomere***. The exomere is very prominent in many polydesmid species and is found in all known macrosternodesmids; conversely it may be entirely absent, as is the case in about half of all *Polydesmus* species and all *Pseudopolydesmus* species. None of the species treated here have an exomere. The prefemorite has a deep depression or fossa on its median surface into which the cannula of the coxa inserts. From this fossa originates an internal channel which has been variously called a "prostatic groove" or a "seminal canal" among other terms. Calling this channel a groove is anatomically inaccurate because combining SEM images with observations through the light microscope reveal that rather than an open groove—as is the case in other Polydesmida—it is (at least in its distal part) a closed tube internal within the gonopod (Zahnle *et al.* 2020). Although some debate remains, it seems that seminal fluid is deposited from the openings (gonopores) in the coxae of the second legpair into the prefemoral pit where the groove originates, and the groove conducts this fluid and nonmotile sperm to the female seminal receptacles during copulation (Tanabe & Sota 2008, Wojcieszek *et al.* 2012, Wojcieszek & Simmons 2013). Here we will refer to it as the ***seminal canal*** pending studies which may show its true functional morphology. In Polydesmidae, the seminal canal originates in the fossa on the median side of the gonopod, but seems to proceed laterally, and in many species, especially those around *Polydesmus,* makes a distinct loop before enlarging to form a ***seminal vesicle***, which, however, may not be present in all members of the Polydesmidae. From the seminal vesicle, a short section of the canal leads to the posterior surface of the gonopod and opens in a ***seminal pore***. The seminal pore in Polydesmidae almost invariably opens on a process or small area which Simonsen (1990), following previous authors (*i.e.,* Attems 1940) called a *Haarpolster* but which more recently has been designated the ***pulvillus***. The pulvillus appears as a more or less prominent knob or shelf set with fine cuticular projections or fimbriae (not socketed true setae) in many genera of the Polydesmidae, but in a few others presently included in the family, the cuticular fimbriae are absent, or the pore may open at the end of an extended tube called the ***solenomere***. The solenomere of polydesmids is likely homologous to the pulvillus, since in some species, for example *Snoqualmia idaho* Shear, 2012, a long tube is present which has the typical pulvillar fimbriae surrounding the pore at its tip. In species of *Bidentogon* dicussed here, the solenomere is either poorly sclerotized or bears widely spaced fimbriae similar to those seen on the pulvillus of species in other genera. On some of the gonopods described here, masses of small, cylindrical objects of constant dimensions are seen on the pulvillus (Fig. 55) and these may be sperm cells, which in millipedes are not motile. Near the pulvillus a relatively small process occurs in almost all species of Polydesmidae, and a few recent authors have called this the "endomere," but this is not consistent with the previous use of the term. This process was designated *m1* in species of *Pseudopolydesmus* in the terminology of Sierwald *et al.* (2019) and Hoffman (1974), but for a more universal application here we call it the ***pulvillar process***. Distal to the pore, the gonopod acropodite is often extended into a more or less elaborate section which previous authors called the tibiotarsus. Rejecting the implied homology of that term, we follow Shelley (1994) who, in describing macrosternodesmid gonopods, designated this distalmost section of the gonopod the ***terminal zone***. The terminal zone may be short and simple or long and elaborate, as it is in species of *Pseudopolydesmus.* Hoffman (1974) devised alphanumerical designations for the various processes developed from this section of the gonopod of *Pseudopolydesmus* species, slightly revised and extended in Sierwald *et al.* (2019). It is not clear that this terminology for terminal zone processes could be used for other genera since to do so could give a false impression of homology. Therefore, we have assigned letters to features of the terminal zone and elaborations of the telopodite to be used in the figure captions and descriptions.

To summarize:

Gonopod = coxa + telopodite
Telopodite = prefemorite (+exomere, if present) + acropodite
Acropodite = pulvillar region (+pulvillar process, if present) + terminal zone

Other Characters

In addition to their small size, a few other characters seem to unite polydesmid millipedes in the United States and Canada (excluding *Bidentogon*, which has a different suite of nongonopodal characters). The alveolate, or dimpled, sculpture of the head, anterior part of the collum, the sides of the body rings and much of the telson or pygidium is found in nearly all species. The labrum, however, appears almost as a separate sclerite and does not have alveolate cuticle. In *Bidentogon,* alveolate cuticle is present over the dorsa of the metazonites, but that is not the case in other genera and species described here; at most, alveolate cuticle may appear at the anterior edge of the second ring. Likewise, all species bear rows of setae set on tubercles on the metazonites. The setae are often clavate and are arrayed in three, four or five rows of 10–16 or as many as 20 in each row. Setae which are acute on anterior rings may become clavate on posterior rings, and in some species the number of rows increases on posterior rings. On the collum, only anterior marginal and posterior marginal rows are present, the anterior row usually with 16 or more setae. Between these collum rows are numerous scattered setae. Generally the anterior rings (1–5) have three rows of setae, with interpolated setae appearing more posteriorly and eventually forming a fourth or even fifth row between the original second and third rows. The penultimate ring may revert to fewer rows or to an irregular distribution except for the anterior and posterior marginal rows. The metazonites are domed, bearing narrow paranota set low on the ring but not extending far laterally. The paranota have strong teeth that are aligned with the rows of seta-bearing tubercles on the dorsum of each metazonite, and each tooth bears a single seta. Pore formulae are 5, 7, 9, 10, 12, 13, 15–18 for the species with 19 rings; those in which the males have 18 rings have the pore series ending on ring 17. The ozopores open from prominent pore calluses. Limbi of the metazonites were not visible using light microscopy, but under SEM were seen to be microspiculate, the spicules usually simple (Fig. 33), but they are forked in *Snoqualmia* species. A few of the genera have distinctive, distally enlarged and/or downturned epiprocts (an elongation of the telson or pygidium). In all species, the epiproct carries four spinnerets arranged in a quadrangle and set in a common pit (see Shear 2008 for a review of spinnerets in Polydesmida).

As with many members of the family Polydesmidae, males have encrassate anterior legs with the prefemora and femora enlarged, and in most species treated here nearly all male legs are modified in this way, the more posterior ones less so. Additional leg modifications are not seen except in *Bidentogon* species, where the femora of the third legpair are swollen and notably larger than in the other pregonopodal legs. Sphaerotrichomes may or may not be present; in contrast to many other polydesmids, when they occur, they are found on the tarsi rather than on the more proximal podomeres, and are of a type that has not been observed before (Fig. 63).

For mostly technical reasons, we have not been able to explore the structure of the female genitalia as has been done recently by Zahnle *et al.* (2020). These authors found that the female genitalia exist in three states: withdrawn into a cavity on the third ring, or partially or wholly everted. Among our specimens we found only a few with everted genitalia, but for some there is evidence that there may be unusual features of the female genitalia present—e.g. paired, heavily sculptured knobs protruding from the female genital orifice (Fig. 24). Zahnle *et al.* (2020) focused on two species of *Pseudopolydesmus* but previous observations suggest that other polydesmid female genitalia may be quite different from the *Pseudopolydesmus* plan (*i.e.*, Shear *et al.* 2009, Fig. 19).

Taxonomy

Order Polydesmida Pocock, 1887

Suborder Polydesmidea Leach, 1815

Superfamily Polydesmoidea Leach, 1815

Family Polydesmidae Leach, 1815

Diagnosing the family Polydesmidae in a way that distinguishes its members from other, closely related and similar families is not easy. We contend that the superfamily Trichopolydesmoidea is superfluous and synonymous with Polydesmoidea, bringing Trichopolydesmidae, Macrosternodesmidae, Mastigonodesmidae, Opisotretidae and Fuhrmannodesmidae into consideration in delineating the family.

The most recent attempt to diagnosis Polydesmidae is that of Enghoff *et al*. (2015). Their account includes qualifying words “usually”, “occasionally” and “often”, and this is necessary because the family presently includes some discordant elements and as has been often stated, the taxa give the characters and not *vice versa.* Nevertheless, it is possible to list a few characters for Polydesmidae that may provide guidance: 1) presence on the gonopod of a fimbriate pad or projection (pulvillus) at the point where the seminal pore opens, 2) presence of a vesicle in the distal part of the seminal canal, 3) the seminal canal with a distinct arch or loop proximal to the vesicle. One or more of these characters may be absent in species presently considered polydesmids, including a few described here. Nonsexual characters that are helpful include a microspiculate limbus and the presence of sphaerotrichomes on at least some of the anterior legs of males. Species of Macrosternodesmidae, in our view the most closely related family and the only other polydesmoid family in North America, lack these gonopod characters, but many do have sphaerotrichomes; in addition, macrosternodesmids have the gonopod prefemorite transverse with respect to the gonocoxae such that the acropodite makes a right angle with it. In Polydesmidae, the acropodite continues the line of the prefemorite. Characteristically, the acropodites of macrosternodesmids are more complex, with at least three major branches, including an exomere.

In the genera and families described herein, even the characters just listed do not always occur together, possibly because of phenotypic simplification associated with a great reduction in size. However, the pulvillus is always present in the species discussed here, the vesicle in only a few, and the loop in the seminal canal in none of the species. *Bidentogon* species are the exception, retained for now in Polydesmidae, but lacking all three of these important characters, unless our hypothesis about the origin of the solenomere in *Bidentogon* species is supported.

Genus *Bidentogon* Buckett & Gardner, 1968

Bidentogon Buckett & Gardner 1968:198. Type species, *Bidentogon helferorum* Buckett & Gardner 1968.
Bidentogon, Shear, 1972:489; Shelley, 2003:9.

Species included: Bidentogon californicus Buckett & Gardner, 1968; *B. expansus* Shelley, 2003; ***B. norcal*** **n. sp**.; and ***B. buttensis*** **n. sp**.

Diagnosis. The simple gonopods of *Bidentogon* species distinguish them from any other small polydesmids; the gonopod acropodite consists of a long solenomere and a simple, unbranched terminal zone (Fig. 5). The gonopod prefemorite is reduced and strongly flattened. Males have the femur of the third leg enlarged (Fig. 11), a character not seen in other polydesmids. From the other genera discussed here, *Bidentogon* species can be diagnosed by the flattened seta-bearing tubercles of the metazonites that somewhat resemble what Sierwald *et al.* (2020) called "blisters" in *Pseudopolydesmus* and by the presence of alveolate cuticle on the metazonites between these tubercles (Figs 1, 2). In addition, *Bidentogon* species never have more than three rows of setae on the metazonites; the other small polydesmid genera described here may have three rows on the anteriormost rings but transition to four or five rows posteriorly.

Distribution. California, from San Mateo Co. and Sacramento north to Shasta Co. (see map in Shelley [2003] and new records below).

Notes. *Bidentogon* is a rather anomalous genus whose inclusion in Polydesmidae *sensu strictu* is questionable. The genus was at first placed in the family Vanhoeffeniidae (Buckett & Gardner 1968), then in Trichopolydesmidae due to the synonymy of Vanhoeffeniidae with that family (Shear 1972). Shelley (2003) included it in Polydesmidae, a better position for the present time. At the least, *Bidentogon* probably represents an undiagnosed tribe in the family, and at most a family of its own. The simple gonopods (Figs 5, 6, 10, 12, 15, 16, 18, 19), in which the acropodite consists of a solenomere (**s,** Fig 18) and an unmodified terminal zone (**tz,** Fig. 18), give few clues to the affinities of the genus. Further complicating things are the absence in the gonopods of its species of the three most reliable polydesmid synapomorphies: a pulvillus, vesicle, and loop in the seminal canal. The gonopod prefemorite is curiously reduced and flattened (**pf,** Fig. 10))

However, SEM examination reveals that the solenomere is weakly sclerotized, which has not been observed using the optical microscope. In fact, there appears to be a continuum from a very lightly sclerotic solenomere with projecting cuticular scales (in *Bidentogon norcal,* **n. sp.**; Figs 18–20) to a solenomere that is more sclerotized (*B. californicus*) but still with thinner, wrinkled cuticle near its base. We hypothesize that the solenomere may have developed from a typical pulvillus that became elongated and eventually more sclerotized. The cuticular scales in *B. norcal* would be homologous to the fimbriae surrounding the seminal pore on other species. A similar trend occurs in species of the genus *Calianotus; C. yosemitensis* (Causey) has a flat pulvillus, while that of *C. sastianus* (Chamberlin) is elongated into a tube and set with hair-like scales, and the solenomere of *C. bituberculatus* (Loomis) is a tube without scales (Shelley 1997). If supported, this hypothesis would argue for keeping *Bidentogon* in Polydesmidae.

Mikhaljova (2005) has speculated that the northeast Asian genus *Uniramidesmus* Golovatch & Mikhalova, 1979 may be related to *Bidentogon.* At least some species of the central Asian genus *Turanodesmus* Lohmander, 1932 strongly resemble *Bidentogon* in their metazonital ornament as well as gonopod anatomy (Spelda *et al.* 1998). Finally, there is a close resemblance of the gonopods of species of *Utadesmus* Chamberlin & Hoffman (Utah, New Mexico) to those of *Bidentogon* species, differing only in the presence of a pulvillar process and a flattened, shelf-like pulvillus; Shelley (1996) described the ornament of the metazonites as being much like that of *Bidentogon* species.

Nonetheless, the general appearance of *Bidentogon* species is polydesmid. An apparently unique character is the large, blunt tubercles that bear the setae of the metazonites—flattened and expanded to resemble the dorsal areas seen in *Polydesmus* and *Pseudopolydesmus*—but separated by alveolate cuticle; in the other genera discussed here, alveolate cuticle does not occur on the dorsa of the metazonites and the seta-bearing tubercles are not flattened. In addition, the third legpair of males is unusually modified in *Bidentogon* species, with a distinctly swollen, almost spherical femur. No sphaerotrichomes were observed on the legs of the males.

Bidentogon californicus **(Chamberlin,1918)**
Figs 1–6

Brachydesmus californicus Chamberlin 1918:9.
Bidentogon helferorum Buckett & Gardner 1968:198; Shear, 1972:490.
Bidentogon californicus, Shelley, 2003:10.

Diagnosis. The terminal zone of the gonopod (**tz**, Fig. 6) is acute, not expanded as it is in the other known species of the genus. The anterior marginal row of setae on the collum ranges in number from 14 to 16 (Fig. 1).

Notes. After some confusion, the name of this species was finally settled by Shelley (2003). Shear (1972) had discovered the supposed type material of Chamberlin's *Brachydesmus californicus* in the collections of the Museum of Comparative Zoology and redescribed that species while applying the genus name *Bidentogon* (at the time Chamberlin described the species, any polydesmid with 19 rings was placed in *Brachydesmus,* now understood as an exclusively European genus). However, Shelley (2003) was able to show that *B. helferorum* was actually a synonym of *B. californicus,* and provided the new name *B. expansus* Shelley, 2003, for Shear's concept of *B. californicus.*

Buckett & Gardner (1968) provided a good detailed description of this species (as *B. helferorum*), supplemented by Shear (1972) with additional illustrations. Shelley (2003) documented and mapped many new localities from Alameda, Marin, Mendocino, San Mateo, Santa Clara and Santa Cruz counties in California. Here we provide SEM illustrations for the first time (Figs 1–6). Using material temporarily mounted on microscope slides, it was possible to trace the seminal canal out to the tip of the shorter gonopod branch, which is therefore referred to as a solenomere. No vesicle could be seen and the course of the canal is more or less direct, though it does sharply change direction laterad near the base of the solenomere. The simple, acute, terminal zone distinguishes this species from *B. expansus,* in which the terminal zone widens distally.

Distribution. San Francisco Bay region of California, and north to Mendocino County (Shelley, 2003)

New records. CALIFORNIA: *Marin Co.:* 1 mi. west of Bolinas (37.308°, -122.706°), 16 January 1960, C. Judson, m ff (FSCA); 3 mi northwest of Inverness (38.124°, -122.903°), 8 May 1976, A. Newton, M. Thayer, m, f (FMNH); 6 mi east of Point Reyes Station (38.094°, -122.735°), A. Grigarik *et al*., 1 March 1960 (FSCA). *San Mateo Co.:* 0.5 mi southeast of Half Moon Bay (37.462°, -121.530°), 18 May 1954, R. Schuster mm ff (FSCA).

Bidentogon expansus **Shelley, 2003**
Figs 7–12

Bidentogon californicus, Shear, 1972:490 (not of Chamberlin, 1918).
Bidentogon expansus Shelley 2003:11.

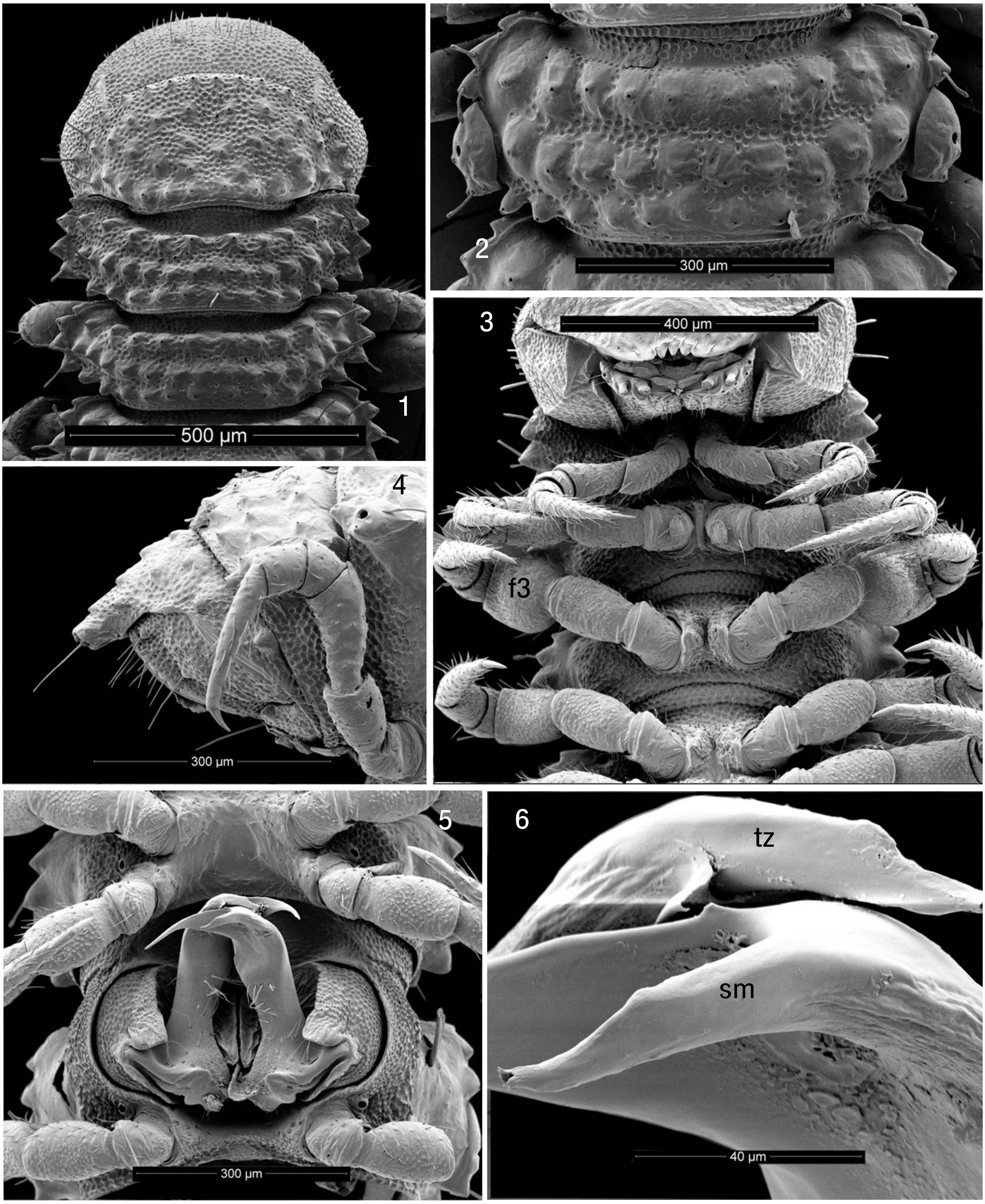
Diagnosis. The expanded tip of the gonopod is bluntly rounded and the solenomere is comparatively long (Figs 10, 12). There are 18 setae in the anterior marginal row on the collum (Fig. 7).

Shelley (2003) provided the new name *B. expansus* for Shear's concept of *B. californicus.* He argued that the types of *californicus* had been mislabelled, since "Chamberlin's clear intent, as evidenced by the published account, was to apply this name to the form at Stanford, the designated type locality (Shelley 2003, p. 10)." Thus, the specimens from Sacramento, on which Shear based his thinking, had probably been somehow mislabelled as the types of *californicus.* Further evidence that this was correct came from the many records of the real *californicus* from near the California coast, as opposed to the inland Central Valley around Sacramento.

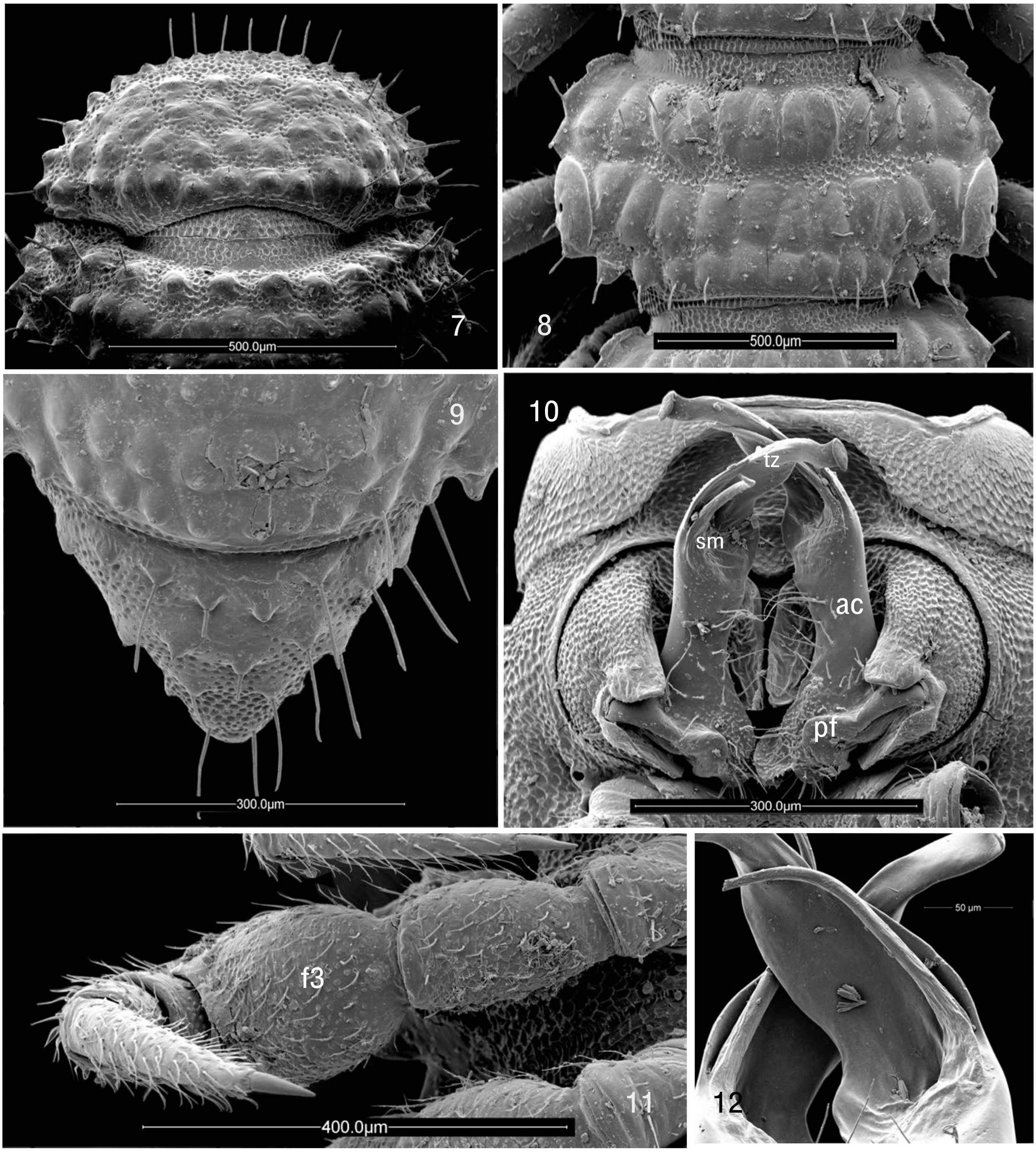
Here we supplement the original description and illustrations with new SEM pictures (Figs 7–12). The expanded tip of the terminal zone (**tz**, Fig. 10) differentiates this species from *B. californicus,* otherwise they are very similar.

