

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: troglloxenes, 3 species; first-level trogllophiles, 21 species; second-level trogllophiles (=unmodified neotroglobites), 5 species. No true trogllobites 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 (Núñez 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 trogllobitic (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.

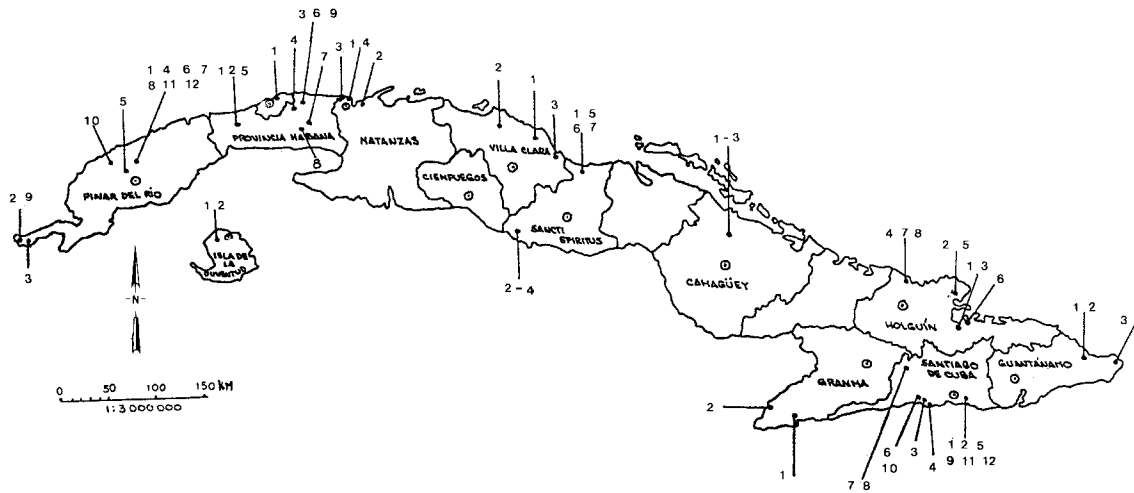
The purpose of this paper is to summarize the available (but

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 Núñez *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).

Figure 1. Outline map of Cuba and its provinces, showing location and code number of caves in which beetles have been found. The code number is the same as in the taxonomic list and in the appendix list of cave names.



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. Troglaxene. 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 trogllobites. 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. Troglomite. 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; Pérez & 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 larochei Bousquet, 1988; reported by Silva (1988: 114) as *D. erythrocerus* LeConte.

Accidental. Predator. Endemic species. Flightless. Halophilic. Cave records: Pinar del Río Province; Hoyo de Fanía 8. Reference: Mateu 1977: 377.

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: Holguín Province; Cueva de los Santos 8. Havana Province; Cueva de los Murciélagos 9. 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)

Accidental. Predator. The species is distributed in lowland and montane forests in Cuba, and eastward to the islands of Guadelupe and Dominica. Winged. Cave records: Santiago de Cuba Province; Cueva Jíbara 8. Reference: Mateu 1977: 378.

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

Accidental. Predator. Endemic species. It is widely distributed across Cuba in lowland and montane forests. Winged. Cave records: Santiago de Cuba Province; Cueva Atabex 1, Cueva Jíbara 8. Reference: Mateu 1977: 377.

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: Holquin 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)

Accidental. Predator. Distributed in moist habitats from southern USA to Mexico and Puerto Rico. Winged. Cave records: Pinar del Río; Hoyo de Fanía 8. Reference: Mateu 1977: 378.

Pentagonica flavipes (LeConte, 1853)

Accidental. Predator. Distributed in moist habitats from southern USA to Mexico and Puerto Rico. Winged. Cave records: Pinar del Río; Hoyo de Fanía 8. Reference: Mateu 1977: 378.

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

Accidental. Predator. Endemic species. Distributed in moist habitats in eastern Cuba. Winged. Cave records: Holquin Province; Cueva Bariay 1. Santiago Province; Cueva Jíbara 8. References: Mateu 1977: 378; Silva 1988: 114.

Selenophorus chalybaeus (Dejean, 1829)

Accidental. Predator. The species ranges from the Bahamas to Jamaica and east to Antigua and Guadalupe. In Cuba it is widely distributed in lowland habitats. Winged. Cave records: Holquin Province; Cueva del Jagüey 6. Reference: Mateu 1977: 378.

