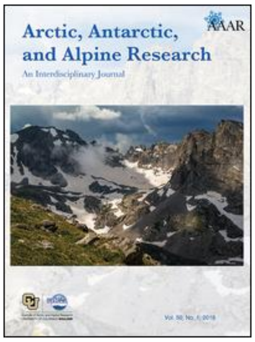

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THE SUBTERRANEAN CRUSTACEAN FAUNA OF CASTLEGUARD CAVE, COLUMBIA ICEFIELDS, ALBERTA, CANADA, AND ITS ZOOGEOGRAPHIC SIGNIFICANCE*

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ABSTRACT

A biological survey of Castleguard Cave has shown that the inner cave is inhabited by two species of aquatic crustaceans, the asellid isopod *Salmasellus steganothrix* and the crangonyctid amphipod *Stygobromus canadensis,* both of which are blind and unpigmented. The isopod is abundant throughout the portions of the system containing sediment-rich pools and was found in areas of the cave which lie beneath the Columbia Icefields. The amphipod, which is unique to Castleguard Cave, was found only in one series of pools about 2 km from the entrance.

The occurrence of these aquatic species so far inside an area fully glacierized during the Wisconsinan and even at present partially under a permanent icefield suggests that they may be remnants of very old preglacial distributions. Since it is known that the cave has remained intact and internally ice free for more than 720,000 yr, it is hypothesized that it has served as a subglacial refugium for these organisms.

INTRODUCTION

The cave faunas of the Northern Hemisphere (Holarctic region) have been extensively sampled and analyzed in the last several decades. As a result, hundreds of species, both aquatic and terrestrial, have been described from subterranean environments in the temperate regions of Europe, Asia, and North America. Obligatory cave species (troglobites) are typically specialized morphologically through the loss or degeneration of eyes and pigment and often exhibit attenuation of the body and appendages. Similarly modified species obligatory to groundwater habitats but not necessarily caves per se are sometimes called stygobionts or phreatobites.

Troglobites are especially well represented in animal groups such as flatworms, snails, crustaceans, arachnids, millipeds, insects, fishes, and salamanders. Stygobionts may occur both within and outside of karst regions and commonly include small crustaceans such as amphipods, isopods, and bathynellids. The distinction between troglobites and styobionts is not always clear, and the two terms are sometimes used interchangeably.

With very few exceptions, the geographic distribution of troglobites in the Holarctic region is restricted to the nonglacial parts of North America and Eurasia. It is

*A version of this paper was presented orally at a symposium, "Karst and Caves of Castleguard Mountain," at the 8th International Congress of Speleology, Bowling Green, Kentucky, U.S.A., 20 July 1981.

assumed that since troglobitic organisms are generally absent from glaciated regions in the Northern Hemisphere, any cave or groundwater faunas that might have existed there prior to the Pleistocene were subsequently extirpated by the effects of glacial or periglacial conditions (Vandel, 1965; and others). This appears to be a valid assumption, inasmuch as troglobitic organisms probably existed at more northern latitudes prior to the climatic changes and geological alterations that accompanied glaciation during the Pleistocene. It is quite conceivable that during glacial maxima large-scale exterminations of cave and groundwater faunas would have resulted from the physical destruction of many subterranean habitats by scouring and mechanical abrasion, drastically lowered groundwater temperatures, and elimination of surface sources of organic nutrients. If this scenario is accepted, it is not surprising that troglobitic organisms are almost nonexistent in recently glaciated regions. In North America the only troglobitic (or stygobiont) organisms recorded from glaciated regions at present are a small number of amphipod and isopod crustaceans, and some workers have attributed their presence there to postglacial dispersal from the south since Wisconsinan time (see Holsinger, 1980; Lewis and Bowman, 1981). Troglobites are also very rare in glaciated areas of Europe (viz., the British Isles and Poland), where they consist primarily of small crustaceans (Jefferson, 1976; Skalski, 1981).

