Stewart B. Peck and Margaret K. Thayer - The Cave-inhabiting rove beetles of the United States (Coleoptera; Staphylinidae; excluding Aleocharinae and Pselaphinae): Diversity and distributions. *Journal of Cave and Karst Studies, v. 65*, n. 1, p. 3-8.

THE CAVE-INHABITING ROVE BEETLES OF THE UNITED STATES (COLEOPTERA; STAPHYLINIDAE; EXCLUDING ALEOCHARINAE AND PSELAPHINAE): DIVERSITY AND DISTRIBUTIONS

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A taxonomic listing is given for new records of 66 species of staphylinid beetles (excluding Aleocharinae and Pselaphinae) collected in caves in the contiguous United States. Most species are judged to be either accidentals or infrequent troglophilic inhabitants of caves. Nine species are classed as frequent troglophiles. When added to the 6 frequent troglophile species of aleocharine staphylinids, this yields a total of 15 species of staphylinid beetles (excluding Pselaphinae) frequently found in US cave ecosystems. No troglobitic species are known from US caves. Troglobitic staphylinids (excluding Pselaphinae) elsewhere in the world are few (some 30 species). They are briefly considered and discussed. Worldwide, troglobitic staphylinids are taxonomically, geographically, and geologically concentrated in the Canary Islands (in volcanic lava tube caves) and in nearby Spain and northwestern Africa.

Worldwide, caves are most frequently and abundantly occupied by beetles in the families Carabidae, Leiodidae, and Staphylinidae. The first two of these families contain a great many cave-specialized and cave-restricted (troglobitic) genera and species in many parts of the world, mostly in Europe (Casale *et al*. 1998; Giachino *et al*. 1998). In contrast, very few cave-specialized or cave-restricted (troglobitic) staphylinid beetles are known. Jeannel and Jarrige (1949) summarized data on about 150 species of Staphylinidae from over 1000 caves worldwide and considered very few of these species to be troglobites. Recent reviews by Bordoni and Oromi (1998) and Outerelo *et al*. (1998) list only 30 troglobitic species worldwide, and most of these are from Europe and North Africa. None are from the USA.

Most staphylinid beetles are distinctive in their appearance, with an exceptionally elongate and flexible body form and very short elytra (front wing covers) over their hind wings (Figs. 1–6). Their English common name, "rove beetle," comes from their behavior of rapidly running about in many directions. Some species in the family are eyeless and without flight wings, but other than the few cave species, these are mostly small to minute litter- or soil-inhabiting species. This beetle family is one of the world's largest, with some 4100 species recorded in the USA and Canada, and over 47,000 species known to science worldwide (Newton *et al*. 2000). Recently, the traditional beetle families Scaphidiidae and Pselaphidae have been combined with the family Staphylinidae, and each is now treated as a subfamily (Kasule 1966; Newton & Thayer 1995). These two groups are not included in the following discussions, which are restricted to the subfamilies traditionally placed in the Staphylinidae. Pselaphines are known from many caves, especially in the USA (Chandler 1992; Chandler & Reddell 2001) and Europe (Poggi *et al*. 1998). Some 53 species of them in 8 genera are considered to be troglobites in the USA (Peck 1998; Chandler & Reddell 2001). We are not aware of any cave records for scaphidiines, which are strictly mycophagous as far as known (Leschen & Löbl 1995), and they seem unlikely to be cave-associated.

Staphylinid beetles occur frequently and commonly in caves in the United States. The published records of staphylinids from US caves are many and scattered in numerous regional and state cave faunal reports. These have been summarized by Roth (2001). After many years of faunal surveys of many caves by many people, no troglobitic species (outside Pselaphinae) have been found in the USA. It now seems most likely that none will be found in the future.

Identification of species in this very large beetle family is difficult and time consuming, even for the specialist, and since troglobitic species are not known from the US, staphylinid beetles have often received little or no specific attention in surveys of cave insect diversity. For these reasons, we have a very scattered and incomplete knowledge of which species of staphylinid beetles are frequent inhabitants of US caves and components of cave ecosystems.

