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Observations on the Cave-Associated Beetles (Coleoptera) of Nova Scotia, Canada

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Abstract:

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The cave-associated invertebrates of Nova Scotia constitute a fauna at a very early stage of post-glacial recolonization. The Coleoptera are characterized by low species diversity. A *staphylinid Quedius spelaeus spelaeus*, a predator, is the only regularly encountered beetle. Ten other terrestrial species registered from cave environments in the province are collected infrequently. They include three other rove-beetles: *Brathinus nitidus, Gennadota canadensis* and *Atheta annexa*. The latter two together with *Catops gratiosus* (Leiodidae) constitute a small group of cave-associated beetles found in decompositional situations. *Quedius s. spelaeus* and a small suite of other guanophiles live in accumulations of porcupine dung: *Agolinus leopardus* (Scarabaeidae), *Corticaria serrata* (Latrididae), and *Acrotrichis castanea* (Ptilidae). Two adventive weevils *Otiorhynchus ligneus* and *Barypeithes pellucidus* (Curculionidae) collected in shallow cave passages are seasonal transients; *Dermestes lardarius* (Dermestidae), recorded from one cave, was probably an accidental (stray). Five of the terrestrial beetles are adventive Palaearctic species. Aquatic beetles are collected infrequently. Four taxa have been recorded: *Agabus larsoni* (Dytiscidae) may be habitual in regional caves; another *Agabus* sp. (probably semivittatus), *Dytiscus* sp. (Dytiscidae), and *Crenitis digesta* (Hydrophilidae) are accidentals. The distribution and ecology of recorded species are discussed, and attention is drawn to the association of beetles found in a Nova Scotia "ice cave".

Keywords: cave fauna, Coleoptera, beetles, Nova Scotia, Canada

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INTRODUCTION

Although they are still in the main poorly described, the invertebrate communities inhabiting caves in the formerly glaciated northern regions of North America are of considerable interest. They are composed almost entirely of species in a dynamic and early phase of post-glacial repopulation and thus may offer opportunities to gain insights into the little understood earliest stages of colonization of subterranean habitats. In Nova Scotia there is evidence that post-glacial recolonization of cave habitats by some species was relatively delayed by zoogeographical barriers and is at an earlier stage than that of neighbouring geographical regions (Moseley, 2007*a*).

Coleoptera are of particular interest in cave biology. As a group, beetles are among the most important cavernicolous insects: Gibert & Deharveng (2002) estimated that the Order contains 73% of the described 'troglobitic' terrestrial insects, and unlike many other organisms found in caves the taxonomy, distribution, and biology of beetles are well investigated. The genus *Quedius* and some other lines display different progressive stages of behavioural, physiological and morphological adaptation to subterranean life (Moseley et al., 2006; Moldova & Rajka, 2007).

Knowledge of the composition and ecology of the beetle fauna of Nova Scotia caves has accumulated slowly as a result of general invertebrate surveys made from time to time since the 1960s. Calder and Bleakney (1967) listed three beetles from a small gypsum cave used as a porcupine den: *Quedius spelaeus spelaeus*, *Brathinus nitidus* (Staphylinidae) and *Aphodius leopardus* [now known as *Agolinus leopardus*] (Scarabaeidae). The next four decades produced new occurrence records of the two staphylinids, the addition of five further terrestrial beetles to the provincial checklist and the first records of aquatic species (Moseley, 1998, 2007a; Majka et al., 2006; Moseley et al., 2006). Subsequent fieldwork has now increased the total to 15 (4 aquatic and 11 terrestrial) taxa, and added further occurrence records of previously listed species.

Moseley et al. (2006) gave some details of the life history of *Q. s. spelaeus*, noted its role as an important predator in subterranean communities, and conjectured that the provincial population may have immigrated from late-glacial offshore refugia, while Majka et al. (2006) briefly discussed the distribution and ecology of *G. canadensis* in Nova Scotia, based mainly on new surface records. Except for the preliminary check-list and summary of

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records that were provided by Moseley (2007*a*) almost nothing is known about other beetle species utilizing subterranean habitats in the province.

This paper describes and discusses the composition, geographical distributions and ecology of the cave-associated Coleoptera of Nova Scotia. It is a contribution to knowledge of the poorly investigated subterranean fauna of glaciated North America.

METHODS

Beetles were collected from caves and abandoned hardrock mines in mainland Nova Scotia and Cape Breton Island intermittently between 1969 and 2007. Invertebrates were sampled from 17 sites mainly by hand, from bulk substrate samples, and in unbaited pitfall traps: set baits and baited traps were used sparingly. Those sites where beetles were collected are shown in Fig. 1. Further details and comprehensive background information including a full list of collecting sites, ecological notes, details of associated fauna, and a bibliography were provided by Moseley (2007*a*).

All specimens were collected by M. Moseley except where otherwise indicated. Voucher specimens are deposited in the Natural History collections of the Nova Scotia Museum (Halifax, Canada) and/or retained by the identifying taxonomist.

Threshold (th.), *deep threshold* (d.th.), and *dark zone* (d.z.) are as defined in Moseley (2007*a*). Use of the ill-defined terms *troglobite*, *troglophile* and *trogloxene* has been avoided as far as possible: where they appear in citations from another author they are to be understood in the sense intended by the writer concerned.

RESULTS

Fifteen beetle taxa have been collected from cave environments in Nova Scotia in the families Dytiscidae (3), Hydrophilidae (1), Ptilidae (1), Leiodidae (1), Staphylinidae (4), Scarabaeidae (1), Dermestidae (1), Latrididae (1), and Curculionidae (2). Individual accounts of all taxa follow.

