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Securicauda hermani and *Carinacauda stormi*, two new genera and species of slug from the Pacific Northwest of the United States (Gastropoda: Stylommatophora: Arionidae), with notes on *Gliabates oregonius* Webb 1959

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Abstract

Two new genera and species of arionid slug, *Securicauda hermani* **n. gen. et n. sp.** and *Carinacauda stormi* **n. gen. et n. sp.**, are described from the United States in northern Idaho and western Oregon, respectively. This taxonomic decision is based on anatomical comparisons to the ten genera of Arionidae native to northwestern North America. *Securicauda* lacks an atrium and atrial accessory structures and the epiphallus is almost entirely buried in the penis; *Carinacauda* has an atrium, a pair of atrial accessory structures, and a long epiphallus that is not embedded in the penis.

Key words: axetails, anatomy, Idaho, Oregon, Cascade Mountains, Northern Rocky Mountains, Western Hemlock Zone

Introduction

The Western Hemlock Zone (Daubenmire 1978; Franklin & Dyrness 1988) of the Pacific Northwest, with its nearly perpetual moisture, is home to a rich biodiversity of litter-dwellers including terrestrial gastropods. A characteristic of this habitat, which is interesting to many naturalists, is a disjunct "island" in the northern Rocky Mountains of northern Idaho, western Montana and southeastern British Columbia (e.g., Wilke & Duncan 2004). Around 200 groups are known to have this disjunct distribution—be it an intraspecific disjunction or one recognized by taxonomists to represent sister species (Brunsfeld *et al*. 2001). The mesic forests of northern Idaho have been known to house a diverse assemblage of terrestrial gastropods, including many endemics, since the work of Horace B. Baker in the 1930s (e.g. Baker 1932), and Allyn G. Smith in the 1940s (e.g. Smith 1943). Some 60 years later, terrestrial invertebrate collecting trips to northern Idaho frequently reveal novel species or large range extensions of terrestrial gastropods (e.g. Frest & Johannes 2000, Leonard *et al*. 2003, Ovaska *et al*. 2004). The year 2000 was no exception. We encountered a small arionid slug that we were unable to identify based on external appearance. Subsequently, we learned of a slug with a similar external appearance in the Cascade Mountains of western Oregon that some naturalists believed to be *Gliabates oregonius* Webb 1959. Due to an incomplete and brief description of *G. oregonius* (Webb 1959, 1977) there has been controversy concerning the taxonomy of this Oregon slug (Roth 2004). Recently, a slide mount of the genitalia of Webb's holotype was uncovered at the Field Museum in Chicago; an image of this mount is presented here. Dissection and examination of a series of slugs from both Idaho and Oregon reveal that both of our new taxa are distinct from *G. oregonius*. A morphological comparison with other arionid slugs native to the western United States leads us to the conclusion that they represent two new genera and species.

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Material and methods

Populations studied. Specimens of the new taxa were collected from three sites in Idaho and ten in Oregon (Fig. 1, Appendix).

Anatomical studies of the new taxa. Our description of the external anatomy is based on the examination of more than 20 living specimens from Oregon and more than 20 from Idaho that were viewed through a 10–60X Nikon SMZ 2T stereo-zoom microscope. Except where stated otherwise, both measurements and relative body proportions are of living animals in movement. Digital photographs were used to assist in describing morphology and coloration. Digital photographs were made using a Nikon D300 digital camera, Nikon 200-mm micro lens, Cannon 250D close-up lens (reverse-mounted), 1.4 Tamron teleconverter and Nikon SB800 speedlight.

Fifteen specimens from Idaho and fifteen specimens from Oregon were dissected in the current study. Specimens for dissection were drowned in water for approximately 24 hrs and then preserved in 70% ethanol. Genitalia were mounted using a small amount of KY-Jelly immersed in 70% filtered ethanol, then imaged with the use of a Visionary Digital BK Plus Imaging System using a Canon 40D camera. A montage of images was compiled using Helicon Focus and edited using Adobe Photoshop CS3. For both groups mounted slides of jaws and radulae were prepared. Where necessary to better understand details of the distal genitalia, slides were prepared and stained with hematoxylin, dehydrated in 95% and 100% ethanol, cleared in toluene and mounted in Permount (Fisher Scientific, Fairlawn, New Jersey).

Comparative anatomy. We made anatomical comparisons of the new taxa and the ten genera of Arionidae native to northwestern North America (Table 1). In constructing the table we depended heavily upon the published literature (Branson 1991; Leonard *et al*. 2003; Ovaska *et al*. 2010; Pilsbry 1948; Pilsbry & Brunson 1954; Roth 2004; Webb 1959, 1977; Webb & Russell 1977). Where the literature was incomplete we examined actual specimens to confirm specific characteristics.

TABLE 1. Comparison of characteristics of *Securicauda* **n. gen.** and *Carinacauda* **n. gen.** with those of the other genera of Arionidae native to northwestern North America.

Characteristic	*Securicauda*	*Carinacauda*	*Gliabates*	*Kootenaia*	*Prophysaon*	*Magnipelta*	*Hemphillia*	*Staala*	*Udosarx*	*Zacoleus*	*Hesperarion*	*Ariolimax*
Pneumostome anterior to middle of mantle: No (0), Yes (1)	0	1	?	0	1	0	0	1	1	0	0	0
Tail < ½ the mantle length: No (0), Yes (1)	1	1	0	0	0	1	0	1	0	0	0	0
Mantle texture lumpy: No (0) Yes (1)	1	1	?	1	0	0	0	0	0	0	0	0
Tail keeled: No (0), Yes (1)	1	1	1	0	0	1	1	0	1	1	1	1
Line of abscission on tail: No (0), Yes (1)	0	0	0	0	1	0	0	0	0	0	0	0
Caudal mucus pore present: No (0), Yes (1)	0	0	0	0	0	0	1	1	0	0	1	1
Sole tripartite: No (0), Yes (1)	0	0	0	0	0	1, 0*	0	0	1	1	0	0
Shell shape: Flat (0), Convex (1)	1	1	1	1	0	1	1	1	1	1	1	1
Shell calcareous: No (0), Yes (1)	1	1	1	1	1	1	0	1	1	1	1	1
Distinct penial verge present: No (0), Yes (1)	1	1	0	0	0	0	1**	1	0	0	1	0***
Penis reduced to penial loop: No (0), Yes (1)	0	0	0	1	1	0	0	0	0	0	0	0
Distinct epiphallus present: No (0), Yes (1)	1	1	0	0	1	1	1	1	1	1	1	1
Penial retractor muscle present: No (0), Yes (1)	1	1	1	1	0	1	1	1	1	0	1	1
Buccal and tentacular retractors converge behind diaphragm: No (0), Yes (1)	0	0	?	0	0	1	1	1****	1	1	1	1

*Pilsbry & Brunson (1954) indicate that "the sole is plain in relaxed specimens"; Webb & Russell (1977) state that the tail tip "was tripartite – this was not evident anteriorly." We examined two specimens – one tripartite, one undivided. We conclude that this is a variable characteristic in this genus. **_Hemphillia glandulosa_ and _Hemphillia burringtoni_ have a penial papilla. ***While this is generally true of the genus, a verge is present in _Ariolimax columbianus._ ****Except the main branch of the left tentacular retractor which originates on the floor of the body cavity.

