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The Taxonomic Revolution of New World dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae)

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After almost two decades of stagnation, the taxonomy of the New World Scarabaeinae dung beetles has since 1988 been going through a period of great effervescence. In the last 35 years, 81 complete revisions and 69 supplements have been produced by 86 authors based in 15 countries, addressing the taxonomic status of 950 species. This is what we christen as the Taxonomic Revolution of New World dung beetles. We review the history and products of this revolution, explore its causes and its apparent exceptionalism among most other New World Coleoptera groups, and point to the many great challenges that still face the scarabaeine taxonomists. An aspect of interest to ecologists is the coevolution of the Taxonomic Revolution with what we call the Ecological Revolution of dung beetles, i.e., the similar expansion in ecological studies about these organisms. We argue that it has been the continuous feedback between these two simultaneous processes that has enabled each of them to exist and flourish: without the Ecological Revolution, the Taxonomic Revolution could not have existed, and vice-versa. Ecologists and taxonomists are partners in the scientific enterprise, symbionts one may say.

KEYWORDS

systematics, Neotropical, Nearctic, scarabs, catalogue, taxonomic revision, taxonomic monograph, phylogenetics

An ongoing revolution

Anyone familiar with the taxonomic literature on the New World Scarabaeinae must have realized that we live in a rather special period. Since 1988, no less than 81 complete revisions have been published, and these were later updated by 69 supplements. Combined, these works address the systematics of 950 species in the Western Hemisphere (Tables 1, 2; Figure 1). This is not to say that, previously, the taxonomic knowledge of the fauna had been static. Rather the contrary, ever since Linnaeus (1758), the number of new taxa

TABLE 1 List of the taxonomic revisions, monographs, and their supplements published during the Taxonomic Revolution of New World dung beetles.

Tribe	Genus	Subgenus or species group	Last major revisions or monographs and supplements	Number of species currently recognised
Ateuchini			Montreuil, 1998; Vaz-de-Mello, 2008	Macrotaxonomic only (tribal, subtribal and generic levels)
	Agamopus Bates, 1887		Costa-Silva et al., 2022	5
	Aphengium Harold, 1868		Silva and Vaz-de-Mello, 2015	4
	Ateuchus Weber, 1801	*Lobidion* Génier, 2010	Génier, 2010; Génier and Cupello, 2018; Montoya-Molina et al., 2021	2
	Deltorhinum Harold, 1867		Génier, 2010; Montoya-Molina and Vaz-de-Mello, 2019a	7
	Feeridium Vaz-de-Mello, 2008		Vaz-de-Mello, 2008	1
	Genieridium Vaz-de-Mello, 2008		Vaz-de-Mello, 2008	7
	Nunoidium Vaz-de-Mello, 2008		Vaz-de-Mello, 2008	1
	Pedaridium Harold, 1868		Ferreira and Galileo, 1993; Vaz-de-Mello, 2008	22 (in Ferreira and Galileo, 1993), 1 described plus 1 undescribed (in Vaz-de-Mello, 2008)
	Pereiraidium Vaz-de-Mello, 2008		Vaz-de-Mello, 2008	1
	Scatimus Erichson, 1847		Génier and Kohlmann, 2003; see also Martínez-Revelo et al., 2020a	13
	Scatrichus Génier and Kohlmann, 2003		Génier and Kohlmann, 2003	3
	Silvinha Vaz-de-Mello, 2008		Vaz-de-Mello, 2008	1
Coprini			Montreuil, 1998; Tarasov and Dimitrov, 2016	Macrotaxonomic only (tribal level)
	Copris Geoffroy, 1862	*Copris s. str.*: incertus group: incertus and laeviceps complexes	Darling and Génier, 2018	9
Deltochilini			Tarasov and Dimitrov, 2016	Macrotaxonomic only (tribal level)
	Anomiopus Westwood, 1842		Canhedo, 2004a, b, 2006; see also Vaz-de-Mello et al., 2011; Edmonds and Figueroa, 2013; Figueroa and Edmonds, 2015; Cano, 2018a, b; Valois et al., 2020	63
	Atlantemolanum González-Alvarado et al., 2019		González-Alvarado et al., 2019	2
	Boreocanthon Halffter, 1958		Edmonds, 2022	13

(Continued)

TABLE 1 Continued

Tribe	Genus	Subgenus or species group	Last major revisions or monographs and supplements	Number of species currently recognised
	Canthon Hoffmannsegg, 1817	*Bajacanthon* Halffter, 2022	Halffter et al., 2022a	1
		Canthon s. str.: humectus group	Halffter et al., 2015	4
		Goniocanthon Pereira & Martínez, 1956	Nunes et al., 2018	3
		Peltecanthon Pereira, 1953	Nunes et al., 2020	4
		Pseudepilissus Martínez, 1954	Vieira et al., 2019	14
	Deltochilum Eschscholtz, 1822	*Deltochilum* s. str.	Génier, 2012	7
		Aganhyboma Kolbe, 1893	Silva et al., 2015, 2018	27
		Deltohyboma Lane, 1946	González-Alvarado and Vaz-de-Mello, 2021a	Macrotaxonomic only (species-group level)
		Deltohyboma Lane, 1946: gilli group	González-Alvarado and Vaz-de-Mello, 2021b	5
		Euhyboma Kolbe, 1893	Nazaré-Silva and Silva, 2021a	1
		Hybomidium Shipp, 1897	González-Alvarado and Vaz-de-Mello, 2014	13
		Parahyboma Paulian, 1938	Nazaré-Silva and Silva, 2021a	2
		Rubrohyboma Paulian, 1939	Nazaré-Silva and Silva, 2021a	1
	Deltepilissus Pereira, 1949		Silva et al., 2022	2
	Hansreia Halffter and Martínez, 1977		Valois et al., 2015, 2017b	6
	Holocanthon Martínez and Pereira, 1956		Sawaris et al., 2019	2
	Scatonomus Erichson, 1835		Valois et al., 2020	11
	Scybalocanthon Martínez, 1948		Silva and Valois, 2019; see also Silva and Génier, 2019	24
	Scybalophagus Martínez, 1953		Ocampo and Molano, 2011	5
	Sylvicanthon Halffter and Martínez, 1977		Cupello and Vaz-de-Mello, 2018	15
	Tetraechma Blanchard, 1841		Nunes and Vaz-de-Mello, 2022	5

(Continued)

TABLE 1 Continued

Tribe	Genus	Subgenus or species group	Last major revisions or monographs and supplements	Number of species currently recognised
Dichotomiini			Montreuil, 1998; Tarasov and Dimitrov, 2016	Macrotaxonomic only (tribal level)
	Chalcocopris Burmeister, 1846		Rossini and Vaz-de-Mello, 2015; see also Cupello et al., 2016, 2023b	2
	Holocephalus Hope, 1838		Smith and Génier, 2001; see also Nunes and Vaz-de-Mello, 2016b	6
	Dichotomius Hope, 1838	*Cephagonus* Luederwaldt, 1929	Nunes and Vaz-de-Mello, 2019	40
		Dichotomius s. str.: buqueti group	Arias-Buriticá and Vaz-de-Mello, 2019	3
		Dichotomius s. str.: mamillatus group	Rossini and Vaz-de-Mello, 2020	4
		Dichotomius s. str.: reclinatus group	Arias-Buriticá and Vaz-de-Mello, 2023	4
		Homocanthonides Luederwaldt, 1929	Maldaner et al., 2018a	1
		Selenocopris Burmeister, 1846: agenor group	Montoya-Molina and Vaz-de-Mello, 2021; see also Solís and Kohlmann, 2022	17
		Selenocopris: assifer group	Nunes et al., 2016	5
		Selenocopris: batesi group	Valois et al., 2023	5
		Selenocopris: globulus group	Valois et al., 2022	10
		Selenocopris: nisus group	Cassenote et al., 2020	1
		Selenocopris: sericeus group	Valois et al., 2017a; see also Silva et al., 2020	9
		Selenocopris: speciosus group	Maldaner et al., 2015; see also Maldaner and Vaz-de-Mello, 2022	5
		Selenocopris: superbus group	Cassenote et al., 2020	1
	Isocopris Pereira and Martínez, 1960		Rossini and Vaz-de-Mello, 2017	7
Eucraniini			Philips et al., 2002; Ocampo and Hawks, 2006	Macrotaxonomic only (tribal level)
	Anomiopsoides Blackwelder, 1944		Ocampo, 2005, 2007	4
	Ennearabdus Van Lansberge, 1874		Ocampo, 2010a	1
	Eucranium Brullé, 1838		Ocampo, 2010b	6
	Glyphoderus Westwood, 1838		Ocampo, 2004	3

(Continued)

TABLE 1 Continued

Tribe	Genus	Subgenus or species group	Last major revisions or monographs and supplements	Number of species currently recognised
Eurysternini	*Eurysternus* Dalman, 1824		Génier, 2009	53
Oniticellini			Philips, 2016	Macrotaxonomic only (tribal and subtribal levels)
	Attavicinus Philips and Bell, 2008		Philips and Bell, 2008	1
Onthophagini	*Digitonthophagus* Balthasar, 1959		Génier and Krell, 2017; Génier and Moretto, 2017	16 (one introduced species in the New World)
	Hamonthophagus Roggero et al., 2016		Roggero et al., 2016	5 (two introduced species in the New World)
	Onthophagus Latreille, 1802		Zunino and Halffter, 1988a, 1997	Macrotaxonomic (species-group level)
		Onthophagus s. str.: chevrolati group	Zunino and Halffter, 1988a, 1988b; Delgado and Capistan, 1996; Delgado, 1999; Delgado and Howden, 2000; Zunino and Halffter, 2005; Arriaga-Jiménez et al., 2016; Moctezuma et al., 2016; Gasca-Álvarez et al., 2018; Sánchez-Huerta et al., 2018; Halffter et al., 2019; Joaqui et al., 2019; Moctezuma and Halffter, 2019a, 2020b, 2020c; Moctezuma et al., 2021b	58
		Onthophagus s. str.: dicranius group: dicranius complex	Howden and Gill, 1993; Génier and Howden, 1999; Kohlmann and Solís, 2001; Solís and Kohlmann, 2003; Génier, 2017; Delgado and Mora-Aguilar, 2019; Moctezuma and Halffter, 2019b	12 plus one undescribed
		Onthophagus s. str.: dicranius group: mirabilis complex	Howden and Gill, 1993; Génier and Howden, 1999; Génier and Medina, 2004; Génier, 2017; Moctezuma et al., 2023b	9
		Onthophaguss. str.: mexicanus group	Moctezuma and Halffter, 2021b; Moctezuma et al., 2023a	20
		Onthophagus s. str.: lecontei-subopacus complex	Howden and Génier, 2004	5
		Onthophagus s. str.: hircus group	Rossini et al., 2018a	Macrotaxonomic only (species-group level)
		Onthophagus s. str.: hircus group: osculatii complex	Rossini et al., 2018b	8
Phanaeini			Arnaud, 2002b (phanaeines sensu Edmonds, 1972 only – i.e., modern Phanaeina less *Bolbites* – except for *Dendropaemon*)	117
	Bolbites Harold, 1868		Cupello et al., 2021a	1
	Coprophanaeus d'Olsoufieff, 1924		Edmonds and Zídek, 2010; see also Kohlmann and Solís, 2012; Cupello and Vaz-de-Mello, 2013a, 2014b; Maldaner et al., 2017; Arnaud, 2018; Maldaner et al., 2018b, 2019	44 (plus six *species inquirenda*)
	Dendropaemon Perty, 1830		Génier and Arnaud, 2016; see also Cupello and Génier, 2017	41

(Continued)

TABLE 1 Continued

Tribe	Genus	Subgenus or species group	Last major revisions or monographs and supplements	Number of species currently recognised
	Diabroctis Gistel, 1857		Valois et al., 2018	5
	Gromphas Brullé, 1838		Cupello and Vaz-de-Mello, 2013b, 2014a, 2015	6
	Megatharsis Waterhouse, 1891		Gillett et al., 2009	1
	Oxysternon Castelnau, 1840		Edmonds and Zídek, 2004; see also Arnaud, 2004; Hielkema, 2017	11
	Phanaeus MacLeay, 1819		Edmonds, 1994; Edmonds and Zídek, 2012; Zunino, 2013; Arnaud, 2018; Moctezuma and Halffter, 2021a; Moctezuma et al., 2021c; Halffter et al., 2022b; Solís and Kohlmann, 2023	83
	Sulcophanaeus d'Olsoufieff, 1924		Edmonds, 2000; Arnaud, 2002a	15
Incertae sedis	*Bdelyrus* Harold, 1869		Cook, 1998, 2000	27
	Canthidium Erichson, 1847	*Neocanthidium* Martínez et al., 1964: gigas group	Carvalho-de-Santana et al., 2019	6
	Cryptocanthon Balthasar, 1942		Cook, 2002; see also Arias-Buriticá and Medina, 2014; Mora-Aguilar and Delgado, 2018; Martínez-Revelo et al., 2020b; Giraldo-Mendoza, 2022	43
	Isacanthon Pacheco and Vaz-de-Mello, 2019		Pacheco and Vaz-de-Mello, 2019a	1
	Ontherus Erichson, 1847		Génier, 1996, 1998; see also González-Alvarado and Medina, 2015	60
	Paracanthon Balthasar, 1938		Pacheco and Vaz-de-Mello, 2019b	15
	Paracryptocanthon Howden and Cook, 2002		Pacheco and Vaz-de-Mello, 2017	2
	Streblopus Van Lansberge, 1874		Cupello et al., 2020	2
	Tesserodoniella Vaz-de-Mello and Halffter, 2006		Vaz-de-Mello and Halffter, 2006	2
	Zonocopris Arrow, 1932		Vaz-de-Mello, 2007a	2

Most revisions are complete revisions, i.e., they reassess the taxonomic status of all taxa included in the group revised, both micro-and macrotaxonomic ones, and propose a classification (even if an unaltered one). A few works, however, are devoted exclusively to macrotaxonomic revisions at the tribal, subtribal, or species-group levels. Faunistic revisions, species descriptions published not in the context of a revision, and purely phylogenetic works without taxonomic decisions (either new or confirmatory ones) are not listed.

described from the New World has been growing steadily (Figure 2). Before the current period – which we name the Taxonomic Revolution of New World dung beetles – there had been two other moments when the fauna was systematically revised: the first, during the late 1860s, was led by Edgar von Harold, who, among other works, monographed four of the most diverse genera on the continent, *Ateuchus*, *Canthidium*, *Dichotomius*, and *Canthon* (Table 3; Figure 3). In this short three-year period between 1867 and 1869, 205 new species-group taxa (i.e., taxa now considered valid species and subspecies) were described, an impressive 70% increase in the known diversity of the subfamily (Figure 2). Thereafter, a 69-year period of revisionary stasis would follow, punctuated in the middle almost solely by d'Olsoufieff's (1924) magnificent phanaeine revision.

Then, in 1938, a second period of revisionary activity started with the publication of the first part of Paulian's (1938) "canthonine" monograph. This second period would eventually be much longer than the Haroldian one. Over the next 33 years, 12 authors writing from 10 countries would produce 29 complete revisions and address the systematics of 266 species (Tables 3, 4; Figure 3). In addition, 12

TABLE 2 Glossary with our definitions of terms used in the text and whose meaning may be confusing, unknown, or disputed among systematists.