Distribution. Western Central Valley of California (Shelley 2003).

New record: CALIFORNIA: *Yolo Co.:* West Sacramento, 11 April 1961, M. E. Irwin, mmff (CAS).



FIGURES 1–6. *Bidentogon californicus* Buckett & Gardner. **1**. Head and anterior rings, dorsal view. **2**. Midbody ring, dorsal view. **3**. Epiproct, lateral view. **4**. Anterior end of male, ventral view. **5**. Gonopods *in situ,* ventral view. **6**. Gonopod tips, ventral view. Abbreviations: **sm**, solenomere; **tz**, terminal zone. SEM stub WS33-8.



FIGURES 7–12. *Bidentogon expansus* Shelley **7**. Collum and first ring, dorsal view **8**. Midbody ring, dorsal view. **9**, Epiproct, dorsal view. **10**. Gonopods *in situ,* ventral view. **11.** Right leg 3, ventral view. **12.** Part of right gonopod, ventral view. Abbreviations: **ac**, acropodite; **f3**, femur of third leg; **pf**, prefemorite; **sm**, solenomere; **tz**, terminal zone. SEM stub WS33-7.

***Bidentogon buttensis* Shear & Marek*,* new species**
Figs 13–16

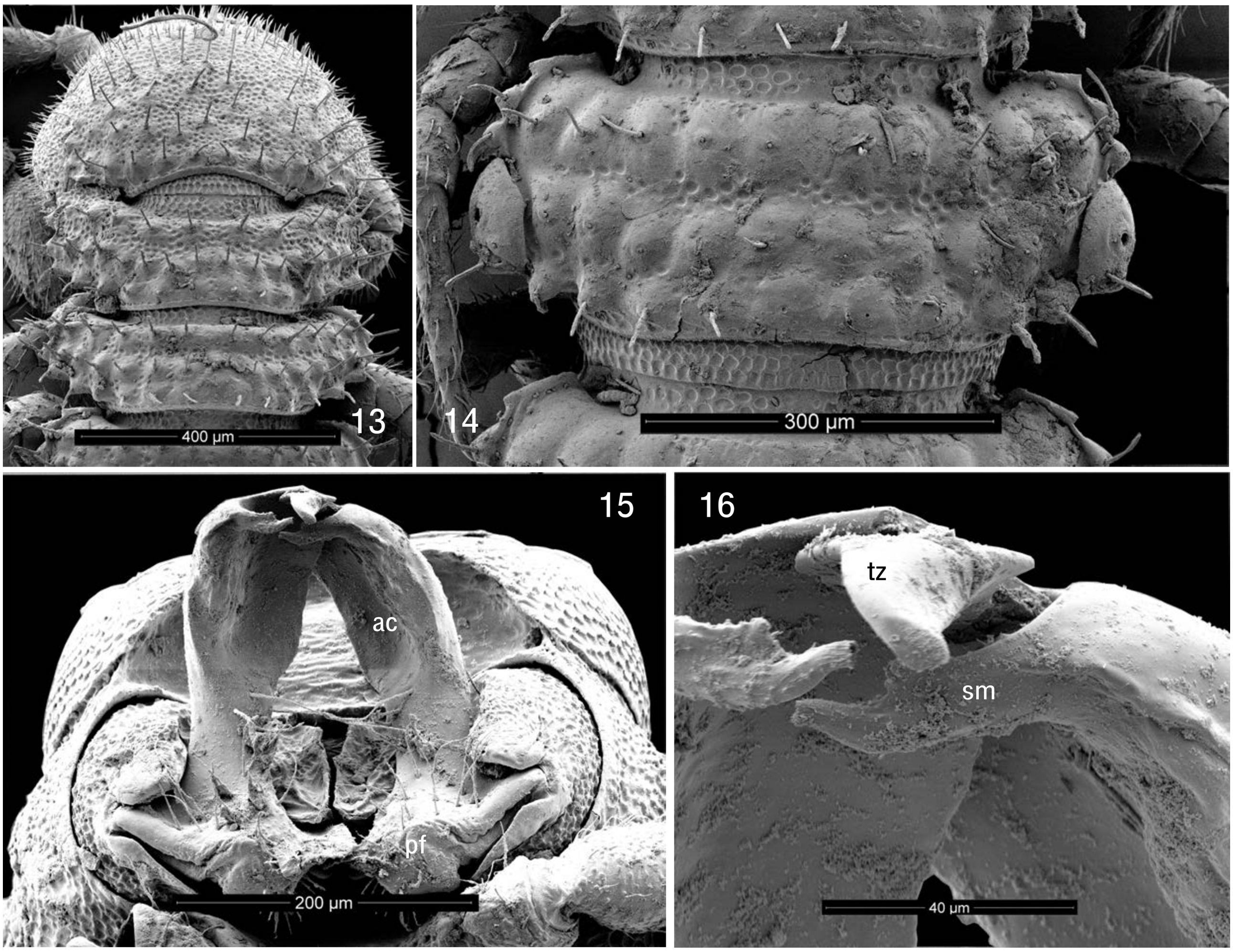
Type. Male holotype from near Stringtown Hill, NE of Oroville, Butte Co., California, collected 9 February 1956 by R. O. Schuster, deposited in the Florida State Collection of Arthropods, Gainesville, Florida. The dissected holotype is mounted on SEM stub WS33-9, deposited in CAS.

Diagnosis. The solenomere (**sm**, Fig. 16) is short and has a low tooth subdistally, nearly appearing bifid; the short terminal zone (**tz,** Fig. 16) is slightly expanded and also has a low subterminal tooth. There are 16 setae in the anterior marginal row of the collum (Fig. 13).

Etymology. The species name, an adjective, is from the type locality in Butte Co., California.

Description. Male holotype. Length about 5–6 mm, maximum width 0.7 mm. Nonsexual characters typical for the genus. Femora of third legpair expanded, nearly spherical. Gonopod prefemora typically flattened (**pf,** Fig. 15). Acropodite (**ac,** Fig. 15) short, distally broadened, solenomere curved, nearly as long as terminal zone. Terminal zone with very low subterminal tooth. Females unknown.

Distribution. Known only from the type locality.



FIGURES 13–16. ***Bidentogon buttensis,*** **n. sp. 13.** Head and anterior rings, dorsal view. **14.** Midbody ring, dorsal view. **15.** Gonopods *in situ,* ventral view. **16.** Gonopod tips, ventral view. Abbreviations: **ac**, acropodite; **pf**, prefemorite; **sm**, solenomere; **tz**, terminal zone. SEM stub WS33-9.

Bidentogon norcal **Shear & Marek*,* new species**
Figs 17–20

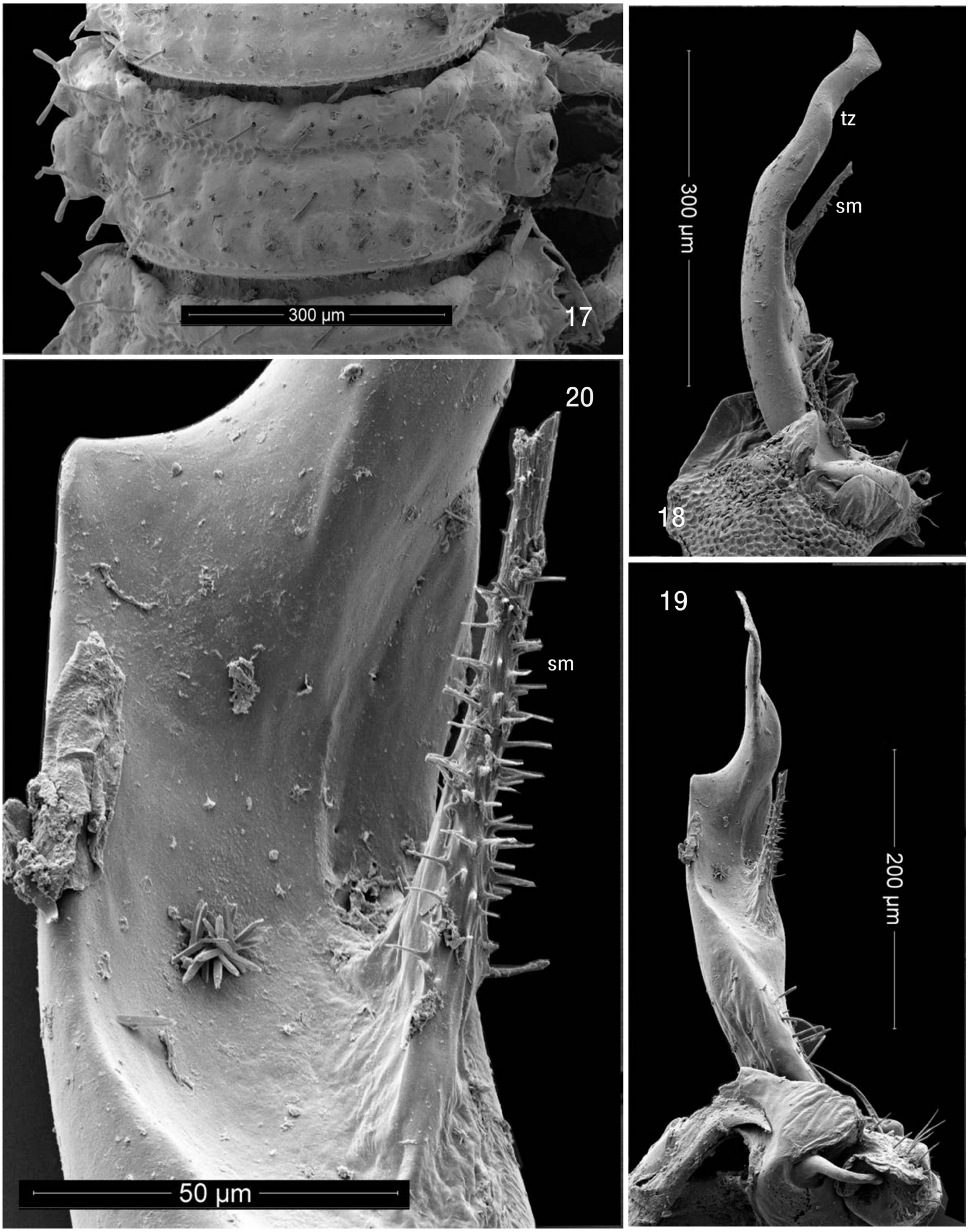
Types. Male holotype and male and female paratypes from Ingot, Shasta Co. California, collected 3 February 1959 by K. W. Gerhardt. The dissected holotype is mounted on SEM stub WS33-10, deposited in CAS.

Diagnosis. The short solenomere of the gonopod (**sm,** Figs 18, 19) is poorly sclerotized and ornamented with fine, hair-like scales; the terminal zone (**tz,** Fig. 18) is long with an expanded tip, but flattened, not blunt as in *B. expansus.* There are 18 setae in the anterior marginal row of the collum.

Etymology. The species name refers to *nor*thern *Cal*ifornia.

Description. Male holotype. Length 5.5 mm, maximum width 0.62 mm. Nonsexual characters typical for the genus. Femora of third legpair expanded. Gonopod prefemora typically flattened. Solenomere (**sm,** Figs 18, 20) narrow, weakly sclerotized, straight, parallel to long axis of acropodite, set with closely spaced fine, hair-like cuticular scales. Terminal zone with flattened, slightly expanded tip (**tz,** Fig. 18; Fig. 19). Females similar in nonsexual characters to males.

Distribution. Known only from the type locality.



FIGURES 17–20. ***Bidentogon norcal,* n. sp. 17**. Midbody ring, dorsal view. **18**. Rght gonopod, lateral view. **19**. Left gonopod, mesal view. **20**. Detail of left gonopod, mesal view. SEM stub WS33-10. Abbreviations: **sm**, solenomere; **tz**, terminal zone.

Genus *Snoqualmia* Shear, 2010

Snoqualmia Shear 2010:8. Type species, *Snoqualmia snoqualmia* Shear, 2010.

Snoqualmia idaho Shear, 2010

Snoqualmia idaho Shear 2010:10.

Species included: Snoqualmia snoqualmia Shear, 2010 and *Snoqualmia idaho* Shear, 2010

Notes. Working through the collections reported on in this study, we found two males and two females of *Snoqualmia idaho* Shear that were a part of the original collection at the type locality. These specimens are hereby designated as paratypes and will be deposited in the California Academy of Sciences. Despite their extraordinarily complex gonopods, species of *Snoqualmia* generally conform to the size and appearance of the other species treated here, except that the teeth of limbus bear one or two serrations (Shear 2010).

Genus *Retrorsia* Shelley, 2003

Retrorsia Shelley, 2003:3. Type species, *Retrorsia leonardi* Shelley, 2003.

Species included: Retrorsia leonardi Shelley, 2003; *Retrorsia benedictae* Shelley, 2003; ***Retrorsia richarti*, n. sp.; *Retrorsia simplicissima*, n. sp.** and ***Retrorsia gracilis*, n. sp**.

Diagnosis. The diagnosis provided by Shelley (2003) is actually a description and does not compare *Retrorsia* to other polydesmid genera. However, he implied that the retrorse branch of the terminal zone of the gonopod distinguished *Retrorsia* species from all others. This branch is very obvious in the two species he described, but less so in the three new species described below. Nevertheless it is present and serves as a diagnostic character.

Distribution. Northwestern Oregon and western Washington, in or west of the Cascade Ranges.

Notes. *Retrorsia* species made up the first component of the diverse minute polydesmid fauna of the Pacific Northwest to be recently described. The general appearance of the two previously described species is typical of the tiny polydesmids, with large, setose heads, relatively small collums with scattered setae, and metazonites with toothed margins and with rows of setae on prominent sockets. Alveolate cuticle is confined to the head, epiproct and sometimes the anterior margin of the collum. The epiproct is short and not swollen. The gonopods are somewhat variable from species to species; the two described by Shelley (2003), *R. leonardi* and *R. benedictae,* have a prominent subterminal branch in the terminal zone, the lateral one of which Shelley termed the endomerite and the mesal one the tibiotarsus. In the terminology used here, the gonopod consists of a simple acropodite (**ac,** Fig 27) bearing the pulvillus, and a terminal zone with two processes, one of which recurves anteriorly (**rp,** Fig. 28) and is the source of the generic name. A further uniting character is a rounded notch just distal to the pulvillus, although this is not obvious in *R. leonardi,* the type species of the genus. Shelley's illustrations of the gonopods show the course of the seminal canal as lacking a loop and a seminal vesicle. Close examination reveals that a loop is indeed lacking, but that the seminal canal at the very least expands just before the pore (Figs 121, 122), so it can be argued that a vesicle is indeed present and perhaps has been reduced, or is in the process of developing. The three new species described below have simpler gonopods than the two described by Shelley (2003) and the retrorse process of the terminal zone is less distinct.

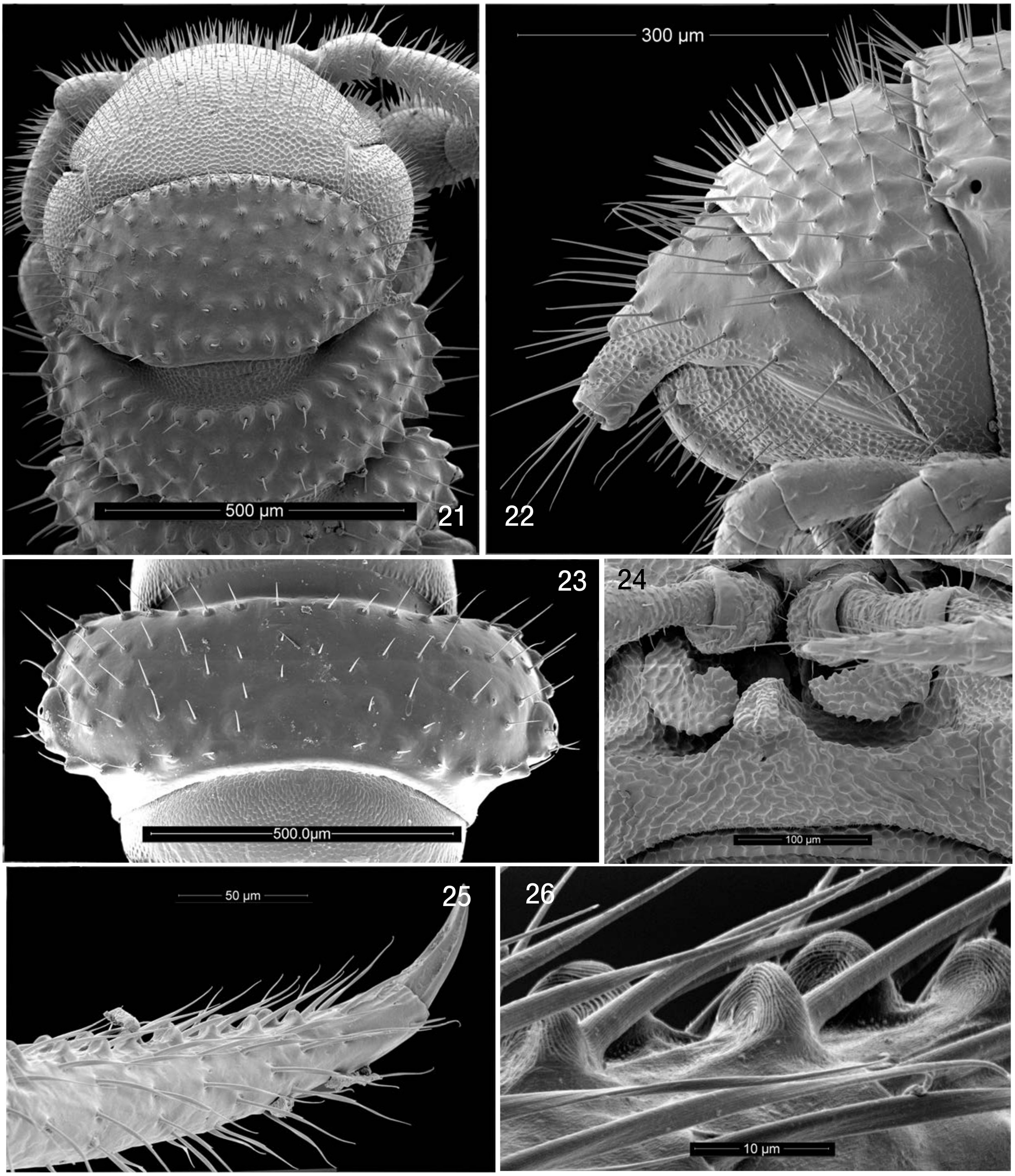
The detailed descriptions of the nonsexual characters of the two species named by Shelley (2003) can serve as well for the three additional species described here. The anterior setal row on the collum consists of 16–20 setae, varying according to species. The anterior metazonites have four rows of 14–18 setae set on stout, discrete tubercles; the number of rows increases to five midbody and may or may not decrease again to four at the posterior end.

Shelley (2003) did not mention *Utadesmus* as possibly related to *Retrorsia,* but there are similarities in the gonopods, especially in the division of the terminal zone into two processes.

***Retrorsia leonardi* Shelley, 2003**
Figs 21–28, 121, 138

Retrorsia leonardi Shelley, 2003:5.

Type locality. Ainsworth State Park, Columbia River Gorge National Scenic Area, 30 mi (48 km) east of Portland, Multnomah County, Oregon.



