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Additions to the millipede family Caseyidae Verhoeff, 1909. VI. Proposal of the new subfamily Opioninae, new species and records of the genus *Opiona* Chamberlin, 1951 and synonymy of *Speyosia* Causey, 1963 with *Opiona* (Diplopoda, Chordeumatida, Striariidea)

WILLIAM A. SHEAR[1,*] & PAUL E. MAREK[2]
[1]*Professor Emeritus, Department of Biology, Hampden-Sydney College, Hampden-Sydney VA 23943 USA*
current address: 1950 Price Drive, Farmville VA 23901 USA
wshear@hsc.edu; https://orcid.org/0000-0002-5887-7003
[2]*Department of Entomology, Virginia Tech, Blacksburg VA 24061 USA*
pmarek@vt.edu; https://orcid.org/0000-0002-7048-2514
[*]*Corresponding author*

Abstract

The caseyid millipede genus *Opiona* Chamberlin, 1951 contains 15 species distributed from southern Alaska and the Canadian province of British Columbia south to Santa Cruz County, California. We provide new records and range extensions of five previously described species and describe five new species: *Opiona arcata* **sp. nov.**, *O. johnsoni* **sp. nov.**, *O. alsea* **sp. nov.**, *O. triangalensis* **sp. nov.**, and *O. laquesis* **sp. nov.**. The following new synonym and combination are proposed: *Opiona* Chamberlin, 1951 = *Speoseya* Causey, 1963, **syn. nov.** and *Opiona grahami* (Causey, 1963) = *Speoseya grahami* Causey, 1963, **comb. nov.**—the valid names being the former. We propose a new subfamily Opioninae, **subfam. nov.**, to include *Opiona; Metopiona* Gardner & Shelley, 1989; *Opionoides* Shear & Marek, 2025*; Paropiona* Shear & Marek 2025; and *Benlomondia* Shear & Marek, 2025.

Key words: taxonomy, California, Oregon, Washington, gonopods, secondary sexual modifications, new synonym

Introduction

The genus *Opiona* Chamberlin, 1951, ranges from Santa Cruz County, California, in the south, north to localities on the southeast coast of Alaska (Alexander Archipelago). Gardner and Shelley (1989) described the range of the genus as comprising two areas: one from Santa Cruz County to Mendocino County in California, and the other from southwestern Oregon to Vancouver Island, Canada [the extension of the range north to Alaska was established by Shelley *et al.* (2007)]. We bridge the gap between these two regions with new records of described species, and new species. All records are from caves or mesic forest habitats, and with the exception of a few records of *O. columbiana* Chamberlin, 1951 from Spokane County, Washington, are west of the Coast and Cascade Ranges. As with nearly all Chordeumatida known from the Pacific tier of U.S. states and Canadian provinces, *Opiona* species are sexually mature, active and collectable during the cooler, wetter season stretching variably from November to May—times when most collectors are unlikely to be active. In the dry, warm summer, individuals, mostly juveniles, appear to retreat to deeper layers of the soil where moisture may be retained. This lack of time-focused activity by collectors may help account for the apparent, but illusory, geographical division of the range of the genus.

Chamberlin (1951) described the genus *Opiona* for the type species *Opiona columbiana*. Twelve years later, Causey (1963) added *Opiona siliquae* Causey, 1963, and following that paper, nothing further of substance appeared on the genus for 26 years. Gardner & Shelley (1989) reviewed the family Caseyidae Verhoeff, 1909 and added 11 new species to *Opiona*, one of which (*Opiona communis* Gardner & Shelley 1989) was described as having 3 subspecies. The type species, *O. columbiana*, originally described from Vancouver Island, British Columbia, was found by Shelley *et al.* (2007) to range from near the Oregon-Washington border to Wrangell Island in southern Alaska—with

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a possible two additional localities as much as 250 miles north of Wrangell Island along the narrow Alaskan coastal strip (these localities were represented by females only but are highly likely to be for *O. columbiana*). Shear (2011) added the first troglobitic species of the genus, *Opiona groeningi* Shear, 2011, from caves in the Marble Mountains of Siskiyou County, California. Shear & Crawford (2019) described the troglophile *Opiona caseophila* Shear & Crawford, 2019 from Oregon Caves National Monument, Josephine County, Oregon.

As suggested by Shear (2011), the previously described species of *Opiona* seem to fall into two groups based on the presence or absence of two gonopod structures, vestigial telopodites and posterior projections of the gonopod sternum. Here we suggest a third group of miniature species (< 5 mm long) with reduced modifications of the anterior legs in males, differently modified ninth legs, and specialized flagellocoxites. However, we have not examined all described species, so such groupings should be considered tentative.

Shear & Leonard (2007) and Shear (2011) did not agree with the interpretation of caseyid gonopods by Gardner & Shelley (1989), though their interpretation was reasonable at the time it was proposed. We elaborate further on this theme in a section below, with special reference to the gonopods of *Opiona* species. It should also be noted that assigning homologous names to the structures of chordeumatidan gonopods is tentative and difficult because of the great degree of modification that has taken place, and this is especially true of the caseyids.

Causey (1963) described the genus *Speoseya* for the type species—troglobite *Speoseya grahami* Causey, 1963. We examined the holotype of *Speoseya grahami* Causey, 1963, and found that the gonopods and other characters are not significantly different from those of species of *Opiona*. Therefore we here synonymize *Speoseya* with *Opiona,* and create the new combination *Opiona grahami* (Causey, 1963), **comb. nov.**

Methods

Specimens were field-preserved in various concentrations of alcohol but are now in 70% ethanol. Morphological studies were done using an Olympus SZH stereomicroscope and an Olympus BX50 compound microscope equipped with Nomarski optics. For scanning electron microscopy (SEM), specimens were first cleaned in an ultrasonic cleaner, then mounted on 12.7 mm diameter aluminum stubs using double-sided adhesive carbon discs and allowed to air-dry. These were sputter coated with a 40-nm thick layer of gold and palladium using a Cressington 208HR sputter coater and a Cressington MTM20 thickness controller. SEM micrographs were taken with a FEI Quanta 600 FEG environmental scanning electron microscope. Micrographs were edited and refined using GIMP, and plates were composed in InkScape. Geographic coordinates were recorded from label data, and in some cases, retrospectively georeferenced in Google Earth; some label data was too imprecise to do so.

List of abbreviations

EMUCB	Essig Museum, University of California, Berkeley, California
FSCA	Florida State Collection of Arthropods, Gainesville, Florida
FMNH	Field Museum of Natural History, Chicago, Illinois
VMNH	Virginia Museum of Natural History, Martinsville, Virginia
ac	angiocoxite
ap	accessory pore
cc	colpocoxite
cg	coxal gland
cl	coxal lobe
col	collum
cp	coxal process
cx#	coxa of numbered leg
cxg	coxa of gonopod
f, ff	female, females
f#	femur of numbered leg
flc	flagellocoxite

flcd	dorsal branch of flagellocoxite
flcm	major branch of flagellocoxite
flct	tubular branch(es) of flagellocoxite
m, mm	male, males
p	pore
prf#	prefemur of numbered leg
ptf#	postfemur of numbered leg
R#	numbered ring
s#	sternum of numbered legpair
sg	gonopod sternum
sp	sternal process
t#	tibia of numbered leg
tar	tarsus of numbered leg
tp	gonopod telopodite
t9	telopodite of leg 9
vd	opening of *vas deferens*

Results

Taxonomy

Order Chordeumatida Pocock, 1894

Suborder Striariidea Cook, 1896

Superfamily Caseyoidea Verhoeff, 1909

Family Caseyidae Verhoeff, 1909

Caseyidae Verhoeff, 1909: 567. Cook & Collins 1895: 68; Chamberlin 1941a: 22, 1941b: 10, 1947: 9, 1951:8, 1952: 2; Causey 1952: 113, 1954: 81, 1955: 90, 1963: 193; Loomis 1966: 225; Shear 1972: 258, 2011: 50, 2021: 109, Shear & Crawford 2019: 575; Shear & Leonard 2007: 23; Gardner & Shelley 1989: 185; Shelley 1993: 168; Shelley *et al.* 2007: 14.
Underwoodiidae Verhoeff, 1909: 568. Palmén 1952: 3; Causey 1963: 193; Shelley 1993:169.

The nominal family Underwoodiidae Verhoeff, 1909, was first synonymized with Caseyidae by Causey (1963). The synonymy was supported in a revision of *Underwoodia* Cook & Collins, 1895, by Shelley (1993).

Subfamilies of Caseyidae

With the diagnosis below of Opioninae, the assignment of known caseyid genera to subfamilies—with the possible exception of *Martenseya* Shear, 2021—is as follows:

Subfamily Caseyinae Verhoeff, 1909. Monobasic with only the genus *Caseya* Cook & Collins, 1895. The subfamily may be diagnosed by the enlargement and modification of the male seventh coxae and the extraordinary complexity of the gonopods (see Gardner & Shelley 1989, and Shear & Leonard 2007).

Subfamily Underwoodiinae Cook & Collins, 1895. *Underwoodia* Cook & Collins, 1895; *Martenseya* Shear, 2021. The subfamily may be diagnosed by its much simpler gonopods, consisting only of anterior and posterior angiocoxites and lacking flagella or pseudoflagella. The inclusion here of *Martenseya* may be subject to later change; the single species of the genus is so different from all other caseyids that the discovery of additional species may require the establishment of a new family. For the time being, it fits here on the basis of the similar modifications of the male

anterior legs to those of *Underwoodia.* According to Shelley (1993), *Underwoodia* includes three species: two from North America and one from the Russian Far East. However, the gonopods of the three species are nearly identical. Given that all three species are ostensibly parthenogenic Shelley (1993) found that the sex ratio among museum specimens was 80:1 in favor of females), it is not inconceivable that there is really just a single species.

Subfamily Opioninae Shear & Marek, ***new subfamily****.* The included genera are listed below and a diagnosis is given.

Subfamily Ochrogrammatinae Shear & Marek, 2024. *Ochrogramma* Gardner & Shelley, 1989; *Vasingtona* Chamberlin, 1941b. The ventrally projecting, flattened process of the male mandible is unique to this subfamily. The gonopods are characterized by highly branched, dendritic angiocoxite processes.

Subfamily Opioninae Shear & Marek, new subfamily

Type genus. *Opiona* Chamberlin, 1951

Diagnosis. Distinct from subfamily Ochrogrammatinae Shear & Marek, 2024 in the unmodified mandibles of males (*vs.* ochrogrammatine mandibular stipes with broad distolateral lamina), from Caseyinae Verhoeff, 1909, in the unmodified seventh coxae of males (*vs*. caseyine seventh coxae enlarged, with 2–4 distal processes), and from Underwoodiinae in having gonopods with flagella or pseudoflagella (*vs.* underwoodiine gonopods lacking flagella or pseudoflagella).

Short description. Male first legs with 6 podomeres, robust, with various specialized setae. Male second legs with gonapophyses (gonapophyses absent in one species); second leg telopodites reduced in size, with 3–6 podomeres. Male third legs with coxal lobes (absent in one species); telopodites reduced in size, often with flattened, broad prefemur, claw lacking or present as a long filament. Fourth through seventh legs of normal size, slightly or not at all crassate. Gonopods highly variable from genus to genus, consisting of angiocoxites (often two-branched), flagellocoxites (absent in one genus) and lobular, poorly sclerotized colpocoxites. Ninth legs greatly reduced, coxae with process; telopodite of one podomere, flattened and button-like or elongate. Tenth coxae enlarged, with prominent coxal glands and usually a distal process varying from a low knob to a long, curved hook.

Included genera. *Opiona* Chamberlin, 1951; *Metopiona* Gardner & Shelley, 1989; *Paropiona* Shear & Marek, 2025a; *Opionoides* Shear & Marek, 2025a; and *Benlomondia* Shear & Marek, 2025b.

Genus *Opiona* Chamberlin, 1951

Opiona Chamberlin, 1951: 8. Gardner & Shelley 1989: 203; Shear 2011: 51. Shear & Crawford 2019: 575.
Speoseya Causey, 1963: 195. **New synonymy.**
Type species*: Opiona columbiana* Chamberlin, 1951. Of *Speyosia, S. grahami* Causey, 1963.

Diagnosis. *Opiona* differs from the other genera of the subfamily in having gonopods with complex flagellocoxites, as described below.

Description and notes. The genus was described in detail by Gardner & Shelley (1989) and we add the following notes. The male head does not differ from the female in any meaningful way and the male mandibles and gnathochilarium are not modified. The eye may consist of as many as 20 ommatidia, as few as two, or be absent altogether (in one of the two troglobitic/troglophilic species). The trunk consists of 30 rings, including the collum and telson. Preserved males often show a "humpbacked" appearance due to the contraction of strong muscles associated with the third legpair; the fourth ring is expanded to accommodate these muscles (Fig. 17). Males can often be identified as such in the field because of the large, single-articled telopodites of legpair 9, which project from the sides of the body at the seventh ring.

The male pregonopodal leg modifications are as follows. The first legpair (Fig. 1, *i.e.*) is robust, but perhaps shorter than pairs 4–7, with 6 podomeres. Parenthetically, Gardner & Shelley (1989) show the telopodites of all legs posterior to legpair 2 (when illustrated) as having 6 podomeres—they missed the trochanter in these legs. The prefemur may be laterally flattened, or have a depressed mesal surface. The postfemur and tibia carry stout setae that

are variously modified, flattened and slightly spiraled, strongly hooked or mace-like. The hooked setae, if present, may have many small spiculate projections; they transition distally to the spatulate type by first losing the spicules, then uncurling, flattening and assuming a spiral shape distally. Similarly, the mace-like setae also transition distally to the spatulate type. In some species, the postfemora and tibiae of the first legpair have distal knobs.

The male second legpair (Fig. 27, *i.e.*) is variously reduced and may consist of as few as three podomeres, or as many as six. A terminal claw is usually absent, or long and filamentous. Gonapophyses arise from the coxae and the openings of the *vas deferens* are at their bases, but there may also be a more distal pore that has been observed via SEM in some species. The gonapophyses may be densely setose, with long, flexuous setae, and are variable in length compared to the telopodites; they can be longer, shorter or about the same length.