In Canada, which was extensively glaciated in the Pleistocene, troglobites or stygobionts were unknown (see Fenton et al., 1973) until the discovery of a subterranean isopod, *Salmasellus steganothrix,* in Alberta (Bowman, 1975; Clifford and Bergstrom, 1976). Shortly thereafter (April 1977), a subterranean amphipod, *Stygobromus canadensis,* was collected from Castleguard Cave by Recklies and Mort and later described by Holsinger (1980). The isopod was also found for the first time in this cave in 1977. More recently, a second subterranean amphipod, *Stygobromus secundus,* was described from a spring near Rocky Mountain House in Alberta by Bousfield and Holsinger (1981). The discovery of these subterranean crustaceans is of great interest zoogeographically, not only because they are the first troglobites or stygobionts reported from Canada, but because they occur in glaciated areas farther north than any other known subterranean species in North America, and two of them inhabit a cave covered in part by active glaciers.

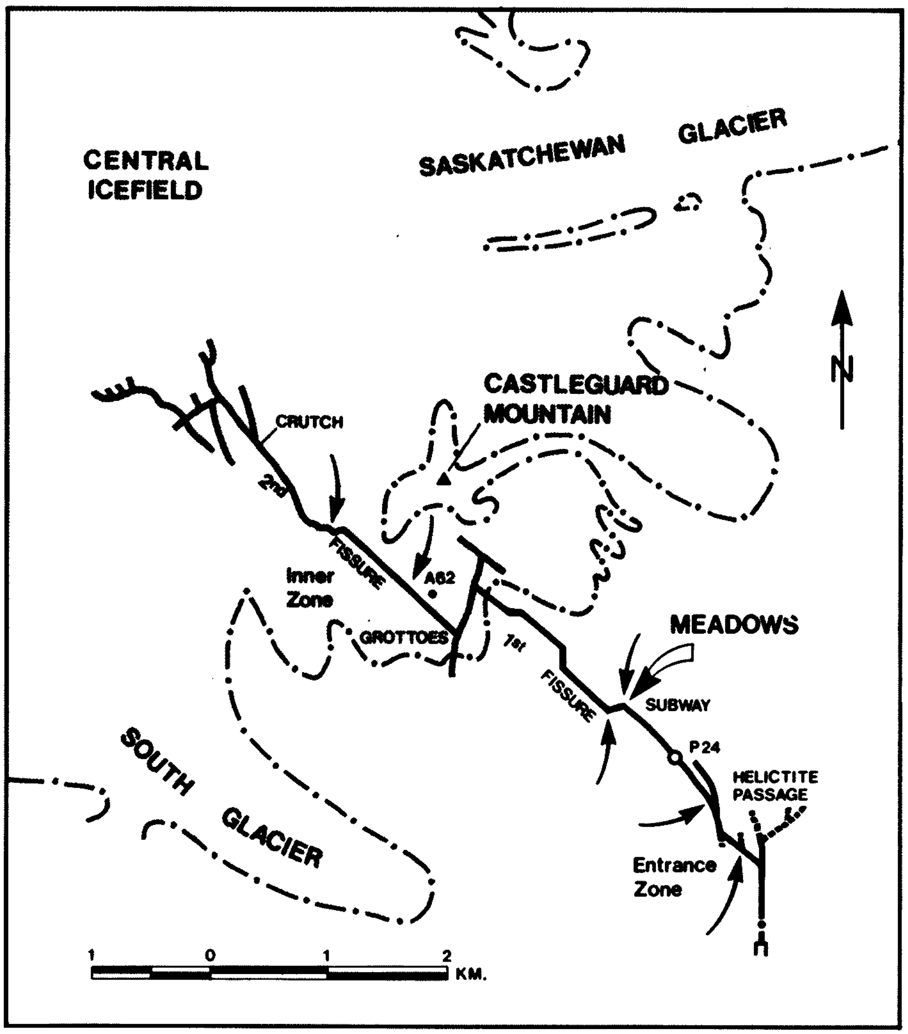

FIGURE 1. Location of collection points in Castleguard Cave. Closed arrows indicate the positions of pools containing the isopod species *S. steganothrix.* The open arrow indicates the pools where the amphipod *S. canadensis* was found.

