A NEW SUBFAMILY OF BLIND BEETLE FROM IDAHO ICE CAVES WITH NOTES ON ITS BIONOMICS AND EVOLUTION (COLEOPTERA: LEIODIDAE)

By Richard L. Westcott
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DOROTHY M. HALMOS

Editor
A NEW SUBFAMILY OF BLIND BEETLE FROM IDAHO ICE CAVES WITH NOTES ON ITS BIONOMICS AND EVOLUTION (COLEOPTERA: LEIODIDAE)

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ABSTRACT: A new genus and species, Glaciacivicola bathyscioides, is described and a new subfamily, Glaciacivicoliniae, is erected. Based upon structure of the front coxal cavities, placement of the hind coxae and structure of the male genitalia, this subfamily appears most closely related to Catopocerinae. Specimens were collected in southern Idaho from three widely separated lava tube ice caves, and were found in direct contact with the ice. The caves are briefly described. Considerations are given as to the evolution and means of dispersal of this new beetle. It appears to be an extremely specialized glacial relict which has extended its range through the porous lavas in which the caves occur.

During the summer of 1965 I discovered a remarkable anophthalmic beetle while exploring a lava tube ice cave in the eastern Snake River Plain of southern Idaho. This cave beetle, which represents a new genus and species, creates, in my opinion, a need for erecting a new subfamily.

I am grateful to W. F. Barr, University of Idaho, for his many helpful suggestions in the preparation of this paper and to Jim Papadakis, Crystal Ice Caves, for allowing access to and providing information about the caves. Thanks are given to T. C. Barr, Jr., University of Kentucky, M. H. Hatch, University of Washington, Martin Prinz, Tufts University, and R. E. Williams, University of Idaho, for information pertaining to this study. I would like also to acknowledge the assistance of my colleague, L. S. Hawkins, Jr., who accompanied me in the exciting discovery of this beetle. Figure one was drawn by Nellie Lambley, University of Idaho.

GLACIACVICOLINAE, New Subfamily

A subfamily of Leiidiidae characterized by the following characters: dorsal surface virtually glabrous; antennae subclavate, eleven-segmented, scape much longer than any other segment, eighth segment not distinctly narrower or shorter than seventh or ninth; terminal segment of maxillary palpi large, longer than any other segment, somewhat fusiform; front coxae elongate, cylindric-conic, contiguous, inserted near hind margin of prothorax, cavities widely open behind; mesocoxae globose, contiguous; metacoxae oval, transverse, widely separated; tarsal formula 5-5-5; abdomen with all but last two visible tergites membranous, with five (♀) or six (♂) visible sternites.

This beetle belongs in the superfAMILY Staphylinoidae, according to the

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characters given to that group by Crowson (1955), but its assignment to family presents some difficulty, primarily because considerable disagreement exists in defining the families of Staphylinoidea. The staphylinid-silphid-leptodirid-leiiodid complex, to which this beetle certainly belongs, is particularly difficult to define, and to do so is beyond the scope of this paper. It seems best to place this beetle in the family Leioididae, as delimited by Hatch (1957), although one of the main characteristics of this family, namely that the eighth antennal segment is conspicuously shorter and narrower than the seventh and ninth, does not apply. The structure of the male genitalia agrees closely with that found among many of the Leioididae, particularly those of the subfamilies Catopocerinae, Bathysciinae, and Catopinae.

The subfamily Glacicaviculinae bears a striking resemblance to many of the elongate cavernicolous species of the almost exclusively European subfamily Bathysciinae. However, the two can readily be separated by the structure of the front coxal cavities, which are closed behind in the Bathysciinae and widely open behind in the Glacicaviculinae. Furthermore the bathyscines have the terminal segment of the maxillary palpi awl-shaped or conical, short, and much smaller than segments two or three. The Leioididae have the front coxal cavities closed behind except in the Catopocerinae and some species of Hydnobius (Leioidae). The Catopocerinae appear almost unique in having the hind coxae separated, and based upon this premise Glacivaciculinae might well be placed near them. However, members of the Catopocerinae always have the eighth antennal segment distinctly smaller than the seventh or ninth. Both the Catopocerinae and Glacivaciculinae lack antennal vesicles (see Crowson, 1955) and possess widely open procoxal cavities. On this basis they might be placed in the Silphidae. Crowson (1955) has referred Catopocerinae to this family. However, the structure of the male genitalia of both subfamilies strongly suggests a leioidid affinity.