The male legpair three (Fig. 3, *i.e.*) has the coxae extended into long or short distal lobes, with the small telopodites articulated laterally at the distal ends of the coxae, the lobes thereafter extending further ventrad. The tips of the lobes are set with distinctive recumbent setae, or with a tuft of erect setae. The telopodites are reduced but usually have fewer than six segments. The prefemur is usually expanded and flattened, with more recumbent setae, while the more distal podomeres are small. The joint between the tibia and the tarsus may be obscure but the distal end of the tibia is marked by a single long seta. The tarsus and tarsal claw are reduced to mere nubbins or a long filament.

Male legpairs 4–7 may be slightly more robust than the postgonopodal legs but not conspicuously so in most species.

The early interpretation of the gonopods in this genus by Gardner & Shelley (1989), while consistent with understanding at the time, was not correct. The gonopod (see Figs 28–32) consists of 3 basic units: the sternum, coxa and, sometimes, the telopodite. The sternum is generally well defined and sclerotized and may completely envelop the coxal base—and sometimes have extended processes which meet in the posterior midline. However, some species trend in the direction of coxal/sternal fusion into a coxosternite. The coxa has a relatively simple body, lacking setae. Anteriorly the coxa is prolonged into an angiocoxite, the largest and most obvious part of the gonopod. Gardner & Shelley (1989) mistakenly called this the "colpocoxite." The angiocoxite usually has two or three divisions, anterior (the largest) and one or two more posterior. These divisions could be considered anterior and posterior angiocoxites, respectively, but do not appear to be separate as in other caseyids such as *Ochrogramma* species, so such a designation is probably not warranted. They can be called anterior and posterior branches. Posteriolateral to the anterior division of the angiocoxite is a complex flagellocoxite, usually divided into three to many pseudoflagella (not independently movable from a base). The flagellocoxite is directed sharply anteriorly, then curving back just as sharply posteriorly to extend lateral to the angiocoxites. The flagellocoxite can be complex. Usually there is a group of pseudoflagella inserted in a sheathing process from the angiocoxite, but in addition, there can be a bladelike process arising from the base of the flagellocoxite—and this too may be sheathed in some species. Another process can be quite thin and set with many long spicules. In Gardner & Shelley's (1989) drawings, the pseudoflagella are depicted as simple, single lines, but this is misleading and probably due to using relatively low magnifications to make the drawings. SEM examination shows that the pseudoflagella are in reality hollow tubes. In one group of species, the posterior division of the angiocoxite forms multiple sheaths for these pseudoflagella, each one evidently in its own slot; this is hard to describe. The flagellocoxite takes a different form in the miniature species described below and will be detailed there. Most posterior on the coxa is the colpocoxite, a poorly sclerotized sac probably homologous to the coxal gland. In SEM these usually collapse, but in the Gardner & Shelley (1989) illustrations they appear as lobes, probably their natural condition. Most lateral on the coxa is the articulation of the telopodite [called "sternal process" by Gardner & Shelley (1989)]. In their drawings, no articulation is shown and the telopodite is drawn as if it arises from the lateral lobe of the sternum. In reality, SEM study shows it is articulated to the coxa or to the coxal part of a coxosternite and may be movable from a socket. The telopodite may be absent in some species but in others it is a small, sometimes curved rod with setae at its tip (this is more evidence it is not sternal because the sterna never bear setae). In other species the distal setae are missing. This suggests a possible trend of reduction to eventual absence of the telopodite.

Causey (1963) misinterpreted the gonopods of *Opiona* in her descriptions of *O. siliquae* and *Speyosia grahami*, a *lapsus* that went unremarked by Gardner & Shelley (1989). Causey thought that the gonopods were composed of both the eighth and ninth pair of legs and thus called the actual ninth legs the tenth legs, and the actual tenth legs the eleventh legs. Causey did not label her drawings, but from her text it would appear that she thought the flagellocoxites were the "posterior gonopods." It is difficult to reconcile the rather simple sketches of *O. siliquae*

gonopods of Gardner & Shelley (1989) with the more detailed drawings of Causey (1963). New material of *O. siliquae* needs to be obtained for restudy.

The male ninth legs (Fig. 7, *i.e.*), called "posterior gonopods" after the fashion of the times by Gardner & Shelley (1989), are typical caseyoid. A globular or flattened coxa carries a mesal process that may be deeply divided or long and hooklike and that projects ventroposteriorly. It may rarely be divided. There is often also a lateral process, and in some species, this is almost membranous and tightly appressed to the telopodite [thus in those cases it was missed by Gardner & Shelley (1989) and revealed only by SEM]. SEM has also revealed small gland openings near the base of the mesal process; the openings were illustrated by Causey (1963) in her descriptions of *O. siliquae* and *S. grahami*, but were not mentioned in her text. The telopodite is either broad or flattened in lateral view—button-like. There may be grooves or rough, toothy areas on the telopodite. In at least two species, Gardner & Shelley (1989) seem to illustrate the telopodite as having two or even 3 articles, but this is actually a groove ("sulcus") or grooves in a single article. In a few species the male ninth leg telopodite seems complexly folded, and in a few others has a patch of triangular teeth.

The male tenth leg coxae (Fig. 8, *i.e.*) have the usual large coxal glands and invariably posteriorly directed, mesal processes which vary in form from a triangular nubbin to a long, but blunt, hook.

Gardner & Shelley (1989) illustrated female genitalia for the species they described, but in most cases we were unable to apply these characters to females not associated with males. The female genitalia (Fig. 15) consist of two pairs of weakly sclerotized lobes anteriorly capped on each side by another lobe referred to as the receptacle. All these structures are densely setose, but Gardner & Shelley (1989) illustrated them without setae. The use of female genitalia in diplopod systematics is a fraught subject because few distinctive characters can be found, in contrast to the often elaborate male gonopods. In addition, the female genitalia, often referred to as "cyphopods," though they are not derived from an appendage, are extensible and their appearance may be quite different in mated or unmated specimens (pers. obs., WAS). In some chordeumatidan taxa, such as the genus *Cleidogona,* there are postgenital plates developed from the second sternum, and these do appear distinctive from species to species (Shear 1972; Snyder & Shear, in press). Such features do not appear in *Opiona* species. It remains an interesting evolutionary question as to why the male intromittent organs are so elaborate and species-specific, while the female organs are so relatively uniform.

Shear (2011) suggested that *Opiona* species fall into two distinct groups. In a group containing the majority of species, including the genotype, the structure of the gonopod is as follows: a vestigial telopodite is present, usually with distal setae but sometimes as a simple rod, or with a long, distal extension. The hollow, tubular pseudoflagella (tubular branches) of the flagellocoxite are numerous and inserted into a sheath proceeding posteriorly from the angiocoxite. There are no posterior sternal processes. We designate this as the Columbiana Group, including the species *columbiana, causalis, goedeni, exigua, graeningi, facetia, fisheri, scytonoides, catorhycha,* and the new species *arcata* and *johnsoni*, described below. The second group suggested by Shear (2011) lacks vestigial gonopod telopodites and the pseudoflagella are not sheathed. In these species, the gonopod sternum is extended posteriomesally on each side into processes which meet in the midline. We call this the Confusa Group, including the species *confusa, distincta, bifurcata,* and *beresseyae*.

We now find a third group of species, which, like the first group, have telopodites and sheathed flagella but are very small (< 5 mm long), with 2–4 ommatidia and reduced ninth legs in which the coxal process is present only as a small nubbin. The flagellocoxite in this group is also of a distinctive form (see descriptions below). This is the Alsea Group, and it consists of three new species described herein: *alsea, trianglensis* and *laqueus*.

Given the present knowledge, two species, *O. siliquae* Causey, 1963 and *O. grahami* (Causey, 1963), cannot be placed in a group. If these species groups were to be considered genera, the name *Opiona* would go with the Columbiana Group, which includes the genotype, and new names would be required for the remaining two groups. However we think that more study, particularly of the Confusa Group, would be required before such a division could be undertaken.

We consider *Speoseya* a synonym of *Opiona* because its only species has the same modifications of the male pregonopodal legs as the other species of that genus, and the morphology of the gonopods conforms to that described for *Opiona* species.

Included species. *Opiona* presently consists of 20 species, a number which includes the new ones described herein and the former *S. grahami*.

Distribution. The genus is distributed from Santa Cruz County, California, north to the Alexander Archipelago

in Alaska (Gardner & Shelley 1989, Shelley *et al.* 2007). Except for collections of *O. columbiana* from Skamania County, Washington, no records are known from east of the Coast Ranges and Cascade Mountains, nor from the Sierra Nevada.

New records of previously described species

Below we provide additional records of the species available to us, as well as descriptive notes focusing on the secondary sexual modifications of the males and the gonopods. SEM reveals details that could be important in distinguishing species but that were not available to Gardner & Shelley (1989) who used only light microscopy.

Opiona columbiana Chamberlin, 1951

Figs 1–8

O. columbiana Chamberlin, 1951: 8. Gardner & Shelley 1989: 215; Shelley *et al.* 2007: 14.
O. hatchi Causey 1954: 81. Synonymized by Gardner & Shelley 1989: 215.

New records. WASHINGTON: *Pacific Co.*: Fish and Wildlife land near crossing of Chinook River on US101, 46.3043°N, -123.9664°W, 15 January 2006, W. Leonard, m. *Skamania Co.*: McCloskey Creek at Maybee Mines Road, 1500' asl, 20 November 2003, C. Richart, mm, ff; Spring Creek Hatchery, 44.728°N, -121.6279°W, 50' asl, 30 November 2003, W. Leonard, mm, ff. *Spokane Co.*: Riverside State Park, 47.807°N, -117.4815°W, 7 November 2004, W. Leonard *et al.,* m, f; near Bowl and Pitcher, Riverside State Park, Spokane, 47.6968°N, -117.4988°W, 18 October 2009, C. Richart, W. Leonard, m. *Thurston Co.*: Fish Pond Creek, Kennedydell Park, 46.9878°N, -112.9702°W, 15 March 2004, W. Leonard, m; Olympia, 223 Foote St. NW, 1–7 April 2005, W. Leonard, m. All specimens deposited in VMNH.

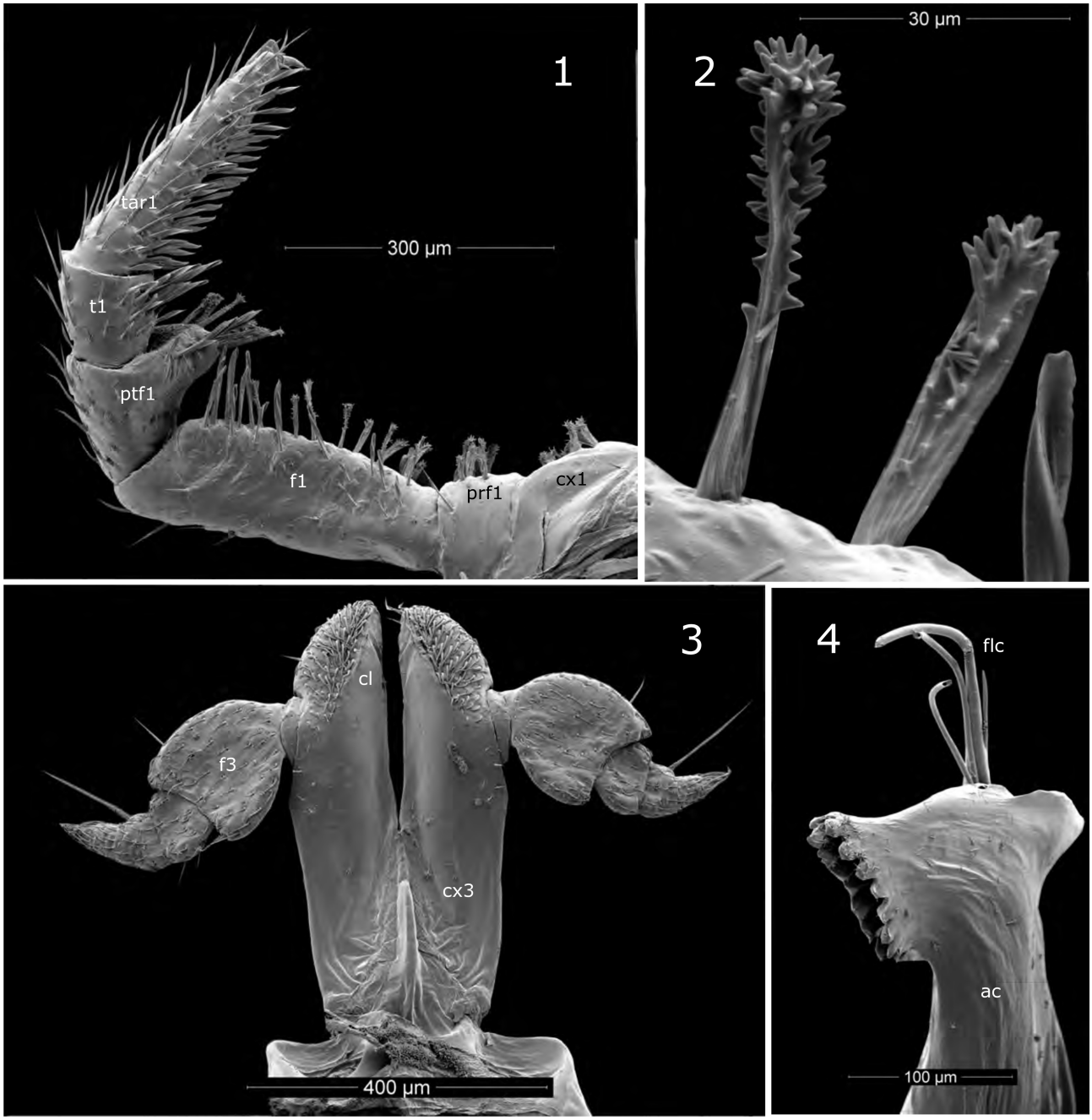
Descriptive notes. *Male*. The first legpair (Fig. 1) is robust but shorter than the fourth. The coxae (**cx1**), prefemora (**pf1**) and femora (**f1**) bear distinctive blunt setae with distal triangular projections (Fig. 2). We call these setae "macelike." Toward the distal end of the femur, the macelike setae lose their characteristic appearance and transition to a flattened, distally spiraled form which then continues on the ventral surfaces of the postfemora (**ptf1**) and tibiae (**t**). The postfemur has a blunt lobe ventrally which carries most of these setae. The tarsi (**tar1**) have typical ventral combs.

The second legpair telopodites are reduced. The gonapophyses are about the same length as the telopodites and have long, flexuous setae. The third legpair (Fig. 3) coxae (**cx3**) are elongate and capped with short distal lobes (**cl**) covered in recumbent setae. The femora (**f3**) are enlarged and flattened, while the distal articles are much reduced.