FAUNAL GEOGRAPHY OF CASTLEGUARD CAVE

A morphological description of Castleguard Cave is given by Ford et al. (1983, this symposium). It can be considered to comprise two faunal zones: (1) the entrance zone extending as far as the shaft, P24, and (2) the rest of the cave beyond the P24 (Figure 1).

The entrance zone consists of one major passage as well as Boon's Blunder and several smaller, not yet fully explored, side passages. It is located at quite shallow depth under the Castleguard Meadows. In the entrance and some way into the cave below the first shaft, P8, abundant evidence (droppings) of pack rats are seen, suggesting regular visits by these animals to this area of the cave. During some expeditions, they have attacked equipment and supplies deposited at the inner limit of the seasonally flooded area, ca. 1 km from the entrance. This signifies that they are active in late March and April, when hibernating mammals of the region remain dormant in the winter conditions prevailing outside.

Specimen collections were conducted during the expeditions of April 1977, 1978, and 1980. At this time the pools in the entrance crawls are frozen for several hundred meters into the cave. As soon as nonfrozen pools were encountered they were found to contain specimens of the isopod *Salmasellus steganothrix.* Since earlier in the year the zone of freezing may have extended farther into the cave and the pools are isolated from each other in this area it is possible that this species withstands short periods of freezing, perhaps by burrowing in the sediment. Most of the pools in this zone were inhabited by members of this species, sometimes with relatively large populations. The innermost part of this zone, Helictite Passage, contains no pools and no specimens were observed here.

Because the outer part of the entrance zone is completely inundated at times during the summer months, it is likely that large amounts of nutrients are brought into the cave at this time and that these support the large population of isopods.

The inner zone, starting with the Subway at the bottom of P24 and leading through many kilometers of fissure passage, is located initially below the Castleguard caprock benches and then under the icefields. A string of small pools located in thick mud beds is found at the end of the Subway. In addition to containing further examples of *Salmasellus steganothrix* they were the only habitat where the amphipod *Stygobromus canadensis* was found. The pools are about 50 cm deep and of varying dimensions, the largest one being approximately 2 m long and 1 m wide. At the time of the expeditions there was no active water supply to these pools.

Throughout the First Fissure no specimens of any kind were found, probably due to the fact that wet areas are all clean washed by summer invasion waters, and no sediment accumulates. The warmest region of the cave, the Grottoes, was thoroughly checked, but no specimens were located. This is a comparatively dry area of the cave. Similarly, the great invasion water shaft, A62, was carefully studied because copious water enters at this point in summer and some supply is maintained throughout the year. As in the First Fissure, however, it was washed clean and no specimens were observed. Farther on towards the end of the Second Fissure (and well underneath the glaciers) pools similar in character to those in the entrance zone were found and these also were inhabited by *Salmasellus steganothrix.* Biological survey of the cave was extended almost to the Crutch area. There is an abundant population of *Salmasellus steganothrix* to this point, but no further examples of *Stygobromus canadensis* were found.

Salmasellus steganothrix appears to be distributed fairly uniformly throughout the entire cave system. *Stygobromus canadensis,* on the other hand, is known to exist only in one isolated area. No other species were observed in the cave. Collection sites of individual specimens are indicated on Figure 1.

DESCRIPTION OF THE CRUSTACEAN FAUNA

Isopod Crustaceans

The only isopod species found in the cave was *Salmasellus steganothrix.* This species was described by Bowman (1975) from numerous specimens taken from the stomachs of rainbow trout in Horseshoe Lake, Jasper National Park, Alberta. It is assumed that living specimens occur in the subterranean waters associated with the lake. Since its original discovery, the species has been recorded from a cave spring near Cadomin, Alberta (and probably in a well near Cadomin) by Clifford and Bergstrom (1976), in Castleguard Cave, and in Deadhorse Cave, a large lava tube located approximately 750 km southwest of the Alberta sites in Skamania County, Washington (identification by J. J. Lewis).