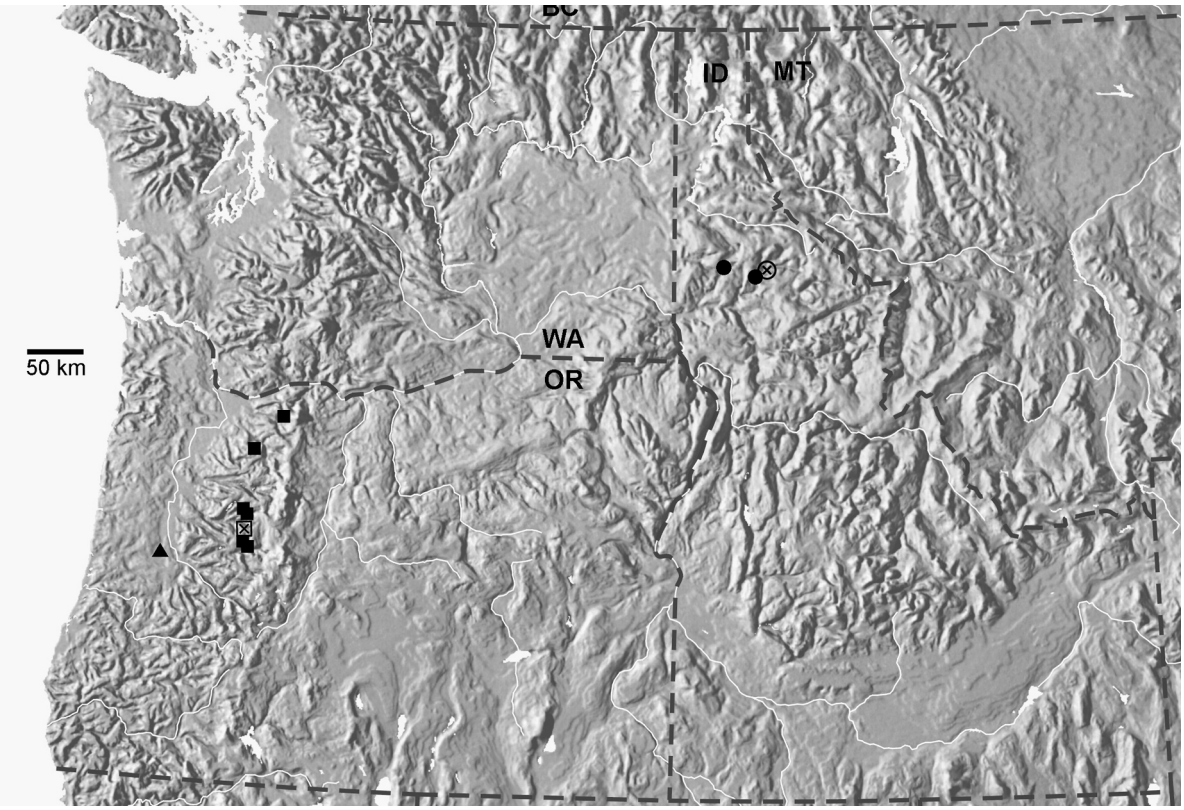

FIGURE 1. Relief map of the Pacific Northwest United States showing the localities of *Securicauda hermani* **n. sp.** (●) and *Carinacauda stormi* **n. sp.** (■); the open symbols containing an "X" represent the type localities. Solid pyramid (▲) = type locality for *Gliabates oregonius*.

Abbreviations

asl	above sea level
CM	Carnegie Museum of Natural History, Pittsburgh, Pennsylvania
DMNH	Delaware Museum of Natural History, Wilmington, Delaware
FMNH	Field Museum of Natural History, Chicago, Illinois
OSAC	Oregon State Arthropod Collection, Corvallis, Oregon

Results

Systematics

Arionidae

Securicauda new genus

Type species. *Securicauda hermani* new species

Diagnosis. Distinguished from all other previously known arionids by small size, strongly keeled tail, and a mantle covering approximately 70% of the extended body length and from *Carinacauda stormi* by the absence of an atrium, the presence of a very short epiphallus partially embedded in the penis and by the lack of atrial accessory structures.

Etymology. The generic name is derived from Latin *securis*, meaning axe, and *cauda*, meaning tail. It describes the sharp, blade-like keel of the animal's tail.

***Securicauda hermani* new species**
Fig. 2, 3, 4

Types. The holotype (CM 104647) and one paratype (CM 104661) were collected on 17 October 2009 by W. Leonard and C. Richart on down woody debris in the riparian zone of Hobo Creek at Hobo Cedar Grove, Idaho Panhandle National Forest, Shoshone County. Additional paratypes were collected by W. Leonard and C. Richart in the riparian zone of Mannering Creek, Benewah County, Idaho (CM 103973) and along Merry Creek, Shoshone County, Idaho (CM 104022).

Etymology. The specific epithet is in honor of Steven G. Herman, Ph.D. A professor at The Evergreen State College since 1971, Dr. Herman has influenced hundreds of students and naturalists for decades in the Pacific Northwest.

Distribution. This species is known from three localities at elevations ranging between 1060 and 1300 m asl in Shoshone and Benewah counties, Idaho (Fig. 1).

FIGURE 2. Photographs of paratypes of *Securicauda hermani* **n. sp.** A. Mannering Creek, Benwah County, Idaho; 10 mm extended length in movement (CM 103973). B. Hobo Cedar Grove, Idaho Panhandle National Forest, Shoshone County, Idaho; 10 mm extended length in movement (CM 104661).

Description. *Size:* Very small, mature adults from 8 to 10 mm extended length while in movement.

External features: Head extending a relatively short distance beyond the mantle; surface smooth with several fine, semi-parallel, longitudinal grooves. Mantle elliptical; covered with glandular lumps; with free flap anterior of pneumostome; posterior edge seated in a slight depression in body; 64 to 80% (mean=72%; SD=0.05; n=7) of length of extended body in movement and 62 to 81% (mean=75%; SD=0.07; n=15) of preserved individuals. Pneumostome slightly anterior to middle of right side of mantle. Sides of body smooth with a series of fine, semi-parallel grooves between edge of mantle and pedal groove. Tail 7 to 20% (mean=17%; SD=0.04; n=7) of length of the extended body in movement; with prominent mid-dorsal keel posterior to edge of mantle; with a series of parallel longitudinal ridges and furrows on sides beneath keel; without line of abscission; caudal mucus pore lacking. Sole undivided. Pedal groove present above foot margin. Foot fringe moderately wide.

Coloration: Head tan; tentacles dark-brown or gray. Neck semi-translucent; adults with distinct white patch on right side. Mantle tan or gray with fine pale-blue flecking and dark-brown or gray blotches; usually with relatively

broad lateral stripe on each side. Sides below mantle gray or tan. Tail light-brown with light-blue flecking, with or without dark-brown markings coincident with furrows. Sole pale-gray to beige with scattered white flecks. Mucus clear.