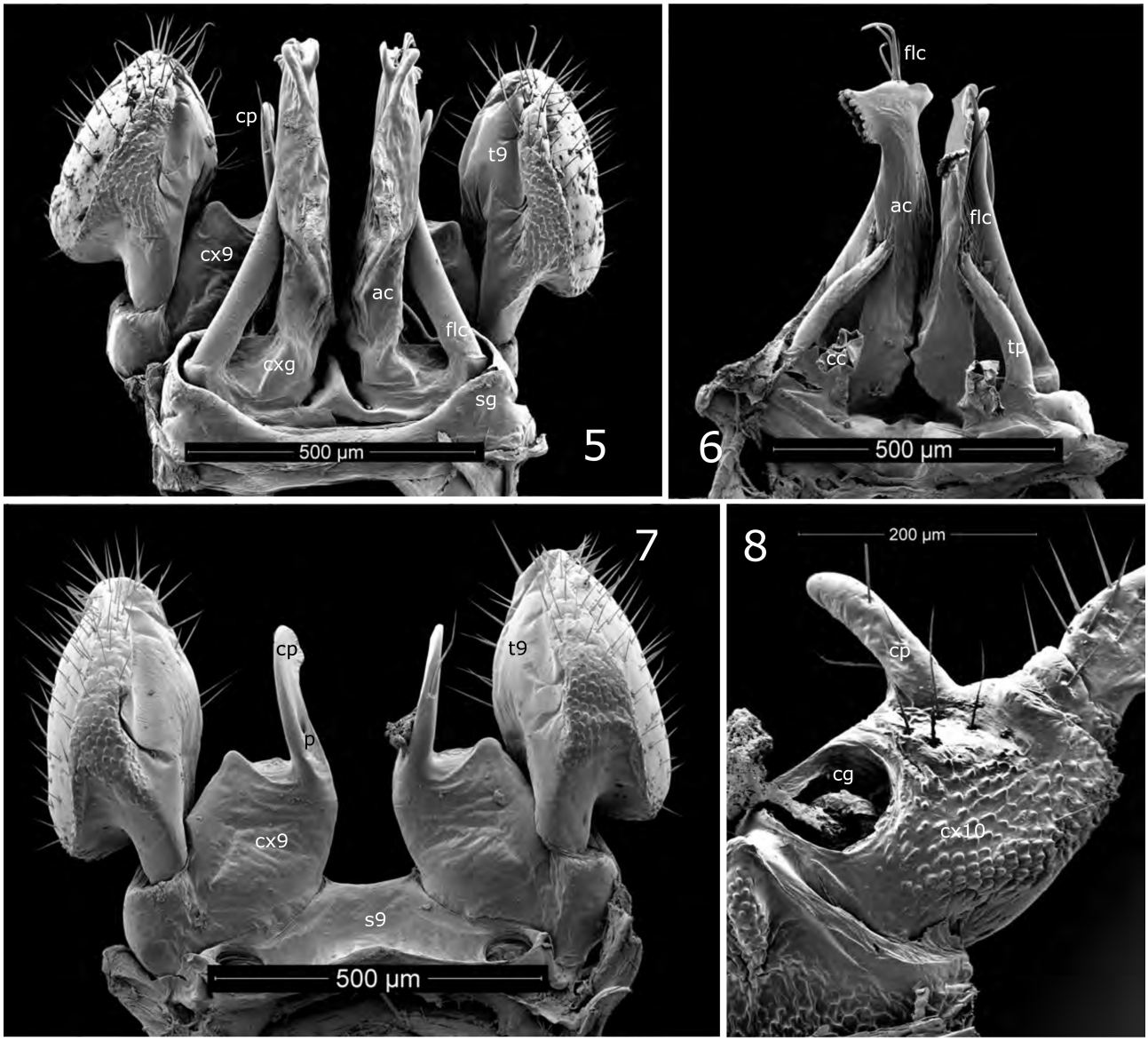
The gonopods (Figs 4–6) are robust. The sternum (**sg,** Fig. 5) is separate but envelops the coxae (**cxg**). The angiocoxites (**ac**) and flagellocoxites (**flc**) arise directly from the coxae and the latter are carried in a complex sheath by the former (Figs 4, 6). The vestigial telopodites (**tp,** Fig. 6) are slightly curved, with a few terminal setae. The colpocoxites (**cc**, Fig. 6) are poorly sclerotized sacs.

The ninth legs (Figs 5, 7) in anterior view (Fig. 7) have a robust sternum (**s**) and blocky coxae (**cx9**), which extend mesodistally beyond the articulation of the telopodites (**t9**) and carry a long, hooked coxal process (**cp**) with a gland pore near its base (**p**, Fig. 7). The tenth legpair coxae (**cx10**, Fig. 8) are enlarged, with a prominent eversible gland (**cg**) and curved, blunt coxal processes (**cp**).

Notes. *Opiona columbiana,* the genotype, was described from Vancouver Island (Chamberlin 1951) and *O. hatchi* by Causey from King Co., Washington (Causey 1954). Shelley *et al.* (2007) greatly extended the range of the species from near the Columbia River in Washington north to Wrangell Island, Alaska; two females that conform to the species were collected even further north to Juneau and to the St. Elias Mountains. This is a range of 1,310 miles (2,096 kilometers), astonishing for a millipede species not evidently aided by human agency. Equally enigmatic are the records (see above) from Spokane Co., some 280 miles (448 kilometers) to the east and in a completely different habitat of the semiarid Columbia Plateau. Some of these Spokane records were first reported by Shelley *et al.* (2007) but we repeat them here to draw attention to the seemingly anomalous occurrence of an *Opiona* species in eastern Washington. What special adaptive qualities are possessed by *Opiona columbiana* that can account for this vast range?



FIGURES 1–4. *Opiona columbiana* Chamberlin, male. Fig. **1**. Right leg 1, anterior view. Fig. 2. Setae from femur of leg 1. Fig. **3**. Legpair 3, posterior view. Fig. **4**. Tip of gonopod angiocoxite and flagellocoxites, posterior view. Abbreviations: **ac**, angiocoxite; **cx1**, coxa of leg 1; **cx3**, coxa of leg 3; **cl**, coxal lobe; **f1**, femur of leg 1; **f3**, femur of leg 3; **flc**, flagellocoxite; **prf1**, prefemur of leg 1; **ptf1**, postfemur of leg 1; **t1**, tibia of leg 1; **tar1**, tarsus of leg 1.



FIGURES 5–8. *Opiona columbiana* Chamberlin, male. Fig. **5**. Gonopods and ninth legpair, anterior view. Fig. **6**. Gonopods, posterior view. Fig. **7**. Ninth legpair, anterior view. Fig. **8**. Coxae of left 10th leg, anterior view. Abbreviations: **ac**, angiocoxite; **cx9**, coxa of leg 9; **cx10**, coxa of leg 10; **cg**, coxal gland; **cc**, colpocoxite; **cp**, coxal process; **cxg**, gonopod coxa; **flc**, flagellocoxite; **p**, …; **s9**, …; **sg**, gonopod sternum; **t9**, telopodite of leg 9; **tp**, gonopod telopodite.

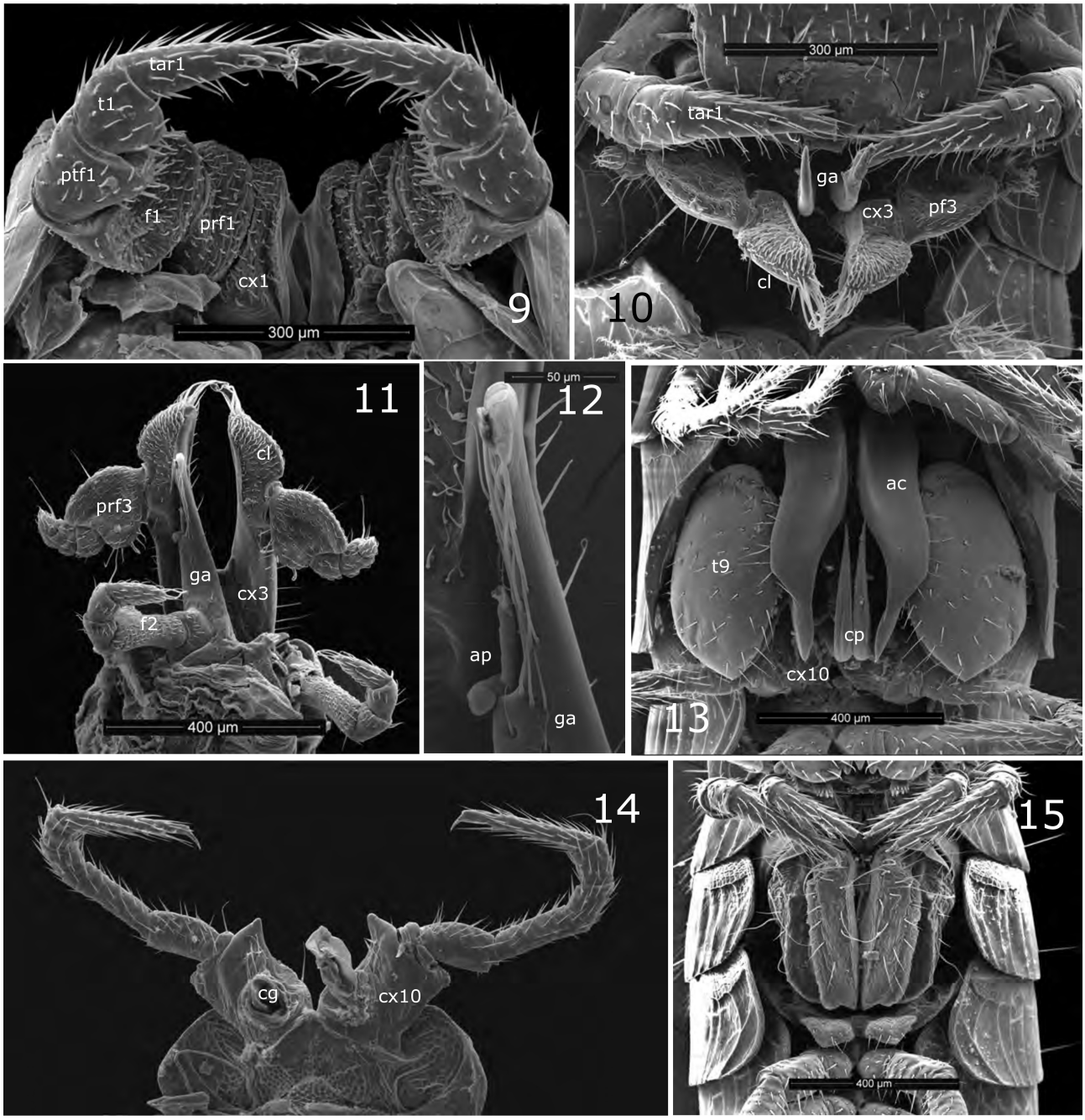
Opiona causalis Gardner & Shelley, 1989

Figs 9–15

O. causalis Gardner & Shelley, 1989: 216.

New record. OREGON: *Benton Co.*: 1 mi. on Botkin Road from Rt. 34, 44.4638°N, -123.4617°W, 25 February 2005, W. Leonard, C. Richart, mm, ff (VMNH).

Descriptive notes. *Male*. The first legpair (Fig. 9) is much shorter than the fourth, with considerably thickened podomeres. Their coxae (**cx1**) are closely appressed, and like the prefemora (**pf1**) and femora (**f1**), are set with short, clavate setae. The postfemora (**ptf1**) and tibiae (**t**) are slightly expanded ventrally and have longer, flattened, spiral setae. The tarsi (**tar1**) lack a ventral comb. The second legpair (Figs 10–12) telopodites are not much reduced, with curved femora (**f2**, Fig. 11) and long, distally hooked gonapophyses (**ga**, Figs 10–12) with only a few long distal setae (Fig. 12) and a distal accessory pore (**ap**, Fig. 12)—in addition to the basal pore of the *vas deferens*.



FIGURES 9–15. *Opiona causalis* Gardner & Shelley, male. Fig. **9**. First legpair, posterioventral view. Fig. **10**. First, second and third legpairs *in situ*, ventral view. Fig. **11**. Second and third legpairs, anterior view. Fig. **12**. Second legpair: tip of gonapophysis, anterior view. Fig. **13**. Gonopods and ninth legs *in situ*, ventral view. Fig. **14**. Legpair 10, anterior view. Fig. **15**. Female genitalia, ventral view. Abbreviations: **ac**, angiocoxite; **ap**, accessory pore; **cg**, coxal gland; **cl**, coxal lobe; **cp**, coxal process; **cx1**, coxa of leg 1; **cx3**, coxa of leg 3; **cx10**, coxa of leg 10; **f1**, femur of leg 1; **f2,** femur of leg 2; **ga**, gonapophysis; **pf1**, prefemur of leg 1; **prf3**, prefemur of leg 3; **ptf1**, postfemur of leg 1; **t1**, tibia of leg 1; **t9**, telopodite of leg 9; **tar1**, tarsus of leg 1.

The gonopods are essentially as illustrated by Gardner & Shelley (1989). We were unable to obtain useful SEM pictures of the gonopods due to the limited available material.

The ninth legpair (Fig. 13) has the typical button-like telopodites (**t9**) and acute, sharply curved coxal processes (**cp**). The tenth legpair coxae (**cx10**, Fig. 14) have eversible coxal glands and bluntly triangular distal coxal processes.

The female genitalia are shown in ventral view in Fig. 15. The small, knobbed structures posterior to the vulvae appear to be projections from the second termite. They have not been noted in previous descriptions of this species.

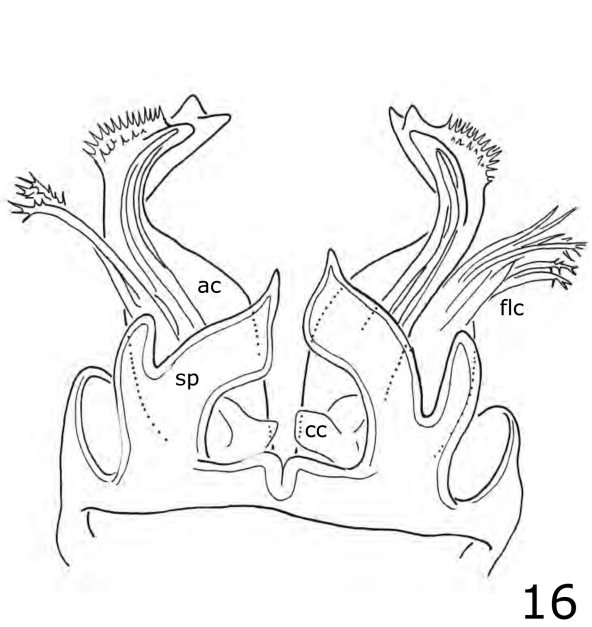
Notes. *Opiona causalis* was previously known from Polk and Lincoln Cos., Oregon. The Lincoln Co. record is based on a single female (Gardner & Shelley 1989).

