Zootaxa 1463: 1–12 (2007)
www.mapress.com/zootaxa/

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

Cave millipeds of the United States. V. The genus *Idagona* Buckett & Gardner (Chordeumatida, Conotylidae, Idagoninae)

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Abstract

The conotylid milliped subfamily Idagoninae presently includes but a single genus and species, *Idagona westcotti* Buckett & Gardner, known from lava tubes in Idaho, USA. This study presents new records of the genus *Idagona*, extending its distribution into Utah and Nevada, its habitat records to limestone caves, and describes two additional species, *Idagona lehmanensis*, n. sp., from limestone caves in the Great Basin National Park in eastern Nevada, and *Idagona jasperi*, n. sp., from a high-altitude limestone cave in northern Utah.

Key words: *Idagona*, Great Basin National Park, troglophile, troglobiont, lava tubes, limestone caves, Idaho, Utah, Nevada, Bear River Range

Introduction

The milliped species *Idagona westcotti* Buckett and Gardner was described in 1967, based on specimens from two lava tubes in Clark and Butte Counties, Idaho. While postulating a relationship to the Conotylidae, Buckett and Gardner determined that this species differed from members of that family to the extent that they proposed a new family, Idagonidae Buckett and Gardner 1967, for this one species. Indeed, at the stage of development of chordeumatidan milliped taxonomy 40 years ago, their proposal seemed justified. The gonopods of *I. westcotti* were unlike those of any other known North American species, in that while two pairs of legs, the eighth and ninth, were profoundly modified, the ninth pair had subsequently become reduced to a small remnant tightly appressed to the eighth pair. In the conotylids to which they compared the new species, the ninth legs bore elaborate coxites which actually play a role in spermatophore transfer, and thus these modified legs can justifiably be called posterior gonopods. In addition, conotylids are characterized by the reduced telopodites of the ninth legs, consisting only of a cylindrical prefemur and a usually swollen, pyriform or oblate femur. In *I. westcotti*, the telopodites of the ninth legs have disappeared completely and only the small colpocoxites remain (Figs. 1, 2; see also Fig 23).

Subsequently I carried out detailed studies of the Conotylidae which resulted in a number of clarifications of the relationships within that family (Shear 1971, 1972, 1976). It was my conclusion in 1972 that Idagonidae was a synonym of Conotylidae in that the fundamental gonopod structure, gnathochilarium, and distribution of coxal glands all fit the conotylid plan. In 1976, I divided the Conotylidae into subfamilies and placed *Idagona* in the subfamily Austrotylinae Shear 1976. I neglected to note that by bringing *Idagona* into this subfamily, I was also bringing in the established family-level name, so the subfamily should have been termed Idagoninae Buckett and Gardner. However, Hoffman (1979) separated *Idagona* and the subfamily name Idagoninae from the austrotylines, solving that nomenclatorial problem and presenting an arrangement with which I now completely agree. Idagoninae is not closest to Austrotylinae, but obviously to Conotylinae,

Accepted by A. Minelli: 3 Feb. 2007; published: 30 Apr. 2007

because the anterior gonopods pass posteriorly lateral to the coxites of the posterior gonopods[1], an arrangement typical of conotylines but not of austrotylines, where the anterior gonopods and posterior gonopod coxites lie parallel to one another in an anterior-posterior position. This represents a synapomorphy for the two subfamilies, since this arrangement is derived compared to the morphology of pairs of unmodified legs.

Collections made by D. A. Hubbard in Idaho in 2000 greatly expanded the known range of this species, and are reported here. More recently, two species distinct from *I. westcotti* were collected from caves in Great Basin National Park, Nevada, and in northern Utah. The new taxa are described below.

The new records and new species are important because relatively little is known of the cave faunas of the Rocky Mountains, and even less of that of the Great Basin. Recent work (Shear and Hubbard 1998, Christiansen and Wang 2006) suggests that many new taxa are present. Collections on hand, and to be reported later, include new milliped species and genera from Colorado, Arizona and Nevada. Indeed it may be said that the general milliped fauna of the whole region is hardly at all understood; the fauna may be quite complex and underestimated because of the many forested habitats isolated from each other by vast stretches of sagebrush desert (for example, see Shelley and Medrano 2006). These habitats are difficult to access and must be visited at exactly the right times, generally in the cooler, wetter seasons, in order to collect soil and litter fauna.

New records and species

Family Conotylidae Cook 1896

Subfamily Idagoninae Buckett and Gardner 1967

Idagonidae Buckett and Gardner 1967, p. 117.
Austrotylinae Shear 1976 (in part, only *Idagona* Buckett and Gardner), p. 19.
Idagoninae, Hoffman, 1979, p. 129.

Idagona Buckett and Gardner 1967

Idagona Buckett and Gardner 1967, p. 120. Shear, 1972, p. 270.

Diagnosis: Distinct from all other North American conotylid millipeds in the complete loss of the telopodite articles of the posterior gonopods and the reduction of those appendages to a small pair of coxites which pass anteriorly between the anterior gonopods (Figs. 1-8, 19, 20). Additionally, the third legpair femora in males are inflated and bear an adenostyle (Figs. 9-12, 14); the tenth coxae in males are enlarged and lobed; the eleventh coxae are unmodified.