Hatch (1933) and Arnett (1960) recognize the family Leptodiridae, though there is some difference of opinion on placement of certain subfamilies. Hatch (1933) describes the Leptodiridae to include generally fragile species with long appendages and thin integuments, while the Leioididae include stocky species with shorter appendages and heavier integuments. Using this as a criterion, the Glacivaciculinae would fall into the leptodirid section. Hatch (1957) subsequently places the leptodirids under Leioididae. For further discussion of the staphylinid-silphid-leioidid complex, the reader is referred to Brown (1933), Hatch (1927), and Horn (1880).

The Glacivaciculinae also bear superficial resemblance to the Brathinidae. Both groups have the procoxal cavities open behind and the structure of the maxillary palpi is very similar. However, the male genitalia of Brathinidae are of the staphylinid type, lacking a pars basalis, and of the visible abdominal tergites, all but the basal are sclerotized, while in the Glacivaciculinae the genitalia possess a pars basalis and all of the visible abdominal tergites are membranous except for the ultimate and a portion of the penultimate. Further-
more, in the Brathinidae the hind coxae are contiguous, conical, and prominent internally, while the Glacicavicolinae have the hind coxae widely separated, oval, and not prominent. The antennal scape in the Brathinidae does not exhibit the proportionately great length evident in the Glacicavicolinae.

The placement herein of Glacicavicolinae is, admittedly, an arbitrary one and I would not argue with those who might wish to define it differently. However, it is firmly believed that its affinities lie with the Silphidae or Leiodidae, as delimited by Hatch (1957), rather than the Brathinidae or Staphylinidae, as defined by Arnett (1960). Perhaps this strange beetle may represent an entirely new family, but to classify it as such at this time would, I believe, obscure its relationships.

Glacicavicola new genus

Type species: Glacicavicola bathyscioides new species.

Head oval, elongate, sharply constricted posteriorly into a well-defined neck; gula roughly triangular, sutures meeting near middle of head, then extending to submentum; eyes absent; labial palpi small, terminal segment cylindrical; antennae extremely long and with very long hairs, inserted dorsolaterally just in front of middle of head under a slightly raised portion of frons which extends forward as a slight ridge; apical swelling of segments nine and ten together with fusiform terminal segment forming a slight club.

Thorax with pronotum longer than wide, sides smoothly rounded; scutellum large, triangular; mesosternum keeled, sharply constricted anteriorly where it is much narrower than the pronotum and bears a depression which is almost divided medially by the pronounced apical portion of the keel and a marginal, backward-projecting triangular piece, so that in lateral view it usually appears notched.

Elytra much longer than wide, much wider than pronotum, inflated, very convex, fused; epipleural fold apparent only on apical half, ending a short distance before apex; hindwings absent.

Legs extremely long, hind legs longer than body, femora clavate, all tibiae with two moderately-developed spurs of equal size; male with patches of tenet hairs beneath pro- and mesotarsi; tarsal claws long, sickle-shaped.

Abdomen with first two visible sternites immovably fused, the suture between them distinct.

Glacicavicola bathyscioides new species

Figs. 1-5

Male: Elongate, length almost twice width, antlike, very fragile, exhibiting false physogastry; color shining brownish-red, elytra translucent, with very faint lateral spots which are particularly noticeable on apical half; setae scarce on dorsum.

Head almost twice as long as wide, widest in front of middle, convex;
Figure 1. *Glacicavicola bathyascioides*, new species.
surface unevenly microreticulate, becoming rugose on neck, dorsal surface of epicranium with a faint median longitudinal depression, with setigerous punctures as follows: a widely-spaced pair immediately behind frontoclypeal suture, one just mesad of ridge in front of each antennal insertion, one just caudo-mesad of each antennal insertion, all bearing a short, recurred seta; and a widely spaced pair between caudal end of median depression and neck, each bearing a conspicuous, long, recurred seta; a few, mostly long, setae present on clypeus, labrum, mentum, submentum, and anterior ventrolateral portion of epicranium; maxillary palpi moderately setose from apex of antepenultimate segment to apical portion of ultimate which is glabrous; ratio of lengths of last three segments 0.8:0.5:1; antennae almost as long as body, approximate ratio of lengths of segments 2.2:1.1:1.3:1.3:1.4:1.5:1.5:1.6:1.4:1.1, scape and pedicel with few hairs, segments 3-6 moderately hairy, remaining segments more densely pubescent.