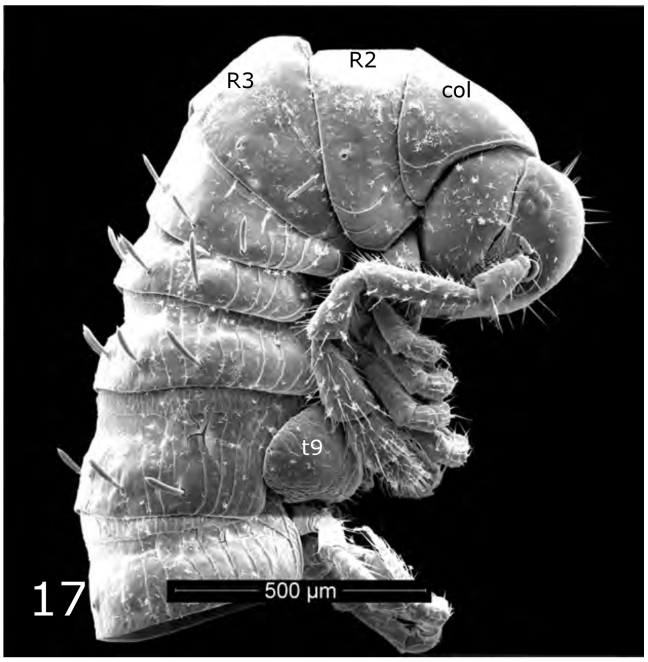
Opiona communis Gardner & Shelley, 1989

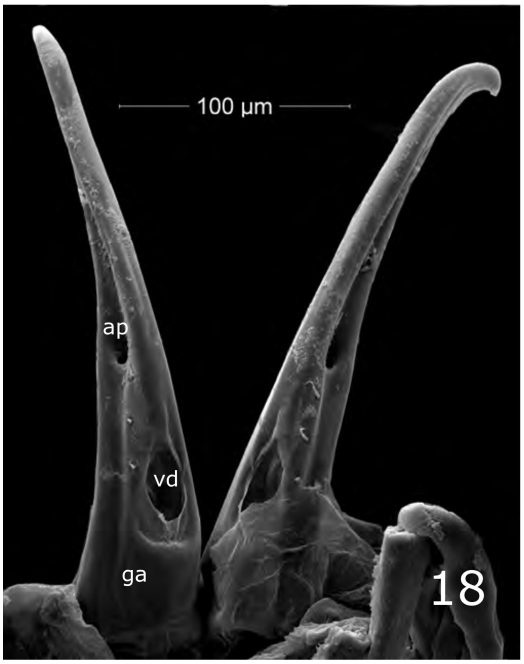
Fig. 16

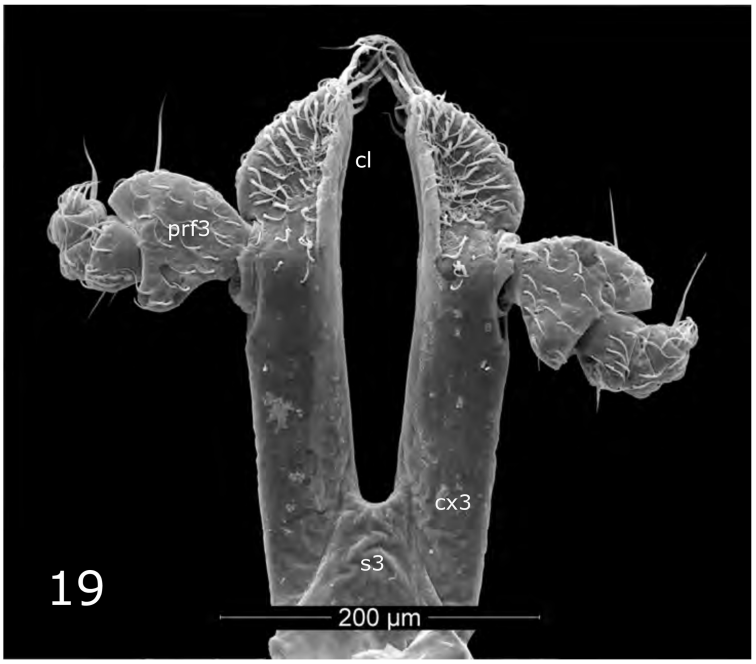
O. communis Gardner & Shelley, 1989: 212.

New records. CALIFORNIA: *Sonoma Co.*: Porter Creek, 10 mi. N of Santa Rosa, undated, J. S. Buckett, m. *Mendocino Co.*: McKerricher State Park, 7 September 1976, J. Doyen, m, f (EMUCB).

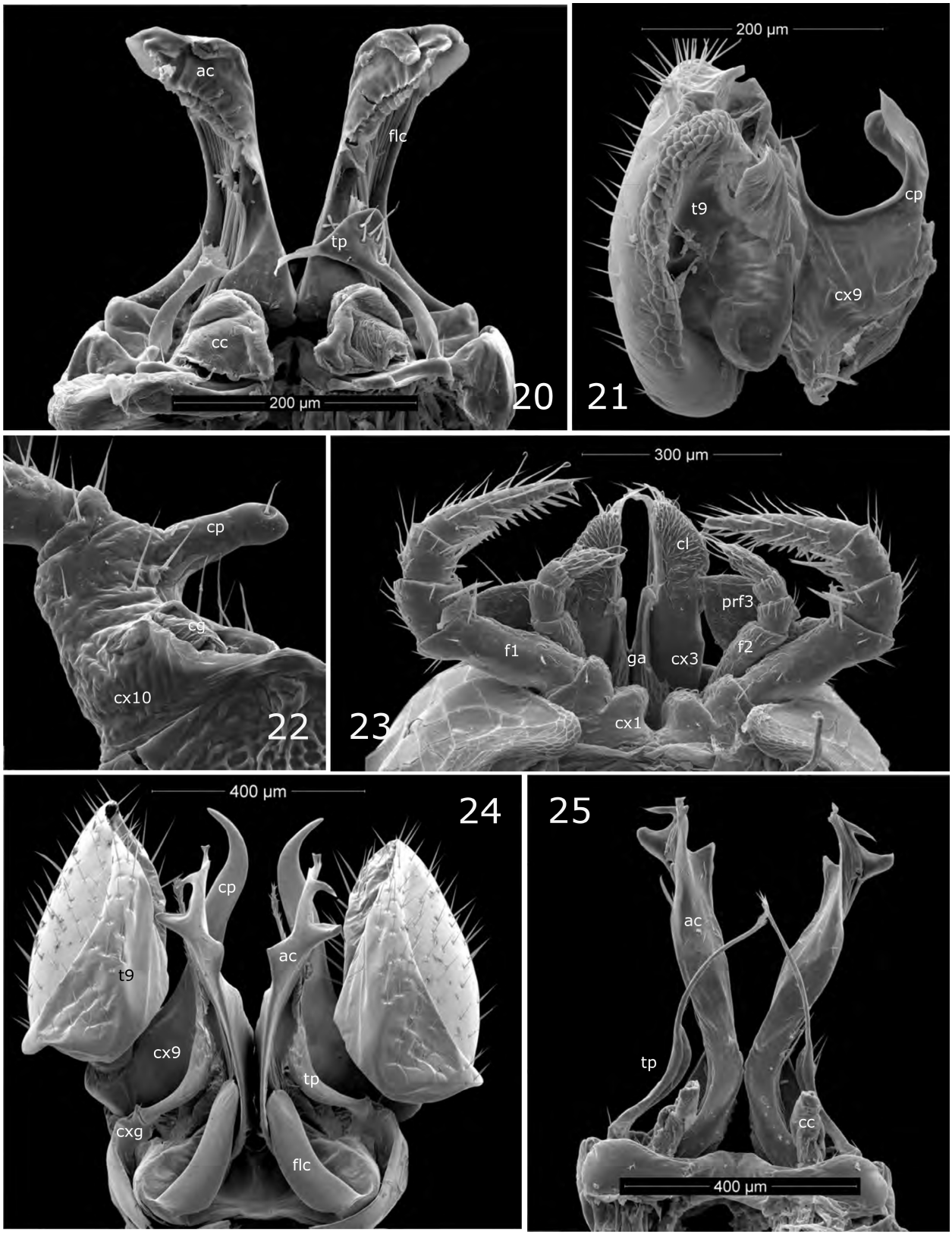








FIGURES 16–19. *Opiona communis* Gardner & Shelley, male and *O. exigua* Gardner & Shelley, male. Fig. **16**. Gonopods of *Opiona communis*, posterior view. Figs **17–19**. *Opiona exigua.* Fig. **17**. Anterior rings, lateral view. Fig. **18**. Second legpair: gonapophyses, anterior view. Fig. **19**. Legpair 3, anterior view. Abbreviations: **ac**, angiocoxite; **ap**, accessory pore; **cc**, colpocoxite; **cl**, coxal lobe; **col**, collum; **cx3**, coxae of leg 3; **flc**, flagellocoxite; **ga**, gonapophysis; **prf3**, prefemur of leg 3; **R2**, second ring; **R3**, third ring; **sp**, sternal process; **s3**, sternite of legpair 3; **t9**, telopodite of leg 9; **vd**, opening of *vas deferens*.



FIGURES 20–25. *Opiona exigua* Gardner & Shelley, male, and *O. facetia* Gardner & Shelley, male. Figs. **20–22**. *Opiona exigua.* Fig. **20**. Gonopods, posterior view. Fig. **21**. Right leg 9, posterior view. Fig. **22**. Coxa of left leg 10, anterior view. Figs **23–25**. *Opiona facetia.* Fig. **23**. Legpairs 1–3, anterior view. Fig. **24**. Gonopods and legpair 9, anterior view. Fig. **25**. Gonopods, posterior view. Abbreviations: **ac**, angiocoxite; **cl**, coxal lobe; **cx**1coxa of leg 1; **cx3**, coxa of leg 3; **cx9**, coxa of leg 9; **cx10**, coxa of leg 10; **cg**, coxal gland; **cc**, colpocoxite; **cp**, coxal process; **cxg**, gonopod coxa; **f1**, femur of leg 1; **f2**,femur of leg 2; **flc**, flagellocoxite; **ga**, gonapophysis; **prf3**,p refemur of leg 3; **t9**, telopodite of leg 9; **tp**, gonopod telopodite.

Descriptive notes. We did not have material suitable for SEM illustrations of this species, and so provide a drawing of the gonopods in posterior view (Fig. 16) to complement the lateral view provided by Gardner & Shelley (1989). The bifid sternal processes (**sp**), mesal branches meet or nearly meet in the midline. The flagellocoxites (**flc**) have cuticular fimbriae at their tips and are not sheathed by the angiocoxites (**ac**), which have distinctive patches of small, triangular teeth at their apices.

Notes. Gardner & Shelley (1989) recognized three subspecies of *O. communis*, all from the San Francisco Bay area: in the counties of Sonoma, Solano and Santa Cruz (*O. communis communis*), Sonoma and Marin (*O. communis angusta*), and Sonoma and Napa (*O. communis prolixa*). They described the subspecies despite not documenting the presence of intermediates and the closely situated records. We have not studied the situation in detail and so simply record our data as pertaining to *O. communis* in general. It does not appear to us from the drawings [Gardner & Shelley (1989: figs 65–75)] that the subspecies would be readily distinguishable. New collecting and molecular data would help resolve the question. The Mendocino Co. record represents a small northward extension of the range.

Opiona exigua Gardner & Shelley, 1989

Figs 17–22

O. exigua Gardner & Shelley, 1989: 217.

New record. CALIFORNIA: *Mendocino Co.*: Mendocino, 17 April 1954, J. Helfer, m, ff (FSCA).

Descriptive notes. Figure 17 illustrates the typical "hunchbacked" appearance of many preserved male *Opiona* due to the contraction of the robust musculature in the collum (**col**) and succeeding two rings (**R2**, **R3**) associated with legpairs two and three; it also illustrates the obvious leg nine telopodites (**t9**). These features, hunchback and t9, allow field recognition of male specimens. The first legpair is as described above for *O. causalis.* The telopodites of the second legpair are shorter than the gonapophyses (**ga**, Fig. 18), which lack long setae but have an accessory pore (**ap**) distal to the basal opening of the *vas deferens* (**vd**). The third legpair coxae (**cx3**, Fig. 19) attached to a trapezoidal sternum (**s3**) are unusually elongate, with broadly curved coxal lobes (**cl**) carrying recumbent setae and distal tuft of longer setae. The third leg telopodites are strongly reduced with an expanded, flattened prefemur (**pf3**).

The gonopods in posterior view (Fig. 20) have flagellocoxites (**flc**) closely appressed to the angiocoxites (**ac**), which receive them in a complex sheathing apparatus. The vestigial telopodites (**tp**) are curved mesad, with narrow stems and broadened tips with sparse setae and a short, acute extension. The colopocoxites (**cc**) are large and prominent.

The male ninth leg coxae (**cx9**, Fig. 21) are flattened; the coxal process (**cp**) is bifid, with an anterior acute branch and a posterior blunt branch. The telopodite (**t9**) is excavated and complexly lobed on its anteriomesal surface. The male coxa 10 (**cx10**, Fig. 22) has the usual large coxal gland opening (**cg**) and a blunt coxal process that is only slightly curved (**cp**).

Notes. *Opiona exigua* was described by Gardner & Shelley (1989) from two localities in Mendocino Co. Our new record is too imprecise for georeferencing.

Opiona facetia Gardner & Shelley, 1989

Figs 23–26

Opiona facetia Gardner & Shelley, 1989: 219.

New records. OREGON: *Linn Co.*: Willamette National Forest, Sweet Home Road, 1–4 July 2001, J. Rykken, mm, ff. WASHINGTON: *Cowlitz Co.*: Pin Creek, Kool Road 0.4 mi west of Fish Pond Road, 47.0742°N, -122.8470°W, 180' asl, 25 January 2004, C. Richart, W. Leonard, m, f. All specimens deposited in VMNH.