Klimaszewski and Peck (1986) presented a comprehensive systematic report on the cave-inhabiting aleocharine staphylinids of the USA. The aim of this paper is to complement that report and the literature summary of Roth (2001). We present a systematic summary of new records of authoritatively identified species of Staphylinidae (excluding Aleocharinae and Pselaphinae) from cave localities throughout the USA. This documentation of the species diversity and distribution of these staphylinid beetles helps to complete an understanding of this previously poorly known part of the fauna of US caves.

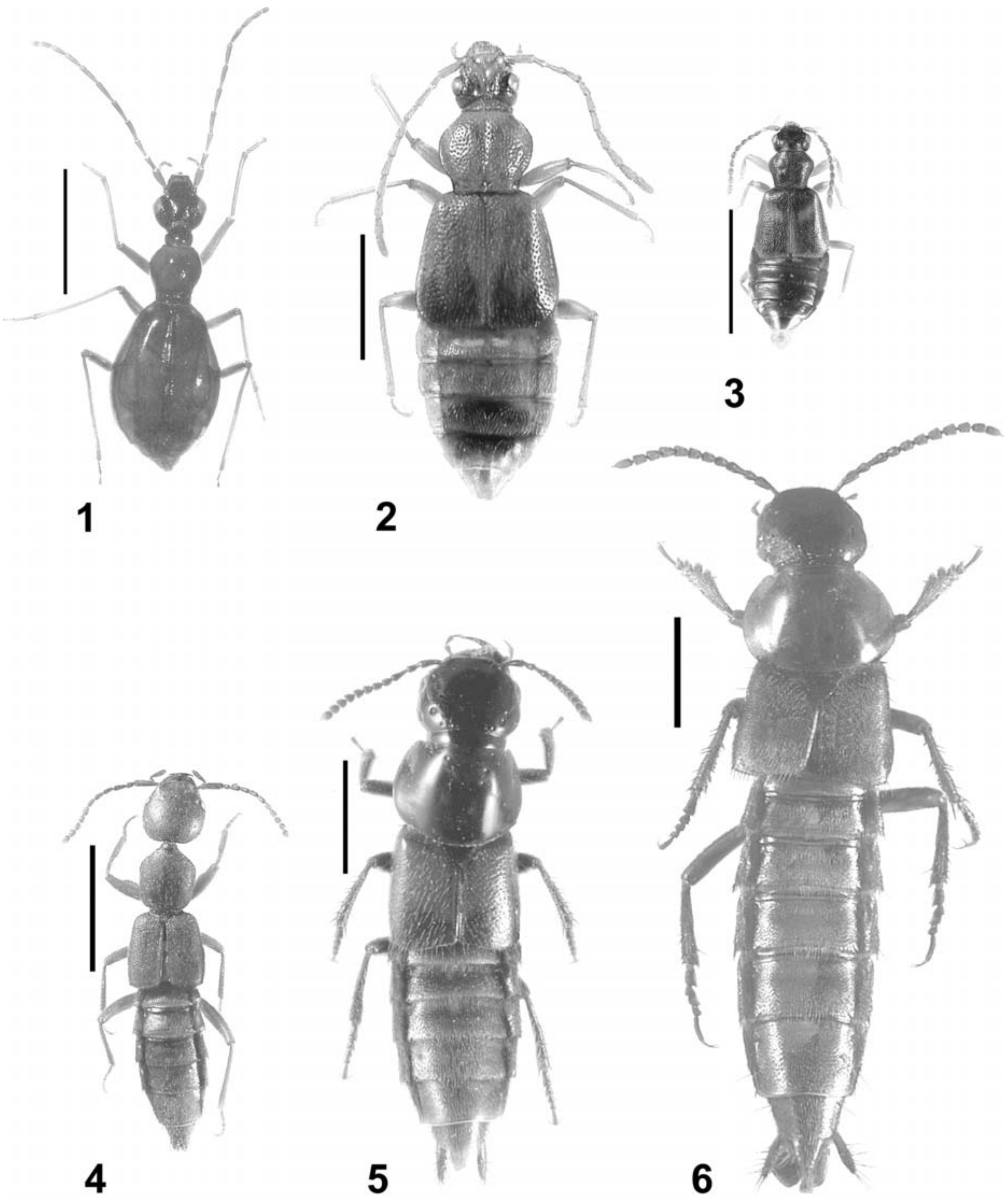

Figure 1. ***Brathinus nitidus.***

Figure 2. ***Geodromicus brunneus.***

Figure 3. ***Lesteva pallipes.***

Figure 4. ***Eustilicus condei.***

Figure 5. ***Quedius erythrogaster.***

Figure 6. ***Quedius spelaeus.***

All scale lines are 2.0 mm.

MATERIALS AND METHODS

Staphylinid beetles are usually collected in caves by general searching and hand collecting, or by setting bait stations and baited pitfall traps. The beetles usually feed as generalized predators on small terrestrial invertebrates and are most frequently found at or near decaying organic matter, which attracts their prey items. Most of the records reported here have been collected by the first author over many years of field work in US caves. Many additional records are included which were made by many other collectors, and these people are thanked in the acknowledgments. This paper reports on 611 collections and 2185 specimens. All specimens reported here have been seen by one of the authors and most specimens are in the collections of the Field Museum of Natural History, Chicago, IL, USA; the American Museum of Natural History, New York, NY, USA; or the Canadian National Collection of Insects, Agriculture Canada, Ottawa, Ontario, Canada.

Identifications were made by the authors, J.M. Campbell, A. Smetana, A. Davies, and A.F. Newton. The species records are arranged in putative phylogenetic sequence by subfamily, tribe, and subtribe following Newton *et al*. (2000, which also provides authorities for generic and family group names) and alphabetically by genus and species. Only records that have been determined to species by a staphylinid taxonomist are given, with names updated where needed, following Herman (2001; all except Paederinae) and an unpublished database maintained by A.F. Newton. There are additional unidentified specimens in the above and other collections, especially the Illinois