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Moss-inhabiting beetles of the West Indies (Insecta: Coleoptera)

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Abstract

This study is the first attempt to assess the diversity of beetles (Coleoptera) in terrestrial moss cushions on three West Indian islands (Hispaniola, Jamaica, and Puerto Rico) based on 10 years of moss sampling in 18 localities. In total 1711 adult beetles were collected. They belong to 234 species from 30 families. The most species and specimen rich families are Staphylinidae (86 morphospecies and 1195 specimens), Curculionidae (61 morphospecies and 131 specimens), and Chrysomelidae (16 morphospecies and 185 specimens). In addition to basic bryobionts feeding on moss tissues, moss cushions host a diverse fauna of mycophagous and saprophagous Coleoptera together with predaceous species of beetles. Our results suggest that community composition in moss inhabiting beetles is determined both by geographical isolation processes and, to a lesser degree, by environmental variation across altitudinal gradients. This confirms that the greater relevance of geographical isolation is a common pattern in organisms with limited dispersal ability. Beetle abundance was not significantly related to either the volume of moss or the substrate. Despite being not significant (but close to), the observed trend was to higher beetle abundance in moss cushions collected on trees than in those collected on soil/rock. This may be resulting from the greater diversity of fungi and higher number of beetle fungivores associated with tree growing moss communities.

Key words: Beetles, biological diversity, bryophytes, bryobionts, fungivory, beetle flightlessness, beetle blindness, island fauna, Neotropics, Greater Antilles, Dominican Republic, Jamaica, Puerto Rico

Introduction

Beetles are one of the largest ordinal taxa among living organisms with about 400,000 known species (McKenna *et al.* 2019). They account for almost 25% of known species on Earth and about 40% of insects (Ślipiński *et al.* 2011). Beetles occur in almost all types of terrestrial and freshwater habitats both as adults and larvae (Crowson 1981). Although many beetles inhabit and can be seen on various vegetative and other surfaces (e.g., upper and lower sides of leaves, stems, and flowers of various plants, soil surface etc.) (Crowson 1981), many also occur inside substrates, such as leaf litter (Chandler 1987), wood at various stages of decay (Gimmel & Ferro 2018) and soil, including deep soil

(Andújar *et al.* 2017, Andújar & Grebennikov 2021). Moss mats and moss cushions are another type of substrate where beetles have been noticed since early days of coleopterology (Westwood 1839; Douglas 1870; Waterhouse 1870).

Moss cushions and bryophyte communities in general occur on the soil surface, forest floor, rocks, on the bark of living and dead trees, and stems and leaves of various plants (Smith 1982). These are “forest bryophyte societies” as defined by Mägdefrau (1982). Bryophyte communities are among the first colonizers of extreme and inhospitable places (Gerson 1982; Porley & Hodgetts 2005) and often are the main components of high-altitude ecosystems forming petriophyte communities 6300–6600 meters above sea level (Mani 1978). Among life forms of bryophytes (Mägdefrau 1982), cushions and mats occupy a layer of still air at the land-air interface which traps heat and moisture (Brown 1976; Porley & Hodgetts 2005). Two additional features make bryophytes unique: their perennial nature, which renders bryophytes as a food source and habitat for overwintering or surviving dry season when many tracheophytes are absent (Glime 2017); and the small size of spaces among the stems and leaves within cushions which serve as shelters for small animals (Gerson 1982). Because of these features, moss cushions are populated by a particular fauna of phytophagous, fungivorous, saprophagous and predatory invertebrates. Several categories have been suggested to classify animals according to their relationship with moss communities. Chernov (1985) called invertebrates living in mosses semi-edophores (which indicates that they spend part of their life cycle in soil). Gerson (1982) divided moss faunae into bryobionts (animals living exclusively within mosses); bryophiles (animals that are usually associated with mosses but can be found elsewhere); bryoxenes (animals spending part of their life cycle within mosses); and occasionals (animals that at times are found in mosses but do not depend on them for survival). Bryobionts obviously include not only beetles that feed on moss tissues, but also those that are associated with fungi that only grow in moss cushions. This classification is adapted herein.

Beetles constitute a substantial part of invertebrates inhabiting moss cushions (Nelson & Hauser 2012). A few beetle families almost entirely consist of bryobionts or bryophiles, closely associated with mosses during entire life span both as adults and larvae – see Armatopodidae (Lawrence 2011) and Byrrhidae (Johnson 1986). In other families where most species feed openly on leaves of their host plants, some groups occur only inside or on the surface of moss cushions and mats [e.g., Chrysomelidae: Chrysomelinae (Leschen *et al.* 2020) and Galerucinae: Galerucini (Lee & Beenan 2020) and Alticini (Damaška *et al.* 2022; Konstantinov & Linzmeier 2020)]. Many carnivorous beetles use moss cushions as their hunting grounds (Bordoni 1972; Lindroth 1974). However, moss cushions have been excluded from the lists of beetle habitats in some major works (e.g., Crowson 1981; Lawrence & Ślipiński 2013). Generally, and unlike leaf litter, moss cushions and their beetle assemblages have not attracted much attention among coleopterists. In this paper we provide an account for beetles that inhabit moss cushions in three of the West Indies Islands of the Greater Antilles: Hispaniola (Dominican Republic only), Jamaica, and Puerto Rico. The region in question is one of the World’s biodiversity hotspots (Myers *et al.* 2000). The West Indian flora and fauna are rich and highly endemic. Seventy-two percent of 11,000 plant species of the West Indies are endemic (BirdLife International 2009). Among vertebrates, 99% of amphibians and 93% of reptiles are endemic (Hedges 2001). A great variety of ecosystems exist in the West Indies, ranging from tropical, moist broadleaf forests to xeric cactus scrublands. Most substantial bryophyte communities occur in the forest on the mountain slopes at significant for West Indies altitudes (Table 1).

Material and methods

Specimen collecting

Beetles for this study were collected by ASK from 2004 to 2014 in the Dominican Republic, Jamaica, and Puerto Rico in 18 localities (Table 1). In total 1711 specimens were collected. The following steps were taken to process moss samples and moss-living beetles (Konstantinov *et al.* 2013; Linzmeier & Konstantinov 2020; Ruan *et al.* 2020):

- 1) Field collection (Figs 1–6): Moss collection was generally reserved for the first part of collecting trips, so that samples can be slowly processed through the entire length of the trip. Clumps of terrestrial moss cushions and mats were taken from various substrates: tree trunks, tree branches, ground, and rocks. Handpicked moss clumps often contained liverworts, traces of soil, small plants growing inside moss cushions, leaf litter and some other decaying plant debris often found on various surfaces in the tropics. Clumps were placed in cloth bags (usually locally purchased pillow covers) and brought to the “field laboratory”.

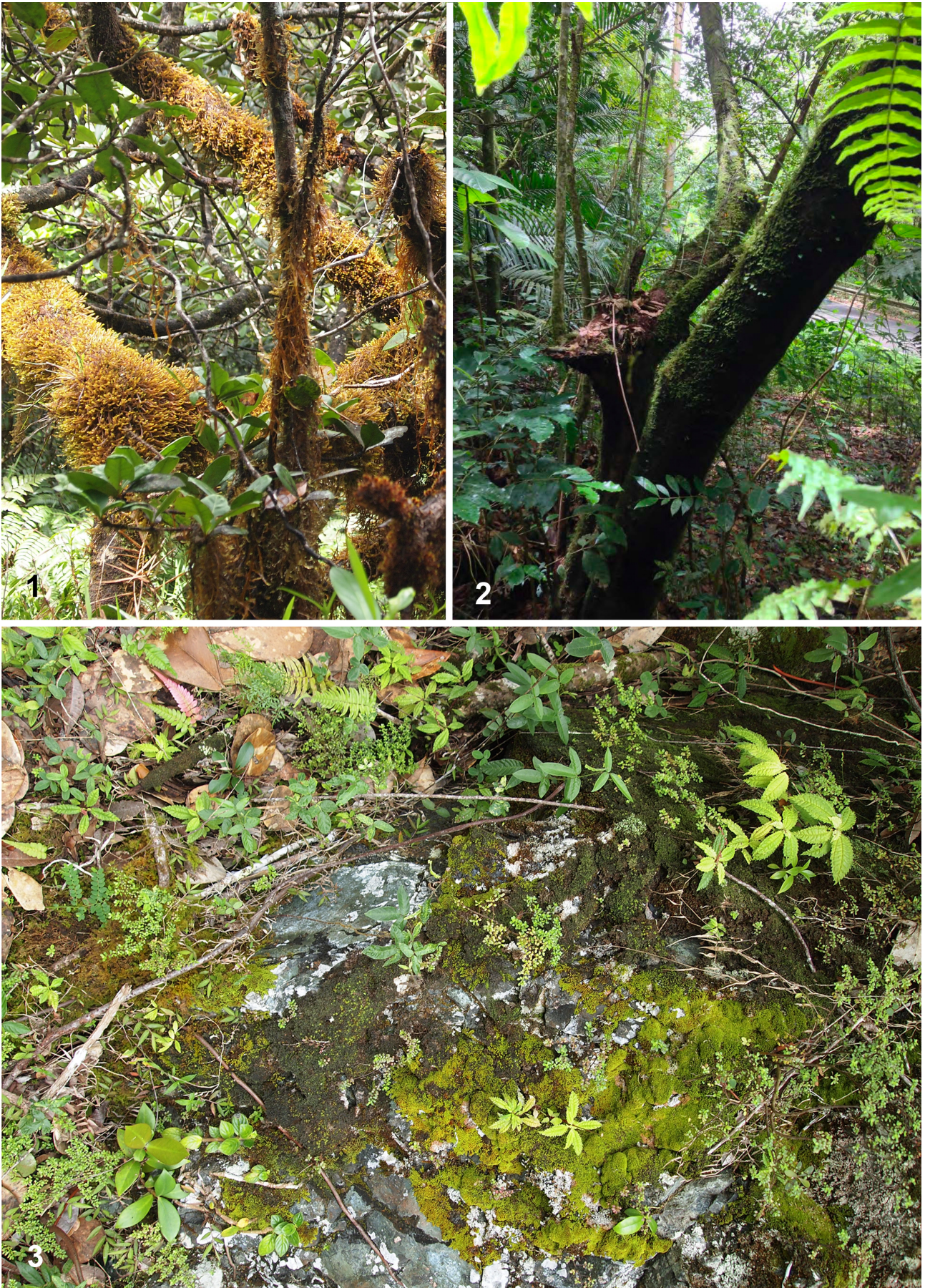
- 2) Berlese funnels (Fig. 7): Bags with unsifted moss were kept moist and away from sun through the trip. Their contents were gradually placed directly in Berlese funnels while keeping the quantity of moss limited so that it would dry after about 12 hours inside the funnel. Moss was replaced in each funnel twice per day, in the morning and in the

evening. If, at the end of a “cycle” moss was still moist, it was kept in the funnel for an additional 12 hours. Altogether four funnels were used simultaneously in each collecting trip (on average eight moss loads per 24 hours). Two kinds of Berlese funnel were used, one called “Collapsible Berlese Funnel Trap” produced by Bioquip (Fig. 7, two funnels in the background) and another called “Tray-type Berlese Funnel” by MegaView Science Co., Ltd (Fig. 7, two funnels at the front of the image). Both kinds of funnels were modified in two ways: net filters with mesh opening of 2–4 mm were put on top of the grill trays to limit the debris falling through, and, instead of vials, whirl packs with labels and alcohol were attached to the apex of the funnel with a duct tape. A new extracting technique was offered by Ruan et al (2020), but it was not used in this study.