Dytiscidae

Agabus larsoni Fery & Nilsson 1993

Nova Scotia cave records: Hayes Cave, 3.VIII.1997, d.z. in large pond (1 adult, det. Y. Alarie).

Geographical distribution and occurrence: known from eastern Canada and northern New England, where it is mainly found in small cold woodland pools (Larson et al., 2000).

Cave ecology: This beetle has also been collected in a limestone stream cave in Kings County, New

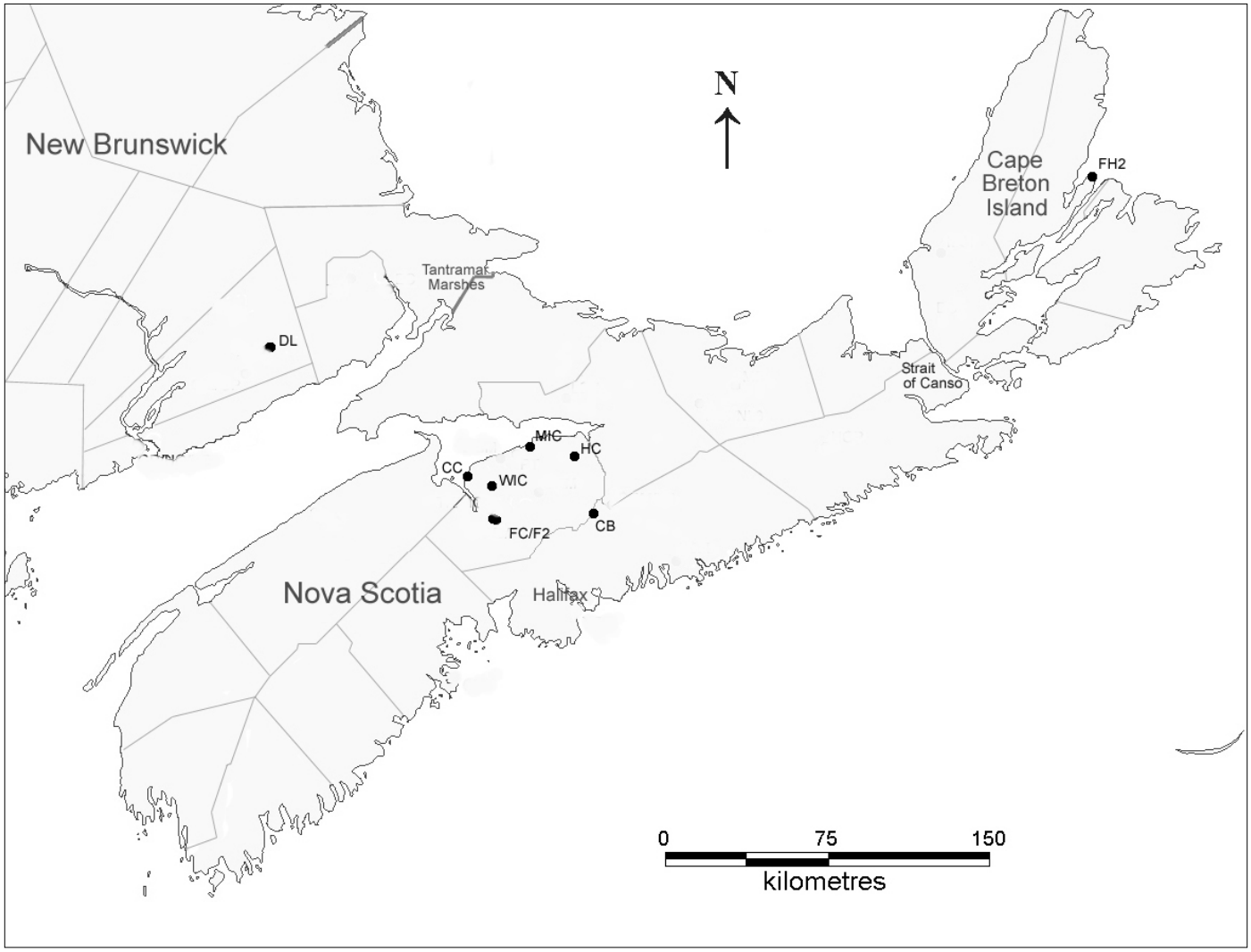

Fig. 1. Outline map to show location of collecting sites [CB = Cave-of-the-Bats; CC = Cheverie Cave/mine; DL = Dalling's Cave; FC = Frenchman's Cave; F2 = Frenchman's II; FH2 = Fairy Hole II; HC = Hayes Cave; MIC = Minasville Ice Cave; WIC = Woodville Ice Cave].

Brunswick, Canada, where there appeared to be a thriving population (Dalling's Cave, 24.VIII.2005, common, th.-d.z. and also in stream outside cave, under stones [det. C. G. Majka]). It is probably habitual within suitable caves in eastern Canada.

Agabus sp. prob. ***semivittatus*** LeConte 1852

NS cave records: Cave-of-the-Bats, 28.VI.1995, d.z. in pool associated with plant flood debris (1 adult, det. Y. Alarie).

Geographical distribution and occurrence: *Agabus semivittatus* is a widespread epigean species that normally occurs in streams, seeps and spring-fed pools (Larson et al. 2000) but, with the exception of the above cave record, is not reported from Nova Scotia (C. G. Majka, *pers. comm.*). The specimen was identified by a recognised specialist but cannot now be located for verification and the taxon is treated here as *Agabus* sp. prob. *semivittatus.*

Cave ecology: Accidental.

***Dytiscus* sp.**

NS cave records: Cave-of-the-Bats, 28.VI.1995,d.z. in stream associated with plant flood debris (one 3rd instar larva).

Cave ecology: Accidental.

