THE CAVE-INHABITING BEETLES OF CUBA (INSECTA: COLEOPTERA): DIVERSITY, DISTRIBUTION AND ECOLOGY

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The known cave-inhabiting beetle fauna of Cuba is summarized. Fifty-three species have been found in 70 low elevation caves in 11 provinces. Distribution of species by family is: Carabidae, 10; Dytiscidae, 4; Gyrinidae, 2; Hydrophilidae, 2; Histeridae, 5; Leiodidae, 2; Ptiliidae, 3; Staphylinidae, 1; Scarabaeidae, 4; Elateridae, 2; Lampyridae, 1; Nitidulidae, 1; Cerylonidae, 1; Tenebrionidae, 12; and Curculionidae, 3. Twenty-four of the species are judged to be accidental cave inhabitants. The remaining 29 species can be placed in the following ecological-evolutionary categories: trogloxenes, 3 species; first-level troglobilhes, 21 species; second-level troglobilhes (=unmodified neotroglobites), 5 species. No true troglobilhes are known (i.e., none of the species is morphologically specialized for cave life). About 59% of the non-accidental inhabitants are endemic to Cuba. The taxonomic composition is similar to that in caves in other West Indian Islands, and impoverished when compared to Neotropical continental caves. The abundance of food (bat guano) seems a prime factor preventing selection for cave-specialization in lowland West Indian and continental Neotropical cave beetles.

Cave-inhabiting insect faunas of the temperate parts of Europe and North America are becoming rather well known. In contrast, the cave insect faunas of many parts of the subtropical and tropical regions of the Americas are still very poorly known (Decu & Juberthie 1994). About 70% of the surface area of Cuba, the largest West Indian island, is underlain by limestone and other soluble calcareous rocks. Under a tropical climate, these limestones have produced vast areas of karst landscapes, and subterranean solution has produced many caves, estimated to be about 10,000 in Cuba (Nuñez Jimenez 1984). Many organisms have occupied these caves and many have come to be evolutionarily highly modified for cave-life. At present, 45 species of aquatic invertebrates and 30 species of terrestrial invertebrates are known to have become troglobilhes (morphologically highly specialized for life in cave habitats) in Cuba (Decu & Juberthie 1994; Armas & Alayon 1984).

Silva (1974) first summarized the entire cave fauna of Cuba and only nine species of beetles were reported from nine cave sites. Simultaneously, a massive program of cave biology field work was undertaken (1969-1973) by a series of joint Cuban-Romanian expeditions. Much has now been published from these expeditions. Silva (1988) contains a more up-to-date list of 388 caves that had been biologically prospected and 807 taxa identified to species level from these caves. Data on fauna from another 68 caves are in Pérez and García-Debrás 1997.

The purpose of this paper is to summarize the available (but often obscure) literature on Cuban cave-inhabiting beetles, to combine it with our new field data, and to provide the first ecological-evolutionary analysis of the Cuban cave beetle fauna.

METHODS AND MATERIALS

We here present a unified summary of both previously published and new information on Cuban cave-inhabiting beetles. In the taxonomic list of species we give (1) our hypothesis of its ecological-evolutionary status in caves, (2) its trophic status in cave food chains, (3) available data on its geographic distribution, (4) condition of its metathoracic flight wings, (5) the cave locations the species is now known from, followed by a map reference code number for the cave, (6) references to all published cave records, and (7) other relevant information. In (3) above we use the word endemic to mean that the species is restricted to Cuba, and in (4) we indicate the presence or absence of fully formed metathoracic flight wings as an available means of dispersal. The cave code numbers are cross referenced to a list of cave localities in an appendix, and on the map in Figure 1. Additional data on the caves is in Nuñez et al. (1973), and Silva (1988). Our new records and additional records that confirm the continued presence of a species in a cave as a perpetuating population are both documented by year and collector. Data on distribution within and outside of Cuba are from a checklist of Cuban beetles (S.B. Peck, unpublished); and beetles of Florida (Peck & Thomas 1998).
New material is deposited in the collections of the institutions of the authors, and some in the collections of the Institute of Ecology and Systematics, Academy of Sciences, Havana, Cuba. The base for much of our field work in eastern Cuba was the former cave research laboratory of the Academy of Sciences at Atabex Cave, Siboney, 15 km southeast of Santiago de Cuba.