Term	Definition
Systematics	The discipline of evolutionary biology concerned with building a general reference inventory of the diversity of life (a system of life). Modern systematics comprises two major subfields: phylogenetics (cf.) and taxonomy (cf.). The end product of systematics is a monographic revision (cf.). Microsystematics is the combination of microphylogenetics and microtaxonomy, whereas macrosystematics is the combination of macrophylogenetics and macrotaxonomy.
Phylogenetics	The subdiscipline of systematics dealing with the reconstruction of the phylogeny, i.e., the pattern of genealogical change and diversification between living beings, from clades, to populations, to organisms, to genes. Phylogeny is the combination of the processes of reproduction, gene flow, hybridization, introgression, lateral gene transfer, population expansion and contraction, cladogenesis, lineage fusion, convergent, divergent, and parallel anagenesis, stasigenesis, and extinction. Microphylogenetics deals with the delimitation of (meta)population lineages and the relationships existing within them, whereas macrophylogenetics deals with the relationships between such lineages, including their organization into clades.
Taxonomy	The subfield of systematics dealing with the classification of organisms, i.e., the delimitation and categorization of taxa, as well as with the naming and identification of these taxa. In modern taxonomy, taxa are delimited based on the phylogenetic relationships of organisms, which are investigated by the other subfield of systematics, phylogenetics (cf.). In a few words, phylogenetics investigates the genealogical diversification of genes, populations, and clades and so constructs a phylogenetic tree; taxonomy, based on a set of principles (metataxonomy), divides this tree into taxonomic units, taxa, which are then named and usually ranked in the Linnean Hierarchy, giving rise to a classification. Finally, diagnoses, descriptions, dichotomous keys, genetic profiles, and other such tools are provided to allow the identification of organisms belonging to each taxon.
Microtaxonomy	The taxonomy of taxa at the level of species and subspecies (coined by Mayr, 1982).
Macrotaxonomy	The taxonomy of taxa at the supraspecific levels (coined by Mayr, 1969).
Taxonomic revision	A study that reevaluates the taxonomic status of a particular taxon or of taxa subordinated to a more comprehensive taxon. This reevaluation may encompass a taxon and all of its subordinated taxa across all ranks and geographical regions (a complete revision), or just the taxon and/or its subordinated taxa in a particular geographical region (a faunistic revision), or only subordinated taxa at a particular taxonomic rank or group of ranks (e.g., tribal-level-only revision, or species-level-only revision). A taxonomic revision implies, as far as existing material allows, an attempt to give equal treatment to all taxa revised and presents a fully comparative analysis between them. Works including comparable descriptions or diagnoses for all the taxa revised, for example, qualify as revisions. The result of a taxonomic revision is a revised classification.
Complete taxonomic revision	A revision that reevaluates the taxonomic status of a taxon and all of its subordinated taxa in all regions of the globe. For example, the revision of a genus that reevaluates the status of this genus and all the species included in it, or the revision of a species that reevaluates the status of this species and all of its known populations and/or subspecies. The result of a complete revision is a fully revised classification.
Faunistic taxonomic revision	A revision that reevaluates the taxonomic status of a taxon and its subordinated taxa in a particular geographical area, not in its full geographical range. For example, the revision of the species of a genus in a given country, state, biogeographic region, or ecosystem to which the genus is not endemic.
Taxonomic review	A study without a particular geographical focus that reevaluates the taxonomic status of some, but not all, the subordinated taxa at a particular taxonomic rank of a more comprehensive taxon, and whose presentation does not allow a fully comparative analysis between these subordinated taxa. For example, the description of a new species accompanied by an identification key to the congeneric species is a review, not a revision, because an identification key does not allow a full comparison between taxa, nor does it imply reevaluation of their taxonomic statuses.
Taxonomic synopsis	A summary of the taxonomic knowledge of a taxon without reevaluating itself the status of the taxonomy addressed (modified from Mayr, 1969).
Taxonomic monograph	A fully revised encyclopedic classification of organisms. It is a work that combines the characteristics of a taxonomic revision with the attempt to compile in a synthetic way the entire knowledge about the concerned taxa. For example, a work that, besides reevaluating the taxonomic status of taxa, also presents sections on their ecology, biogeography, evolution, complete taxonomic history, list of references, and whatever other aspect worthy of mention qualifies as a taxonomic monograph.
Taxonomic character	Characters that present different states between different taxa. Whether a character is a taxonomic character depends on the level of universality of the analysis. For instance, if one is addressing beetles, whether the forewings are modified into elytra or not is not a taxonomic character, for the forewings of all beetles are modified into elytra. But if one is talking about insects as a whole, whether the forewings are modified into elytra or not becomes a taxonomic character, for there are insects with elytra (beetles) and others without them (the other insects). Definition modified from Mayr (1969).

reviews also appeared in this period, as well as some faunistic revisions (e.g., Howden and Cartwright, 1963; Matthews, 1966; Vulcano and Pereira, 1966). This second period of taxonomic revisions eventually ended in the 1970s, microtaxonomically with Howden's (1971) revision of *Bdelyropsis* and macrotaxonomically with the final part of Halffter and Martínez's (1966, 1967, 1968, 1977) "Canthonina" monograph. In comparison with the Haroldian period, this mid-20th-century phase was much less prolific in the description of new species-group taxa: over 33 years, a "mere" 268 new such taxa were discovered, raising by 28% the number for the year preceding the start of the period, 1937. A special trend of this period, however, and one which reaches maximum expression today, was the geographical transition of the taxonomic center of investigation from its cradle in Europe in the late 1930s (with authors like Balthasar, Paulian, and Blut) to the New World countries in the mid-1940s onwards (especially Howden, Matthews, Halffter, Martínez, Pereira, and Vulcano) (Figures 4–6). Likewise, the role of Maria Aparecida Vulcano (or d'Andretta, her married name used to sign her debuting scarabaeinae papers in 1955) and Violeta Halffter (Gonzalo Halffter's wife) as the first women to participate in the description of new species-group taxa is yet another relevant social change initiated in this period (Figure 7).

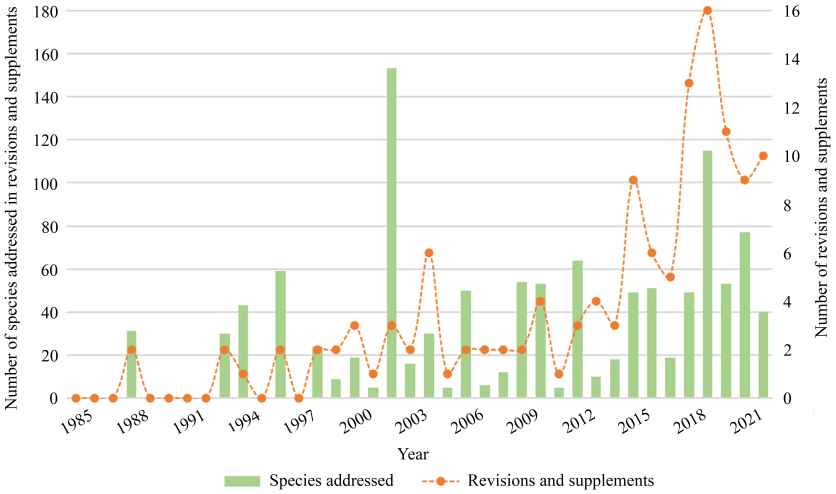

FIGURE 1
Taxonomic progress during the New World Scarabaeinae Revolution. Note that the number of revisions and monographs published each year has been growing since the start of the Revolution in 1988 (see also Table 1). The last year that saw no published work was 26 years ago, in 1997.

The late 1980s would then mark the beginning of a new era. Starting with Zunino and Halffter's 1988 revision of the *Onthophagus chevrolati* species group, the last 35 years have witnessed both a quantitative and a qualitative transformation in the systematics of the New World Scarabaeinae, one without parallel in the history of the discipline. The frequency of new revisions being published has exploded and continues to grow (Figures 1, 2, 8). As said, 150 complete revisions and supplements have appeared and 950 species, revised. The authors of these works are no longer a few researchers based in separate countries as in the mid-20th-century period. There are now instead active research groups widespread in the Americas based in countries like Canada, the US, Costa Rica, Mexico, Colombia, and Brazil, at least the latter three vibrantly composed of both established researchers and numerous students (Table 5). The Brazilian case illustrates the scale of change: in the entire pre-1990s history of the country's entomology, there had been merely eight people who published on the taxonomy of scarabaeines (Vaz-de-Mello, 2000; see Table 6). In contrast, during the 35 years of the Scarabaeinae Taxonomic Revolution, no less than 34 people living in the country have authored at least one taxonomic paper on the group, an almost fourfold increase. In Colombia, there had been none, but the Taxonomic Revolution has seen the work from 21 researchers based in the country so far. The same phenomenon is observed throughout the continent (Table 5). In all, 147 people have contributed with at least one work in the last 35 years, 63 of whom have authored at least one revision.

Qualitatively, the revisions composing this new age are characterized by seven features. First, most of them follow a phylogenetic rather than a faunistic approach. That is, instead of revising the species from a certain area in the Americas (e.g., Halffter, 1961; Howden and Cartwright, 1963; Howden, 1966; Matthews, 1966; Howden and Young, 1981; Kohlmann, 1984), they seek to study the entire diversity of whole taxa, usually genera, but sometimes focused on particular subgenera or species groups. A second characteristic is that they are no longer limited to the holdings of a few collections most easily accessible in their home countries, but are now based on an exhaustive search for specimens in as many collections as possible, including the nomenclaturally pivotal type specimens in European museums. Thirdly, these new revisions are lavishly illustrated, showing the most important taxonomic characters through either drawings or high-resolution photographs. The compilation of published data, usually with a catalog for each species and a section on ecological knowledge, is the fourth characteristic of the new phase. Fifthly, a detailed list of material examined is given for each species. Not only does it provide readers with the information necessary to locate the specimens and re-evaluate the observations noted in the revisions, but they also present additional data such as the date of collection that may prove useful to workers researching other questions about the taxa. Sixthly, modern taxonomists have much richer material available for their studies. Large local and geographical series, with detailed collection data, caught usually by the taxonomists themselves or by ecologists doing large-scale fieldwork, provide much richer data on intra- and interspecific variation than the small, geographically scattered series used by earlier workers. Lastly, the seventh characteristic is the increasing attention paid to the male genitalia, not only to the tegmen, as often done before, but also to the endophallus.

Of course, each of these characteristics can be found in works published before 1988. The study of the male genitalia for taxonomic studies on New World dung beetles was already present in d'Olsoufieff's (1924) revision of the Phanaeini, whereas comprehensive museum studies, including of the type specimens, were certainly a preoccupation of as early authors as Harold. But, generally speaking, works published before the current revolution lacked one or more of the characteristics listed above. Perhaps the closest pre-1988 examples are Kohlmann's (1984) revision of the North American *Ateuchus*, Matthews' (1966) revision of the

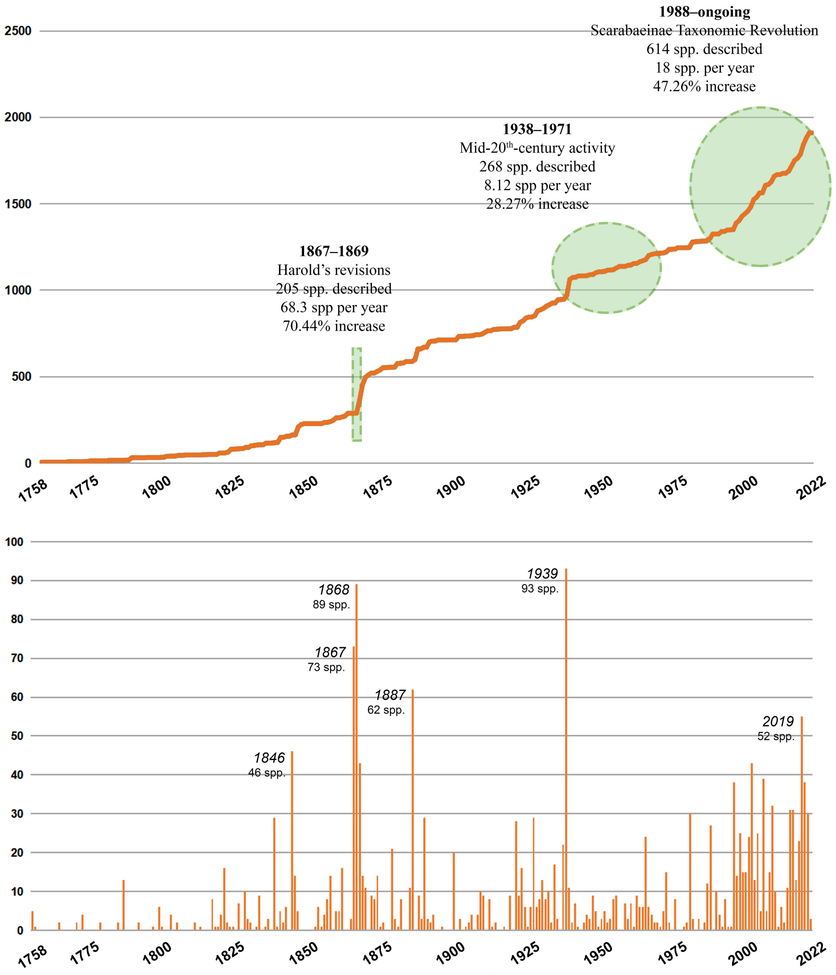

FIGURE 2
Progress in the discovery of new species-group taxa (i.e., species and subspecies) of New World Scarabaeinae since Linnaeus (1758). The upper graph shows the species-group taxa accumulation curve for the continent. Note that, although the number of known species and subspecies has never been truly static, the current Revolution is the longest period of consistent increase. The lower graph shows the number of species-group taxa discovered by year; the years highlighted are the six with the highest figures. Note that two of these years belong to the Haroldian period, one to the mid-20th-century period, and one to the current Revolution. In both graphs as well as in the rest of the paper, we consider the year of the discovery of a species-group taxon as the year of publication of its valid name, even if this name was originally used to denote a taxon whose circumscription matches only partially that of the currently denoted taxon (e.g., a name originally coined for a species taxon encompassing populations that are now considered heterospecific; therefore, the taxon which the name currently denotes – the one including solely the population of the name-bearing type(s) – does not correspond to the original taxon – the one including this and other populations). Data compiled from Schoolmeesters (2022).

TABLE 3 Taxonomic revisions and reviews published for the New World Scarabaeinae in the period preceding the Revolution (1860–1987).

Taxa revised	Revision	Number of species recognised
Eucraniini	Burmeister (1861)	12
Canthidium	Harold, (1867a, b)	61
Uroxys, *Trichillum*	Harold (1868a)	11
Ateuchus (as *Choeridium*)	Harold (1868b)	30
Canthon	Harold (1868c)	97
Dichotomius (as *Pinotus*)	Harold (1869)	39

(Continued)

TABLE 3 Continued

Taxa revised	Revision	Number of species recognised
Holocephalus (as *Atrichius* Gillet, 1907)	Gillet (1907); see also Gillet (1909)	3
Phanaeini	d'Olsoufieff (1924)	136
Eudinopus, *Deltochilum* [in part]	Paulian (1938)	40
Canthonidia, *Canthotrypes*, *Deltochilum* [in part], *Glauconia* (*Megathoposoma*), *Ipsepilissus* (= *Canthochilum*), *Megathopa*, *Paracanthon*, *Sinapisoma*, *Streblopus*	Paulian (1939)	24
Dendropaemon	Blut (1939)	28
Dichotomius: bitiensis section (as *Pinotus*)	Pereira (1942a)	4
Dichotomius: semianeus section (as *Pinotus*)	Pereira (1942b)	11
Anomiopsoides	Martínez, (1945a, b)	8
Zonocopris	Pereira (1946)	1
Dichotomius: batesi section (as *Pinotus*)	Pereira (1947)	7
Phanaeus (*Metallophanaeus*) (currently, a subgenus of *Coprophanaeus*)	Pereira (1949a)	3
Deltorhinum	Pereira (1949b)	1
Oniticellini	Janssens (1953)	7
Dichotomius: speciosus section	Pereira (1953)	3
Scatonomus	Pereira (1954)	7
Canthonella, *Xenocanthon*	Martínez (1954)	2
Deltochilum (*Calhyboma*)	Pereira and d'Andretta (1955b)	12
Anisocanthon, *Holocanthon*	Martínez and Pereira (1956)	4
Paracanthon	d'Andretta and Martínez (1957)	4
Canthomoechus (= *Canthon*), *Francmonrosia* (currently, a subgenus of *Canthon*), *Trichocanthon* (currently, a subgenus of *Canthon*)	Pereira and Martínez (1959)	4
Bdelyropsis, *Bdelyrus*	Pereira et al. (1960)	3
Vulcanocanthon (= *Canthon* (*Pseudepilissus*))	Pereira and Martínez (1960)	1
Gromphas	Barattini and Sáenz (1961)	4
Copris	Matthews (1961)	23
Sisyphus	Howden (1965)	2
Eudinopus, *Megathopa*, *Megathoposoma*, *Malagoniella*, *Streblopus*	Halffter and Martínez (1966)	16
Antillacanthon (= *Canthochilum*), *Canthochilum*, *Canthonella*, *Chapincanthon* (= *Canthochilum*), *Nesocanthon* (currently, a subgenus of *Canthon*)	Vulcano and Pereira (1966)	10
Oniticellus (species now in *Euonicitellus*), *Drepanocerus* (species now in *Anoplodrepanus*), *Canthochilum*, *Canthonella*	Matthews (1966)	19
Canthonella, *Ipselissus* (= *Canthochilum*), *Peltecanthon* (currently, a subgenus of *Canthon*)	Halffter and Martínez (1967)	10
Agamopus, *Canthon* (*Pseudepilissus*), *Canthotrypes*, *Ipselissus* (= *Canthochilum*), *Scybalophagus*, *Sinapisoma*	Halffter and Martínez (1968)	16
Bdelyropsis	Howden (1971)	2
"Phanaeines" (i.e., Phanaeini less Gromphadina and *Bolbites*)	Edmonds (1972)	Macrotaxonomic (genus and subgenus levels)

(Continued)

TABLE 3 Continued

Taxa revised	Revision	Number of species recognised
"Canthonina" (part of Deltochilini)	Halffter and Martínez (1977)	Macrotaxonomic (genus and subgenus levels)
Eurysternus	Jessop (1985)	20
Taxa reviewed	**Review**	**Number of species recognised**
Canthon	Schmidt (1922)	144
Ontherus	Luederwaldt (1931)	31
Uroxys	Arrow (1933)	29
Diabroctis (as *Taurocopris*)	Pessôa (1935)	4
Scatimus	Balthasar (1938)	8
Ateuchus (as *Choeridium*)	Balthasar (1939a)	69
Canthon	Balthasar (1939b)	162
Trichillum	Balthasar (1939c)	13
Scybalophagus	Martínez (1954)	5
Geocanthon [= *Canthon* (*Glaphyrocanthon*)], *Glaphyrocanthon* (currently, a subgenus of *Canthon*), *Goniocanthon* (currently, a subgenus of *Canthon*), *Ipselissus* (= *Canthochilum*), *Nesocanthon* (currently, a subgenus of *Canthon*), *Scybalocanthon*	Pereira and Martínez (1956)	49
Boreocanthon, *Melanocanthon*	Halffter (1958)	14
Isocopris, *Vulcanocanthon* [= *Canthon* (*Pseudepilissus*)]	Pereira and Martínez (1960)	3
Ipselissus (= *Canthochilum*)	Pereira and Martínez (1963)	4
Glaphyrocanthon (currently, a subgenus of *Canthon*)	Martínez et al. (1964)	27
Trichillum s. str.	Martínez (1967)	7

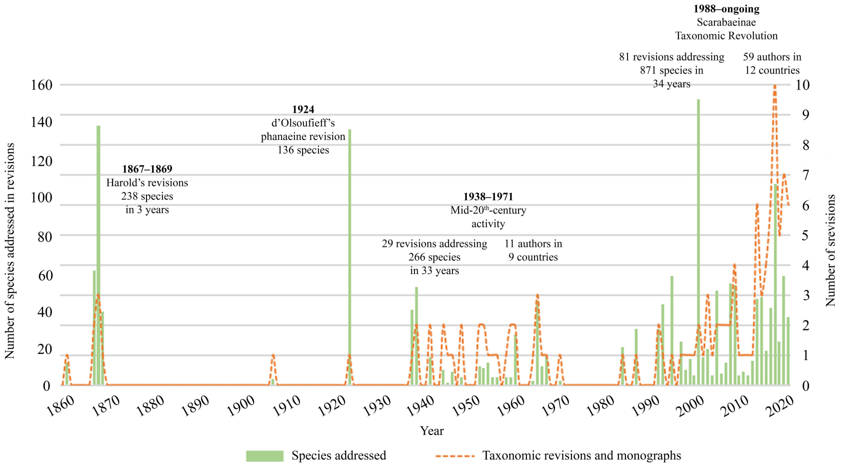

FIGURE 3
Revisionary activity over the history of the New World Scarabaeinae taxonomy. It is possible to see that there have been three well-delimited periods of revisionary effervescence: the first one, in the late 1860s, was the work of a single author, Edgar von Harold. The second, during the mid-20th century, was much longer and carried out by a larger number of people, but never reached the intensity and scale of the current period, the Taxonomic Revolution started in 1988.