Notes: The species of *Idagona* have been recorded from five discrete areas (Map 1). The new species *I. lehmanensis* occurs in southeastern Nevada, far separated from the other localities; this species is highly distinctive: the fourth as well as the third prefemora are modified in males, and the gonopods differ in their much greater complexity and the proportions of the several elements. *I. westcotti* is known from three clusters of lava tubes in southern Idaho, and *I. jasperi* is from two high-altitude caves in Logan Canyon, Cache Co., Utah, not far over the border between Idaho and Utah. Accordingly, *jasperi* more closely resembles *westcotti* and can be separated from that species only by the details of gonopod shape (Figs. 3, 7. 19. 20). The distinct habitat and locality reinforces the hypothesis that *jasperi* is a reproductively isolated population, while the

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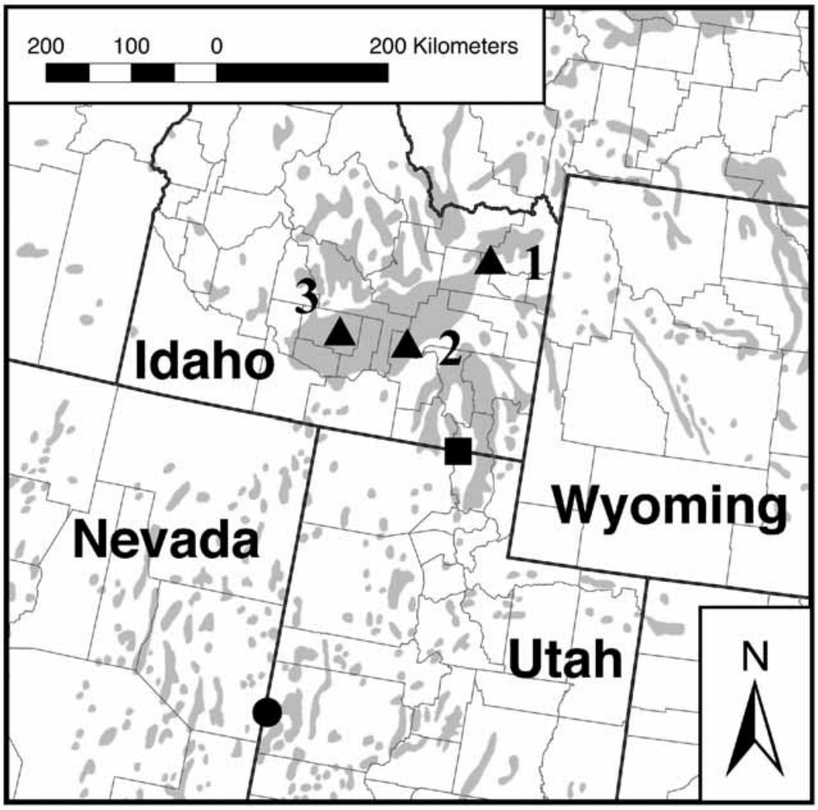
1. In point of fact, it is the reduced coxites of the posterior gonopods that are extended *anteriorly* between the anterior gonopods, but this is an homologous arrangement necessitated by the extreme reduction of the posterior gonopods, which in *Idagona* consist only of the small coxites.

three clusters of *westcotti* localities harbor populations not distinguishable by gonopod or other differences (Figs. 1, 2, 5, 6, 9. 10, 15. 16).

For conservation reasons, and at the request of the collectors, the exact locations of caves mentioned in this paper are not given. Map 1 represents geometrically average locations for clusters of caves, or the approximate location of an individual cave.

The types of the new species described below are deposited in the collections of the Field Museum of Natural History (FMNH), Chicago.



MAP 1. Central Rocky Mountain and Great Basin region of the United States, showing distribution of *Idagona* species. Shaded areas are karst or pseudokarst (lava beds). Triangles, *I. westcotti;* square, *I. jasperi;* circle, *I. lehmanensis.* Triangle 1, general location of Blowhole-Sand Lake, Ice Capades, and London Tunnel Caves; triangle 2, general location of Government Cave; triangle 3, general location of Giant Arch and Pot O' Gold Caves (may be two names for the same cave). Map by S. J. Taylor.

Key to species of *Idagona,* based on males

1a. Legs 4 with femora swollen and bearing a median pore (Fig. 13); gonopod with complex, fimbriate subterminal branch (Figs. 4, 21, 22); SE Nevada.. ***lehmanensis* n. sp**.

1b. Legs 4 with femora not swollen, not bearing a median pore, subterminal branch of gonopod lacking......2.

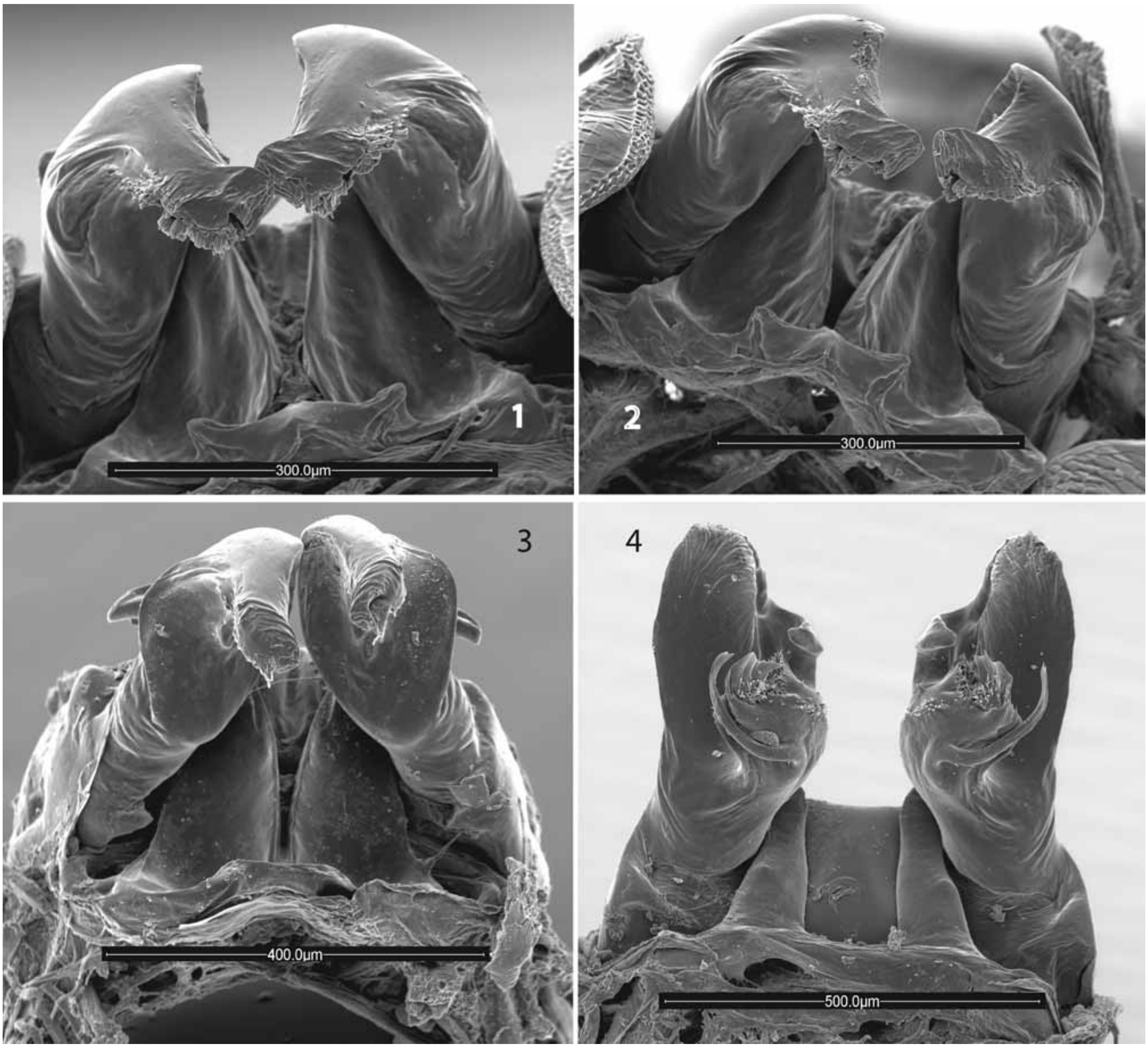
2a. Anterior gonopod with few teeth along apicolateral surface (Figs. 3, 7); adenostyles of legs 3 with distinct basal constriction (Fig. 11); N Utah.. ***jasperi* n. sp**.