**ECOLOGICAL ASSOCIATION WITH CAVES**

Various schemes have been proposed as the basis of an ecological-evolutionary classification of cave faunas (Vandel 1965). We here use a slightly modified version of that of Hamilton-Smith (1971) which has the following categories relevant to populations of beetles in caves.

1. **Accidental.** Species that have no regular association with caves, and which do not complete their life cycle in caves.
2. **Trogloxene.** Species that regularly associate with caves, but for only part of their life cycles.
3. **First-level troglophile.** Species that complete their entire life cycle in caves, but are also known to occur in non-cave habitats.
4. **Second-level troglophile.** Species that are known only from caves, but show no morphological specialization for cave life. These have also been considered as “neotroglobites” or recent troglobites. Because cave faunas have often received more sampling attention than nearby forest habitats, it can be expected that some species now known only from caves as second-level troglophiles will eventually be found outside of caves and are actually first-level troglophiles.
5. **Troglobite.** Species that occur only in cave habitats and have ecological-morphological specializations for cave life (e.g., loss of eyes, wings, pigment, etc.). It is becoming common practice to use the terms “stygobite” or “stygobiont” for such organisms that live in aquatic subterranean habitats.

**RESULTS**

A total of over 400 Cuban caves have now been searched for arthropods by the 1969-1973 Cuban-Romanian expeditions, by later Cuban expeditions (Silva 1988; Peréz & García-Debras 1997) and by us. Beetles that have been identified to species level were found in 70 of these caves. The annotated taxonomic list follows.

**SYSTEMATIC LIST**

**Family Carabidae**

*Dyschirius larocheli* Bousquet, 1988; reported by Silva (1988: 114) as *D. erythrocerus* LeConte.


*Macranthus* (= *Masoreus*) *brevicillus* (Chevrolat, 1863)

First-level troglophile. Predator in moist guano. Infrequent in moist lowland forest habitats in Cuba; also known from caves in Puerto Rico (Peck 1981). Winged. Cave records: Holquin Province; Cueva de los Santos 8. Reference: Mateu 1974: 28. The species is considered by Decu (1983) to be the most frequent and most abundant Cuban cave beetle in moist and guano rich areas.

*Paratachys (= Tachys) abruptus* (Darlington, 1934)


*Paratachys (= Tachys) cubax* (Darlington, 1934)

Repeated searching in Atabex Cave has not found the species again.

*Paratachys (= Tachys) striax* (Darlington, 1934)
Accidental. Predator. Endemic species. Widely distributed in open lowland habitats. Winged. Cave records: Holquín Province; Cueva Bariay 1. This cave had a large population of these beetles in a room with an elevated temperature (28°C), but because they have not been found again in other caves, we class them as accidentals. Reference: Mateu 1977: 378.

*Paratachys (= Tachys) vorax* (LeConte, 1852)

*Pentagonica flavipes* (LeConte, 1853)

*Platynus (= Colpodes) carabai* (Darlington, 1937)

*Selenophorus chalybaeus* (Dejean, 1829)

*Selenophorus pyritosus* (Dejean, 1829)

Family Dytiscidae

*Copelatus posticus* (Fabricius, 1801)

*Derovatellus lentus lentus* (Wehncke, 1876)
Accidental. Predator. The species is also distributed throughout the West Indies, to Trinidad and South America, and in Florida. It is infrequently known from streams in Cuba. Winged. Cave records: Camagüey Province; Cueva del Agua (de los Lagos) 1. References: Spangler 1981a: 145; Silva 1988: 114.

*Laccophilus proximus* Say, 1823

*Laccophilus venustus* Chevrolat, 1863

Family Hydrophilidae

*Oosternum costatum* (Sharp, 1882)
First-level troglophil. Scavenger in moist guano. The species is widespread from the United States through the West Indies and Central America to South America. Winged. Cave records: Provincia de Santiago de Cuba; Cueva de los Majaes 9 (many in moist guano, collected by Peck in 1995). This is not a frequent cave inhabitant.