Selenophorus pyritosus (Dejean, 1829)

Accidental. Predator. The species ranges from the Bahamas to Puerto Rico, and Mexico south to South America. In Cuba it is widely distributed in lowland habitats. Winged. Cave records: Havana Province; Cueva Cinco Cuevas 3. Santiago Province; Cueva Atabex 1. References: Mateu 1977: 378; Silva 1988: 114.

Family Dytiscidae

Copelatus posticatus (Fabricius, 1801)

Accidental. Predator. The species occurs in all of the Greater Antilles, as well as the Lesser Antilles, and Central and South America. Winged. Cave records: Pinar del Río; Hoyo de Fanía. References: Spangler 1981a: 153; Silva 1988: 114.

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

Accidental. Predator. Distributed from south Florida

through all the Greater Antilles to Barbados. It occurs in streams throughout Cuba. Winged. Cave Records: Pinar del Río; Hoyo de Fanía. References: Spangler 1981a: 150; Silva 1988: 114.

Laccophilus venustus Chevrolat, 1863

Accidental. Predator. The species is also distributed in the Bahamas, Haiti, Guatemala, Mexico, and Florida. It is known from streams throughout Cuba. Winged. Cave records: Santiago de Cuba Province; Cueva Jíbara 8. References: Spangler 1973: 354; Silva 1988: 114.

Family Gyrinidae

Dineutus americanus (Linneus, 1767)

Accidental. Predator. The species is distributed throughout the Bahamas and Jamaica to the Virgin Islands, and in Florida. It occurs in streams throughout Cuba. Winged. Cave records: Santiago de Cuba Province; Cueva Jíbara 8. References: Spangler 1981a: 145; Silva 1988: 115.

Dineutus longimanus cubensis Ochs, 1938

Accidental. Predator. The species also occurs in Jamaica, Hispaniola, and Puerto Rico. It occurs in streams throughout Cuba. Winged. Cave records: Santiago de Cuba Province; Cueva Jíbara 8. Saneti Spiritus Province; Cueva Caja de Aqua. References: Pérez and García-Debras 1997: 26; Spangler 1981a: 145; Silva 1988: 115.

Family Hydrophilidae

Oosternum costatum (Sharp, 1882)

First-level troglophile. 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)

Accidental. Scavenger. Distributed from Cuba to Mexico and south to Costa Rica. Winged. Cave records: Pinar del Río; Hoyo de Fanía 8. References: Spangler 1981a: 161; Silva 1988: 115.

Family Histeridae

Acritus analis LeConte, 1853

First-level troglophile. Predator. The species also occurs in Puerto Rico, Guatemala and Mexico. The species is common in Cuba outside of caves. Winged. Cave records: Havana Province; Cueva Galera 6. Pinar del Río Province; Cueva Incógnita 7. References: Decu and Therond 1977: 403; Silva 1988: 115.

Carcinops troglodytes (Paykull, 1811)

First-level troglophile. Predator. The species is tropicopolitan in distribution, and widespread across Cuba. Winged. Cave records: Granma Province; Cueva del Fustete 2. Holquin Province; Cueva de las Cuatrocientas Rozas 2. Sancti Spiritus Province; Cueva Guanayara 3. Matanzas Province; Cueva la Eloisa 2. Havana Province; Cueva el Mudo 8. References: Decu and Therond 1977: 403; Silva 1988: 115. Santiago de Cuba Province, Cueva de los Majaes 9 (collected by Peck in 1995).

Epieurus antillarum (Marseul, 1854)

First-level troglophile. Predator. The species occurs east to Puerto Rico, and is in Mexico, and the southeastern USA. Winged. Cave records: Guantánamo Province; Cueva de la Patana 3. Holguin Province; Cueva de las Cuatrocientas Rozas 2. References: Decu and Therond 1977: 404; Silva 1988: 115.

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.