Thorax with pronotum one and one-fifth times as long as wide, widest at middle, wider at base than apex; surface slightly convex, evenly microreticulate, becoming smooth at sides, with a pair of setigerous punctures close behind anterior margin; sides broadly rounded for apical three-fourths, then converging toward base; anterior margin evenly curved, fitting contour of neck; posterior margin slightly emarginate. Scutellum large, triangular; surface rugose. Propleura smooth. Prosternum faintly alutaceous, with two long and several shorter setae near front margin, which bears a series of minute, forward-projecting setae. Mesosternal depression bearing dense, long, golden pile.

Legs long and slender except for femoral clubs, which make up sevenths of the profemora, one-half the mesofemora, and slightly over two-fifths of the metafemora; ratio of leg lengths (excluding coxa and trochanter) approximately 6:7:9; pro- and mesofemora with ventral row of long hairs which increase in length for about basal three-fourths, hairs of apical fourth shorter and equal to those covering other surfaces of club, posterior surfaces with fewer, shorter hairs; tibiae about equal in length to femora, pro- and mesotibiae bearing a preapical comb of stout setae on anterior and posterior faces; protarsi with apical segment longest, twice as long as basal segment, basal three segments slightly dilated and bearing patches of trumpet-shaped tenet hairs; mesotarsi with basal segment subequal in length to apical segment, basal two segments bearing trumpet-shaped tenet hairs in sparser patches than on protarsi; basal segment of metatarsi noticeably longer than apical segment.

Elytra swollen, elongate, one and three-fourths times as long as wide, twice as wide as pronotum; surface covered with fine, irregularly, widely spaced punctures except at sides; apical fourth, sides, and a narrow strip on either side of suture exhibiting an extremely fine granular appearance; disc with a few, fine, recurred hairs which appear to be arranged in three longitudinal rows beginning near suture, a few small, fine submarginal hairs on apical fifth, mostly in immediate vicinity of apex; sides broadly overlapping
abdomen; lateral margins sinuate near middle then gradually, arcuately converging to separately, narrowly rounded apices.

Figures 2-5: *Glaciacicola bathyscioides*. 2: male genitalia. 3: median portion of female genitalia. 4: posterior margin of fifth visible (penultimate) abdominal sternite of male. 5: posterior margin of fifth visible (ultimate) abdominal sternite of female.
Abdomen with sternum finely alutaceous, sparsely clothed with long, suberect hairs; fifth visible sternite with apex broadly, shallowly emarginate, almost subtruncate. Genitalia as in Fig. 2.

Length: 5.9 mm. Width: 1.9 mm.

Female: Agrees with description of male except for the following: pronotum with additional pair of setigerous punctures at middle. Protarsi not dilated, pro- and mesotarsi without tenet hairs. Abdomen with apical margin of fifth (last) visible sternite broadly rounded. Genitalia as in Fig. 3.

Length: 5.9 mm. Width: 1.9 mm.

Type Material and Localities: HOLOTYPE male, Crystal Falls Cave, Clark County, Idaho, June 11, 1965 (R. L. Westcott & L. S. Hawkins, Jr.); ALLOTYPE female, same locality, June 12, 1965 (R. L. Westcott); both deposited in the California Academy of Sciences on indefinite loan from the University of Idaho. PARATYPES: Same locality as holotype and allotype: 1 ♂, 3 ♀♀, same data as holotype; 6 ♂♂, 4 ♀♀, same data as allotype; 16 ♂♂, 14 ♀♀, VII-16-1965 (R. L. Westcott); 1 ♂, 2 ♀♀, VIII-7-1965 (R. L. Westcott); 1 ♂, VII-5-1966 (W. F. Barr); 2 ♀♀, VI-8-1967 (R. L. & J. A. Westcott).