2b. Anterior gonopod with many strong teeth along apicolateral surface, teeth arranged in irregular, overlapping rows (Figs. 1, 2, 5, 6); adenostyles of legs 3 lacking basal constriction (Figs. 9, 10); S Idaho ....
.... *westcotti* Buckett & Gardner.

***Idagona westcotti* Buckett and Gardner 1967**
Figs. 1, 2, 5, 6, 9, 10, 15, 16

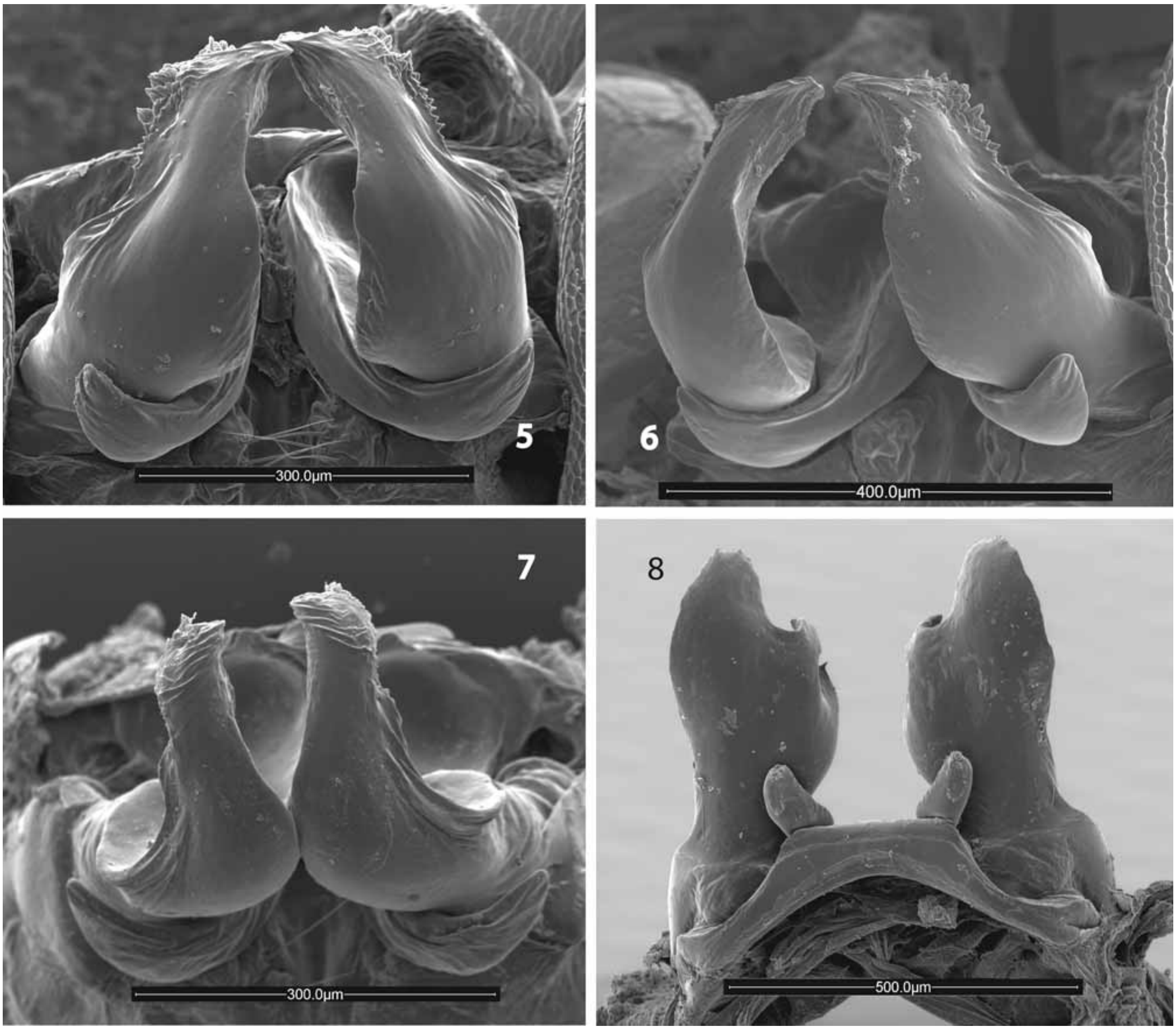
Idagona westcotti Bucket and Gardner 1967, p. 120, figs. 1-8. Shear, 1972, p. 270, figs. 479-481.