Euspilotus sterquilinus (LeConte, 1860)

First-level troglophile. Predator. Endemic species. Widely distributed in Cuba. Winged. Cave records: Ciudad de la Habana Province; Cueva de la Virgen, 5. Guantánamo Province; Cueva de Majana 2 (collected by Ruiz & Garcés in 1985), Cueva de La Patana 3 (collected by Ruiz & Garcés in 1985). Havana Province; Cueva del Mundo 6. Santiago de Cuba Province; Cueva Cativar 3, Cueva del Humo 6, Cueva de los Majaes 9 (collected in December 1984 by Ruiz & Garcés and Peck (1995) feeding on decomposing remains of bats (*Phyllonectris poeyi* Gundlach)). Sancti Spiritus Province; Cueva Guanayara 3. Pinar del Río Province; Cueva Clara 4. References: Decu and Therond 1977: 403; Silva 1988: 115.

Family Leioididae*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 de 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) (Bolívar Pieltain 1944: 302, 303; Silva 1974: 28; 1988: 114) are for this species because *Ptomaphagus* does 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 (Jardin Botanico 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.

First-level troglophile. Scavenger. Winged. In drier guano.

Ptiliidae genus 1 sp.2.

First-level troglophile. Scavenger. Winged. In drier guano.

Ptiliidae genus 2 sp.1.

First-level troglophile. Scavenger. Winged. In drier guano. Cave records combined for above 3 species: Santiago de Cuba Province; Cueva de los Majaes 9 (collected by Ruiz & Garcés in 1984), Cueva de Cativar 3. Granma Province; Cueva del Fustete 2. Havana Province; Cueva de Emilio 5. References: Decu 1983: 15; Silva 1988: 115.

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 in 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 Scarabeidae*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:

Silva 1988: 115.

Gymnetis lanius sternalis (Chevrolat, 1865)

Trogloxene. Scavenger. Endemic species. Widely distributed across Cuba. Winged. Cave records: Villa Clara Province; Cueva El Gato 2 (collected by Luis Grande in 1986), Cueva El Majá 3 (collected by Luis Grande in 1986). Havana Province; Cueva del Mudo 8. References: Decu 1983: 16; Silva 1988: 115. These beetles were found in large numbers in caves where there is guano as a food for the larvae. The larvae occurred in balls of rather dry guano.

Tiarocera cornuta (Gory & Percheron, 1833)

Trogloxene. Scavenger. Endemic species. Widely distributed across Cuba. Cave Records: Havana Province; Cueva de la Mariana 7. References: Silva 1974: 28; 1988: 115. These beetles are found in caves when there is guano near the entrances as a food for the larvae. Other cetonine scarabs are known to occur as larvae and adults in guano deposits in caves in Trinidad (S.B. Peck, unpub.).

Family Elateridae

Conoderus posticatus var. *sticturus* Candeze, 1859 (as *C. p. esticturus* in Silva 1988: 114).

Trogloxene. Predator. Scavenger. Widespread across Cuba. The species is also widespread from Mexico to Brazil. Winged. Cave records: Havana Province; Cueva de los Murcielagos 9. References: Hardy 1963: 160; Silva 1988: 114. The larvae develop in guano, and this is known for other elaterids (Martin 1980).

Pyrophorus noctilucus Linnaeus, 1758

First-level troglophile. Predator. Scavenger. The species is widespread in the West Indies, and from Mexico to Argentina. Winged. Cave records: Santiago de Cuba Province; Cueva del Humo 7 (collected by Ruiz in 1986), Cueva de los Majaes 9. Sancti Spiritus Province; Cueva de Colón 1, Cueva de la zona de Guanayara 4. Villa Clara Province; Cueva de los Bichos 1 (collected by Luis Grande in 1986), Cueva El Majá 3 (collected by Luis Grande in 1986). Havana Province; Cueva del Mudo 8. Pinar del Río Province; Cueva de las Catacumbas 3 (collected by Ruiz & Garcés in 1985), Cueva de las Columnas 5 (collected by Ruiz & Garcés in 1985). References: Decu 1983: 16; Hardy 1963: 160; Silva 1988: 114. These luminescent beetles occur in caves when there is guano for the larvae to feed on. Larvae were found in Cueva El Mudo and Cueva de los Majaes.

Family Lampyridae

Photinus nefarius J.E. Olivier, 1912

Accidental. Predator. Endemic species. The distribution in Cuba is poorly known. Winged. Cave records: Havana Province; Cueva de la Marina 7. References: Silva 1974: 28; 1988: 115.

Family Nitidulidae

Carpophilus sp.

Accidental. Scavenger. Some 12 species in this genus occur in Cuba. Winged. Cave records: Ciudad de Havana

Province; Cueva del Tunel 4. Reference: Silva 1988: 115.