Natural History Survey, but it is unlikely that they contain any additional species of frequently occurring troglophiles not listed here. Full label data such as date of collection, name of collector and other label information are available as Access or other digital files from the authors. Frequently, a species has been taken many times in a cave and by the same or other collectors on many separate occasions. Such duplicate records are not indicated.

Frequency of association of the species with cave habitats is given as (1) "accidental" (for which there about 5 records or fewer and there is no apparent or regular association with cave habitats) or (2) as "troglophile" (having an apparently regular association with dark-zone cave habitats, and for which there are usually more than 5 records). The troglophiles are further divided into the subcategories of (2A) "infrequent troglophiles" (with ~5-10 cave records) and (2B) "frequent troglophiles" (for which there are generally many >10 cave records). These categorizations are subjective, and may be modified by the accumulation of additional data; in particular, more records may elevate some infrequent troglophile species into the category of frequent troglophiles. Supplementary data available at http://www.caves.org/pub/journal/Peck-Thayer Appendix.rtf include a brief summary of the general distribution of the species, microhabitat associations of the species in caves when known or suspected, and, for species previously reported from caves, a list of state abbreviations as a summary of previous records (see Roth 2001).

RESULTS

No cave-limited or cave-evolved species (troglobites) have been found in caves in the contiguous USA. In a world list of troglophilic Staphylinidae, Bordoni and Oromi (1998) list 44 species, 8 of which are from the USA. From the data reported here, 9 species of staphylinids (excluding Aleocharinae and Pselaphinae) are considered to be regularly occurring or frequent troglophiles in US caves. Adding these to the data on the 6 frequently occurring troglophilic species of Aleocharinae (from Klimaszewski & Peck 1986) and that presented in Roth (2001), 15 species of frequently occurring troglophile staphylinids are now known from US caves. Their names and general geographical distributions in caves are in Table 1. Species judged to be infrequent troglophiles or accidentals in US caves are listed in Table 2. Full data on cave names for all specimen records are at
http://www.caves.org/pub/journal/Peck-Thayer Appendix.rtf