*Tropisternus mergus* (Say, 1835)

Family Histeridae

*Acritus analis* (Linneus, 1767)

*Dineutus americanus* (Linneus, 1767)

*Family Gyrinidae*

*Oosternum costatum* (Sharp, 1882)
First-level troglophil. Scavenger in moist guano. The species is widespread from the United States through the West Indies and Central America to South America. Winged. Cave records: Provincia de Santiago de Cuba; Cueva de los Majaes 9 (many in moist guano, collected by Peck in 1995). This is not a frequent cave inhabitant.

*Selenophorus pyritosus* (Dejean, 1829)

Family Dytiscidae

*Copelatus posticus* (Fabricius, 1801)
Epieurus antillarum (Marseul, 1854)

Epieurus pulicarius (Erichson, 1834)
Accidental. Predator. The species is otherwise known only from Mexico. The only Cuban records are from one cave. Winged. Cave records: Santiago de Cuba Province; Cueva Atabex 1. References: Decu and Therond 1977: 404; Silva 1988: 115. The species has not been found in this cave again in spite of repeated searching.

Eusiptilotus sterequilinus (LeConte, 1860)

Family Leiodidae

Aglyptinus sp.
First-level troglophile. Scavenger in guano of fruit bats. Endemic species (first record of the genus from Cuba). The genus is widespread in the Neotropics, and species are often associated with guano in caves (Peck 1977). Winged. Cave records: Pinar del Río Province; Cueva la Barca, in fresh guano of Artibeus fruit bats. We have since found it frequently in forests near Santiago de Cuba.

Proptomaphagus apodemus (Szymczakowski, 1969)
First-level troglophile. Scavenger in guano of fruit bats. Endemic species. Widely distributed across Cuba, but previously reported only from caves. Winged. Cave records: Guantánamo Province; Cueva de Majana 2 (collected by Ruiz & Garcés in 1985), Cueva de La Patana 3 (collected by Ruiz & Garcés in 1985). Santiago de Cuba Province; Cueva de la Cantera 2 (collected by Ruiz & Garcés in 1985), Cueva de los Majaes 9 (collected by Ruiz & Garcés in 1984), Cueva Atabex (collected by Peck in 1995). Granma Province; Cueva del Fustete 2, Cueva del Hoyito 5. Camagüey Province; Cueva del Agua (de los Lagos) 1, Cueva del Indio 2, Cueva de la Lechuza 3. Sancti Spiritus Province; Cueva de las Columnas 2, Cueva Grande de Caguanes 5, Cueva Humbolt 6, Cueva del Túnel 7. Ciudad de La Habana Province; Cueva del la Virgen 1, Pinar del Río Province; Cueva del Abono 1 (collected by Ruiz & Garcés in 1985), Cueva de Pio Domingo 9, Cueva de la Vela 11 (collected by Ruiz & Garcés in 1985). Isla de Juventud Province, Cueva del Abono 2. References: Decu 1973: 367; Silva 1988: 114.

Notes. References to Ptomaphagus sp. in Cueva de Bellamar 1 (Matanzas Province) and Cueva del Cura 4 (Havana Province) (Bolivar Pieltain 1944: 302, 303; Silva 1974: 28; 1988: 114) are for this species because Proptomaphagus did not occur in Cuba. Proptomaphagus also occurs in Mexico as small-eyed flightless soil species and as winged species in caves in Hispaniola and Puerto Rico (Peck 1983). Because the Hispaniola and Puerto Rico cave-dwelling species also occur in forests, we predicted that P. apodemus would also be found in forests in Cuba. We actually found it there by using baited pitfall traps and flight intercept traps in the Santiago Botanical Garden (Jardín Botánico T. Roig) in December 1995. The species was previously considered to be a second-level troglophile (a neotroglobite), but our discovery of it in several non-cave sites reduces it to the status of a first-level troglophile. Proptomaphagus darlingtoni (Jeannel) is another species in the genus known from lowland forests at Soledad; near Cienfuegos, Cuba (Peck 1970).

Family Ptiliidae

Ptiliidae genus 1 sp.1.

Ptiliidae genus 1 sp.2.

Ptiliidae genus 2 sp.1.

Note: These are all undescribed species (H. Dybas, pers. comm.).