Family Cerylonidae

Euxestus erithaeus Chevrolat, 1863

First-level troglophile. 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)

First-level troglophile. Scavenger. Cosmopolitan and in stored products. Widespread throughout Cuba. Winged. Cave records: Sancti Spiritus Province; Cueva de Guanayara 3. Villa Clara Province; Cueva el Gato 2 (collected by Luis Grande in 1986). Havana Province; Cueva de la Mariana 7; Cueva el Mudo 8. References: Ardoin 1977: 383; Silva 1988: 115. The species is especially found in dry guano, and populations may number in the tens of thousands. It is known in guano caves, attics, chicken coops, etc. from Ontario to Venezuela (Peck 1981, 1992).

Alphitobius laevigatus (Fabricius, 1781)

First-level troglophile. Scavenger. Cosmopolitan, common in stored products. Winged. Cave records: Santiago de Cuba Province; Cueva de las Golondrinas 5, Cueva de los Majaes 9 (collected by Ruiz & Garcés in 1984, and S.B. Peck in 1995). Granma Province; Cueva del Fustete 2. Huguin Province; Cueva de las Cuatrocientas Rozas 2. Sancti Spiritus Province; Cueva Guanayara 3. Havana Province; Cueva Galera 6, Cueva el Mudo 8. Villa Clara Province; Cueva de los Bichos 1. References: Ardoin 1977: 391; Silva 1988: 115. The species is known to be abundant in bat caves in Texas, Mexico, and the West Indies (Peck 1992). It may build up to very large populations in moist guano.

Blapstinus cubanus Marcuzzi, 1962

Accidental. Scavenger. Distributed throughout Cuba and the Bahamas. Winged. Cave records: Havana Province; Cueva Cinco Cuevas 3, reported from a single specimen. References: Ardoin 1977: 390; Silva 1988: 116.

Blapstinus cf. *fortis* LeConte, 1878

First-level troglophile. Scavenger. Endemic species. Widespread throughout Cuba. Winged. Cave records: Sancti Spiritus Province; Cueva Colón 1, Cueva Grande de Caguanes 5. References: Silva 1974: 28; 1988: 116.

Orghidania torrei Ardoin, 1977

First-level troglophile. Scavenger. Endemic species. Probably widespread throughout Cuba. Winged. Cave records: Sancti Spiritus Province; Cueva Colón 1. References: Ardoin 1977: 384; Silva 1988: 116.

Trimytantron cavernicolous Garrido and Gutiérrez, 1997

First-level troglophile. 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 epigeal locality (Punta de Judas, Yaguajay). Reference: Garrido and Gutiérrez 1997: 34.

Trimytantron cubanum Ardoin, 1977

Second-level troglophile. Scavenger. Endemic species. Known only from one cave locality. Wingless. Cave records: Holguin Province; Cueva de los Panaderos (type locality) 7. References: Ardoin 1977: 388; Silva 1988: 116.

Trimytantron decui Ardoin, 1977

Second-level troglophile. Scavenger. Endemic species. Known only from caves. Wingless. Cave records: Santiago de Cuba Province; Cueva Cativar (type locality) 3, Cueva de las Golondrinas 5 (collected by Ruiz & Garcés in 1984), Cueva del Humo 6, Cueva de los Murciélagos 10, Cueva del Terrarium 11 (collected by Ruiz & Garcés in 1984), Cueva de la Virgen 12 (collected by Ruiz & Garcés in 1984). Granma Province; Cueva de los Petroglifos. Guantanamo Province; Cueva de la Patana 3 (collected by Ruiz & Garcés in 1985). References: Ardoin 1977: 382; Garrido & Gutiérrez 1997: 21; Silva 1988: 116.

Trimytantron negreai Ardoin, 1977

Second-level troglophile. Scavenger. Endemic species. Known only from one cave. Wingless. Cave records: Holguin Province; Cueva del Guano (type locality) 4. References: Ardoin 1977: 387; Silva 1988: 116.