Salmasellus steganothrix is one of approximately 45 hypogean species of the family Asellidae found in North America to date. It is the only species of the genus *Salmasellus* known to date and is therefore unique in constituting the basis for a monotypic genus. This species is blind and unpigmented and of typical hypogean facies (Figures 2 and 3). The sizes of the specimens were variable and up to 8 mm (Figure 2a). Figure 2b illustrates an egg-bearing specimen. This species is relatively abundant; in some pools 40 to 50 specimens could easily be counted under the low-light conditions available. Also, as the animals tend to travel along the sediment floors of the pools, numerous tracks could be seen in undisturbed areas. Asellid isopods are also common and widespread in caves and other groundwater habitats in the unglaciated parts of North America, Europe, and Asia.

Amphipod Crustaceans

Stygobromus canadensis was described by Holsinger (1980) and to date is known only from Castleguard Cave. It is extremely rare—only five specimens have been collected. Specimens were found in pools at the end of the Subway as described earlier. The species is blind and unpigmented, of typical hypogean facies (Figures 4 and 5), and measures up to 5 mm in length. Specimens were easily distinguished from the much more abundant *Salmasellus steganothrix* by their remarkably rapid movement through the pools.

Stygobromus canadensis belongs to the large, exclusively subterranean genus *Stygobromus*, of which 97 species from North America (north of Mexico) and one from south-central Siberia have been described to date (see Holsinger, 1978). Species of *Stygobromus* are common and widespread in caves and groundwater habitats in unglaciated parts of North America. The species is unique enough to be placed in a separate species group in the genus and has no close relatives elsewhere.

DISCUSSION

To date a total of 12 subterranean amphipod species in the family Crangonyctidae and seven subterranean isopods in the family Asellidae have been recorded from areas north of the southern limits of continental glaciation in North America. Six of the amphipods and six of the isopods occur in glaciated areas of the Central Lowland Province in the east-central United States and most of them range both north and south of glacial bound-