Hydrophilidae

Crenitis digesta (LeConte, 1855)

NS cave records: Frenchman's II (cave), 14.X.1996,d. th. (1 adult, det. S.B. Peck).

Geographical distribution and occurrence: Widespread in eastern North America (S. Peck, *pers. comm.*).

Cave ecology: Accidental.

Ptilidae

Acrotrichis castanea (Matthews, 1877) [Fig. 2A]

NS cave records: Frenchman's II (cave), 5.X.1997 and 18.X.1997, abundant d.th. to d.z. in 'moderately decomposed' (pH 6.5) porcupine dung (det. M. Sörensson); 18.X.1997, d.th. in wet plant debris (1).

Geographical distribution and occurrence: a widely distributed Nearctic species (in Canada from British Columbia to Nova Scotia) (Majka & Sörensson, 2007).

Cave ecology: This guanophile species was abundant in Frenchman's II and has also been collected from a cave in Illinois (Sörensson, 2003) suggesting that it may be more common in such habitats than presently known. Ptilids are probably often overlooked in cave collections due to their small size and secretive habits.

Leiodidae: Cholevinae

Catops gratiosus (Blanchard, 1915)

NS cave records: Woodville Ice Cave, 9.IX.2007, d.th. (broken rock and leaf litter) in unbaited pitfall trap (1♂,1♀, det. C. G. Majka); 22.IX.2007, d.th. in unbaited pitfall (1♀, det. C. G. Majka).

Geographical distribution and occurrence: *Catops gratiosus* is an infrequently collected species reported from central Nova Scotia to northern Cape Breton (Majka & Langor, 2008). It has not otherwise been recorded in Atlantic Canada and the nearest records to the region are from southern Maine, Ontario, and Quebec (Peck & Cook, 2002)

Cave ecology: Peck & Cook (2002) recorded the species from 62 caves in Alabama, Georgia, Illinois, Indiana, Iowa, Kentucky, Maryland, Massachusetts, New York, Ohio, Pennsylvania, Tennessee, Virginia, and West Virginia. Although it has a behavioural affinity for caves, it exhibits no apparent morphological specializations for subterranean life. While most specimens collected in western and northeastern North America are from deciduous and coniferous forests, most of the collections at lower elevations in the southeastern USA are from caves (usually near the entrances) which it is thought may serve as cool and moist refugia in warmer and drier low elevation regions (Peck & Cook, 2002). However cave records from Ontario (Peck, 1988) and now from Nova Scotia show that it does utilize caves in the north, suggesting that it is probably present in such habitats throughout its geographical range. Beetles have been taken in forests on carrion, decaying fungi, and mammal dung and in caves on dead mice and bats but not on bat guano (Peck & Cook, 2002).

Staphylinidae: Omaliinae

Brathinus nitidus LeConte, 1852

NS cave records: Frenchman's Cave, no details (1, det. T. Barr) (Calder & Bleakney, 1967); Fairy Hole II, 24.X.1971, on deposit of fish bones in d.z. (1, det. J. M. Campbell) (Moseley, 2007*a*).

Geographical distribution and occurrence: *Brathinus nitidus* is a Nearctic species distributed from Newfoundland and Nova Scotia westwards to the Lake Superior region and south along the Appalachians to northern Alabama (Peck, 1975). It is associated with shaded cool wet habitats with most of the more southerly records being from caves (Peck, 1975). The Canadian National Collection has 88 examples all collected 9.VII.1984 – 25.IX.1984 in Cape Breton from litter, moss, dead logs, mushrooms etc., often along streams or near waterfalls (A. Davies, *pers. comm.*). The Frenchman's Cave record is the sole mainland Nova Scotia report of the species. Careful searching of both the cave and its immediate vicinity in 2007 failed to secure additional specimens.

Cave ecology: Because it is often encountered underground Peck & Thayer (2003) regarded this beetle as a 'troglophile'. Peck (1975) stated that it survives quite well in the dark zone as well as the threshold and also noted that a probable larva had been reported from a cave in Tennessee but was unable to find any larvae in caves himself. In the absence of proof of an ability to breed in them, it is possible that only adults in search of cool humid conditions enter

caves.

Staphylinidae: Staphylininae

Quedius (Microsaurus) spelaeus spelaeus Horn, 1871 [Figs. 2B; 3A,D]

NS cave records: Cheverie Cave/mine, 21.VII.2007, running across mud floor in d.z. (1 adult); 5.VII.2007, d.z. under pork liver bait (1 late-instar larva); 5.VII.2007, d.z. under rocks on loamy floor (2 adults); 15.VIII.2007, d.z. in worm casts (1 larva). Frenchman's Cave, 19.VIII.2007, d.th. in porcupine dung (1 larva, parasitized by a wasp [Hymenoptera: Proctotrupidae]; 19.VIII.2007, d.th. under stone (♂♀ pair, collected live and observed mating in culture). Woodville Ice Cave, 9.IX.2007, d.th. in unbaited pitfall placed in scree (1 adult). For records prior to 2007 see Moseley et al. (2006).