Descriptive notes. *Male*. The first legpair is only a little reduced (Fig. 23). The coxae (**cx1**) and pre femora lack specialized setae, while the femora (**f1**), post femora and tibiae have a few long, ensiform setae. The postfemora and tibia are not ventrally expanded and do not have ventral lobes. The tarsi bear typical tarsal combs. The second legpair telopodites (**f2**, Fig. 23) are considerably longer than the gonapophyses (**ga**, Fig. 23). The third legpair coxae

are not as elongate as in the previously described species (**cx3**, Fig. 23). The coxal lobes (**cl**) are relatively long and bear the usual recumbent setae, and distal tuft. The prefemora (**pf3**) are expanded and flattened.

The gonopods (Figs 24, 25) are typical of the group. The flagellocoxites (**flc**, Fig. 24) are sheathed by the angiocoxites (**ac**, Figs 24, 25) that are complexly branched at the tips. The curved, vestigial telopodites (**tp**, Figs 24, 25) articulate to the gonopod coxae (**cxg**) and are distally expanded, with a few setae, and have long, thin extensions that are fimbriate at the tips. The colpocoxites (**cc**, Fig. 25) are small.

The ninth legpair coxae (**cx9**, Fig. 24) are attached to a pentagonal sternum (**s10**) and gradually transition mesally to a large, flattened, slightly sinuous coxal process (**cp**). The telopodites are mesally excavate and have an anterior ridge (**t9**). The tenth leg coxae (**cx10**, Fig. 26) are enlarged and glandular (**cg**) with a short, blunt coxal process (**cp**).

Notes. *Opiona facetia* was described by Gardner & Shelley (1989) from localities in Clackamas and Marion Cos., Oregon, so the Cowlitz Co., Washington, record below is a considerable range extension. The Sweet Home Road locality (see below) is not precise enough for georeferencing. The collection date for this locality is also unusually late, since adults of *Opiona* species have generally not been collected after early May.

Opiona goedeni Gardner & Shelley, 1989

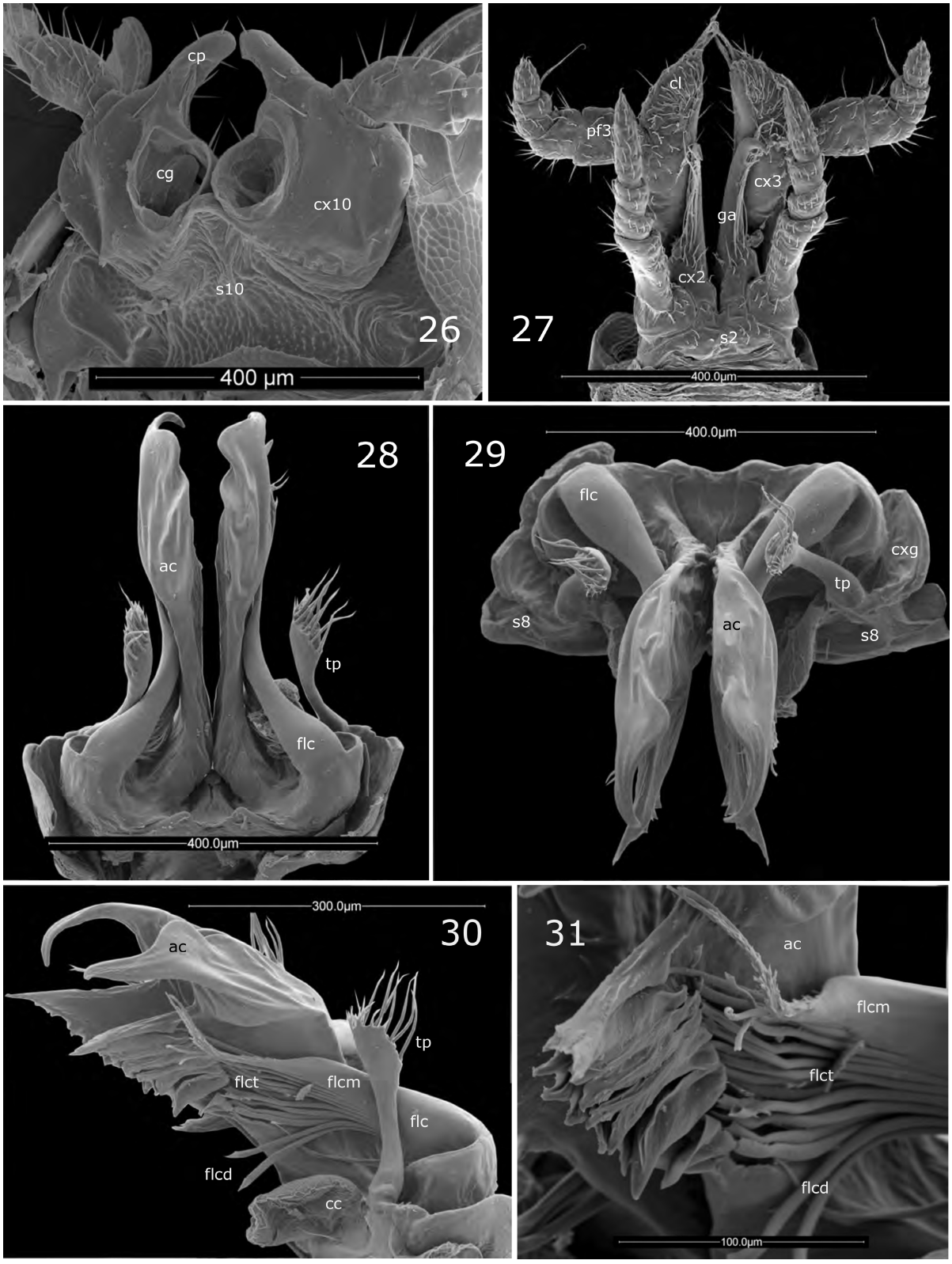
Figs 27–34

O. goedeni Gardner & Shelley, 1989: 214.

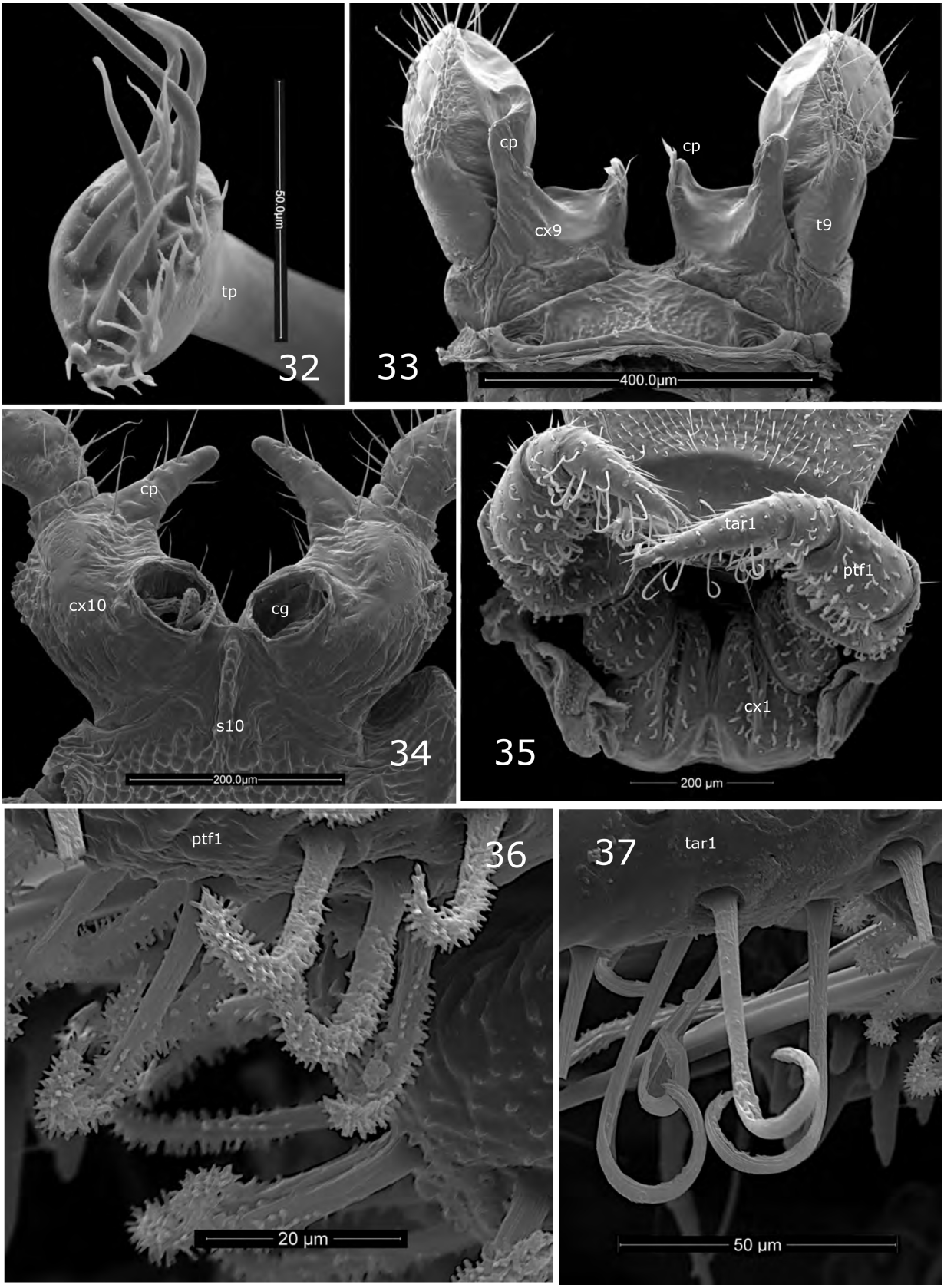
New records. OREGON: *Clatsop Co.*: SR30, 0.9 mi. W of Taylor Valley/Wavra overpass, 2.9 mi. W of Westport 46.1578°N, -123.4272°W, 336’ asl, 6 Febrary 2004, C. Richart, W. Leonard, m, f. *Linn Co.*: Wells Creek Road, 0.7 mi. from SR34 (6.3 mi. from SR20), 9 December 2005, W. Leonard, C. Richart, m. *Tillamook Co.*: FR14, 2.2 mi NE of FR22, Suslaw National Forest, 45.6582°N, -123.8387°W, 900’ asl, 10 December 2005, W. Leonard, C. Richart, m, ff.

WASHINGTON: *Grays Harbor Co.*: Canyon River, 6 mi. W, 1.25 mi. N of Matlock, 17 January 2003, W. Leonard *et al.*, m; 9 mi. N of SR12 on Middle Satsop Road, 47.0332°N, -123.5259°W, 26 November 2004, W. Leonard, m, ff; Inner Creek at Quinalt Lake Loop Road, 47.5025°N, -123.782167°W, 13 February 2005, W. Leonard, C. Richart, m, ff; locality not specified, 47.314°N, -123.6237°W, 13 October 2003, W. Leonard, m; Wynoochee River, 47.3131°N, -123.6075°W, 973’ asl, 28 September 2003, W. Leonard, m. *Jefferson Co.*: 5.9 mi. E of US101 on road to Queets Campground, Olympic National Park, 47.5726°N, -124.1378°W, 5 March 2005, W. Leonard, C. Richart, m, f; Olympic National Park, north shore on Lake Quinalt Road, 4.2 mi. E of US101 47.499533°N, -123.097217°W, 10 November 2003, W. Leonard, m, ff; Olympic National Park, 6 mi. E of US101 on Queets Road, 47.5722°N, -124.1368°W, 5 March 2005, W. Leonard, C. Richart, m; Willougby Creek at Hoh River, 3.5 mi E of US101, 28 March 2003, W. Leonard, m; Nolan Creek at US101, 47.7505°N, -124.3198°W, 1 March 2002, W. Leonard, m, ff. *Pacific Co.*: Long Beach, Willows Rd. 0.6 m from 30th Street, 15 January 2006, W. Leonard, C. Richart, m; 3.5 mi S of Naselle on SR401, at Cement Creek, 46.3341°N, -123.8003°W, 15 January 2006, W. Leonard, C. Richart, m, f; 1.1 mi S of US6 on Trap Creek Road, 46.5432°N, -123.6151°W, 19 November 2005, W. Leonard, C. Richart, m, f; 4.3 mi. N of SR4 on US101, at Middle Nemah River, 46.4871°N, -123.8866°W, 15 January 2006, W. Leonard, C. Richert, m, ff; Ellsworth Creek, Nature Conservancy Preserve, 14 March 2003, W. Leonard, *et al.*, m, ff; Ellsworth Creek Preserve, 46.3981°N, -123.8899°W, 23 November 2003, W. Leonard *et al.*, mm, ff; tributary to Ellsworth Creek, Nature Conservancy Preserve, 46.3847°N, -123.8840°W, 150’ asl, 17 January 2004, m, f. *Thurston Co.*: Hospital Creek, 5 mi. S, 1 mi. E of Vail, 12 October 2003, W. Leonard, m, ff; Evergreen State College campus, Olympia, 22 March 2003, W. Leonard, m; Hospital Creek, above confluence with Skoocumchuck River, 46.7733°N, -122.5856°W, 13 December 2003, W. Leonard, K. McAllister, mm, ff. *San Juan Co.*: Patos Island, 27–29 October 2003, T. Burke, N. Hedges, mm. *Wahkiakum Co.*: 10.9 mi. up Elochoman Valley Road from SR4, 46.3044°N, -123.2617°W, 28 March 2004, C. Richart, mm. All specimens deposited in VMNH.

Descriptive notes. *Male*. The first legpair is as described above for *O. facetia.* The second legpair is articulated to a small sterum **(s2**, Fig. 27). The coxae (**cx2) and** telopodites are shortened but are still longer than the gonapophyses (**ga**, Fig. 27), which carry long, flexuous setae. The third legpair coxae (**cx3**, Fig. 27) are elongate and lobed. The coxal lobes (**cl**) have normal, rather than recumbent, setae on their anterior surfaces, and distal tuft. The prefemora (**pf3**) are not expanded and flattened; the tarsus lacks a claw.