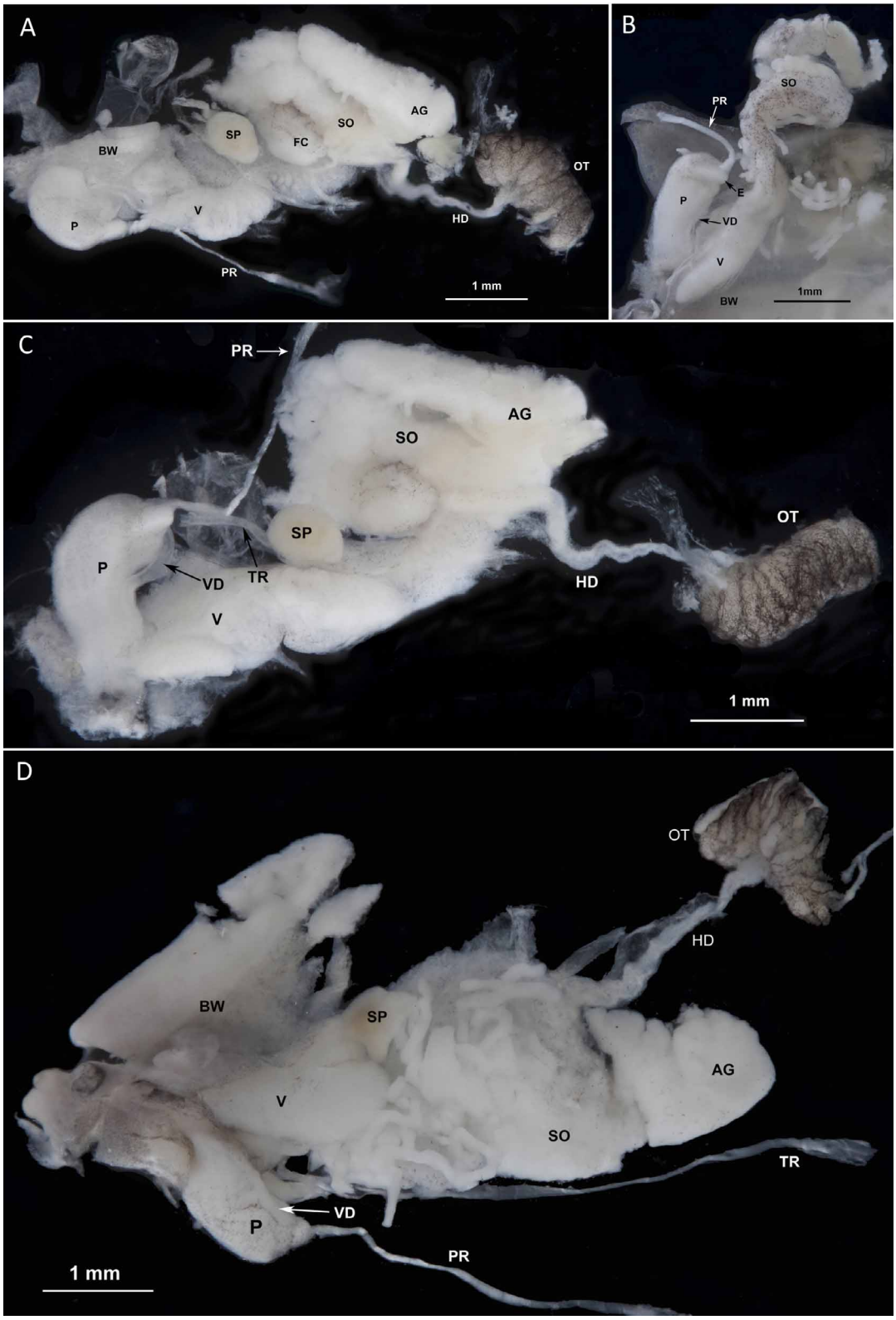

FIGURE 3. Photographs of the genitalia of three specimens (C and D are different views of the same individual) of *Securicauda hermani* **n. sp.** from Hobo Cedar Grove, Shoshone County, Idaho (CM 104661). AG = albumen gland; BW = body wall; E = epiphallus; FC = fertilization chamber; HD = hermaphroditic duct; OT = ovotestis; P = penis; PR = penial retractor muscle; SO = spermoviduct; SP = spermatheca; SPD = spermatheca duct; TR = tentacular retractor muscle; V = vagina; VD = vas deferens.

Internal features. Shell: Dome-shaped, situated toward rear of mantle; with marginal horny layer and fingernail-shaped, calcareous central portion.

Jaw and radula: Jaw a slender palisade arc composed of about 50 transverse inscribed subdivisions. Radula of typical arionid type with tricuspid middle tooth and bicuspid laterals. Mesocones elongated and blade-like; ectocones much shorter and thorn-like, becoming increasingly shorter and blunter in lateral rows.

Reproductive system: Ovotestis situated just under the posterior margin of the diaphragm and partially buried in the digestive gland; consisting of 15 or more lobules (Fig. 3). Hermaphroditic duct long and thick; leading to fertilization chamber; partially surrounded by very large albumen gland. Spermoviduct a bicolored coil that develops many digitate outgrowths in sexually mature individuals. Vagina a very broad, but shallow structure that leads directly to gonopore. Duct of the small ovoidal spermatheca very short, arising from the vagina near its junction with the spermoviduct. Vas deferens originating from spermoviduct just before spermoviduct-vagina junction; continuing over one face of the vagina and then ascending alongside of the penis to which it is loosely adherent. As the vas deferens approaches the top of penis it joins a very short U-shaped epiphallus that becomes partially buried in and wrapped around penis. Penis thick-walled. Penis retractor muscle especially robust, originating at the diaphragm; its muscle fibers insert in penis apex and continue internally into a large verge. Verge acorn-shaped with nipple-like projection at its free end. This projection serving as the opening for a duct that appears to connect with the buried portion of the epiphallus. Projection supported by very short rods that surround the duct opening. Fig. 4 shows the nipple-like tip and a portion of duct. Penis leading directly to the gonopore.

Buccal and tentacular retractor muscles: Paired buccal retractor muscles joining close to rear margin of buccal mass. The resulting broad retractor originates at rear middle of diaphragm very close to the ovotestis and a loop of the intestine. Optical tentacle retractors originating at lateral margins of diaphragm. Right-hand retractor passing between vagina and penis.

Digestive system: Esophagus leading to the very long, thin-walled crop that extends nearly to the rear limit of body cavity. Crop connecting to short stomach that turns toward left side where it gives rise to the short intestine that curves up and back to right side and toward the pneumostome. Paired ducts at crop-stomach junction lead to a pair of digestive glands.