It is interesting to note that of the species in Table 1, *Quedius fulgidus* and *Quedius mesomelinus* were probably accidentally introduced into North America (Smetana 1971). They are, thus, historically recent additions to the fauna of US caves. At present, they seem to be geographically and ecologically peripheral in US cave ecosystems, although at least the last species is also troglophilic in Europe (Outerelo *et al*. 1998), with some populations possibly being subtroglobitic (Hennicke & Eckert 2001). The total taxonomic and numerical abundance of terrestrial predators in US cave ecosystems would have been less before the accidental introduction of these species into North America. It is evident that these species have found niche space in US cave habitats, but there is no present evidence that they displaced other terrestrial predators from US caves. Rather, they have slightly enriched the diversity of terrestrial insect predators in US cave ecosystems.

DISCUSSION

Staphylinids in caves. Staphylinids are an ecologically very diverse group of beetles.

Nevertheless, most occupy habitats that are moist and have very low light levels. This general preference would seemingly preadapt them for life in caves. However, in view of the great number of species known from the USA, comparatively few have actually been found to establish populations in caves. This may be because they are somehow restricted by microhabitat requirements, by food types, by competition with already-established species, or perhaps by a need for environmental temperature fluctuations. Alternatively, those that do occur regularly in caves might do so because (1) they are more omnivorous or tolerant of the limited foods available in caves, or (2) caves present suitable extensions of the microhabitats they favor in non-cave environments, or (3) they are tolerant of the dark, humidity, and relatively constant temperatures of caves.

Distributional patterns. A few of the records represent new state records for the species, which is not unexpected in a group of beetles that has not been well studied. Some troglophiles appear to be more prevalent in caves in the southern part of their ranges than in the northern parts. It is assumed that this is because more southerly caves offer cooler and moister habitats than are generally found outside of caves, and the troglophiles use caves more frequently in the south as environmental refuges. This pattern is present in at least *Brathinus nititdus*, *Lesteva pallipes*, *Quedius erythrogaster* and *Q. fulgidus* and may occur in other troglophilic staphylinids, but distributional data are not adequate to demonstrate its generality.

The problem of defining a troglobitic staphylinid. In a world list of 29 species of troglobitic Staphylinidae, Bordoni and Oromi (1998) note that categorizing a staphylinid as a troglobite is not as easy or clear-cut as for some other groups of cave insects. Outerelo *et al*. (1998) add one additional

Table 1. Staphylinidae frequently occurring as troglophiles in US caves. Additional supportive data are at http://www.caves.org/pub/journal/Peck-Thayer Appendix.rtf and also available from the NSS library and NSS archives (see masthead for NSS address).

Omaliinae: Anthophagini
Geodromicus brunneus (Say, 1823): eastern-central USA; from VA and IL south to OK and GA. Fig. 2.
Lesteva pallipes LeConte, 1863: eastern-central USA; from IA and MD south to AR and GA. Fig. 3
Aleocharinae
Aleocharini
Aleochara (*Echochara*) *lucifuga* (Casey, 1893): eastern-central USA; PA and IA to VA and AL.
Athetini
Aloconota laurentiana Blatchley, 1910, (reported as *Aloconota insecta* (Thomson, 1856) in Klimaszewski and Peck (1986), by Gusarov 2001): eastern-central USA; NY and IL to MO, VA, and AL.
Atheta (subgenus undetermined) *annexa* Casey, 1910: eastern-central USA; IA and VA to MO, GA, and FL.
Atheta (*Dimetrota*? subgenus uncertain) *lucifuga* Klimaszewski and Peck, 1986: eastern-central USA; MO and KY to GA and FL.
Atheta (*Dimetrota*) *troglophila* Klimaszewski and Peck, 1986: eastern-central USA; PA and IA to AR, GA, and FL.
Oxypodini
Blepharrhymenus illectus (Casey, 1911): central to south eastern USA; MO to TN and AL.
Paederinae: Paederini: Stilicina
Eustilicus condei (Jarrige, 1960): southwestern USA; TX and NM. Fig. 4.
Staphylininae: Staphylinini
Quediina
Quedius erythrogaster Mannerheim, 1852: OR, CA, and eastern states; IL to NY and south to TN and AL. Fig. 5.
Quedius fulgidus (Fabricius, 1792): eastern USA; IL to PA and south to AL and AR.
Quedius mesomelinus (Marsham, 1802): northcentral-north eastern USA; MN to PA south to IA and VA
Quedius spelaeus Horn, 1878: widespread eastern-central and western USA; MN to NY and south to MO and VA; also WA to WY and south to CA and UT. Fig. 6.
Philonthina
Belonuchus aphaobius Smetana, 1995: southwestern USA; central TX.
Belonuchus troglophilus Smetana, 1995: southwestern USA; AZ, OK, TX.