Trimytantron poeyi Ardoin, 1977

Second-level troglophile. Scavenger. Endemic species. Known only from caves. Wingless. Cave records: Granma Province; Cueva del Futete (Fustete) 2. Guantanamo Province; Cueva de la Patana 3 (type locality) (collected by Ruiz & Garcés in 1985). Habona Province; Cueva del Mundo 6. Sancti Spiritus Province; Cueva de Colón 1, Cueva de las Columnas 2. Santiago de Cuba Province; Cueva de Cativar 3; Cueva del Humo 6. References: Ardoin 1977: 383; Garrido & Gutiérrez 1997: 21; Silva 1988: 116.

Trimytantron vinai Ardoin, 1977

Second-level troglophile. Scavenger. Endemic species. Known only from one cave locality. Wingless. Cave records: Matanzas Province; Cueva La Pluma (type locality) 4. References: Ardoin 1977: 388; Silva 1988: 116.

Zophobas rugipes Kirsch, 1866

First-level troglophile. Scavenger. Widespread from Mexico to Brazil, and from Cuba to the Lesser Antilles. It is distributed throughout Cuba (Garrido & Gutierrez, 1994). Wingless. Cave records: Guantanamo Province; Cueva de la Patana 3 (collected by Ruiz & Garcés in 1985). Villa Clara Province; Cueva el Majá 3 (collected by Luis Grande in 1986). References: Ardoin 1977: 385; Garrido and Gutierrez 1994: 243; Silva 1988: 116.

Family Curculionidae

Anchonus suillus (Fabricius, 1792)

Accidental. Scavenger. Widespread in West Indies, from the Bahamas and Cuba, through to Puerto Rico and south to Guadeloupe. Winged. Cave records: Santiago de Cuba Province; Cueva de los Majaes 9 (one collected by Peck in 1995 in bat guano). A soil-litter dwelling feeder on roots and litter.

Caecocossanus sp. (cf. *decuanus* Osella, 1973)

Accidental. Scavenger. Only one species, *C. decuanus*, is reported from Cuba. This is an eyeless and flightless soil-inhabiting species (see Howden 1992: 18). Cave records: Matanzas Province; doline of Cueva la Pluma 4. References: Silva 1988: 114; Osella 1977: 399.

Stenancylas colomboi Casey, 1892

Accidental. Scavenger. Reported from Jamaica, St. Vincent, and south Florida (Anderson & Peck 1994) as well as Cuba. Winged. Cave Records: Santiago de Cuba Province; Cueva de los Majaes (one collected by Peck in 1995 in bat guano). Known from roots and foliage of *Asplenicum* ferns and litter in coastal deciduous forests.

DISCUSSION

In addition to the above records, Nuñez *et al.* (1973), Orghidan *et al.* (1977), Perez and García-Debrás (1977), and Silva (1988) mention beetles in other caves, but give no species level identifications. We have not repeated these records in the above list because they cannot be used in the following analysis.

The known fauna of beetles that have been found in caves in Cuba and identified or segregated to species are now 53 species. Of these, 24 are judged to be accidentals, with no repeated pattern of ecological-evolutionary relationship with cave habitats. The following analysis, thus, treats only the remaining 29 species that have a non-accidental association with caves, and these are summarized in Table 1. This cave-dwelling beetle fauna is richer than that of caves in the island of Puerto Rico (10 species, Peck 1974, 1981a, 1994) and similar to that in the island of Jamaica (23 species, Peck, 1992). By contrast, a single continental tropical cave, Cueva del Guacharo in Venezuela, has 29 resident beetle species (Peck *et al.*, 1989).

CAVE RESTRICTION AND ENDEMISM

The Cuban cave beetle fauna has no morphologically specialized cave-limited species (troglonites). There are five tenebrionid species that are now known only from caves (second-level troglonites) but all of these are expected by us to occur in epigeal habitats (Table 1); we predict that these are actually first-level troglonites. The rest of the fauna (24 species) are more frequently known from non-cave habitats. Of the 29 non-accidental cave-occurring beetles, 17 (59%) are thought to be endemic to Cuba (Table 1). This compares favorably with the entire Cuban beetle fauna, which contains about 55% endemic species (S.B. Peck, unpublished). Three of the caver-

Table 1. Summary of characteristics of the non-accidental cave beetles of Cuba.