3) Sifting (Figs 10–12): To save time for field collecting, moss was sifted in the “field laboratory” while collecting was not possible due to bad weather or by the end of the trip when it became clear that there was not enough time to process all the collected moss through Berlese funnels without sifting. Therefore, moss samples were sifted into mesh bags, which dramatically reduced the size of the remaining substrate. At times flea beetles crawled on the sides of the bags and were collected there. Sifted substrate was then processed through Berlese funnels. It is assumed that sifting may cause a loss of beetle specimens (Konstantinov *et al.* 2013).

Table 1. Moss collecting events

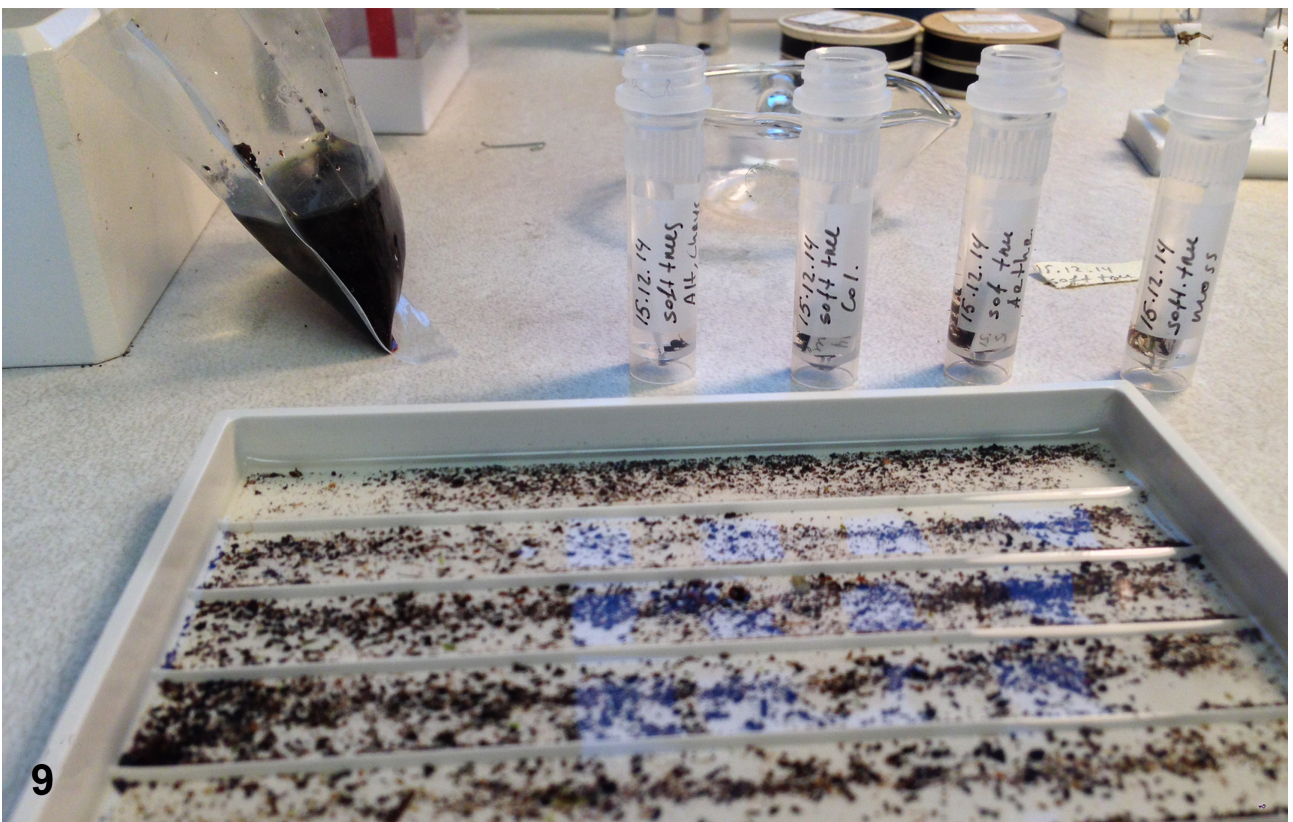
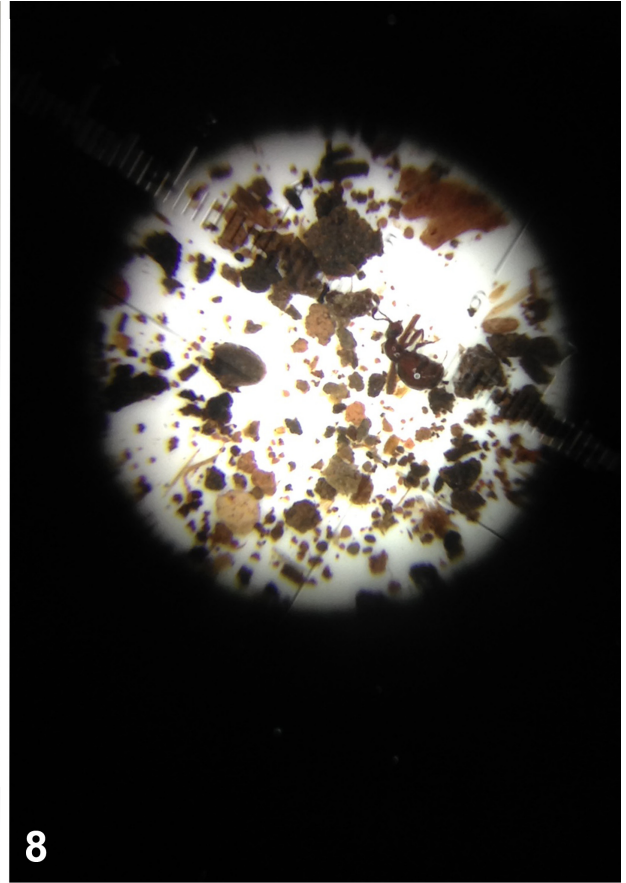
| Country | locality | coordinates | date | WP | altitude m | volume of moss | method of extraction | moss kind and place | # of taxa | # of adult specimens |
|--------------------|-----------------|----------------------------|--|-----|---------------|-------------------|-----------------------------------|------------------------|--------------|-------------------------|
| Dominican Republic | Los Tablones | N19°08.22 W70°27.73 | 29.6.2004 | | 1200 | 1 bag | Berlese, unsifted moss | ground, trees | 22 | 360 |
| Dominican Republic | Pico Duarte | N19°01.75 W70°54.65 | 30.6.2004 | | 1900 | 1 bag | Berlese, unsifted moss | ground, trees | 12 | 101 |
| Dominican Republic | Pico Duarte | N19°02.15 W70°59.10 | 1.7.2004 | | 2590 | 2 bags | Berlese, sifted and unsifted moss | ground, trees | 6 | 44 |
| Dominican Republic | Las Abejas | N18°09.008' W71°37.338' | 18.6.2005 | | 1270 | 1 bag | Berlese, unsifted moss | trees | 27 | 77 |
| Dominican Republic | Las Abejas | N18°09.132' W71°37.430' | 17.7.2006 | | 1230 | 2 bags | Berlese, sifted and unsifted moss | trees | 8 | 12 |
| Dominican Republic | Sierra de Neiba | N18°41.644' W71°46.457' | 12.7.2006 | | 1597 | 1 bag | Berlese, sifted and unsifted moss | trees | 36 | 166 |
| Dominican Republic | El Cachote | N18°03.295' W71°09.778' | 08.12.2014 | 189 | 961 | ¾ bag | moss | trees | 26 | 91 |
| Dominican Republic | Zapoten | N18°19.655' W71°41.994' | 15.12.2014 | 522 | 1705 | 1 bag | Berlese, sifted and unsifted moss | thick/rock | 20 | 24 |
| Dominican Republic | Zapoten | N18°19.655' W71°41.994' | 15.12.2014 | 522 | 1705 | 1 bag | Berlese, sifted and unsifted moss | thick/soil | 3 | 4 |
| Dominican Republic | Zapoten | N18°19.655' W71°41.994' | 15.12.2014 | 522 | 1705 | 1 bag | Berlese, sifted and unsifted moss | thin/rock | 27 | 52 |
| Dominican Republic | Zapoten | N18°19.655' W71°41.994' | 15.12.2014 | 522 | 1705 | 2 bags | Berlese, sifted and unsifted moss | thick/trees | 19 | 456 |
| Jamaica | Troy | N18°15.915' W77°39.220' | 12.7.2015 | | 705 | 1 bag | Berlese, unsifted moss | trees, ground | 5 | 7 |
| Jamaica | Dolphin Head | N18°22.546' W78°10.694' | 15.7.2015 | | 315 | 2 bags | Berlese, sifted and unsifted moss | ground, trail side | 10 | 22 |
| Puerto Rico | El Yunque | N18°16.541 W65°50.238 | 14.VI.2008, 16.VI.2008, 08.IX.2014 | 488 | 952 | 3 bags | Berlese unsifted moss | trees | 20 | 136 |
| Puerto Rico | Toro Negro | N18°09.478 W66°31.202 | 01.09.2014 | 472 | 917 | 1 bag | Berlese with and without light | trees | 12 | 29 |
| Puerto Rico | Toro Negro | N18°10.335 W66°35.504 | 03.09.2014 | 478 | 1350 | ½ bag | Berlese, sifted and unsifted moss | trees, ground | 19 | 88 |
| Puerto Rico | Maricao | N18°08.041 W66°57.290 | 04.09.2014 | 483 | 702 | ¼ bag | Berlese, sifted and unsifted moss | trees | 6 | 17 |
| Puerto Rico | Maricao | N18°08.089 W66°58.932 | 06.09.2014 | 486 | 902 | ¾ bag | Berlese, sifted and unsifted moss | ground | 8 | 25 |
| Total | | | | | | | | | (285) | 1711 |



Figures 1–3. Moss cushions sampled in Puerto Rico. **1,** El Yunque; **2,** Toro Negro; **3,** Maricao.