TABLE 4 Authors who published taxonomic revisions and reviews of New World Scarabaeinae prior to the Taxonomic Revolution.

Country (current borders)	Authors
Slovakia	V. Balthasar (1938)
Czechia	V. Balthasar (1939)
Germany	**H. Blut** (1939), **H. Burmeister** (1861), **E. von Harold** (1867–1869), A. Schmidt (1922)
Belgium	**J.-J.E. Gillet** (1907), **A. Janssens** (1953)
France	**R. Paulian** (1938–1939), **G. d'Olsoufieff** (1924; or Madagascar? See Vinson, 1946: 89)
United Kingdom	**L. Jessop** (1985)
Canada	**H.F. Howden** (1965–1971)
United States	**W.D. Edmonds** (1972)
Mexico	**G. Halffter** (1958–1977)
Puerto Rico	**E.G. Matthews** (1961–1966)
Brazil	H. Luederwaldt (1931), **F.S. Pereira** (1942–1966), S.B. Pessôa (1935), **M.A. Vulcano** (D'Andretta) (1955–1966)
Argentina	**A. Martínez** (1945–1977)
Uruguay	**L.P. Barattini** (1961), **A. Sáenz** (1961)

In bold are the authors of at least one taxonomic revision, whether complete or only macrotaxonomic (see Table 3). Authors are classified by country of affiliation at the moment of publication (modern boundaries considered, though); this information is usually present on the first page of their works, but in a few cases (e.g., d'Olsoufieff) it is inferred from other sources. Years in parentheses following each author's name indicate their first and last work published in the period.

Antillean scarabaeines, and Halffter and Martínez's (1966, 1967, 1968, 1977) canthonine series. But while they can certainly be seen as legitimate precursors of the current phase – see, e.g., Kohlmann's pioneering usage of the endophallus for species delimitation – they still differ from the typical work of the Revolution for having a faunistic rather than a phylogenetic perspective, in the first two cases, and for the rather small series available for examination in the case of Halffter and Martínez.

A milestone in this Scarabaeinae Taxonomic Revolution has been the publication of Vaz-de-Mello et al.'s (2011) identification key to the New World genera. Until then, the information available for identifying these taxa was dispersed across the taxonomic literature, there existing no comprehensive and reliable tool allowing ecologists, conservationists, systematists, museum curators, and other specialists and amateurs to identify the specimens of their studies. Eighty-eight genera and 42 subgenera were included in the key, as well as a list of the most relevant publications for species-level identification. The relevance of Vaz-de-Mello et al.'s work cannot be overstated: as we write these lines, Google Scholar lists no less than 333 citations of the key in the scientific literature, whilst Research Gate counts 3,158 reads. However, as inevitably happens to any publication in an active field of scientific inquiry, the work is, at some points, already outdated. Four new genera have since been described (Génier, 2010; Roggero et al., 2016; González-Alvarado et al., 2019; Pacheco and Vaz-de-Mello 2019a) (one of them, *Lobidion* Génier, 2010, not included in the key, has since been lowered to a subgenus of *Ateuchus*; Génier and Cupello, 2018), a subgenus has been re-elevated to genus, *Boreocanthon* (Edmonds, 2022), a new subgenus has been described, *Canthon* (*Bajacanthon*) (Halffter et al., 2022a), the subgeneric classification of *Dendropaemon* has been completely modified, including the recognition of 12 subgenera in contrast to the previous three (Génier and Arnaud, 2016; Cupello and Génier, 2017), some names used as valid in the key have now been invalidated (*viz.*, *Eucanthidium* Martínez and Halffter, 1986, *Luederwaldtinia* Martínez, 1951, *Telhyboma* Kolbe, 1893, *Tetramereia* Klages, 1907, and *Vulcanocanthon* Pereira and Martínez, 1960) (Génier, 2012; Génier and Arnaud, 2016; Cupello, 2018; Nunes and Vaz-de-Mello, 2019; Vieira et al., 2019), some genera have been re-delimited and the key is no longer adequate to identify them completely (e.g., *Sylvicanthon* and *Tetraechma*) (Cupello and Vaz-de-Mello, 2018; Nunes and Vaz-de-Mello, 2022), and some names, due to nomenclatural problems discovered since 2011, have changed their allocation and denote different taxa in the key than they now do (e.g., *Selenocopris* and *Canthidium s. str.*) (Cupello, 2018; Nunes and Vaz-de-Mello, 2019). Moreover, some later works have found errors in the key that need correction (e.g., the supposed lack of a margin between the pygidium and the propygidium in all of the species of *Gromphas*, or an excavated hypomera in all the *Ateuchus*) (Cupello and Vaz-de-Mello, 2013b; Cupello, 2022). Despite all this, Vaz-de-Mello et al.'s key continues to be the main identification tool used by New World scarabaeine specialists and will likely remain so until a revised version is published.

Progress has also been made on other fronts. Catalogs have been published for almost every South American country since the 2000s, as well as for Panama, Costa Rica, Nicaragua, El Salvador, Mexico, Canada, and several of the Antilles (Table 7; Figures 9, 10). Like for the key, many of these catalogs are already outdated as new species are discovered every year and dozens of new country records (as well as refutations of previous records) appear in the taxonomic revisions. Rather than something to regret, the short time these catalogs are superseded is a sign of the vigor of the field. The only country that has had its catalog first published and then updated

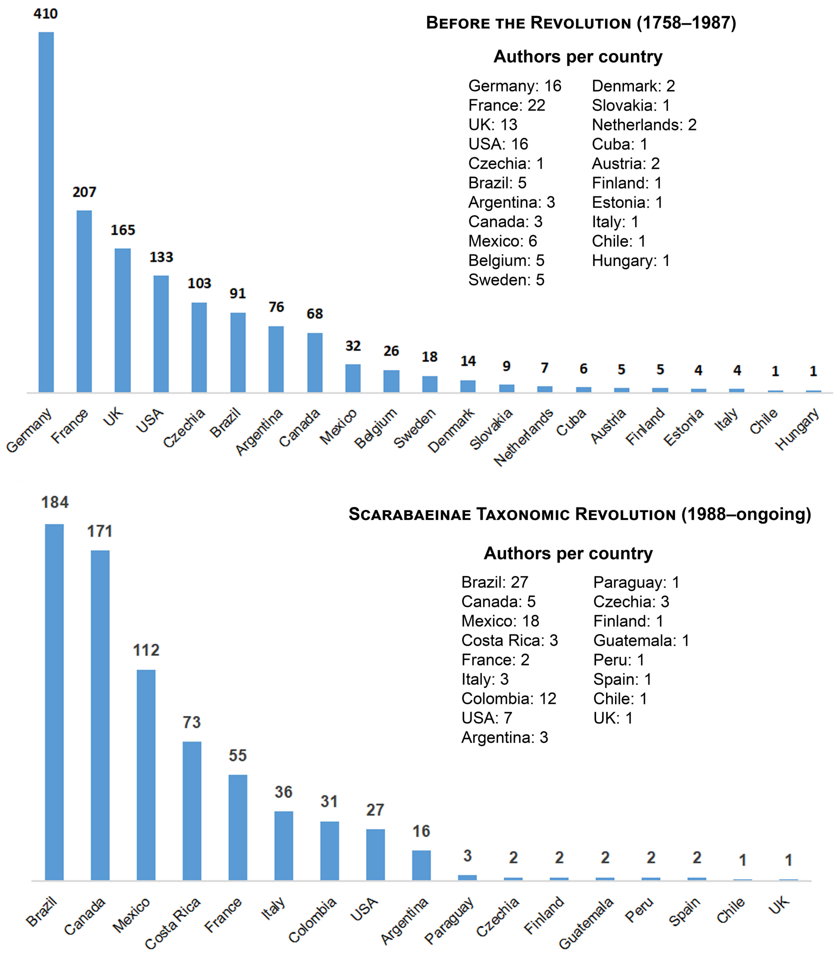

FIGURE 4
Number of new species-group taxa of New World Scarabaeinae described by authors based in each country before (above) and during (below) the Revolution. Countries are treated by their modern borders and names, even though they may not have been the same at the author's time. While new taxa were usually discovered by authors based in European countries during the first 229 years of the taxonomic history of the group, the last 35 years have seen a shift to authors based in the Americas. As noted in the text, the start of this trend actually dates back to the mid-20th-century period. Note that, if a taxon was described in a work whose authors are based in different countries, the species is counted again for each of these countries; therefore, the summed numbers will be greater than the total number of known species-group taxa from the continent. Data compiled from Schoolmeesters (2022).

during the Revolution, Brazil, epitomizes the period: whereas at the turn of the millennium 617 species were known from the country (Vaz-de-Mello, 2000), this figure has now risen to 784 (Vaz-de-Mello, 2023), a ~20% increase. This should be no different for the other South American countries. The Brazilian catalog also points to the direction that others should follow: openly available online, it allows additions and corrections in real-time, with the inclusion of newly discovered species, corrections associated with nomenclatural novelties, and updates in geographical distribution, among others. Currently, only the valid name, invalid synonyms, and the distribution of each species among the Brazilian states are available. In the future, further data such as type material, life habits, and habitat occupied will be added. We envision a future where the same tool will be available for each of the New World countries.

Much of the Revolution's success has been due to the great expansion that our Scarabaeinae museum collections have been experiencing since the second half of the 20th century, particularly during this millennium in South America. Until then, specimens were usually caught fortuitously by general entomologists who, by not being particularly interested in dung beetles, applied collection methods not properly suited to find them (e.g., active search with insect nets, light traps, Malaise traps). Now, the scarabaeine taxonomists themselves and, most importantly, a host of ecologists using the group as bioindicators are going regularly to the field in their search. They have designed and continuously perfected methods to collect ever more efficiently the highest richness and abundance of dung beetles as possible, including pitfall traps baited with as diverse materials as dung, carrion, mushrooms, decaying fruits, and dead millipedes (see, e.g., Lobo et al., 1988; Kryger, 2009; Araújo et al., 2022), as well as flight interception traps for both generalist species and those not regularly attracted to baits (e.g., Puker et al., 2020) (see Mora-Aguilar et al., 2023 for a review).

And field collections have not only become more frequent and efficient, but also more geographically encompassing. Though it is

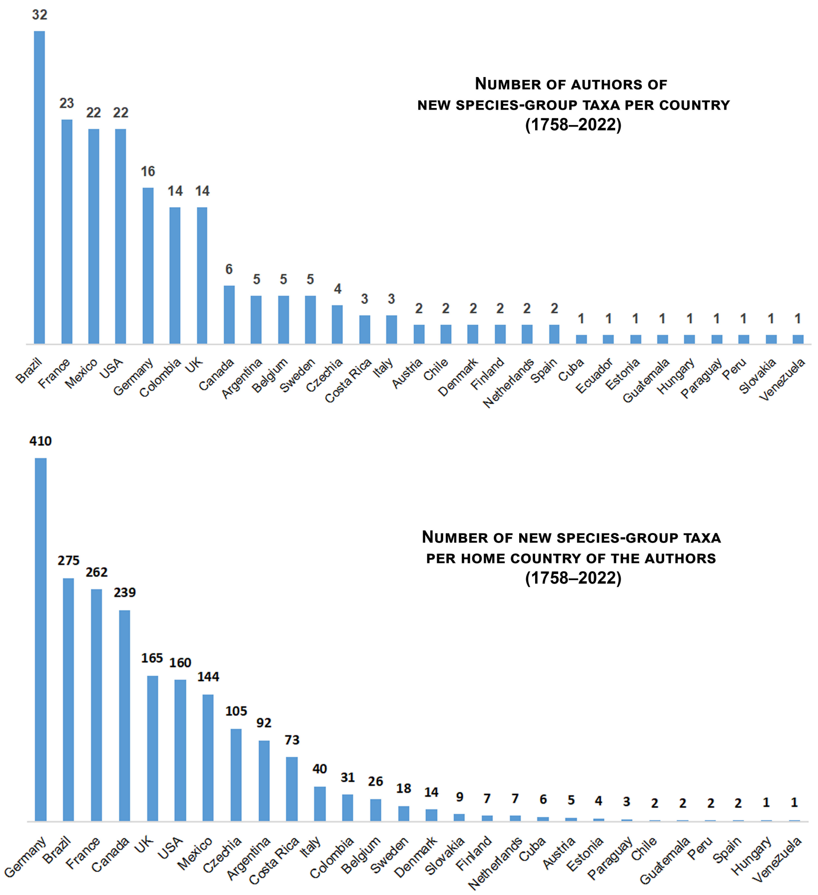

FIGURE 5
Species-group taxa, authors, and home countries across the taxonomic history of the New World Scarabaeinae. Like in Figure 5, countries are treated by their modern borders and names. The upper graph shows for each country the number of authors who have over the past 265 years discovered at least one New World species-group taxon of dung beetles. The graph below, in turn, shows the number of such taxa discovered by authors based in each of the countries. As in Figure 4, if a taxon was discovered by two or more authors based in different countries, it was counted again for each of those countries. Note that, although the last Germany-based author to discover a new species-group taxon was Blut (1939), the country still leads the number of discovered species by a wide margin. This is primarily due to the amazing efforts of Edgar von Harold in the latter half of the 19th century, who alone was responsible for the discovery of 275 species-group taxa, or ~69% of the German share and ~15% of the entire fauna (see Figure 6). Data compiled from Schoolmeesters (2022).

true that more intrepid naturalists have been exploring the most isolated corners of the New World since the 18th century in search of insects (see Papavero, 1971, 1973), most of the dung beetle specimens accumulated in collections until the 1950s–1970s came from more easily accessible localities, usually closer to the coast and larger urban centers, including the temperate forests of the eastern United States, localities in Mexico and Central America explored by the *Biologia Centrali-Americana* naturalists and, later, by US biologists, the West Indies, the southern Brazilian Atlantic Forest, and the Pampas grasslands of southern Brazil, Argentina, and Uruguay. Over the past decades, however, vast areas that, for centuries, had been seldom visited by naturalists have now turned into the ground of frequent fieldwork. These locations include the southern, eastern, and western Amazon rainforest in Ecuador, Peru and the Brazilian states of Rondônia, Mato Grosso and Pará, as well as the forests around Manaus and in French Guiana; the savannas, shrublands, and dry forests of the Cerrado in central Brazil; the tropical rainforests and cloud forests of southern Central America, particularly those of Costa Rica; the montane tropical forests of Los Chimalapas region of southern Mexico; the Pacific rainforests of Ecuador; the forests of the Magdalena Valley in Colombia; and the last remnants of Atlantic Forest in northeastern Brazil. The combination of adequate collecting techniques and broader geographical coverage, as well as the development of scientific institutions, including museums, in Latin America, have transformed the character of the material available for taxonomic investigation. It changed from being composed of scattered, usually poorly labeled specimens preserved in European museums until the mid-20th century to huge geographical and population series bearing precise collecting information housed in countries throughout the Americas.