FIGURES 26–31. *Opiona facetia* Gardner & Shelley, male and *O. goedeni* Gardner & Shelley, male. Fig. **26**. Coxae of legpair 10 of *O. facetia.* Figs **27–31**. *Opiona goedeni.* Fig. **27**. Legpairs 2 and 3, anterior view. Fig. **28**. Gonopods, anterior view. Fig. **29**. Gonopods, ventral view. Fig. **30**. Gonopods, lateral view. Fig. **31**. Sheathing process of gonopod angiocoxite, lateral view. Abbreviations: **ac**, angiocoxite; **cl**, coxal lobe; **cx2**, coxa of leg 2; **cx3**, coxa of leg 3; **cx10**, coxa of leg 10; **cg**, coxal gland; **cc**, colpocoxite; **cp**, coxal process; **cxg**, gonopod coxa; **flc**, flagellocoxite; **flcd**, dorsal branch of flagellocoxite; **flcm**, main branch of flagellocoxite; **flct**, tubular branches of flagellocoxite; **ga**, gonapophysis; **pf3**, prefemur of leg 3; **s2**, sternum of legpair 2; **s8**, sternum of gonopods; **s10**, sternum of legpair 10; **tp**, gonopod telopodite.



FIGURES 32–37. *Opiona goedeni* Gardner & Shelley, male and *Opiona arcata,* **sp. nov.**, male. Figs **32–34**. *Opiona goedeni.* Fig. **32**. Tip of gonopod telopodite, distal view. Fig. **33**. Legpair 9, anterior view. Fig. **34**. Coxae of legpair 10, anterior view. Figs **35–37**. *Opiona arcata,* **sp. nov.** Fig. **35**. Legpair 1, ventral view. Fig. **36**. Setae of legpair 1 postfemur. Fig. **37**. Setae of legpair 1 tarsus. Abbreviations: **cx1**, coxa of leg 1; **cx9**, coxa of leg 9; **cx10**, coxa of leg 10; **cg**, coxal gland; **cp**, coxal process; **ptf1**, postfemur of leg 1; **s10**, sternum of legpair 10; **t9**, telopodite of leg 9; **tar1**, tarsus of leg 1; **tp**, telopodite of gonopod.

The gonopods (Figs 28–32) are among the more complex in the genus. In anterior (Fig. 28) and ventral view (Fig. 29), the gonopod coxae (**cxg**, Fig. 29) are seen to be bilaterally fused. The angiocoxites (**ac**, Fig. 28) are basally narrow and distally expanded, with bifid tips (Fig. 29); the mesal bifurcation is strongly hooked. In lateral view (Fig. 30) the flagellocoxite (**flc**) curves sharply posterior and has three distinct branches: the ventralmost branch (**flcm**, Figs. 30, 31) is basally broad then tapers to a fine filament with many small cuticular scales; the mesal branch (**flct**, Figs 30, 31) consists of as many as 11 tubular pseudoflagella which are sheathed in a complex process from the angiocoxite; and the dorsalmost branch (**flcd**, Figs 30, 31) consist of two thin, hastate filaments that are not tubular. The vestigial telopodites (**tp**, Figs 28–30, 32) are basally narrow, distally expanded, and bear both setae and unsocketed cuticular branches (Fig. 32). Interestingly, Gardner & Shelley (1989) also counted 11 tubular pseudoflagella and seven telopodite setae in the holotype, suggesting a surprising degree of detailed consistency from individual to individual.

The ninth legpair coxae (**cx9**, Fig. 33) are broadly separated and saddle-shaped with processes on both the lateral and mesal sides (**cp**). The lateral processes are bluntly quadrate and closely appressed to the telopodites; the mesal processes consist of a rather thin anterior branch and a rounded posterior branch. The telopodites (**t9**) are ovoid, with a distinct sulcus giving the impression of consisting of two podomeres. The tenth legpair coxae (**cx10**, Fig. 34) are enlarged, with the usual gland openings (**cg**) and a blunt, straight coxal process (**cp**).

Notes. These new records significantly extend the known range of *O. goedeni,* previously known only from Washington, Polk and Clatsop Cos., Oregon. The range of Washington records suggests that the species may eventually be collected in British Columbia, Canada.

New species

Opiona arcata Shear & Marek, new species

Figs 35–43

Types. Male holotype and three male paratypes from Jacoby Creek Road and Kirkpatrick (South) Quarry Road, 40.8279°N, -124.0391°W, 100–200 ft (30.5–61 m) asl, Humboldt Co., California, collected 5 and 24 November 1977 by A. K. Johnson (FSCA). Additional male paratype from Jolly Giant Canyon, Arcata, 40.8777°N, -124.0614°W, Humboldt Co., California, collected 20 December 1975 by A. K. Johnson (FSCA).

Etymology. The species name is a noun in apposition referring to the town of Arcata, near the type localities.

Diagnosis. This species differs from all other *Opiona* species in the recurved, hooded appearance of the gonopod angiocoxites (**ac**, Figs 39, 40); the long, thin, slightly twisted vestigial telopodite (**tp**, Fig. 40); and from all except *Opiona johnsoni,* **sp. nov.***,* in the distinctive setation of the male first legpair (Figs 35–37). From *O. johnsoni,* **sp. nov.,** the species differs in the form of the male ninth leg coxal process (cf. Figs 42 *vs*. 47); in *O. johnsoni* the coxal process has two long, thin, curved branches, while in the present species there are two short, acute processes.

Description. *Male holotype*. Length, about 6.2 mm (specimen tightly coiled), width about 0.55 mm. Head with 9 ommatidia in three irregular rows on each side. Legpair one (Figs 35–37) robust. Postfemora (**ptf1**) and tibiae with curled, papillose setae (Fig. 36); tibiae with slight distal swelling; tarsi (**tar1**) with ventral combs and smooth, curled setae (Fig. 37). Second legpair (Fig. 38) with long, nearly straight gonapophyses (**ga**) with accessory pore (**ap**) distal to the basal opening of the *vas deferens* (**vd**); telopodites reduced, slightly shorter than gonapophyses; femur (**f2**) the longest podomere; claw as a long, thin filament. Legpair three (Fig. 38) with coxae (**cx3**) twice as long as coxal lobe (**cl**); coxal lobe with recumbent setae and distal tuft; telopodites much reduced; prefemur (**pf3**) enlarged, flattened; claw vestigial or absent.

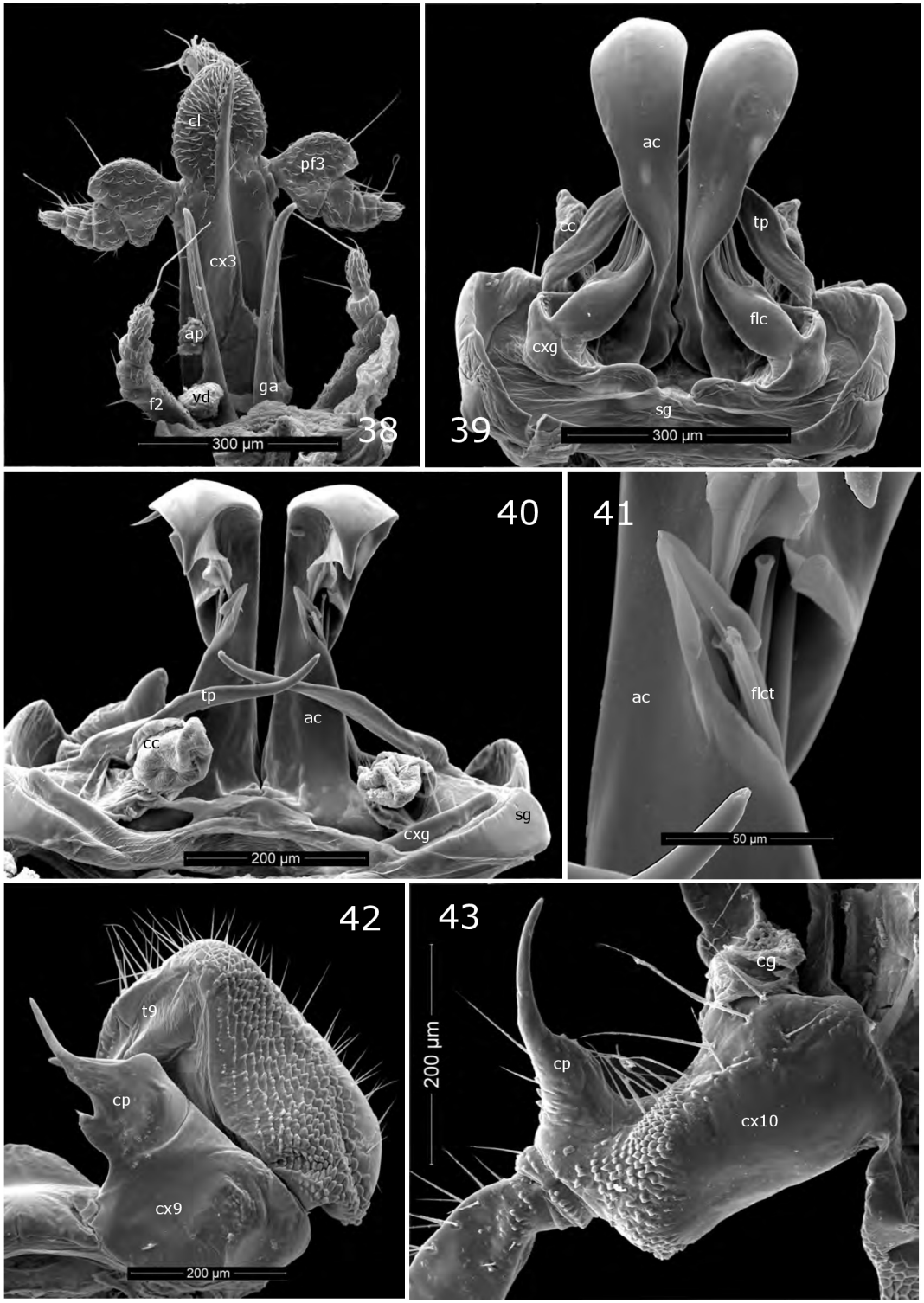
Gonopods (Figs 39–41) with broad sternum (**sg**, Fig. 39) and low, flattened coxae (**cxg**) with angiocoxites (**ac**) distally broadened, hooded, posteriorly with complex sheathing process entirely hiding flagellocoxites (**flc**). Telopodites (**tp**) simple, slightly curved and flattened. Colpocoxites (**cc**) widely separated, relatively large.

Legpair nine (Fig. 42) with trifid coxal process (**cp**); telopodite (**t9**) typical, slightly scaley. Legpair ten (Fig. 43) with elongate coxae (**cx10**) bearing coxal glands (**cg**); coxal process (**cp**) long, acute, curved.

Females not collected.

Distribution. Known only from the type localities in the vicinity of Arcata, California.

Notes. This species belongs in the Columbiana group, having vestigial telopodites, sheathed flagellocoxites and lacking posterior sternal processes.



FIGURES 38–43. *Opiona arcata,* **sp. nov.**, male Fig. 38. Legpairs two and three, anterior view. Fig. **39**. Gonopods, anterior view. Fig. **40**. Gonopods, posterior view. Fig. **41**. Sheathing process of gonopod angiocoxite, posterior view. Fig. **42**. Left leg 9, anterior view. Fig. **43**. Coxa of right leg 10, posterior view. Abbreviations: **ac**, angiocoxite; **ap**, accessory pore; **cl**, coxal lobe; **cx3**, coxa of leg 3; **cx9**, coxa of leg 9; **cx10**, coxa of leg 10; **cc**, colpocoxite; **cp**, coxal process; **cxg**, gonopod coxa; **f2**, femur of leg 2; **flc**, flagellocoxite; **flct**,, tubular branches of flagellocoxite; **ga**, gonapophysis; **pf3**, prefemur of leg 3; **sg**, gonopod sternum; **t9**, telopodite of leg 9; **tp**, gonopod telopodite; **vd**, opening of *vas deferens*.

Opiona johnsoni Shear & Marek, new species

Figs 44–48

Types. Male holotype from Abraham Haas Grove, 40.297°N, -123.895°W, Avenue of the Giants, Humboldt Redwoods State Park, Humboldt Co., California, collected 25 November 1977 by A. K. Johnson (FSCA). Male and female paratypes from 3.5 miles north, 1 mile east of Pepperwood on Rt. 36, 40.479°N, -123.959°W, 250 ft asl, collected 12 November 1977 by A. K. Johnson (FSCA).

Etymology. The species is named for A. K. Johnson, its collector. A noun in genitive.

Diagnosis. *Opiona johnsoni,* **sp. nov.**, is very similar to *O. arcata* Shear & Marek, **sp. nov.**, described above, but differs in the coxal processes of male ninth legs (cf. Figs 42 *vs*. 47). The coxal process of the male tenth coxa is much shorter and not curved (Fig. 48). The distal ends of the gonopod angiocoxites are differently shaped (Fig. 45 *vs.* 40) in the two species.

Description. *Male paratype.* Length, about 6.0 mm, width about 0.5 mm. Nine ommatidia on each side of head. First legpair (Fig. 44) robust, with short, recurved papillate setae on coxae (**cx1**), prefemur (**prf1**) and femur (**f1**); these setae longer on postfemora (**ptf1)** and tibiae (**t1**), transitioning to smooth, hooked setae on tarsi (**tar1**). Tarsus with ventral comb; coxae, prefemora and femora ventrally depressed. Second and third legpair as described for *O. arcata* Shear & Marek, **sp. nov.**, above.

Gonopods (Figs 45, 46) similar to those of *O. arcata*, but angiocoxites (**ac**) not so broadened distally and with differently shaped sheathing processes. Flagellocoxites (**flc**) completely enclosed by angiocoxites, including main flagellocoxite branch (**flcm**, Fig. 46) and tubular branches (**flct**, Fig. 46). Telopodites (**tp**) articulated to coxae (**cxg**, Fig. 45), simple, slightly expanded just below tips, crossing in midline. Colpocoxites (**cc**) prominent.

Legpair nine (Fig. 47) with coxal processes (**cp**) elongate, bifid, curved. Telopodites (**t9**) typical, with deep posterior excavation. Tenth leg coxae (**cx10**, Fig. 48) enlarged, glandular (**cg**), with short, acute, straight coxal process (**cp**).