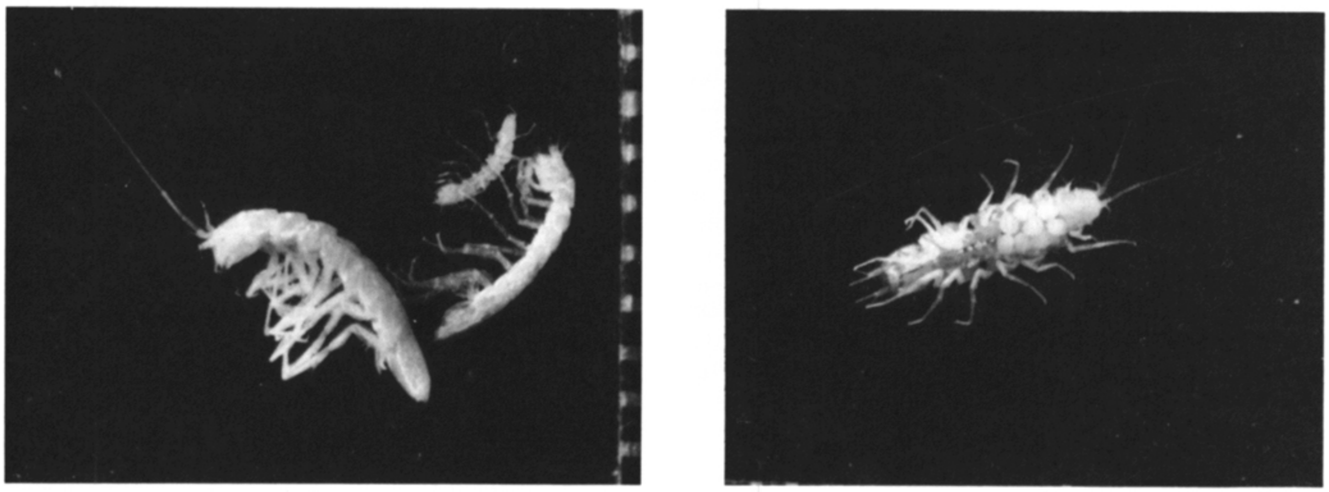

FIGURE 2. *Salmasellus steganothrix*. Panel (a) illustrates the size variation of collected specimens. Panel (b) shows a female specimen with eggs. The scale is in millimeters.

FIGURE 3. *Salmasellus steganothrix*, scanning electron micrograph showing mouth parts. Bar represents 0.1 mm.

FIGURE 4. *Stygobromus canadensis*, male and female specimens. Scale is in millimeters.

aries with generally contiguous distributions (for details, see Bowman and Beckett, 1978; Holsinger, 1981; Lewis and Bowman, 1981). The majority of these species are stygobionts which live in interstitial or shallow groundwater habitats often developed in loosely consolidated glacial drift, and it is a reasonable assumption that these species have spread north into glaciated areas from "southern refugia" following retreat of glaciers in the late Pleistocene.

In contrast to those species whose occurrence in glaciated areas can probably be explained by postglacial dispersal are at least five amphipods and one isopod that are either endemic to glaciated regions or represented there by disjunct populations far removed from those in unglaciated regions to the south. In three recent papers, one of us (Holsinger, 1978, 1980, 1981) suggested that under certain conditions some aquatic subterranean species might have survived extended periods of glaciation in deep groundwater refugia beneath the ice, and that their present ranges have not resulted from northward migration since Wisconsinan time but instead probably reflect very old, preglacial distributions. Similarly, the possibility of subglacial refugia in Europe has been raised in recent papers by Ginet (1971), Jefferson (1976), and Skalski (1981).

FIGURE 5. *Stygobromus canadensis*, scanning electron micrograph. Bar represents 0.1 mm.

The arguments in support of the subglacial refugium hypothesis may be summarized as follows: (1) A small number of hypogean crustaceans living in glaciated areas at present are either local endemics or represented by highly disjunct populations, and some are only distantly related taxonomically to congeneric species living in unglaciated areas. (2) It is improbable that tiny, hypogean crustaceans would have migrated great distances northward in the relatively short period of time since the Wisconsinan glacial age. It has been shown that the Castleguard area was fully glacierized during the late Wisconsinan (Ford, 1983, this symposium). (3) The fact that groundwater remains unfrozen beneath temperate glaciers and is thus potentially available for colonization by subterranean crustaceans. (4) The occurrence of certain species of crustaceans beneath the Ross Ice Shelf, 475 km from the open Ross Sea in Antarctica (Bruchhauser et al., 1979). (5) The low metabolic rate, slow growth rates, reduced energy budgets, and tolerance for lowered water temperature of hypogean crustaceans which might permit their extended existence in an austere, food-poor, subglacial environment. (6) Castleguard Cave itself, which is presently inhabited by both troglobitic amphipods and isopods, extends in part beneath modern alpine glaciers, and has apparently remained internally ice-free and available as a potential habitat for aquatic organisms for at least 145,000 yr and probably for more than 720,000 yr (Gascoyne et al., 1983, this symposium).