Figures 4–6. Moss cushions sampled. **4**, Jamaica, Troy; **5**, Dominican Republic, Zapoten; **6**, Dominican Republic, El Cachote.



Figures 7–9. Methods for collecting moss inhabiting beetles. 7, Berlese funnels at work with attached whirls packs; 8, sorting residue, view through microscope ocular; 9, tray for sorting moss sifting residue with vials for storing beetles and other arthropods.



Figures 10–12. Methods for collecting moss-inhabiting beetles. **10**, bag of moss and sifter attached to a bag for sifting residue; **11**, flea beetle inside a bag for storing sifting residue; **12**, moss sifting in progress.

4) Sorting (Figs 8–9): Whirl packs were taken to the USNM for sorting and specimen processing. Contents of whirl packs were gradually unloaded into a sorting tray and examined under a microscope. To prevent overlooking specimens, some of which were less than 1 mm in length, small amounts of material were placed into the sorting trays each time. Beetles and other arthropods were then sorted into following categories placed in separate alcohol filled vials: Chrysomelidae, adults and larvae; other Coleoptera, adults and larvae; other insects, adults and larvae; other invertebrates; moss samples (Linzmeier & Konstantinov 2020).

This sampling technique is not perfect and it must be assumed that some specimens can be lost at every step of the sampling process: a) in the field during moss picking and dropping it in the bag, b) while moss clumps are placed in Berlese funnels, c) during sifting, d) not all specimens placed in Berlese funnels end up in the whirl packs, e) and possibly overlooked during sorting.

Collecting methods described above do not assure that all collected beetles are bryobionts. There are many small plants, liverworts, and fungi growing within or through the moss cushions. Some of them are being picked up when moss is collected, so arthropods that may be associated with them may also end up in our samples. Collected samples also contained traces of soil, leaf litter and other decaying plant debris. As a result, some collected beetles are bryoxenes and occasionals as defined by Gerson (1982).

Specimen processing

Beetles were mounted, labeled, and sorted to families and morphospecies by AKT, Curculionidae and Staphylinidae except Pselaphinae were further identified by RSA and VIG accordingly. Pselaphinae were identified by BEO and CC. Chrysomelidae were identified by ASK. Other “small” families were identified by MAI and IMS.

Mosses were not identified for the following reasons: 1) moss feeding beetles are widely polyphagous (Konstantinov *et al.* 2019), as many other moss feeding insects (Gerson 1982); 2) moss clumps were collected in a way that more than one moss species was placed in the same collecting bag; 3) many beetles living with moss cushions use them as a substrate, not as a food source, so physical qualities of moss clumps such as density and size of spaces in-between plants is a factor; 4) some saprophagous beetles are such generalists that moss species on which they feed on may not be important.

We used some distributional categories suggested by Ivie *et al.* (2008) for beetles collected in Montserrat. In addition, a few categories applicable for beetles of Greater Antilles were used. The source of the flea beetle diversity numbers is an unpublished World flea beetle genus and species compilation, which is a FileMakerPro database maintained by ASK since 2006. It is cited as follows: (Konstantinov unpublished compilation). Digital images of beetles were taken with Macropod Pro photomacrography system (Macroscopic Solutions, LLC, Tolland, CT, USA), processed with Zerene Stacker, version 1.04 and edited with Adobe Photoshop Elements 2020.

Voucher specimens are deposited in the following collections:

USNM – National Museum of Natural History, Smithsonian Institution, Washington, D. C. – Chrysomelidae and other families not mentioned below.

CMNC – Canadian Museum of Nature, Ottawa, Canada – Curculionidae.

LSAM – Louisiana State Arthropod Museum, Baton Rouge, Louisiana – Pselaphinae.

WIBF – West Indian Beetle Fauna Project Collection, Montana State University, Bozeman, Montana – Anamorphidae, Tenebrionidae.

ZMUN – Natural History Museum, University of Oslo, Norway – Staphylinidae, except Pselaphinae.

Statistical analyses

We first assessed whether beetle abundance was related to the volume of moss collected in each sample (linear regression) or the substrate (trees vs. soil/rock via Wilcoxon test) of the different sampling events included in Table 1. We then analyzed the patterns of variation in species richness and community composition (i.e., beta diversity). For this, the four samples collected in Zapoten (Dominican Republic) were pooled into a single community, as all were taken in the same location (i.e., identical geographical coordinates and altitude) on the same day. This yielded a total of 15 local communities, for which we built a presence/absence table. This table included 15 sites (rows) and 234 species (columns). All statistical analyses were conducted in R. From this table, we computed species richness for each community and analyzed whether the variation in species richness was related to the amount of moss sampled, the spatial coordinates or altitude. To do this, species richness was linearly regressed against the volume of moss sampled, spatial coordinates or altitude. We also assessed whether community composition varied in relation to spatial position (longitude and latitude) and altitude. Variation in community composition was measured as Simpson dissimilarity (Simpson 1960), an index that is independent of richness differences and thus accounts only for the replacement of

species from site to site (Baselga 2010). Pairwise Simpson dissimilarity between local communities was computed using package *betapart* (Baselga & Orme 2012; Baselga *et al.* 2022). The resulting dissimilarity matrix was submitted (i) to a Nonmetric Multidimensional Scaling (NMDS) to visually describe the pattern of variation in community composition across sites, and (ii) to a Distance-Based Redundancy Analysis (db-RDA) that assessed whether the variation in species composition was explained either by spatial position or altitude. Both analyses were conducted in R using package *vegan* (Oksanen *et al.* 2022). Finally, we also assessed the relationship between community similarity (i.e., 1 – Simpson dissimilarity) and spatial distance. For this, we computed geodesic distance between geographical coordinates using package *geodist* (Padgham & Sumner 2021), and then fitted an exponential distance-decay model using *betapart* and following the same methods described in Gómez-Rodríguez and Baselga (2018) and Martínez-Santalla *et al.* (2022).

Results and Discussion

In total, 1711 adult beetles belonging to 234 species from 30 families (Figs 13–43) were collected (Table 2). The most species and specimen rich families are Staphylinidae (86 morphospecies and 1195 specimens, 13 species and 949 specimens of which are Pselaphinae), Curculionidae (61 and 131 respectively), and Chrysomelidae (16 and 185). Fourteen families are represented by one or two species and by one or two specimens (Table 2). They may be bryoxenes or occasional. The other families with a few species have more specimens that may indicate that they are substantially associated with mosses (e.g., Latridiidae with seven specimens of two species; Ptilodactylidae with seven specimens of four species; and Sylvanidae with ten specimens of two species). Most collected beetles were adults and only a few larvae of Chrysomelidae (Tables 3 and 4) and Carabidae were collected (not identified). The small number of larvae in moss samples is similar to what was reported for endogean beetles in Madagascar (Andújar & Grebennikov 2021). Byrrhidae were not found in our samples as they mostly occur in the Holarctic and none are known from the West Indies (Blackwelder 1944).

Bordoni's (1972) study of beetle assemblages in bryophyte communities in Italy comparable in size to the present one revealed 4024 specimens of 179 species from 25 families. As in our study, Staphylinidae (with Pselaphinae) were the most species and specimen rich group with 72 species and 875 specimens (Bordoni 1972). Bordoni (1972) reported more Staphylinidae *sensu stricto* (655) than Pselaphinae (220), which in our study was reversed (Table 2). Carabidae were the second-best represented family with 24 species and 121 specimens, but in our study we found only three specimens of three species, which are most likely bryoxenes. Chrysomelidae, Curculionidae, and Latridiidae were found in negligible numbers (Bordoni 1972), however they are one the most species and specimen rich in our study. The other families that Bordoni (1972) found in relatively small numbers are: Anobiidae, Corylophidae, Cryptophagidae, Scirtidae, Hydrophilidae, Phalacridae, Ptiliidae, Scaphidiidae, Scydmaenidae (both within Staphylinidae now), Tenebrionidae, Throscidae. To compare it with our list of families see Table 2.

A study of beetle assemblages in a mature *Sphagnum* bog in Ontario, Canada (Runtz & Peck 1994) using pan and emergence traps during 3 months resulted in 5734 specimens belonging to 30 beetle families. In that study, Carabidae, Ptiliidae and Staphylinidae represented more than 80% of total specimens. Staphylinidae and Carabidae were the most taxonomically diverse (Runtz & Peck 1994). As with Bordoni (1972) study, Chrysomelidae and Curculionidae were collected in small numbers. The difference in taxon samples between Runtz & Peck (1994) and our study may be partly explained by the difference in collecting methods. Pan traps may be better at capturing beetles that move to find food (such as predators) and our methods may be better to collect beetles that are more sedentary feeders, such as leaf beetles or beetles feeding on fungi. Altogether, the vast majority of beetles in *Sphagnum* bog were not “bog-specific” (Runtz & Peck 1994). Considering the prevalence of Staphylinidae in our study, it may largely agree with these results.

How well known are moss inhabiting beetles?