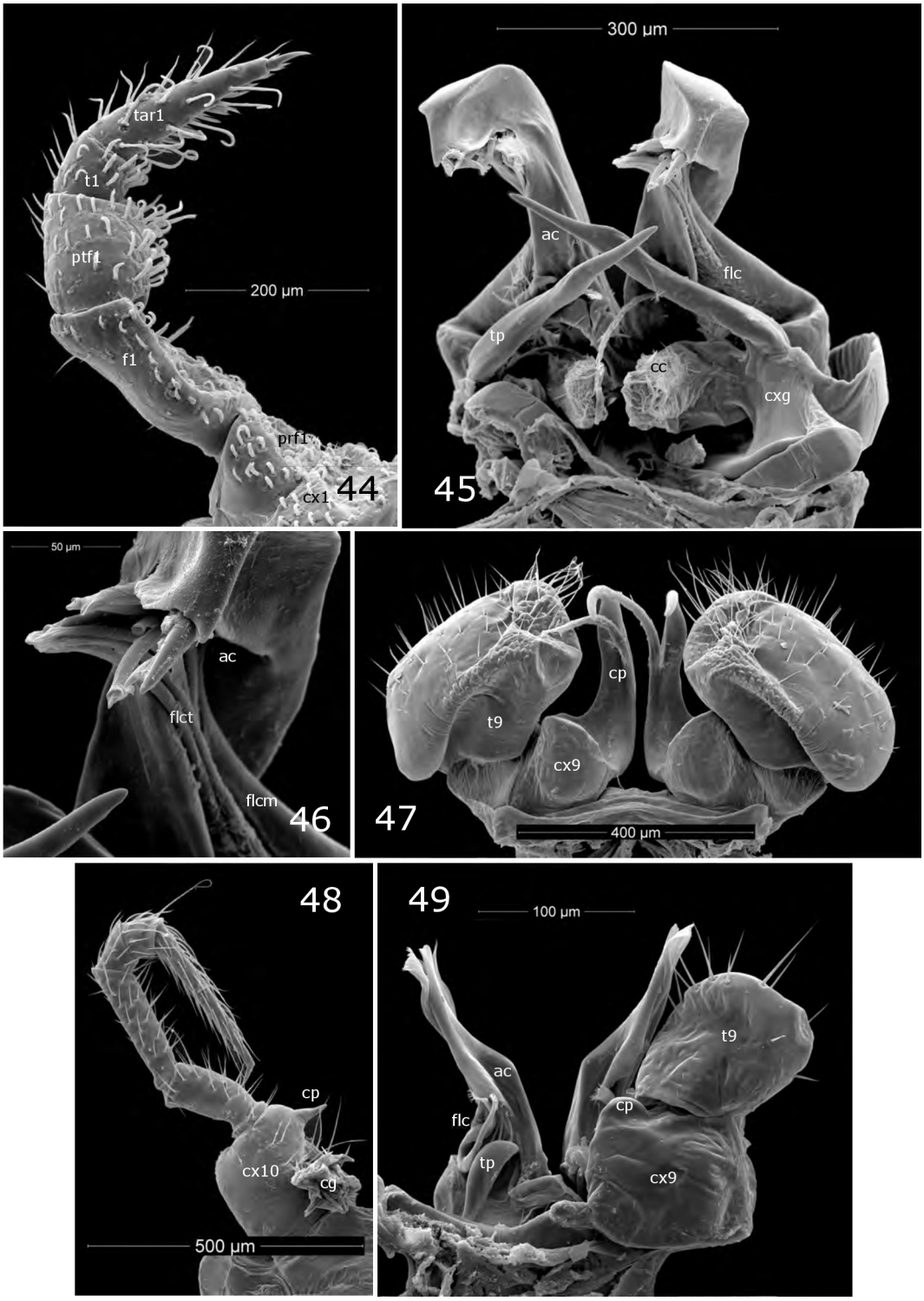
Females similar to males in nonsexual characters.

Distribution. Known only from the type localities.

Notes. We describe this species as separate from *O. arcata*, which occurs further north in Humboldt County, based on differences in the ninth and tenth legs and slight differences in the angiocoxites. Humboldt Redwoods State Park preserves about 160 named groves of redwood trees, including the Abraham Haas Grove.

Alsea group

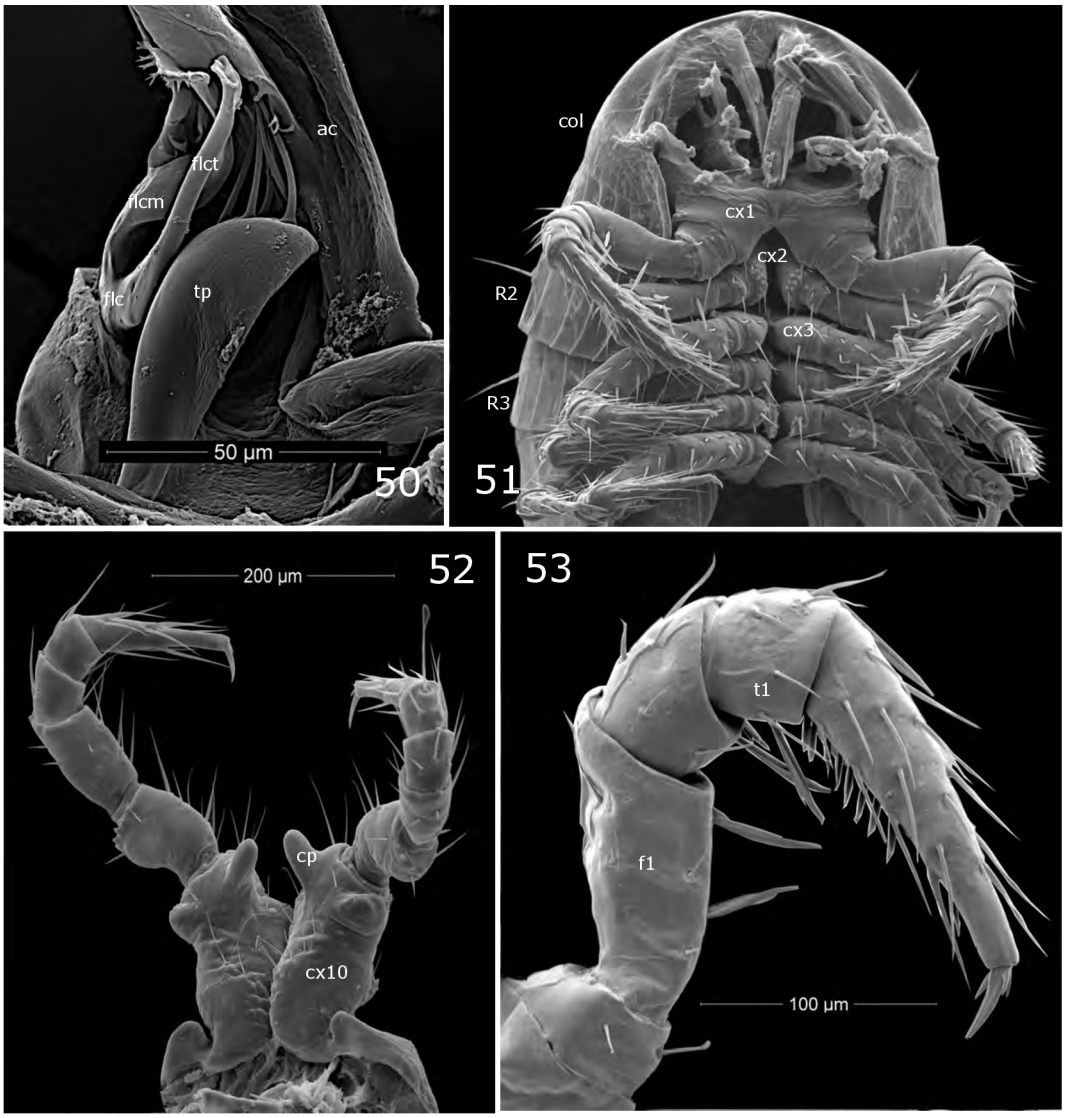
The following three new species are in some ways similar to members of the Columbiana group but differ in a number of characters. All three are much smaller (< 5 mm) than previously described *Opiona* species and have only two ommatidia in each eyepatch. The modifications of the first three legpairs are significantly reduced. The first legs do not have special setae, except for a few ensiform ones on the femora and postfemora. The second leg telopodites are of nearly normal size and the gonapophyses are short. The coxal lobes of the third legs are small and do not have the usual recumbent setae or tufts, usually just a single distal seta; the telopodites are not reduced or modified. The gonopods have vestigial telopodites but the flagellocoxites are quite different from those of the Columbiana group (see species descriptions below). The ninth legpair sternum and coxae are fused to form a coxosternum and the coxal processes are simply short nubbins, while the telopodites are comparatively very small. The tenth legs have elongated coxae with eversible glands but the coxal processes are short and peglike. A good case could be made for placing them in a separate new genus but pending more study on the range of *Opiona* species, we keep them in that genus.



FIGURES 44–49. *Opiona johnsoni*, **sp. nov.**, male and *Opiona alsea*, **sp. nov.**, male. Figs. **44–48**. *Opiona johnsoni,* **sp. nov.**, male. Fig. **44**. Right leg 1, anterior view. Fig. **45**. Gonopods, posterior view. Fig. **46**. Sheathing process of gonopod angiocoxite, posterior view. Fig. **47**. Legpair 9, posterior view. Fig. **48**. Left leg 10, anterior view. Fig. **49**. Gonopods and left leg 9 of *Opoiona alsea*, **sp. nov.** Abbreviations: **ac**, angiocoxite; **cx1**, coxa of leg 1: **cx9**, coxa of leg 9; **cx10**, coxa of leg 10; **cg**, coxal gland; **cc**, colpocoxite; **cp**, coxal process; **cxg**, gonopod coxa; **f1**, femur of leg 1; **flc**, flagellocoxite; **flcm**, main branch of flagellocoxite; **flct**, tubular branches of flagellocoxite; **prf1**, prefemur of leg 1; **ptf1**, postfemur of leg 1; **t1**, tibia of leg 1; **tar1**, tarsus of leg 1; **t9**, telopodite of leg 9; **tp**, gonopod telopodite.

***Opiona alsea* Shear & Marek, sp. nov.**
Figs 49–52

Types. Male holotype from Philomath, 1 mile on Botkin Road from State Route 34, 44.4638°N, -123.4617°W, Benton Co., Oregon, collected 25 February 2005 by W. Leonard and C. Richart (VMNH). Male paratype and two female paratypes from Clemens Park, Alsea, Seeley Creek Road 0.3 miles from State Route 34, along North Fork of Alsea River, 44.4092°N, -123.5678°W, 400 ft asl, Benton Co., Oregon, collected 4 December 2005 by W. Leonard and C. Richart (VMNH).



FIGURES 50–53. *Opiona alsea,* **sp. nov.**, male and *Opiona trianglensis,* **sp. nov.**, male. Figs. **50–52**. *Opiona alsea*, **sp. nov.**, male. Fig. **50**. Right gonopod, posterior view. Fig. **51**. Anterior rings of male, ventral view. Fig. **52**. Legpair 10, posterior view. Fig. **53**. Left leg 1 of *Opiona trianglensis*, **n.sp.**, male. Abbreviations: **ac**, angiocoxite; **col**, collum; **cx1**, coxa of leg 1; **cx2**, coxa or leg 2; **cx3**, coxa of leg 3; **cx10**, coxa of leg 10; **cp**, coxal process; **f1**, femur of leg 1; **flc**, flagellocoxite; **flcm**, main branch of flagellocoxite; **flct**, tubular branch of flagellocoxite; **R2**, Ring 2; **R3**, Ring 3; **t1**, tarsus of leg 1; **tp**, gonopod telopodite.

Etymology. The species name is a noun in apposition, after the town of Alsea and the Alsea River.

Diagnosis. Distinct from all other *Opiona* species in lacking gonapophyses on the male second coxae and coxal lobes on the male third coxae (Fig. 51). The telopodites of these legpairs are of normal size, not reduced or modified.

Description. *Male paratype.* Length about 4.2 mm, width about 0.40 mm. Two ommatidia on each side of head. Color white (after long preservation). First legpair robust: coxae (**cx1**, Fig. 51) broad, not modified; femur, postfemur and tibia with few ensiform, slightly twisted long setae, not ventrally expanded; tarsus with tarsal comb.

Second legpair with coxae lacking gonapophyses (**cx2**, Fig. 51) but with sculpture of small nodules, telopodite not reduced. Third legpair coxae (**cx3**, Fig. 51) without coxal lobes, telopodite not reduced or modified.

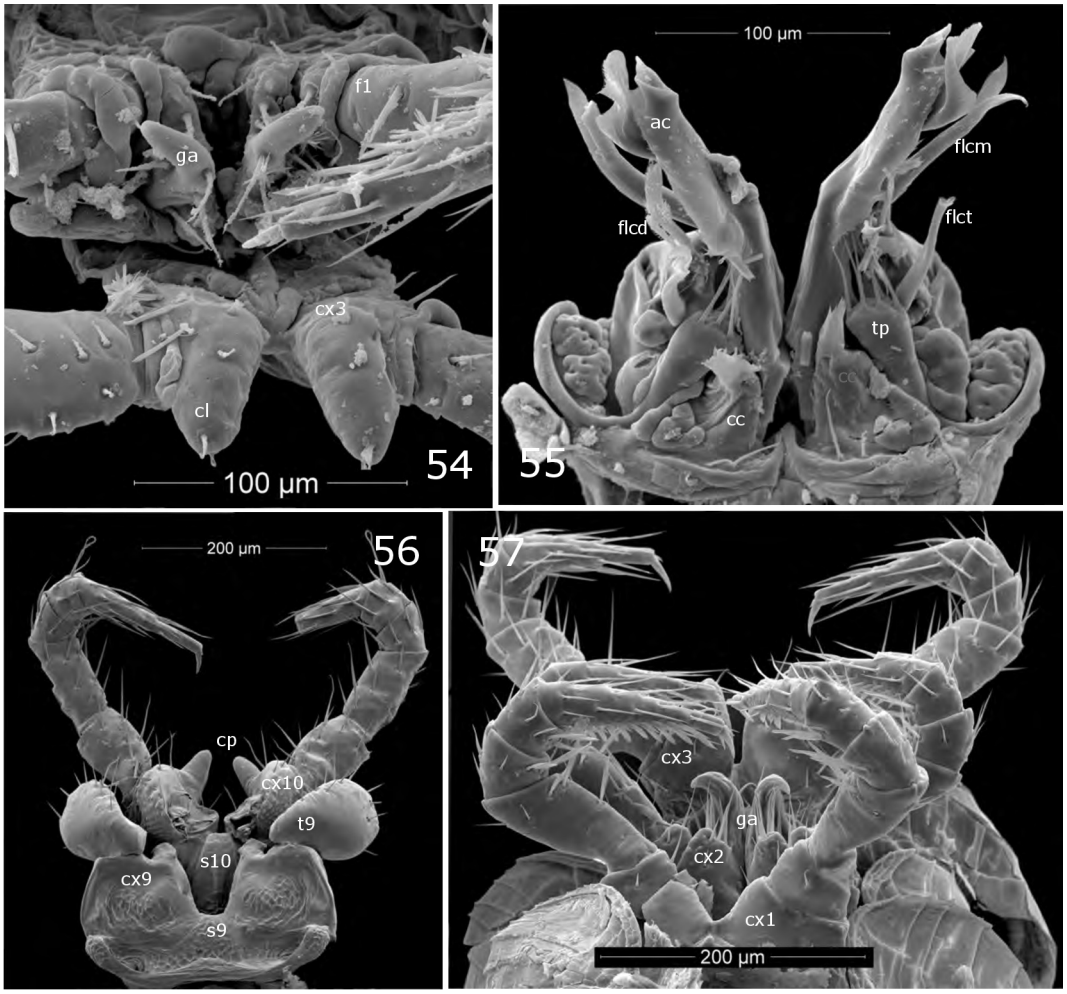
Gonopods (Figs 49, 50) with slender, bifurcate angiocoxite (**ac**), partially sheathing flagellocoxite (**flc**). Flagellocoxite 3-branched: major branch (**flcm**, Fig. 50) sigmoid, distally flabellate, distal margin with tiny acute branched cuticular projections; tubular branch (**flct**) single, dorsal branch not observed. Telopodite (**tp**, Figs. 49, 50) distally broadened, with four to six distal setae.