Types. Male holotype in Department of Entomology, University of California, Davis, California. "…one male paratype sent to H. F. Loomis, Miami, Florida; allotype retained in the authors' private collection; remainder of paratypes divided between University of Idaho, Moscow, Idaho, and the authors' private collection (Buckett and Gardner 1967, p. 124)." The entire type series consisted of the male holotype, one female allotype, three male and three female paratypes. The series was collected in Crystal Falls Cave, 20 mi. (32.2 km) northeast of Dubois, *Clark Co*., **Idaho**, 16 July 1965, by R. L. Westcott. An additional female specimen, not designated as a paratype, was collected by Westcott on 18 August in Boy Scout Cave, Craters of the Moon National Monument, *Butte Co*., **Idaho** (Buckett and Gardner 1967).



FIGURES 1–4. Gonopods of *Idagona* species. 1, *Idagona westcotti*, Giant Arch Cave, posteriorventral view. 2. *I. westcotti*, Ice Capades Cave, posterioventral view. 3. *I. jasperi*, n. sp. posterioventral view. 4. *I. lehmanenesis*, n. sp., posterior view.

New Records: **Idaho:** *Clark Co*., Blowhole-Sand Lake Cave, 14 July 2000, D. A. Hubbard, males, females; Ice Capades Cave, 14 July 2000, D. A. Hubbard, males, females. *Blaine Co.,* Government Cave, 16 July 2000, D. A. Hubbard, males, females. *Fremont Co.,*London Tunnel Cave, 15 July 2000, D. A. Hubbard, juveniles presumably this species. *Lincoln Co.:* Giant Arch Cave, 16 July 2000, D. A. Hubbard, males, females; Pot O'Gold Cave, 16 July 2000, D. A. Hubbard, males, females (Giant Arch Cave and Pot O'Gold Cave may be parts of the same lava tube, or different names for the same cave). These specimens are at present in the author's personal collection but will be deposited in the Field Museum of Natural History, Chicago, when studies are complete.



FIGURES 5–8. Gonopods of *Idagona* species. 5. *Idagona westcotti,* Giant Arch Cave, anterioventral view 6. *I. westcotti,* Ice Capades Cave, anterioventral view. 7. *I. jasperi*, n. sp., anterioventral view. 8. *I. lehmanensis* n. sp., anterior view.

Notes. The drawings in Shear (1972, figs. 479–481) are in general accurate and serve for recognition of the species. Other drawings and a detailed written description are given in Buckett and Gardner (1967). Scanning electron micrographs are provided here for additional detail; they show that what Shear (1972) interpreted as fimbriate, or hairy, margins on the anterior gonopods are actually arrays of stout cuticular teeth.

The species may be general in lava tubes through the extensive Snake River Plain lava beds of southern Idaho (Map 1). Comparing the specimens from the listed localities, I found no differences of note and therefore treat the populations as a single species. Even those from the two most distant clusters of records have gonopods, and third and tenth legpair modifications that are virtually identical (Figs. 1, 2, 5, 6, 9, 10, 15, 16). It is worth noting ,however, that the available collections represent samples from within a larger potential distribution; more collecting and examination of molecular evidence is needed to clarify the actual status of these populations. Howarth (1973; see also Peck 1973, 1982) emphasized that troglophilic or troglobitic animals in lava beds may occupy small spaces in the lava inaccessible to collectors and use these spaces to spread to new lava tubes. Thus *I. westcotti* in the Idaho lava beds may well be a single panmictic population, rather than a series of discrete populations isolated in larger lava tubes. Because of their northerly location and the insulating properties of the porous lava, many, but not all, of the tubes in which *I. westcotti* occurs have permanent ice and constant temperatures around 4°C. This does not seem to have an adverse effect on the diverse fauna found there, which includes beetles, centipeds, and opiliones as well as millipeds (Briggs 1973, 1974; Peck, 1973).

Idagona westcotti shows few consipicuous adaptations to cave life, such as enlongate appendages, depigmentation and reduction or loss of eyes. Most specimens are only slightly paler than epigean conotylid species found in the Rocky Mountains and the Pacific Northwest, and while ocelli appear to be somewhat reduced in number and size, the change is not very conspicuous. However, given the bleak sagebrush desert and dry juniper woodland habitat surrounding the lava tubes, it seems unlikely that surface populations exist, and that the animals are now effectively limited to subterranean habitats.

The prevailing theory of the colonization of western North American lava tubes emphasizes that the arthropod faunas of these caves are derived from taxa that are mesic forest litter inhabitants. During glacial maxima in the Pleistocene, such forest habitats occupied much lower elevations than they do now, and litter animals were available to enter, survive, and reproduce in caves. As the climate became warmer and much drier under interglacial conditions, the forests retreated to higher elevations, leaving behind remnant animal populations in caves, the surrounding environment having become inhospitable for them. Depending on such factors as time since isolation, population size and selective regime, the isolates may diverge and eventually speciate (Peck 1973, 1982). The pattern of distribution seen in *I. westcotti* indicates that the species was widespread on the surface prior to environmental change and since then the lava tube populations have diverged little, at least morphologically.