Moss inhabiting beetles are much less known than those living openly. In Chrysomelidae all beetle species found in mosses prior to this study were undescribed and four genera out of six turned out to be new to science (all described now – Konstantinov *et al.* 2020b). A new genus and species of a recently resurrected family Cerasommatidiidae, was described from boreal mosses of Toro Negro (Puerto Rico) (Arriaga-Varela *et al.* 2022). Not counting Chrysomelidae, out of 222 morphospecies only 11 were identified to species. Among Staphylinidae (excluding Pselaphinae), 29 morphospecies out of 73 were identified to genus and none to species. And among Curculionidae (excluding Scolytinae),

35 morphospecies out of 60 were identified to genus and only four to species. The world fauna of *Micropsephodes* Champion (Anamorphidae) contains two described species, yet there are nine species of this genus in our sample, all are likely undescribed. As for other beetles, not all unidentified taxa are necessarily new to science, but these considerations confirm how little is known about beetle diversity and specifically that occurring in moss cushions.

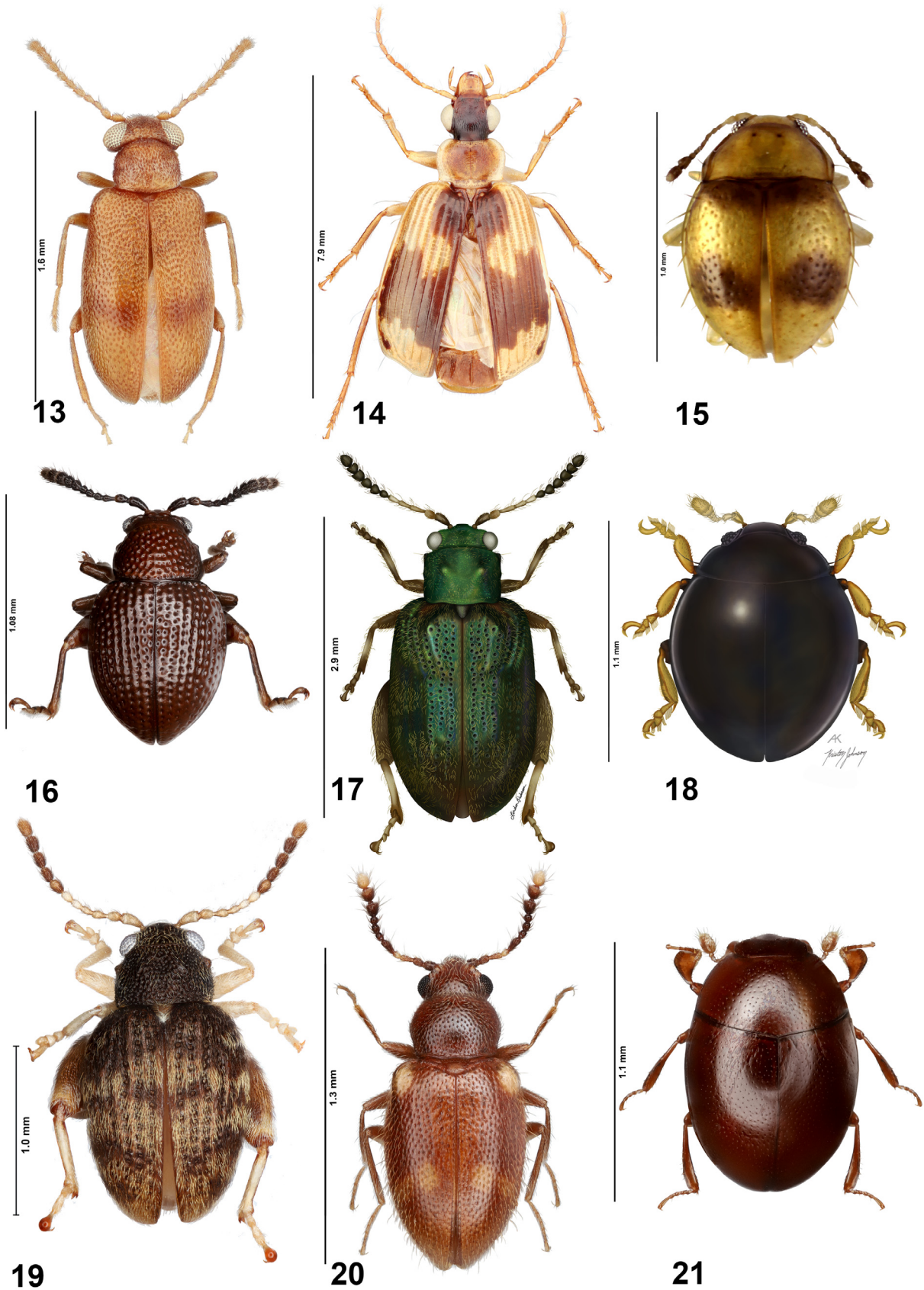
Table 2. Moss inhabiting beetle families, number of species and specimens

| # | Family | # species | # adult specimens | Id to genus | Id to species |
|----|----------------------------|-----------|-------------------|-------------|---------------|
| 1 | Aderidae | 1 | 1 | 1 | 0 |
| 2 | Anamorphidae | 9 | 47 | 9 | 0 |
| 3 | Anobiidae | 1 | 2 | 1 | 0 |
| 4 | Anthribidae | 1 | 1 | 0 | 0 |
| 5 | Brentidae | 1 | 1 | 0 | 0 |
| 6 | Carabidae | 3 | 3 | 3 | 2 |
| 7 | Cerasomatidiidae | 1 | 1 | 1 | 1 |
| 8 | Chrysomelidae | 16 | 185 | 6 | 16 |
| 9 | Ciidae | 3 | 5 | 1 | 0 |
| 10 | Coccinellidae | 3 | 6 | 1 | 0 |
| 11 | Corylophidae | 2 | 3 | 2 | 0 |
| 12 | Curculionidae s.str. | 56 | 125 | 31 | 3 |
| | Curculionidae, Scolytinae | 5 | 6 | 5 | 2 |
| 13 | Endomychidae | 2 | 2 | 0 | 0 |
| 14 | Erotylidae | 4 | 4 | 3 | 0 |
| 15 | Histeridae | 5 | 6 | 5 | 0 |
| 16 | Lampyridae | 1 | 1 | 1 | 0 |
| 17 | Latridiidae | 2 | 7 | 2 | 0 |
| 18 | Leiodidae | 4 | 4 | 4 | 1 |
| 19 | Lycidae | 1 | 1 | 0 | 0 |
| 20 | Melandryidae | 2 | 2 | 2 | 0 |
| 21 | Melyridae | 1 | 1 | 1 | 0 |
| 22 | Monotomatidae | 1 | 1 | 1 | 0 |
| 23 | Nitidulidae | 1 | 1 | 1 | 0 |
| 24 | Ptiliidae | 2 | 10 | 0 | 0 |
| 25 | Ptilodactylidae | 4 | 7 | 4 | 0 |
| 26 | Scarabaeidae | 2 | 2 | 1 | 0 |
| 27 | Staphylinidae s.str. | 73 | 246 | 29 | 0 |
| | Staphylinidae, Pselaphinae | 13 | 949 | 13 | 1 |
| 28 | Sylvanidae | 2 | 10 | 2 | 0 |
| 29 | Tenebrionidae | 6 | 63 | 3 | 1 |
| 30 | Zopheridae | 6 | 8 | 6 | 0 |
| | total | 234 | 1711 | 140 | 27 |

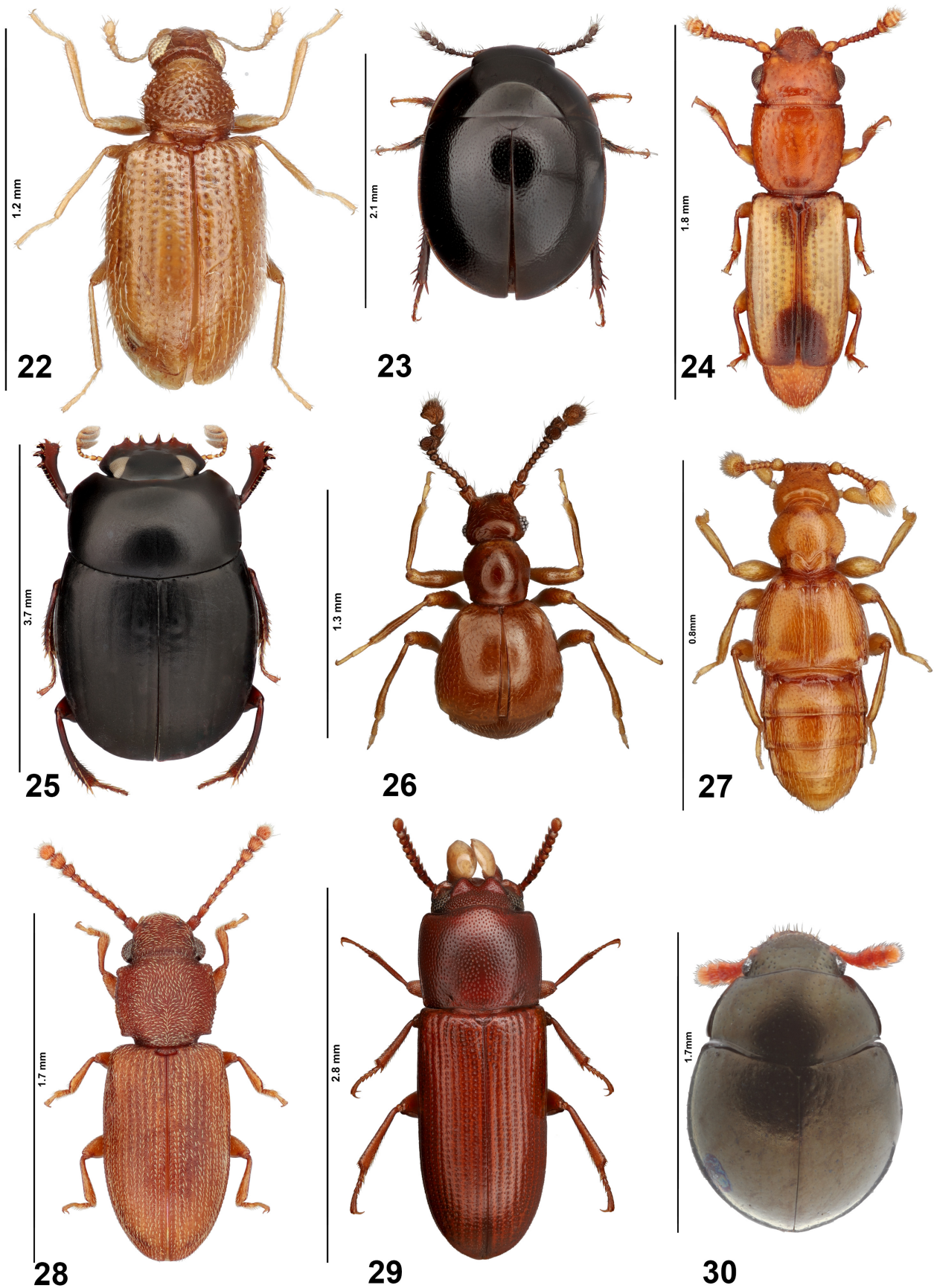
Morphological traits

Moss inhabiting beetles from many families share similar morphological traits with beetles living in other substrates such as leaf litter (Konstantinov & Tishechkin 2004) and deep soil (Andújar & Grebennikov 2021). They are generally small, on average smaller than openly living members of the family. One of the smallest is an unidentified Ptiliidae, 0.6 mm long (Fig. 41).