FIGURES 21–26. *Retrorsia leonardi* Shelley. 21. Head and anterior rings, dorsal view. **22**. Pygidium, lateral view. **23**. Midbody ring, dorsal view. **24**. Retracted female genitalia, ventral view. **25**. Tarsus of left leg 7, posterior view. **26.** Sphaerotrichomes on tarsus of leg 7. SEM stub WS32-15

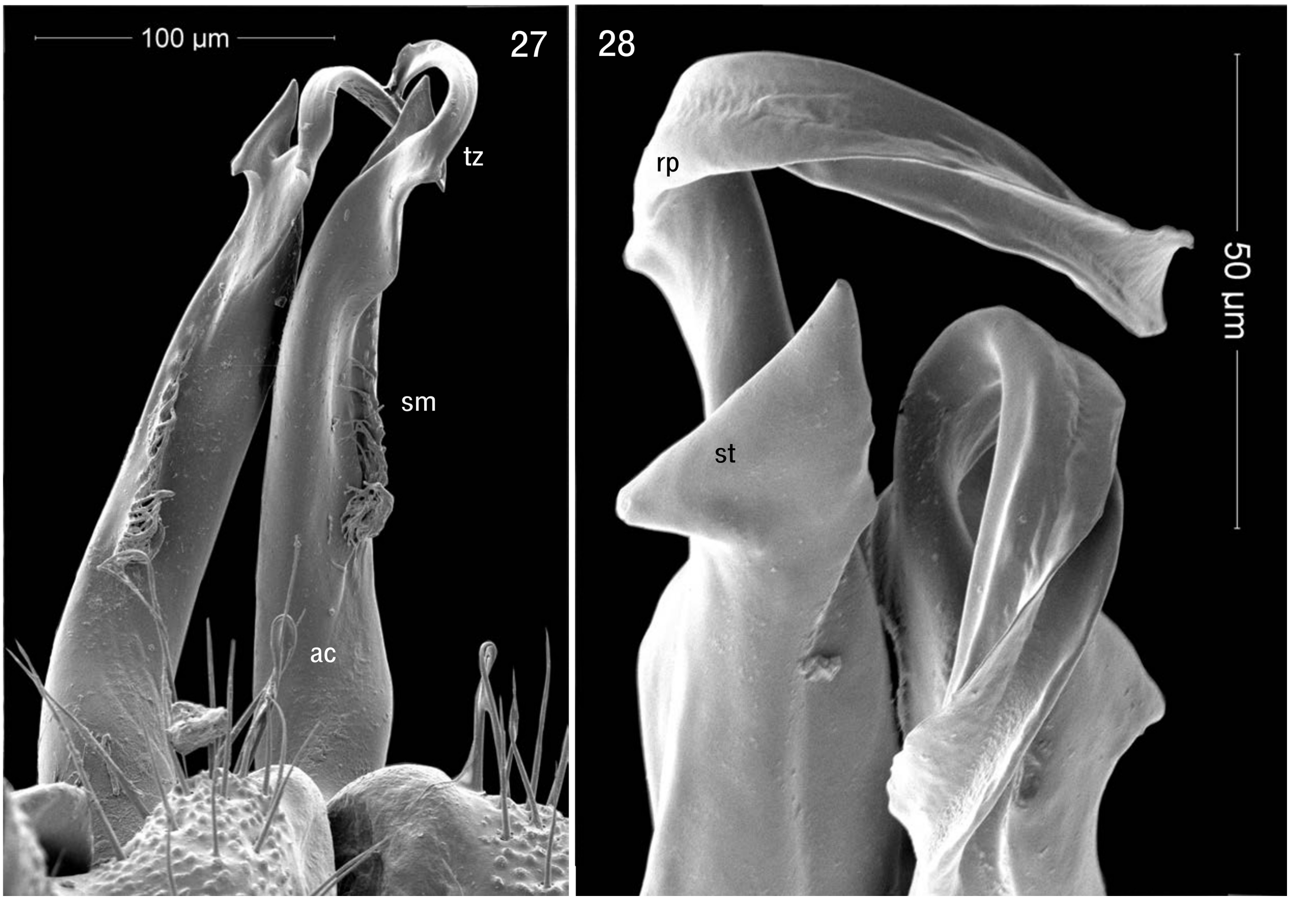
Diagnosis. The retrorse process (**rp,** Fig. 28) terminating the terminal zone is strongly curved and the subterminal process (**st,** Fig. 28) is broadly spatulate. The notch above the pulvillus seems almost entirely suppressed in this species. The anterior marginal row of setae on the collum may consist of as many as 20 setae (Fig. 21).

Notes. Males have sphaerotrichomes on the tarsi (Fig. 25) of the anterior legs, the bases of which are proximodistally flattened and have fingerprint-like wrinkles (Fig. 26). The cuticular fimbriae around the seminal pore of the pulvillus extend distally along the posterior surface of the gonopod in a diminishing line (Figs 27, 120). Posterior metazonites may have up to six rows of setae, but the rows tend to become less distinct on rings 16–18. The epiproct is short, not decurved or swollen (Fig. 22).

The female genitalia may be unusual and deserve further study. In their retracted position (Fig. 24) paired projecting structures can be seen which have the same cuticular sculpture as the sternite. It is not clear if these are the cyphopod valves or not.

Distribution. The new records for this species expand the range into Washington well north of the Columbia River.

New records. OREGON: *Columbia Co.:* Keystone Creek, Clatskanie Valley, 132 ft asl, 40.0822°, -123.1569°, 8 February 2002, W. Leonard, C. Richart, mm ff. *Yamhill Co.:* near Amity, 45.4594°, -122.4600°, 30 December 1915, P. Nosler, mm ff. WASHINGTON: *Cowlitz Co.:* 11.4 mi east of I-5, 410 ft asl, 7 March 2004, W. Leonard, mm ff; Pin Creek, Kool Road 0.4 mi west of Fishpond Road, 180 ft asl, 47.0742°, -122.8470°, 29 January 2004, W. Leonard, C. Richart, mm ff; SR503, 3.9 mi east of I-5, hillside north of Lewis River, 45.9412°, -122.6874°, 7 March 2004, W. Leonard, mm ff; SR504, 3.9 mi east of Toutle, 500 ft asl, 46.3483°, -122.7067°. 1 March 2005, W. Leonard, C. Richart. *Lewis Co.:* 8.5 mi south of Rendell on FS25, Gifford Pinchot National Forest, 46.4415°, -121.9982°, 21 December 2003, W. Leonard, m ff; same locality, 6 December 2003, W. Leonard, C. Richart, mm ff; Iron Creek Campground, 9.6 mi south of Rendell on FS25, Gifford Pinchot National Forest, 45.4297°, -121.9869°, 21 December 2003, W. Leonard, m; Shafer Park, 244 ft asl, 46.7530°, -122.9380°, 29 February 2004, C. Richart, m; SR508 at Bremer, 750 ft asl, 45.5917°, -122.4319°, 6 December 2006, W. Leonard, C. Richart, mm ff. *Wahakiaium Co.:* County Line Par, north of SR14, 46.1743°, -121.2183°, 22 February 2004, W. Leonard, mm ff; Rock Creek at Elochoman River, 46.2763°, -123.2796°, 10 January 2004, W. Leonard, C. Richart, mm ff.

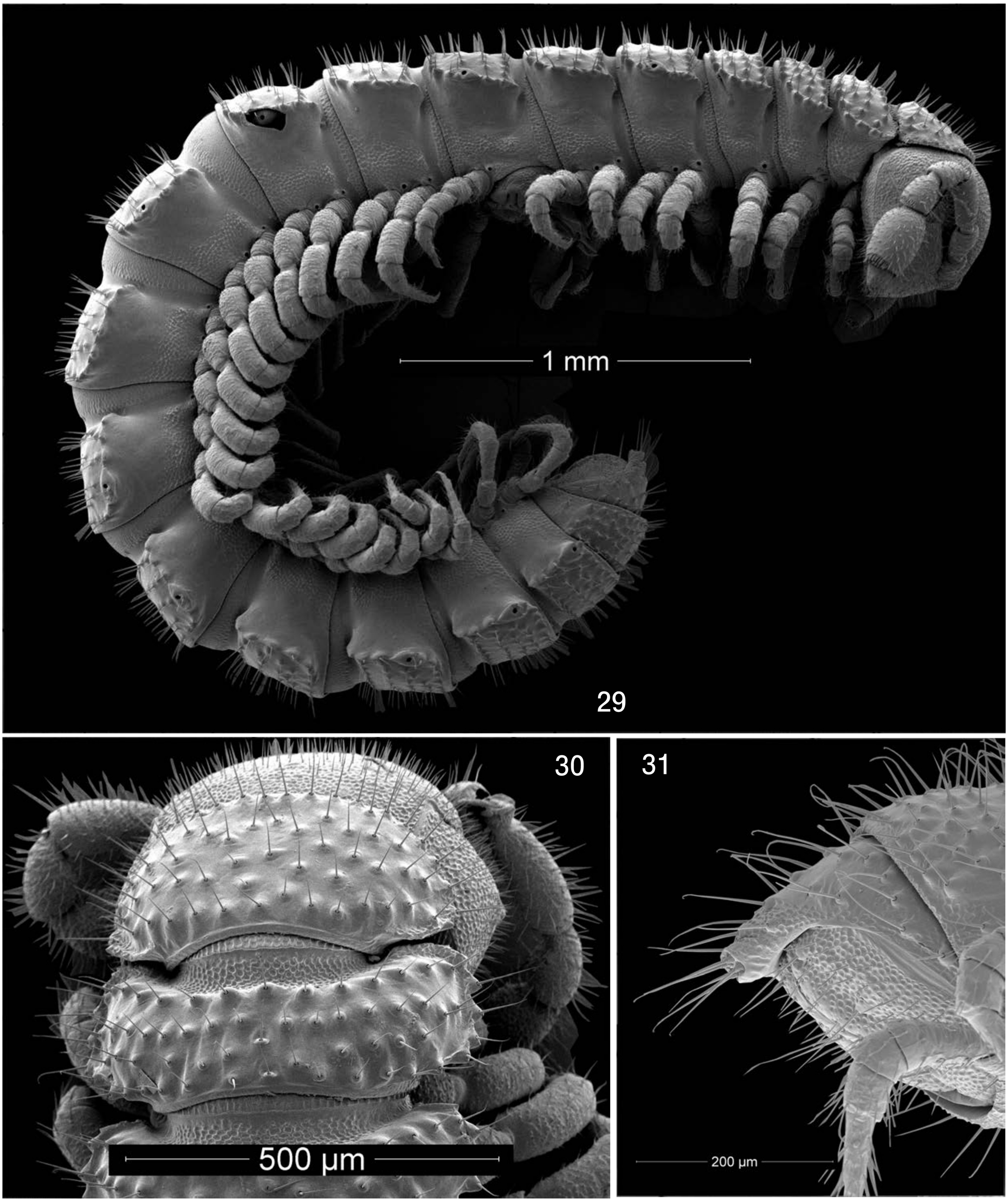


FIGURES 27, 28. *Retrorsia leonardi* Shelley gonopods. **27**. Gonopods *in situ*, posterior view. **28**. Gonopod tips. SEM stub WS32-15. Abbreviations: **ac**, acropodite; **rp**, retrorse process; **sm**, solenomere; **tz**, terminal zone.

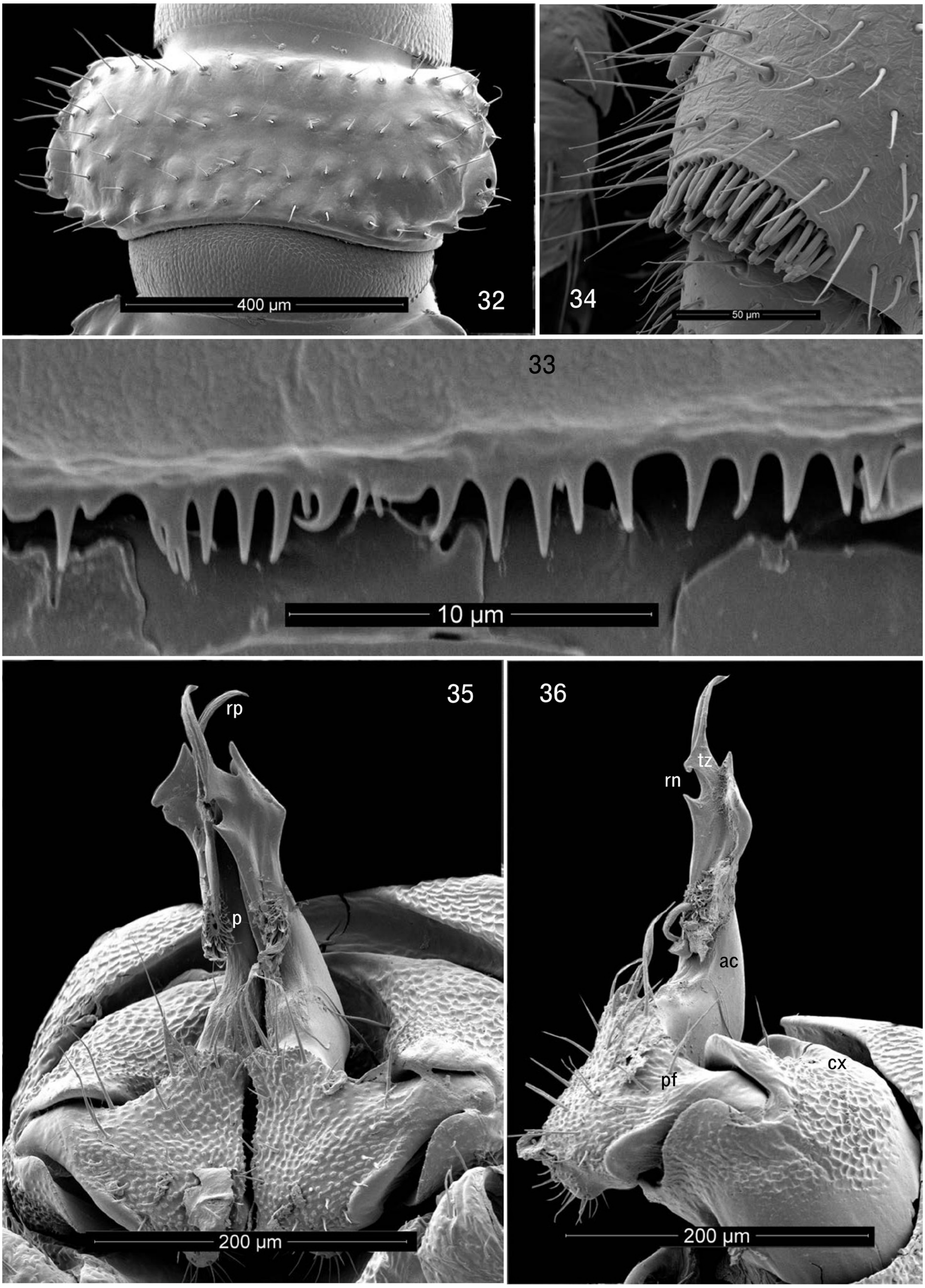
***Retrorsia benedictae* Shelley**
Figs 29–39, 122

Retrorsia benedictae Shelley, 2003:7

Type locality. Along Oregon Rt. 202, 3 mi (4.8 km) SE of Olney, Clatsop County, Oregon.



FIGURES 29–31. *Retrorsia benedictae* Shelley. **29**. Male, lateral view. **30**. Head and anterior rings, dorsal view. **31**. Pygidium, lateral view. SEM stub WS32-14.

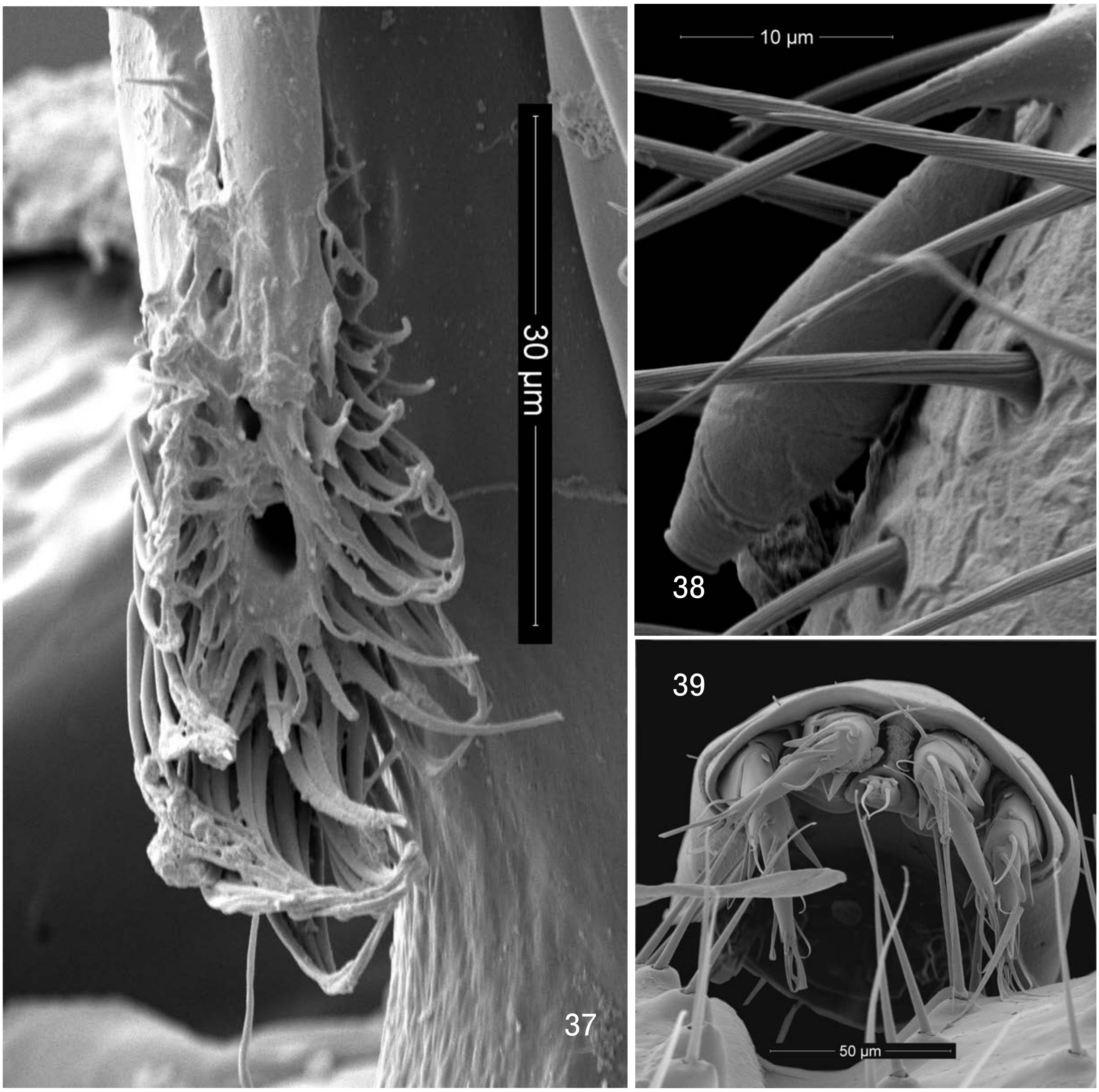


FIGURES 32–36. *Retrorsia benedictae* Shelley. **32**. Midbody ring, dorsal view. **33**. Limbus. **34**. Accessory sensory area on sixth segment of antenna, lateral view. **35**. Gonopods *in situ*, posterior view. **36**. Left gonopod, lateral view. SEM stub WS32-14. Abbreviations: **ac**, acropodite; **cx**, coxa; **p**, pulvillus; **pf**, prefemorite; **rn**, rounded notch distal to pulvillus; **rp**, retrorse process; **tz**, terminal zone.

Diagnosis. The semicircular notch in the gonopod is prominent (**rn,** Fig. 36) but separated from the pulvillus (**p,** Fig. 35) by half the length of the terminal zone (see also Fig. 121). There are 16 or 18 setae in the anterior marginal row of the collum (Fig. 30). A detailed description is available in Shelley (2003).

Notes. The male specimen we used for SEM examination (Figs 29–39) had some interesting commensals/parasites, including a fungal capilliconidia (amphoromorph) of the genus *Basidiobolus* (Enghoff & Reboleira 2017) on an antenna (Fig. 38) and the hypopis of an unidentified mite attached to the fifth ring (Fig. 39).

Distribution. Clatsop Co., Oregon (Shelley 2003), and Pacific Co., Washington (new records below).

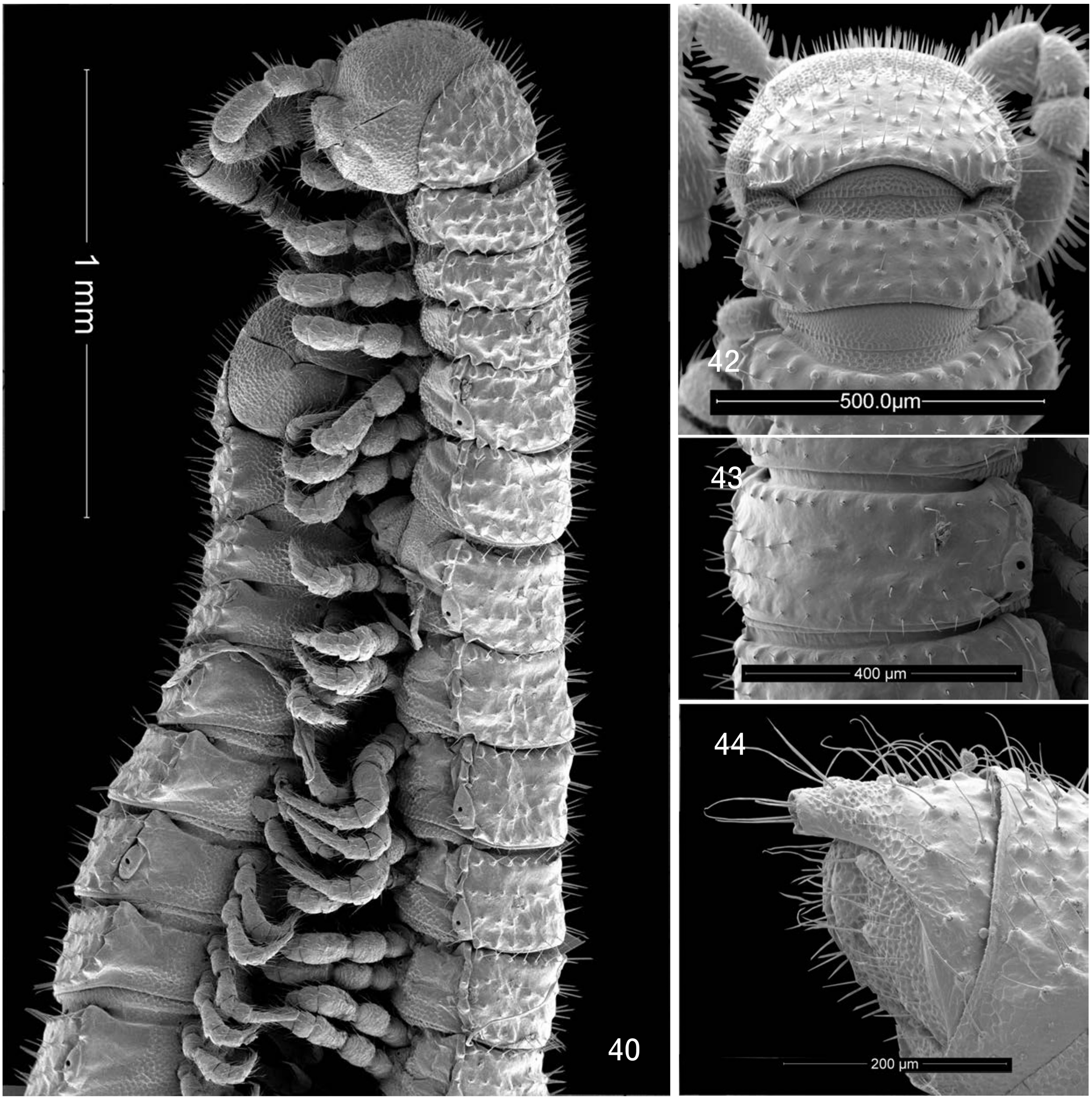


FIGURES 37–39. *Retrorsia benedictae* Shelley. **37**. Pulvillus of gonopod, posterior view. **38**. Suspected fungal theca on antenna. **39**. Hypopis of unidentified mite on fifth body ring. SEM stub 32-14.