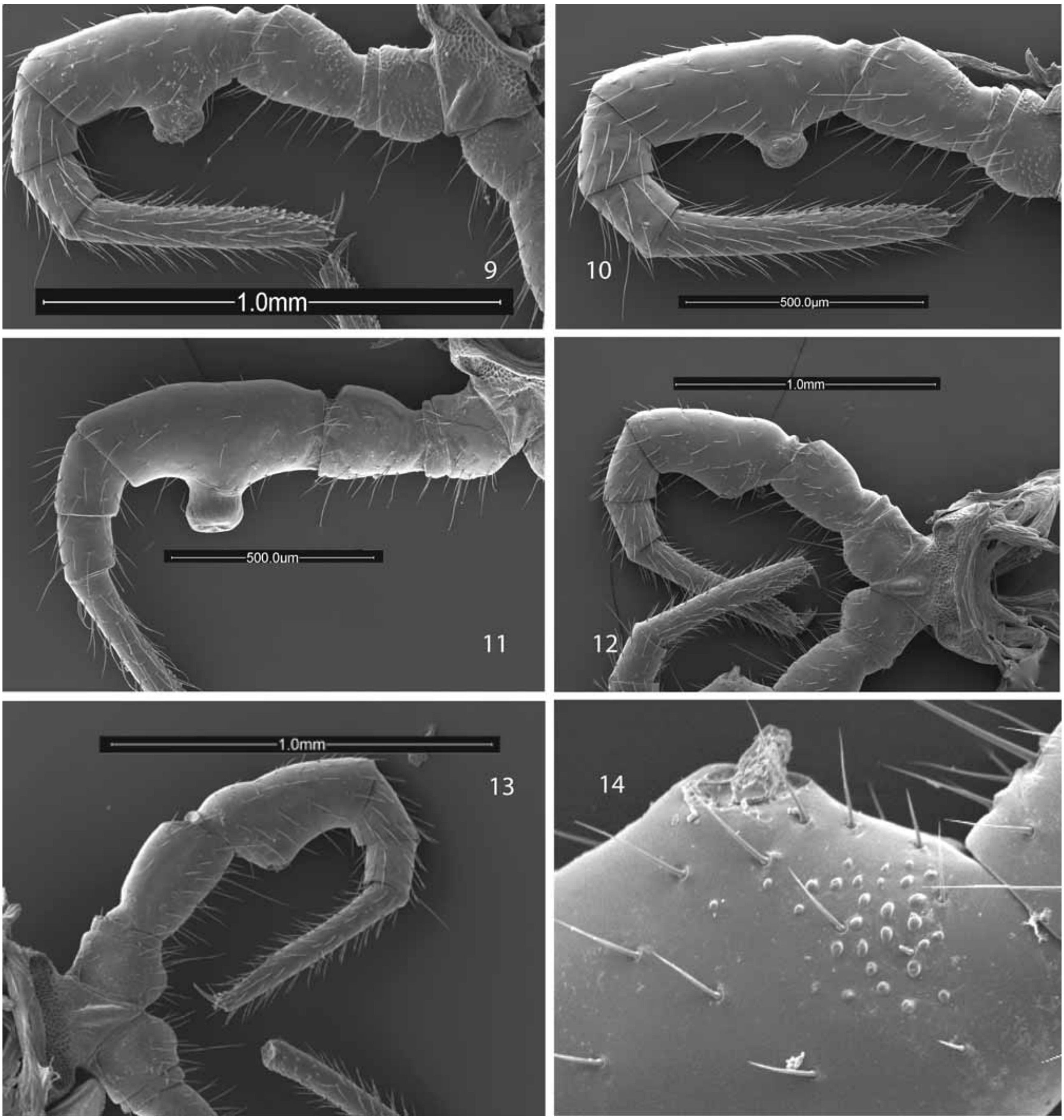
***Idagona jasperi*, n. sp.**
Figs. 3, 7, 11, 17, 19, 20

Types: Male holotype, paratypes from **Utah:** *Cache Co.,* Nielsen's Cave, Tony Grove Recreation Area, 8100' (2469 m) elevation, Wasatch-Cache National Forest, J. Jasper, August 2006. Additional male paratype from same locality, but Main Drain Cave. 9 September 2006, G. Baker (all specimens FMNH).

Diagnosis: Distinct from *I. westcotti* in the more gracile gonopods (Fig. 7), with many fewer lateral teeth (Fig. 3); the posterior gonopod sternum of *westcotti* has a median flange with acute corners; this is not seen in *jasperi*. The adenostyle of femur three (Fig. 11) is more strongly constricted at the base in *jasperi,* and has a very obvious apical depression and large pore; in *westcotti* there are multiple small pores.

Etymology: The species is named for the collector, Jon Jasper.

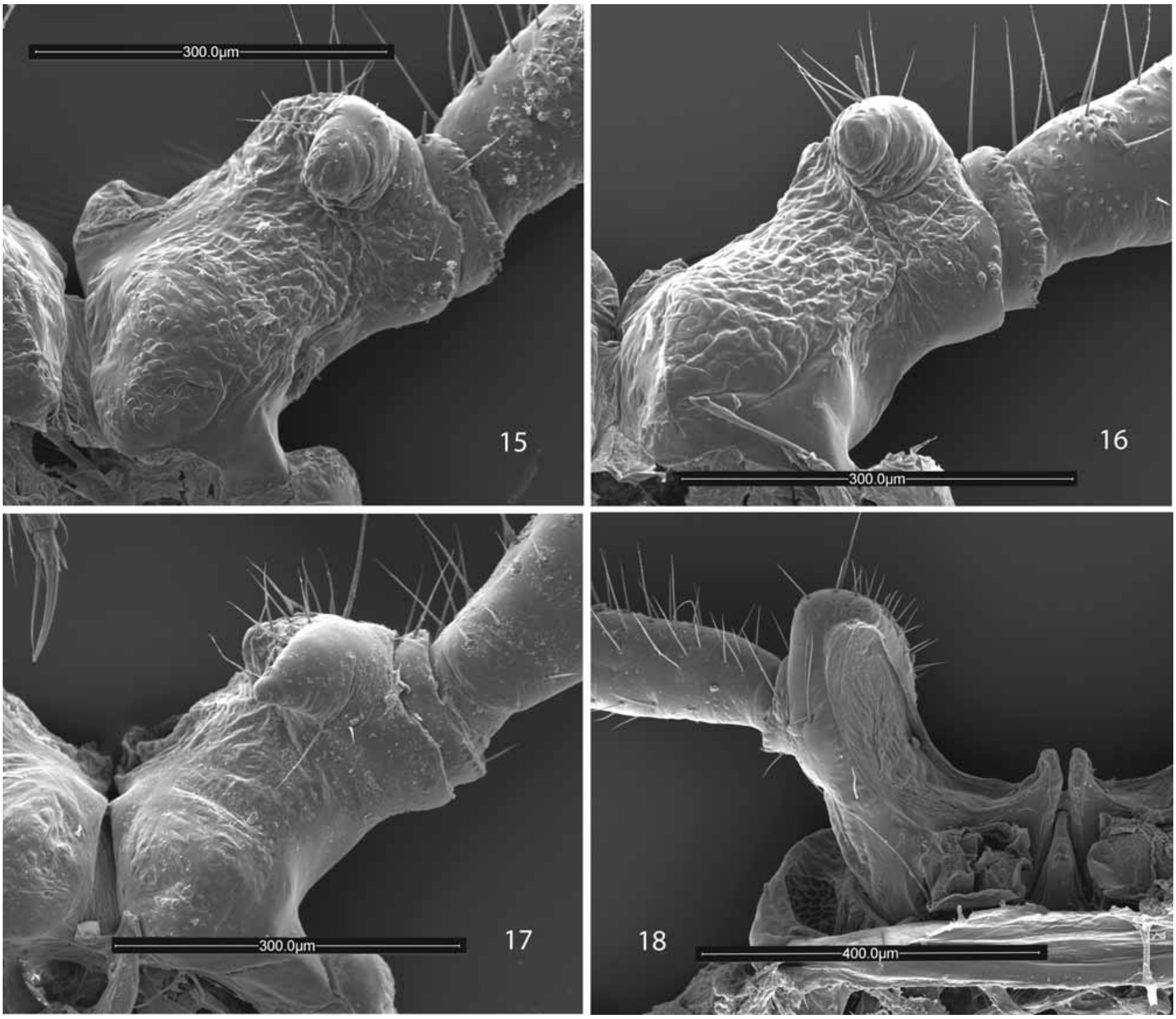
Description: Male: 13.5 mm long, 1.0 mm wide. Fourteen ocelli in oval patch, ocelli round, black, compactly arranged. Legpair 3 (Fig. 11) with femur enlarged, bearing prominent median adenostyle strongly constricted at base. Legpair 4 enlarged but with unmodified femora. Gonopods (Figs. 3, 7, 19, 20) similar to those of *I. westcotti*, but markedly more slender, more abruptly tapered distally; lateral apical teeth much reduced, median extension of posterior gonopod sternum low. Coxae 10 (Fig. 17) enlarged but not extended distal to trochanteral joint, distal knob strongly acute, gland opening ventral. Coloration medium tan, extensively mottled with darker purplish-brown.