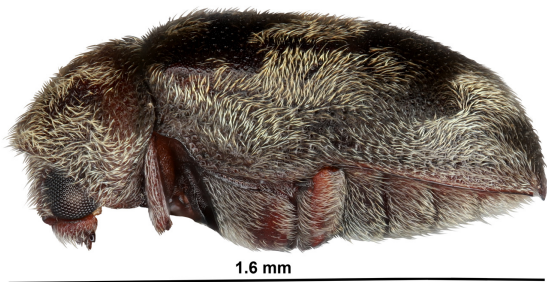
Moss inhabiting beetles are characterized by roundish bodies and often by the absence or reduction of wings to the extent that their elytra are fused. As the result of flightlessness, their flight muscles and many thoracic structures are reduced (Konstantinov & Chamorro-Lacayo 2006). This is especially true for Chrysomelidae, which, in addition to features mentioned above, tend to have antennomeres gradually enlarging from base to apex (Fig. 16) which makes them appear clavate (Fig. 18) (Konstantinov & Konstantinova 2011). The vast majority of openly living leaf beetles have filiform or, less often, serrate antennae. Antennae of some other moss-inhabiting flea beetles have reduced number of antennomeres compared to openly living (*Kiskeya* - nine antennomeres). As a result, moss-inhabiting beetles from different families have very similar body shape and size and general antennal structure [see *Kiskeya* in Chrysomelidae (Fig. 18) and *Prototyrtaeus* in Tenebrionidae (Fig. 30)]. While openly living beetles from the same families are wildly different. All moss inhabiting Chrysomelidae known so far have eyes, but *Borinken* Konstantinov & Konstantinova (Konstantinov *et al.* 2020a) have a few facets. In beetles from other families blindness occurs (e.g., Curculionidae).



Figures 13–21. Dorsal habiti of moss-inhabiting beetles. **13**, Aderidae: *Vanonus* sp.; **14**, Carabidae: *Lebia* sp.; **15**, Cerasommatidiidae: *Yamuy marginatus* [cortesy of Emmanuel Arriaga-Varela (Centro de Estudios en Zoología, Universidad de Guadalajara, Mexico)]; **16**, Chrysomelidae: *Borinken elyunque*; **17**, *Erinacealtica janestanleyae* (illustration by L. Pederson, SEL scientific illustration internship program, 2018); **18**, *Kiskeya baorucae* (illustration by AK, edited by K. Johnson, SEL scientific illustration internship program, 2017); **19**, *Menudos maricao*; **20**, Erotylidae: *Toramus* sp.; **21**, Histeridae: *Bacanius* sp.



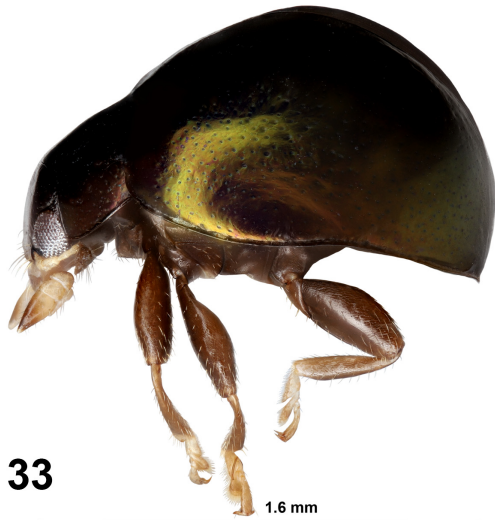
Figures 22–30. Dorsal habiti of moss-inhabiting beetles. 22, Latridiidae: *Melanophthalma* sp.; 23, Leiodidae: *Aglyptinus* sp.; 24, Monotomatidae: *Europs* sp.; 25, Scarabaeidae: *Canthochilum* sp.; 26, Staphylinidae: Pselaphinae: *Bythinogaster* sp., 27, *Dalmosanus* sp.; 28, Sylanidae: *Ahasverus* sp.; 29, Tenebrionidae: *Gnathocerus* sp., 30, *Prototyrtaeus obrieni* (modified from Spiessberger and Ivie 2020)



31



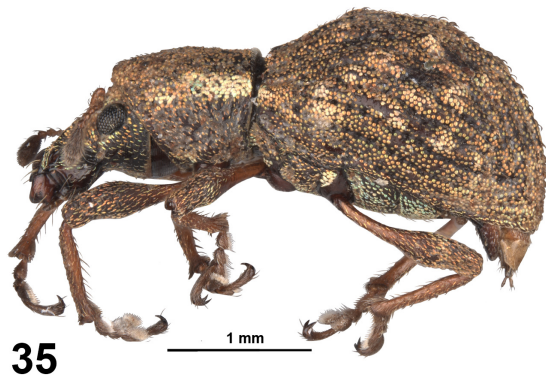
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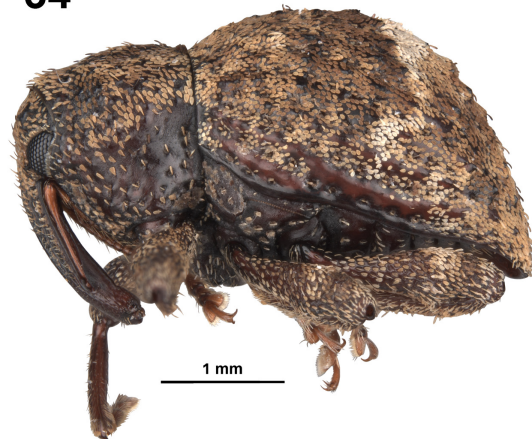
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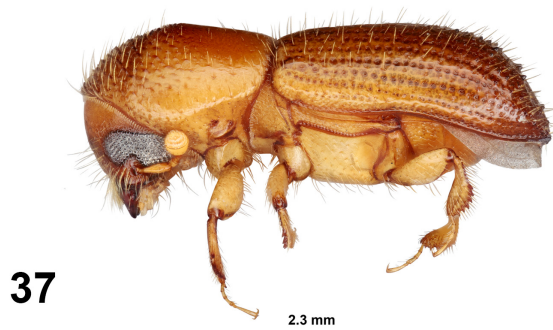
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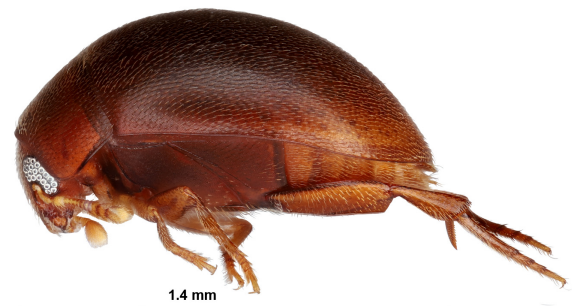
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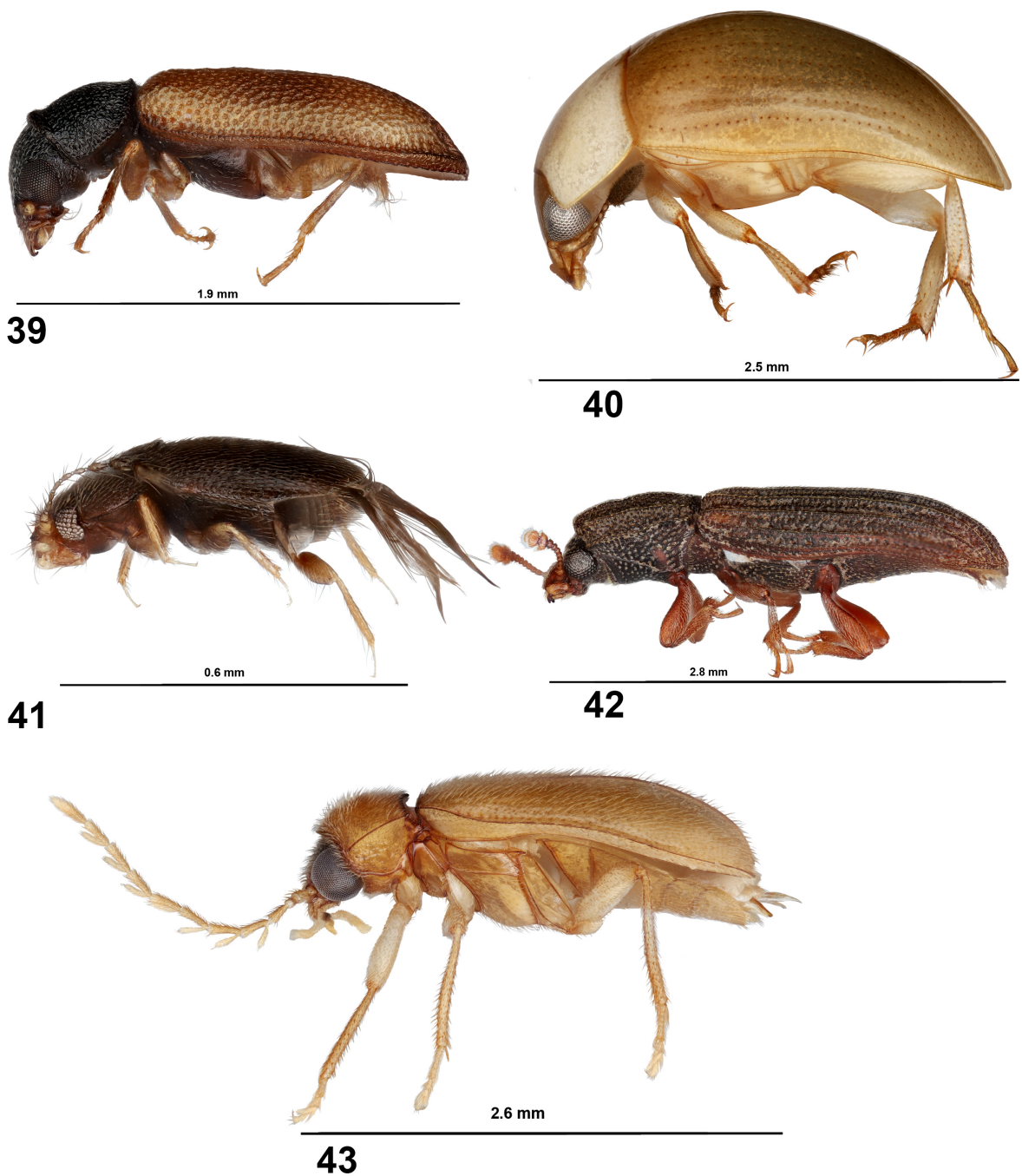