New records. WASHINGTON: *Pacific Co*.: 1.0 mi on Walberg Road, 0.4 mi west of Icwaco Water Park, 46.3236°, -123.9417°, 2 January 2005, W. Leonard, C. Richart, m f; 1.1 mi south of SR6 on Trap Creek Road, B-line, 46.5432°-123.6152°, 19 November 2005, W. Leonard, C. Richart, m; 2 mi west of Astoria Bridge on US101, 10 ft asl, 46.2569, -123.9250°, 2 January 2005, W. Leonard, C. Richart, mm ff; 3.5 mi south of Naselle on SR401 at Cement Creek, 46.3341°, -123.8003°, 15 January 2006, W. Leonard, C. Richart, mm; 4.5 mi north of SR4 on US101, at Middle Nemah River, 46.4874°, -123.8865°, 15 January 2006, W. Leonard, C. Richart, mm ff; 5.9 mi south of SR6 on Trap Creek Road, Alder Creek drainage of Naselle River, 46.4973°, -123.6439°, 19 November 2005, W. Leonard, C. Richart, m; east side of Ellsworth Creek, The Nature Conservency Preserve, 100 ft asl, 46.3838°, -123.8679°, 12 January 2004, W. Leonard, mm ff; Long Beach, 30th St., 0.2 mi from US101, 50 ft asl, 46.3239°, -124.0598°, 15 January 2006, W. Leonard, C. Richart, mm ff; Long Beach, Willows Road, 0.6 mi from 30th St., 46.3229°, -124.0575°, 16 January 2006, W. Leonard, C. Richart, mm ff; SR401 8 mi south of SR4, 40 ft asl, 46.2752°, -123.8158°, 2 January 2005, W. Leonard, mm ff.

Retrorsia richarti **Shear & Marek, n. sp.**
Figs 40–46, 124

Types. Male holotype and male and female paratypes from Thurston Co., Washington, Hospital Creek above confluence with Skookumchuck River, 46.7733°, -122.5855°, collected 12 December 2003, by W. Leonard, K. McAllister. All types deposited in CAS.



FIGURES 40–44. ***Retrorsia richarti*, new species. 40**. Mating pair, lateral view. **41**. Head and anterior rings, dorsal view. **43**. Midbody ring, dorsal view. **44**. Pygidium, lateral view. SEM stub WS33-1.

Diagnosis. The pulvillus (**p,** Fig. 45) is midlength in the acropodite of the gonopod, with the pulvillar notch (**rn,** Fig. 45) immediately distal; the terminal zone processes are short, the anterior only slightly retrorse. The anterior marginal row on the collum consists of 20 setae (Fig. 42).

Etymology. The species name honors Dr. Casey Richart, Santa Barbara Botanical Garden, master naturalist and prolific collector of millipedes for this and other studies.

Description. Paratype male. Length, about 4.0 mm, greatest width 0.48 mm. Anterior marginal setal row on collum Fig. 42) of 20 setae. Anterior metazonites (Figs 42, 43) with four rows of setae, posterior rows somewhat irregular; transitioning to five rows about ring nine. Epiproct (Fig. 44) short, not decurved or swollen, with typical four spinnerets. Anterior legs crassate (Fig. 44), tarsi with sphaerotrichomes. Gonopod (Fig. 46) with large, inflated prefemorite. Acropodite long, slender, pulvillus (**p,** Fig. 46) about midway in their length, with pulvillar notch immediately above. Retrorse process of terminal zone (**rp,** Fig. 46) nearly straight, slightly inclined anteriorly. Subterminal process (**st,** Fig. 46 short, pointing directly posterior. Females similar to males in nonsexual characters.

Notes. The type locality collection included a mating pair (Fig. 40)

Distribution. Much of coastal northwestern Washington in the Puget Sound region, including the countes of Cowlitz, Grays Harbor, Jefferson, Lewis, Mason, Pacific, Thurston, and Wahakiakum.

Records: WASHINGTON: *Cowlitz Co.*: Germany Creek, at end of county road, 5.5 mi north of Stella, 450 ft asl, 46.2564°, -123.1345°, 22 November 2003, W. Leonard, C. Richart, mm; Germany Creek, 5.3 mi north of SR14, 46.2590°, -123.1350°, 11 November 2004, W. Leonard, mm; Germany Creek, 5.5 mi north of SR14, 46.2608°, -123.1343°, 8 December 2003, W. Leonard, mm. *Grays Harbor Co.*: Garrard Road at Weyerhauser D-line, 15 ft asl, 46.8040°, -123.3165°, 7 February 2005, m. *Jefferson Co.*: Falls View Campground, 7.8 mi west of Brinnon, 47.7896°, -122.9255°, 22 February 2003, W. Leonard, mm. *Lewis Co.*: Shaefer Park, 244 ft asl, 46.7530°, -122.9385°, 29 February 2003, W. Leonard, mm ff; end of Lepisto Road, north fork of Lincoln Creek, 46.7324°, -123.2303° 14 January 2004, C. Richart, m f. *Mason Co.*: 1.5 mi south, 0.5 mi west of Grapeview, 47.3354°, -122.8292°, 21 January 1968, E. Benedict, m; 2.5 mi north of Grant, 47.2761°, -122.9606°, 21 January 1968, E. Benedict, m; Beerbower Road at Schafer State Park Road, beside park, 47.1007°, -123.3873°, 11 December 2004, W. Leonard, m; Kennedy Creek, 47.0954°, -123.0820°, 30 March 2003, W. Leonard, m; Kennedy Creek, 0.6 mi upstream from Old Olympic Highway, 47.0901°, -123.1008°, 8 February 2003, W. Leonard, mm. *Thurston Co.*: Evergreen State College, Olympia, 47.0729°, -122.9779°, 16 March 2003, 26 January 2004, W. Leonard, mm ff; Intersection of Prather Road SW and Bicknell Road, 46.7767° -123.0505, 14 January 2004, C. Richart, mm f; McAllister Springs, 47.0491°, -122.7280°, 22 January 2000, 7 February 2004, W. Leonard, mm ff; Priest Point Park, Olympia, 47.06682°, -122.3952°, 5 January 2003, 1 February 2003, 16 February 2003, 11 January 2004, W. Leonard, mm ff; Tolmie State Park, 47.1204°, -122.7758°, 3 February 2003, W. Leonard, mm ff; Woodward Bay Natural Resource Conservation Area, 47.1271°, -122.8547°, 2 March 2003, W. Leonard, mm ff. *Wahakiakum Co.*: Swede Park, residence at 309 Loop Road, Grays River, 50 ft asl, 46.3075°, -123.6688°, 17 January 2004, W. Leonard, C. Richart, mm ff. *Whatcom Co.*: White Cap Road, 48.6623°, -122.4922°, 20 February 2004, C. Richart.

Retrorsia gracilis **Shear & Marek, n. sp.**

Figs 47–49, 124, 125

Types. Male holotype and male and female paratypes from Lewis Co., Washington, 604 Roswell Road, Centralia, 46.7223°, -122.9444°, collected 25 January 2004 by W. Leonard and C. Richart. All types deposited in CAS.

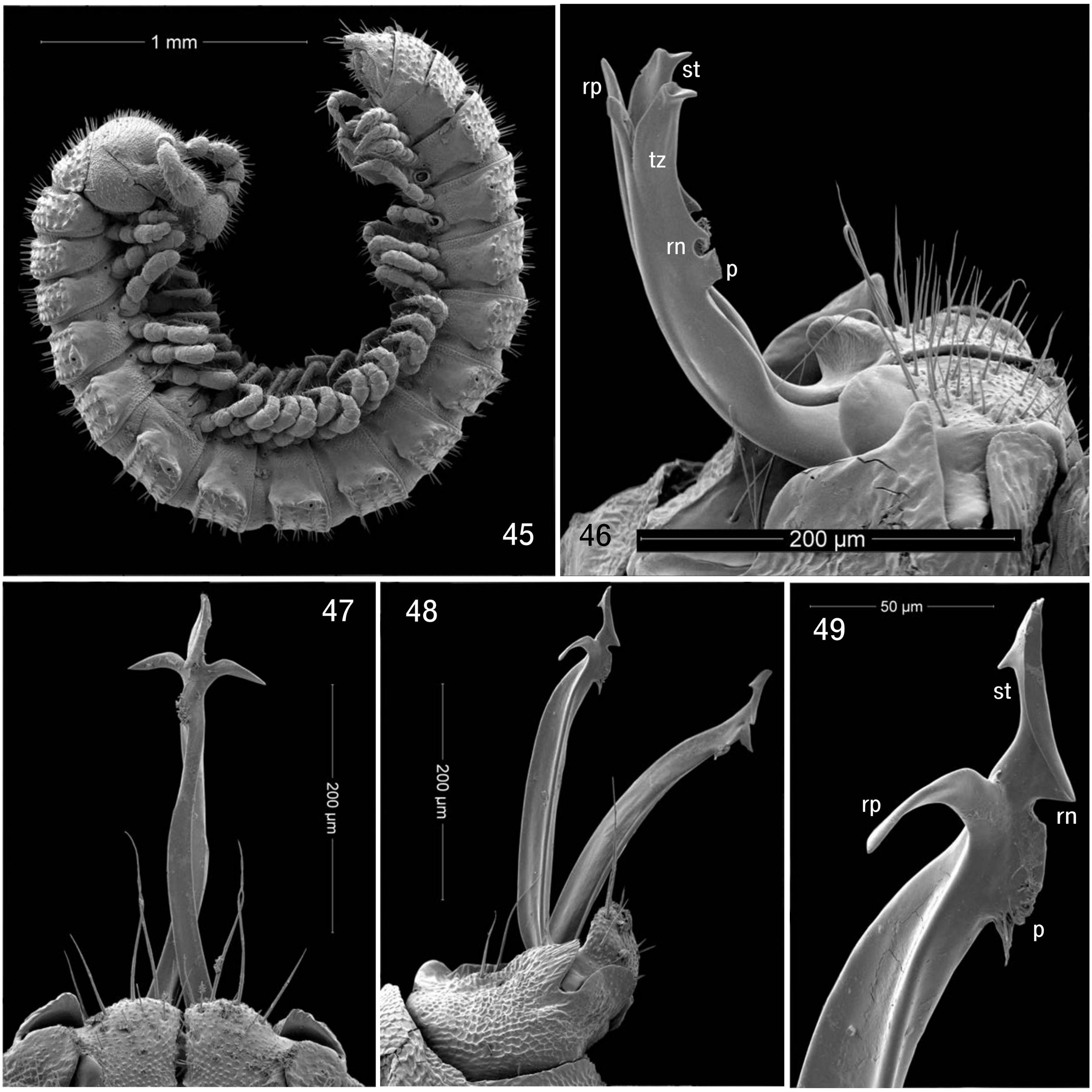
Diagnosis. The pulvillus (**p,** Fig. 49) is displaced to the distal one-fifth of the gonopod, with the pulvillar notch (**rn,** Fig. 49) immediately distal. The retrorse process (**rp,** Fig. 49) is sharply recurved. There are 18 setae in the anterior marginal row of the collum.

Etymology. The species name, an adjective, refers to the slender gonopods.

Description. Male holotype. Length 4.5 mm, greatest width 0.5 mm. Anterior metazonites with three rows of setae, distribution irregular on seventh ring, transitioning to four rows (Fig. 50) on eighth and ninth ring; a few posterior segments may appear to have five rows due to intercalated setae. Epiproct not swollen, short. Anterior legs crassate, tarsi with sphaerotrichomes. Gonopod (Figs 47–49, 124, 125) with large, inflated prefemorite. Acropodite long, slender, pulvillus (**p,** Fig. 49) in distal fifth of acropodite, pulvillar notch immediately distal. Retrorse process of terminal zone strongly decurved (**rp,** Fig. 49, relatively long. Subterminal process (**st,** Fig. 49) with small tooth subdistally. Females similar to males in nonsexual characters.

Distribution. Lewis Co., Washington.

Records*:* WASHINGTON: *Lewis Co.*: Iron Creek Campground, 9.6 mi south of Rendell on FS25, Gifford Pinchot National Forest, 45.4297°, -121.9869°, 21 December 2003, W. Leonard, m ff; North Fork Newaukam River, below confluence with Middle Fork, 46.6046°, -122.8482°, 29 December 2004, W. Leonard, m ff.

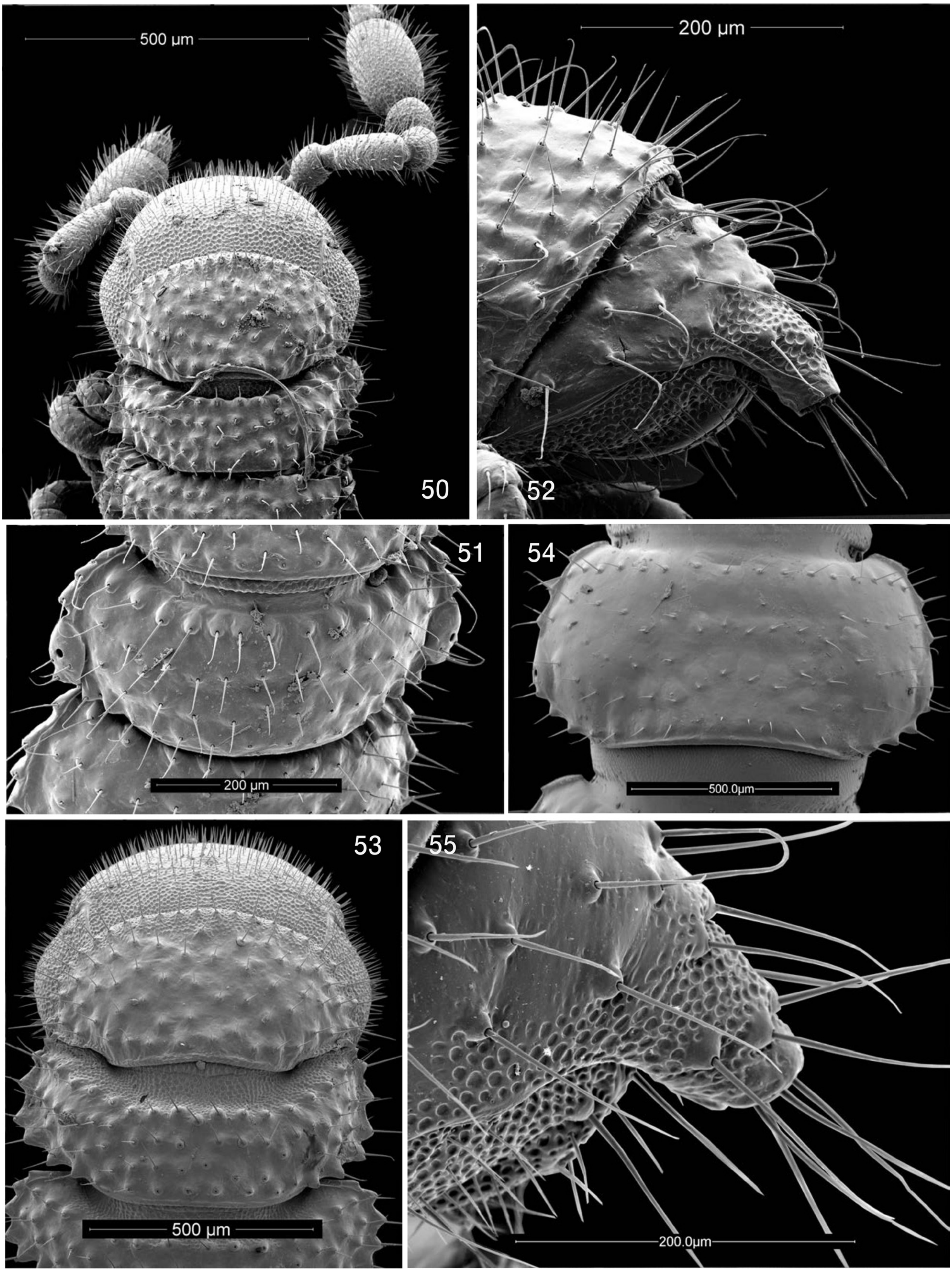


FIGURES 45–49. Species of *Retrorsia.* **45, 46**. ***Retrorsia richarti*, new species. 45**, Male, lateral view. **46**. Gonopods *in situ*, lateral view. SEM stub 33-1. **47–49**. ***Retrorsia gracilis*, n. sp. 47**. Gonopods *in situ,* anterior view. **47**. The same, lateral view, anterior to the left. **49**. Gonopod tip. SEM stub WS33-2. Abbreviations: **p**, pulvillus; **rn**, rounded notch distal to pulvillus; **rp**, retrorse process; **st**, subterminal process; **tz**, terminal zone.

Retrorsia simplicissima Shear & Marek*,* n. sp.

Figs 50–52, 126

Type. Male holotype from Stillman Basin, 1.8 miles on Weyerhauser Road 4200 from Road 4000, 2116 ft asl, 46.4956°, -123.2134°, Lewis Co., Washington, collected 4 December 2004 by W. Leonard and C. Richart. The holotype is mounted on SEM stub WS 33–11, deposited in CAS.



FIGURES 50–55. Species of *Retrorsia* and ***Retrorsioides,* n. gen**. **50–52**. ***Retrorsia simplicissima,* n. sp. 50.** Head and anterior rings, dorsal view. **51**. Midbody ring, dorsal view. **52**. Pygidium, lateral view. SEM stub WS33-11. **53–55**. ***Retrorsioides castellum,* n. sp. 53**. Head and anterior rings, dorsal view. **53**. Midbody ring, dorsal view. **55**. Pygidium, lateral view. SEM stub WS32-17.

Diagnosis. The gonopod (Fig 126) is extremely simple, with the pulvillus about midway in its length, and only a hint of a pulvillar notch. The terminal zone tip is undivided and slightly retrorse. The anterior marginal setal row of the collum consists of 22 setae (Fig. 50).

Etymology. The species name, an adjective, refers to the simple gonopods.

Description. Length about 5.0 mm, greatest width 0.46 mm. Anterior metazonites (Figs 50, 51) with four rows of setae, a few posterior segments may appear to have five rows due to intercalated setae. Epiproct not swollen, short. Anterior legs crassate, tarsi with sphaerotrichomes. Gonopod (Fig. 126) with small prefemorite. Acropodite relatively short, stout, pulvillus near midlength of acropodite, pulvillar notch small, shallow, indicated by slight swelling immediately distal. Terminal zone simple, only slightly retrorse. Female unknown.

Distribution. Only known from the type locality.

Notes. This species seems marginal to our concept of *Retrorsia,* though the general appearance of the gonopod in comparison to the other species suggests it belongs here. The gonopod is among the simplest to be found in the family Polydesmidae.

Retrorsioides Shear & Marek, new genus

Type species: *Retrorsioides castellum,* n. sp.

Species included: ***Retrorsioides castellum,*** **n. sp.,** ***R. linnensis,*** **n. sp.,** ***R. kittitas,*** **n. sp.,** ***R. bammerti,*** **n. sp.,** and ***R. arbora-magna,*** **n. sp.**

Diagnosis. Clearly related to *Retrorsia,* species of this genus are distinct in the gonopod having a prominent, anteriodorsally directed process at about the level of the pulvillus (absent in *Retrorsia* species), and in having a pulvillar process rather than a pulvillar notch (present in *Retrorsia* species).

Etymology. The name of the genus is based on the similarity of the included species to species of *Retrorsia.*

Distribution. Washington, Oregon and northern California.

Notes. *Retrorsioides* species encompass a wide distribution, from Humboldt Co. in northern California north to Thurston Co., Washington. The general appearance of the species is much like that of *Retrorsia* species, and the other polydesmids described herein. In addition to the accessory sensory area on the sixth antennal segment, there may also be a small cluster of sensilla near the distal end of the seventh segment. There may be up to 24 setae in the anterior marginal row on the collum, and alveolate cuticle, while present on the anterior part of the collum, is not seen on the dorsa of any of the anterior metazonites. However, the epiprocts of all the species have alveolate cuticle posteriorly. Males have crassate legs and typical (for this group of genera) sphaerotrichomes on the anterior tarsi. In two of the species, the pygidium or epiproct is swollen and curved ventrally, as it is in *Snoqualmia* species. The gonopod prefemora may be bulbous or small and flattened. The gonopod acropodites are shorter and stouter than in *Retrorsia* species and are not apically recurved, nor are they distally divided. Instead, a long, acute process arises at about the level of the pulvillus, which is not associated with a semicircular notch, but with a short pulvillar process.

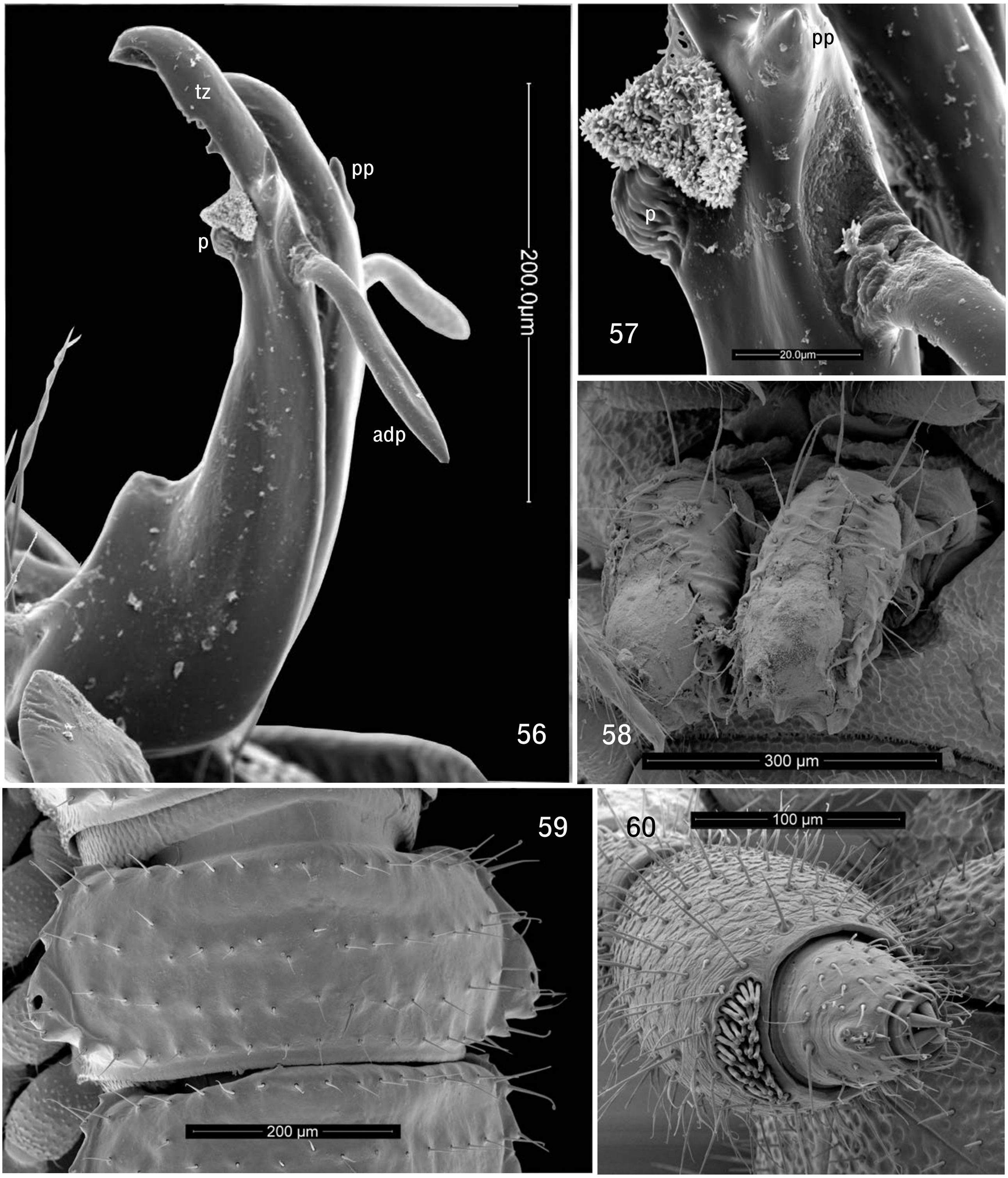
Retrorsioides castellum Shear & Marek, n. sp.