Name	Cave Status	Trophic Status	Flight Wings	Distribution	Cuban Status	Habitat Association
Carabidae						
<i>Macranthus brevicillus</i>	1st troglophile	predator	yes	West Indies,	native	wet guano
Hydrophilidae						
<i>Oosternum costatum</i>	1st troglophile	scavenger	yes	Neotropics	native	wet guano
Histeridae						
<i>Acritus analis</i>	1st troglophile	predator	yes	Neotropics,	native?	moist guano
<i>Carcinops troglodytes</i>	1st troglophile	predator	yes	Neotropics,	introduced?	moist guano
<i>Epiurus antillarum</i>	1st troglophile	predator	yes	Neotropics,	native	moist guano
<i>Euspilotus sterquilinus</i>	1st troglophile	predator	yes	Cuba	endemic	moist guano
Leiodidae						
<i>Aglyptinus sp.</i>	1st troglophile	scavenger	yes	Cuba	endemic	moist guano
<i>Proptomaphagus apodemus</i>	1st troglophile	scavenger	yes	Cuba	endemic	moist guano
Ptiliidae						
Species 1	1st troglophile	scavenger	yes	Cuba	endemic	moist guano
Species 2	1st troglophile	scavenger	yes	Cuba	endemic	moist guano
Species 3	1st troglophile	scavenger	yes	Cuba	endemic	moist guano
Staphylinidae						
Species 1	1st troglophile	predator	yes	Cuba	endemic?	moist guano
Scarabaeidae						
<i>Ataenius gracilis</i>	1st troglophile	scavenger	yes	Neotropics	native	moist guano
<i>Gymnetis lanius</i>	trogloxene	scavenger	yes	Cuba	endemic	moist guano
<i>Tiarocera cornuta</i>	trogloxene	scavenger	yes	Cuba	endemic	moist guano
Elateridae						
<i>Conderus posticatus</i>	trogloxene	predator	yes	Neotropics,	native	dry guano
<i>Pyrophorus noctilucus</i>	1st troglophile	predator	yes	Neotropics,	native	dry guano
Cerylonidae						
<i>Euxestus erithaeus</i>	1st troglophile	scavenger	yes	West Indies	native	moist guano
Tenebrionidae						
<i>Alphitobius diaperinus</i>	1st troglophile	scavenger	yes	Neotropics,	introduced?	moist guano
<i>A. laevigatus</i>	1st troglophile	scavenger	yes	Neotropics,	introduced?	moist guano
<i>Blapstinus cf. fortis</i>	1st troglophile	scavenger	yes	Cuba	endemic	dry guano
<i>Orghidania torrei</i>	1st troglophile	scavenger	yes	Cuba	endemic	moist guano
<i>Trimytantron cavernicolous</i>	1st troglophile	scavenger	no	Cuba	endemic	moist guano
<i>T. cubanum</i>	2nd troglophile	scavenger	no	Cuba	endemic	moist guano
<i>T. decui</i>	2nd troglophile	scavenger	no	Cuba	endemic	moist guano
<i>T. negreai</i>	2nd troglophile	scavenger	no	Cuba	endemic	moist guano
<i>T. poeyi</i>	2nd troglophile	scavenger	no	Cuba	endemic	moist guano
<i>T. vinai</i>	2nd troglophile	scavenger	no	Cuba	endemic	moist guano
<i>Zophobas rugipes</i>	1st troglophile	scavenger	no	Neotropics,	native	dry guano

nicolous 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

Table 2. Comparison of numbers of known species in the cave-evolved invertebrate faunas of the Greater Antilles (data from Decu & Juberthie, 1994; Peck 1992, 1994, and unpublished).

	Cuba	Jamaica	Hispaniola	Puerto Rico +Virgin Islands
Aquatic - Marine (eyeless or small-eyed stygobites)				
Platyhelminthes	0	1	0	0
Oligochaeta	0	0	1	0
Crustacea				
Remipedia	0	0	0	0
Ostracoda	3	3	4	0
Copepoda	19	0	1	0
Mysidacea	5	2	1	1
Thermosbaenacea	4	1	4	6
Isopoda	4	1	7	0
Amphipoda	2	4	15	6
Decapoda	7	2	3	1
Insecta (Coleoptera)	0	0	3	0
Total	45	14	39	14
Terrestrial (troglobites)				
Onychophora	0	1	0	0
Arachnida				
Pseudoscorpiones	2	4	0	0
Opiliones	2	2	0	0
Schizomida	2	1	0	0
Amblypygi	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
Collembola	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