37



38

Figures 31–38. Lateral habiti of moss-inhabiting beetles. **31**, Anobiidae: *Protheca* sp.; **32**, Ciidae: *Cerasis* sp.; **33**, Coccinellidae: Sticholotidini; **34**, Corylophidae: *Sericoderus* sp.; **35**, Curculionidae: Anypotactini; **36**, *Neotyloides* sp.; **37**, Scolytinae: *Xyleborus volvulus* sp.; **38**, Melandryidae: *Microscapha* sp.



Figures 39–43. Lateral habiti of moss-inhabiting beetles. **39**, Melyridae: *Melyrodes* sp.; **40**, Nitidulidae: *Pallodes* sp.; **41**, Ptiliidae; **42**, Zopheridae: *Bitoma* sp.; **43**, Ptilodactylidae: *Ptilodactyla* sp.

Trophic association

In our estimation 1430 moss inhabiting beetles in our samples are phytophagous or saprophagous. That is assuming that all non-pselaphine Staphylinidae are carnivores. A study of general predation in moss cushions in the submontane forest of the Beskydy and Jeseníky Mountains in the Northern Moravia (Czech Republic) revealed that on the surface of the cushions the main predators are ants, spiders, and birds, but inside the cushions millipedes, carabids and staphylinids are the dominant predators (Drozdová *et al.* 2009). Carabids were also dominant in moss cushions of another European locality (Bordoni 1972).

Similarly, Runtz & Peck (1994) reported that the majority of beetles in their study were generalist predators and scavengers and only a few phytophagous. Some staphylinids in our samples come from tribes or genera other species of which feed on fungi or their spores. Although phytophagous Chrysomelidae and Curculionidae represent a large part of the entire species diversity in our study, predators may be more diverse. It may look as broadly phytophagous beetles tend to be bryobionts, while many non-phytophagous beetles (Staphylinidae) are bryoxenes or occasionals.

Predator pressure may explain why some potentially moss surface-living flea beetles are flightfull and have camouflage color to evade visual predators (e.g. *Erinaceiatica* Konstantinov & Linzmeier 2020, Fig. 17) in comparison to deep moss-living flea beetles that are flightless and uniformly brown or black (for example *Kiskeya*, Fig. 18).

Direct evidence of bryophagy in moss inhabiting beetles is rare and none is known for the West Indies. In Chrysomelidae, bryophagy was observed directly in the field [United States (Konstantinov *et al.* 2019), Malaysia (Takizawa & Konstantinov 2018) and Taiwan (Lee & Beenan 2020)]. Examination of a beetle gut content in the laboratory revealed remnants of bryophyte cell tissues (Duckett *et al.* 2006, Ruan *et al.* 2020). As was mentioned above, moss inhabiting Chrysomelidae are generally broadly polyphagous as many other moss feeding insects (Gerson 1982). For example, adults and larvae of *Distigmoptera borealis* Blake consumed liverwort *Reboulia hemisphaerica* (L.) Raddi (Aytoniaceae) and gametophytes of moss *Weissia controversa* Hedw. (Pottiaceae) and adults were observed eating capsules (sporophytes) of *Weissia* sp. (Konstantinov *et al.* 2019).

Distribution patterns

We attempt to assess distributional patterns of moss inhabiting beetles based on the categories suggested for Montserrat beetles (Ivie *et al.* 2008) [Island endemic, Local endemic (a few islands), West Indian endemic] and categories more applicable for beetles of the Greater Antilles. Since the majority of beetles identified at most only to genus, this analysis is far from rigorous. However, what is apparent is that the ranges of surface-living beetles occurring in the same localities as moss-inhabiting beetles are much larger. Among them are beetles distributed in the entire Greater Antilles, West Indies and even Central America (e.g., *Cerotoma ruficornis* Olivier and *Diabrotica graminea* Baly among Chrysomelidae).

Most moss-inhabiting West Indian beetles identified to species are highly endemic (Island endemic or single location endemic). *Prototyrtaeus* species (Tenebrionidae) inhabit different mountain ranges in the Dominican Republic, with a high degree of endemism on the tops of the mountain ranges (Spiessberger & Ivie 2020). Similar pattern is known for *Kiskeya* (Chrysomelidae) in Hispaniola with two species occurring in two neighboring but isolated mountain ranges: Sierra de Neiba and Sierra de Baoruco (Konstantinov & Chamorro-Lacayo 2006). In Puerto Rico, three species of *Kiskeya* are located at the mountain tops of three main mountain regions of the island: El Yunque, Maricao, and Toro Negro (Konstantinov *et al.* 2020a).

Some West Indian endemics have a close relative on South American continent (e.g., *Yamuy* Arriaga-Varela, Tomaszewska & Szawaryn with two species in Puerto Rico and Venezuela) (Arriaga-Varela *et al.* 2022).

Openly living and moss inhabiting beetle communities

The only data for comparing openly-living and moss-inhabiting beetle communities at the same localities is available for Chrysomelidae in two places in Puerto Rico: Maricao and Toro Negro (Tables 3 and 4). Obviously lists of beetles for both locations, especially surface-living are not complete. However, it is clear that surface-living communities are drastically different from moss-living. There is not a single species and even a genus of leaf beetles that occurs on the surfaces and inside moss cushions. Taxonomic diversity as well as specimen abundance is also much greater for surface-living beetles. Representatives of Cassidinae, Cryptocephalinae, Eumolpinae, and Lamprosomatinae collected in Maricao are not found in mosses (Table 3). In Toro Negro (Table 4), tree-fern feeding *Leptophysa* Baly is collected on the leaf surface while *Borinken*, a sister group to *Leptophysa* (Damaška *et al.* 2022, Douglas *et al.* 2023), is found in moss cushions. Interestingly, another Toro Negro fern-feeding flea beetle, *Normaltica obrieni* Konstantinov, belongs to the same clade together with moss-living Bolivian *Stevenaltica* Konstantinov (Douglas *et al.* 2023).

Community ecology

Beetle abundance was not significantly related to either the volume of moss reported in Table 1 ($r^2=0.048$, $F_{1,16}=0.91$, $p=0.38$) or the substrate (Wilcoxon $W=7$, $p=0.065$). Despite being not significant (but close to), the observed trend was to higher beetle abundance in moss cushions collected in trees than in those collected in soil/rock. Given the low sample size ($n=13$ after removing samples taken in pooling moss from both substrates), this result suggests that substrate might be a relevant predictor of beetle abundance in moss cushions (Fig. 44). Species richness was not significantly related to either the volume of moss ($r^2=0.0041$, $F_{1,16}=0.06$, $p=0.80$) or the geographical coordinates of

sampling sites ($r^2 < 0.0001$, $F_{1,12} < 0.1$, $p = 0.99$), or altitude ($r^2 = 0.063$, $F_{1,12} = 1-86$, $p = 0.36$). In turn, the NMDS ordination based on Simpson similarity ($k=2$, stress = 0.038) suggested a clearly structured pattern of variation in community composition, following both spatial and altitudinal gradients (Fig. 45). This was confirmed by the db-RDA analysis, as variation in community composition was significantly explained by spatial coordinates (pseudo- $r^2 = 0.25$, $p < 0.001$), and by altitude (pseudo- $r^2 = 0.10$, $p < 0.043$). A model including all significant predictors (latitude, longitude, and altitude) explained a third of the variation in species composition (pseudo- $r^2 = 0.33$, $p < 0.001$), implying that the contribution of spatial coordinates and altitude to the explained variance were mostly independent. Finally, an exponential distance-decay model (Fig. 46) explained 36% of the variance (pseudo- $r^2 = 0.36$, $p < 0.001$). In sum, all these results suggest that although species richness is not structured along spatial or altitudinal gradients, the species composition of communities of moss inhabiting beetles varies consistently across spatial and altitudinal gradients. Because these two gradients are independently related to beta diversity, our results suggest that community composition in moss inhabiting beetles is determined both by geographical isolation processes and, to a lesser degree, by environmental variation across altitudinal gradients. The greater relevance of geographical isolation is a common pattern in organisms with limited dispersal ability (Saito *et al.* 2015, Gómez-Rodríguez & Baselga 2018, Salces-Castellano *et al.* 2021, Baselga *et al.* 2022)