Ninth leg (Fig. 49) with blocky, subglobular coxa (**cx9**); coxal process (**cp**) small nubbin; telopodite (**t9**) slightly smaller than coxae, sparsely setose. Tenth legpair (Fig. 52) with elongate coxae (**cx10**) and coxal glands (**cg**) coxal process short, rounded (**cp**), coxae with low posterior knob.

Females similar to males in nonsexual characters.

Distribution. The two known localities, Philomath and Clemens Park, are separated by about 13 km (8.5 mi).

Notes. More specimens of males are needed to confirm that the lack of modifications of second and third legs are not anomalous.



FIGURES 54–57. *Opiona trianglensis,* **sp. nov.**, male and *Opiona laquesis,* **sp. nov.**, male. Figs. **54–56**. *Opiona trianglensis,* **sp. nov.**, male. Fig. **54**. Legpairs 1, 2 and 3, ventral view. Fig. **55**. Gonopods, posterior view. Fig. **56**. Legpairs 9 and 10, anterior view. Fig. **57**. Legpairs 1, 2 and 3 of *Opiona laquesis*, **sp. nov.**, male. Abbreviations: **ac**, angiocoxite; **cx3**, coxa of leg 3; **cl**, coxal lobe; **cx9**, coxa of leg 9; **cx10**, coxa of leg 10; **cc**, colpocoxite; **cp**, coxal process; **f1**, femur of leg 1; **flcd**, dorsal branch of flagellocoxite; **flcm**, main branch of flagellocoxite; **flct**, tubular branch of flagellocoxite; **ga**, gonapophysis; **s9**, sternum of legpair 9; **s10**, sternum of legpair 10; **t9**, telopodite of leg 9; **tp**, gonopod telopodite.

Opiona trianglensis Shear & Marek, sp. nov.

Figs 53–56

Types. Male holotype and paratype from Triangle Lake, 44.178°N, -123.548°W, 710' asl, Lane Co., Oregon, collected 7 June 1957 by H. S. Dybas (FMHN). Male paratype and two female paratypes from 6 miles south, 1 mile east of Oakridge, near Hills Creek Lake, 43.657°N, -122.424°W, 1500' asl, Lane Co., Oregon (VMNH).

Etymology. The species name, a noun in apposition, refers to the holotype locality, Triangle Lake. The coordinates given are for Triangle Lake State Park.

Diagnosis. Differing from *Opiona alsea* **sp. nov.** in having the male second coxae with short gonapophyses (**ga**, Fig. 54) and the male third coxae with small lobes (**cl**, Fig. 54). From *Opiona laquesis* Shear & Marek, **sp. nov.**, in the more complex gonopod angiocoxites of *Opiona trianglensis* **sp. nov.** (**ac**, Fig. 55).

Description. *Male paratype.* Length, about 4.7 mm, width about 0.40 mm. Two ommatidia on each side of head. Color white (after long preservation). First legpair (Fig 53) robust, femur (f**l)** ,postfemur a**nd** tibia (t1) each with tow or three ensiform, slightly twisted macrosetae, not expanded ventrally. Second legpair (Fig. 54) coxae with short, curved gonapophyses (**ga**); telopodites not reduced. Third legpair coxae (**cx3**, Fig. 54) with short coxal lobes (**cl**) bearing single terminal setae; telopodite not reduced or modified.

Gonopods (Fig. 55) with complex angiocoxites (**ac**), an anterior branch curves around a posterior sheathing process. Flagellocoxite major process (**flcm**) robust, bladelike, distally divided; dorsal process (**flcd**) with two flabellate branches, the lateral branch smaller; tubular process (**flct**) single, slightly curved. Telopodites (**tp**) small, distally expanded, with 3–4 terminal setae. Colpocoxites (**cc**) with flattened, sclerotic tips.

Ninth legs (Fig. 56) with sternite (**s9**) and coxae (**cx9**) fused to form coxosternum; coxal process a small nub, directed posteriorly; telopodites (**t9**) small, subglobular, mesally excavate.

Coxae of tenth legs (**cx10**, Fig. 56) elongate, glandular (**cg**), free from sternum (**s10**); coxal processes (**cp**) short, blunt.

Females resemble males in nonsexual characters.

Distribution. Known only from the two type localities.

Notes. It appears that the paratype used for SEM examination was infected with an entomopathic fungus, which can be seen protruding from the soft membrane between the lateral sternal lobes and the coxae of the gonopods in Fig. 55. The same condition was seen in other joint membranes of this specimen.

Opiona laquesis Shear & Marek, sp. nov.

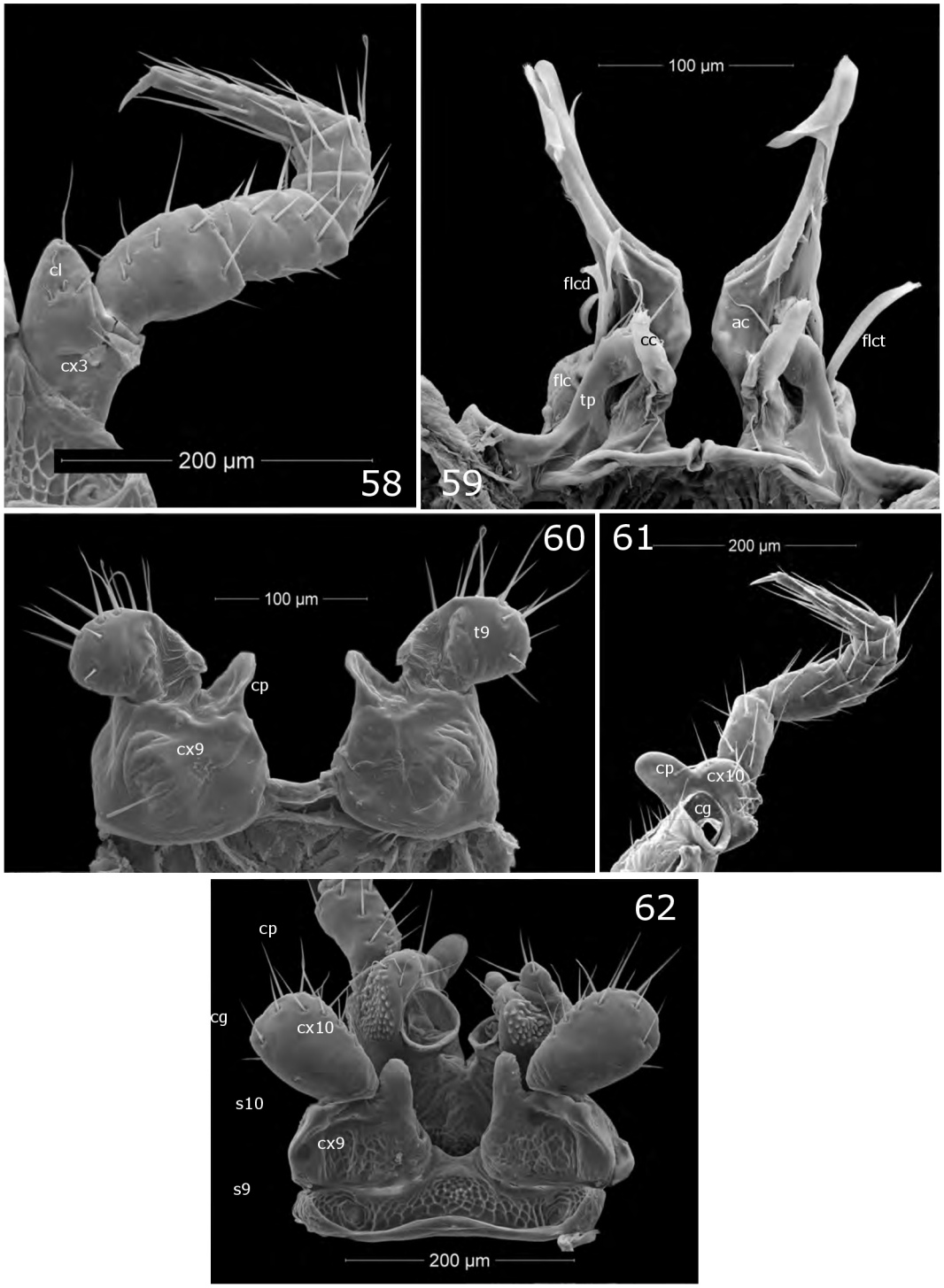
Figs 57–62

Types. Male holotype from State Route 401, 8 miles south of State Route 4, 46.2753°N, -123.8158°W, 40 ft asl, Pacific Co., Washington, collected 2 January 2005 by W. P. Leonard; male paratype from Trap Creek, 1.1 mile north of State Route 12, Pacific Co., Washington, collected 3 May 2003 by W. P. Leonard; Male, female paratypes from 1.7 miles south of State Route 6 on Trap Creek Road, Trap Creek Basin, 46.5403°N, -123.6298°W, Pacific Co., Washington, collected 19 November 2005 by W. P. Leonard & C. Richart; male, female paratypes from State Route 503, 11.4 miles east of Interstate 5, 45.9688°N, -122.5498°W, Cowlitz Co., Washington, collected 7 March 2004 by W. P. Leonard. All specimens deposited in VMNH.

Etymology. The species name is a Latin noun in apposition, meaning "trap," and referring to the collection of the species in the Trap Creek Basin, Pacific Co., Washington.

Diagnosis. Similar to the foregoing two species but with the gonopod angiocoxites much more slender and with a retrorse distal process.

Description. *Male paratype from Trap Creek.* About 4.0 mm long, 0.40 mm wide. Two black ommatidia on each side of head. Color white. First legpair (Fig. 57) robust; coxae (**cx1**) broad; few ensiform, slightly twisted macrosetae on femora; postfemora and tibiae, tarsi with combs. Second leg coxae (**cx2**, Fig. 57) with short, curved gonapophyses (**ga**) with long, basal setae; telopodites not reduced; tarsi with combs. Third leg coxae (**cx3,** Figs 57, 58) with small basal lobes (**cl**, Fig. 58) bearing single terminal setae.



FIGURES 58–62. *Opiona laquesis*, **sp. nov.**, male. Fig. **58**. Right leg 3, anterior view. Fig. **59**. Gonopods, posterior view. Fig. **60**. Legpair 9, posterior view. Fig. **61**. Right leg 10, anterior view. Fig. **62**. Legpairs 9 and 10, anterior view. Abbreviations: **ac**, angiocoxite; **cx3**, coxa of leg 3; **cx9**, coxa of leg 9; **cx10**, coxa of leg 10; **cg**, coxal gland; **cl**, coxal lobe; **cc**, colpocoxite; **cp**, coxal process; **flc**, flagellocoxite; **flcd**, dorsal branch of flagellocoxite; **flct**, tubular branch of flagellocoxite; **s9**, sternum of legpair 9; **s10**, sternum of legpair 10; **t9**, telopodite of leg 9; **tp**, gonopod telopodite.

Gonopods (Fig. 59) with angiocoxite (**ac**) proximally broad, distally narrowing to curved, retrorse tip. Flagellocoxite (**flc**) with dorsal branch (**flcd**) short; flattened, median branch bifurcate; both branches flabellate but lacking cuticular fringes; tubular branch (**flct**) single. Telopodites (**tp**) apically broadened, setose. Colpocoxites (**cc**) small, narrow.

Legpair nine (Figs 60, 62) with well separated blocky coxae (**cx9**); coxal process (**cp**) short, blunt, flattened; telopodite (**t9**) small, posteriorly with deep groove. Legpair 10 (Figs 61, 62) with elongate coxae (**cx10**) and gland (**cg**) and rounded, blunt coxal process (**cp**).

Females similar to males in nonsexual characters.

Distribution. Known from the listed type localities. The Cowlitz Co. record suggests a wider possible distribution for this species. A number of collections from Pacific and Cowlitz Cos. included only females, which may be this species.

Discussion

Opiona now includes 20 species, roughly divided into three species groups, each of which could be regarded as a distinct genus when more study of *Opiona* can be carried out. The divided distribution of the genus as postulated by Gardner & Shelley (1989) can no longer be considered valid, since records presented here indicate a more continuous range from northern California to Alaska. As with almost all known chordeumatidans from the Pacific Northwest and California, collections of mature specimens can evidently be made only from October to May, the wetter, cooler season as opposed to the warm, dry summer.

Acknowledgements

We again express our debt to Bill Leonard and Casey Richart for the specimens described in this and many other papers. Their efforts have nearly doubled the number of millipede taxa known from the Pacific Northwest of the United States, and more material remains to be studied. This work was supported by a National Science Foundation grant to P. Marek (Division of Environmental Biology # 2433355). Steve McCartney in the Nanoscale Characterization and Fabrication Laboratory at Virginia Tech assisted with scanning electron microscopy. We thank Elena Mikhaljova for suggestions which improved the manuscript, and special thanks to Dragan Antić for his meticulous editing.

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