FIGURES 9–14. Pregonopodal leg modifications of *Idagona* species. 9–12, third legs, anterior views. 9. *Idagona westcotti*, Giant Arch Cave. 10. . *I. westcotti*, Ice Capades Cave. 11. *I. jasperi* **n. sp.** 12. *I. lehmanensis* **n. sp.** 13. Leg 4 of *I. lehmanensis* **n. sp.**, anterior view. 14. Denticles near adenostyle of leg 3 femur of *I. lehmanensis* **n. sp.**

Distribution: Known only from the type localities. The caves with *I. jasperi* are in the upper reaches of Logan Canyon, about 20-25 miles northeast of Logan, Utah, in the southeast flank of the Bear River Range.

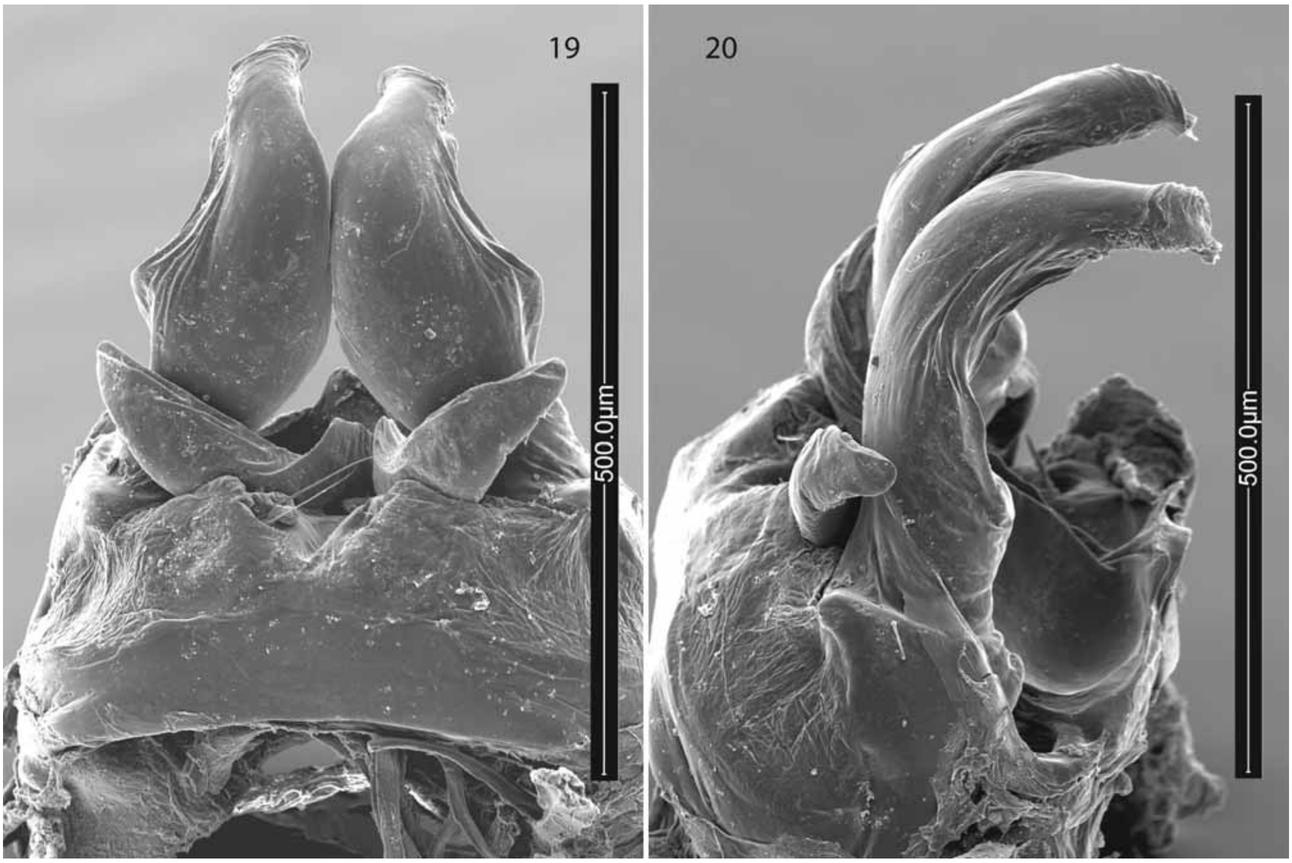
Notes: There is extensive karst development in Logan Canyon (Spangler 2001; Jasper 2006) and many of the caves are at high altitudes, above 8000'. Nielson's Cave, among others, harbors permanent ice or snowpack, as do some of the Snake River Plain lava tubes. *Idagona jasperi* specimens are recorded as actively walking over ice and snow, and like other elements of the faunas of these caves, are well-adapted to near-freezing temperatures. The millipeds are described by collectors as being very abundant on wood and other organic debris in the caves (J. Jasper, pers. comm..to WS).