Family Staphylinidae

Aleocharinae sp.
First-level troglophile. Predator. Cave records: Santiago de Cuba Province; Cueva del Humo 7 (collected by Ruiz en 1986), Cueva de los Majaes 9 (collected by Peck in guano in 1995). These beetles are notoriously difficult to identify. They must exist in other Cuban caves.

Family Scarabaeidae

Ataenius gracilis (Melsheimer, 1845)
First-level troglophile. Scavenger. Widely distributed from southeastern USA and West Indies to Peru. Winged. In moist guano. Cave records: Provincia de Santiago de Cuba; Cueva de los Majaes 9 (several collected by Peck in guano in 1995). Not previously known to maintain populations in caves.

Canthochilum histeroides (Harold, 1868)
Accidental. Scavenger. An endemic in lowland forest in northern and western Cuba. Winged. Cave records: Matanzas Province; Gran Caverna de Fuentes. Reference:
Pyrophorus noctilucus Linnaeus, 1758


Photinus nefarius J.E. Olivier, 1912

Family Lampyridae

Carpophilus

Family Nitidulidae


Family Cerylonidae

Euxestus erithaeus Chevrolat, 1863

First-level trogophile. Scavenger. Widespread but uncommon in litter in Florida and Greater Antilles. Winged. Cave records: Santiago de Cuba Province; Cueva Atabex 1 (collected in bat guano by Peck in 1995), Cueva de los Majaes 9 (in bat guano by Peck in 1995). These are the first Cuban cave records. The species is also known from bat guano in a cave in Jamaica (Peck 1992).

Family Tenebrionidae

Alphitobius diaperinus (Panzer, 1832)


Alphitobius laevigatus (Fabricius, 1781)


Blapstinus cubanus Marcuzzi, 1962


Blapstinus cf. fortis LeConte, 1878


Orphidania torrei Ardoin, 1977


Trimyctantron cavernicolous Garrido and Gutiérrez, 1997

First-level trogophile. Scavenger. Endemic species. Wingless. Cave records: Sancti Spiritus Province; Cueva
el Pirata, Cayo Caguanes (type locality); Cueva de Colon 1; Cueva de los Chivos; also from one epigean locality (Punta de Judas, Yaguajay). Reference: Garrido and Gutiérrez 1997: 34.

**Trimytantron cubanum** Ardoin, 1977

**Trimytantron decui** Ardoin, 1977

**Trimytantron negrei** Ardoin, 1977

**Trimytantron poeyi** Ardoin, 1977

**Trimytantron vinai** Ardoin, 1977

**Zophobas rugipes** Kirsch, 1866

**Family Curculionidae**

**Anchonus suillus** (Fabricius, 1792)
niculous species have been introduced to Cuba through human commerce, so the faunal mix of cave beetles is now richer than in Pre-Columbian times.

**Cave Adaptations**

Many of the adaptations that species have for life in caves are physiological, such as an ability to live in perpetual darkness, and in moist environments. These leave no morphological evidence on the body of the beetle. What can be taken as morphological evidence for cave restriction is reduction or loss of pigmentation, eyes, and flight wings; and elongation of antennae, legs and sensory hairs. None of the Cuban cave beetle species shows cave-related loss or gain of either pigmentation, eyes, appendages, or flight wings (Table 1). There are seven species of Tenebrionidae which have lost the metathoracic flight wings, but these are in phylogenetically wingless lineages associated with semi-arid environments. The wings were probably lost in ancestral species before cave colonization occurred. Thus, no Cuban cave beetles show evidence of morphological adaptation to cave habitats.

**Habitat Association**

Cuban cave environments. The physical conditions of caves, which seem to especially affect terrestrial tropical cave life, are: 1. elevation; 2. temperature; 3. humidity; 4. food availability.

1. **Elevation.** Cuba is a relatively low island. More than 80% of its surface is below 300 m elevation. Most of the caves that have been studied are at elevations between sea level and 100 m. Only a few are as high as 150 m elevation. This may have an impact on the suitability of the caves for the development of troglobitic species. It is a general observation that most terrestrial troglobites in tropical caves occur at higher elevations, from 1000 to 2000 m.
(Peck & Finston, 1993; Vandel, 1965). More data are needed on this topic.