Geographical distribution and occurrence: The geographical distribution of this Nearctic rove-beetle was discussed by Moseley et al. (2006). The Nova Scotia population appears to be disjunct and may have immigrated from late-Pleistocene offshore

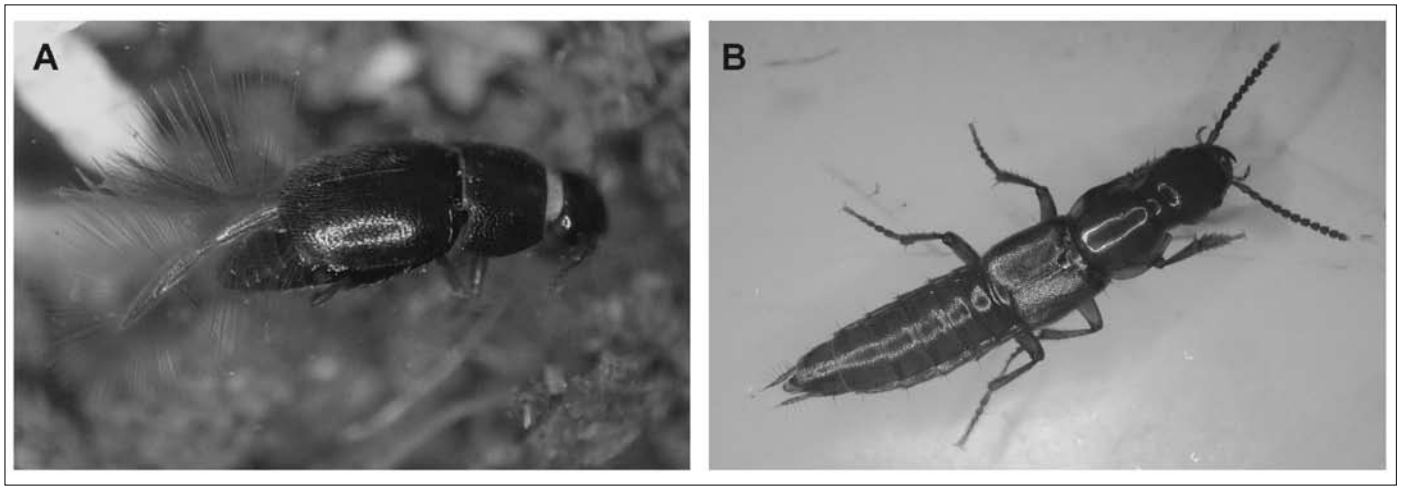

Fig. 2.: A: *Acrotrichis castanea*, preserved adult [Frenchman's II, 5.X.1997] (photo: C. Majka). B: *Quedius s. spelaeus*, live adult [Cheverie Cave/mine, 21.VII.2007] (photo: author).

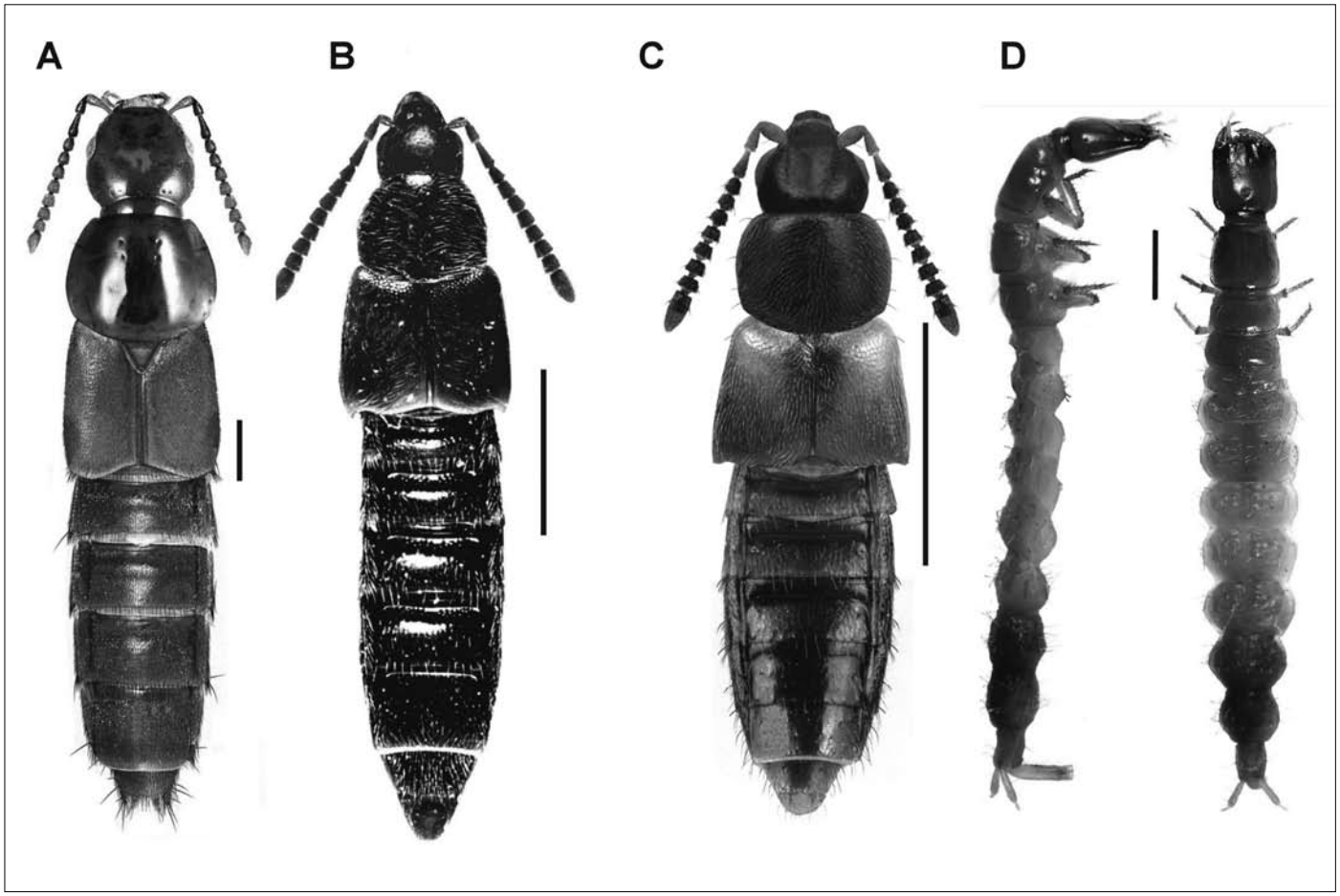

Fig. 3. Illustrations of Staphylinidae (photos: G. Pelletier) (3B: after Majka et al., 2006). A: *Quedius s. spelaeus*, adult. B: *Gennadota canadensis*, adult. C: *Atheta annexa*, adult. D: *Q. s. spelaeus*, late-instar larva [All scale lines = 1 mm].