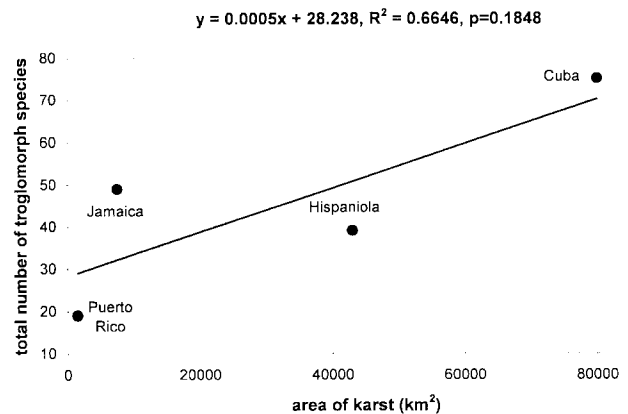


Figure 2. Linear regression of the total number of known troglomorph (troglobite + stygobite) species against island karst area. The relationship is suggestive but not statistically significant.

Table 3. Summary of characteristics of Greater Antilles and their cave faunas.

Island	Total Area (km ²)	Area of Karst (km ²)	No. Sp. aquatic stygobites	No. Sp. terrestrial troglobites	Total No. Sp.
Cuba	111,000	80,000	45	30	75
Hispaniola	76,476	≈43,000	39	0	39
Jamaica	11,700	≈7,500	14	35	49
Puerto Rico (+ Mona & Virgin Islands)	9,399	≈1,500	14	5	19

terrestrials are arachnids, not insects. Within insects, there are only 5 troglotic beetles for the whole Caribbean, and only 2 are terrestrial species. Why there are more tropical troglotic arachnids than troglotic 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 troglotic 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 troglotic 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 troglotic beetles in both continental and insular tropical lowland caves. This general-

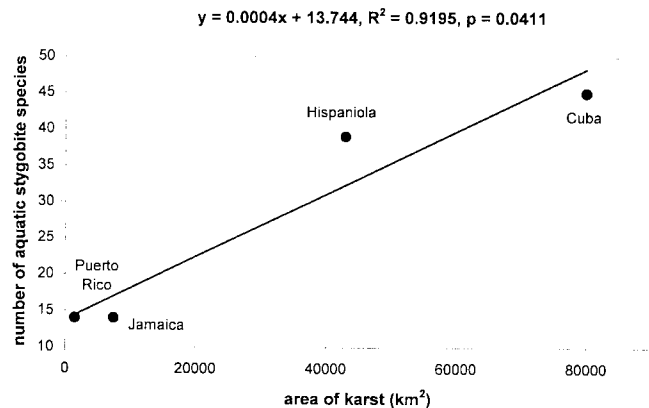


Figure 3. Linear regression of the total number of aquatic stygobite species against island karst area. The relationship is statistically significant.

ization in the New World is based on an analysis of 241 terrestrial troglotic beetles 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 troglotic beetles is not due to a lack of evolutionary time. The islands are certainly old enough, and many other terrestrial troglotic beetles 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 troglotic beetles do occur there is a strong selective factor of limited food availability. Terrestrial troglotic beetles 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.

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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 neighbouring 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.
4. Catacumbas, Cueva de las; Gran Caverna de Sto. Tomás. El Moncada.
5. Clara, Cueva; Los Portales, San Diego de los Baños.
6. Columnas, Cueva de las; Gran Caverna de Sto. Tomás. El Moncada.
7. Fango, Cueva del; Gran Caverna de Sto. Tomás. El Moncada.
8. Hoyo de Fanía; Gran Caverna de Sto. Tomás. El Moncada.
9. Incógnita, Cueva; Gran Caverna de Sto. Tomás. El Moncada.
10. Jagüey, Cueva del; Península de Guanahacabibes.
11. Pio Domingo, Cueva de; Sumidero, Minas de Matahambre.
12. Represas, Cueva de las; Gran Caverna de Sto. Tomás. El Moncada.
13. Vela, Cueva de la; 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. Eloisa, Cueva de la; 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. Jagüey, Cueva del; Cuesta de Seboruco, Mayarí.
7. Panaderos, Cueva de los; Gibara.
8. Santos, Cueva de los; Gibara.

Granma Province

1. Banega, Cueva; Matias.
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, Guaná.
7. Humo, Cueva del; Los Negros, Baire, Tercer Frente.
8. Jíbara, 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.