species (*Anotylus subanophthalmicus*) to bring the total to 30 species. Some of these species may actually be endogeans (species whose primary habitat is in either soil or deep rock cracks and crevices or the superficial subterranean zone). For such species, caves are only secondary habitats. Many eyeless and wingless endogean species are known worldwide. They frequently occur in regions with Mediterranean-type climates and are most often collected by soil-washing techniques (Campbell & Peck 1990). Because of their limited dispersal abilities, many endogean species may be useful indicators of past regional biogeographic history. For example, Campbell and Peck (1990) suggest that the eyeless and flightless endogean species *Omalonomus relictus* is evidence that the Cypress Hills of southern Alberta and Saskatchewan, Canada, were not ice-covered during times of Pleistocene glaciations.

Where do troglobitic staphylinids occur? The distributions of the 30 species of supposed troglobites listed by Bordoni and Oromi (1998) and Outerelo *et al*. (1998) are as follows: Canary Islands and Madeira Island, 12; Morocco, 7; Spain, 4; Algeria, 2; Italy, 1; Romania, 1; Galapagos Islands, 1; Mexico, 1; and India, 1. There are 3 notable patterns of species concentration in this list. The first is the *taxonomic* concentration of 15 species in the genera *Domene* and *Apteranopsis* in the Canary Islands and nearby Spain and northwestern Africa (see below). The second is the *geographic* concentration of 25 species in the Canary Islands and the western Mediterranean region of Spain and North Africa. The third is the *geologic* concentration of 13 species in lava tube caves on oceanic volcanic islands of the Canaries, Madeira, and the Galapagos. Statistically, there is a much higher frequency of troglobites in volcanic cave habitats than would be normally expected, since volcanic caves on islands are certainly much rarer habitats than are solution caves in limestone on continents. Additionally, volcanic (lava tube) caves are thought to be much younger than limestone solution caves. While this may be true on a cave by cave basis, we would argue that volcanic landscapes themselves may generally be as old as limestone karst landscapes as sites for origins of troglobitic species.

What is the evolutionary origin of troglobitic staphylinids? About half of the troglobitic staphylinids are scattered in various genera. Thus, these troglobites have evolved independently from several ancestral stocks in several different regions, and probably at different times. But there may have been some general or common adaptive theme in their cave specialization. The species in the western Mediterranean region may represent subterranean occupation by diverse ancestors in response to regional Pleistocene interglacial climatic change and increasing aridity, as is widely thought for so many troglobitic arthropods. This explains multiple adaptations to subterranean habitats in many different ancestral lines. However, 2 taxonomic patterns are also present. The paederine genus *Domene* is represented by 9 troglobitic species in Spain, the Canary Islands, and Morocco, and the aleocharine genus *Apteranopsis* by 6 species in the Canary Islands. These 2 genera have been the most successful in penetrating and speciating in cave habitats. Secondly, a total of 11 of these species are in the Canary Islands. This concentration must be meaningful. Seemingly these isolated, oceanic, and volcanic islands have a different ecological structure or history in their subterranean habitats that collectively allowed more formation of troglobitic species of staphylinids than any other region in the world.