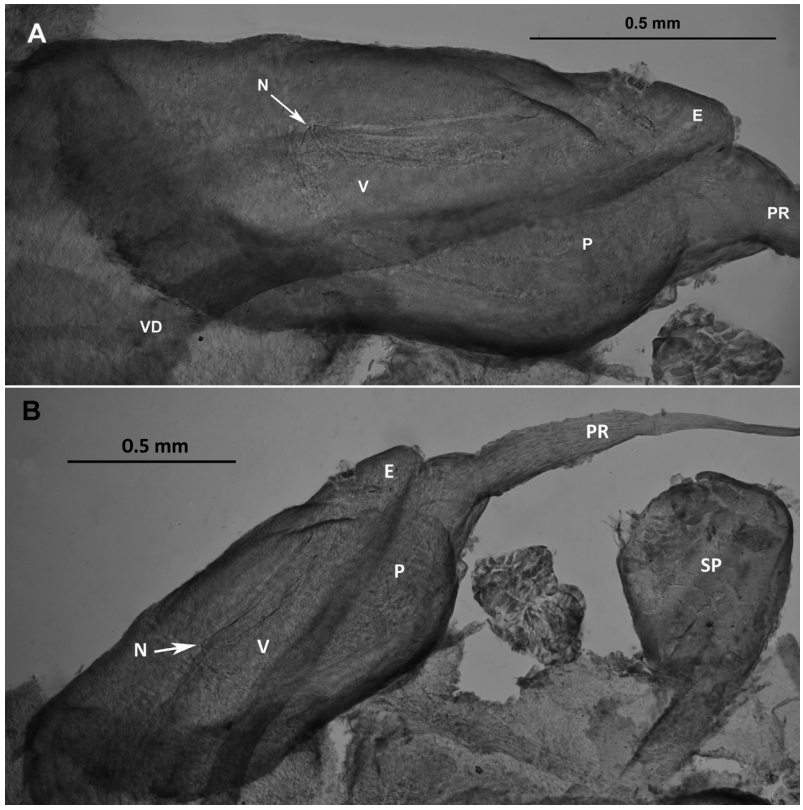

FIGURE 4. The penis of *Securicauda hermani* **n. sp.** from Hobo Cedar Grove, Shoshone County, Idaho stained and mounted on a slide (CM 104661). E = epiphallus; N = nipple-like tip of verge; P = penis; PR = penial retractor muscle; SP = spermatheca; V = verge.

Natural history. This species' range apparently is limited to areas of high winter snowfall in the Western Hemlock Zone of northern Idaho. Western Redcedar (*Thuja plicata*) is a dominant tree species at the three known collection sites. All specimens were collected either on the underside of woody debris, especially long slender stems of Western Redcedar, or in moss. During the early spring this species has been found in upland forest up to 30 m from streams; however once the habitat conditions dried, detections were limited exclusively to mossy seeps, wetlands and stream margins. On several occasions we have found slugs on small woody debris that prior to its removal by us had been embedded up to several centimeters in the needle-duff layer. It appears that this species' diminutive size enables it to move through spaces in the needle-litter layer, which is likely important in helping to modulate ambient temperature and moisture. Research is needed on the natural history and distribution of this species.

Comparative anatomy. We place *Securicauda hermani* in the Arionidae on the basis of its ribbed jaw, which is the only characteristic its shares with all other arionids. It differs from *Carinacauda stormi* in that it lacks an atrium and paired atrial accessory structures and has a very short epiphallus, partially buried in the penis. It differs from *Kootenaia* and *Prophysaon* by virtue of its keeled tail and from all other genera in Table 1 by its divergent buccal and tentacular retractors.

Additional comments. We suggest the common name Rocky Mountain Axetail in recognition of the geographic area from which the species is known and to reflect the hypothesized close relationship between *Securicauda* and *Carinacauda*. The name axetail was first applied to *C. stormi* by John Applegarth of Eugene, Oregon due to the presence of a sharp mid-dorsal keel that, when the slug is contracted, protrudes upward suggesting the head of an axe.

Carinacauda new genus

Type species. *Carinacauda stormi* new species

Diagnosis. Distinguished from all other previously known arionids by small size, strongly keeled tail and a mantle covering approximately 60% of the extended body length; distinguished from *Securicauda hermani* by the presence of an atrium, a very long and coiled epiphallus and a pair of atrial accessory structures.

Etymology. The name refers to the keeled morphology of the tail; *carina* is Latin for keel, *cauda* for tail.

Carinacauda stormi new species

Fig. 5, 6, 7

Types. The holotype (CM 104044), taken on 15 November 2008 from the Upper Blue River Watershed, and one paratype (CM 104023), taken on 05 November 2009 from the Upper Canyon Creek, were collected by T. Young from Douglas-fir needle duff litter (*Pseudotsuga menziezii*) on the Willamette National Forest, Linn County, Oregon. An additional paratype (CM 104045) was collected on 15 April 2010 by T. Young in the Canyon Creek Watershed, Willamette National Forest, Linn County, Oregon.

Etymology. The species name honors Dr. Robert M. Storm, professor emeritus of natural history and vertebrate zoology at Oregon State University.

Distribution. This species was detected at more than 50 localities at elevations ranging between 610 to 1190 m asl in Willamette and Mt. Hood National Forests in Clackamas, Marion, Linn and Lane counties, Oregon (Fig. 1).

Description. *Size:* Very small, extended length of adults in movement 12 to 15 mm; length reduced by approximately 40% after preservation.

External features: As in *Securicauda* except the following: mantle 58 to 64% (mean=61%; SD=0.04; n=15) of the extended body in movement and 55 to 80% (mean=77%; SD=0.07; n=12) of preserved specimens; pneumostome located in the middle (sometimes slightly posterior) of right side and bottom of mantle; tail 20 to 27% (mean=24%; SD=0.03; n=15) of the extended body in movement.

Coloration: Head pale-gray or translucent tan-white; tentacles dark-brown/gray. Neck semi-translucent; adults with a distinct white patch on right side. Mantle tan or pale-gray with light-blue flecking and dark-brown or gray irregular blotches, with a relatively broad lateral stripe on each side. Pneumostome located below lateral stripe and surrounded by light-gray "halo." Sides below mantle pale-gray, with or without dark-brown or gray markings. Tail pale- to dark-gray with fine white flecking and dark-brown or gray markings coincident with furrows; usually with a pale-gray stripe on mid-dorsal keel. Sole pale-gray with scattered white flecks. Mucus clear.

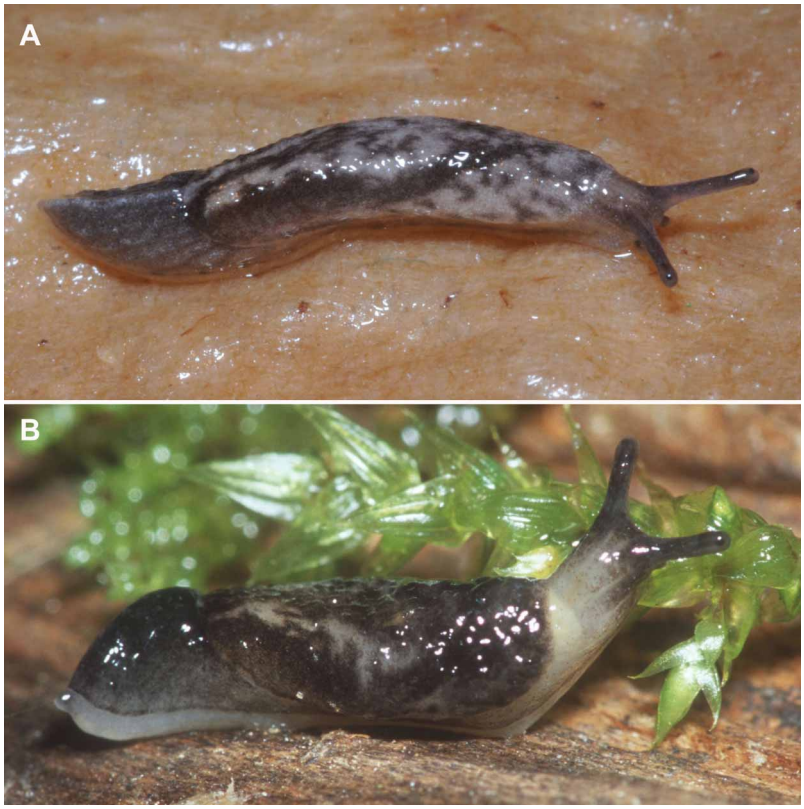

FIGURE 5. Photographs of two paratypes of *Carinacauda stormi* **n. sp.,** Upper Blue River Watershed, Willamette National Forest, Linn County, Oregon. A. adult, 15 mm extended length in movement (CM 106751). B. juvenile, 10 mm extended length in movement (#8 in Appendix).