Table 3. Leaf beetles (Chrysomelidae), Maricao, Puerto Rico

| Subfamily, tribe, subtribe | Name | Maricao, 4.IX.14 h=720m adult / larva | Maricao, 6.IX.14 h=802m adult / larva | moss habitat # species/# specimens | open habitat # species/# specimens | adult/ larva |
|------------------------------------|---|---------------------------------------|---------------------------------------|------------------------------------|------------------------------------|--------------|
| Cassidinae, Cassidini | <i>Coptocyclus</i> sp. | 1 | | | X | adult |
| Cryptocephalinae, Cryptocephalini | <i>Cryptocephalus</i> sp. | 1 | | | X | adult |
| Cryptocephalinae, Cryptocephalini | <i>Diachus</i> sp. | 1 | | | X | adult |
| Eumolpinae | <i>Metachroma</i> sp. | | 1 | | X | adult |
| Galerucinae, Galerucini | <i>Ectmesopus vitticollis</i> Blake | 1 | 1 | | X | adult |
| Galerucinae, Galerucini | <i>Yngaresca variicornis</i> (Weise) | 4 | 2 | | X | adult |
| Lamprosomatinae | <i>Oomorpha longifrons</i> (Lacordaire) | 10 | 10 | | X | adult |
| Galerucinae, Alticini | <i>Apraea portoricensis</i> (Blake) | 4 | | | X | adult |
| Galerucinae, Alticini | <i>Centralaphthona</i> sp. | 2 | | | X | adult |
| Galerucinae, Alticini | <i>Heikertingerella krugi</i> (Weise) | | 50 | | X | adult |
| Galerucinae, Alticini | <i>Heikertingerella</i> sp. | 12 | 18 | | X | adult |
| Galerucinae, Alticini | <i>Homoschema</i> sp. | | 5 | | X | adult |
| Galerucinae, Alticini | <i>Longitarsus</i> sp. | | 5 | | X | adult |
| Galerucinae, Alticini, Monoplatina | <i>Aedmon sericellus</i> (Clark) | | 6 | | X | adult |
| Galerucinae, Alticini, Monoplatina | <i>Aedmon</i> sp. | 2 | 6 | | X | adult |
| Galerucinae, Alticini, | <i>Kiskeya micheliorum</i> Konstantinov and Linzmeier | 2 | | | X | adult |
| Galerucinae, Alticini, Monoplatina | <i>Menudos maricao</i> Linzmeier and Konstantinov | | 4/2 | | X | adult/ larva |
| | | 40 | 108/2 | 2/4 (2 larvae) | 15/144 | |

Table 4. Leaf beetles (Chrysomelidae), Toro Negro, Puerto Rico

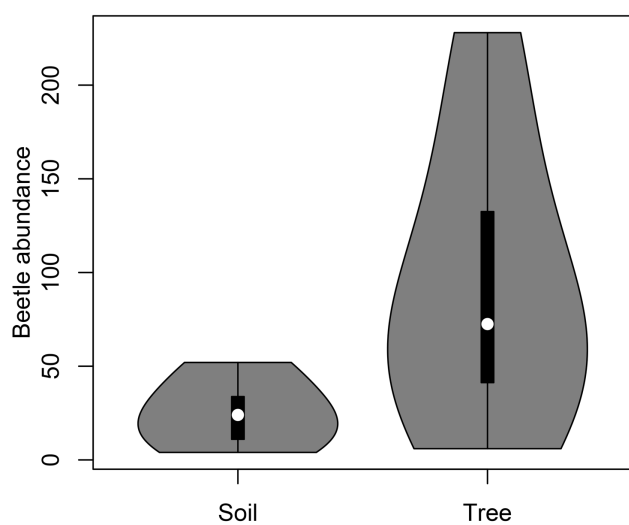
| Subfamily, tribe, subtribe | Name | Toro Negro, 1.IX.14 h=924m adult / larva | Toro Negro, 3.IX.14, h=1350m adult / larva | moss habitat # species/# specimens | open habitat # species/# specimens | adult/ larva |
|---------------------------------------|---|--|--|--|--|-----------------|
| Galerucinae, Alticini | <i>Chaetocnema</i> sp. | 2 | | | X | adult |
| Galerucinae, Alticini | <i>Leptophysa hoffmani</i> (Bryant) | 5 | | | X | adult |
| Galerucinae, Alticini | <i>Normaltica obrieni</i> Konstantinov | 41 | | | X | adult |
| Galerucinae, Galerucini | <i>Cerotoma ruficornis</i> Olivier | 11 | | | X | adult |
| Galerucinae, Galerucini | <i>Diabrotica graminea</i> Baly | 2 | | | X | adult |
| Galerucinae, Alticini, | <i>Borinken toronegro</i> Konstantinov and Linzmeier | | 3 | X | | adult |
| Galerucinae, Alticini, | <i>Kiskeya segarrai</i> Konstantinov and Linzmeier | | 24 | X | | adult |
| Galerucinae, Alticini, Monoplatina | <i>Menudos illariosus</i> Linzmeier and Konstantinov | | 1/1 | X | | adult/ larva |
| Galerucinae, Alticini, Monoplatina | <i>Menudos toronegro</i> Linzmeier and Konstantinov | 12 / 7 | 8 | X | | adult/ larva |
| Total | | 73/7 | 36/1 | 4/109 (8 larvae) | 5/61 | |

Focus taxa:**Anamorphidae and effect of substrates on their distribution**

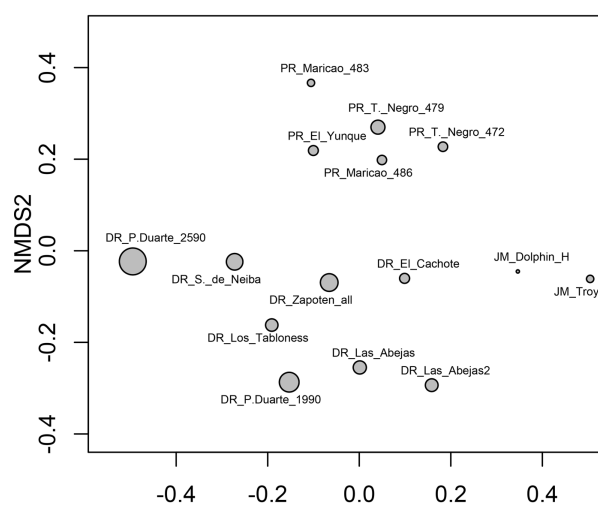
Anamorphidae is a small family with 36 genera and about 170 species worldwide according to most recent World catalog (Shockley *et al.* 2009b). All nine species in our samples belong to the genus *Micropsephodes* Champion (Table 1), which, according to the aforementioned catalog, contains only two species, one from the United States and the other from Guatemala. Species in our samples are likely undescribed, but their distribution may provide some insight into the effect of different substrates on beetle fauna in moss cushions. Anamorphidae are obligate mycophagous spore-feeders (Pakaluk 1986, Shockley *et al.* 2009a). For one species, *Micropsephodes lundgreni* Leschen and Carlton, which is presumably mycophagous spore specialist (Shockley *et al.* 2008), it was reported that the absolute majority of collected specimens had been found within a few meters of the ground, on logs, limbs and branches of different trees or captured in flight intercept traps suspended well above the ground (Shockley 2012).

Recent studies have revealed an unexpectedly high diversity of fungi associated with forest bryophytes (Davey *et al.* 2014; Heilmann-Clausen & Christensen 2005). The diversity of fungi associated with mosses is comparable to or even exceeds the diversity of fungal communities associated with vascular plants (Davey & Currah 2006). This high fungal diversity may be related to water absorption capacity of bryophytes growing on tree trunks that leads to an increase in bark moisture, which positively influence its decomposition rate (Dilks & Proctor 1979; Shorohova *et al.* 2016). It is shown that thick moss cushions may stabilize the microclimate of the decaying wood and advance fruitbody production of fungi (Purhonen *et al.* 2021).

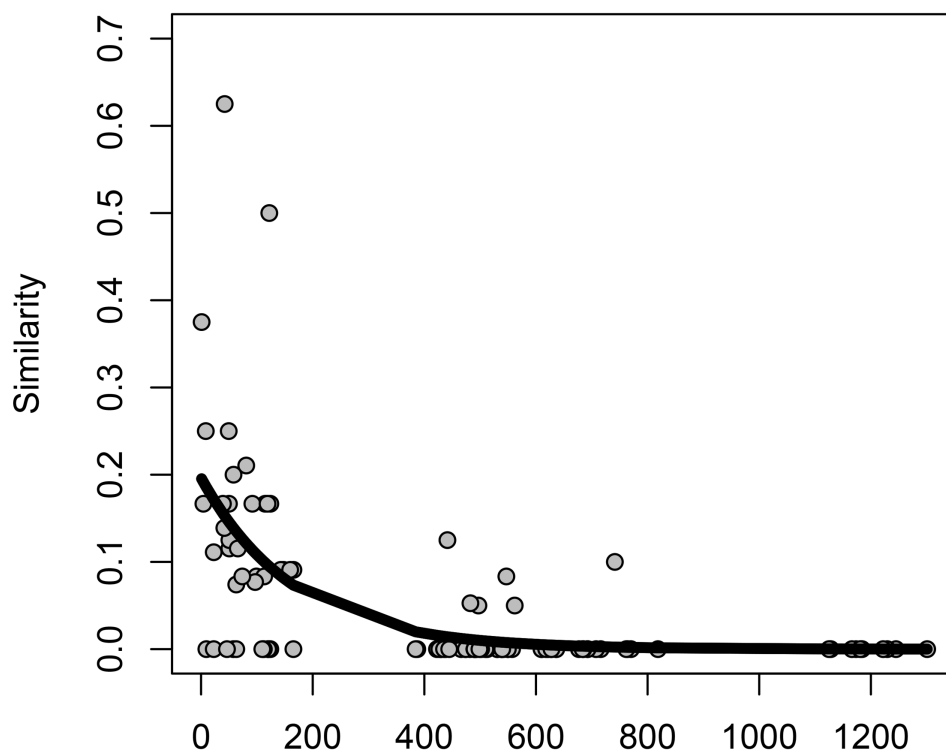
Therefore, it may be assumed that moss cushions host a diverse fauna of mycophagous or saprophagous coleopterans together with predaceous species of beetles besides basic bryobionts feeding on moss tissues. In a case of moss cushions growing on trees we may expect an increase in abundance of mycophagous species as a result of cumulative effect of moss and bark fungal communities. During our survey representatives of *Micropsephodes* spp. were extracted in a greater number from moss cushions taken from tree trunks in comparison with moss cushions taken from rocks or from the ground.



44



45



46

Distance

Figures 44–46. Statistical analyses. **44**, Comparison of the distribution of beetle abundance between substrates (soil/rock vs. trees). The violin plots illustrate kernel probability density, white dots are the median, black bars are the quartiles, and vertical lines are 1.5 times the interquartile range; **45**, Non-metric Multidimensional Scaling of moss inhabiting beetle communities of the West Indies. The NMDS ordination was based on Simpson dissimilarity and was performed in two dimensions ($k=2$), which accounted for >96% of the variance in the dissimilarity matrix (stress=0.038). The size of the dots representing each local community is proportional to the altitude of the sampling site; **46**, Decay of community similarity with spatial distance. Community similarity was quantified with the Simpson index, and spatial distance is geodesic distance between sampling sites (in km). The black curve is the fitted negative exponential function (pseudo- $r^2=0.36$, $p<0.001$).