Perhaps the abundance of carabid beetle predators elsewhere in the world has suppressed the evolution of troglobitic staphylinids; that is, the niche of troglobitic predatory beetles may be filled by carabids nearly worldwide. But at least 4 species of troglobitic trechine carabids are known from the Canary Islands (Casale *et al*. 1998), so this cannot be the full answer. Additionally, the relative proximity of these islands to

Table 2. Staphylinidae judged to be infrequent troglophiles or accidentals in US caves. Additional supportive data are at http://www.caves.org/pub/journal/Peck-Thayer Appendix.rtf and also available from the NSS library and NSS archives (see masthead for NSS address).

Subfamily Omaliinae
Tribe Omaliini
Omalium rivulare (Paykull, 1789), accidental.
Tribe Anthophagini
Brathinus nitidus LeConte, 1852, infrequent troglophile. Fig. 1.
Lesteva cribratula (Casey, 1894), infrequent troglophile.
Olophrum obtectum Erichson, 1840, accidental.
Orobanus ?simulator LeConte, 1878, accidental.
Subfamily Proteininae
Megarthrus americanus Sachse, 1852, accidental.
Subfamily Tachyporinae
Tribe Deropini
Derops divalis (Sanderson, 1947), infrequent troglophile.
Tribe Tachyporini
Coproporus laevis LeConte, 1863, accidental.
Nitidotachinus horni (Campbell, 1973), accidental.
Nitidotachinus scrutator (Gemminger & Harold, 1868), accidental.
Sepedophilus crassus (Gravenhorst, 1802), accidental.
Sepedophilus littoreus (Linnaeus, 1758), accidental.
Sepedophilus opicus (Say, 1832), accidental.
Tachinus canadensis Horn, 1877, accidental.
Tachinus fimbriatus Gravenhorst, 1802, accidental.
Tachinus frigidus Erichson, 1839, accidental.
Tachinus fumipennis Say, 1832, accidental.
Tachyporus jocosus Say, 1832, accidental.
Tribe Mycetoporini
Lordithon obsoletus (Say, 1832), accidental.
Subfamily Trichophyinae
Trichophya pilicornis (Gyllenhal, 1810), accidental.
Subfamily Oxytelinae
Tribe Deleasterini
Deleaster trimaculatus Fall, 1910, accidental.
Tribe Oxytelini
Anotylus exiguus (Erichson, 1840), accidental.
Anotylus insignitus (Gravenhorst, 1806), accidental.
Anotylus tetracarinatus (Block, 1799), accidental.
Oxytelus nimius Casey, 1894, accidental.
Subfamily Steninae
Dianous chalybeaus LeConte, 1863, accidental.
Stenus (*Tesnus*) *alacer* Casey, 1884, accidental.
Stenus (*Stenus*) *bilentigatus* Casey, 1884, accidental.
Stenus (Stenus) *renifer* LeConte, 1963, accidental.
Subfamily Paederinae
Tribe Paederini
Subtribe Lathrobiina
Lathrobium (*Tetartopeus*) *angulare* LeConte, 1863, accidental.
Lathrobium (*Apteralium*) *brevipenne* LeConte, 1863, accidental.
Lobrathium gnoma (Casey, 1905), accidental.
Subtribe Scopaeina
Orus (*Leucorus*) *rubens* (Casey, 1905), accidental.
Subtribe Stilicina
Eustilicus tristis (Melsheimer, 1844), infrequent troglophile.
Rugilus dentatus Say, 1831, accidental.
Rugilus opaculus (LeConte, 1880), accidental.
Subtribe Cryptobiina
Homaeotarsus badius (Gravenhorst, 1802), accidental.
Homaeotarsus bicolor (Gravenhorst, 1802), accidental.
Homaeotarsus capito (Casey, 1884), accidental.
Homaeotarsus carolinus (Erichson, 1840), accidental.
Homaeotarsus cinctus (Say, 1830), accidental.
Homaeotarsus pimerianus (LeConte, 1863), accidental.
Subtribe Paederina
Paederus littorarius Gravenhorst, 1806, accidental.
Subfamily Staphylininae
Tribe Xantholinini
Neohypnus obscurus (Erichson, 1839), accidental.
Stenistoderus rubripennis (LeConte, 1880), accidental.
Tribe Staphylinini
Subtribe Quediina
Heterothops campbelli Smetana, 1971, accidental.
Quedius capucinus (Gravenhorst, 1806), accidental.
Quedius laticollis (Gravenhorst, 1802), accidental.
Quedius montanicus (Casey, 1915), accidental
Subtribe Philonthina
Erichsonius nanus (Horn, 1884), accidental.
Erichsonius patella (Horn, 1884), accidental.
Erichsonius pusio (Horn, 1884), accidental.
Gabrius micropthalmus (Horn, 1884), accidental.
Hesperus baltimorensis (Gravenhorst, 1802), accidental.
Neobisnius paederoides (LeConte, 1863), accidental.
Neobisnius sobrinus (Erichson, 1840), infrequent troglophile.
Philonthus caeruleipennis (Mannerheim, 1830), accidental.
Philonthus thoracicus (Gravenhorst, 1802), accidental.