The abundance of material available for study led, in turn, to a new character of the taxonomic revisions. If, before, little could be said about intraspecific variation, now work after work has been revealing how diverse the dung beetle species can be across their distribution, often showing complex patterns of population structure (e.g., Edmonds, 1994; Edmonds, 2000; Solís and Kohlmann, 2002; Génier and Kohlmann, 2003; Génier, 2009;

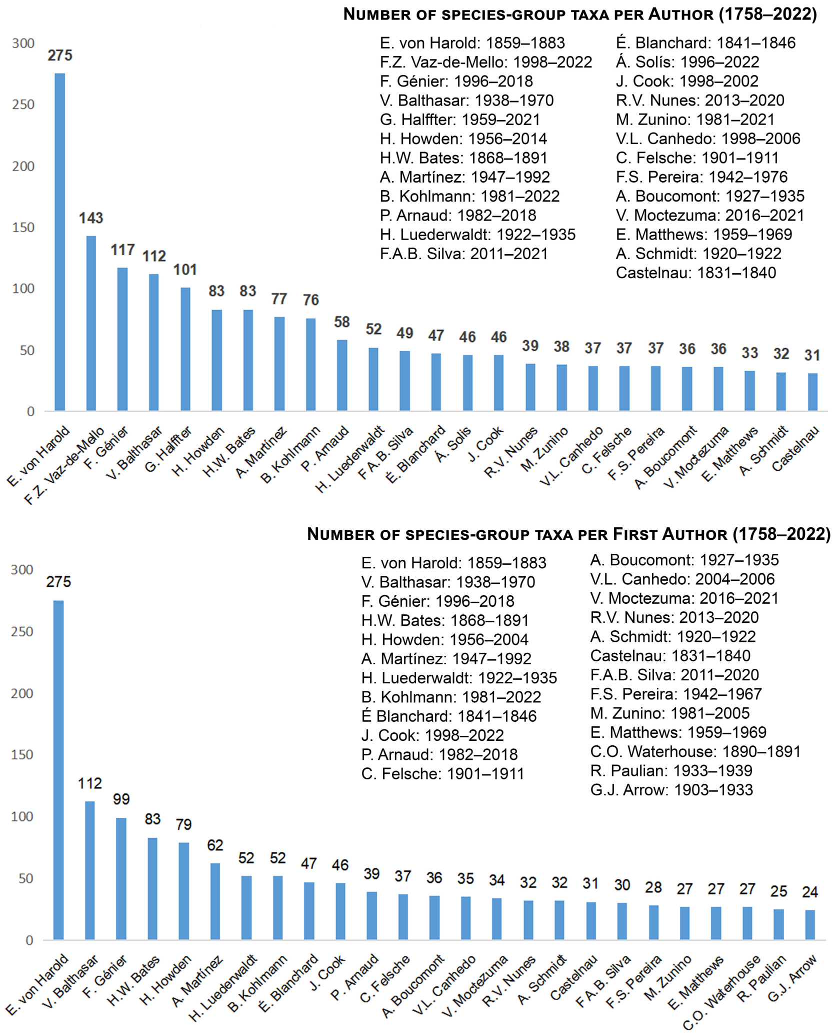

FIGURE 6
Number of new species-group taxa by the 25 most prolific authors over the taxonomic history of the New World Scarabaeinae. The upper graph shows all authors combined regardless of their position in the authorship of the name of the taxon. The lower graph shows only the figures as first authors. The years next to the name of the authors refer to the period in which they described new species-group taxa. Refer to Table 5 for more details. Data compiled from Schoolmeesters (2022).

Cupello and Vaz-de-Mello, 2018; Maldaner et al., 2019; Cupello et al., 2020, 2021a; Nazaré-Silva and Silva, 2021b; Costa-Silva et al., 2022; Solís and Kohlmann, 2023). Also, while the scarcity of material previously prevented the recognition of subtler interspecific taxonomic characters, now the abundance of specimens for comparison has led to the discovery of cryptic species among the continent's dung beetles (e.g., Cupello and Vaz-de-Mello, 2013b, 2018; Darling and Génier, 2018; Génier, 2019a). This discovery posed the necessity of exploring other character systems in addition to the ones traditionally used by the taxonomists, so leading to the revelation of the diversity and taxonomic informativeness of the endophallus (see Zunino, 2012 for part of this history) and the first attempts at species delimitation using genetic data (Solís and Kohlmann, 2012; Nolasco-Soto et al., 2017; Maldaner et al., 2019; Nolasco-Soto et al., 2020).

Another major result of the revolution in field collecting has been the re-discovery of long-disappeared species. These include, for instance, *Sulcophanaeus rhadamanthus* (Harold, 1875), a phanaeine species that had vanished before the 1950s and was re-found 60 years later in Rio Grande do Sul, Brazil, more than 1,000 km south of its previously known range in Rio de Janeiro state (da Silva et al., 2011, 2012, 2013). More recently, another new population was found in the state of Santa Catarina (Simões-Clivatti and Hernández 2022). These discoveries suggest that the presence of this species in the Argentinian province of Buenos Aires, as indicated by the label of a specimen in the Museu de Zoologia, São Paulo, and called into question by Pereira and d'Andretta (1955a), may, after all, be correct. Another example of a species that has recently reappeared is *Paracryptocanthon borgmeierei* (Vulcano et al., 1976). Until the last decade, it was known from just seven females, all collected in the 1960s and 1970s from a forest fragment in the heart of the city of Rio de Janeiro (Vulcano et al., 1976; Howden and Cook, 2002). It was then re-discovered, in 2013, through the collection of a larger series of

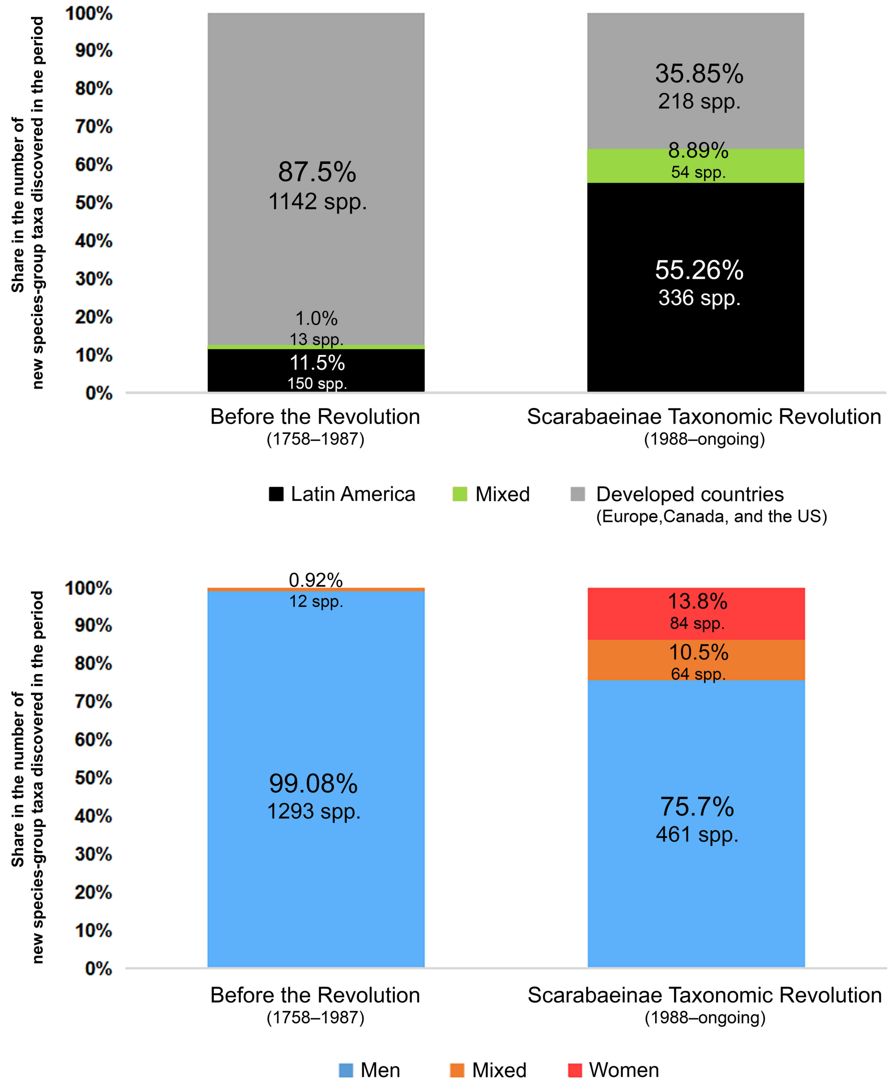

FIGURE 7
Social changes in the community of New World scarabaeine taxonomists. The upper bar chart shows the relative participation of authors based in Latin America and the developed world in the discovery of new species-group taxa before and during the Revolution; "mixed" refers to taxa described by pairs or groups of authors distributed across countries belonging to the two groups. Note that whereas before the Revolution authors based in Latin American countries participated in the description of less than 13% of new taxa, their share has grown to more than 60% over the past 35 years. As argued in the text, this was made possible at least partly by the expressive economic expansion experienced by these countries since the mid-20th century. The lower chart depicts the differential participation of men and women in the same process. "Men" and "women" refer to taxa described by either a single person or by a group of people of the same sex, whereas "mixed" refers to taxa discovered by composite groups of both men and women. Women's participation has greatly expanded in recent decades. Among the 112 authors who published new species-group taxa in the 230 years preceding the Revolution, only two, or 1.78%, were women, the Brazilian Maria Aparecida Vucano (d'Andretta) (starting in Pereira and d'Andretta 1955a) and the Mexican Violeta Halffter (idem in Martínez et al., 1964), and they were always co-authored by men. During the Revolution, this number has so far risen to 17, or 20% of all the 85 authors. The Revolution has also seen the first women to ever publish new species-group taxa without being co-authored by men, Ana Margarete Ferreira and Maria Helena Galileo, in their 1993 revision of *Pedaridium*; this was later followed by Joyce Cook (Cook, 1998, 2000, 2002) and Virgínia Canhedo (Canhedo, 2004a, b, 2006). Altogether, the percentage of new species-group taxa whose description had at least a woman involved has risen from less than 1% before the Revolution to ~24% in the last 35 years.

specimens of both sexes at the same locality from where it had been previously known (Pacheco and Vaz-de-Mello, 2017). A third example is *Dichotomius malyi* Maldaner et al., 2015, originally known from two old, possibly 19th-century specimens labeled simply as "São Paulo" and then re-discovered in 2014 living in Minas Gerais state (Maldaner and Vaz-de-Mello, 2022). Other groups, such as *Aphengium*, *Deltorhinum*, *Megatharsis*, *Coprophanaeus* (*Metallophanaeus*), *Dendropaemon*, *Paracanthon*, and *Streblopus*, that used to be among the rarest of the Scarabaeinae have now, thanks to the intensified collection efforts, become, if not common, at least more frequently found in the field and numerous in collections (Gillett et al., 2009; Edmonds and Zídek, 2010; Génier, 2010; Gillett et al., 2010; Silva and Vaz-de-Mello, 2015; Génier and Arnaud, 2016; Montoya-Molina and Vaz-de-Mello, 2019a; Pacheco and Vaz-de-Mello, 2019b; Cupello et al., 2020).

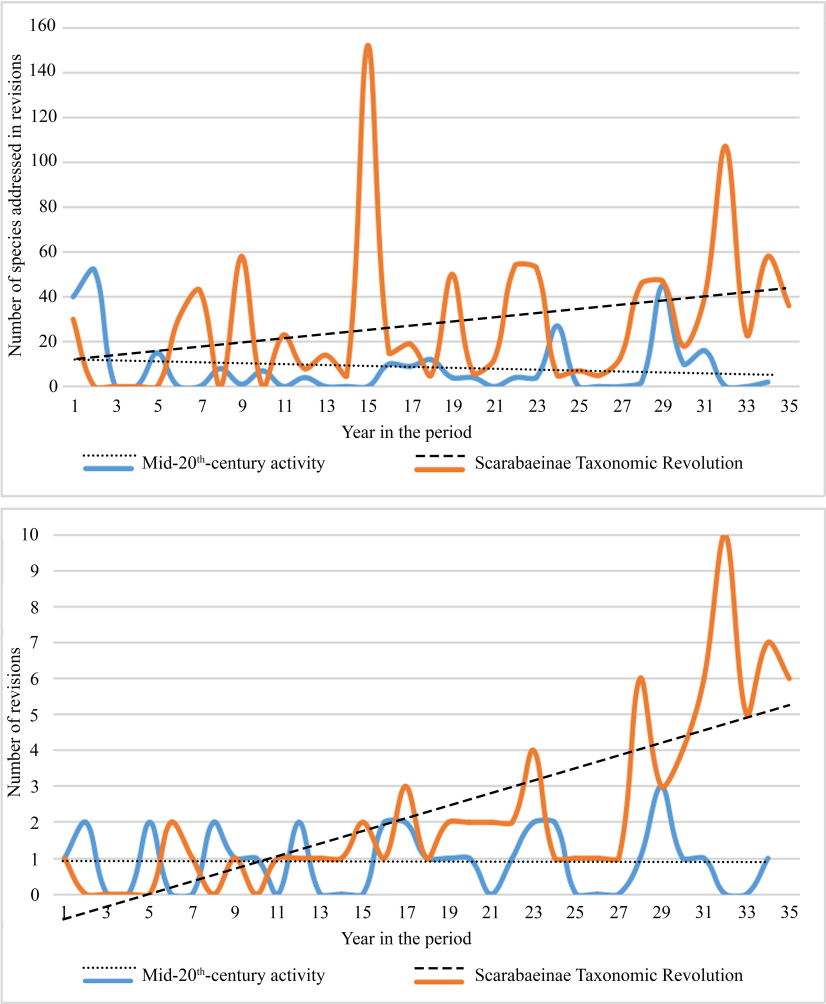

FIGURE 8
Comparisons between the 34 years of the mid-20th-century period (1938–1971, with macrotaxonomic extension to 1977) and the so far 35 years of the Taxonomic Revolution (1988–ongoing). Year 1 corresponds to 1938 and 1988, respectively, and so on. The upper graph compares the rhythm in the number of species addressed annually during each of the two periods. Dashed lines indicate the overall trend for each period. Note that, in the mid-20th-century period, the trend was of a slow decrease, whereas for the current Revolution, it is of consistent growth. The lower graph compares the rhythm of new revisions and monographs appearing in each year of the two periods. Note that the trend in the number of new works remained stagnated throughout the mid-20th-century period, whereas, in the Revolution, it has been in steep increase.

TABLE 5 Authors who have published systematic papers on Scarabaeinae during the Taxonomic Revolution (1988–ongoing).

Country	Authors
Canada	**J. Cook** (1998–2002), **J.D.G. Darling** (2018), **F. Génier** (1996–2021), **B.D. Gill** (1993–2003), **H.F. Howden**† (1993–2014)
United States	**K.L. Bell** (2008), **W.D. Edmonds** (1994–2022), **D.C. Hawks** (2006), M. Ivie (1990–2008), F.-T. Krell (2016–2017), S. McCleve (2005), **F.C. Ocampo** (2002–2004), **T.K. Philips** (1990–2016), D. Price (2007–2009), B.C. Ratcliffe (1998–1999), **A.B.T. Smith** (1999–2001), W.B. Warner (1990)
Mexico	**A. Arriaga-Jiménez** (2016–2022), J. Blackaller-Bages (1993), F. Capistan (1996), D.J. Curoe (2014), L. Delgado (1990–2019), C. Deloya (1990–2019), F. Escobar (2019), F. Escobar-Hernández (2019), M.E. Favila (2017–2020), H.J. Gasca-Álvarez (2018), J. González-Astorga (2017–2020), **G. Halffter**† (1988–2023), **V. Halffter**† (2003–2015), Ben. Hernández (2021–2023), T. Joaqui (2019), **V. Lizardo** (2021–2023), P.A. Martínez-Rodríguez (2021), **V. Moctezuma** (2016–2023), **A.E. de los Monteros** (2017–2022), E.F. Mora-Aguilar (2015–2023), J.L. Navarrete-Heredia (1993–2023), G. Nogueira† (2020–2022), **J. Nolasco-Soto** (2017–2022), M. Pensado (1998), L.N. Peraza (2006), G.A. Quiroz-Rocha (2023), **L.E. Rivera-Cervantes** (1999–2015), **S. Rivera-Gasperín** (2022), M. Rös (2018–2020), J.L. Sánchez-Huerta (2017–2023), J. Valdez-Carrasco (2020), F.Z. Vaz-de-Mello (2005–2006)
Guatemala	E.B. Cano† (2003–2018)
Nicaragua	Blas Hernández (2020), J.-M. Maes (2020)
Costa Rica	G.E. Alvarado (2019), **B. Kohlmann** (1996–2023), Á Solís (1996–2023)

(Continued)