One of the more difficult problems with the subglacial refugium model is how to account for a food source that would have sustained the growth and reproduction of hypogean organisms. This problem probably would not have been insurmountable, however. The basis for most food chains in subterranean ecosystems is allochthonous organic material that supports the growth of heterotrophic bacteria and fungi (Dickson and Kirk, 1975). All such food originates at the surface and is then carried into underground habitats by flooding, seepage, or filtration (or some combination of these), where it undergoes slow decomposition. The principal food source for hypogean amphipod and isopod crustaceans is either the decomposing organic matter itself or the microorganisms, or perhaps both (Holsinger, 1980). Although transportation of organic nutrients into groundwater habitats should be significantly curtailed in areas covered by thick masses of ice above the annual firn line, it might not be cut off entirely. Open drainage systems beneath glacial ice that allow the free flow of water from the ice surface into the underlying bedrock have been shown to exist under the central Columbia Icefield today (Smart, 1983, this symposium). Schroeder and Ford (1983, this symposium) have described sedimentological evidence in the cave for the circulation of considerable volumes of water during some parts, at least, of "full" glacial conditions. Several European workers have suggested similar means of moving organic material into groundwater habitats in former subglacial karst areas (see Skalski, 1981).

Considering the low metabolic rates, slow growth rates, and reduced energy budgets generally associated with hypogean organisms, the amount of nutrients necessary to sustain life might be quite small. So small, in fact, that small particles of organic detritus flushed into groundwater habitats prior to glaciation, or organically enriched sediments with decomposer micro-organisms already present in subterranean channels before glaciation, or even particles that might have been transported into hypogean habitats by free-flowing groundwater beneath the ice, conceivably could have provided at least a minimally adequate food supply for small populations of hypogean crustaceans for long periods of time.

One possible source of food for the crustaceans living in Castleguard Cave at present, and possibly in the past as well, is a red alga which is common on the icefields above the cave in the summer. It is possible that some of this material is being carried into the cave by glacial meltwater, where it could serve as an organic nutrient.

The presence of *Stygobromus canadensis,* and possibly *Salmasellus steganothrix,* in Castleguard Cave offers the most compelling evidence gathered to date in support of a theory of subglacial refugia. *Stygobromus canadensis* occurs approximately 500 km north of the southern limit of continental glaciation, is locally endemic, and is only distantly related taxonomically to other amphipods in the Cordilleran region of North America (Holsinger, 1980, 1981). *Salmasellus steganothrix,* on the other hand, is found outside of Castleguard Cave, but all but one highly disjunct population in southern Washington are known only from a relatively small geographic area in western Alberta. The possibility that populations of *Salmasellus steganothrix* might have survived Wisconsinan glaciation in a low-elevation refugium in an ice-free corridor, hypothesized by some workers to have existed between the Laurentide and Cordilleran ice sheets on the eastern side of the Canadian Rockies in the late Pleistocene (see Rutter, 1980), has also been raised by Clifford and Bergstrom (1976). If such an ice-free corridor existed, however, it would have been far to the east of the Castleguard Cave area.

Chronological study of speleothems indicates that Castleguard Cave has remained intact and internally ice-free for >720,000 yr (Gascoyne et al., 1983, this symposium). The age of this cave and the evidence that it has remained wet but unfrozen suggest that it could have been a potential habitat for subterranean crustaceans since, at least, the Yarmouth Interglacial, and that it could have provided a subglacial refugium for these organisms during glacial maxima in both Illinoian and Wisconsinan times.

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REFERENCES CITED

Bousfield, E. L. and Holsinger, J. R., 1981: A second new subterranean amphipod crustacean of the genus *Stygobromus* (Crangonyctidae) from Alberta, Canada. *Canadian Journal of Zoology,* 59: 1827–1830.

Bowman, T. E., 1975: Three new troglobitic asellids from western North America (Crustacea: Isopoda: Asellidae). *International Journal of Speleology,* 7: 339–356.

Bowman, T. E. and Beckett, D. C., 1978: A redescription of the troglobitic isopod, *Caecidotea stygia,* from the environs of Cincinnati, Ohio (Crustacea: Isopoda: Asellidae). *Proceedings of the Biological Society of Washington,* 91: 294–302.

Bruchhauser, P. M., Raymond, A., Jacobs, S. S., DeVries, A. L., Throndike, E. M., and DeWitt, H. H., 1979: Fish, crustaceans, and the sea floor under the Ross Ice Shelf. *Science,* 203: 449–451.