continental sources of colonist species also seems important–e.g., no troglobitic staphylinids are found in the Hawaiian Islands. Another potentially important factor is the availability of suitable habitats outside of caves. If the habitats are highly suitable for staphylinids, there would be less selective pressure for staphylinids to occupy and become isolated in cave environments. This might well be important because of the general aridity of the islands and areas which do posses troglobitic staphylinids. Increasing regional aridity would tend to make caves distinctly more "attractive" to moisture-loving insects such as staphylinid beetles.

ACKNOWLEDGMENTS

Milton W. Sanderson, formerly of the Illinois Natural History Survey, introduced the first author to a need to accumulate data on cave-inhabiting staphylinids. Principal collectors who gathered the material reported here are: T.C. Barr, Jr., K. Christiansen, J. & K. Craig, K. Dearolf, W. Elliott, J.E. Gardner, J.R. Holsinger, W.B. Jones, K. Krekeler, J. Lewis, L.M. Ferguson, O. Park, S.B. Peck, J. Reddell, and D.C. Rudolph. Additional collectors are: S. Bamberg, H.S. Barber, R. Baroody, D.P. Beiter, E.M. Benedict, J. Black, J.E. Cooper, D. Cowan, D. Culver, D. Davis, R. Deike, H.S. Dybas, J. Fish, A. Fiske, R.E. Graham, C.W. Greever, A.G. Grubbs, O. Helmy, P. Hertl, M. B. Hills, D.A. Hubbard, Jr., L. Hubricht, C. Hybner, T.C. Kane, G.T. Lane, C. Laing, T. Marsh, B. Martin, R. McAdams, D. McKenzie, P. Miller, R. Mitchell, T. Mollhagen, P. Moss, D. Newson, R.M. Norton, B. Opell, G. Park, J.A. Payne, J. Peck, A. Pursell, J. Porter, C. Remington, P.O. Ritcher, J. Rittman, W. Russell, T. Rossen, M. W. Sanderson, F. Shires, W. Stannard, H.R. Steeves, Jr., G. Steyskal, W. Tozer, J.M. Valentine, S. Wiley, and N. Youngsteadt. J.M. Campbell, A. Davies, and A. Smetana provided identifications of the less common species, and A.F. Newton provided new Idaho records from material furnished by R.L. Hoffman. Anthony Davies also helped with literature and distributional records. Without the aid of both the above collectors and taxonomists, our knowledge of these cave beetles would be much the poorer. Field work of S.B. Peck was partly supported by grants from the Natural Sciences and Engineering Research Council of Canada. We thank A.F. Newton for access to his species database.

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