Chrysomelidae

Most of about 32,500 species of Chrysomelidae live on the surfaces of their host plants (Lawrence & Ślipiński 2013). Bryophyte association is reported for two sister subfamilies (as shown in Douglas *et al.* 2023) Chrysomelinae (four genera, about 30 species – Leschen *et al.* 2020) and Galerucinae. Within Galerucinae, moss association is reported for one genus and three species of Galerucini (Lee & Beenan 2020). In Alticini with about 600 valid genera and 9900 species, moss association is reported for 22 genera and 75 species (Konstantinov unpublished compilation). Moss inhabiting flea beetles come from various, often distant, lineages (Damaška *et al.* 2022, Douglas *et al.* 2023). Damaška *et al.* (2022) reported nine independent origins of an association with moss as habitat shifts from an angiosperm leaf-surface-living lifestyle. Altogether, there are eight genera and 20 species of moss-inhabiting flea beetles known to occur in the West Indies. *Apleuraltica* Bechyne and *Monotalla* Bechyne are only known from the Lesser Antilles. Species of West Indian moss inhabiting flea beetles involved in this study belong to six genera and 16 species:

| | | | |
|-----------------------|--------------------------------|--|--|
| <i>Andersonaltica</i> | Linzmeier & Konstantinov | | |
| 2 species | 17 adults, 4 larvae | | Dominican Republic (Sierra de Neiba, Zapoten) |
| <i>Borinken</i> | Konstantinov & Konstantinova | | |
| 2 species | 10 adults, 2 larvae | | Puerto Rico (El Yunque, Toro Negro) |
| <i>Erinacealtica</i> | Konstantinov & Linzmeier | | |
| 3 species | 10 adults, 3 larvae | | Dominican Republic (Las Abejas, El Cachote, Zapoten) |
| <i>Kiskeya</i> | Konstantinov & Chamorro-Lacayo | | |
| 5 species | 123 adults, 1 larva | | Dominican Republic (Las Abejas, Sierra de Neiba), Puerto Rico (El Yunque, Maricao, Toro Negro) |
| <i>Menudos</i> | Linzmeier & Konstantinov | | |
| 3 species | 25 adults, 10 larvae | | Puerto Rico (Maricao, Toro Negro) |
| <i>Ulrica</i> | Scherer | | |
| 1 species | 2 adults | | Puerto Rico (El Yunque) |

They are highly endemic as most genera except *Kiskeya* are restricted to a single island and very few species are known from a locality other than type. Interestingly, no leaf beetles were found in moss cushions in Jamaica.

West Indian moss inhabiting flea beetles belong to three flea beetle clades: Monoplatina—*Andersonaltica*, *Erinacealtica*, *Menudos*, and *Ulrica*; so-called *Disonycha* group of Damaška *et al.* (2022)—*Kiskeya*; and Manturine-Leptophysine clade of Damaška *et al.* (2022)—*Borinken*. West Indian moss inhabiting Monoplatina have their immediate relatives among surface-living West Indian endemic genus *Aedmon* Clark. However, *Kiskeya* seems to be nested among various New World genera within *Disonycha* group (Damaška *et al.* 2022) and a very distant group of genera that includes Neotropical *Apraea* Jacoby, *Chanealtica* Konstantinov, and *Heikertingerella* Csiki. It is remarkably morphologically similar to Asian leaf litter and moss-inhabiting *Clavicornaltica* Scherer. But they are placed in the distant clades both in Damaška *et al.* (2022) and Douglas *et al.* (2023). *Clavicornaltica* seems to be associated with *Charbia* group in Damaška *et al.* (2022) and *Parategyrius*+*Aptonini* clade in Douglas *et al.* (2023).

Twenty larvae belonging to all aforementioned genera except *Ulrica* confirms that moss-inhabiting flea beetles are likely bryobionts. All found larvae are similar to openly living leaf beetle larvae such as *Altica* Geoffroy and *Ivalia* Jacoby (Duckett *et al.* 2006, Konstantinov *et al.* 2019, Ruan *et al.* 2020). Their descriptions are forthcoming.

Curculionidae

The Curculionidae are one of the most hyperdiverse families of organisms known. With over 62,000 described species, they are found in almost all geographic regions and in almost all habitats (Oberprieler *et al.* 2007). They are almost all phytophagous or saprophagous with the adults and larvae feeding on living, dead or dying plants, plant parts or plant products. An association with mosses has not been widely noted although some well-studied species from the Subantarctic Islands in the Ectemnorhinini feed and shelter in bryophytes (Chown & Scholtz 1989). Kuschel (1964, 1971) also noted species in the south temperate genera *Athor* Broun and *Baeosomus* Broun (as *Bryocatus* Broun) (both Eriirhininae, Stenopelmini) as feeding on mosses.

Although there are some records of moss feeding among weevils, mosses have not been carefully sampled for curculionids and this is the first study examining bryophytes as a potential habitat and food source for weevils. Leaf litter sampling on the other hand has been carried out extensively throughout Central America and Mexico and parts of South America and the West Indies and almost all of the genera with species collected in this study are represented in general leaf litter samples. Although these leaf litter samples may contain moss the prevalence of these genera over

a large number of samples and multiple locations suggests that's as far as this study goes, they are at best occasional and not bryobionts; however, careful separate contemporaneous sampling in moss and leaf litter would be needed to establish a clear association with mosses.

Among the curculionids collected during this study are 8 species of *Anchonus* Schoenherr and a variety of small undescribed Cryptorhynchinae and Molytinae in genera that are commonly found in leaf litter samples. The 4 species of *Decuanellus* Osella represent another genus where almost all previous specimens have been collected in leaf litter. Species of *Anthonomus* Germar, *Plocetes* LeConte, *Penestes* Schoenherr, *Sicoderus* Vanin and *Phyllotrox* Schoenherr are likely tourists or incidental occurrences. Species in all of these latter genera have a known biology that does not include association with mosses.

The best candidates for bryobionts among the Curculionidae collected here are the various unidentified higher elevation species assigned to the Polydrusini of the Entiminae. These species represent undescribed taxa closely related to the polydrusine genus *Apodrosus* Marshall, species of which are widespread across Cuba, Hispaniola and Puerto Rico (Girón & Franz 2010, Anderson & Zhang 2017). Collections of two species related to these polydrusines have been made on mosses in Costa Rica and Panama as species of *Sciomias* Sharp (Anne Howden, *in litteris*, as cited in Chown & Scholtz 1989), one associated with lichens the other with mosses. In addition, another related species has been collected from mosses in Guatemala. Vouchers of all are in the CMNC. These moss associations are likely derived within the Polydrusini as most other related species feed on angiosperms.

Although it is not suspected that they feed on mosses, some large Curculionidae in the genus *Gymnopholus* Heller in Papua New Guinea are hosts to small gardens on their backs which often include mosses (Gressitt *et al.* 1968).

Staphylinidae (except Pselaphinae)

Moss cushions, as a porous and humid substrate, are well suited for many staphylinids, provided the beetles can find food there. Wood under the cushions may act as a water buffer and contribute to high humidity inside the cushions.

Phytophagy in the broad sense (e.g., including feeding on pollen and nectar) is known in five subfamilies of the Staphylinidae (Thayer 2005) but it is certain that none of the species recorded in this study feed on mosses. Members of the subfamily Staphylininae (two species of *Gabrius* Stephens and several species of Xantholinini), Paederinae (*Dibelonetes* Sahlberg, *Echiaster* Erichson, *Lithocharis* Dejean, *Paederus* Fabricius, *Palaminus* Erichson and *Pinophilus* Gravenhorst) and Euaesthetinae (*Edaphus* Motschulsky) are predators and most of them may also occur in forest litter. Many species of *Palaminus* are arboreal and in wet tropical environment can be observed even during daytime while running on exposed leaf surface. A large number of the recorded species are associated with fungi growing on the bark and dead wood under moss cushions: four species of Scaphidiinae, four species of *Sepedophilus* Gistel, two species of *Gyrophaena* Mannerheim and likely many of the fourteen recorded species of the subtribe Bolitocharina). These mycophagous species may feed on spores (*Gyrophaena*) or hyphae or have a mixed diet of both (Thayer 2005). The five recorded species of Osoriinae (*Holotrochus* Erichson, *Osorius* Guérin-Méneville, *Thoracophorus* Motschulsky, two species of *Tannea* Blackwelder) are associated with dead wood under the moss cushions and may feed on decaying wood and/or fungi. *Myllaena* Erichson (one species recorded) is typically associated with very wet substrates next to water or, more rarely, wet forest litter. *Carpelimus* Leach (one species recorded) is also associated with wet habitats at water edge.

Staphylinidae (Pselaphinae)

Bythinogaster Schaufuss, 1887 is a genus of relatively large (ca. 1.7–1.8mm long) pselaphines in the tribe Brachyglutini (Supertribe Goniaceritae). Five described species are restricted to the Greater Antilles, with the genus recorded from Cuba, the Dominican Republic, Haiti, Jamaica, and Puerto Rico. Collection data do not associate any specimens outside of the current study with moss. Specimens were taken mainly from forest litter, at lights, or in flight intercept traps. Additionally, previous collection events yielded only short specimen series, with most represented by fewer than four specimens. The undescribed species of *Bythinogaster* in this study is unique in both the incredibly large number of specimens (over 900), and the collection method (exclusively from arboreal moss sifting). Thus, unlike the other pselaphines collected in this study, the undescribed species of *Bythinogaster* likely represents a hyper-abundant micropredator specific to arboreal moss.

A few other pselaphines are associated with mossy habitats. Most potential associations are based on a few studies and scattered collection records from temperate and boreal bogs. Various species of *Reichenbachia* Leach, *Brachygluta* Thomson (both Brachyglutini), *Tychobythinus* Ganglbauer (Bythinini), and *Pselaphus* Herbst (Pselaphini) are known from collections from sphagnum moss in temperate and boreal bogs, and other forested wetlands (Carlton 2003; Sabella *et al.* 2015; Reichle 1969), but their obligate associations with moss mat habitats are uncertain.

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