Figs 53–58, 127

Types. Male holotype and male paratypes from Delemeter Road, 10.1 mi southwest of Castle Rock, 46.2175°, -123.0178°, 400 ft asl, Cowlitz Co. Washington, collected 23 November 2003, by W. Leonard and C. Richart. All types deposited in CAS.

Diagnosis. The anteriorly directed process of the gonopod (**adp,** Fig. 56) is about as long as the terminal zone, thin and acute; the pulvillar process (**pp,** Figs 56, 57) is in the form of a blunt tooth; the terminal zone (**tz,** Fig. 56) is simple and curved. The anterior marginal row of setae on the collum consists of 24–26 setae; anterior metazonites have 4 rows of setae.

Etymology. The species name, a noun in apposition means "castle" in Latin and refers to the town of Castle Rock, near the type locality.



FIGURES 56–60. Species of ***Retrorsioides,*** **n. gen.**. **56–58**. ***Retrorsioides castellum,*** **n. sp. 56**. Gonopods, lateral view, anterior to the right. **57**. Pulvillus with probable spermatic mass.**58**. Female genitalia, ventral view. SEM stub WS32-17. **59, 60**. ***Retrorsioides linnensis,*** **n. sp. 59**. Midbody ring, dorsal view. **60**. Tip of antenna, apical view. SEM stub WS33-15. Abbreviations: **adp**, anteriorly directed process; **p**, pulvillus; **pp**, pulvillar process.

Description. Male holotype. Length about 6.0 mm, greatest width 0.8 mm. Head densely setose, cuticle alveolate (Fig. 53). Collum (Fig. 53) with anterior marginal row of 24 setae (26 in some paratypes). Anterior metazonites with four rows of setae (Figs 53, 54), a few posterior segments may appear to have five rows due to intercalated setae; setal tubercles becoming low on posterior segments. Epiproct (Fig. 55) not swollen, short. Anterior legs crassate, tarsi with sphaerotrichomes. Gonopod (Figs 56, 57, 127) with subglobular prefemorite. Acropodite relatively long, narrow. Pulvillus (**p,** Figs 56, 57) in distal third of acropodite, pulvillar process (**pp,** Fig. 56) a short, slightly curved tooth. Anteriorly directed process (**adp,** Fig. 56) long, evenly tapering. Terminal zone (**tz,** Fig. 56) simple, curved. Females similar to males in nonsexual characters; vulvae as in Fig. 58.

Distribution. Cowlitz Co., Washington.

Records*:* WASHINGTON: *Cowlitz Co.*: Germany Creek at end of county road, 5.5 mi north of Stella, 46.2564°, -123.1345°, 450 ft asl, 27 November 2003, W. Leonard, C. Richart, m; Germany Creek, 5.5 mi north of SR4, 47.2608°, -123.1343°, 350 ft asl, 8 December 2003, W. Leonard, mm f.

Note*:* at the Germany Creek localities, this species is syntopic with *Retrorsia richarti,* **n. sp.** It is almost 50% larger. There is a region of wrinkled, seemingly less sclerotized cuticle at the base of the anteriorly directed process (Fig. 56), suggesting that this feature might be movable. Figure 56 shows a probable spermatic mass exuded from the pore of the pulvillus. Millipedes do not produce motile sperm.

Retrorsioides linnensis **Shear & Marek, n. sp.**

Figs 59–68, 128

Types. Male holotype and male and female paratypes from Wells Creek Road, 0.7 mi from SR34, 44.4696°. -123.4899°, Linn Co., Oregon, collected 9 December 2005 by W. Leonard and C. Richart. All types deposited in CAS.

Diagnosis. The seventh segment of the antenna has a small distal knob set with 6–8 sensilla (Fig. 60). The gonopod (Figs 66, 128) is short and stout with all processes and the pulvillus clustered near the tip. The prefemorite (**pf,** Fig. 66) is flattened. The anteriorly directed process has a small basal tooth.

Etymology. The species epithet is an adjective referring to the type locality in Linn Co., Oregon.

Description. Length about 4 mm, greatest width 0.42 mm. Head densely setose, cuticle alveolate. Collum with anterior marginal row of 18 setae. Anterior metazonites with three rows of setae, transitioning to four rows (Fig. 62) at about ring 5; setal tubercles becoming low on posterior segments. Epiproct (Fig. 63) not swollen, short. Anterior legs (Fig. 65) crassate, tarsi with sphaerotrichomes (Fig. 64). Gonopod (Figs 66–68, 128) with flattened prefemorite (**pf,** Fig. 66). Acropodites (**ac,** Fig. 66) short stout, processes and pulvillus crowded toward tip. Pulvillus (**p,** Fig. 68) in distal third of acropodite; pulvillar process (**pp,** Fig. 68) a short, triangular tooth. Anteriorly directed process (**adp,** Fig. 68) long, flattened, with marginal teeth. Terminal zone (**tz,** Fig. 68) bifurcate, bent laterally. Female similar in nonsexual characters.

Distribution. Linn and Tillamook Cos., Oregon.

Records*:* OREGON: *Tillamook Co.*: 1 mi west, 0.5 mi south of Lee's Camp, 700 ft asl, 45.5883°, -123.5349°, 4 November 1972, E. M. Benedict, mm, ff; FR14, 4.2 mi northeast of SR22, Suislaw National Forest, 900 ft asl, 45.2248°, -123.8337°, 10 December 2005, W. Leonard, C. Richart, m. f.

Retrorsioides kittitas **Shear & Marek, n. sp.**

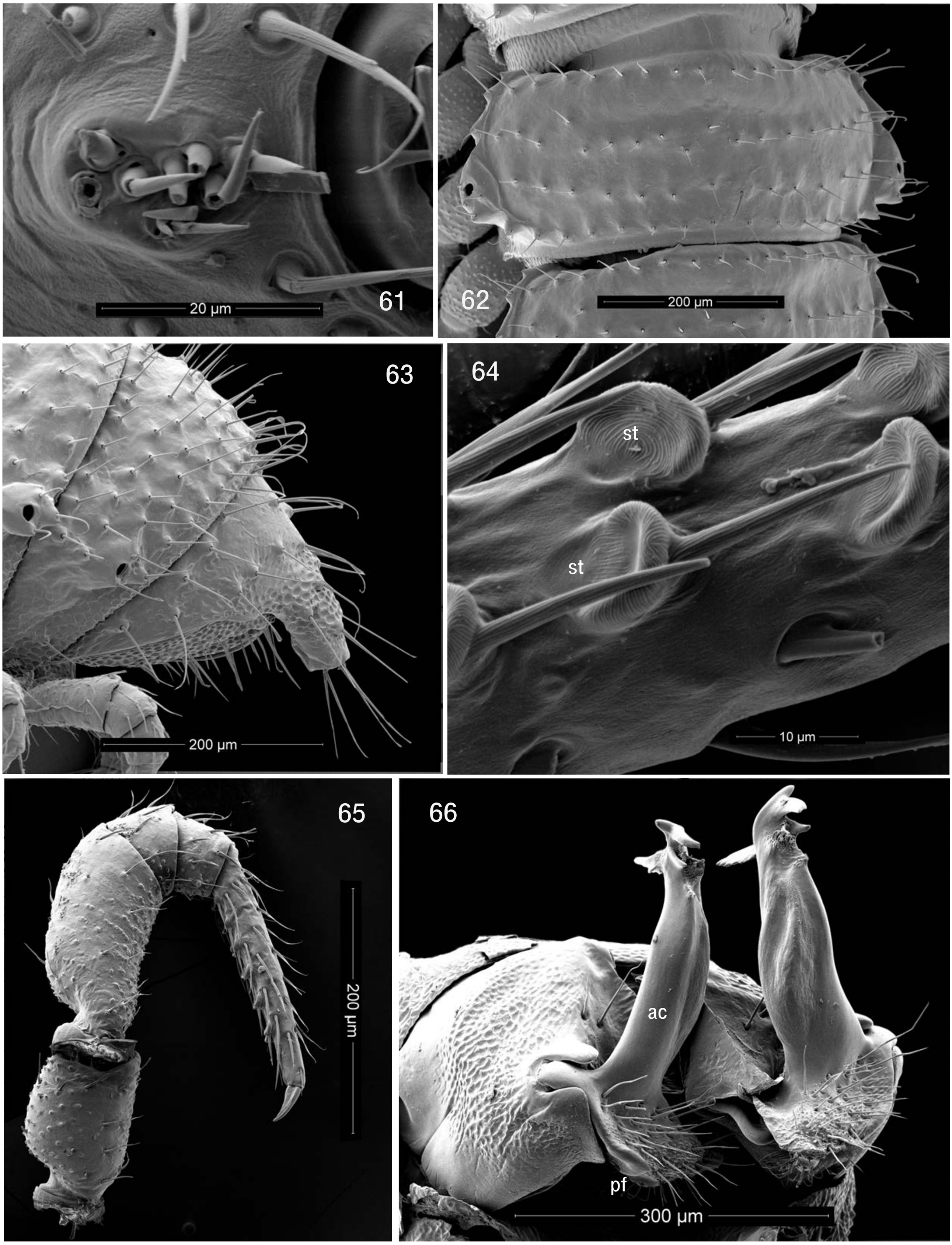
Figs 69–75, 129

Types. Male holotype and male and female paratypes from the confluence of Stafford Creek and the North Fork of the Teanway River, Wenatchee National Forest, 2900 ft asl, 47.3497°, -120.8483°, Kittitas Co., Washington, collected 31 October 2004 by W. Leonard and J. Baugh. All types deposited in CAS.

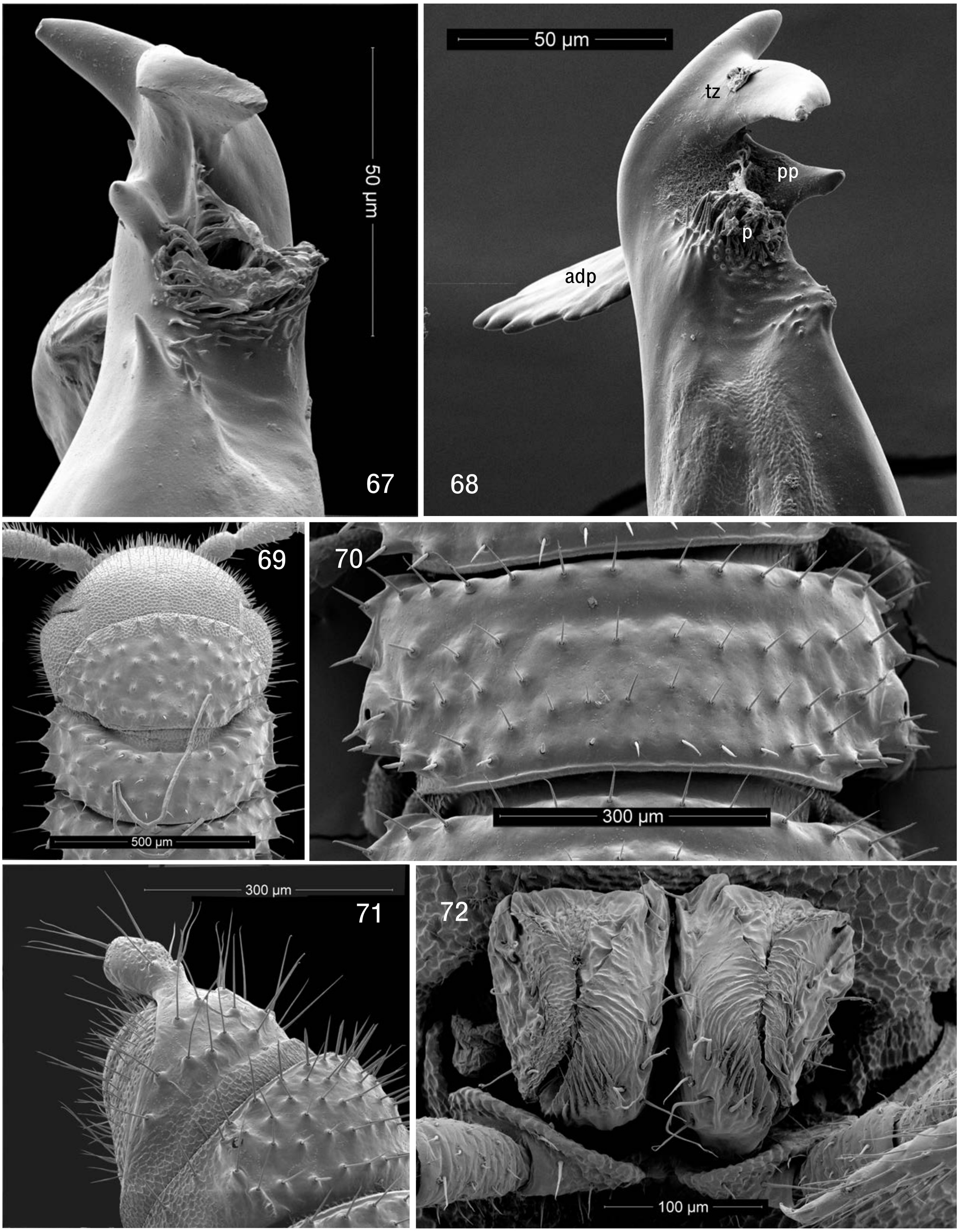
Diagnosis. The epiproct (Fig. 71) is swollen and decurved. Like the preceding species, the gonopod (Figs 73–74, 129) is short with the pulvillus and other features crowded at the distal end, but in *R. kittitas,* the prefemorite (**pf,** Fig. 73) is inflated and oblong with an enlarged, asetose distal part. The anteriorly directed process (Fig. 75) is set on all sides with acute teeth.

Etymology. The species epithet is a noun in apposition referring to Kittitas Co., Washington.

Description. Male holotype. Length about 4.5 mm, greatest width 0.65 mm. Head (Fig. 69) densely setose, cuticle alveolate. Collum (Fig. 69) with anterior marginal row of 16 setae. Anterior metazonites with four rows of setae (Fig. 69, 70), some of the rows irregular; transitioning to five rows posteriorly but many rows irregular. Setal



FIGURES 61–66. ***Retrorsioides linnensis*, n. sp. 61**. Accessory sensory area on seventh antennal segment. **62**. Midbody ring, dorsal view. 63. Pygidium, lateral view. **64.** Sphaerotrichomes on tarsus of third leg. **65**. Left third leg, posterior view. **66**. Gonopods *in situ*, posteriolateral view. SEM stub WS33-15. Abbreviations: **ac**, acropodite; **pf**, prefemorite; **st**, sphaerotrichome.



FIGURES 67–72. Species of ***Retrorsioides*** **n. gen**. **67, 68**. ***Retrorsioides linnensis,*** **n. sp. 67**. Gonopod tip, posterior view. **68**. Same, mesal view. **69–72**. SEM stub WS33-15. ***Retrorsioides kittitas,*** **n. sp. 69**. Head and anterior rings, dorsal view. **70**. Mid-body ring, dorsal view. **71**. Pygidium, lateral view. **72.** Female genitalia, ventral view. SEM stub WS32-17Abbreviations: **adp**, anteriorly. directed process; **p**, pulvillus; **pp**, pulvillar process; **tz**, terminal zone.

tubercles becoming low on posterior segments. Alveolate cuticle absent from metazonites except for anterior margin of ring 2. Epiproct (Fig. 71) swollen, short, bent ventrally. Anterior legs crassate, tarsi with sphaerotrichomes. Gonopod (Figs 73–75, 129) with oblong, inflated prefemorite (**pf,** Figs 73, 74). Acropodite (**ac,** Fig. 73) short, stout. Processes and pulvillus crowded toward tip, pulvillus (**p,** Fig.75) in distal third of acropodite. Pulvillar process (**pp,** Figs 74, 75) long, acute, hooked; anteriorly directed process (**adp,** Figs 73, 74, 75) rounded, tapering slightly, with many acute teeth, terminal zone (**tz,** Fig. 75) bifurcate, straight. Female similar in nonsexual characters, vulvae as in Fig. 72.

Distribution. Kittitas Co., Washington.

Record*:* WASHINGTON: *Kittitas Co.*: Taneum Creek, Kittitas National Forest, 2700 ft asl, 47.1138°, -120.8848°, 26 March 2004, C. Richart, m.

***Retrorsioides bammerti* Shear & Marek, new species**

Figs 76–78, 130

Types. Male holotype and male paratypes from Bob Bammert Grove, Capitol State Forest, 287 ft asl, 46.8960°, -123.0963°, Thurston Co., Washington, collected 14 November 2004 by W. Leonard. All types deposited in CAS.

Diagnosis. The sigmoid terminal zone of the gonopod (**tz,** Fig. 130) and the basal position of the pulvillus (**p,** Fig. 130) set this species apart from all others in the genus.

Etymology. The species name recognizes Robert (Bob) Bammert (1926–2019), noted Washington conservationist for whom the type locality, a grove of old-growth trees, is named.

Description. Male holotype. Length about 4.0 mm, greatest width 0.50 mm. Head densely setose, cuticle alveolate (Fig. 76). Collum (Fig. 76) with anterior marginal row of 14 setae. Anterior metazonites with three rows of setae (Fig. 76), transitioning to four rows (Fig. 77) about ring 5, posteriormost segments with five rows (Fig. 78); setal tubercles becoming almost obsolete on midbody to posterior rings. Alveolate cuticle absent from metazonites posterior to collum. Epiproct (Fig. 78) swollen, short, bent ventrally, without alveolate cuticle. Anterior legs crassate, tarsi with sphaerotrichomes. Gonopod with oblong, inflated prefemorite (**pf,** Fig. 130) similar to previous species. Acropodite short, stout. Pulvillus (**p,** Fig. 130) in basal third of acropodite, pulvillar process (**pp,** Fig. 130) long, acute, directed distally. Anteriorly directed process (**adp,** Fig. 130) rounded, tapering slightly, without teeth. Terminal zone (**tz,** Fig. 130) not bifurcate, sigmoidally curved. Females unknown.

Distribution. Northwestern Washington in Thurston, Pacific and Lewis Counties.

Records*:* WASHINGTON: *Lewis Co.*: Stillman Basin, 1.8 mi on Weyerhauser 4200 from road W4000, 2116 ft asl, 48.4956°, -123.2134°, 4 December 2004, W. Leonard, C. Richart, mm. *Pacific Co.*: 1.1 mi south of SR6 on Trap Creek Road, B-line, 46.5432°, -123/6152°, W. Leonard, C. Richart, m.

Note*:* At the Stillman Basin locality, this species is syntopic with *Retrorsia simplicissima.*

***Retrorsioides arboramagna* Shear & Marek, n. sp.**

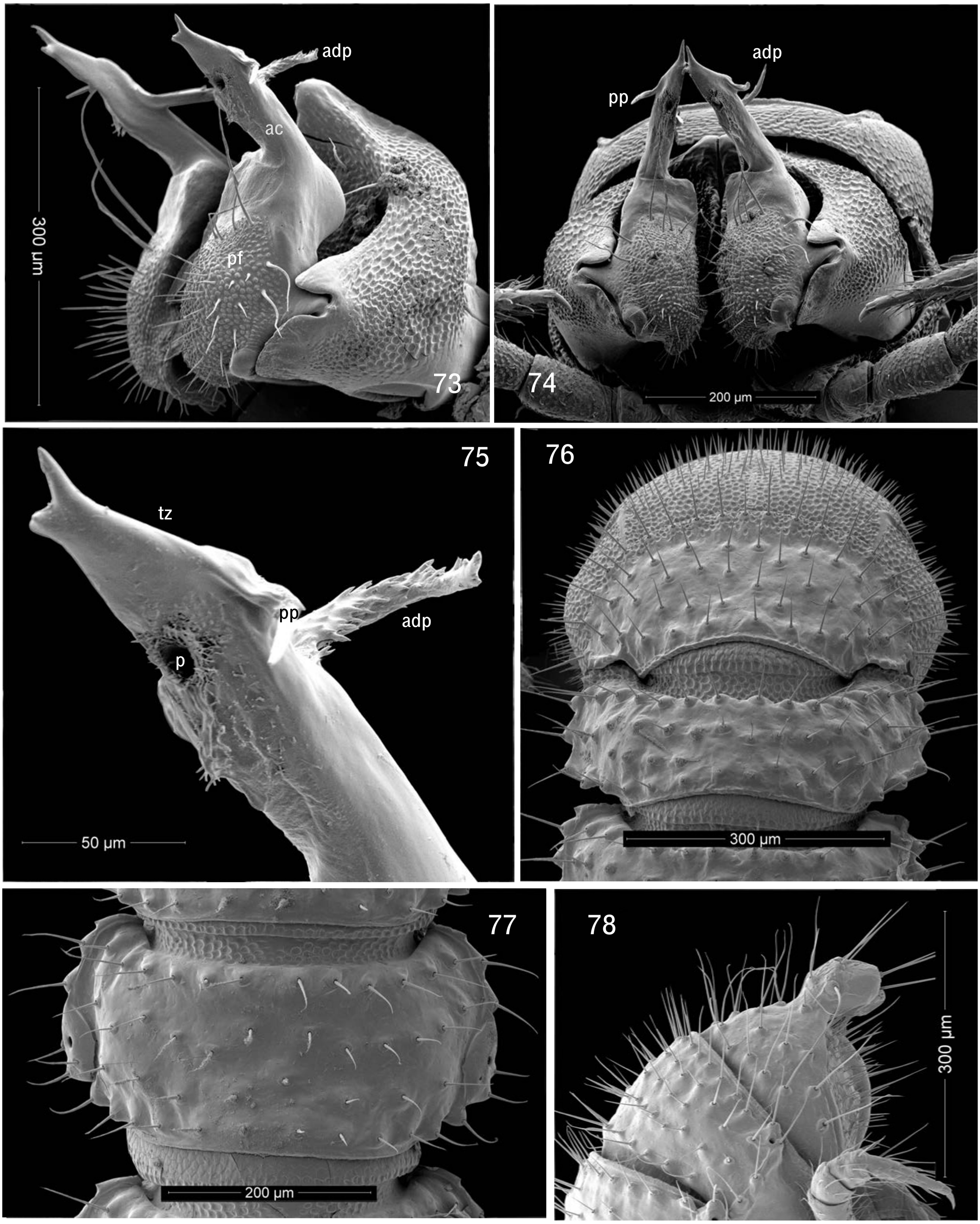
Figs 79–84

Type. Male holotype from Prairie Creek Redwoods State Park, "Big Trees," 252 ft asl, 41.4006°, -124.0003°. Humboldt Co. California, collected 2 December 2006 by C. Richart. The holotype is mounted on SEM stub WS33-16, deposited in CAS.