2. Temperature. The air temperature in Cuban caves generally ranges from 21°-28°C with 22°-26°C being frequently encountered. Some upper chambers with impediments to air flow (heat traps) may reach temperatures as high as 37°C. These chambers are often occupied by the pollen feeding bat _Phyllonycteris poeyi_ Gundlach, and the elevated temperature is caused by metabolic heat from the bats and their decomposing guano. If humidity is high and food abundant, our observations are that beetles are present without regard to high or low cave temperatures.

3. Humidity. The relative humidity (RH) of Cuban cave air ranges from “dry” caves with about 70% RH, to the usual condition of near saturation from 95-98% RH. With high humidities, a variety of beetles are usually present. In dry caves, only some species of tenebrionids (which are normally drought adapted beetles) are present.

4. Food. Perhaps up to 90% of Cuban caves are occupied by bats. These have diverse diets and different species are specialist feeders on insects, fruit, pollen, and nectar. This produces a mix of guano types of varying nutrient content, which occur in scattered patches. In some caves the guano may be present in tremendous amounts. The guano varies in moisture content from dry to wet. Guano of intermediate moisture content has the richest assemblage of scavenger beetle species and the largest population sizes, which may reach tens of thousands of individuals. In the guano in Cuban caves, predator beetles are fewer in individual numbers and number of species (8) than are scavenger species (16). The predators feed on a variety of scavenging arthropods, such as mites, collembola, and fly larvae in the guano.

One of the common themes of specialization to life in temperate caves is adaptations to low levels of unpredictable food resources (Vandel 1965). The overabundance of predictable food resources (especially guano) has been seen as one factor retarding the development of cave-restricted terrestrial species in tropical caves (Vandel 1965). This matches our experiences, but this is not the place to present data on this topic.

### Why are there no troglobitic beetles in Cuba?

Because of the abundance of caves in Cuba, it would be reasonable to expect the presence of cave-evolved species. The absence of troglobitic beetles raises the question about why they are absent. To set the stage we present a summary (Table 2) of the known troglobites of the Greater Antilles. Totals and island characteristics are given in Table 3.

Notice that there are appreciable numbers of aquatic species modified for subterranean life (stygobites) on all four of the Greater Antillean islands. There are also appreciable numbers of terrestrial troglobites, except for Hispaniola which has not had any survey effort for terrestrial cave faunas. Notice also that the bulk of aquatics are crustaceans, and the bulk of

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**Table 2. Comparison of numbers of known species in the cave-evolved invertebrate faunas of the Greater Antilles**  

<table>
<thead>
<tr>
<th></th>
<th>Cuba</th>
<th>Jamaica</th>
<th>Hispaniola</th>
<th>Puerto Rico + Virgin Islands</th>
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<tr>
<td><strong>Aquatic - Marine</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td>Platyhelminthes</td>
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<td>0</td>
<td>0</td>
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<td>Oligochaeta</td>
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<td>0</td>
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<td>0</td>
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<td>Crustacea</td>
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<td></td>
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<tr>
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<td>0</td>
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<td>0</td>
</tr>
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</tr>
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<td>0</td>
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<tr>
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<td>4</td>
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<td>6</td>
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<tr>
<td>Decapoda</td>
<td>7</td>
<td>2</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>Insecta (Coleoptera)</td>
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<td>3</td>
<td>0</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>45</td>
<td>14</td>
<td>39</td>
<td>14</td>
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</table>

| **Terrestrial (troglobites)** |      |         |            |                              |
| Onychophora          | 0    | 1       | 0          | 0                            |
| Arachnida            |      |         |            |                              |
| Pseudoscorpiones     | 2    | 4       | 0          | 0                            |
| Opiliones            | 2    | 2       | 0          | 0                            |
| Schizomida           | 2    | 1       | 0          | 0                            |
| Amphiropygi          | 1    | 0       | 0          | 0                            |
| Aranea               | 2    | 9       | 0          | 1                            |
| Isopoda              | 5    | 1       | 0          | 0                            |
| Diplopoda            | 0    | 1       | 0          | 1                            |
| Chilopoda            | 2    | 0       | 0          | 0                            |
| Insecta              |      |         |            |                              |
| Thysanura            | 3    | 0       | 0          | 1                            |
| Collombola           | 7    | 2       | 0          | 0                            |
| Orthoptera           | 3    | 0       | 0          | 0                            |
| Blattodea            | 1    | 1       | 0          | 1                            |
| Homoptera            | 0    | 2       | 0          | 1                            |
| Coleoptera           | 0    | 2       | 0          | 0                            |
| **Total**            | 30   | 35      | 0          | 5                            |

