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Cave millipeds of the United States. III. Two new species from the western states. (Diplopoda: Polydesmida, Chordeumatida).

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ABSTRACT

Two new species of cave millipeds are described. *Speodesmus aquiliensis* (Polydesmidae) is from Fulford Cave, Eagle Co., Colorado, and *Macromastus umpqua* (Conotylidae) is from a lava tube near North Umpqua, Douglas Co., Oregon. The closest relative of *S. aquiliensis* is *S. tujanbius*, found in Carlsbad Caverns in southern New Mexico. These two species are distinct from the compact group of *Speodesmus* species found in caves in the Edwards Plateau of Texas. *Macromastus umpqua* is the second species of its genus to be described; *M. marginandus* is an epigean species from Idaho.

INTRODUCTION

This paper is the third in a series of occasional articles on the milliped fauna of North American caves, complimentary to my series on Mexican and Central American cave millipeds (Shear, 1982). The first paper in the series (Shear, 1969) presented a synopsis at the generic level of cave millipeds in the United States and gave a key to the genera. The second (Shear, 1974) described a new *Colactis* from an isolated desert cave in California and redescribed *Speodesmus tujanbius* (Chamberlin) from Carlsbad Caverns, New Mexico. In the present article, I describe a fourth species of *Speodesmus*, *S. aquiliensis*, and a second species of *Macromastus*, an important genus of the chordeumatid family Conotylidae. This latter species also adds to the growing list of troglobites from lava tubes in the Pacific northwest of the United States.

TAXONOMY AND DISCUSSION

Order Polydesmida

Family Polydesmidae

Genus **Speodesmus** Loomis**Speodesmus aquiliensis**, new species, Figs. 1-7.

Types: Male holotype from Fulford Cave, 21 mi SE of Eagle, Eagle Co., Colorado, collected 6 July 1980 by J. R. Holsinger, J. V. Ward, J. Meacham, and R. Goke. Deposited in the American Museum of Natural History.

Name: The species epithet is a Latin adjective referring to the type locality, Eagle Co., Colorado.

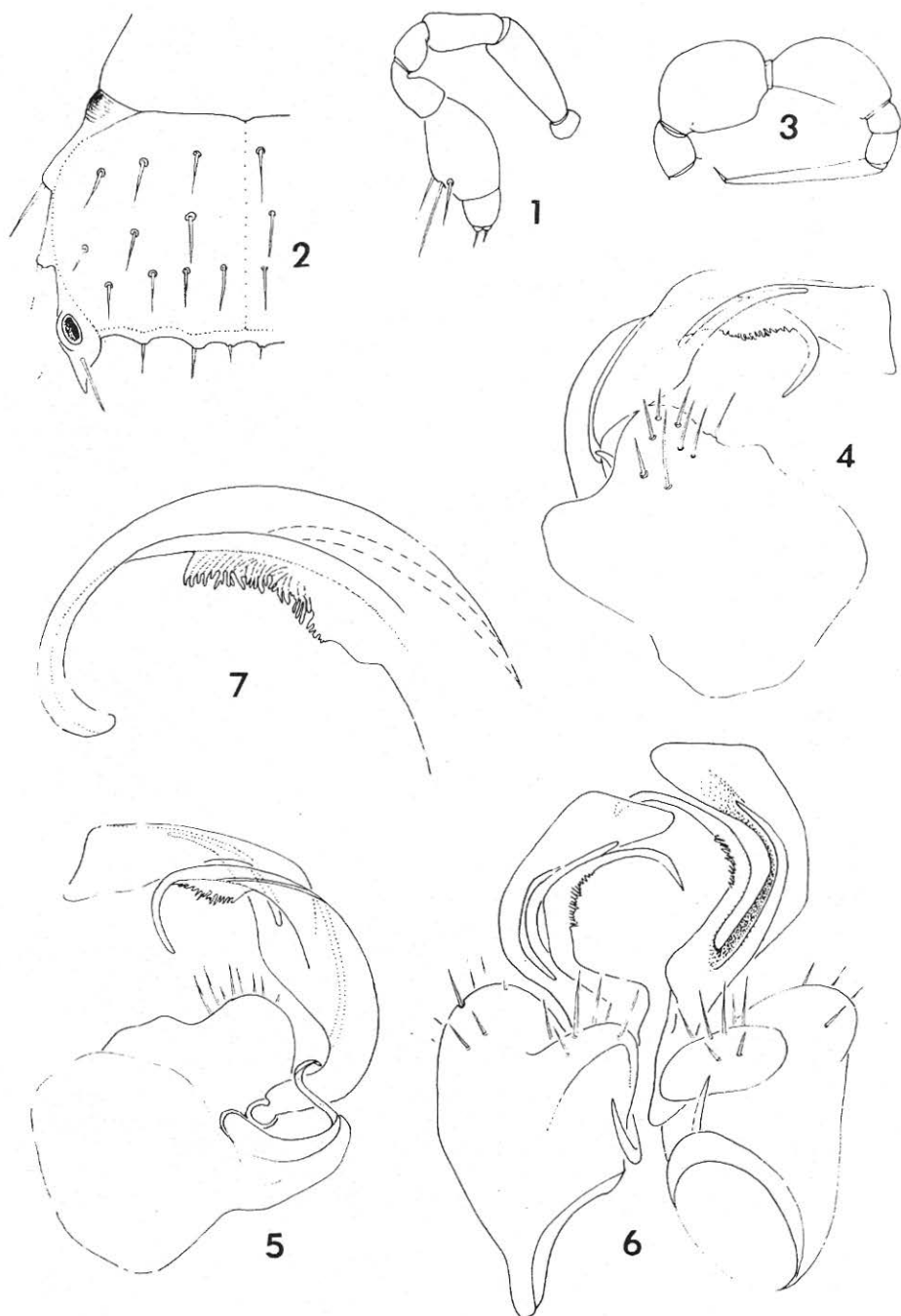
Diagnosis: Distinct from *S. bicornourus* and *S. echinourus* in lacking the retrorse barb on the major anterior branch of the gonopod. Distinct from *S. tujanbius* in being only two-thirds as large and in the much deeper divisions between the gonopod branches.