Diagnosis. Distinct from other species of the genus in the extended pulvillus (**p,** Fig. 83), and a strong tooth (**x,** Fig. 83) at the base of the anteriorly directed process.

Etymology. The species epithet (Latin) is a noun in appostion meaning "big tree" and refers to the type locality, famous for its gigantic Coast Redwoods.

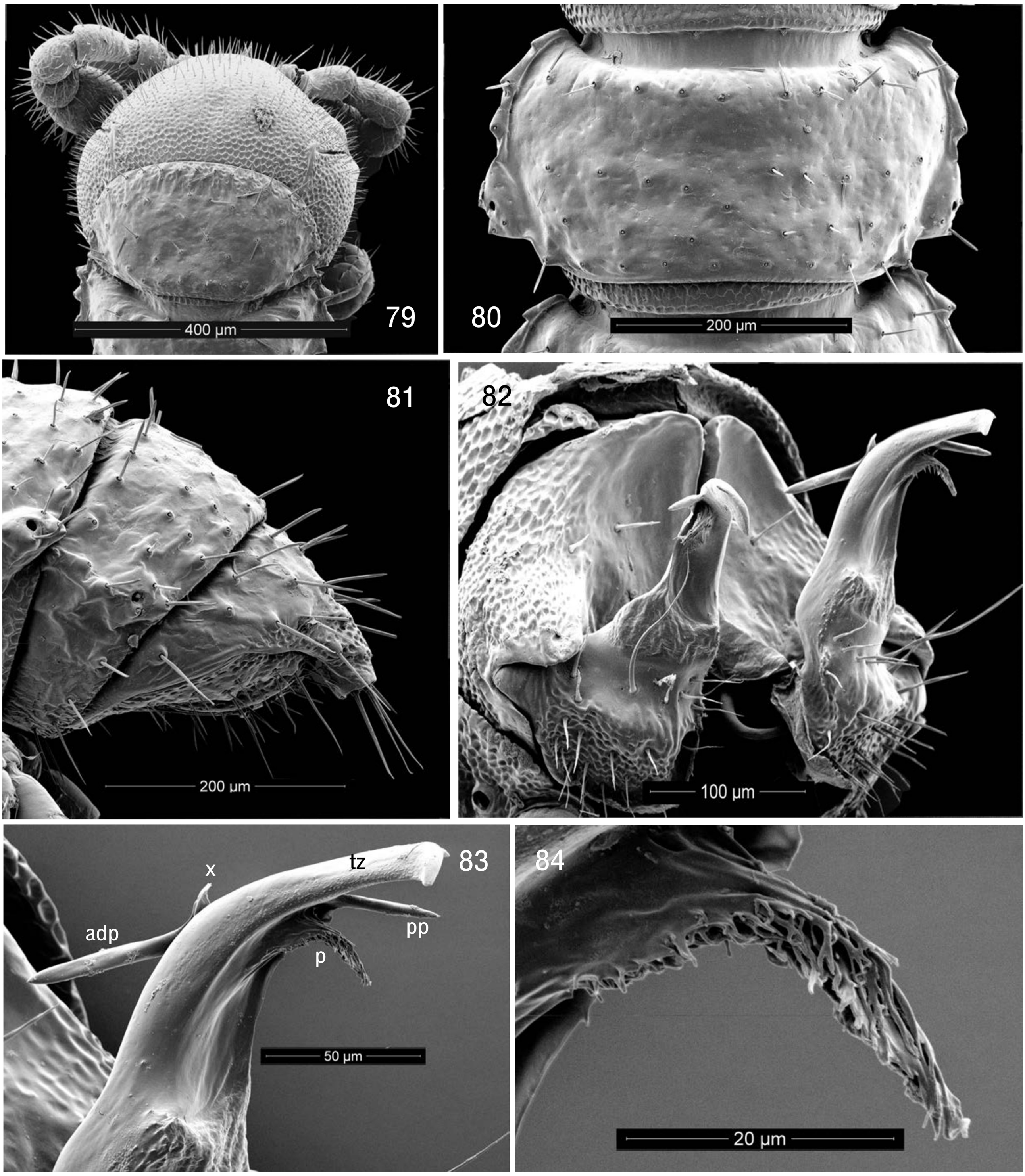
Description. Male holotype. Length about 3.0 mm, greatest width 0.45 mm. Head densely setose, cuticle alveolate (Fig. 79). Collum (Fig. 79) with anterior marginal row of 16 setae. Anterior metazonites with three rows of setae, transitioning to four rows about ring 5, setal tubercles becoming almost obsolete on midbody to posterior rings (Fig. 80). Alveolate cuticle absent from metazonite posterior to collum. Epiproct (Fig. 81) not swollen, short, straight, with alveolate cuticle. Anterior legs crassate, tarsi with sphaerotrichomes. Gonopod (Figs 82–84)



FIGURES 73–78. Species of ***Retrorsioides,*** **n.gen**. **73–74**. ***Retrorsioides kittitas*****, n. sp. 73**. Gonopods *in situ*, posteriolateral view. **74**. Same, posterior view. **75**. Gonopod tip, lateral view. SEM stub WS32-17. **76–78**. ***Retrorsioides bammerti*****, n. sp. 76**. Head and anterior rings, dorsal view. **77**. Midbody ring, dorsal view. **78.** Pygidium, ventral view. SEM stub WS33-1. Abbreviations: **ac**, acropodite; **adp**, anteriorly directed process; **p**, pulvillus; **pf**, prefemorite; **pp**, pulvillar process.

with moderately inflated prefemorite. Acropodite long, robust, basally thickened. Pulvillus (**p,** Fig. 83; Fig. 84) in distal third of acropodite, its dorsal side prominently extended. Pulvillar process (**pp,** Fig. 83) short, thin, directed posteriorly. Anteriorly directed process (**adp,** Fig. 83) long, tapering to acute point, without small teeth along length but with single, sharp, slightly curved tooth (**x,** Fig. 83) at base. Terminal zone (**tz,** Fig. 83) not bifurcate, flattened. Females unknown.

Distribution. Known only from the type locality.



FIGURES 79–84. ***Retrorsioides arboramagna*, n. sp. 79**. Head and anterior rings, dorsal view. **80**. Midbody ring, dorsal view. **81**. Pygidium, lateral view. **82**. Gonopods *in situ*, lateroposterior view. **83**. Gonopod tip, mesal view. **84**. Pulvillus of gonopod. SEM stub WS33-16. Abbreviations: **adp**, anteriorly directed process; **p**, pulvillus; **pp**, pulvillar process; **tz**, terminal zone, **x**, unnamed gonopod process.

Rowlandesmus Shear & Marek, new genus

Type species: *Rowlandesmus millicoma* Shear & Marek, new species.

Species included: ***Rowlandesmus millicoma* n. sp.** and ***R. dentogonopus*, n. sp.**

Diagnosis. In their somatic characters, the two species of this genus are similar in nonsexual traits to the others described here, except that the metzonital tubercles carrying setae are generally lower and the surface of the metazonites of the midbody rings nearly smooth. The distinction lies in the gonopods Figs 88–90, 93, 94, 131, 132), in which the acropodite is sharply bent and reflexed in its distal third to half. Just distal or just proximal to this "kink" in the gonopod (**k,** Fig. 88) is a short process. The pulvillus is basal to the "kink" and in *R. millicoma*, much expanded.

Etymology. The genus is named for our late and much respected colleague, Rowland M. Shelley (1942–2018), one of the most productive millipede taxonomists of 20th and 21st centuries. He initiated the modern study of the small polydesmids of western North America with careful redescriptions of known genera and species and the description of *Retrorsia* Shelley, 2003.

Distribution. Douglas and Coos Cos., Oregon.

Notes. We are placing both of these species in *Rowlandesmus* due to the similarity of the gonopods, with a sharp bend or "kink" in the acropodite causing the distal third to be reflexed at a right or lesser angle in relation to the basal part. Nevertheless there are some differences, and subsequent species discoveries may result in the two species being separated.

Rowlandesmus millicoma Shear & Marek, n. sp.

Figs 85–90, 131

Types. Male holotype and male and female paratypes from 14 mi. E, 2 mi. S of Allegany, Weyerhauser Millicoma Tree Farm, company Road 6000, riparian zone of Fall Creek, 43.3983°, -123.7770°, Coos Co., Oregon, collected 23 November 1971 by E. M. Benedict. All types deposited in CAS.

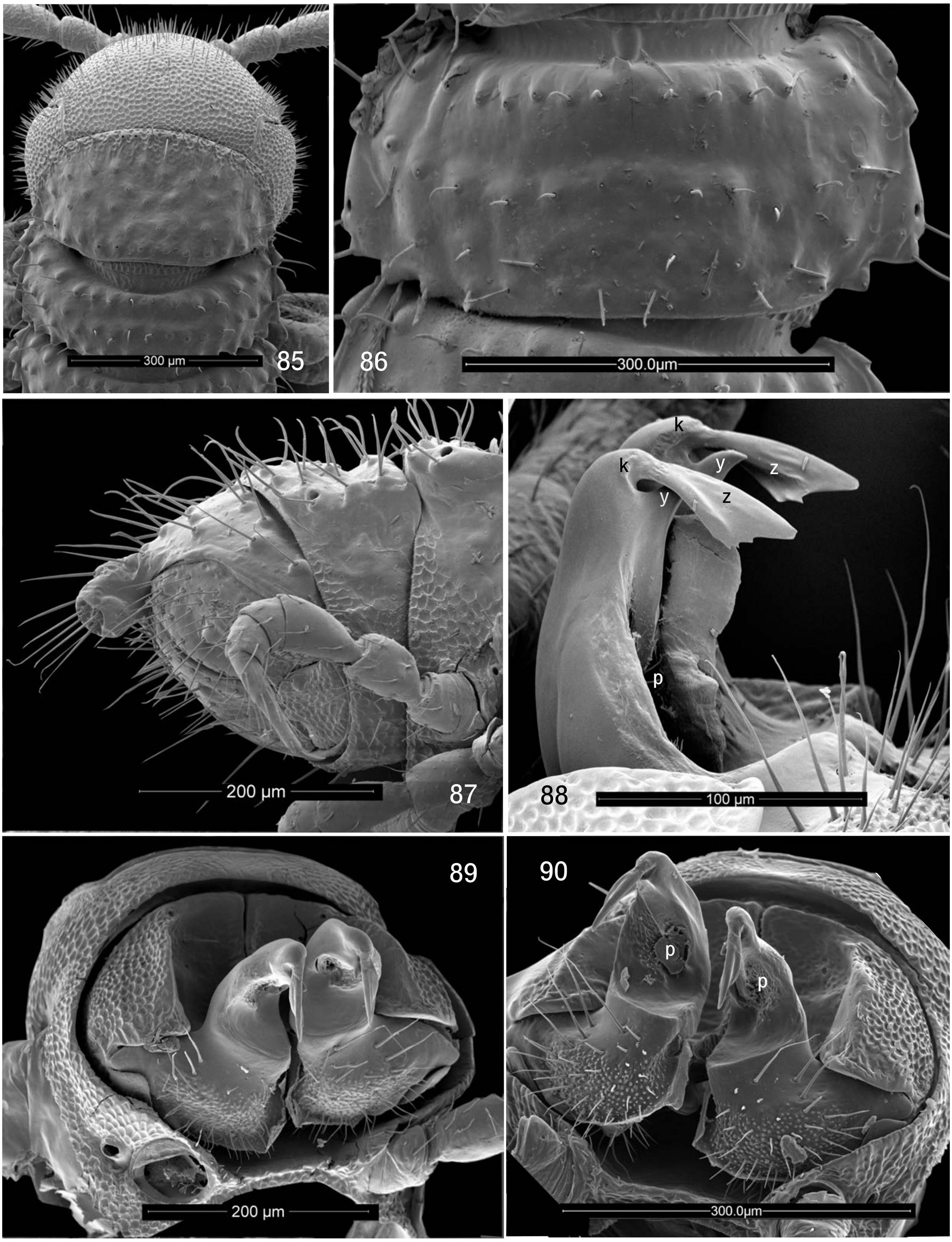
Diagnosis. Distinct from *R. dentogonopus* in lacking prominent teeth in the terminal zone of the gonopod and in the more basal position and larger extent of the pulvillus (**p,** Fig. 90).

Etymology. The species name is a noun in apposition and refers to the type locality, the Millicoma Tree Farm.

Description. Male holotype. Length about 3.5 mm, greatest width 0.45 mm. Head densely setose, cuticle alveolate (Fig. 85). Collum with anterior marginal row of 20 setae (Fig 85). Anterior metazonites with three rows of setae, transitioning to four rows about ring 5, setal tubercles low on anterior segments, becoming almost obsolete on midbody (Fig. 86) to posterior rings; some rings with interpolated setae nearly forming fifth row. Alveolate cuticle absent from metazonites posterior to collum. Epiproct (Fig. 87) swollen, short, decurved, lacking alveolate cuticle. Anterior legs crassate, tarsi with sphaerotrichomes. Femur of third leg slightly enlarged. Gonopod (Figs 88–90, 131) with moderately inflated prefemorite. Acropodite short, robust. Pulvillus (**p,** Figs 88, 90) basal, enlarged, pulvillar process absent. Terminal zone bifurcate, longer distal process (**z,** Fig. 88) narrow at base, then broadened, bent posteriorly at slightly less than right angle, crossing lateral to shorter basal process (**x,** Fig. 88). Females similar to males in nonsexual characters.

Distribution. Coos Co., Oregon.

Records*:* OREGON: *Coos Co.*: 11 mi east, 4 mi south of Allegany, Weyerhauser Millicoma Tree Farm, company road 6040, 43.3429°, -123.8435°, 21 November 1971, E. M. Benedict, mm; 6 mi east, 2 mi south of Allegany, Weyerhauser Millicoma Tree Farm, company road 5000, 43.3944°, -123.9111°, 20 November 1971, E. M. Benedict, m, f; 6 mi east of Allegany, Game Commission cabin, 43.4311°, -123.9094°, 20 November 1971, E. M. Benedict, mm.



FIGURES 85–90. ***Rowlandesmus millicoma*, n. gen., n. sp. 85**. Head and anterior rings, dorsal view. **86**. Midbody ring, dorsal view. **87**. Pygidium, lateral view. **88**. Gonopods *in situ*, lateral view. **89**. Same, ventral view. **90**. Same, ventrolateral view. SEM stub 33-5. Abbreviations: **k**, "kink" in gonopod; **p**, pulvillus; **x, y, z**, processes of terminal zone.

Rowlandesmus dentogonopus Shear & Marek, n. sp.

Figs 91–95, 132

Type. male holotype from 2 mi north of Melrose, Douglas Co., Oregon, 43.2084°, -123.4612°, 400 ft asl, collected 7 February 1972 by E. M. Benedict. The holotype is mounted on SEM stubs WS33-3 and WS33-4, deposited in CAS.

Diagnosis. The gonopod has a hood-like structure with numerous acute teeth overhanging the bent terminal zone. The "kink" in the gonopod is basal to the division of the terminal zone and the pulvillus is more distal than in the preceding species.

Etymology. The species epithet is an adjective referring to the teeth on the gonopod.

Description. Male holotype. Length about 5.5 mm, greatest width 0.62 mm. Head (Fig. 91) densely setose, cuticle alveolate. Collum with anterior marginal row of 20 setae (Fig. 91). Anterior metazonites with three rows of setae, transitioning to four rows about ring 5, setal tubercles becoming almost obsolete on midbody to posterior rings (Fig. 95). Alveolate cuticle absent from metazonite posterior to collum. Epiproct (Fig. 92) swollen, short, slightly decurved, with some slight alveolate cuticle. Anterior legs crassate, tarsi with sphaerotrichomes. Gonopod (Figs 93, 94, 132) with moderately inflated prefemorite. Acropodite short, robust, basally swollen. Pulvillus (**p**, Fig. 93) distal, just below deflexed part of terminal zone, pulvillar process absent. Terminal zone bifurcate. Longer distal process (**x**, Fig. 93) broad at base, then curved, narrowed, bent posteriorly at acute angle; shorter basal process (**y,** Fig. 93) distal to "kink (**k**, Fig. 93)". Bent portion of terminal zone overhung by hood-like structure bearing numerous teeth, teeth larger on margin. Females unknown.

Distribution. Known only from the type locality.

Benedictesmus Shear & Marek, new genus

Type Species: *Benedictesmus aureus* Shear & Marek, n. sp.

Species included: ***Bendictesmus aureus,* n. sp., *B. ellenae,* n. sp., *B. yaquina*, n. sp.** and ***B. timber,* n. sp.**

Diagnosis. Males of some *Benedictesmus* species have only 18 postcephalic rings, while females have 19. The short, simple gonopods have a bifurcate terminal zone (**tz,** Figs 101, 105); the pulvillus may be extended into a tube (*B. ellenae,* **n. sp.**, Fig. 106).

Etymology. The genus is named for the late Ellen M. Benedict (1931–2005), a pseudoscorpion specialist who provided much of the material for this study. Dr. Benedict taught at Portland State University, Malhuer Field Station and Pacific University.

Distribution. Coastal eastern Oregon.

Benedictesmus aureus Shear & Marek, n. sp.

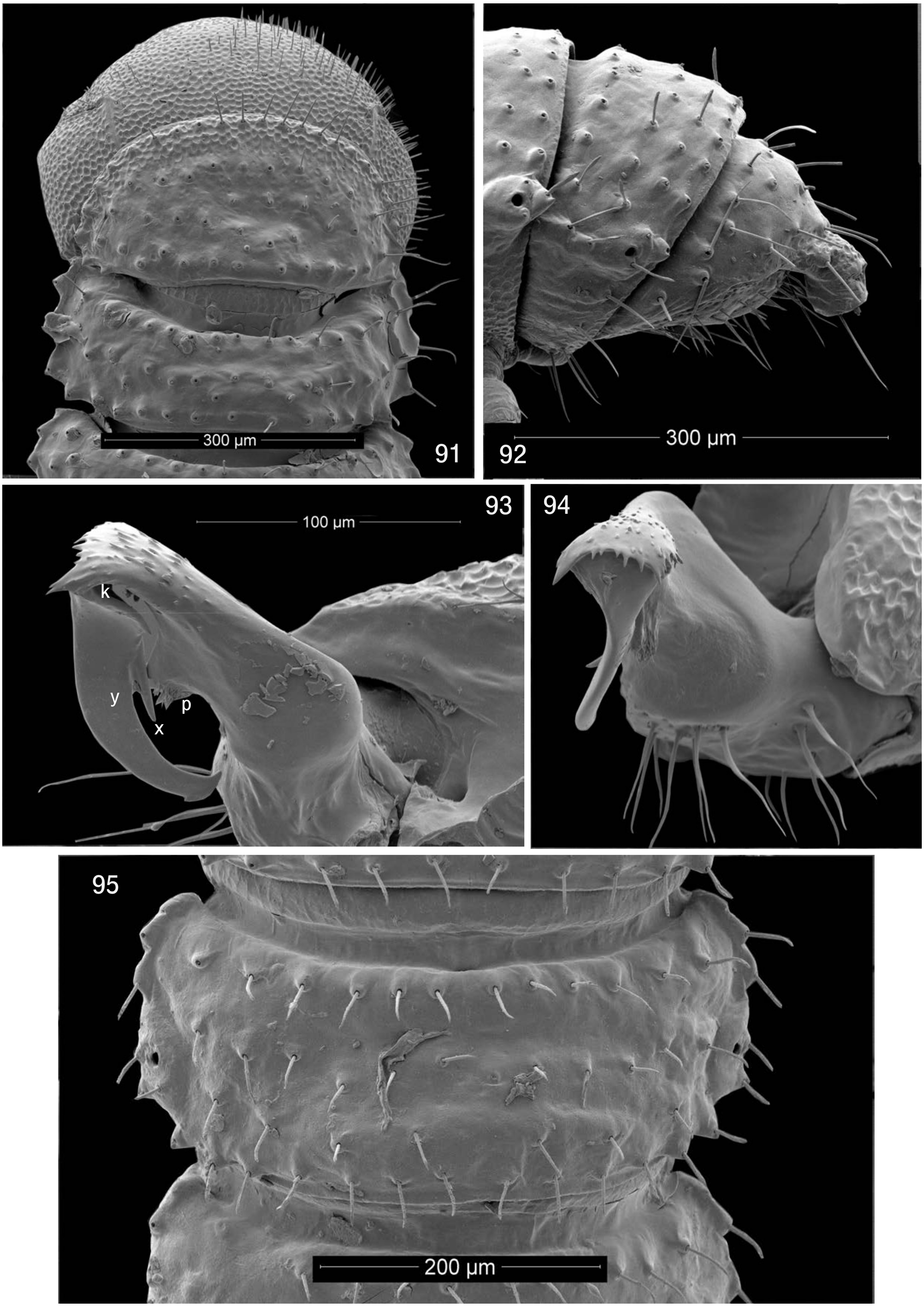
Figs 96–101, 133

Types. Male holotype and male and female paratypes from 13 mi East of Gold Beach on the road to Agness, 42.4932°, -124.2194°, Curry Co., Oregon, collected 10 March 1972 by E. M. Benedict. All types deposited in CAS.