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**Figure 2.** Linear regression of the total number of known troglomorph (troglobite + stygobite) species against island karst area. The relationship is suggestive but not statistically significant.
terrestrials are arachnids, not insects. Within insects, there are only 5 troglobitic beetles for the whole Caribbean, and only 2 are terrestrial species. Why there are more tropical troglobite arachnids than troglobite insects is an unaddressed question.

There are interesting trends in these figures when explored as species-area relationships, a common analytical approach in comparative biogeography. In summary, for total subterranean faunas the species-area relationship is not significant (Fig. 2). When only aquatics are analyzed, there is a significant species-area relationship for the islands’ karst areas (Fig. 3). It is interesting to note that, for the aquatic species, species number in relation to total island area is an even more significant regression than that for area of karst (not shown). This is reasonable because we know that the groundwater fauna can occupy groundwater spaces in non-limestone terranes as well as those in limestones.

The scarcity or absence of troglobite beetles is not unique to Cuba, but is a generalization for the entire West Indian cave fauna. The three species known from Hispaniola are aquatic elmids (Spangle, 1981b). And since the two eyeless beetle species known from Jamaica are from montane regions, the generalization can be extended to an absence of terrestrial troglobite beetles in lowland West Indian caves. This fits the general picture for tropical lowland terrestrial faunas as a whole, and the scarcity or absence of troglobite beetles in both continental and insular lowland caves. This generalization in the New World is based on an analysis of 241 terrestrial troglobites in Mexico, Guatemala, and Belize, of which 86% were from upland caves, and the bulk of the 14% from lowland caves were arachnids, terrestrial isopods, and collembola; not beetles (Peck & Finston 1993).

The absence of troglobitic beetles is not due to a lack of evolutionary time. The islands are certainly old enough, and many other terrestrial troglobites have evolved in these islands. The resolution of the question must be one of an absence of selective pressure and appropriate environmental conditions. These have been present for other groups such as West Indian arachnids, terrestrial isopods, and some insects, mostly collembola. Again we turn to the most obvious factor. Where troglobites do occur there is a strong selective factor of limited food availability. Terrestrial troglobites occur most frequently in food-poor (bat-poor) montane caves, and in food-rich (bat-rich) lowland caves they usually occur only in the food-poor part of the caves. Other terrestrial groups have responded to these environmental conditions and selective pressures to become cave limited and morphologically evolved for cave life, but West Indian beetles have not.

ACKNOWLEDGEMENTS

Field work of SBP was partly supported by a research grant from the Natural Sciences and Engineering Research Council of Canada. We thank the many members of the Cubano-Romanian cave biology expeditions who were the first to make known the true richness of the cave arthropods of Cuba. SBP is grateful to V. Decu for making available the four volumes of results of the Cubano-Romanian cave biology expeditions, to Lazaro Roque Abeló for the copy of Silva (1988), and to many other Cuban speleologists who shared their cave publications. Field work of AERB was partly supported by a research grant from the RARE Center for Tropical Conservation of Philadelphia. We thank many specialists for help in making identifications, especially R.A. Anderson (Curculionidae) and P. Kovarik (Histeridae).

REFERENCES


APPENDIX

Cuban cave localities from which beetles are known. Province symbol and number of cave as in list of beetle taxa (see Fig. 1). Following the cave name may be the neighboring town or village, and then the municipality in which it is located.

Pinar del Río Province
1. Abono, Cueva del; Gran Caverna de Sto. Tomás. El Moncada.
2. Agua, Cueva del; Península de Guanahacabibes.
3. Barca, Cueva la; Península de Guanahacabibes.
5. Clara, Cueva; Los Portales, San Diego de los Baños.
7. Fango, Cueva del; Gran Caverna de Sto. Tomás. El Moncada.
10. Jaguey, Cueva del; Península de Guanahacabibes.
11. Pío Domingo, Cueva de; Sumidero, Minas de Matahambre.
12. Represas, Cueva de las; Gran Caverna de Sto. Tomás. El Moncada.