Male. Length 6 mm, greatest width, 0.74 mm. Nineteen segments. Body completely unpigmented, cuticle transparent. Head broader than collum, densely setose. Antennae relatively short, penultimate segment enlarged (Fig. 1). Collum roughly oval in outline, lacking paranota, with three transverse rows of setae. Pore formula 5, 7, 9, 10, 12-18. Midbody segments with fairly narrow paranota (Fig. 2); three marginal teeth subtending marginal setae; ozopore (when present) large, opening from a low callus at posteriolateral corner, this corner in the form of posteriorly projecting tooth. Posterior margin of metazonite with row of six small setae, metazonal surface with three rows of six, six, and eight setae (lateral marginal setae not counted). Epiproct acute, with terminal group of five setae; periproct lips margined, flared, prominent. Typical leg (Fig. 3) with femur and prefemur greatly enlarged, as in *S. tujanbius*; legs not so enlarged in juvenile females, less so in penultimate instar males.

Gonopods (Figs. 4-7) with typical tripartite structure. Solenomerite not as long as bifurcate prefemoral process, apically sharply curved, with fimbriate pad somewhat reduced but still prominent near opening of seminal canal (Fig. 5). Prefemoral process divided into broad, blade-like mesal part and smaller, acute lateral part.

Mature females not available for study.

Distribution: At present the species is known only from the type locality, but according to James Meacham (letter of 6 March 1982): "A nearby cave was named White Centiped [sic] Cave after them and the same milliped (first recovered from Lime Creek Caverns in the mid-seventies) is found in a series of caves in the Lime Creek Karst by the hundreds of thousands." Of course, without examining males from each of the populations, it is not possible to state with assurance that all of them are *S. aquiliensis*.



Figs. 1-7. *Speodesmus aquiliensis* male. Fig. 1. Right antenna, Anterior view. Fig. 2. Left half of midbody segment, dorsal view. Fig. 3. Leg from midbody segment, anterior view. Fig. 4. Right gonopod, lateral view. Fig. 5. Right gonopod, mesal view. Fig. 6. Gonopods, posterior view. Fig. 7. Solenomerite tip, lateral view.