TABLE 5 Continued

Country	Authors
Suriname	**C.P.T. Gillett** (2009), A.J. Hielkema (2017–2019)
Venezela	J. Clavijo (1990)
Colombia	G. Amat-García† (2014), **J.A. Arias-Buriticá** (2012–2019), J. Castillo-García (2014), W. Chamorro (2020–2021), **C. Giraldo-Echeverri** (2021), **A. González-Alvarado** (2009–2015, 2021), M.S. Herrera (2019), L.C.P. Locarno (2014), A. Lopera-Toro (2001–2021), D.E. Martínez-Revelo (2020), C.A. Medina (2001–2020), **F. Molano-Rendón** (2009–2019), J.C. Neita-Moreno (2020), J.A. Noriega (2020), C. Pardo-Diaz (2019), D.A. Parrales (2015), C. Salazar (2019), R. Sarmiento-Garcés (2014–2019), E. Torres (2020), S.A.P. Tovas (2019), A. Vítolo (2001)
Ecuador	W. Chamorro (2019), D. Marin-Armijos (2019), S. Villamarin (2009)
Peru	L. Figueroa (2012–2015), Giraldo-Mendoza (2022), F. Meza-Velez (2012)
Brazil	J.F. Araújo (2022), **J.A. Arias-Buriticá** (2023), A. Asenjo (2019), **V.L. Canhedo**† (1998–2006), **M.S.G. Carvalho** (2016), **E.C. Carvalho de Santana** (2019–2022), **S. Cassenote** (2020), W. Chamorro (2014), **V. Costa-Silva** (2020–2022), **M. Cupello** (2013–2022), **A.B.M. Ferreira** (2022), **A.M. Ferreira** (1993), **D.C. Ferreira** (2017–2019), **M.H. Galileo** (1993), M. Gavino (2001), **A. González-Alvarado** (2019–2021), **L. Harada** (2018), L. Iannuzzi (2022), **J. Louzada** (2001–2015), **M.E. Maldaner** (2015–2022), **S. Montoya-Molina** (2019–2021), A.B.G. Moura (2022), R.C. de Moura (2022), **E.E. Nazaré-Silva** (2021), **L.G.O.A. Nunes** (2018–2022), **R.V. Nunes** (2013–2020), **T.L. Pacheco** (2017–2019), **C.S. Ribeiro-Costa** (2020–2022), **L. Sawaris** (2019), **F.A.B. Silva** (2011–2023), **D.M. Takiya** (2018–2019), **M.C. Valois** (2015–2023), **F.Z. Vaz-de-Mello** (1998–2004, 2007–2023), **M.K. Vieira** (2019)
Bolivia	A.C. Hamel-Leigue (2006), S.K. Herzog (2006)
Paraguay	C. Aguilar (2001–2009)
Argentina	Adr. Martínez (1990), Ant. Martínez† (1990–1992), **F. Ocampo** (2007–2011)
Chile	M. Pino (2021), F. Tello (2021), J. Mondaca (2023)
Norway	**D. Dimitrov** (2016), **S. Tarasov** (2015–2016)
Finland	M. Rossini (2020–2021)
Czechia	V. Malý (2008), S. Pokorný† (2008), **J. Zídek**† (2004–2012)
Switzerland	E.F.A. Toussaint (2020)
Italy	**E. Barbero** (2016), P. Gandini (2009), **C. Palestrini** (2016), **A. Roggero** (2016), **M. Rossini** (2015–2020), **M. Zunino** (1988–2021)
France	**P. Arnaud** (1996–2018), **M. Dierkens** (2016), **O. Montreuil** (1998), **P. Moretto** (2016), O. Boilly (2021)
Belgium	P. Schoolmeesters (2011)
Netherlands	M.A. Hielkema† (2019)
United Kingdom	M.V.L. Barclay (2018), D.J. Mann (2006)
Spain	E. Galante (1997–2020), J.R. Verdú (1997–2021)
South Africa	E. Pretorius (2004), C.H. Scholtz (2002–2004)

In bold are the authors of at least one complete taxonomic revision (see Table 1). Authors are classified by country of affiliation as stated in each of their works; authors may be listed for different countries if they changed their affiliation over the years. Years in parentheses following each author's name indicate the year of publication of their first and so far last taxonomic work during the Revolution while based in the respective country. Dagger (†) indicates authors known to be deceased.

TABLE 6 Authors who have described New World dung beetle species-group taxa.

Author	Species described	As first author	Country	Author	Species described	As first author	Country
E. von Harold (1859–1883)	275	275	Germany	M.H. Galileo (1993)	3	3	Brazil
F..Z. Vaz-de-Mello (1998–2022)	143	16	Brazil/ Mexico	A. Lopera-Toro (2020–2021)	3	3	Colombia
F. Génier (1996–2018)	117	99	Canada	M.E. Maldaner (2015–2021)	3	3	Brazil
V. Balthasar (1938–1970)	112	112	Czechia/ Slovakia	E. Nazaré-Silva (2021)	3	3	Brazil

(Continued)

TABLE 6 Continued

Author	Species described	As first author	Country	Author	Species described	As first author	Country
G. Halffter (1959–2021)	101	12	Mexico	J. Neita-Moreno (2020)	3	3	Colombia
H.F. Howden (1956–2014)	83	79	Canada	L.W. Saylor (1935–1943)	3	3	USA
H.W. Bates (1868–1891)	83	83	UK	E.L. Taschenberg (1870)	3	3	Germany
A. Martínez (1947–1992)	77	62	Argentina	E. Torres (2020)	3	3	Colombia
B. Kohlmann (1981–2022)	76	52	Mexico/ Costa Rica	C. Aguilar-Julio (2001–2009)	2	2	Paraguay
P. Arnaud (1982–2018)	58	39	France	G.E. Alvarado (2019)	2	2	Costa Rica
H. Luederwaldt (1922–1935)	52	52	Brazil	J.G. Audinet-Serville (1828)	2	2	France
F.A.B. Silva (2011–2021)	49	30	Brazil	H. Blut (1939)	2	2	Germany
É. Blanchard (1841–1846)	47	47	France	J.B.L. Buquet (1844)	2	2	France
A. Solís (1996–2022)	46	12	Costa Rica	M. Carvalho (2016)	2	2	Brazil
J. Cook (1998–2002)	46	46	Canada	W. Chamorro (2020–2021)	2	2	Ecuador/ Colombia/ Brazil
R.V. Nunes (2013–2020)	39	32	Brazil	L.A.A. Chevrolat (1834–1844)	2	2	France
M. Zunino (1981–2021)	38	27	Italy	V. Costa-Silva (2020–2022)	2	2	Brazil
V. Canhedo (1998–2006)	37	35	Brazil	J. Curtis (1844)	2	2	UK
C. Felsche (1901–1911)	37	37	Germany	J.W. Dalman (1824)	2	2	Sweden
F.S. Pereira (1942–1976)	37	28	Brazil	P.A.J. Drapiez (1819–1820)	2	2	Belgium
A. Boucomont (1927–1935)	36	36	France	D. Drury (1773)	2	2	UK
V. Moctezuma (2016–2021)	36	34	Mexico	L. Figueroa (2013–2015)	2	2	Peru
E. Matthews (1959–1969)	33	27	USA	P. Gandini (2009)	2	2	Italy
A. Schmidt (1920–1922)	32	32	Germany	J. Gistel (1857)	2	2	Germany
Castelnau (Laporte) (1831–1840)	31	31	France	H.L. Gory (1831–1844)	2	2	France
C.O. Waterhouse (1890–1891)	27	27	UK	Ben. Hernández (2021)	2	2	Mexico
R. Paulian (1933–1939)	25	25	France	H.G. Hubbard (1894)	2	2	USA
G.J. Arrow (1903–1933)	24	24	UK	P.A. Latreille (1812)	2	2	France
O.P. Young (1981)	24	0	USA	A.L.M. Le Peletier de Saint-Fargeau (1828)	2	2	France
L. Delgado (1990–2019)	22	16	Mexico	F. Ocampo (2007–2010)	2	2	USA/ Argentina
M. Valois (2015–2020)	19	11	Brazil	G.W.F. Panzer (1794)	2	2	Germany
W.F. Erichson (1835–1848)	18	18	Germany	L.N. Peraza (2006)	2	2	Mexico
B. Gill (1987–2003)	18	3	Canada	M. Rös (2018)	2	0	Mexico
A. González-Alvarado (2010–2021)	17	15	Colombia/ Brazil	J. Sturm (1826–1843)	2	2	Germany
T.L. Pacheco (2017–2020)	17	14	Brazil	J.R. Verdú (1997–2021)	2	1	Spain
E.F. Germar (1813–1823)	16	16	Germany	W.B. Warner (1990)	2	2	USA

(Continued)

TABLE 6 Continued

Author	Species described	As first author	Country	Author	Species described	As first author	Country
J. Louzada (2001–2015)	16	0	Brazil	M. Weber (1801)	2	2	Denmark
G. d'Olsoufieff (1924)	16	16	France	G. Amat-Garcia (2014)	1	0	Colombia
H. Burmeister (1848–1874)	14	14	Germany/ Argentina	J.F. Araújo (2020)	1	0	Brazil
J.C. Fabricius (1775–1801)	12	12	Denmark	M. Barclay (2017)	1	0	UK
M. Ivie (1990–2008)	12	5	USA	G.J. Billberg (1815)	1	1	Sweden
A.G. Olivier (1789)	12	12	France	J. Blackaller-Bages (1993)	1	0	Mexico
T.K. Philips (1990–2008)	12	7	USA	O. Boilly (2021)	1	1	France
A. Preudhomme de Borre (1880–1886)	12	12	Belgium	C. Bruch (1925)	1	1	Argentina
M. Robinson (1940–2051)	12	12	USA	G.A. Brullé (1838)	1	1	France
O.L. Cartwright (1956–1970)	11	0	USA	F. Capistan (1996)	1	0	Mexico
J.L. LeConte (1847–1866)	11	11	USA	J. Clavijo (1990)	1	0	Venezuela
L.E. Rivera-Cervantes (1999–2015)	11	10	Mexico	D.J. Curoe (2014)	1	0	Mexico
J.J.E. Gillet (1907–1911)	10	10	Belgium	S. Endrödi (1962)	1	1	Hungary
M. Perty (1830)	10	10	Germany	F. Escobar-Hernández (2019)	1	0	Mexico
M. Rossini (2015–2021)	10	5	Italy/Finland	L. Fairmaire (1893)	1	1	France
J.L. Sánchez-Huerta (2017–2021)	10	2	Mexico	E. Fleutiaux (1889)	1	1	France
M. Cupello (2015–2020)	9	7	Brazil	C.J. Gahan (1894)	1	1	UK
V. Halffter (1964–2009)	9	0	Mexico	E. Galante (1997)	1	0	Spain
P.H. Lucas (1859)	9	9	France	H.J. Gasca-Álvarez (2018)	1	1	Colombia
W.J. Brown (1927–1946)	8	8	Canada	M. Gavino (2001)	1	0	Brazil
W.D. Edmonds (1979–2022)	8	7	USA	C. Giraldo-Echeverri (2021)	1	0	Colombia
F.E. Guérin-Méneville (1838–1855)	8	8	France	S.S. Haldeman (1843)	1	1	USA
T. Say (1823–1835)	8	8	USA	L. Harada (2018)	1	0	Brazil
M.A. Vulcano (d'Andretta) (1955–1976)	8	4	Brazil	J.F.W. Herbst (1789)	1	1	Germany
J.O. Westwood (1835–1842)	8	8	UK	J. Huijbregts (1984)	1	1	Netherlands
C.H. Boheman (1858)	7	7	Sweden	A. Janssens (1932)	1	1	Belgium
C. Linnaeus (1758–1767)	7	7	Sweden	T. Joaqui (2019)	1	0	Mexico
W.S. Macleay (1819)	7	7	UK	E.A. Klages (1906)	1	1	USA
B.G. Nevinson (1889–1892)	7	7	UK	H.J. Kolbe (1893)	1	1	Germany
T. Kirsch (1871–1873)	6	6	Germany	J.T. Lacordaire (1855)	1	1	Belgium
C. Medina (2010–2020)	6	0	Colombia	R.B. Lange (1945)	1	1	Brazil

(Continued)

TABLE 6 Continued

Author	Species described	As first author	Country	Author	Species described	As first author	Country
S. Montoya-Molina (2019–2021)	6	6	Brazil	S.I. Ljungh (1799)	1	1	Sweden
J.W. Van Lansberge (1874)	6	6	Netherlands	V. Malý (2008)	1	1	Czechia
de Zayas (1966)	6	6	Cuba	S. McCleve (2005)	1	1	USA
J. Darling (2018)	5	5	Canada	A.B.G. Moura (2020)	1	0	Brazil
C. Deloya (1990–2019)	5	5	Mexico	R.C. de Moura (2020)	1	0	Brazil
G.H. Horn (1875–1894)	5	5	USA	A. Murray (1856)	1	1	UK
C.G. de Mannerheim (1828)	5	5	Finland	J.L. Navarrete-Heredia (1993)	1	0	Mexico
E.F. Mora-Aguilar (2015–2019)	5	5	Mexico	G. Nogueira (2020)	1	0	Mexico
G. Nunes (2018–2020)	5	5	Brazil	H. d'Orbigny (1905)	1	1	France
B. Ratcliffe (1980–1999)	5	5	USA	D.A. Parrales (2015)	1	0	Colombia
E. Carvalho de Santana (2019–2022)	4	4	Brazil	M. Pensado (1998)	1	0	Mexico
E.A. Chapin (1930–1935)	4	4	USA	S.B. Pessôa (1934)	1	1	Brazil
J.F. Eschscholtz (1822)	4	4	Estonia	R.A. Philippi (1859)	1	1	Chile
Adr. Martínez (1982–1990)	4	4	Argentina	S. Pokorný (2008)	1	0	Czechia
D.E. Martínez-Revelo (2020)	4	4	Colombia	L.J. Reiche (1848)	1	1	France
F. Molano (2010–2015)	4	4	Colombia	A. Sallé (1889)	1	0	France
A.M.F.J. Palisot de Beauvois (1805)	4	4	France	R. Sarmiento-Garcés (2014)	1	1	Colombia
L. Redtenbacher (1868)	4	4	Austria	L. Sawaris (2019)	1	1	Brazil
C. Schaeffer (1906–1915)	4	4	USA	J.C.D. von Schreber (1759)	1	1	Germany
A.B.T. Smith (1999–2001)	4	4	USA	C. Schreibers (1802)	1	1	Austria
M. Vieira (2019)	4	4	Brazil	D. Sharp (1877)	1	1	UK
J. Arias-Buriticá (2014)	3	3	Colombia/ Brazil	J.W. Shipp (1897)	1	1	UK
A. Arriaga-Jiménez (2018–2019)	3	2	Mexico	F. Tello (2021)	1	1	Chile
W.S. Blatchley (1918–1928)	3	3	USA	N.A. Vigors (1825)	1	1	UK
E. Cano (2003–2018)	3	3	Guatemala	J. Zídek (2012)	1	0	Czechia
A.M. Ferreira (1993)	3	3	Brazil				

"Species described" and "As first author" refer to the number of new species-group taxa that each author described, respectively, regardless of his/her position in the authorship of the newly established species-group name and exclusively as its first (or sole) author. Data retrieved from Schoolmeesters (2022). "Country" refers to the country where the author was based when the new species description was published. Note, however, that we take into consideration modern borders and names, not necessarily those contemporary to the authors. The only exception – made in recognition of his pivotal role in the history of entomology – is the Dane J.C. Fabricius, who is listed for Denmark even though the city where he was based, Kiel, is now part of Germany; at Fabricius's time, even though part of the Holy Roman Empire, Kiel was under Danish rule. Underline indicates authors who have published species-group taxa during the Taxonomic Revolution. Authors are ordered in decreasing order by the number of "Species described".

Often treated as a minor, almost esoteric subject, important contributions have also been made toward the nomenclature of the American scarabaeines. The allocation of species-group names established by 19th- and early 20th-century workers was, most of the time, difficult to define with the paucity of information usually available in the original descriptions. This insufficiency of the majority of the old descriptions (but see Harold's for exceptions) is something typical of a by-gone era when the emphasis was given

TABLE 7 Number of species of Scarabaeinae for each New World country and other major political units.