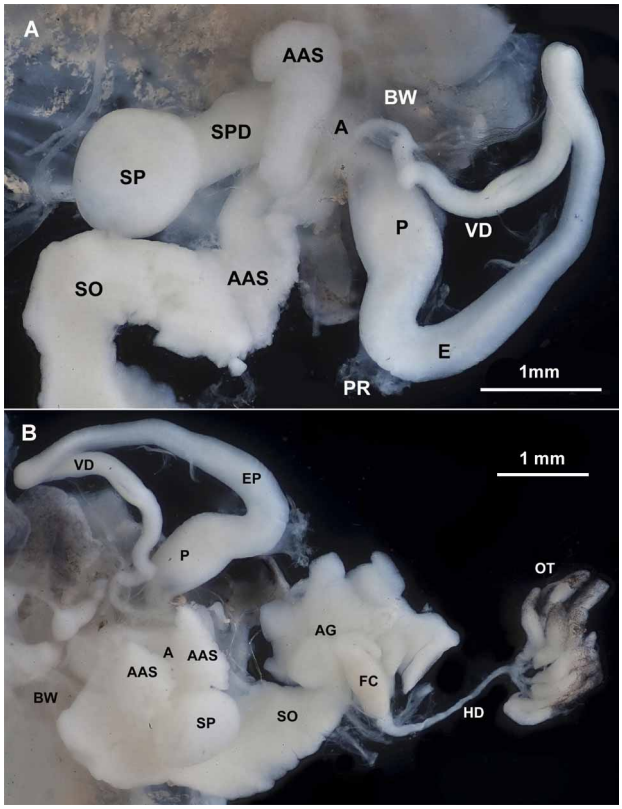

FIGURE 6. Photographs of the proximal and distal genitalia of a paratype of *Carinacauda stormi* **n. sp.** from Linn County, OR (CM 106749). A = atrium; AG = albumen gland; AAS = atrial accessory structure; BW = body wall; E = epiphallus; FC = fertilization chamber; HD = hermaphroditic duct; OT = ovotestis; P = penis; PR = penial retractor muscle; SP = spermatheca; SO = spermoviduct; SPD = spermatheca duct; VD = vas deferens.

Internal features. Shell: Similar to *S. hermani* in both position and composition.

Jaw and Radula: Similar to *S. hermani* in structure.

Reproductive System: Ovotestis consisting of 12 or more lobules; located on midline just under posterior margin of diaphragm and partially surrounded by the digestive gland. Hermaphroditic duct of moderate length and thickness; leading to fertilization chamber, which is largely surrounded by the large albumen gland. The whitish, loosely coiled spermoviduct leads to the tubular free oviduct that opens into the atrium. The spermathecal duct, which arises near junction of free oviduct and atrium, generally becomes thick in sexually mature individuals; in two of our individuals the duct remained slender for at least a portion of its length. Spermatheca large and globular. The slender vas deferens arising from spermoviduct; traveling across the free oviduct and connecting with the long, thick and highly coiled epiphallus. Penis retractor muscle inserting in wall of epiphallus just before duct joins penis apex. Epiphallus internally connecting with a large verge that is about half as long as the penis. In sexually mature individuals the distal portion of the verge is so opaquely white that it can be seen through the translucent wall of the penis (in Fig. 7 these opaquely white areas show up as densely black). Penis opening into atrium, which also receives the free oviduct and spermathecal duct. The atrium also bears a pair of accessory structures of unknown function. In immature animals, these structures resemble the cotyledons on a bean sprout. As animals mature the pair becomes much larger and more complex. They are sufficiently opaquely white for the more lateral member of the pair to be seen through the thin body wall. Examination under a compound microscope failed to reveal any fine detail—no darts, or ducts or muscle bands that might suggest a special function.

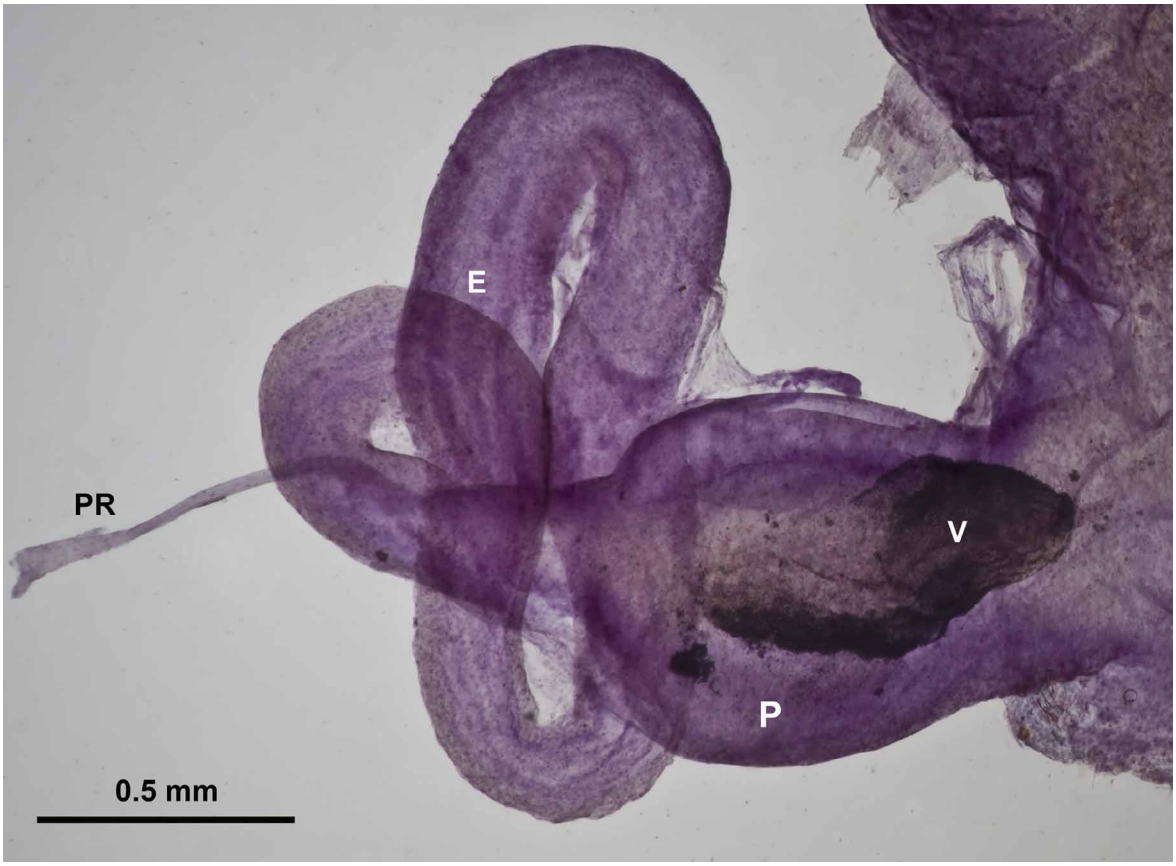

FIGURE 7. The penis of *Carinacauda stormi* **n. sp.** from Linn County, OR stained and mounted on a slide (CM 106751). E = epiphallus; P = penis; PR = penial retractor muscle; V = verge.