Male. Total length 23 mm, greatest width, 2.5 mm. About 15 ocelli in three irregular rows on each side of head, ocelli variable in size, not touching each other, totally unpigmented, lenses low, nearly flat. Antennae long, when fully extended reaching nearly to posterior margin of seventh trunk segment. Head typical of family, densely setose. Trunk segments as described for *M. marginandus* (Loomis and Schmitt, 1971) with very prominent paranota, producing an almost flat dorsal surface; paranota broadly rounded and with pronounced lateral rims. Mesal pairs of segmental setae relatively short for conotylids, lateral pair even further reduced, at posterior margin of paranotum, blunt and spatulate. Head and trunk completely unpigmented, cuticle so transparent that all muscles and internal organs are clearly visible.

Pregonopodal legs more crassate than other legs, but otherwise little modified; as in *M. marginandus*, fifth and sixth legpair with small, fungiform, perforate knobs on femora. Legpairs 10 and 11 unmodified except for usual coxal glands on pair 10.

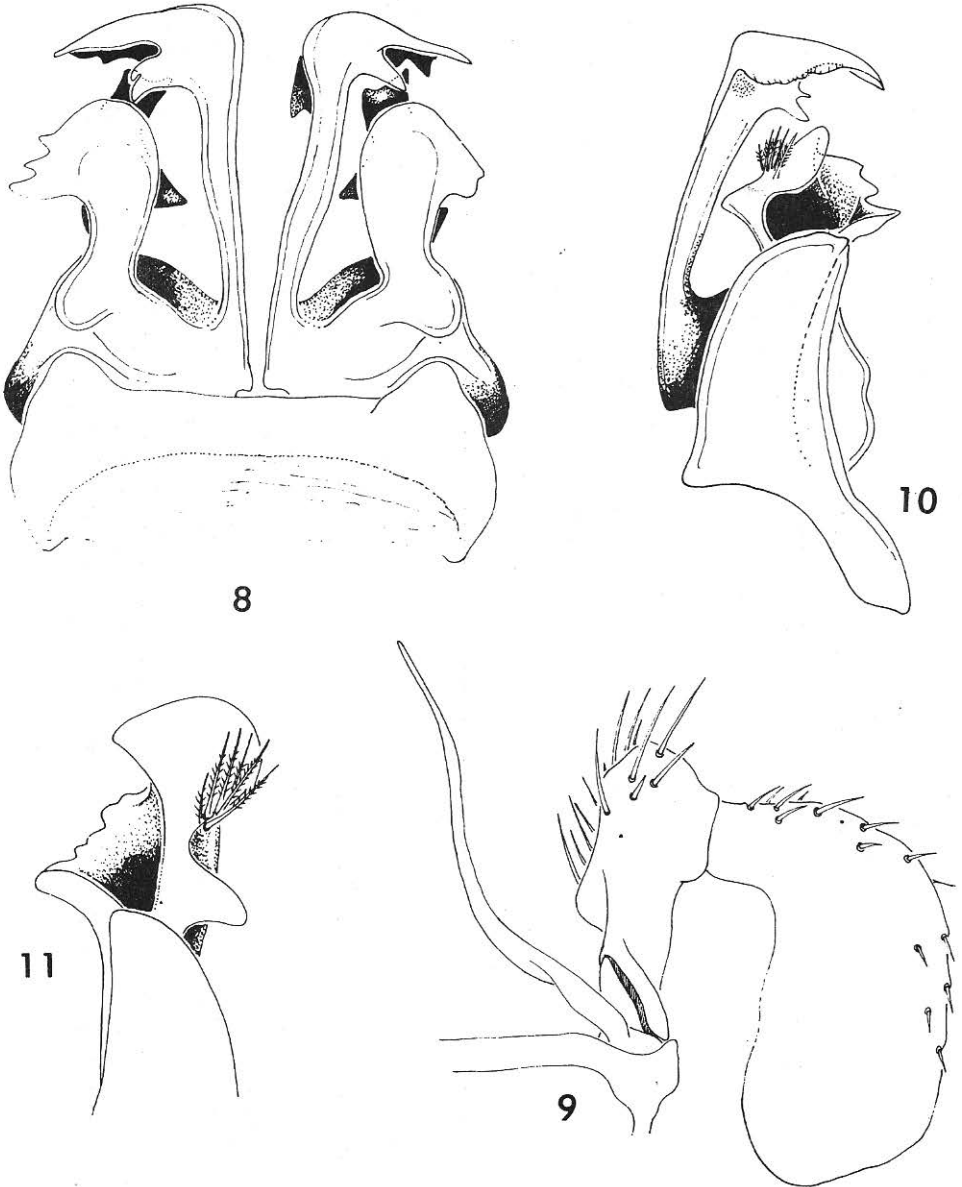
Anterior gonopods (Figs 8-11) similar in general form to those of *M. marginandus* (Shear, 1976, fig. 29). Sternum transverse, mesally bandlike, laterally expanded by evident fusion with gonopod coxae. In posterior view coxosternum large, fused with telopodite only in lateral portion, substantially drawn out distally to blunt angle. Telopodite with two branches, the mesal branch longer, simple, rodlike, with broadly expanded distal part sharply curved, forming thin, cuticular canopy; expanded part subtended by a tooth on the lateral side. Lateral telopodite branch (Fig. 11) shorter, posteriorly excavate, with irregularly formed teeth and processes, mesal group of fringed setae. Posterior gonopods just as in *M. marginandus*, coxa very small, drawn out into large flagelliform structure which, in situ, inserts between branches of anterior gonopod telopodite. Prefemur erect, tibiotarsus typical of family, but unusually large, especially prominent in undissected animal.