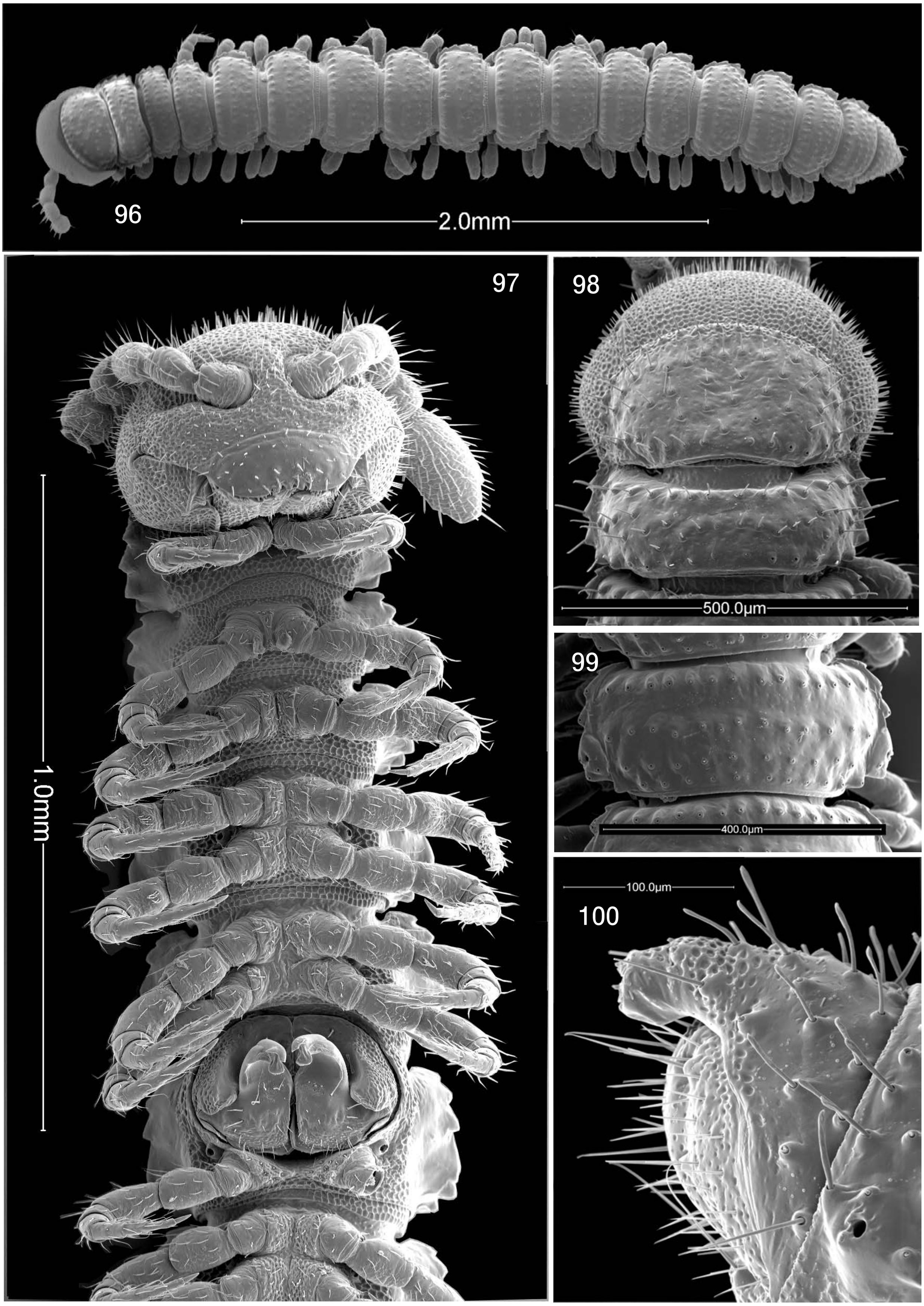
Diagnosis. Distinct from *B. ellenae,* **n. sp.**, which also has 18 rings in males, in the much shorter terminal zone of the gonopod and in having 20, rather than 18 setae in the anterior marginal row on the collum. The other two species of *Benedictesmus* have 19 rings in males. Females of all known species of *Benedictesmus* have 19 rings.

Etymology. The species name, an adjective, refers to Gold Beach, Oregon, the type locality.

Description. Male holotype. Eighteen rings (Fig. 96). Length about 3.0 mm, greatest width 0.41 mm. Head densely setose, cuticle alveolate (Fig. 98). Collum with anterior marginal row of 20 setae (Fig. 98). Anterior metazonites with three rows of setae, transitioning to four rows about ring 5, setal tubercles becoming almost obsolete on midbody (Fig. 99) to posterior rings. Alveolate cuticle absent from metazonites posterior to collum. Epiproct (Fig. 100) slightly swollen, short, slightly decurved, with alveolate cuticle. Anterior legs crassate (Fig. 97), tarsi with



FIGURES 91–95. ***Rowlandesmus dentogonopus*, n. gen., n. sp. 91**. Head and anterior rings, dorsal view. **92**. Pygidium, lateral view. **93**. Right gonopod, mesal view. **94**. Left gonopod, lateral view. **95**. Midbody ring, dorsal view. SEM stub WS33-4. Abbreviations: **k**, "kink" in gonopod, **p**, pulvillus; **x, y**, processes of terminal zone.



FIGURES 96–100. ***Benedictesmus aureus*, n. gen., n. sp. 96**. Male, dorsal view. **97**. Anterior part of male, ventral view. **98**. Head and anterior rings, dorsal view. **99**. Midbody ring, dorsal view. **100**. Pygidium, lateral view. SEM stub WS33-6.

sphaerotrichomes. Gonopod (Fig. 101, 133) with moderately inflated prefemorite, distal part of prefemorite with pore field, 3 or 4 setae (**ppf,** Fig.101). Acropodite short, robust, basally flattened. Pulvillus a short tube (**p,** Fig. 101). Distal, pulvillar process (**pp,** Fig. 101) extending over pulvillus as short hood. Terminal zone (**tz,** Fig. 101) short, bifurcate. Females with 19 rings, similar to males in nonsexual characters.

Distribution. Known from the type locality and one site a mile away (14 mi east of Gold Beach), where males and females were collected by E. M. Benedict on the same day as the types.

Notes. The pore field at the distal part of the gonopod prefemorite seems to be unique in this group of small polydesmids; among the pores are three or four long, curled setae.

Benedictesmus ellenae **Shear & Marek, n. sp.**

Figs 102–110, 134

Types. Male holotype and male paratype from 4 mi south of Pistol River on US 101, 42.3286°, -124.4219°, 200 ft asl, Curry Co., Oregon, collected 12 February 1972 by E. M. Benedict. All types deposited in CAS.

Diagnosis. The pulvillus of the gonopod is well separated from the terminal zone, a pulvillar process is absent, and the pulvillus is extended into a moderately long, membranous tube (Fig. 105). The anterior marginal setal row of the collum has 18 setae (Fig. 102).

Etymology. The species name recognizes the collector, Ellen M. Benedict.

Description. Male holotype. Eighteen rings. Length about 4.0 mm, greatest width 0.45 mm. Head densely setose, cuticle alveolate (Fig. 101). Collum (Fig. 102) with anterior marginal row of 18 setae. Anterior metazonites with three rows of setae, transitioning to four rows (Fig. 103) about ring 5, setal tubercles becoming almost obsolete on midbody to posterior rings. Alveolate cuticle absent from metazonites posterior to collum. Epiproct (Fig. 104) slightly swollen, short, strongly decurved, with alveolate cuticle. Anterior legs crassate, tarsi with sphaerotrichomes. Gonopod (Figs 105, 106, 134) with moderately inflated prefemorite. Acropodite short, robust. Pulvillus (**p,** Fig. 104, Fig. 105) basal to midlength of acropodite, extended as a tube (Fig. 106). Pulvillar process absent. Terminal zone (**tz,** Fig. 105) bifurcate, longer distal process flattened, curved; shorter process subtriangular. Females unknown, probably with 19 rings.

Distribution. Curry Co., Oregon.

Records*:* OREGON: *Curry Co.*: 1 mi north, 3 mi west of Brookings, 42.0708°, -124.3081°, sea level, 2 February 1972, E. M. Benedict, mm. These specimens had dried out and have been rehydrated.

Note*:* One of the male paratypes carried several minute nematodes attached to the head (Figs 107, 109, 110) and on some of the rings (Fig. 108). The nematodes, while firmly attached to the millipede's cuticle by their tails, are probably not parasites since there is no indication that the cuticle of the millipede has been penetrated—some nematodes have glands in the tail or spinnerets that secrete adhesives. More likely, they are commensal and phoretic. The nematodes appear as *Geraldius* or *Chambersiella* spp. and their coiling may indicate that they are anhydrobiotic (J. Eisenback, per. comm.).

Benedictesmus yaquina **Shear & Marek, n. sp.**

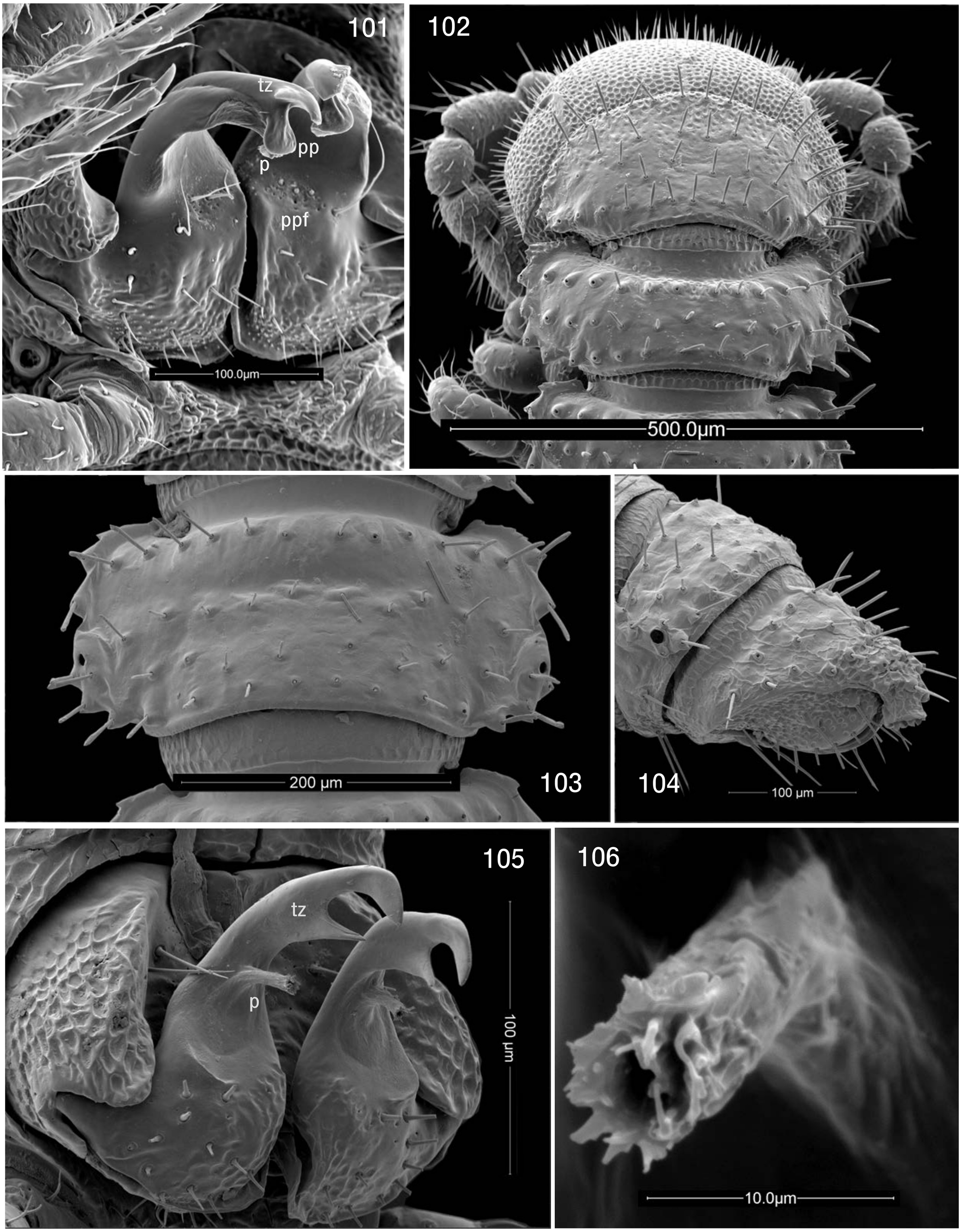
Figs 111–117, 135

Types. Male holotype and male and female paratypes from 0.6 m west of Elk City, Yaquina River, 44.6233°, -123.8918°, Lincoln Co., Oregon, collected 20 December 1971 by E. M. Benedict. All types deposited in CAS.

Diagnosis. Distinct from other species of the genus in having an unenlarged, straight epiproct (Fig. 113) and four rows of setae on the anterior metazonites (Fig. 112), increasing to five rows on the most posterior rings (Fig. 113).

Etymology. The species epithet, a noun in apposition, refers to the type locality along the Yaquina River.

Description. Holotype male. Nineteen rings (Fig. 111; the telson or 19th ring is concealed in the figure by the crassate anterior legs). Length about 5.5 mm, greatest width 0.62 mm. Head densely setose, cuticle alveolate (Fig. 112). Collum with anterior marginal row of 20 setae (Fig. 112). Anterior metazonites with four rows of setae, transitioning to four rows (Fig. 113) about ring 15, setal tubercles prominent throughout. Alveolate cuticle absent from metazonites posterior to collum. Epiproct (Fig. 114) not swollen, relatively long, straight, with extensive alveolate

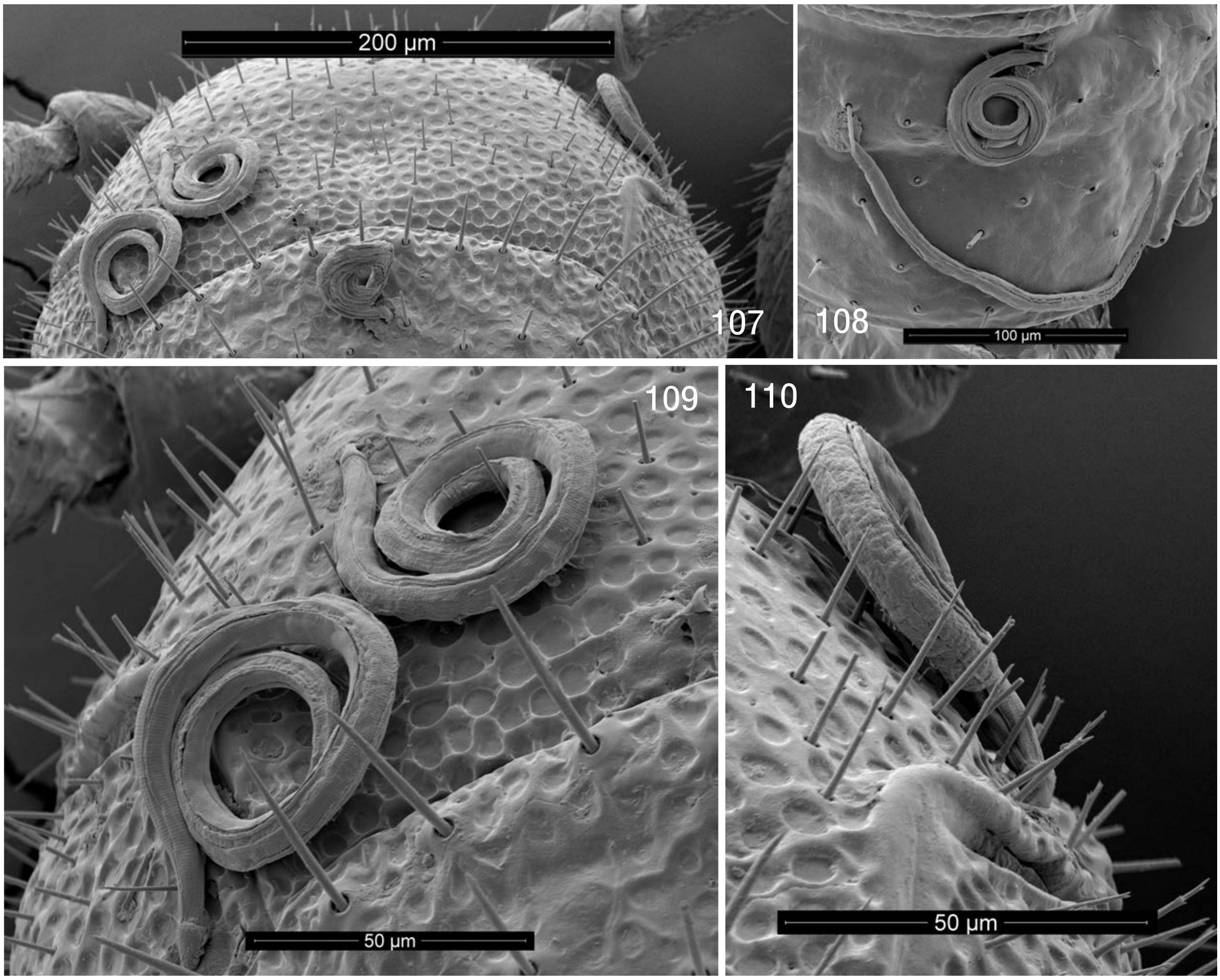


FIGURES 101–106. Species of ***Benedictesmus,* n. gen**. **101**, Gonopods of ***Benedictesmus aureus*, n. sp.**, ventral view. SEM stub WS33-6. **102–106**. ***Benedictesmus ellenae*, n. sp. 102**. Head and anterior rings, dorsal view. **103**. Midbody ring, dorsal view. **104**. Pygidium, lateral view. **105**. Gonopods *in situ*, lateroventral view. **106**. Pulvillus of gonopod. SEM stub WS33-13.Abbreviations: **p**, pulvillus; **pp**, pulvillar process; **ppf**, prefemorite pore field; **tz**, terminal zone.

cuticle. Anterior legs crassate (Fig. 111), tarsi with sphaerotrichomes. Gonopod (Figs 115–117, 135) with rather flattened prefemorite. Acropodite short, robust. Pulvillus (**p,** Fig. 116, 117) just distal to midlength of acropodite, somewhat elongate. Pulvillar process (**pp,** Fig. 116, 117) with short tooth on lateral side. Terminal zone entire (**tz,** Fig. 116, 117), with distinct apical tooth. Females similar to males in nonsexual characters.

Distribution. Benton, Douglas and Lincoln Cos., Oregon.

Records: OREGON: *Benton Co.*: 2.3 mi northwest of Glenbrook on South Fork of the Alsea River access road, 44.3313°, -123.4314°, 1200 ft asl, 4 December 1971, E. M. Benedict, mm; Clemens Park, Seely Creek Road, 0.3 mi from SR34, 44.4092°, -123.4644°, 400 ft asl, 4 December 2005, W. Leonard, C. Richart, mm, ff. *Douglas Co.*: 3.2 mi northeast of Scottsburg, 43.6617°, -123.7877°, 400 ft asl, 11 December 1971, E. M.Benedict, mm, f. *Lincoln Co.*: 1.4 mi west of Nashville, 44.6716°, -123.6100°, 600 ft asl, 20 December 1971, E. M. Benedict, mm.



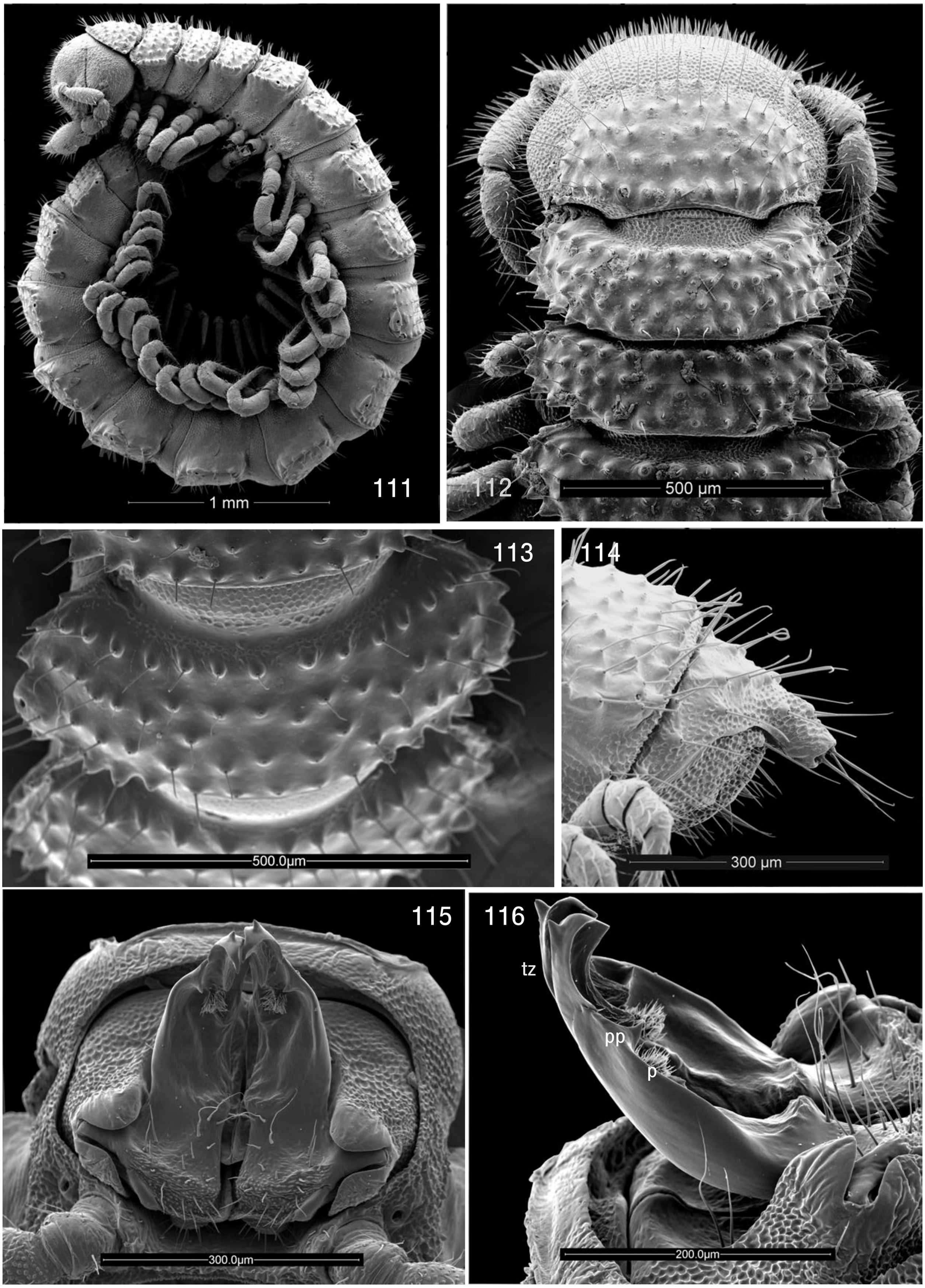
FIGURES 107–110. Commensal nematodes on ***Benedictesmus ellenae,*** **n. sp**. **107**. Four nematodes attached to head and collum. **108**. Two nematodes attached to a metazonite. **109**. Detail of nematodes attached to head. **110**. Nematode attached to head, lateral view. SEM stub WS33-13.