Paratypes are deposited in the collections of the American Museum of Natural History; British Museum (Natural History); California Academy of Sciences; Chicago Natural History Museum; Entomology Research Institute, Canada Department of Agriculture, Ottawa; Los Angeles County Museum of Natural History; Museum of Comparative Zoology, Harvard University; Purdue University; United States National Museum; University of California, Davis; University of Idaho; University of Washington; T. C. Barr, Jr. (University of Kentucky); G. H. Nelson (Kansas City); and the writer.

Variability: Relatively little variation in size, form, or color can be detected. Perhaps most obvious is a variability in the size of the notch formed between the independently rounded elytral apices. Females from Crystal Ice Caves and Boy Scout Cave usually have the last visible abdominal sternite more broadly rounded or even truncate. Some specimens have been taken which are testaceous in color, but these undoubtedly are teneral adults.

Variation in sculpture and setal arrangement is evident. There are differences in the degree of fine granulation present on certain portions of the elytra. This character appears to be almost lacking in some specimens from Crystal Falls Cave, but it is readily observable in specimens from Crystal Ice Caves. However, the two populations do not diverge significantly enough to warrant subspecific differentiation.
An interesting variation in setal pattern is exhibited by the setigerous punctures of the head and pronotum, particularly the latter. The setigerous punctures of the dorsal surface of the epicranium almost always conform to the pattern exhibited by the holotype. In referring to these structures, the anterior and posterior locations are not morphological but positional, owing to the prognathous condition of the head. The setae born by these punctures are not of uniform size. Those immediately behind the frontoclypeal suture and those caudomesad of the antennal insertions are recurved, of about the same size, and usually quite evident when viewed at the correct angle with proper lighting. Those in front of the antennal insertions are not always recurved, usually much smaller and difficult to see, while the posterior pair are almost always much larger than any of the other setae, strongly recurved forward, and with the anterior portion in contact with the surface of the head. In addition, there may be present a few minute setae, especially on the median discal area of the epicranium. Quite often there is a pair located not far in front of the large posterior setae. A few specimens possess extremely reduced posterior setae and some appear to have the setigerous puncture lacking on one side.

A much greater degree of variation is evident in the setal pattern of the pronotum. Over half of the specimens examined exhibit the same pattern as the allotype, possessing an anterior and median pair of setigerous punctures, each of which bears a moderately long, backward-recurving seta. Other specimens exhibit wide variation, as shown in Table 1. Each setigerous puncture of a pair is not always evenly placed with respect to its counterpart. The anterior pair are almost always evenly placed, but a considerable number of specimens show anterior or posterior displacement of one of the median punctures, and one

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<th>Pattern of Setigerous Punctures</th>
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<tr>
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<td>TOTAL</td>
<td>38</td>
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Variation in setal pattern of pronotum (cf. Fig. 1). R = right, L = left, A = anterior, P = posterior. A lone "A" or "R" indicates the presence of both members of the pair.
specimen exhibits a lateral displacement. Two of the specimens examined have an extra anterior setigerous puncture on one side. Care must be taken to look for the punctures themselves, as the setae often break off.

A paramere of the male genitalia may possess an additional seta located a short distance below the apical pair of setae.

Bionomics

*Glacicavicola bathyscioides* has been taken from three widely separated lava tube ice caves on the eastern Snake River Plain of Idaho. The primary collecting site was Crystal Falls Cave, but specimens were taken also from Boy Scout Cave and Crystal Ice Caves, which are approximately 160 km and 184 km respectively from Crystal Falls Cave.

Crystal Falls Cave, about 30 km northeast of Dubois, is a lava tube cave located at an elevation of approximately 1891 m (6200 ft) in an area of numerous craters and lava outcroppings. The surrounding area exhibits a more extensive vegetation than that found at the other caves mentioned, which may indicate an older age for this cave. It consists of at least three levels, only one of which was readily accessible. This section was estimated to be 305 m in length, including the spacious chamber into which the large entrance opens. At the far end of this chamber, a much smaller opening leads downward into the portion of the lava tube in which permanent ice is found. Here there is an extensive ice floor and several ice mounds and stalagmites. During the summer and early fall, considerable melting takes place except in the terminal portion of the cave. Maximum-minimum thermometer readings taken where melting occurs showed the temperature to fluctuate by no more than a degree from freezing during a period from July to mid-September, but the winter low during the 1966-67 season was \(-5.5^\circ C\).