Atlantic refugia (Moseley et al., 2006).

Cave ecology: *Quedius s. spelaeus* is a subterranean species that, with the exception of examples from animal burrows in western North America, has never been collected outside caves (Smetana, 1971). The Nova Scotia population may be restricted to subterranean habitats. Adults and larvae are top predators in cave invertebrate communities (Moseley et al., 2006). It is by far the most frequently collected beetle in Nova Scotia caves, and probably present in all or almost all such underground sites throughout the province. It is found both in the threshold near entrances and in the dark zone, usually associated with porcupine dung but also with other organic substrates (Fig. 4). Most adults have been collected as single individuals from under stones, but they are mobile and have also been observed running across a cave floor in the open and have been taken in unbaited pitfall traps. Male-female pairs are sometimes found under stones, and have been observed mating in culture.

Adults held in culture become agitated even in subdued light and are observed to attempt where possible to burrow into porcupine dung or other unconsolidated substrate. However, when offered stones placed on the surface they often preferentially locate under these, even in the absence of ambient light, rather than burrowing. This is in line with field observations.

Larvae are found within deposits of dung or other suitable organic materials such as worm casts, although the capture of one late-instar larva under recently set pork liver bait implies that they do on occasion move around. Late instar larvae (length 7.0-14.4 mm. Mean 10.6 mm) are frequently seen and have been collected in June, July and October but smaller larvae have never been found despite collecting over many years including Tullgren extractions of bulk dung samples.

A late-instar *Q. s. spelaeus* larva collected from a cave threshold proved to be parasitized by a proctotrupid wasp (*Exallonyx* sp?). Although it remained undersized (length = 8 mm), the reared larva behaved in the same way as healthy larvae (Moseley et. al., 2006) excavating a cavity in dung adjacent to the wall of the culture jar and pupating therein before emergence of the wasp.

Fig. 4. Broken rock embedded in deposits of partly-decomposed porcupine dung in Frenchman's Cave, Hants County, Nova Scotia. This is typical habitat for Q. s. spelaeus (photo: author).

Staphylinidae: Aleocharinae

Gennadota canadensis Casey, 1906 [Fig. 3B]

NS cave records: Woodville Ice Cave, winter 1997-1998,d.th. in molasses-baited pitfall (1 adult, det. J. Klimaszewski; 1 presumptive larva associated with adult) (Majka et al., 2006).

Distribution and occurrence: This is a rarely-collected Nearctic species known only from Pennsylvania, Quebec, and Nova Scotia. Half of the known specimens have been collected in caves, the balance in various epigean decomposition situations (Majka et al., 2006)

Cave ecology: Although the few existing collection records do indicate that this beetle has some propensity for entering caves it is not known if it can establish permanent breeding populations underground.

Atheta annexa Casey, 1910 [Fig. 3C]

NS cave records: Woodville Ice Cave, 3.VIII.2007, d.th. in sample of leaf litter and soil (1 adult, det. J. Klimaszewski); 9.IX.2007, d.th. in unbaited pitfall (1 adult, det. M. Moseley).

Geographical distribution and occurrence: This Nearctic aleocharine is distributed from Iowa, Illinois, and Indiana, south to Florida and Alabama, east to Virginia, and west to Missouri (Klimaszewski & Peck, 1986) and in Canada in Nova Scotia, New Brunswick, and Ontario (Majka & Klimaszewski, 2008). Adults have been collected from organic debris, fungi near cave entrances, raccoon dung, *Neotoma* nests (Klimaszewski & Peck, 1986), compost heaps, forest litter, and decaying gill fungi (Majka & Klimaszewski, 2008).

Cave ecology: *Atheta annexa* is one of the most frequent and regular aleocharines in caves in the USA (Peck & Thayer, 2003). This suggests that it may be able to establish breeding populations underground, though this has not been proven: Klimaszewski & Peck (1986) imply that it is usually found near cave entrances.

Scarabaeidae

Agolinus leopardus (Horn, 1870)

NS cave records: Frenchman's Cave, X.1964, D. Calder, d.th. on porcupine dung (1 adult), (Calder & Bleakney, 1967; D. Calder, *pers. comm.*); IX-X.1964, D. Calder, th.-d.th. in porcupine dung (six larvae probably this species by virtue of adult occurrence).

Geographical distribution and occurrence: *Agolinus leopardus* is a Nearctic species, widespread in Canada and the USA, usually found in deer dung.

Cave ecology: Guanophile. Not usually considered a cave species.

Dermestidae

Dermestes lardarius Linnaeus, 1758

NS cave records: Frenchman's II, 5.X.1997,d.th. on

wall (1 adult).

Geographical distribution and occurrence: This is a widespread cosmopolitan species, commonly associated with stored food products in anthropogenic situations. The earliest records in North America are from 1670 and in Nova Scotia from 1827 (Majka, 2007).

Cave ecology: Accidental.

Latrididae

Corticaria serrata (Paykull, 1798)

NS cave records: Minasville Ice Cave, 23.IX.1995, d.th. in dry 'well decomposed' porcupine dung, pH 7.2 (1♀, det. C. G. Majka).