La Habana Province
1. Animales, Cueva de los; Las Cañas, Artemisa.
2. Baño, Cueva del; Las Cañas, Artemisa.
3. Cura, Cueva del; Tapaste.
4. Emilio, Cueva de; Las Cañas, Artemisa.
5. Galera, Cueva; Galera, Sta. Cruz del Norte.
6. Mudo, Cueva del; Catalina de Güines.

Ciudad de La Habana Province
1. Cinco Cuevas, Cueva; Boca de Jaruco, Sta. Cruz del Norte.
2. Mariana, Cueva de la; Quivicán.
3. Murciélagos, Cueva de los; Boca de Jarúco, Sta. Cruz del Norte.
4. Tunel, Cueva del; Quivicán.
5. Virgen, Cueva de la; 15 km east of Puerto de La Habana.

Matanzas Province
1. Bellamar, Cueva de; Matanzas.
2. Eloísa, Cueva de; Camarioca, Varadero.
3. Jarrito, Cueva del; al SE de Matanzas.
4. Pluma, Cueva la; Bacunayagua, Matanzas.

Villa Clara Province
1. Bichos, Cueva del los; Zuleta.
2. Gato, Cueva El; Mogote de Sagua.
3. Majá, Cueva El; Caibarien.

Sancti Spiritus Province
1. Colón, Cueva de; Cayo Caguanes, Yaguajay.
2. Columnas (del Veterano), Cueva de las; 10 km west of Trinidad.
3. Guanayara, Cueva; 10 km al W de Trinidad.
4. Guanayara, Caves in the area of; 10 km west of Trinidad.
5. Grande de Caguanes, Cueva; Cayo Caguanes, Yaguajay.
6. Humbolt, Cueva; Cayo Caguanes, Yaguajay.
7. Túnel, Cueva del; Caya Caguanes, Yaguajay.

Camagüey Province
1. Agua (de los Lagos), Cueva del; Sierra de Cubitas.
2. Indio, Cueva del; Sierra de Cubitas.
3. Lechuza, Cueva de la; Sierra de Cubitas.

Holguín Province
1. Bariay, Cueva; Loma El Pilón, Mayarí.
2. Cuatrocientas Rosas, Cueva de las; Banes.
3. Grande de Pilón, Cueva; Mayarí Abajo.
4. Guano, Cueva del; Gibara.
5. Hoyito (de las Cuatrocientas Rozas #2), Cueva del; Banes.
6. Jaguey, Cueva del; Cuesta de Seboruco, Mayarí.
7. Panaderos, Cueva de los; Gibara.
8. Santos, Cueva de los; Gibara.

Granma Province
1. Banega, Cueva; Matías.
2. Fustete, Cueva del; Niquero.

Santiago de Cuba Province
1. Atabex, Cueva; Playa Siboney, Santiago de Cuba.
2. Cantera, Cueva de la; Playa Siboney, Santiago de Cuba.
3. Cativar, Cueva; Guamá.
4. Colorada del Maso, Cueva de la; Guamá.
5. Golondrinas, Cueva de las; Playa Siboney, Santiago de Cuba.
6. Humo, Cueva del; La Uvita, Guamá.
7. Hymn, Cueva del; Los Negros, Baire, Tercer Frente.
8. Jibara, Cueva; Tercer Frente.
9. Majaes, Cueva de los; Siboney, Santiago de Cuba.
10. Murciélagos, Cueva de los, La Uvita, Guamá.
11. Terrarium, Cueva del; Playa Siboney, Santiago de Cuba.
12. Virgen, Cueva de la; Playa Siboney, Santiago de Cuba.

Guantánamo Province
1. Golondrinos, Cueva de los; Majana, Baracoa.
2. Majana, Cueva de; Majayara, Baracoa.
3. Patana, Cueva La; Maisí, Baracoa.

Municipio Especial Isla de la Juventud
1. Abono, Cueva del; Sierra de Casas.
2. Agua, Cueva del; Sierra de Casas.