FIGURES 15–18. Leg 10 coxae of *Idagona* species, posterior views. 15. . *Idagona westcotti*, Giant Arch Cave. 16. *I. westcotti*, Ice Capades Cave. 17. *I. jasperi* **n. sp.** 18. *I. lehmanensis* **n. sp.**, anterior view.

In contrast to the lava tubes of the Snake River Plain, the fauna of the caves of the Bear River Range is little known, and this report is the first for troglobitic or troglophilic terrestrial animals there. The compact, well-formed eyepatch and relatively dark pigmentation (when compared to *I. westcotti*) would indicate a minimal degree of cave-adaptation in this species.

Earlier, Peck (1981) described invertebrate collections from the Uinta Mountains, to the southeast, and found that of 38 species collected in caves there, only three could be regarded as cave-limited. Peck (1981) attributed the relatively low number of troglobionts to the short time available since colonization. Up to about 12,000 years ago, severe periglacial conditions would have obtained, and as the glaciers melted, caves would have been scoured by powerful streams. No doubt this same analysis can also be applied to the high altitude caves of Logan Canyon, but with even less time available since colonization, as the montane glaciers in the more northerly Bear River Range would have retreated more slowly. Moist conferous forests surround the caves where *I. jasperi* has been found, and surface-dwelling populations may well exist there, but no collecting has been done. The caves may in fact only be refuges for the millipeds from the severe winter conditions that obtain in the region, and the animals may move freely between caves and forest litter. I strongly suspect that other, as yet uncollected, species of *Idagona* exist in caves and high altitude forests in other Utah (and Idaho) mountain ranges.



FIGURES 19, 20. *Idagona jasperi* **n. sp.** 19. Gonopods, anterior view. 20. Gonopods, lateral view.

***Idagona lehmanensis*, n. sp.**
Figs. 4, 8, 12-14, 18, 21-23

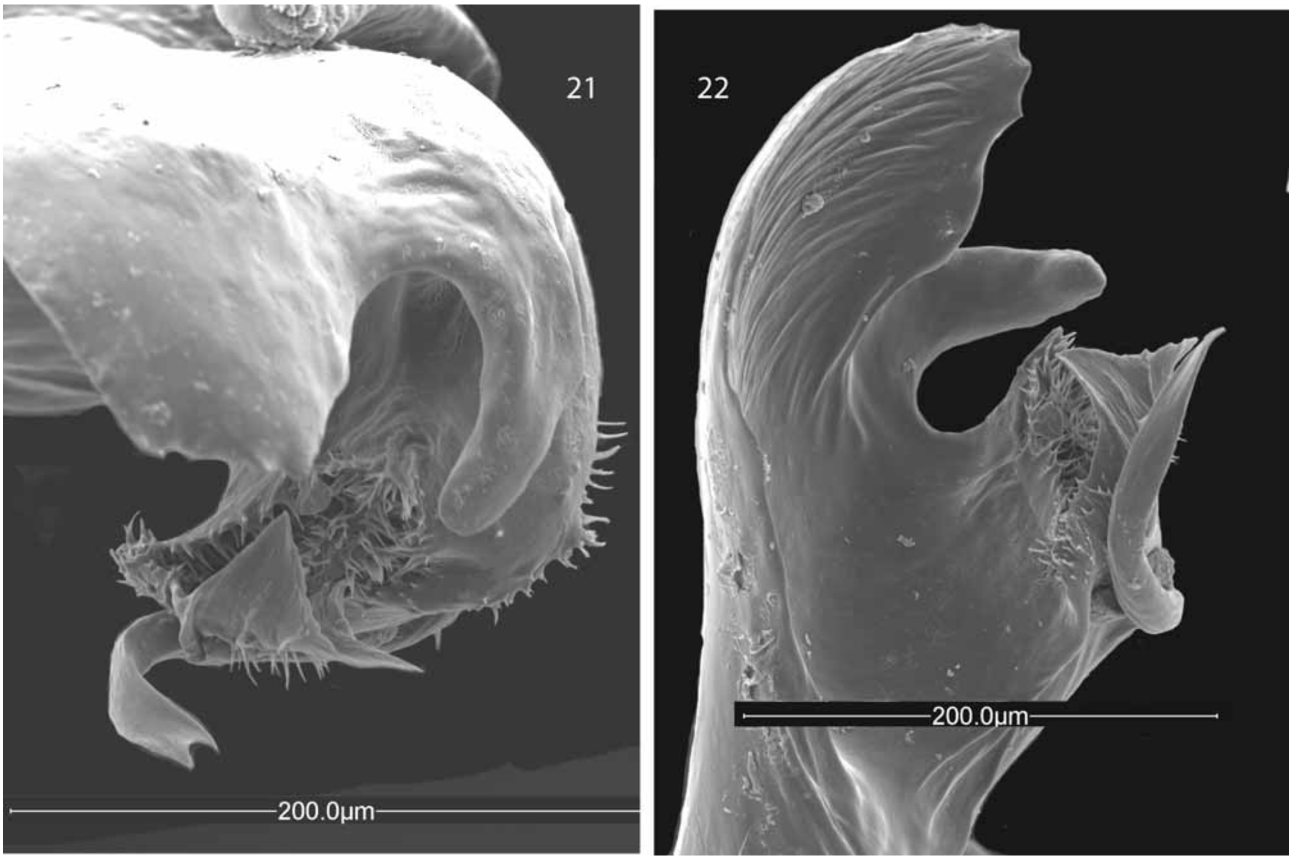
Types: Male holotype, two male paratypes and female paratype from Water Trough Cave, Great Basin National Park, Nevada, collected 24 May 2006 by S. J. Taylor, J. K. Krejca, M. G. Slay and G. Baker (FMNH). Additional immature specimens were collected at the same time.