Buccal and tentacular retractor muscles: Similar to the architecture of *S. hermani*.

Digestive system: As in *S. hermani* the crop and the pair of digestive glands are the major feature of the digestive system. The intestine is short and oriented as in *S. hermani*.

Natural history. This species is currently known from montane areas of the Oregon western slope Cascades where Douglas-fir (*Pseudotsuga menziesii*) is a dominant overstory species and minor tree species include Western Hemlock (*Tsuga heterophylla*) and Vine Maple (*Acer circinatum*). We located approximately 100 individuals at more than 50 sites in Willamette National Forest; all individuals were found in Douglas-fir–Western Hemlock forests where needle litter was almost exclusively Douglas-fir at the microsite. Forest age class did not seem to be a

factor in detecting this species; detections occurred in forests 25 years to over 150 years in age. Areas where down wood retained pockets of moisture and where Vine Maple leaves formed a layer to hold moisture are preferred habitats. In addition, small topographic depressions where water collects or saturation occurs as the rainy season develops appear to be important microhabitat features. Detections occurred almost exclusively in semi- to fully saturated needle litter between the most recent and previous year's needle-duff layers (approximately 2.5 to 5 cm below the surface). Shrub, fern and moss layers were lacking in the areas where detections occurred. This species was rarely detected in forest stands where either Incense-cedar (*Calocedrus decurrens*) or Western Redcedar (*Thuja plicata*) was a dominant tree species. Though it has been found at the margins of small streams, this species is not associated with seeps or wetlands.

Detections have occurred primarily in the fall, but recent spring surveys have detected adults and juveniles in conditions where litter was still saturated due to snowmelt. Four specimens have been successfully kept in captivity for 24 months (November 2008 to November 2010) and over 20 collected in November 2009 are currently in captivity to document biological and reproductive behavior. Eggs were documented in February 2009 and March 2010; however, none of the eggs produced hatchlings. The clutch in 2010 contained 12 eggs that were semi-translucent white, oblong and approximately 2 mm long.

Comparative anatomy. We place *Carinacauda stormi* in the Arionidae on the basis of its ribbed jaw, which is the only character it shares with all other arionids. It differs from *Securicauda hermani* by possessing an atrium and paired accessory structures and a well developed, coiled epiphallus. It differs from *Kootenaia* and *Prophysaon* by virture of its keeled tail and from all other genera in Table 1 by its divergent buccal and tentacular retractors.

Additional comments. We suggest the common name Cascade Axetail in recognition of the Cascade Mountains where the species resides and to reflect its hypothesized close relationship with *Securicauda*.

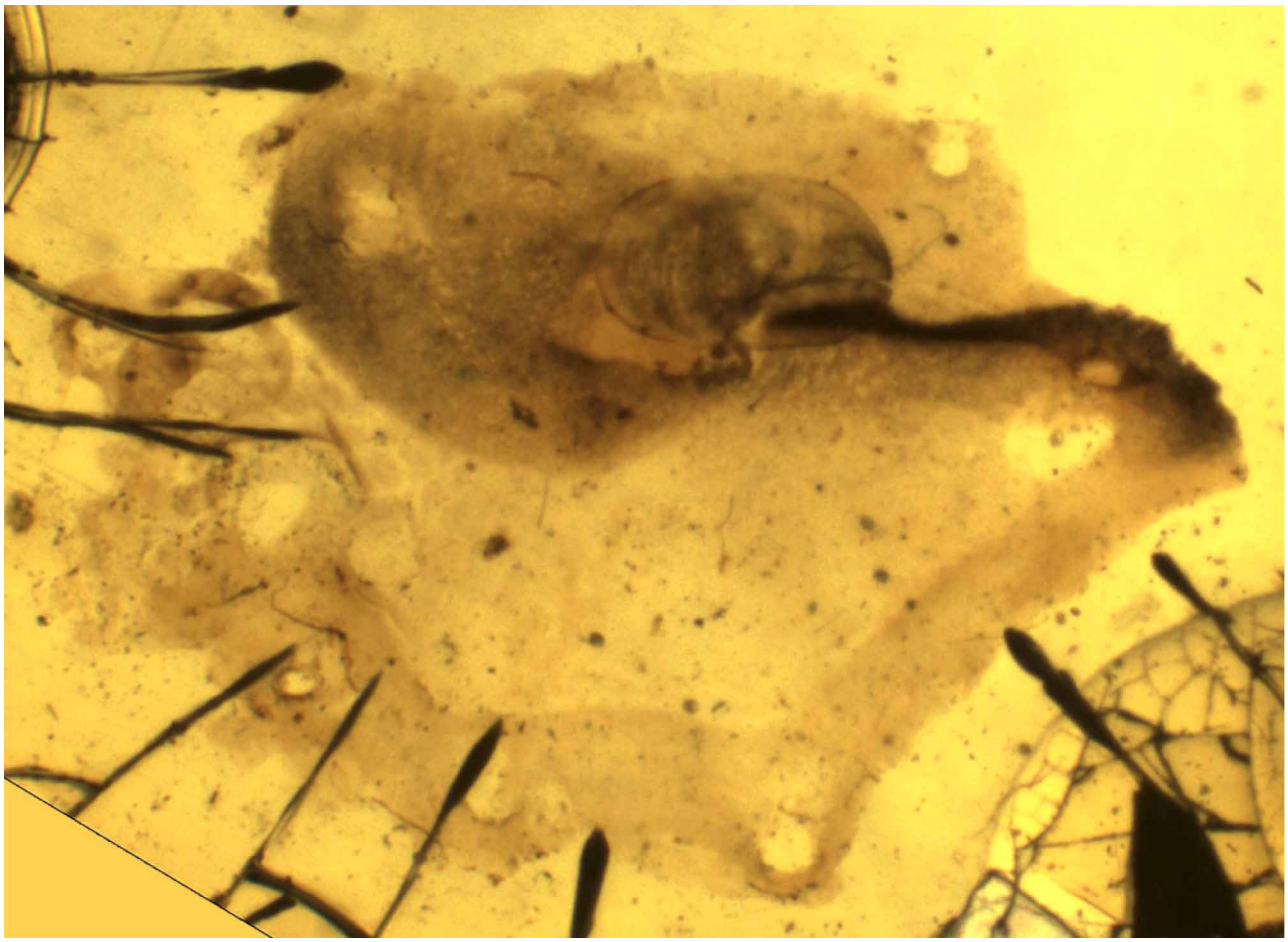

FIGURE 8. The slide-mounted holotype of *Gliabates oregonius* Webb 1959 (FMNH 308279). The keel on the tail is identifiable as a dark brown stripe on the upper right side of the photo. The mantle is identifiable by a dark-brown ovoid area immediately forward (left) of the tail. The shell is partially exited from the mantle and overlapped onto the tail. Several cracks in the slide cover show as dark brown lines along the left and lower sides of the image. Photo courtesy of Jochen Gerber, FMNH.