Geographical distribution and occurrence: An adventive European beetle, which is now widespread in Nova Scotia (Majka et al., in press). It is frequently associated with stored products and is found in mouldy plant debris (Majka et al. in press).

Cave ecology: A guanophile. Not known to regularly inhabit caves in Europe (Rücker, 2005).

Curculionidae: Entiminae

Otiorhynchus ligneus (Olivier, 1807)

NS cave records: Frenchman's II, 18.X.1997, d.th. in molasses trap set in area of clean damp sand, gravel and pebbles (1 adult, det. C. G. Majka).

Geographical distribution and occurrence: This adventive European root weevil was first recorded in North America in 1917 in New Brunswick (Brown, 1940) and is now found throughout Atlantic Canada and in Maine (Majka et al., 2007).

Cave ecology: This phytophagus weevil is not normally associated with caves, and probably only occurs in such habitats as a seasonal transient.

Barypeithes pellucidus (Boheman, 1834)

NS cave records: Frenchman's Cave, 28.VII.2007, th. on moss (1 adult, det. C. G. Majka): Cheverie Cave, 30.VII.2007, d.th. on rock surface (1 adult, det. C. G. Majka).

Geographical distribution and occurrence: First recorded from the northeastern USA early in the 20th century (Blatchley & Leng, 1916), this Palaearctic weevil is now widespread throughout much of North America including Nova Scotia (Majka et al., 2007). It was common 2.VII.1998 in litter and damp moss on the surface outside Frenchman's Cave.

Cave ecology: This phytophagus weevil is not normally associated with caves, and is probably a seasonal transient.

Sciaphus asperatus (Bonsdoff, 1785)

This weevil, recorded by Moseley (2007*a*) from a cave in Nova Scotia, was reported in error. The record refers to *O. ligneus.*

DISCUSSION

Overview

Beetles are infrequently collected in caves and mines in Nova Scotia. With one exception, all recorded species are uncommon to very rare in underground collections and it is also noticeable that few of the records are from dark zone situations. The prominent exception is the native Nearctic rove-beetle *Q. s. spelaeus*. Half of the beetles collected in the period 1969-2007 were this species. Although based on purely qualitative collecting, there is little doubt that this reflects a genuine scarcity of these insects at such sites: most beetles are relatively conspicuous and easily-collected in caves, and thus collecting bias ought to lead to their over-representation rather than under-representation.

The cave-associated coleopteran fauna of Nova Scotia is also impoverished taxonomically. The most speciose family Staphylinidae is represented by four of a total fifteen taxa. Three dytiscids and two curculionids are also represented with the balance being from six miscellaneous families. There are no records of carabids. Five of the terrestrial beetles are adventive Palaearctic species. All the staphylinids are native, whereas only three of the remaining seven terrestrial beetles (*A. leopardus, A. castanea,* and *C. gratiosus*) are Nearctic species. Thus, if only native North American beetles are considered, the preponderance of staphylinid species (4/7 terrestrial beetles) is striking.

There are no anopthalmic troglomorphs although *Q. s. spelaeus* is primarily subterranean and the Nova Scotia population probably exclusively so. A small suite of guanophiles are associated with accumulations of porcupine dung that constitute a major energy source in Nova Scotia caves (Moseley, 2007*a*): *A. castanea*, *Q. s. spelaeus, A. leopardus* and *C. serrata.* Two of the rove-beetles, *G. canadensis* and *A. annexa*, together with *C. gratiosus*, constitute a small group of cave-associated beetles commonly found in decompositional situations. An omaliine, *B. nitidus*, is a Nova Scotia representative of a fairly large suite of cave-associated staphylinids that, on the surface, are usually found in moist habitats near water (Assing, 2007). Two adventive weevils, *O. ligneus* and *B. pellucidus,* collected in shallow cave passages, are probably seasonal transients while the remaining species, *D. lardarius*, recorded from one cave, was probably an accidental (stray).

Aquatic beetles are rarely collected. Of the four recorded taxa only *A. larsoni* is likely to be habitual in caves in this region: records of two other predaceous diving beetles (*A.* sp. prob. *semivittatus* and *Dytiscus* sp.) and *C. digesta* , a scavenger, are considered to represent accidentals (strays).

Predaceous terrestrial beetles

The distribution pattern of predaceous terrestrial beetles in Nova Scotia cave communities is unusual and difficult to explain. It is characterized by very low species diversity (4 species) and is restricted to a single family, the Staphylinidae. There are no trechines or other carabids. Within the Staphylinidae there is only one relatively frequently collected species (*Q. s. spelaeus*) with other cavernicolous rove

beetles that are known to be present in the province being uncommon, rare, or absent in underground collections.

The absence of species of Carabidae is puzzling. Throughout much of the world this family occupies the niche of dominant predatory cave beetles (Peck & Thayer, 2003) and is also represented in most cave guano communities (Gnaspini & Trajano, 2000). Together with the Leiodidae, the Carabidae (especially Trechinae) constitutes more than 90% of known 'troglobitic' Coleoptera (Gibert & Deharveng, 2002; Moldova & Rajka, 2007).

Although the very large family Staphylinidae with more than fifty thousand described species is only represented in cave communities worldwide by a handful of 'troglobites', and relatively few other cavernicolous species (Gibert & Deharveng, 2002; Peck & Thayer, 2003; Hlavac et al., 2006), this does not reflect the ecological significance of rove-beetles in subterranean habitats. Those few species that have established populations in caves are commonly present and frequently-collected, especially in North America (Peck & Thayer, 2003).