Diagnosis; *Idagona lehmanensis* is easily distinguished from all other known *Idagona* species by the complicated subterminal branch of the anterior gonopod (Figs. 21, 22) and the presence of modified, pore-bearing femora on the fourth, as well as the third, legpair (Fig. 13). The tenth coxae of *lehmanensis* (Fig. 18) have much less well-developed apical knobs and are extended beyond the trochanteral joint; the anterior surfaces are poorly sclerotized and the coxal gland openings are frontal rather than ventral.

Etymology: The species epithet, *lehmanensis*, was suggested by S. J. Taylor and makes reference to the former Lehman Caves National Monument, which became Great Basin National Park in 1986.

Description: Male (Fig. 23): Length, 13.0 mm, width 1.0 mm. Ocelli 23-27, round, black, in compact oval patch, dorsal row of ocelli somewhat indistinct. Third legpair (Fig. 12) with expanded femur bearing adenostyle as low mound; adenostyle subtended on anterior side by cluster of small, cuticular granules (Fig. 14).

Fourth legpair similar (Fig. 13). Gonopods (Figs. 4, 8, 21, 22): anterior gonopods large, upright, distally expanded, with complex posteriorly located subterminal branch (Figs. 21. 22) bearing numerous cuticular fimbriae, narrow bifid subbranch, and distally expanded subbranch. Apex of gonopod deeply divided, medial division broad, trullate; lateral division narrow, evenly curved. Posterior gonopod coxites with poorly sclerotized sternum, basal gonopodal elements much reduced, coxites relatively small, not scooplike, with small posterior nodule, clusters of microteeth near apex. Tenth coxae (Fig. 18) extended beyond trochanteral articulation, posterior knob low, anterior surface poorly sclerotized, membranous, gland opening on anterior surface. Coloration white to pale tan, anterior segments and head lightly mottled purplish-brown, legs white (Fig. 23).



FIGURES 21, 22. *Idagona lehmanensis* **n. sp.** 21. Tip of anterior gonopod, ventral view. 22. Tip of anterior gonopod, lateral view.

Female similar to male in nonsexual characters.

Distribution: In addition to Water Trough Cave, juvenile idagonines undoubtedly this species were collected in the nearly adjacent Model Cave.

Notes: Idagona lehmanensis differs strongly from the other two species and might have been considered the type of a new genus. However, such designation, if justified, can wait for the discovery of more species of idagonines and a fuller understanding of their relationships. The more complex gonopods of *I. lehmanensis*, when compared to the other two, mirrors a similar situation in the eastern North American genus *Conotyla* (Conotylidae, Conotylinae), in which species with simpler gonopods are found in the northern part of the generic range, and moving south, one finds gonopods become progressively more complex. The more northerly occurring species of *Conotyla* are also more widely distributed; southerly species may have ranges restricted to single ridgetops or summits (Shear 1971). At this point we do not know enough about the diversity or distribution of *Idagona* to draw a parallel.

FIGURE 23. *Idagona lehmanenesis,* **n. sp.** Anterior end of male paratype. Note the swollen femora on both legpairs 3 and 4 and the absence of conotyliform telopodites on the posterior gonopods. Photo by S. J. Taylor.

The caves of this immediate region are closely clustered and many are isolated from one another only by relatively recently formed erosional features. *Idagona lehmanensis* very likely will be found in most or all of these caves. As with *I. westcotti,* the presence of this species, not highly adapted for life underground, in these caves is probably attributable to the latest Pleistocene climatic events: as the Great Basin climate became drier, forested habitats retreated to higher altitudes on the many inselberg ranges (Vandevender and Spaulding 1979), but because of the significantly more southerly location of the caves, this may have happened much earlier than in northern Utah and southern Idaho. As with the Snake River lava beds, the present surrounding ecosystem is sagebrush desert and dry juniper woodland—inhospitable for chordeumatid millipeds. Besides *I. lehmanensis,* the two caves also host a new genus and species of polydesmidan milliped, to be described later.

Despite its likely isolation in caves, as with its congeners, little special adaptation can be discerned in this species; indeed the number of ocelli present is considerably greater than that in the two northern species.
The Great Basin is a region of North America where crustal extension has resulted in the tipping and down-dropping of blocks of strata, producing the characteristic basin-and-range topography. Isolated mountain ranges, many high enough to have forested habitats in the otherwise desertlike or arid grassland terrain, are separated by basins that often have only internal drainage and may harbor short-lived, saline bodies of water. Particularly in eastern Nevada, many of these inselbergs contain karst (Map 1). At higher elevations in Great Basin inselberg ranges, where moist forests occur, relict populations of this or other *Idagona* species may exist, just as they may in areas of the Rocky Mountains, to the northeast. These habitats in eastern Nevada remain almost entirely unexplored for invertebrate biodiversity, as do the many other karst regions of the state.

Acknowledgements

I am grateful to all of the collectors listed above, but especially to Gretchen Baker, National Park Service ecologist, Jon Jasper, Carlsbad, New Mexico, and Steven J. Taylor of the Illinois Natural History Survey for the special efforts they made to collect material for this study. In addition, Steven Taylor provided valuable information on the caves of the Great Basin National Park, composed Map 1, and contributed Fig. 23; Jon Jasper provided data on the caves of Logan Canyon. David Hubbard's continued help and collaboration is much appreciated; more publications on his Idaho collections are forthcoming. Thanks to Jason Bond for the use of the scanning electron microscope at East Carolina University, Greenville, North Carolina, and to Matt Walker and Paul Marek for technical assistance there. This paper is published under the auspices of a PEET grant from the National Science Foundation of the United States to the author, Jason Bond and Petra Sierwald. Asa Kreevich is thanked for sharing his biological wisdom over a long period of time.

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