Discussion

Systematic considerations. Based on the shared character states of external and internal morphology, we believe that the two genera described in this paper are sister taxa within a common clade, which we refer to as axetails. This hypothesis is also supported by a preliminary genetic analysis of mitochondrial markers that indicates that *Securicauda* and *Carinacauda* form a monophyletic group within the family Arionidae; this analysis suggests a divergence time between the two genera of several million years (Wilke & Ziegltrum 2003 [identified in Fig. 2 as *Gliabates* sp.]; Thomas Wilke, Animal Ecology & Systematics, Justus Liebig University, Giessen, Germany, pers. comm.). Shared character states of axetails include the following unique combination of traits: small size (8–15 mm extended); approximately 60–70% of the body covered by the mantle; a long free anterior mantle lobe; a short (approximately 17–24% of extended body length) and strongly keeled tail; buccal and tentacular retractor muscles diverge to their attachments in the posterior and lateral margins of the diaphragm respectively; absence of viscera in the tail; verge present. Yet despite having what is outwardly a remarkably similar appearance, the distal genitalia of the two genera exhibit great differences. For example, in *Securicauda* an atrium and atrial accessory structures are lacking and the epiphallus is almost entirely buried in the penis. *Carinacauda* has an atrium, a pair of atrial accessory structures, and a long epiphallus that is not embedded in the penis. To some degree, this phenomenon parallels what occurs in the arionid genus *Prophysaon* wherein all species have shared external characteristics, yet within the genus there are such significant differences in the genitalia that Pilsbry (1948) felt compelled to recognize two subgenera. However, the genitalic difference seen in the axetails are considerably greater than occurs in *Prophysaon*. For this reason we believe that the creation of two new genera is warranted.

***Gliabates oregonius* Webb 1959.** In 1959 Glenn Webb described the enigmatic species *Gliabates oregonius* (as *G. oregonia*) and despite providing fairly detailed information on the distal genitalia the description includes minimal additional information on internal and external characteristics of the species. A subsequent paper by Webb (1977) provides additional information on the holotype, including illustrations of the radula, shell, partial mantle and distal genitalia; it also clarifies that the description had been based on just a single specimen in what appears to have been the early stages of decomposition. Lacking from both these papers are descriptions of several characters and character states, including the buccal and tentacular muscles, sole, pneumostome position, relative body proportions, mantle texture, presence/absence of a line of abcission on tail, and presence/absence of a caudal mucus pore.

To gain additional information on *G. oregonius* we examined a series of high-resolution digital photographs of the slide-mounted holotype, provided to us by Jochen Gerber (FMNH). From one of these photographs (Fig. 8) we were able to establish that the tail lacks both a line of abscission and a caudal mucus pore and that the shell is most probably concave.

A few naturalists in the Pacific Northwest have suggested that axetails might be *G. oregonius* and our working hypothesis at the start was that we would confirm that at least *C. stormi* was *G. oregonius*. This hypothesis stemmed from Webb's description on the external morphology of *G. oregonius*, which is partially consistent with axetails. Two shared characters are a body length of "about 1 cm long" and a "strong keel on tail." However, a few external characters are incongruent with axetails. Webb states that the "mantle overlies about half the body"; measurements of the photo of the holotype (Fig. 8) confirm that the mantle is approximately 50% of the body length, which compares to means of 72% and 61% for *Securicauda* and *Carinacauda*, respectively. Our measurements of this same photo also enabled us to establish that the tail of *G. oregionius* is 42% of the body length, approximately double that of either axetail; the tail was also determined to be 94% the length of the mantle, significantly greater than either axetail. One of the more striking characteristics of preserved axetails is an anterior free mantle flap; we believe that the normally detail-oriented Webb would have mentioned this characteristic had it been present in *Gliabates*.

The most compelling evidence on the relationship between *Gliabates* and axetails is found in the characteristics of the internal anatomy. The jaw of both species of axetails has about 50 evenly spaced ribs as compared with 17 ribs in the holotype of *Gliabates*. Webb indicates that *Gliabates* had a two-chambered penis, no well-developed verge, no atrial or vaginal accessory structures and had a short epiphallus. *Carinacauda stormi* differs from *Gliabates* in possessing atrial accessory structures, an undivided penis, a well-developed verge and a very long, coiled epiphallus. *Securicauda hermani* differs from *Gliabates* in possessing a well-developed verge, an undivided penis, a much reduced epiphallus and a slender spermathecal duct.

The type locality of *G. oregonius* along with Webb's description of habitat provides information that is insightful in terms of assessing the potential relationship between *Gliabates* and axetails. The holotype was collected in the Oregon Coast Range on the "east-bank of the Long Tom River, adjacent to Alderwood State Park," Lane County, Oregon (Webb 1959). This site is situated at an elevation of 170 m, approximately 370 m lower than either of the axetails is known to occur. Both Tiffany Young and John Applegarth (pers. comm.) independently made several visits to this site and were unsuccessful in locating any specimens of *G. oregonius*. The habitat at this location was found to be quite different from that where axetails are known to occur. Douglas-fir and Vine Maple were present, but a substantial needle-duff layer was not developed at the site. Swordfern (*Polystichim munitum*) and moss were found to be the dominant ground cover. Vine Maple was also sparse and did not provide an adequate leaf layer to hold moisture. In addition, down wood was present in very low quantity (two pieces/acre).

Webb (1959) stated that *G. oregonius* had a general appearance approximating *Hesperarion* spp., but he noted some differences in the genitalia. *Hesperarion* was not well documented in Oregon until 1991 when Branson (1991) described *Hesperarion mariae* based on specimens collected at Cape Lookout, Tillamook County, Oregon—thus raising the possibility that *G. oregonius* might actually be a *Hesperarion*. Using Webb's published description and illustrations, Roth (2004; pers. comm.) compared *G. oregonius* to *Hesperarion hemphilli* and noted significant differences in the genitalia; he also pointed to similarities of the genital morphology with the genus *Milax* and suggested that *G. oregonius* was probably assignable to Milacidae. Having reviewed photographs of Webb's holotype, we conclude that the slug does not fit the criteria for consideration as a milacid. The holotype lacks a tripartite sole and a subdivided mantle, which are characteristic of milacids, and the jaw is definitely of the arionid type. Unfortunately, the poor quality of the holotype and the lack of additional confirmed specimens of *G. oregonius* preclude more robust morphological comparisons that could shed light on the species' identity and its relationship with other taxa.

The significant differences of the distal genitalia have led us to the conclusion that axetails are not members of the genus *Gliabates*. Despite our certainty on this point, we are unable to contribute new insights into *G. oregonius*. While it seems improbable that Webb could have collected the last individual of a now extinct group, on the basis of Webb's description and photos of the holotype, we are unable to ascribe it to any extant species—native or introduced. A number of factors, which have been discussed in the preceding paragraphs, raise serious question regarding *G. oregonius*. Until such a time when additional slugs are found that match Webb's description, especially in the distal genitalia, we suggest that it be considered a *species inquirenda*.

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References

Baker, H.B. (1932) New land snails from Idaho and eastern Oregon. *The Nautilus*, 45, 82–87.

Branson, B.A. (1991) *Hesperarion mariae* (Gastropoda: Arionidae: Ariolimacinae), a new slug species from Oregon. *Transactions of Kentucky Academy of Science*, 52, 109–110.

Brunsfeld, S.J., Sullivan, J., Soltis, D.E. & Soltis, P.S. (2001) Comparative phylogeography of northwestern North America: A synthesis. *In*: Silvertown, J. & Antonovics, J. (Eds.), *Integrating ecology and evolution in a spatial context.* Blackwell Publishing, Williston, VT, pp. 319–339.

Daubenmire, R. (1978) *Plant geography with special reference to North America*. Academic Press, New York, 338 pp.

Franklin, J.F. & Dyrness, C.T. (1988) *Natural vegetation of Oregon and Washington*. Oregon State University Press, Corvallis, OR, 452 pp.