Country and other territories	Species recorded in the last catalog for the country	Species recorded in Schoolmeesters (2022)	Species per thousand km^2 of land surface	Endemic species according to Schoolmeesters (2022)	Endemic species per thousand km^2	Proportion of endemic species over total richness
Canada	14 (Bousquet et al., 2013)	14	0.001	0	0	0%
United States	58 (Leng, 1920)	99	0.010	38	0.004	38.38%
Mexico	228 (Morón, 2003)	344	0.176	186	0.095	54.06%
Belize	Never published	42	1.841	0	0	0%
Guatemala	Never published	94	0.877	2	0.018	2.12%
El Salvador	52 (Pablo-Cea et al., 2023)	35	2.509	1	0.048	1.92%
Honduras	Never published	42	0.373	0	0	0%
Nicaragua	87 (Maes et al., 2020)	78	0.725	1	0.008	1.28%
Costa Rica	185 (Solís and Kohlmann, 2012; Solís and Kohlmann, 2023)	202	3.623	40	0.783	19.80%
Panama	133 (Ratcliffe, 2002)	158	2.125	16	0.215	10.12%
Bahamas[1]	2 (Turnbow and Thomas, 2008)	1, correct figure 2	0.199	0	0	0%
Turks and Caicos Islands	Never published	0	0	0	0	0%
Cuba[2]	12 (Peck, 2005), 11 (Ivie and Philips, 2008)	13	0.118	10	0.091	76.92%
Cayman Islands	1 [introduced] (Thomas et al., 2013)	0, correct figure 1 [introduced] (Thomas et al., 2013)	3.787	0	0	0%
Jamaica	6 (Ivie and Philips, 2008)	6	0.553	4	0.369	66.66%
Haiti[3]	6 (Perez-Gelabert, 2008)	5, correct figure 7	0.253	2	0.072	28.57%
Dominican Republic[4]	11 (Perez-Gelabert, 2008)	23, correct figure 22	0.455	16	0.331	72.72%
Puerto Rico	7 (Ivie and Philips, 2008)	7	0.768	6	0.659	85.71%
British Virgin Islands[5]	1 (Valentine and Ivie, 2005; Ivie and Philips, 2008)	0, correct figure 1	6.622	0	0	0%
US Virgin Islands	2 (Ivie and Philips, 2008)	2	5.780	0	0	0%
Anguilla	1 [introduced] (Peck, 2016)	0, correct figure 1	10.989	0	0	0%
Sint Maarten[6]	1 [introduced] (Colijn et al., 2019)	0, correct figure 1	24.390	0	0	0%
Saba (Caribbean Netherlands)	0 (Colijn et al., 2019)	0	0	0	0	0%

(Continued)

TABLE 7 Continued

Country and other territories	Species recorded in the last catalog for the country	Species recorded in Schoolmeesters (2022)	Species per thousand km^2 of land surface	Endemic species according to Schoolmeesters (2022)	Endemic species per thousand km^2	Proportion of endemic species over total richness
Sint Eustatius (Caribbean Netherlands)[6]	1 [introduced] (Colijn et al., 2019)	0, correct figure 1	47.619	0	0	0%
Saint Kitts and Nevis[7]	2 (Peck, 2016)	0, correct figure 2	7.662	0	0	0%
Antigua and Barbuda[8]	1 [introduced] (Peck, 2016)	0, correct figure 1	2.262	0	0	0%
Montserrat[9]	2 (Peck, 2016)	1, correct figure 2	19.607	0	0	0%
Guadeloupe	5 (Peck, 2016)	5	3.071	2	1.228	40%
Dominica[4]	3 (Peck, 2016)	0, correct figure 3	3.994	1	1.331	33.33%
Martinique[4]	6 (Peck, 2016)	4, correct figure 6	5.514	0	0	0%
Saint Lucia[4]	3 (Peck, 2016)	3	4.950	2	3.300	66.66%
Barbados	0 (Peck, 2009a)	0	0	0	0	0%
Saint Vincent and the Grenadines[10]	6 (Peck, 2016)	4, correct figure 6	15.424	0	0	0%
Grenada[11]	7 (Peck, 2016)	5, correct figure 7	20.348	0	0	0%
Bonaire (Caribbean Netherlands)	0 (Colijn et al., 2019)	0	0	0	0	0
Curaçao[12]	1 (Colijn et al., 2019)	0, correct figure 1	2.252	0	0	0%
Aruba	0 (Colijn et al., 2019)	0	0	0	0	0%
Trinidad and Tobago	Never published (Peck et al., 2002 list 9 species from Tobago alone)	24	4.680	1	0.195	4.16%
French Guiana	130 (Hielkema and Hielkema, 2019)	160	1.915	8	0.095	5.00%
Suriname	117 (Hielkema and Hielkema, 2019)	120	0.750	1	0.006	0.83%
Guyana	79 (Hielkema and Hielkema, 2019)	83	0.401	4	0.020	4.81%
Venezuela	72 (Roze, 1955)	167	0.189	26	0.029	15.56%
Colombia	283 (Medina et al., 2001)	366	0.352	54	0.051	14.75%
Ecuador	223 (Chamorro et al., 2019)	245	0.955	46	0.179	18.77%
Peru	278 (Ratcliffe et al., 2015)	285	0.222	28	0.021	9.82%
Brazil	782 (Vaz-de-Mello, 2023)	800	0.094	344	0.040	43.00%
Bolivia	216 (Hamel-Leigue et al., 2006)	254	0.234	30	0.027	11.81%
Paraguay	Never published	161	0.405	15	0.037	9.31%

(Continued)

TABLE 7 Continued

Country and other territories	Species recorded in the last catalog for the country	Species recorded in Schoolmeesters (2022)	Species per thousand km^2 of land surface	Endemic species according to Schoolmeesters (2022)	Endemic species per thousand km^2	Proportion of endemic species over total richness
Chile	10 (Mondaca, 2023)	11, correct figure 10[13]	0.013	3	0.004	27.27%
Argentina	202 (Martínez, 1959)	247	0.090	41	0.016	16.59%
Uruguay	Never published	62	0.354	5	0.028	8.06%

[1] Schoolmeesters (2022), following Matthews (1966), listed *Euoniticellus cubiensis* (Castelnau, 1840) as the sole species present in the Bahamas. He overlooked, however, Ivie and Philips's (2008) more recent record of a second species for the country, *Pseudocanthon perplexus* (LeConte, 1847). For this reason, we use Ivie & Philips's number for our calculations.

[2] Ivie and Philips (2008) overlooked Peck's (2005) record of the presence in Cuba of the introduced African species *Digitonthophagus gazella* (Fabricius, 1787). This record was also overlooked by Schoolmeesters (2022), who, in turn, added two other species to Peck's list, *Onthophagus fragosus* Génier and Howden, 2014 and *O. marginicollis* Harold, 1880. While the first is certainly present in Cuba (Génier and Howden, 2014), why Schoolmeesters cites the latter for the country is unknown to us; as far as we know, *O. marginicollis* is restricted to the New World mainland. Putting everything together, we follow Peck (2005) while adding the confirmed *O. fragosus* to his 12-species list.

[3] Schoolmeesters (2022) overlooked literature records (Matthews, 1966; Vulcano and Pereira, 1966) of *Canthon violaceus* (Olivier, 1789) for Haiti, listing it solely from the Dominican Republic. Furthermore, the Haitian species recorded by Matthews (1969) as *Canthochilum* sp. was also not included in Schoolmeesters' catalog. Because of these two omissions, we use Perez-Gelabert's (2008) number for our calculations added by the taxonomic rearrangements of Ivie and Philips (2008). The two endemic species to Haiti are *Canthochilum* sp. (sensu Matthews, 1969) and *C. ciboney* Matthews, 1969. In contrast, all the species that Matthews (1966) had recorded as endemic to Haiti have since then been discovered living in the Dominican Republic: *Canthon callosus* (Harold, 1868) (Vulcano and Pereira, 1966), *C. signifer* (Harold, 1868) (Vulcano and Pereira, 1966), and *Onthophagus capitatus* (Castelnau, 1840) (Ivie and Philips, 2008). It is also worth mentioning that Perez-Gelabert (2008) listed *Digitonthophagus gazella* from Hispaniola without specifying in which of the two countries, Haiti or the Dominican Republic, the species was found; his record was explicitly based on Ivie and Philips' then-still unpublished data. In the latter's publication itself (Ivie and Philips, 2008), it is clarified that all the known records of this species concern the Dominican Republic. Though it is very likely that the species has also invaded Haiti by now, formal confirmation is still lacking. We thus do not include *D. gazella* in our numbers for the country.

[4] Schoolmeesters (2022) confused Dominica with the Dominican Republic and cited *Pseudocanthon caeranus* Matthews, 1966 and *P. sylvaticus* Matthews, 1966 as present exclusively in the latter country. In actuality, neither species occurs in the Dominican Republic; they are both endemic to the Lesser Antilles, the first occurring in Dominica and Martinique, the second only in Dominica (Matthews, 1966; Peck, 2006; Peck, 2016). A third and final Dominica species, *Onthophagus antillarum* Arrow, 1903, is widespread in the Lesser Antilles, but its presence in Dominica as recorded by Matthews (1966) and Peck (Peck, 2006; Peck, 2016) was omitted by Schoolmeesters. At the same time, Saint Lucia, an island that is not inhabited by the *O. antillarum* (Matthews, 1966; Peck, 2009b; Peck, 2016), is misreported for the species by Schoolmeesters. On the other hand, the presence of the invasive species *Digitonthophagus gazella* in St. Lucia, as first reported by Ivie (2009), has not been taken into account by Schoolmeesters. Finally, *Onthophagus albicornis* Palisot de Beauvois, 1805, whose presence in the Dominican Republic has been confirmed in the literature (Matthews, 1966; Ivie and Philips, 2008), is listed as occurring in "Santo Domingo, Hispaniola" by Schoolmeesters; though this is not technically incorrect, as Santo Domingo was indeed the colonial name of the current country, it is inconsistent with the other records from there given in his catalog under the modern name Dominican Republic. Due to all these errors, Dominica is not cited in the Schoolmeesters catalog, and the Dominican Republic is said to harbor one more species than it actually does; St. Lucia, in turn, has the number incidentally correct in Schoolmeesters, since, whilst one of its species is omitted (*D. gazella*), another is incorrectly assigned to it (*O. antillarum*). As for Martinique, Schoolmeesters also erred in not citing for it *O. antillarum* and the African introduced *Digitonthophagus gazella* (Fabricius, 1787) (see Peck, 2011b; Peck, 2016), resulting in the number of Martinique species in the catalog being two less than the correct figure. Given these errors, we decided to use the data provided by Matthews (1966) and Peck (Peck, 2006; Peck, 2009b; Peck, 2011; Peck, 2016) for these places in our calculations instead of Schoolmeesters'.

[5] Schoolmeesters (2022) overlooked Ivie and Philips's (2008) record of *Canthochilum taino* Matthews, 1966 from the island of Tortola, in the British Virgin Islands. The species is further known from two other islands, St. John, in the US Virgin Islands, and Puerto Rico.

[6] Schoolmeesters (2022) overlooked Colijn et al.'s (2019) record of *Digitonthophagus gazella* from the islands of Saint Martin and Sint Eustatius. Concerning the former, the original record is from Yokoyama's (2013) field guide to the wildlife of Saint Martin. This island is politically divided into two regions: the northern part is the Collectivity of Saint Martin, part of the French Republic, whereas the southern part is Sint Maarten, one of the four constituent countries of the Kingdom of the Netherlands. It is unclear in which part of the island the specimen shown by Yokoyama was found, but since the island is so small (87 km^2) and *D. gazella* is spreading so fast through the Caribbean (Ivie and Philips, 2008), there is little doubt that the species should now be widespread on Saint Martin, occurring in both the Dutch and the French areas.

[7] Schoolmeesters (2022) listed no species for Saint Kitts and Nevis, overlooking the records for the island of St. Kitts of *Ateuchus illaesus* (Harold, 1868) by Matthews (1966) and Peck (2011a, 2016) and of *Digitonthophagus gazella* by Peck (2011a, 2016).

[8] Schoolmeesters (2022) assigned no species to Antigua and Barbuda, overlooking Peck's (2011a, 2016) record of *Digitonthophagus gazella* from the island of Antigua.

[9] Schoolmeesters (2022), following Matthews (1966), listed only one species, Ateuchus illaesus, from Montserrat, overlooking Ivie et al.'s (2008a, 2008b) record of *Digitonthophagus gazella* from there, a record also repeated by Peck (2016).

[10] Schoolmeesters (2022) overlooked the presence of *Digitonthophagus gazella* and *Canthon perseverans* Matthews, 1966 in Saint Vincent and the Grenadines (Peck, 2016).

[11] Schoolmeesters (2022) overlooked the presence of *Onthophagus antillarum* and *Digitonthophagus gazella* in Grenada (Matthews, 1966; Woodruff et al., 1998; Peck, 2016). Schoolmeesters (2022) also recorded *Canthon perseverans* uniquely from Grenada, implying that it was endemic to the island. Although it was indeed originally described solely from there (Matthews, 1966) and this situation remained unchanged for many decades, Peck (2016) has recently added a new record from the island of Union, in Saint Vincent and the Grenadines.

[12] Colijn et al. (2019) mentioned the existence of a photo of a dung beele from Curaçao that they identified as *Pseudocanthon* sp., possibly belonging to *P. chlorizans*.

[13] Schoolmeesters's (2022) list of species present in Chile contains a number of errors related both to species incorrectly assigned to the country and species erroneously omitted from it. Among the former are *Sulcophanaeus imperator* (Chevrolat, 1844) (actually endemic to Bolivia, Paraguay and Argentina; Edmonds, 2000), *Deltochilum variolosum* Burmeister, 1873 (apparently restricted to the same countries as *S. imperator*), and *Onthophagus ptox* Erichson, 1847 (range still dubious, but certainly not encompassing Chile; Rossini et al., 2018a). The ones incorrectly omitted, in turn, are two introduced species, *Onitis vanderkelleni* Van Lansberge, 1886 and *Digitonthophagus gazella*, both of which are present in Chile only on the island of Rapa Nui (i.e., Easter Island) (Mondaca, 2023). In addition to these inaccuracies, we have two changes recently established by Mondaca (2023) that Schoolmeesters could obviously not have incorporated into the 2022 version of his catalog: the new junior subjective synonymy of *Pinotus dahli* Landin, 1955 under *Homocopris torulosus* (Eschscholtz, 1822) (the name is listed as valid in Schoolmeesters for a Chilean species as *Dichotomius dahli*) and the revalidation of *Copris punctatissimus* Curtis, 1844 for a endemic species of *Homocopris* (the name is listed by Schoolmeesters as an invalid junior synonym of *Homocopris torulosus torulosus*). Altogether, this leaves us with 10, as indicated by Mondaca (2023), rather than 11 species as listed in Schoolmeesters (2022). Due to these errors and modifications, we use Mondaca's more recent and accurate figure for our calculations, including for the number of endemic species.

to characters now known to hold poor diagnostic value such as details in colouration and punctation, whereas more informative characters such as, as mentioned above, the shape of the endophallites (the term itself has a recent history; Génier, 2019b) and secondary sex characteristics were most often ignored. To overcome this difficulty, all the taxonomic revisions listed in Table 1 have sought to study the original type specimens, designating, when necessary, neotypes. Further nomenclatural problems, including, but not always limited to, the identity of the types, have also been dealt with in papers outside revisions (e.g., Génier, 2001; Génier and Vaz-de-Mello, 2002; Vaz-de-Mello and Génier, 2005; Cupello, 2013; Cupello and Vaz-de-Mello, 2014a; Cupello et al., 2016; Cupello and Génier, 2017; Génier and Krell, 2017; Hielkema, 2017; Maldaner et al., 2017; Cupello, 2018; Cupello and Vaz-de-Mello, 2019; Cupello, 2020; Kohlmann et al., 2020; Cupello et al., 2021b, 2022, 2023b). Two of us have also started a

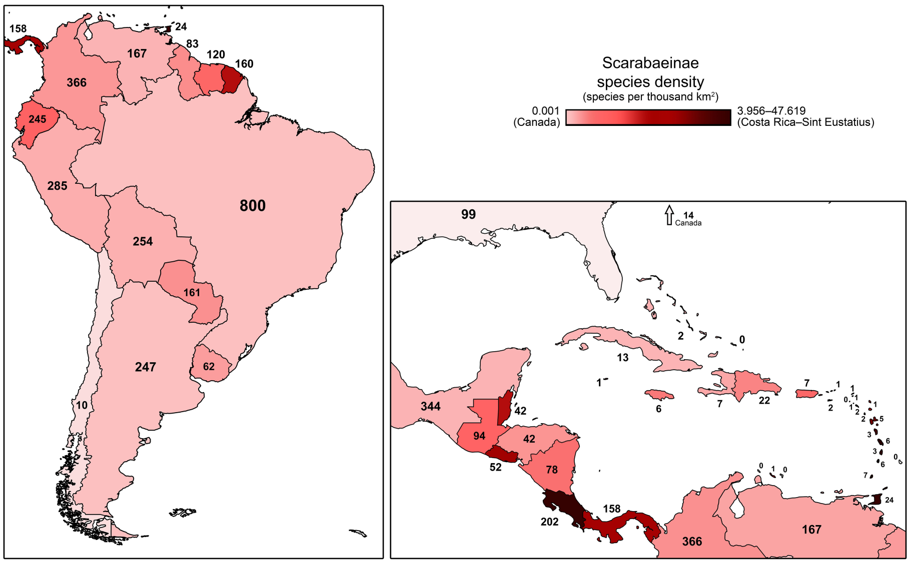

FIGURE 9
Species richness of each New World country and other territories. Numbers indicate the number of species so far recorded for each political entity, color grade marks species/area ratios. Brazil has the largest number of species, but it is one of the poorest countries in terms of species per area. The richest from the latter point of view include Costa Rica, Trinidad and Tobago, and most of the small Antillean islands. But note that no native scarabaeines are known for some of the latter, the recent invader *Digitonthophagus gazella* being their sole representative of the subfamily. See Table 5 for more details.

series dedicated to the study of historical type specimens (Vaz-de-Mello and Cupello, 2018a, b).