Clifford, H. F. and Bergstrom, G., 1976: The blind aquatic isopod, *Salmasellus,* from a cave spring of the Rocky Mountains' eastern slopes, with comments on a Wisconsin refugium. *Canadian Journal of Zoology,* 54: 2028–2032.

Dickson, G. W. and Kirk, P. W., Jr., 1975: Distribution of heterotrophic micro-organisms in relation to detritivores in Virginia caves (with supplemental bibliography on cave mycology and microbiology). *In* Parker, B. C. and Roane, M. K. (eds.), *The Distributional History of the Biota of the Southern Appalachians.* Pt. IV, *Algae and Fungi.* Charlottesville: University Press of Virginia, 205–226.

Fenton, M. B., Peck, S. B., and Syme, R. G., 1973: A biological survey of caves in and around Nahanni National Park, N.W.T., Canada. *Canadian Caver,* 5: 35–42.

Ford, D. C., 1983: Physiography of the Castleguard karst and Columbia Icefields area, Alberta, Canada. *Arctic and Alpine Research,* 15: 427–436.

Ford, D. C., Smart, P. L., and Ewers, R. O., 1983: The physiography and speleogenesis of Castleguard Cave, Columbia Icefields, Alberta, Canada. *Arctic and Alpine Research,* 15: 437–450.

Gascoyne, M., Latham, A. G., Harmon, R. S., and Ford, D. C., 1983: The antiquity of Castleguard Cave, Columbia Icefields, Alberta, Canada. *Arctic and Alpine Research,* 15: 463–470.

Ginet, R., 1971: Biogéographie de *Niphargus* et *Caecospheroma* (Crustacés troglobies) das les départements francais du Jura et de l'Ain-Origine; influence des glaciations. *Actes du 4e Congrès suisse de Spéléologie, Neuchâtel, septembre 1970,* 186–198.

Holsinger, J. R., 1978: Systematics of the subterranean amphipod genus *Stygobromus* (Crangonyctidae), Part II: Species of the eastern United States. *Smithsonian Contributions to Zoology,* 266: 1–444.

———, 1980: *Stygobromus canadensis,* a new subterranean amphipod crustacean (Crangonyctidae) from Canada, with remarks on Wisconsin refugia. *Canadian Journal of Zoology,* 58: 290–297.

———, 1981: *Stygobromus canadensis,* a troglobitic amphipod crustacean from Castleguard Cave, with remarks on the concept of cave glacial refugia. *Proceedings of the 8th International Congress of Speleology, Bowling Green, Kentucky, July 1981,* 1: 93–95.

Jefferson, G. T., 1976: Cave faunas. *In* Ford, T. D. and Cullingford, C. H. D. (eds.), *The Science of Speleology.* London: Academic Press, 359–421.

Lewis, J. J. and Bowman, T. E., 1981: The subterranean asellids (*Caecidotea*) of Illinois (Crustacea: Isopoda: Asellidae). *Smithsonian Contributions to Zoology,* 335: 1–66.

Rutter, N. W., 1980: Late Pleistocene history of the western Canadian ice-free corridor: Report I.G.C.P. 73/1/24 Subgroup, Quaternary Stratigraphy, Eastern Cordillera, University of Alberta, Edmonton. *Canadian Journal of Anthropology,* 1: 1–8.

Schroeder, J. and Ford, D. C., 1983: Clastic sediments in Castleguard Cave, Columbia Icefields, Alberta, Canada. *Arctic and Alpine Research,* 15: 451–461.

Skalski, A. W., 1981: Origin and composition of underground fauna in Poland. *Proceedings of the 8th International Congress of Speleology, Bowling Green, Kentucky, July 1981,* 2: 403–406.

Smart, C. C., 1983: The hydrology of the Castleguard Karst, Columbia Icefields, Alberta, Canada. *Arctic and Alpine Research,* 15: 471–486.

Vandel, A., 1965: *Biospeleology.* Oxford: Pergamon Press. 524 pp.