Peck & Thayer (2003) listed 67 species of staphylinid beetles (excluding Aleocharinae and Pselaphinae) from caves in the continental United States, of which 9 are 'frequently occurring'. Klimaszewski & Peck (1986) recorded 20 species of aleocharines from caves in eastern North America, including 6 'frequently occurring' species, whilst Chandler (1997) recorded 43 species of pselaphines from caves on the continent.

Most of those species found in caves are non-troglomorphic forms that have well-developed eyes and are capable of flight. The majority are thought to be species that are either associated with rotting organic matter, or alternatively with moist habitats near water (Assing, 2007) and those recorded from caves in Nova Scotia fit this pattern.

The observed low diversity of predaceous cave-associated Coleoptera in Nova Scotia reflects in part the well-documented relative impoverishment of the provincial invertebrate fauna in comparison with that of neighbouring regions of northeastern North America. However there are a number of species that are widespread in surface habitats in Nova Scotia yet have never been found in caves there despite being often present in subterranean habitats elsewhere. The absence of carabids (including species of genera such as *Agonum*, *Bembidion* and *Trechus* that commonly have cave-associated representatives in other geographical regions) has already been mentioned. Three staphylinids, *Lesteva pallipes* LeConte, *Quedius mesomelinus* (Marsham) and *Quedius curtipennis* Bernhauer, are other examples of Nova Scotia species that occur in caves elsewhere, but have not been found in subterranean habitats in Nova Scotia.

Quedius mesomelinus is a compelling example. This Palaearctic species was an early anthropogenic introduction to North America being found in archaeological deposits dating from the 17th century (Prévost & Bain, 2006) and it is now widespread in Nova Scotia and elsewhere in eastern North America (Majka & Smetana, 2007). It is one of the species frequently collected in caves in the eastern USA (Peck & Thayer, 2003), and there are cave records from the northern part of its range in Ontario (Peck, 1988) and New Brunswick (Moseley, 2007*a*). In Europe it is common and widespread in caves (Smetana, 1971). However, this conspicuous beetle has never been collected underground in Nova Scotia and it is probably either extremely rare or entirely absent from caves there.

The Nearctic species *Lesteva pallipes* is widespread in eastern Canada, including Nova Scotia, and in the eastern and central USA where it is another of the staphylinids 'frequently occurring' in caves (Peck & Thayer, 2003).

Quedius curtipennis is another introduced European species. The earliest North American records are from 1934 in Seattle (Smetana, 1971) and the species is established in Nova Scotia (Majka & Smetana, 2007). It is occasional in caves in Europe but apparently not in Nova Scotia, although a single pupa found in moss outside the entrance of Woodville Ice Cave (5.VIII.2007) shows that it occurs in habitats in the immediate vicinity of caves.

Although it is possible that *Q. curtipennis, L. pallipes* or other infrequently-collected beetles will turn up in Nova Scotia caves, they are certainly scarce and the preponderance of *Q. s. spelaeus* in underground collections, the rarity (especially in cave dark zones) of other recorded staphylinids, and the general absence of other species including, tellingly, the common and vigorous *Q. mesomelinus* and all carabids, all point to the former species as the almost exclusive occupant of the niche of predatory beetle in provincial caves. This can be seen as a rather extreme instance of the pattern elsewhere in North America where although introduced troglophilic rove-beetles including *Q. mesomelinus* have occupied and become established in niche spaces in American caves, they have not displaced native species (Peck & Thayer, 2003).

The failure of most coleopteran predators to become established contrasts with the pattern observed in other terrestrial invertebrates many of which appear to have met few ecological or competitive barriers in colonizing caves in Nova Scotia. It is speculated that these species occupied empty niches that existed because subterranean ecosystems in the region are at a very early stage of repopulation following the Pleistocene (Moseley, 2007*a*). It appears that, in contrast, the native *Q. s. spelaeus* has been able to competitively exclude other native and invasive predatory beetles from this habitat.

The ecological success of *Quedius s. spelaeus* is probably due to relatively advanced adaptation to this environment. Several authors have made the plausible argument that highly-adapted cave species may be able to defend their subterranean niche from subsequent colonists (White et al., 2009).

Quedius spelaeus is a somewhat distinct species that differs from other members of the large sub-genus *Microsaurus* by the explanate pronotum, impunctate scutellum and a strongly asymmetrical male copulatory

organ (Smetana, 1971). The relationships between these species-specific morphological features and its mode of life are unclear. However the pale colouration observed in most populations is due to absence of pigmentation other than the underlying amber colour of chitin: unlike many other organisms cave-beetles are never white and the colour of *Q. spelaeus* matches that of highly adapted troglomorphic Coleoptera. Behaviours such as the excavation of occupation cells by larvae (Moseley et al., 2006) may be associated with living in darkness: Turquin (1983) found that in the absence of other shelter cave-dwelling *Quedius mesomelinus* builds burrows in clay substrate.

Leiodidae: Cholevinae

The new cave records of *C. gratiosus* are of interest. Leiodidae and especially the subfamily Cholevinae are one of the two most speciose groups of 'troglobitic' beetles (Gibert & Deharveng, 2002; Moldova & Rajka, 2007). Of the more than 80 species of Cholevinae found in North America (Peck & Cook, 2007) several are variously associated with caves including a number that are anopthalmic troglomorphs (e.g. *Ptomaphagus* spp. in the southeastern USA) (Peck,1973, 1984). Although it has no obvious morphological adaptations for cave life *C. gratiosus* is frequently though not exclusively found in caves (usually near the entrances) in the southeastern USA and has also been found in caves in Ontario in eastern Canada (Peck, 1988) and now in Nova Scotia. Surface collections in western North America and the northeastern USA and Canada are from various decomposition situations in forested environments, whilst in caves they have been found on dead mice and bats (Peck & Cook, 2007).