Distribution: Known only from the type locality, but very likely occurs in other lava tubes of the region.

Loomis & Schmitt's 1967 paper was a survey of the millipeds of Montana, in which they described several unusual chordeumatids. One of these, *Macromastus marginandus*, came from a mine shaft in Idaho Co., Idaho. Loomis & Schmitt described a new family, Macromastidae, to accommodate the new species. However, my review of conotylid genera (Shear, 1976) revealed that the family status was not justified, and that, while more primitive in gonopod organization than any other conotylid, *M. marginandus* could easily be accommodated in the family; more biological information was imparted by reducing Macromastidae to a subfamily under Conotylidae.

The original description of *Macromastus marginandus* by Loomis and Schmitt was incomplete and the illustrations lacked detail. My study of 1976 showed that there was a clear continuity between Macromastinae and the other subfamilies of Conotylidae found in North America (Conotylinae, Idagoninae¹, and

¹I called this subfamily Austrotylinae, but as it includes *Idagona*, the type genus of the nominal family Idagonidae, the name has to be changed. Subfamily Idagoninae should be attributed to Buckett & Gardner, 1967. I thank Richard L. Hoffman for bringing this point to my attention.



Figs. 8-11. *Macromastus umpqua* male. Fig. 8. Anterior gonopods, anterior view. Fig. 9. Left posterior gonopod, posterior view. Fig. 10. Left anterior gonopod, posterior view. Fig. 11. Lateral telopodite branch of right anterior gonopod, view slightly mesal of lateral.

Lophominae). Idagoninae and Conotylinae include four genera each, but Macromastinae and Lophominae are monogeneric, and each includes just two species. Of course there may be others as yet uncollected; the distribution of conotylinids in the western United States runs to high altitudes and cave habitats, both difficult of access and not thoroughly collected for millipeds. *Macromastus marginandus* is an epigeal species, with pigment and well-formed dark ocelli; probably its being found in a "short, damp mine shaft" was simply the result of the usual tendency of millipeds to seek out cool, moist habitats.

Macromastus umpqua and *M. marginandus* are very closely related, and if it were not for the considerable distance separating the localities, coupled with the strong troglitic modifications of *M. umpqua* (transparent, unpigmented cuticle and much reduced, irregular unpigmented ocelli) it would be tempting to look at them as divergent populations of the same species. But no *Macromastus* specimens have been found in the intervening territory, and it is likely that *M. umpqua* is cave-limited, a true troglitic. The evident division between the coxosternum and telopodite of the anterior gonopod suggests that this species is closer to the ancestral stock of *Macromastus* than is *M. marginandus*.

Explorations of lava tubes in the Pacific and Rocky Mountain States are proving fruitful in that a surprising number of troglitic arthropods have been detected (see Peck, 1973, 1974; Briggs, 1973, 1974; and others). So far the millipeds are all conotylinids: *Plumatyla humerosa* (Loomis), from caves in northern California and southern Oregon, *Idagona westcotti* Buckett & Gardner, from two widely separated tubes in Idaho, and the present species from the Umpqua Valley in southwestern Oregon. Skamania County, Washington, is another area of extensive lava tube development, but so far no millipeds have been found in these caves.