Approximately 160 km southwest, at an elevation of about 1769 m (5800 ft) in Craters of the Moon National Monument, is Boy Scout Cave. It lies in an area of numerous lava flows and sparse vegetation (cf. Stearns, 1947). This lava tube cave occurs in pahoehoe lava, is small, and has permanent ice only in limited areas.

Crystal Ice Caves are located approximately 64 km to the south of Boy Scout Cave in a small lava field west of Aberdeen at an elevation of approximately 1525 m (5000 ft). They occur in the southern portion of a volcanic rift known as the Great Rift. The lavas of Craters of the Moon also flowed from this rift. Unlike the other caves, Crystal Ice Caves were formed by great explosions which took place along the Great Rift. The ice in these caves presents a fantastic display, occurring in such forms as stalactites and stalagmites of all shapes and sizes, delicate crystals, ice falls, and a solid floor (Fig. 6). The most interesting caves were virtually inaccessible without special equipment, but through the efforts of Jim Papadakis they are now open to the public.

Other lava tube caves were examined, but none of them appeared to
contain appreciable amounts of permanent ice, if any, and no beetles were found. Shoshone Ice Cave, north of Twin Falls, has extensive permanent ice, but due to interference by man there was a long period when this ice was absent. No evidence of *G. bathyscioides* was found there.

Figure 6. Ice formations at Crystal Ice Caves. Photo courtesy of Jim Papadakis.
All of the beetles have been found either on the ice, where they crawl slowly, or floating in meltwater above the ice floor, where many drown. Perhaps the beetles occur on the walls and ceilings of the caves and fall onto the ice, where they are readily visible. They would be extremely difficult to see on the lava rock. They appear to be particularly partial to ice mounds or large ice stalagmites, the former frequently harboring a variety of arthropods, dead as well as alive. Those arthropods which likely are regular inhabitants of the ice caves include staphylinid beetles, collemobolans of the family Entomobryidae, a dipluran of the family Japygidae, several small flies of uncertain affinity, a phalangid, and a recently described millipede, Idaognath westcottii Buckett & Gardner (1967). One staphylinid, Quedius spelaeus Horn, has also been reported from lava tube caves in western Washington (Halliday, 1963). Anthomyiid flies, ichneumonid wasps, and coleopterous larvae of the family Cantharidae have been found, and these represent epigeic insects which are classified as cave accidentals. These forms cannot live long in the caves, but doubtless serve as an important source of food for some cavernicolous. Small staphylinids of the subfamily Aleocharinae were observed feeding on dead cave accidentals as well as on a white fungus that grows abundantly on organic matter in the caves.

Very little of the biology of Glacicavicola bathyscioides has been ascertained. Only a single mating has been observed and this took place in the presence of an additional "audience" of half a dozen beetles about seven feet up a stalagmite. This may suggest that a sex-attractant is involved, which would certainly not be surprising considering these beetles are blind. During the summer of 1967, Don Horning, University of California at Davis, discovered several G. bathyscioides in Boy Scout Cave and was fortunate enough to observe a single beetle chewing on sclerotized portions of a dead individual of the same species. Fungus was observed growing on the dead beetle. Further observations are necessary before elaboration can be made upon feeding habits as well as other aspects of the biology of this unique cavernicole.

Evolution

Terrestrial cavernicolous are considered to have evolved from forms which lived in such media as the soil (endogeans), snow-packets (nivicoles), mosses (muscicoles), and humus or duff (humicoles). These media approximate the uniform, stable environment found in most caves. For a classification of cavedwellers, the reader is referred to Barr (1964) and Vandel (1965).

Glacicavicola bathyscioides is an obligate cavernicolous (troglobite) with specialized features which make hypothesizing its phylogeny and evolution difficult. However, its lack of known close epigeic relatives may imply a great antiquity, and the fact that it has been found associated with ice strongly suggests that it represents a glacial relict.