Another leiodid, *Prionochaeta opaca* (Say), is a further example of a beetle that is unexpectedly absent from Nova Scotia cave collections. Its distribution and ecology are similar to those of *C. gratiosus*. It is a widely distributed North American species primarily found associated with carrion in forested environments but also found on bat guano in caves in the southeastern United States (Peck 1977). Peck (1977) and Peck & Cook (2002) reported records from 52 caves in 12 states in the southeastern United States west to Arkansas, Oklahoma, Missouri, and Iowa, and it is also present in caves in the northern part of its range in Ontario (Peck, 1988). It has been recorded from epigean habitats in New Brunswick, Prince Edward Island, and Nova Scotia (Majka & Langor, 2008) but not from caves.

Guanophiles

Four beetles *A. castanea*, *Q. s. spelaeus, A. leopardus,* and *C. serrata* constitute a small suite of species associated with the extensive deposits of porcupine dung that constitute a major food source in Nova Scotia caves (Moseley, 2007*a*).

The historical view that animals inhabiting guano in caves are 'false cave-dwellers' (Ruffo, 1957; Vandel, 1964) has been challenged by some recent authors who have advanced arguments that all animals regularly found in such habitats underground should be considered *bona fide* cavernicoles (Gnaspini, 1992; Moseley, 2007*a*). In this context it can be argued that *Q. s. spelaeus* is an instructive example that provides addition evidence in support of this view. This beetle is almost exclusively subterranean, yet it is primarily a predator exploiting and restricted to animal dung and other high-energy environments. The guano habitat in caves is presumably a route by which some organisms first colonize subterranean environments

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Woodville Ice Cave

Finally, mention needs to be made of the diversity of beetles found in Woodville Ice Cave. Four species have been recorded, all cavernicolous to a greater or lesser extent: three staphylinids (*Q. s. spelaeus, A. annexa,* and *G. canadensis*) and *C. gratiosus*. Although the site is a small shallow cave with no significant accessible dark zone (Figs. 5, 6), it contains a uniquely diverse and hence notable cave-associated coleopteran fauna in

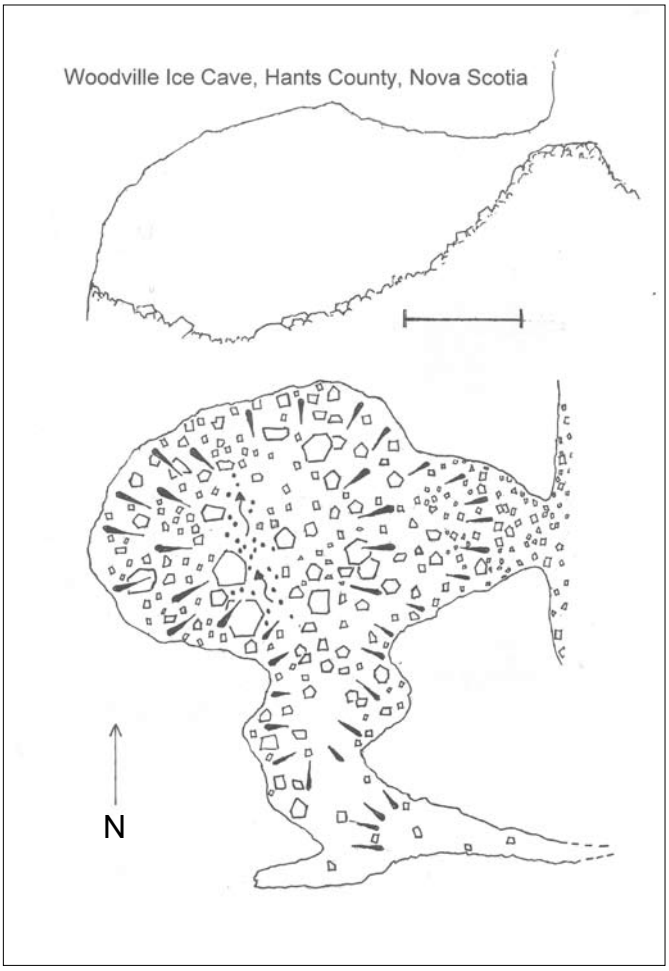

Fig. 5. Woodville Ice Cave, map and projected elevation. Scale line = 5 m

Fig. 6: Entrance of Woodville Ice Cave, Hants County, Nova Scotia (photo: author).

Nova Scotia. The accessible cave is comprised primarily of a deep threshold environment with only a small area of dark zone in a side passage. Ice regularly persists in the cave chamber until early August. Air temperature just above the floor at this time can be 2.5°C while the temperature within the large, deep talus pile that almost seals the entrance is <0.5°C (Moseley, 2007*b*). All species were taken in pitfall traps sited near leaf litter on the talus inside the cave entrance: a deep threshold area in cool air below the thermocline which forms during the summer months. The beetles and other cavernicolous invertebrates found here are believed to represent a sample of the subterranean fauna inhabiting deep cavities within the talus. This is an environment comparable with European Alpine *Kaltlöcher* and similar sites where cavernicolous and psychro-hydrophilous organisms are found associated with stable, cold habitats in cavities in scree or solid rock (e.g. Core, 1968; Růžička et al., 1995; Punz et al., 2005).

Conservation implications

None of the cave-associated beetles recorded in Nova Scotia are believed to be under threat. The only cave-restricted species, *Q. s. spelaeus*, occurs at all or almost all sites and the remaining species, though rarely collected underground, are widespread in epigean habitats. However, the preservation and protection of caves and abandoned mines that support representative populations of these beetles and characteristic species and communities of other organisms is important. Woodville Ice Cave is a provincially significant site, and is especially deserving of protection.

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