Both *P. humerosa* and *M. umpqua* are highly adapted troglitics, with the usual suite of characters: loss of pigmentation and eye structure, lengthened legs and antennae, and weakened cuticle. *Idagona westcotti* sports normal pigmentation and ocellar development for a conotylinid species, so probably is not a troglitic. The fact that it occurs in widely separated locations suggests that it will be found in appropriate epigeal habitats away from lava beds; I would suggest moist canyons at fairly high altitudes.

Certainly both of the cave-adapted species cannot be (in a meaningful sense) long-term inhabitants of the lava tubes in which they are now found. Peck (1973) reports troglitic species from lava tubes reliably dated as less than 2500 years old. Other tubes, especially those in California and Oregon, may be no more than 15,000 years old. Even 15,000 years may seem a very short time in which to develop divergence between cave and surface populations and presumably for speciation to occur.

However, at least three factors suggest that the problem may be more apparent than real. First, we now have evidence that speciation may occur in somewhat different ways than originally conceived. Long periods of phenotypic stability or slow change may be "punctuated" by relatively brief bouts of rapid evolution (arguments summarized in Stanley, 1979). These periods of change may be due to the passage of a population through a bottleneck in which the size of the population is drastically reduced. Many alleles could be either fixed or lost

essentially at random, and the remaining genomes might undergo further drastic reorganization under severe selection pressures, in which regulatory genes might, within only a short space of time, alter the phenotype.

Troglobitic species probably evolve from small initial populations cut off from their parent populations, in the case of arthropods, usually soil-dwelling forms from the surface (Barr, 1968). These populations are expected, in caves of the temperate zones, to be small and to remain small because of the limited supplies of food. Secondly, severe selection pressures may result from intense competition, as well as the scarcity of food. For these reasons, evolution in cave populations should be rapid. Further, many of the phenotypic modifications induced by cave life are of a degenerative nature and thus could easily be brought about by changes in regulatory genes. The morphological alterations have to do with sense organs (used to find food) and the physiological ones probably with more efficient energy use. The first appearance of troglobitic animals in lava tubes thus seems less problematic.

It would be naive to assume that each troglobitic species found in a given lava tube evolved in situ. Some, such as the Idaho beetle *Glacicavicola bathyscioides*, are evidently old troglobites even given the assumption of rapid evolution outlined above (Peck, 1974). Yet this beetle is found in lava tubes only a couple of thousand years old, which it must have invaded from other, preexisting, tubes. Howarth (1972 et seq) has maintained that lava tube environments and lava flows in general are highly permeable to invertebrates. This backs up my own experience collecting millipeds in the lava beds near Albuquerque, New Mexico, in a sagebrush desert inhospitable to soil animals which require a damp microclimate. These millipeds² would emerge to forage after summer rains, thousands of individuals coming out of cracks and crevices in the lava. When confined deep in the lava during the dry season, they might easily have subsisted on wind-blown organic material (Howarth, 1979).

Lava tubes in northern California are not far from limestone caves. *Plumatyla humerosa* evidently can disperse from one cave locality to another, though just how is not at all clear. This species, for example, might have evolved in limestone caves and now uses its unusual dispersal ability to colonize lava tubes and even mine shafts.

Many of the species found in lava tubes in the northwestern United States are relicts of old groups (Briggs, 1974) and most of their epigeal relatives are found in isolated pockets, frequently in very moist, hospitable habitats or at high altitudes, suggesting that their endemism might date, at least as species, from the last episode of continental glaciation. Lava tubes were available at this time and may have been colonized as the climate became drier and warmer. The troglobitic species that eventually resulted might move through porous lava to other tubes in the same beds, or to new tubes formed in superimposed, later flows, once these had cooled and organic matter had accumulated in them (lava tubes are usually shallow and plant roots may even penetrate them from the forests above). The species we see today are those which successfully traveled from tube to tube over the millenia. Probably many more lava tube troglobites became extinct because

²*Orthoporus ornatus* (Spirostreptidae), a large, hard-bodied cylindrical species.

they were not able to get to new tubes; but even a collapsed lava tube would still allow plenty of space for a small arthropod, and organic debris might likewise be abundant enough to support them as crevice-dwellers. Later, when tubes became available, they were colonized (Howarth, 1983).

Just as plausibly, the tube habitat may be entirely secondary and small crevices the real reservoir of these troglobitic populations.

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