Following the terminology of Vandel (1965), it is postulated that the phyletic line of Glacicavicola underwent a long period of "preparation" for a
cavernicolous existence, possibly beginning sometime during the first half of the Tertiary when the climate was more tropical in northern latitudes. The onslaught of cooler weather, which forecast the beginning of the Ice Ages, invoked the southward migration of many animals, while others gradually adjusted to the changing climate. Probably as a result of physiological regression, some terrestrial forms, such as any of those mentioned previously, became dependent upon a more humid environment. As the climate remained cold, glaciers came into being, and many of these animals could not survive. However, some were able to exist as nivicoles in the cool, moist, periglacial environment. Some, such as the ancestral glacicavicolines, may have even inhabited the glaciers themselves. Many nivicoles exist today, and several cavernicolous bathysciines are known to inhabit ice caves in the mountains of Europe (Vandel, 1965).

The eastern Snake River Plain, where G. bathyscioides lives, is largely underlain with basalt of different ages (Stearns et al., 1939; Mundorff et al., 1964). Much of this is exposed, particularly in areas of the more recent lava flows. Many caves exist throughout the area, the majority of them being lava tubes. Some of them contain ice the year around. The Snake River basalt is believed to range in age from Pliocene to Recent, and considering the plain as a whole, eruptions have continued from earliest Pleistocene to comparatively recent times (Hamilton, 1965). At least twice during the Pleistocene, glaciers have occupied areas not far from Crystal Falls Cave. Extensive glaciation was located in the Yellowstone area to the east and, to a lesser degree, north in the region of the Continental Divide (Stearns et al., 1939).

It is not difficult to imagine the ancestral glacicavicolines taking refuge in the lava tube ice caves from the warmer, more arid climate which brought about a rather rapid recession of the glaciers. Conditions were no doubt favorable for this more than once during the Pleistocene, and it seems likely that this refuge began during one of the earlier interglacial periods. Had it occurred after the last and most extensive glacial period, it seems doubtful if G. bathyscioides would yet have attained such a high degree of specialization.

From this discussion it can be hypothesized that G. bathyscioides had its origin somewhere in the vicinity of Crystal Falls Cave, possibly in the once glaciated region just to the north or east, and from there it spread westward and southward to caves at lower elevations.

**Dispersal**

*Glacicavicola bathyscioides* occurs in caves which are separated by distances of over 160 km, thus creating a problem in explaining its means of extending its range. Since its extreme specialization must involve a physiology which renders it fit to live only in an underground environment, it is highly improbable that any extension of its range has been made above ground, either by accident or otherwise. However, this possibility must be explored. An unsuccessful attempt to bring these beetles out of the caves and keep them
alive without some form of protection from the epigean environment leads me to believe that even a brief exposure to warm temperatures and/or sunlight is fatal. Thus it must be assumed that *G. bathyiscioides* has extended its range by underground dispersal.

One of the most extensive groundwater systems known lies beneath the Snake River Plain (Mundorff *et al.*, 1964). Water flow beneath the plain is generally in a southwesterly direction and according to R. E. Williams (pers. comm.), an average movement of about 11 feet per day is not unreasonable. Under isolated conditions the rate of flow may be much higher. Groundwater in the lava beneath the plain occupies pores between unconsolidated materials such as cinders and blocks, joints and fractures, and irregular openings in and between lava flows (Mundorff *et al.*, 1964; Olmsted, 1963). Such irregularities occur above the water table as well and numerous cracks and crevices are apparent on the surface of the lava flows and in the lava tube caves. It is easy to imagine a small beetle, such as *G. bathyiscioides*, being able to move or be carried considerable distances through this system of subterranean channels in a relatively short period of time.

Another means of dispersal can be explored. It was mentioned previously that the ancestral glacialicelines probably took refuge in the ice caves after one of the earlier glacial periods. There they may have remained until, during some subsequent glacial advance, the climate became cold and wet enough for them to move about at or near ground level. However, for reasons already mentioned, this explanation appears less likely.

Either explanation (particularly the former) poses the question of how food is obtained under such extreme conditions. However, it would seem that the food problem is not a limiting factor, since Vandel (1965) has reported that some bathyscielines have been kept alive for eight months without food and certain troglobites are known to derive nourishment from organic or mineral deposits in silt or clay.

The foregoing discussions concerning the evolution and dispersal of *G. bathyiscioides* are by no means complete, but I hope they may serve as a stimulus for further investigation into this most interesting subject.

**Literature Cited**


Brown, W. J. 1933. Two undescribed species of the old family Silphidae with notes on some characters that have been used to divide the group. Canadian Ent. 65:213-215.


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