Lastly, while most of the taxonomic novelties in this Revolution have appeared in revisions and monographs and later papers published to complement them as listed in Table 1, smaller, independent works have also appeared addressing a single or a few species, usually new ones, in supraspecific taxa yet to be revised (e.g., Zunino and Halffter, 1988c; Delgado-Castillo and Deloya, 1990; Ivie and Philips, 1990; Martínez and Clavijo, 1990; Martínez and Martínez, 1990; Warner, 1990; Martínez, 1991, 1992; Delgado

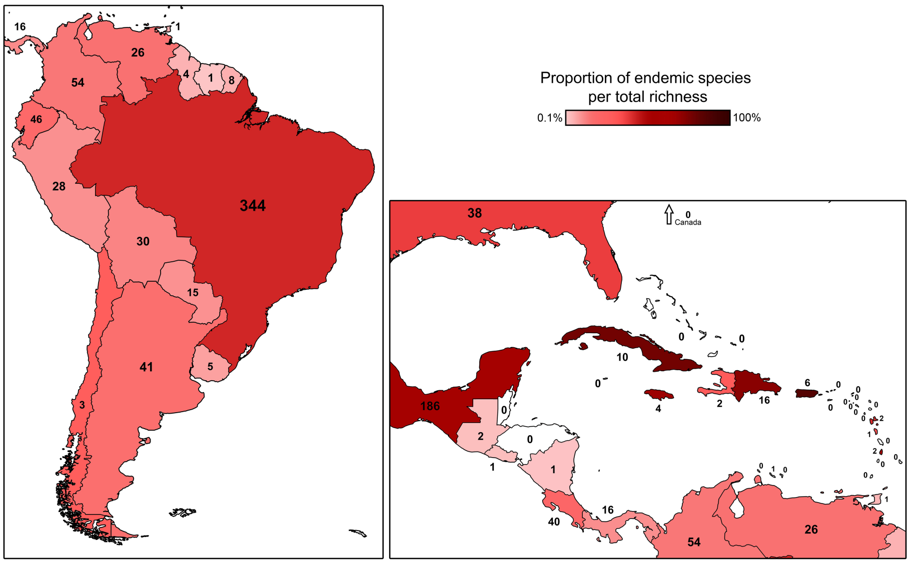

FIGURE 10
Species endemicity in each New World country and other territories. Numbers indicate the number of endemic species so far recorded from each political entity; color grade marks the percentage of endemic species in the fauna. Brazil is the country with the highest number of endemic species, as well as that in South America with the highest proportion of endemics. In the entire New World, the insular countries of Jamaica, Cuba, the Dominican Republic, and Saint Lucia, as well as the Commonwealth of Puerto Rico, are the political entities with the highest proportion of endemic species. See Table 5 for more details.

et al., 1993; Delgado, 1995; Verdú and Galante, 1997; Zunino and Halffter, 1997; Delgado and Pensado, 1998; Ratcliffe, 1998; Ratcliffe and Smith, 1999; Génier, 2000a, b; Aguilar-Julio, 2001; Delgado and Kohlmann 2001; Vaz-de-Mello et al., 2001; Halffter and Halffter, 2003; Kohlmann et al., 2003; Solís and Kohlmann, 2003; Howden and Génier, 2004; Vaz-de-Mello and Génier, 2005; Delgado et al., 2006; Peraza and Deloya, 2006; Ivie and Philips, 2008; Philips and Ivie, 2008; Halffter and Halffter, 2009; Gandini and Aguilar-Julio, 2009; González-Alvarado et al., 2009; Arias-Buriticá and Vaz-de-Mello, 2012; Figueroa et al., 2012; Génier, 2012; Nunes and Vaz-de-Mello, 2013; Chamorro et al., 2014; Delgado and Curoe, 2014; Génier and Howden, 2014; Silva and Vaz-de-Mello, 2014; Génier, 2015; Mora-Aguilar and Delgado, 2015; Moctezuma et al., 2016; Nunes and Vaz-de-Mello, 2016a; Vaz-de-Mello and Nunes, 2016; Kohlmann and Vaz-de-Mello, 2018; Moctezuma et al., 2018; Arriaga-Jiménez et al., 2019; Génier, 2019a; Moctezuma et al., 2019a, b; Montoya-Molina and Vaz-de-Mello, 2019b; Mora-Aguilar and Delgado, 2019; Lopera-Toro et al., 2020; Moctezuma and Halffter, 2020a; Moctezuma et al., 2020; Vaz-de-Mello et al., 2020; Boilly and Vaz-de-Mello, 2021; Chamorro et al., 2021; González-Alvarado and Vaz-de-Mello, 2021a; Moctezuma, 2021; Moctezuma et al., 2021a, d), including some fossil species (Tarasov et al., 2016; Tello et al., 2021a; Tello et al., 2021b; see also Zunino, 2013; Cantil et al., 2018). And while faunistic rather than phylogenetic, Bert Kohlmann and Ángel Solís' successive revisions of the Costa Rican species have also played a key role in pushing forward the systematics of the group (Kohlmann, 1997; Kohlmann and Solís, 1997, 2001; Solís and Kohlmann, 2002; Kohlmann and Solís, 2006b, 2009, 2012; Solís and Kohlmann, 2013; Kohlmann et al., 2019; Solís and Kohlmann, 2023). Thanks to their effort, today, the Costa Rican fauna is likely the best known in the New World, with the highest number of known species per area in all of the continent (Figure 9). Also valuable are the faunistic revisions of the North American *Canthidium* (Kohlmann and Solís, 2006a; Kohlmann et al., 2018), the Mexican *Canthon* (*Glaphyrocanthon*) (Rivera-Cervantes and Halffter, 1999), the Mexican and Guatemalan *Uroxys* (Delgado and Kohlmann, 2007), the South American *Pseudocanthon* Bates, 1887 (Nazaré-Silva and Silva, 2021b), and the Colombian *Dichotomius* (Sarmiento-Garcés and Amat-García, 2014). Adding the numbers from these independent works and the faunistic revisions to those from the revisions and their supplements, 614 new species-group taxa have so far been discovered during the Revolution, increasing by more than 47% the number of species and subspecies known to exist in the New World in 1987.

Expanding the frontiers

Despite the past 30 years of splendid progress, much still has to be done to modernize the systematics of the New World dung beetles. This is most obvious when we check what has been done with the most speciose groups. Of the twelve genera with 50 species or more in the Americas, only five have modern complete revisions published, one of them in need of being redone, while another four are being revised in parts (Table 8; Figures 11, 12). The remaining three, as argued by Cupello (2018), are the major gaps in the taxonomic knowledge of the American Scarabaeinae: *Uroxys* Westwood, 1842, *Canthidium* Erichson, 1847, and *Ateuchus* Weber, 1801. All three, while abundant in collections, have been sidelined by a number of difficulties they present to taxonomists. They are mostly composed of small (2–15 mm), black, and externally homogeneous beetles whose main taxonomic characters are found in the male genitalia, thus requiring careful dissection and anatomical study. The last global revision for each of them dates back to the works of Harold, in the mid-19th century, and neither has so far benefited from all the progress in theory, techniques, and material stored in collections made over the last 150 years. But precisely because of this, it is expected that, once properly studied, it

TABLE 8 The most speciose dung beetle genera in the New World fauna.

Genera	Number of recognized species in the Americas	Taxonomic status (percentage of species revised)
Onthophagus Latreille, 1802	226 (2,257 worldwide)	Partly revised (49.5%)
Dichotomius Hope, 1837	200	Partly revised (52.5%)
Canthidium Erichson, 1847	178	Under revision (F. Génier)
Canthon Hoffmannsegg, 1817	163	Partly revised (15.9%)
Deltochilum Eschscholtz, 1822	114	Partly revised (49%)
Ateuchus Weber, 1801	102	Under revision (M. Cupello)
Phanaeus MacLeay, 1819	83	Revised
Anomiopus Westwood, 1842	63	In need of a new revision
Ontherus Erichson, 1847	60	Revised
Uroxys Westwood, 1842	59	In need of revision
Eurysternus Dalman, 1824	53	Revised
Coprophanaeus d'Olsoufieff, 1924	50	Revised

Limited to genera with at least 50 species in the area. Numbers from Schoolmeesters (2022).

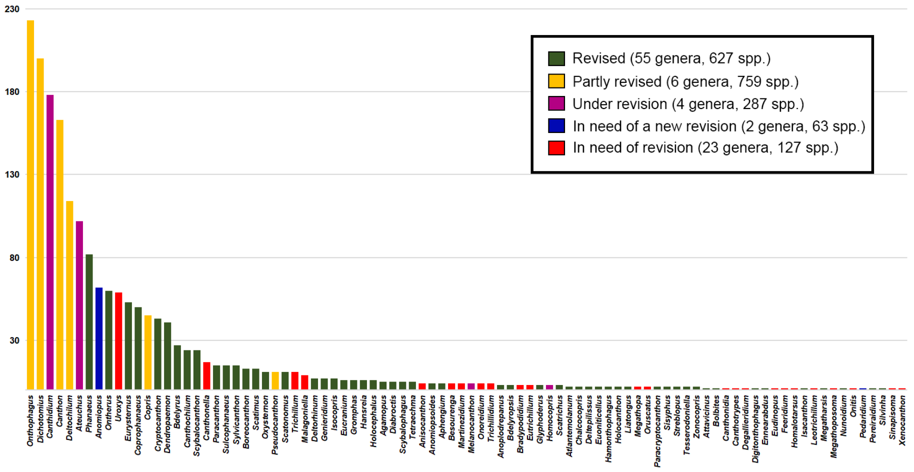

FIGURE 11
Number of currently recognized species and status of taxonomic resolution of each genus in the New World fauna. Notice that these numbers shall likely increase for most genera still unrevised or incompletely revised. At the same time, one of us (MC) feels that the numbers for a few of the groups, particularly *Phanaeus* and *Onthophagus*, are likely inflated under his preferred species definition (see Cupello and Vaz-de-Mello, 2018; Cupello et al., 2021a). Note also that whereas a relatively great number of medium- and small-sized genera have already been revised during the Revolution, the six most speciose groups either have only partial revisions published (ranging from ~16% to ~52% of their species composition; see Table 8) or, though currently under study, still have to see the first results of their revisions published. *Uroxys* is the largest genus still needing to attract any taxonomic attention other than that of faunistic revisions (Delgado and Kohlmann, 2007; Solís and Kohlmann, 2013). It is important to keep in mind, however, that having been revised does not mean being fully resolved: the revision is expected, for more difficult cases, to be just the first step in the investigation; more research will be needed to solve many of the problems still existing with the revised groups (see, e.g., Cupello et al.'s [2023a] comments about the revised *Sylvicanthon*). Finally, notice that six of the genera also encompass species in other parts of the globe: *Onthophagus*, *Copris*, *Euoniticellus*, *Onitis*, *Digitonthophagus*, and *Hamonthophagus*. The latter three are human-introduced in the Americas. The other three, though arriving on the continent spontaneously, are, in geological terms, newcomers, and only one, *Onthophagus*, has experienced significant radiation beyond North and Central America. As a likely result of this recent arrival in the Western Hemisphere, all of them are more diverse in the Old World.

will be these groups that will likely reveal the most interesting discoveries. The first author has been working for the past five years on a revision of one of these genera, *Ateuchus*, and can confirm that the predictions are indeed precise.

Progress must also be made in terms of fieldwork. Although, as we have seen, the places explored by dung beetle specialists have been broadening over the past decades, there are still areas mostly untouched. These include especially the northern Amazon,

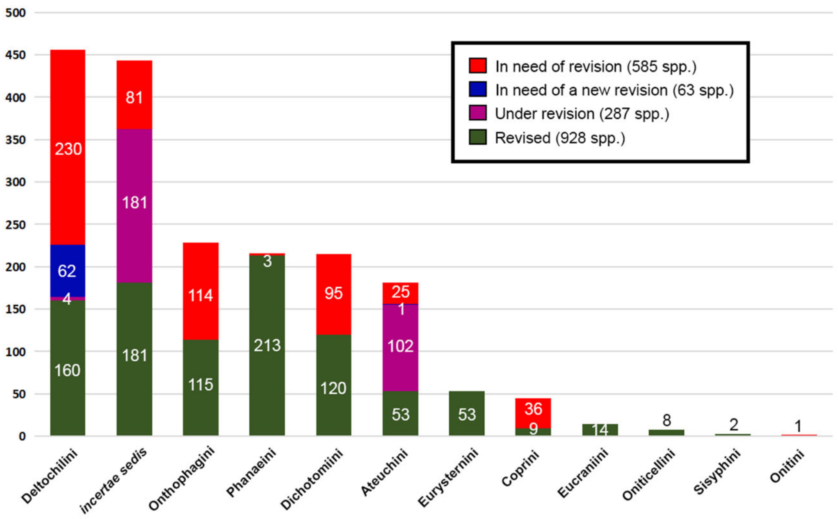

FIGURE 12
Status of taxonomic resolution of each tribe in the New World fauna. Bars show, for each tribe or the group of *incertae sedis* genera, the number of species classified by us in each of the four resolution categories. Phanaeini is, by far, the best resolved among the six most diverse groups; in contrast, Ateuchini, as far as published works are concerned, is, with only ~29% of its species revised during the Revolution, in the most precarious situation.

particularly in the Upper Rio Negro area of northwestern Brazil and Colombia, as well as the entire Venezuelan Amazon. Also almost entirely unexplored are the xerophytic forests of the Dry Chaco in southern Bolivia, northern Paraguay, and northwestern Argentina. As previously noted by Cupello et al. (2021a), distribution maps of South American taxa usually present a great void over the Dry Chaco (see, e.g., *Bolbites onitoides* Harold, 1868, *Holocanthon fuscorubrus* (Blanchard, 1846), *Ontherus appendiculatus* (Mannerheim, 1829), and *Gromphas inermis* Harold, 1869), and recent examination of the two main collections in Paraguay by the first author has revealed that even they house almost no specimens collected there (Cupello et al., 2023a). Also poorly represented in collections are the faunas of the Bolivian and, especially, Argentinian Yungas, as well as that of the tropical forests of the northern Central American countries, namely Guatemala, Honduras, and Nicaragua.

Efforts are also needed toward the re-discovery of species that, despite increasing collection activity, still fail to be caught. Examples are *Gromphas dichroa* (Blanchard, 1846) and *Deltepilissus diabolicus* (Harold, 1880), both of which have not been encountered in the field since the mid-20th century (Cupello and Vaz-de-Mello, 2013b, 2015; Silva et al., 2022), *Homalotarsus impressus* Janssens, 1932 and *Atlantemolanum costalimai* (Pereira and d'Andretta, 1955), both known exclusively from a few old, likely 19th-century specimens (Edmonds, 1972; González-Alvarado et al., 2019), and *Dendropaemon piceus* (Perty, 1830) and *Ateuchus procerus* (Harold, 1883), two even more drastic cases as they have vanished since the first half of the 19th century (Génier and Arnaud, 2016; Cupello, 2022). What is most curious about the majority of these examples is that these species inhabit one of the most intensively collected areas during the last 20 years in South America, the Brazilian Atlantic Forest. Why have they not been found again? Is it possible that they have become extinct due to the extensive deforestation of their habitat (cf. Ribeiro et al., 2009)? At least some of these vanished taxa have been hypothesized to be social insect inquilines, and it may be that if special attention is paid to investigating ant and termite nests, they will finally be re-discovered. The history of the Mexican endemic *Attavicinus monstrosus* (Bates, 1887) shows that we should be cautious before treating these myrmecophilous dung beetles as extinct simply because they are presumably microendemic and have disappeared for a time (Navarrete-Heredia, 1996).

A further issue that must be tackled by the scarabaeine systematists is their macrotaxonomic criteria and methodology. That is, how they infer supraspecific relationships and convert them into a classification. Of the 150 complete revisions and supplementary works listed in Table 1, just 14 have based their macrotaxonomy on explicit phylogenetic analyses, i.e., by presenting formal lists of characters and the analytical methods employed to infer phylogenetic relationships from them (Génier, 1996; Cook, 1998, 2000, 2002; Génier and Kohlmann, 2003; Vaz-de-Mello, 2007a, 2008; Cupello and Vaz-de-Mello, 2015; Génier and Arnaud, 2016; Roggero et al., 2016; Génier and Moretto, 2017; Maldaner et al., 2018b; Martínez-Revelo et al., 2020a; Halffter et al., 2022a). Eight others have based their macrotaxonomy on the phylogenetic results of previous publications (Ocampo, 2004, 2005, 2007, 2010a, 2010b, who relied upon Philips et al., 2002 and Ocampo and Hawks, 2006, and Cupello et al., 2020, 2021a, who relied on Philips et al., 2004a, Cupello and Vaz-de-Mello, 2015 and Tarasov and Génier, 2015, among others) or on then-unpublished data (Philips and Bell, 2008; finally published by Philips, 2016). The remaining ones have, in contrast, built their classifications following more vague, undisclosed procedures, relying on less disciplined, more superficial morphological comparisons to infer the phylogenetic relationships of the species (if the goal of presenting a phylogenetic classification was stated at all; sometimes, even the kind of classification that is aimed – e.g., if it is a phylogenetic or purely phenetic classification – is left vague). For one of these groups originally revised without such an adequate phylogenetic treatment, the phanaeine genera, subsequent workers have started to investigate its phylogeny using these more sophisticated computational methods (Philips et al., 2004a; Price, 2007, 2009; Maldaner et al., 2018b; Gillett and Toussaint, 2020), though this still has to be reflected in a revised macrotaxonomy (Maldaner et al., 2018b is an exception). Incipient treatment has also been given to *Dichotomius* (Pardo-Diaz et al., 2019).

The challenge, then, is to improve this scenario. First, authors, including ourselves, should strive to be more formal and disciplined in our phylogenetic analyses. This is not simply a formal need, the necessity to comply with a more explicit methodology and principles simply for the sake of it or to publish in journals with higher impact factors, but because these methods – i.e., those involved with computational parsimony and parametric (i.e., model-based) phylogenetic analyses – have demonstrated over the decades to be much better at inferring phylogenetic hypotheses that seem to be correct than the unaided, undisciplined human impression. Also, new character systems will be open to exploration once these more sophisticated techniques are dominated by us, scarabaeine systematists, including genetic and morphometric characters. Finally, we should seek to establish formal ranking criteria. What is a genus, a tribe, or a subtribe? Why is it that a taxon is ranked, let us say, as a subgenus and not as a genus or species group? Zunino and Halffter (1981), Génier (2017), and Cupello (2022) have given the first steps in this direction, but much is still to be done. By applying these methods and criteria explicitly and exploring a broad array of data, we will better understand the phylogenetic relationships of the New World dung beetles, and this will, in turn, lead us to a truly phylogenetic macrotaxonomy.