Frest, T.J. & Johannes, E.J. (2000) An annotated checklist of Idaho land and freshwater mollusks. *Journal of the Idaho Academy of Science*, 36, 1–51.

Leonard, W.P., Chichester, L., Wilke, T. & Baugh, J. (2003) *Kootenaia burkei*, a new genus and species of slug from northern Idaho, United States (Gastropoda: Pulmonata: Arionidae). *Zootaxa*, 355, 1–16.

Ovaska, K., Chichester, L. & Sopuck, L. (2010) Terrestrial gastropods from Haida Gwaii (Queen Charlotte Islands) British Columbia, Canada, including description of a new endemic slug (Gastropoda: Stylommatophora: Arionidae). *The Nautilus*, 124, 25–33.

Ovaska, K., Leonard, W.P., Chichester, L., Burke, T.E., Sopuck, L. & Baugh, J. (2004) *Prophysaon coeruleum* Cockerell, 1880, blue-gray taildropper (Gastropoda: Arionidae): new distributional records and reproductive anatomy. *Western North American Naturalist*, 64, 538–543.

Pilsbry, H.A. (1948) Land Mollusca of North America (north of Mexico). *The Academy of Natural Sciences of Philadelphia Monographs*, 3, volume 2 part 2, i–xlvii, 521–1113.

Pilsbry, H.A. & Brunson, R.B. (1954) The Idaho-Montana slug *Magnipelta* (Arionidae). *Notulae Naturae*, 262, 1–6.

Roth, B. (2004) Observations on the taxonomy and range of *Hesperarion* Simroth, 1891 and the evidence for genital polymorphism in *Ariolimax* Mörch, 1860 (Gastropoda: Pulmonata: Arionidae: Ariolimacinae). *The Veliger*, 47, 38–46.

Smith, A.G. (1943) Mollusks of the Clearwater Mountains, Idaho. *Proceedings of the California Academy of Sciences*, 4, 537–554.

Webb, G.R. (1959) Two new north-western slugs, *Udosarx lyrata*, and *Gliabates oregonia*. *Gastropodia*, 1, 22–23, 28.

Webb, G.R. (1977) Additional data on *Gliabates oregonia*. *Gastropodia*, 1, 108.

Webb, G.R. & Russell, R.H. (1977) Anatomical notes on a *Magnipelta*: Camaenidae? *Gastropodia*, 1, 107–108.

Wilke, T. & Duncan, N. (2004) Phylogeographical patterns in the American Pacific Northwest: lessons from the arionid slug *Prophysaon coeruleum. Molecular Ecology*, 13, 2303–2315.

Wilke, T. & Ziegltrum, J. (2003) Genetic an anatomic analyses of the jumping slugs. Technical report prepared for the Olympic National Forest, Olympia, WA (contract 43-05G2-1-10086), 26 pp.

APPENDIX. Collection localities and associated information for the individuals studied.

Locality	Catalog #
Securicauda hermani	
Hobo Grove Botanical Area, Idaho Panhandle National Forest, Shoshone County, Idaho; elevation 1370 m asl; 47°5'4.38"N 116°6'59.66"W; 3 July 2005; 17 Oct 2009 (WL, CR)	CM 104647 (holotype) CM 104661 (paratypes)
Merry Creek headwaters, Idaho Panhandle National Forest, Shoshone County, Idaho; elevation 1300 m asl; 3 Oct 2000 (WL), elevation 1290 m asl; 47°4'35.78"N 116°8'40.19"W; 3 July 2005 (WL, CR)	DM 221708, DM 221706 CM 104022
Mannering Creek at State Route 6, Benewah County, Idaho; elevation 1050 m asl; 47°3'59.74"N 116°40'28.61"W; 3 July 2005; 18 Oct 2009 (WL, CR)	CM 103973
Carinacauda stormi	
Willamette National Forest, McKenzie Ranger District, Upper Blue River Watershed, Linn Co., Oregon; elevation 1128 m asl; 44°18'47.19"N 122°14'53.61"W; 15 Nov 2008 (TY)	CM 104044 (holotype)
Willamette National Forest, McKenzie Ranger District, Upper Blue River Watershed, Linn Co., Oregon; elevation 961 m asl; 44°17'23.64"N 122° 9'46.18"W; 19 Nov 2008 (TY)	CM 106751
Willamette National Forest, Sweet Home Ranger District, Trout Creek Watershed, Linn Co., Oregon; elevation 900 m asl; 44°23'7.44"N 122°21'13.22"W; 16 Nov 2009 (TY)	CM 106750
Willamette National Forest, Sweet Home Ranger District, Upper Canyon Creek Watershed, Linn Co., Oregon; elevation 1010 m asl; 44°17'38.25"N 122°20'0.67"W; 05 Nov 2009 (TY)	CM 104023 (paratype)
Willamette National Forest, Sweet Home Ranger District, Canyon Creek Watershed, Linn Co., Oregon; elevation 940 m asl; 44°22'33.07"N 122°21'34.57"W; 15 April 2010 (TY)	CM 104045 (paratype)
Willamette National Forest, Sweet Home Ranger District, Upper Canyon Watershed; Linn Co., Oregon;elevation 1240 m asl; 44°20'28.79"N 122°16'17.73"W; 20 Nov 2008 (TY)	CM 106749
Willamette National Forest, Sweet Home Ranger District, Upper Canyon Creek Watershed, Linn Co., Oregon ; elevation 1160 m asl; 44°17'49.51"N 122°17'5.67"W; 05 Nov 2009 (TY)	*
Headwaters to Blue River, H.J. Andrews Experimental Forest, Willamette National Forest, Linn Co., Oregon; elevation 1010 m asl; 44°16'52.91"N 122°10'10.58"W; 15 July 2005 (WL, CR); 5 May 2006 (Adrian Richart, CR, WL)	*
Willamette National Forest, Sweet Home Ranger District, Galena Creek Watershed, Linn Co., Oregon; elevation 690 m asl; 44°33'58.62"N 122°16'42.81"W; Nov 2009 (TY)	*
Willamette National Forest, Sweet Home Ranger District, Sheep Creek Watershed, Linn Co., Oregon; elevation 1100 m asl; 44°25'4.70"N 122°11'1.05"W; 16 Nov 2009 (TY)	*
Willamette National Forest, Sweet Home Ranger District, Sheep Creek Watershed, Linn Co., Oregon; elevation 780 m asl; 122°21'13.22"W 122°12'33.58"W; 16 Nov 2009 (TY)	*
Clackamas County, Oregon; elevation 1040 m asl; 45°21'14.22"N 121°54'52.41"W; elevation 960 m asl; 45°7'19.07"N 122°15'48.06"W; 25 Nov 2002; D. Lysgaard-Rutz	OSAC 0000156989
Clackamas County, Oregon; elevation 970 m asl; 45°7'19.07"N 122°15'48.06"W; 31 May 2002; D. Lysgaard-Lutz	OSAC 0000156990
Linn County, Oregon; elevation 730 m asl; 44°37'12.88"N 122°20'50.44"W; 20 Oct 2005; D. Lysgaard-Lutz	OSAC 0000156991 OSAC 0000156992
Linn County, Oregon; 19 Oct 2005; elevation 930 m asl; 44°37'27.61"N 122°21'20.68"W; D. Lysgaard-Lutz	OSAC 0000156993

*Specimen not available for museum donation.