Benedictesmus timber **Shear & Marek, n. sp.**

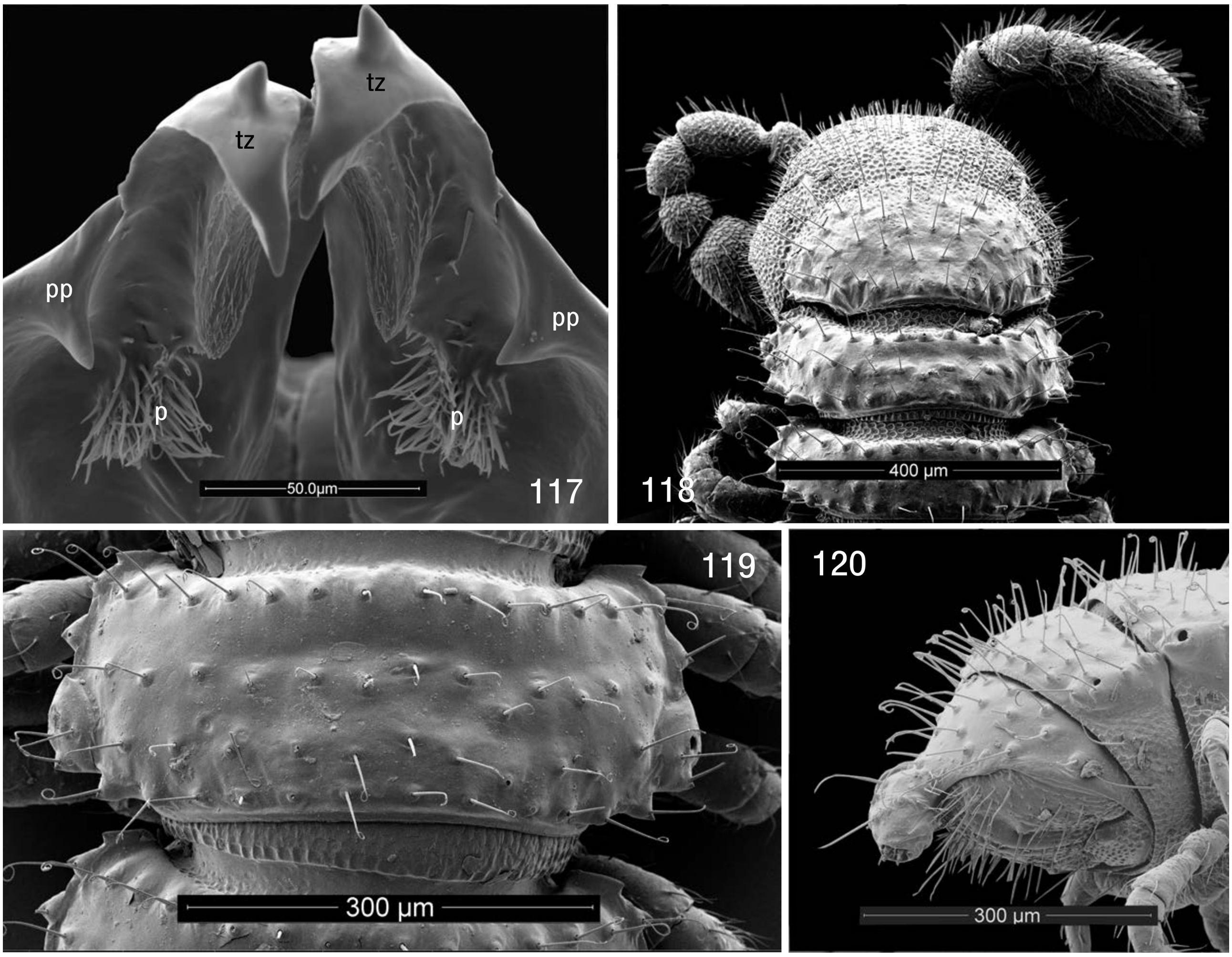
Figs 118–120, 136, 137

Type. Male holotype from 0.3 mi west of SPRR overpass on SR26, 3 mi west of Timber, 45.5251°, -123.2390°, Washington Co., Oregon, collected 27 November 1971 by E. M. Benedict. The holotype is mounted on SEM stub WS33-12, deposited in CAS.

Diagnosis. The terminal zone of the gonopods is unique among *Benedictesmus* species in that both terminal processes are bent or curled into hooks (Figs 136, 137).



FIGURES 111–116. ***Benedictesmus yaquina*, n. gen., n. sp. 111**. Male, lateral view. **112**. Head and anterior rings, dorsal view. **113**. Midbody ring, dorsal view. **114**. Pygidium, lateral view. **115**. Gonopods *in situ*, ventral view. **116**. Same, lateral view. SEM stub WS33-14. Abbreviations: **p**, pulvillus; **pp**, pulvillar process; **tz**, terminal zone.

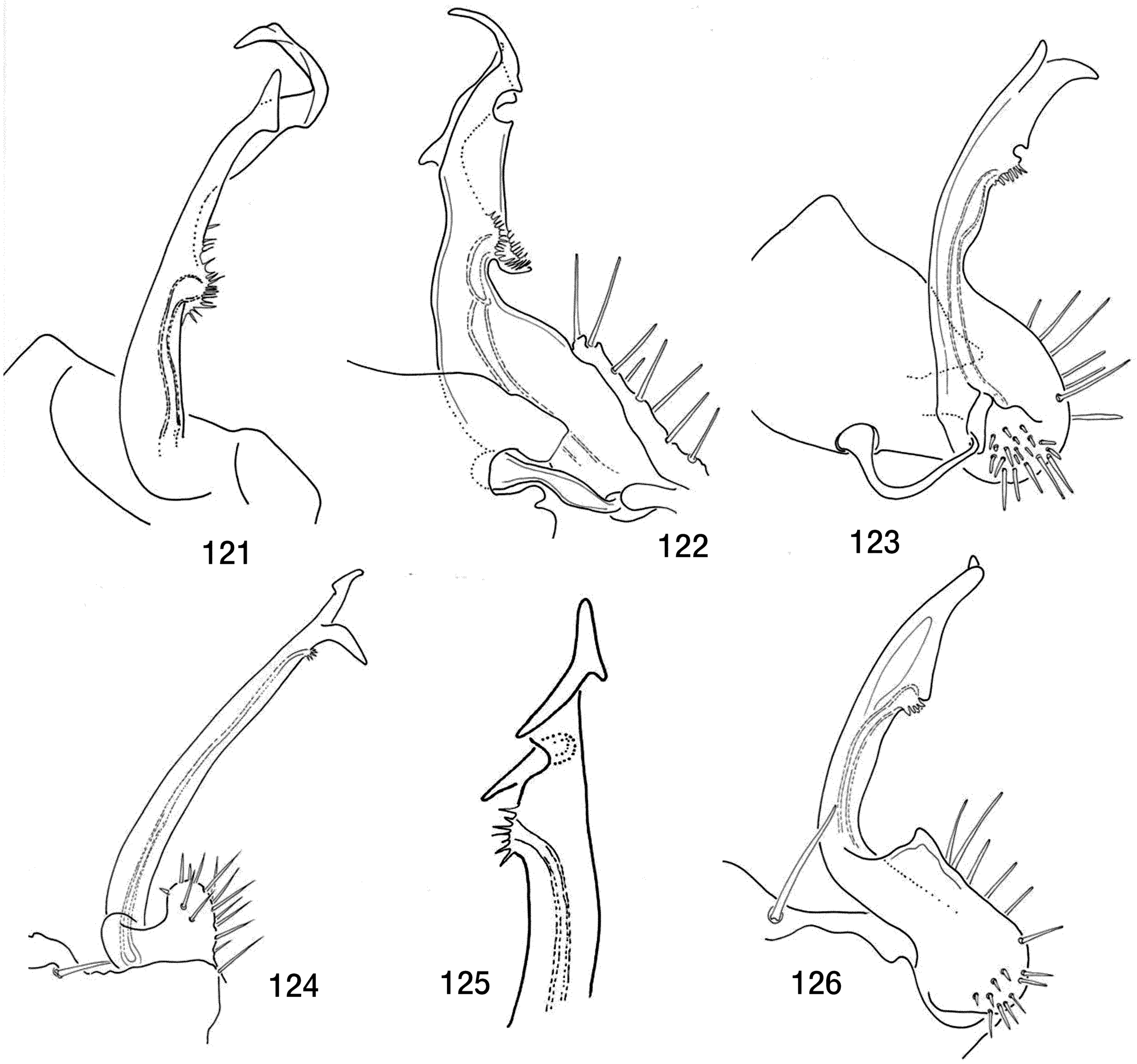


FIGURES 117–120. Species of ***Benedictesmus*, n. gen**. **117**. Gonopod tips of ***Benedictesmus yaquina*, n. sp.**, posterior view. SEM stub WS33-14. Figs **118–120**. ***Benedictesmus timber*, n. sp. 118**. Head and anterior rings, dorsal view. **119**. Midbody ring, dorsal view. **120**. Pygidium, lateral view. SEM stub WS33-12/ Abbreviations: **p**, pulvillus; **pp**, pulvillar process; **tz**, terminal zone.

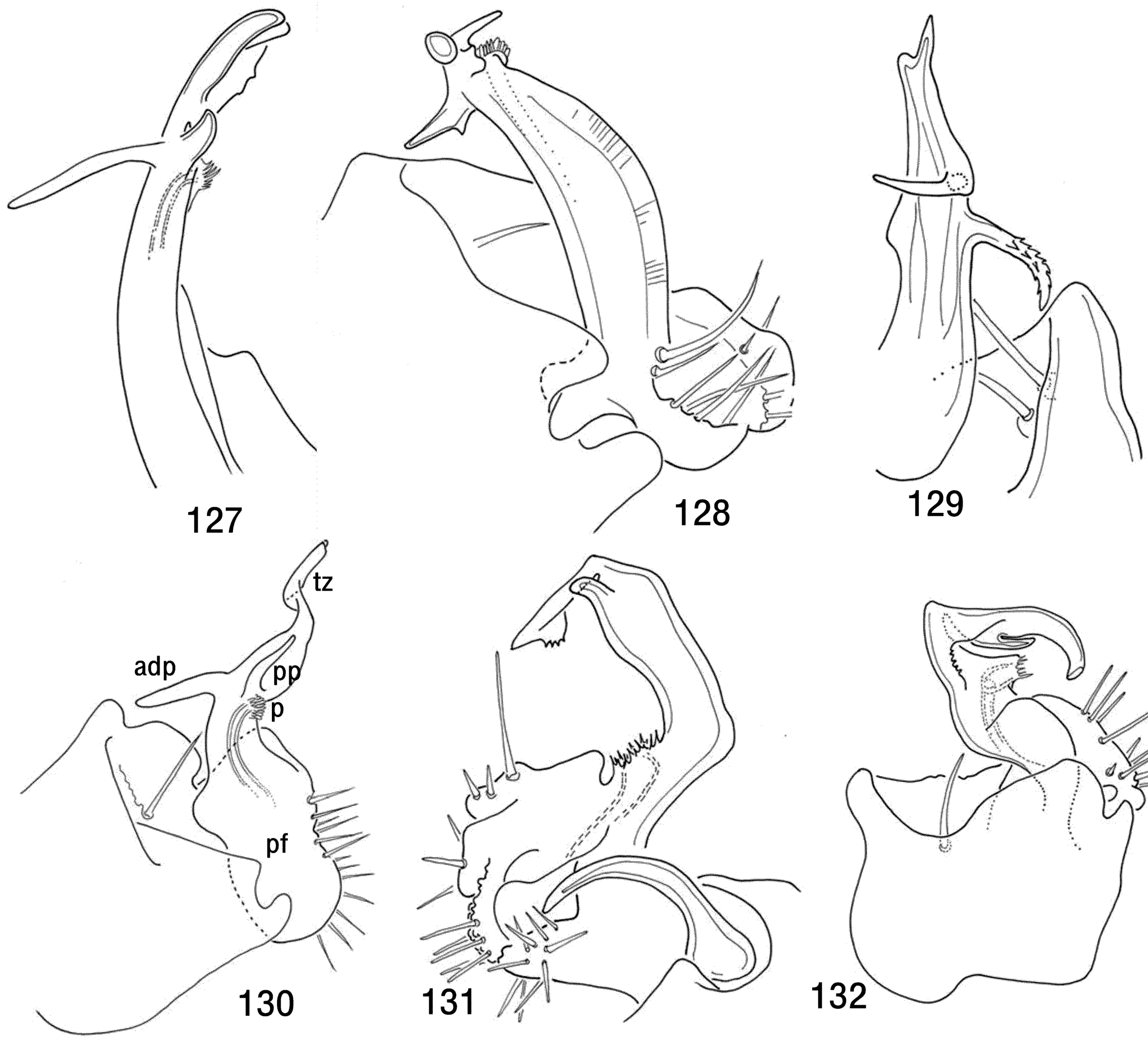
Etymology. The species name is a noun in apposition referring to the type locality near Timber, Oregon.

Description. Male holotype. Nineteen rings. Length about 5.0 mm, greatest width 0.52 mm. Head densely setose, cuticle alveolate (Fig. 118). Collum (Fig. 118) with anterior marginal row of 18 setae. Anterior metazonites with three rows of setae, transitioning to four rows (Fig. 119) about ring 7, setal tubercles becoming almost obsolete on midbody to posterior rings. Alveolate cuticle absent from metazonite posterior to collum. Epiproct (Fig. 120) greatly swollen, short, strongly decurved at nearly right angle, without alveolate cuticle. Anterior legs crassate, tarsi with sphaerotrichomes. Gonopod with flattened prefemorite. Acropodite short, robust. Pulvillus (**p,** Fig. 136) distal just below terminal zone, pulvillar process absent. Terminal zone bifurcate, both processes strongly curved, hook-like (Figs 136, 137). Females unknown.

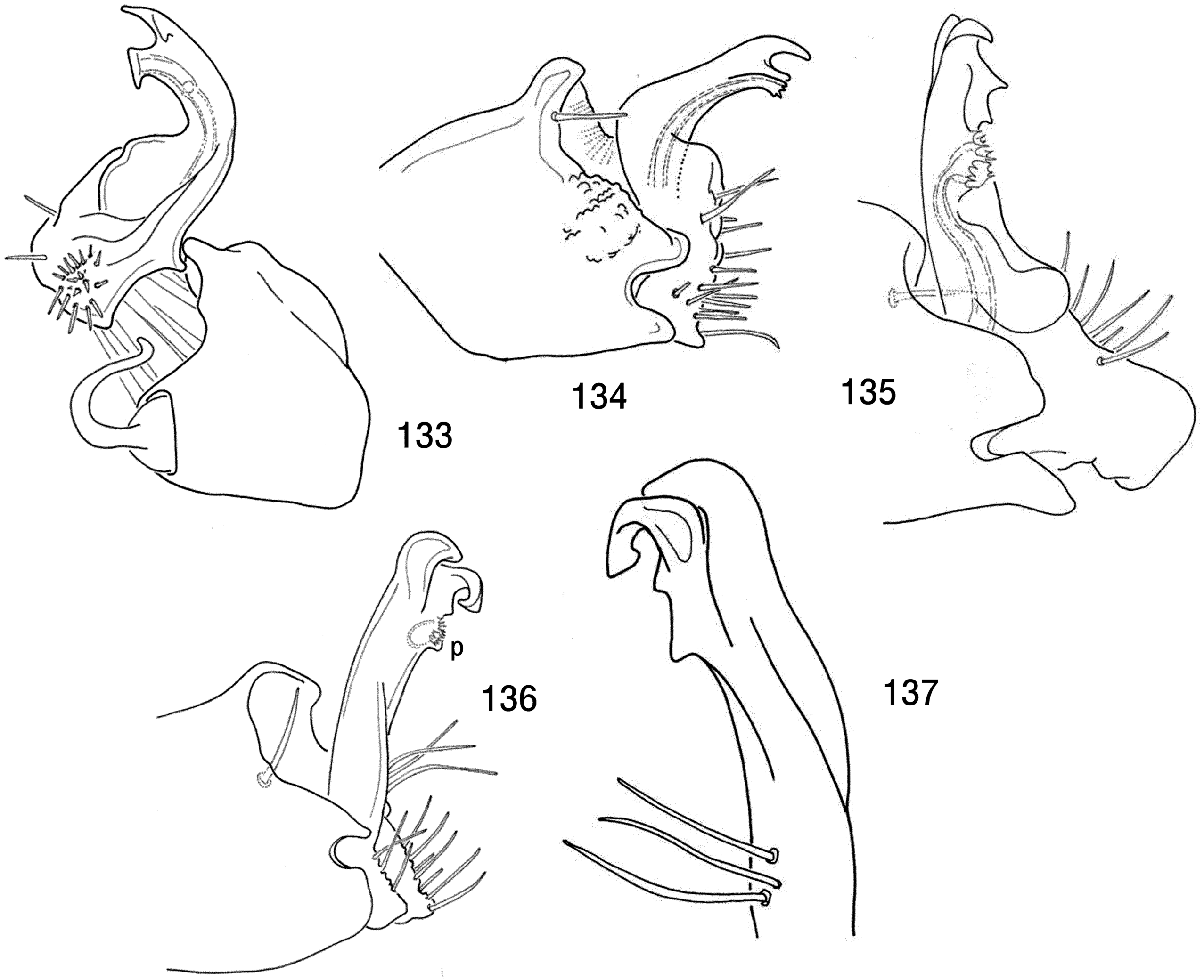
Distribution. Known only from the type locality.



FIGURES 121–126. Drawings of gonopods of polydesmid species. **121**. Left gonopod of *Retrorisia leonardi*, mesal view. **122**. Left gonopod of *Retrorsia benedictae,* mesal view. **123**. Left gonopod of ***Retrorsia richarti,*** **n. sp.**, mesal view. **124**. Right gonopod of ***Retrorsia gracilis,*** **n. sp.**, lateral view. **125**, Gonopod tip of *Retrorsia gracilis,* mesal view. **126**. Right gonopod of ***Retrorsia simplicissima***, **n. sp**., lateral view.

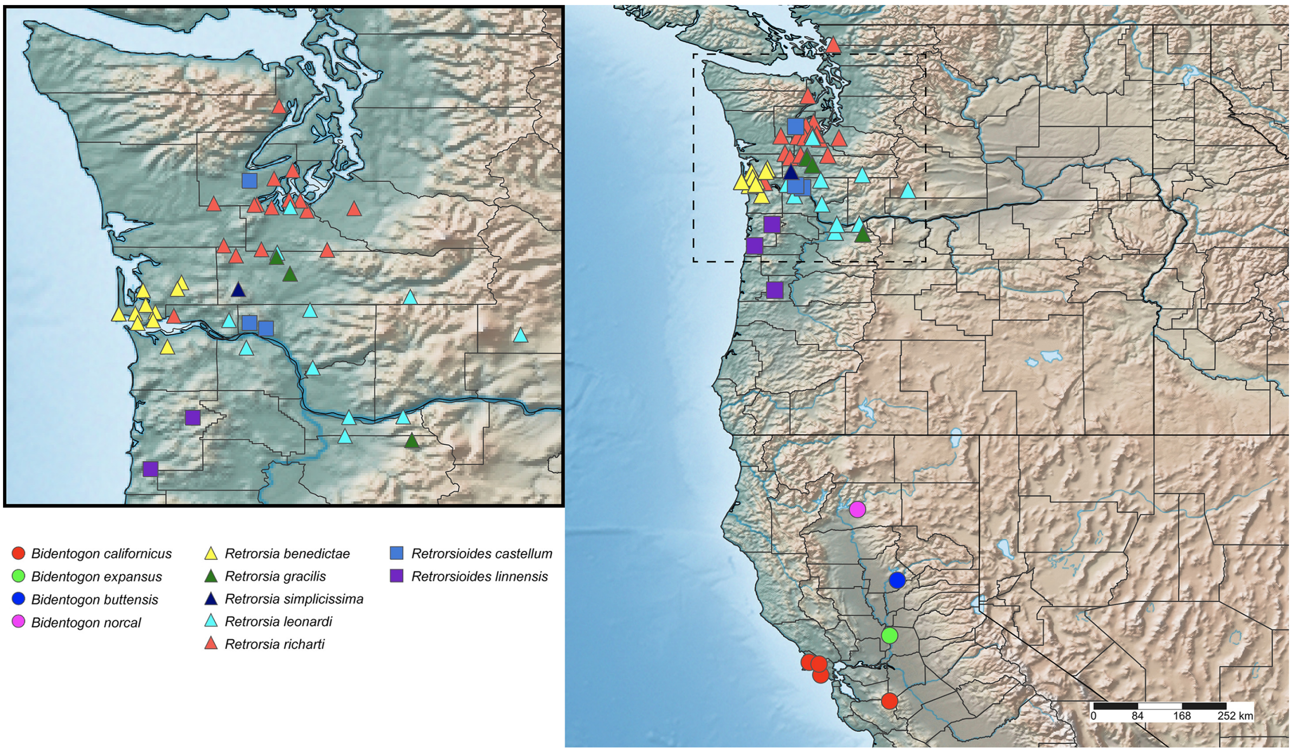


FIGURES 127–132. Drawings of gonopods of polydesmid species. **127**. Tip of gonopod of ***Retrorsioides castellum***, **n. sp.**, mesal view. **128**. Right gonopod of ***Retrorsioides linnensis***, **n. sp.**, lateral view. **129**. Left gonopod of ***Retrorsioides kittitas,*** **n. sp.,** lateral view. **130**. Right gonopod of ***Retrorsioides bannerti,*** **n. sp.**, lateral view. **131**. Right gonopod of ***Rowlandesmus millicoma***, **n. sp.**, mesal view. **132**. Right gonopod of ***Rowlandesmus dentogonopus***, **n. sp.**, lateral view. Abbreviations: **adp**, anteriorly directed process; **p**, pulvillus; **pf**, prefemorite; **pp**, pulvillar process; **tz**, terminal zone.



FIGURES 133–137. Drawings of gonopods of polydesmid species. **133**. Right gonopod of ***Benedictesmus aureus,*** **n. sp.**, mesal view. **134**. Right gonopod of ***Benedictesmus ellenae,*** **n. sp.**, lateral view. **135**, Right gonopod of ***Benedictesmus yaquina***, **n. sp.**, lateral view. Fig. **136**, **137**, ***Benedictesmus timber.*** **n. sp. 136**, Right gonopod, lateral view. **137**, Tip of right gonopod, mesal view. Abbreviation: **p**, pulvillus.

FIGURE 138. *Retrorsia leonardi* Shelley*,* living specimen in habitat. Photograph by William Leonard.



MAPS 1, 2. **Map 1**. Northwestern United States, records of small polydesmidans in California, Oregon and Washington; only records in this paper shown. Dashed lines show extent of Map 2. **Map 2**. Western Washington and northwestern Oregon, records of small polydesmidans; only records in this paper shown.

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