The level of classification that is currently most in need of such an advanced treatment is, no doubt, that of the tribe. This is a truly monumental task, for, since the New World fauna has a polyphyletic origin, the problem actually goes beyond the realm of the local fauna, encompassing the global diversity of the subfamily. Tarasov and Dimitrov (2016), in their groundbreaking phylogenetic study of the Scarabaeinae, have started the revisionary process, and now, with subsequent contributions, the number of recognized tribes in the whole subfamily has increased to 19, 11 of which, as listed in the Appendix, are present in the Americas (one, Onitini, introduced, six, Ateuchini, Dichotomiini, Deltochilini, Eucraniini, Eurysternini, and Phanaeini, endemic) (Scholtz et al., 2009; Tarasov and Dimitrov, 2016; Tarasov, 2017; Davis et al., 2019;

Daniel et al., 2020; Rossini et al., 2022). But the work is still far from being complete, and a great number of New World genera remain *incertae sedis* in the subfamily (Tarasov and Dimitrov, 2016; see the Appendix). And though we are calling special attention to the problems of the tribes, we should not lose sight that the genus-level classification is also in dire need of a more methodologically rigorous systematic treatment: the problems involving *Canthon* and related genera have been exposed 20 years ago by Medina et al. (2003) and are still to be resolved (cf. Cupello and Vaz-de-Mello, 2018), and it is well possible that, when investigated more seriously, genera like *Uroxys* and *Ateuchus*, as currently defined, may also prove to be polyphyletic (Vaz-de-Mello, 2007b).

Finally, the principles and methods of the microtaxonomic investigation – i.e., the delimitation and naming of species and subspecies – must also seek advancement. As we said above for macrotaxonomy, systematists must have clear definitions for the microtaxonomic ranks. That is to say, they need to have clear in their minds as to what kind of entities they want to apply the species and subspecies levels in the Linnean hierarchy (cf. Dubois, 2011). This is pivotal for two main reasons. First, for different taxonomies to be comparable, they have to share the same definitions for the taxonomic ranks. If different authors employ the term "species" to refer to different biological entities (e.g., reproductive communities versus diagnosable populations versus population lineages), taxonomic disagreements will usually have more to do with semantics than with the reality of the biological world. Saying "I don't agree that taxon A as delimited by author X is a good species" means nothing if the word "species" is not expressly defined and, even if it is, if the debaters do not agree on this definition (or are not at least aware that the word is being employed with different denotations). Second, species delimitation methods and ranking criteria, whatever they may be, derive directly from the definition of what a species (or subspecies) is; one can only have a method for discovering X if one defines what is meant by X. If a taxonomist has not defined what a species is (i.e., what kind of entity should be classified in the species category), delimiting species taxa is logically impossible.

But having a definition per se is not enough. This definition must be based on sound, educated reasoning and criteria, not on vague, intuitive ideas of what a species or subspecies is supposed to be. If our goal as systematists of building a classification system based on the evolution of dung beetles is to succeed, we must be better acquainted with the latest developments in the theory of speciation and other microevolutionary processes (e.g., Avise, 2000; Coyne and Orr, 2004; Price, 2008; Grant and Grant, 2014; Barraclough, 2019). We must also make good use of one of the greatest advantages that we have over our pre-1980s predecessors: the availability of large population and geographical series. They allow us to have a better understanding of the population structure of our species in terms of both connectivity between the populations and how their characters, both phenotypic and genetic, are distributed across the geographical space. In analyzing this material, another obvious advantage of modern systematics is, as mentioned above for macrotaxonomy, our capacity of exploring genetic and morphometric characters. Both of these character systems can provide a much vaster volume of data than the traditional qualitative (or vaguely quantitative) morphology to which our predecessors were mostly limited. And the power of these two character systems, genetics and morphometrics, goes beyond sheer volume of data: they allow us to complement traditional descriptive procedures with sophisticated statistical analyses for species delimitation and the study of population structure (Barraclough, 2019), something so far still rarely applied in taxonomic studies on New World dung beetles (but see, e.g., Nolasco-Soto et al., 2017, 2020; see also Matthews, 1961 for simple morphometrics). Yet, as recently demonstrated by Solís and Kohlmann (2023), difficult cases that defy dung beetle microtaxonomists' abilities to find a proper resolution relying on traditional morphological analyses can be clarified with the help even of the simplest molecular analyses. A study of the taxonomic literature listed in Table 1 will show many other cases that would benefit from these approaches, both simple and more sophisticated ones (see, e.g., discussions in Edmonds and Zídek, 2012, Cupello et al., 2021a, 2023a). Though still not easily accessible, behavioral, ecological, spectrophotometric, and biochemical characters shall also play a central role in microtaxonomy once proper methodology is learned or developed. The future will say which new character systems will be opened up by technological advancements for taxonomic exploration.

By paying attention to the population nature of biological diversity, we will put behind old typological biases leading to conceptualizations of species as homogeneous, "minimally diagnosable" units, and, in its place, adopt a biologically grounded conceptualization of species as composed of individuals interacting through interbreeding and so giving emergence to a new level of biological integration, the evolving population and its gene pool. This will have two effects. First, it will make us look for variation, the raw material of evolution, as opposed to present variation in short, almost exculpatory sentences as if recognizing its existence in our species other than in color or size was to admit that the taxonomy is possibly faulty (e.g., "until more evidence is found, we will prefer to treat as these specimens as a single species"). Second, it will make us more cautious before publishing (or accepting) new species taxa based on subtle variation, particularly microgeographic ones and in groups whose taxonomy is still largely unresolved such as *Onthophagus*, *Deltochilum*, and *Canthidium*. Population and geographical variation exist, and our taxonomic methods and concepts must be formulated in accordance.

Species, taxonomists must have in mind, are historically dynamic entities, and the understanding of their nature will remain incomplete until their phylogeographies are fully explored (see Maldaner et al., 2019 and Nolasco-Soto et al., 2017, 2020 for incipient attempts). But, at the same time, we must take care not to confuse population structure with speciation (Sukumaran and Knowles, 2017). Discontinuity in variation may not be due to discontinuity in reproductive connectivity, but an artifact of low geographical sampling of clinally variable, but still connected populations. And even if reproductive discontinuity between (meta)populations is the case, it still may not be evidence of speciation, for the discontinuity may be due to geographical rather than biological reproductive isolation (see Cupello et al., 2021a). All these factors must be taken into account by the microtaxonomist. We must look not only for patterns of variation, but for causes. Not only to know if the organisms or populations are different or "evolving separately", but why they are different and are evolving separately. Our microtaxonomic activities must, in essence, evolve from being solely descriptive to also embracing, like the phylogenetic macrotaxonomy, an explanatory goal.

Why is there a revolution?

Why has the Scarabaeinae Taxonomic Revolution been happening? And why did it start in the late 1980s and not, let us say, in the 2010s or the 1940s? What are the historical factors involved? We suppose that a general increase in scientific funding at least in some of the countries involved, particularly in Brazil in the 2000s, has played a major role. This at least in part was made possible due to the expressive economic growth and rise in general prosperity that most countries across the Americas have been experiencing since WWII (Roser, 2013; Pinker, 2018). Latin America's GDP per capita as a whole has risen by more than 365% since 1940, and this figure is even greater for some of the major countries in the Revolution taken individually such as Costa Rica (~422%), Mexico (~544%), and Brazil (~771%) (Our World in Data, 2020; Figure 7); the situation has been no different for the other two main players in the Americas, the US (~360%) and Canada (~424%) (Our World in Data, 2020). The vast population expansion experienced across much of the continent in the latter half of the 20th century, especially in the US, Mexico, Colombia, and Brazil (Roser et al., 2013), as well as the concomitant increasing participation of women in science (Figure 7) and the widespread rising in literacy and the betterment of education in general (Roser and Ortiz-Ospina, 2016; Pinker, 2018; Roser and Ortiz-Ospina, 2018) have also impacted the field by simply increasing the pool from which new dung beetle taxonomists are drawn. Also important have likely been the sharply declining costs for long-distance transport, particularly airfare (Thompson, 2013; Our World in Data, 2015; Gondim and Daraya, 2016; Pinker, 2018), which enabled much easier access to remote areas for fieldwork and overseas travels for the study of collections. If, before, taxonomists were mostly limited to the museums of their countries and seldom had access to the material housed overseas, including the precious type material, now they have the world before them. This alone could explain the change from a faunistic to a phylogenetic approach during the Revolution.

The advent and spread since the 1990s of personal computers, the internet, and e-mail communication (Roser et al., 2015) has also certainly played a central role in creating and expanding the Revolution. They made the exchange of information between researchers much more efficient, and enabled those based away from the major centers of scientific activity, particularly in Latin America, to effectively be part of the global community of systematists. Another, perhaps even more significant consequence of our digitally connected world has been the growing online accessibility of the taxonomic literature, particularly of historical, rarer works, freely available on websites such as the Biodiversity Heritage Library and Google Books. If, previously, to read a short description written two centuries ago by, say, Fabricius or Blanchard, a researcher may have needed to travel hundreds of kilometers to a library in another city, state, or even country, or endure long weeks of wait until someone mailed (or faxed) him a photograph or photocopy of the page he wanted to see, now the same information can be accessed within a few seconds from almost anywhere on the globe. The digital revolution has also greatly facilitated and reduced the cost of the publication process. Writing and editing a text on a word processing software such as Microsoft Word is undoubtedly easier and faster than using a typewriter or paper and pen. Digital imaging, both digital photography and digital drawing and related digital editors, is much more efficient than traditional line drawing or analog photography. The movement of manuscripts between authors, editors, and reviewers, which formerly had to rely on slow mail services (especially if international and involving third-world countries), is now as quick as a keystroke. And the costliest and slowest phase in the publication process has been pretty much eliminated: since 2012, provided that a few requirements are met, printing is no longer necessary for a taxonomic work to be formally published for nomenclatural purposes (ICZN, 2012). So, from beginning to end, producing a taxonomic revision is, nowadays, a much more practical task than it was a few decades ago.

But how does the history of the modern New World Scarabaeinae taxonomy compare with that of other scarab, beetle, and insect groups in this part of the globe? Is our revolution unique? Or have other groups experienced the same phenomenon? If the Revolution is something special of the Scarabaeinae at least among other scarabs as it seems to be, then there must be additional factors to the ones pointed out above, for they would facilitate the work on any biological group indiscriminately. Perhaps the answer is simply contingency: it just happened that the idiosyncratic interest from a few founding members met the right environment when the above conditions emerged in the late 1980s to the 2000s, and everything simply followed. Another factor to consider, however, is that, simultaneously with the Taxonomic Revolution, there has also been an Ecological Revolution: dung beetles have been transformed during the past decades into one of the major taxa used as bioindicators by ecologists interested in the conservation of tropical biomes (Halffter and Favila, 1993; Favila and Halffter, 1997; Spector, 2006; Nichols et al., 2007; Gardner et al., 2008; Kryger, 2009; Nichols and Gardner, 2011; Rivera and Favila, 2022; Arellano et al., 2023; Mora-Aguilar et al., 2023). This Ecological Revolution itself was largely the result of the emergence of conservation biology as a scientific discipline in the 1980s (Soule and Wilcox, 1980; Soulé, 1985; Quammen 1996; Meine et al., 2006; Van Dyke, 2008; Franco, 2013). The Ecological Revolution has had a two-fold effect on the systematics of the Scarabaeinae: on the one hand, it has put great pressure on the advancement of the discipline, for reliable identifications and identification tools are needed by a community much broader than the taxonomists themselves and museum curators. On the other hand, as we have already discussed, this widespread interest in dung beetles for environmental studies has brought an unprecedented volume of specimens to the collections, a golden opportunity for taxonomic investigations. The great majority of the new populations and species studied by modern taxonomists, particularly in South

America, originate from such ecological inventories. Without this co-evolution of the Taxonomic and Ecological Revolutions, neither could have happened.

And how have the different taxonomic schools in each country been interacting? The first impression is that the current revolution has its root in two major centers of origin, both founded around the 1950s: one in Canada, by Henry F. Howden (1925–2014), and another in Mexico, by Gonzalo Halffter (1932–2022). The latter has greatly flourished, with ramifications throughout Latin America, having been in the partial genesis of at least the modern Brazilian and Costa Rican schools through Halffter's former students Fernando Z. Vaz-de-Mello and Bert Kohlmann, respectively. The Canadian school, in turn, has been active mainly through the work of François Génier. But to what extent has this "polyphyletic" origin influenced the outcome of the Revolution? Are there perceptible differences in style or approaches by the descendants of each of the two schools? Has this influenced their results? And what about the individual researchers in the United States not genealogically related to either of the schools? Have they contributed unique elements? W.D. Edmonds, for instance, one of the major figures in the Revolution, became interested in dung beetle systematics in the early 1960s completely independent of Howden or Halffter, though he came to be close to the latter afterward (e.g., Edmonds and Halffter, 1978; Halffter and Edmonds, 1982). The same could be said of another close US collaborator of Halffter's, Eric Matthews (1932–2022) (Halffter and Matthews, 1966), as well as of Howden's US associate Oscar L. Cartwright (1900–1983) (e.g., Howden and Cartwright, 1963). The influence of Francisco Pereira (1913–1991) in Brazil, Antonio Martínez (1922–1993) in Argentina, and Mario Zunino in Italy in forging their partner Halffter's Mexican school is also worthy of further investigation. The history of the Scarabaeinae Taxonomic Revolution can be itself a subject of fruitful research for those interested in the social dynamics of scientific progress.

Conclusion

While we should all celebrate the progress made in the past three decades, it is important to have clear in our minds that the Scarabaeinae Taxonomic Revolution has just started. It needs to expand to the most difficult groups still unworked in the New World, as well as to grow outwards and reach the faunas of the other parts of the globe, especially those of the Oriental and Ethiopian Regions. In these two latter regions, the hyperdiverse genus *Onthophagus*, with 2,257 species already described (only a small minority in the Americas), is, no doubt, the greatest challenge, and it must eventually be tackled. Closer to home, in the Americas, with the revision of *Ateuchus* nearing completion (though still unpublished; Cupello, 2022), *Dichotomius*, *Canthon*, *Deltochilum*, *Uroxys*, and *Canthidium* remain the most demanding challenges. As these revisions progress, new character systems should also be explored. Is it possible, for example, that, once the female genitalia has been more thoroughly scrutinized, its anatomy will prove to be as important for the systematics of dung beetles as the male endophallus has been since the pioneering works of Mario Zunino and Bert Kohlmann in the 1970s and 1980s? Preliminary results have given support to this idea (e.g., Zunino, 1971, 1972, 1975, 1976, 1978, 1979; Kohlmann, 1984; Zunino and Halffter, 1988a; Marchisio and Zunino, 2012; Cupello et al., 2020). The same may also be true for the mouthparts and wing venation (see, e.g., Philips et al., 2004a, b; Tarasov and Génier, 2015; Cupello et al., 2020; Palestrini et al., 2020). The study of immature stages, which experienced some progress in the latter half of the 20th century (e.g., Edmonds and Halffter, 1978), has, with a few exceptions (e.g., Hernández-Martínez and Martínez, 2003; Martínez and Lumaret, 2005; Sánchez et al., 2010), pretty much stagnated since then. Why can they not prove to be as taxonomically informative as the adults? And what about the molecular data? Will molecular phylogeographical analyses, for example, reveal more complex population dynamics in the scarabaeine species than our morphological studies have so far been capable of detecting? And the macrotaxonomy, will it be revolutionized or only fine-tuned when explicit phylogenetic methodologies, whether employed for molecular or morphological characters, are more widely adopted? Only time and effort will tell. But we are confident that, should funding continue to be available, the Scarabaeinae Revolution will keep producing fascinating discoveries about this so charismatic and ecologically relevant insect group, the dung beetles.

Author contributions

MC conceptualized the paper, reviewed the literature, compiled the data, prepared the figures and tables, and wrote and reviewed the text. FS conceptualized the paper, wrote an early version of the text, and reviewed its final version. FV-d-M conceptualized the paper, provided much of the literature reviewed by MC, and reviewed the text. All authors contributed to the article and approved the submitted version.

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Conflict of interest

Publisher's note

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Appendix: Current macrotaxonomy of the New World Scarabaeinae

Tribal-level classification based on Cupello and Vaz-de-Mello (2013b), Philips (2016), and Tarasov and Dimitrov (2016). Tribal-level nomenclature based on Bouchard et al. (2011) and the updates by Bousquet (2016) and Bouchard and Bousquet (2020).

- **Ateuchini Perty, 1830 (21 gg., 181 spp.)**
  - **Ateuchina Perty, 1830 (3 gg., 113 spp.)**
    - *Aphengium* Harold, 1868 (4 spp.)
    - *Ateuchus* Weber, 1801 (102 spp.)
      - *Ateuchus* s. str. (100 spp.)
      - *Ateuchus* (*Lobidion*) Génier, 2010 (2 spp.)
    - *Deltorhinum* Harold, 1867 (7 spp.)
  - **Scatimina Vaz-de-Mello, 2008 (17 gg., 63 spp.)**
    - *Besourenga* Vaz-de-Mello, 2008 (4 spp.)
    - *Bradypodidium* Vaz-de-Mello, 2008 (3 spp.)
    - *Degallieridium* Vaz-de-Mello, 2008 (1 sp.)
    - *Eutrichillum* Martínez, 1969 (3 spp.)
    - *Feeridium* Vaz-de-Mello, 2008 (1 sp.)
    - *Genieridium* Vaz-de-Mello, 2008 (7 spp.)
    - *Leotrichillum* Vaz-de-Mello, 2008 (1 sp.)
    - *Martinezidium* Vaz-de-Mello, 2008 (4 spp.)
    - *Nunoidium* Vaz-de-Mello, 2008 (1 sp.)
    - *Onoreidium* Vaz-de-Mello, 2008 (4 spp.)
    - *Pedaridium* Harold, 1868 (1 sp.)
    - *Pereiraidium* Vaz-de-Mello, 2008 (1 sp.)
    - *Scatimus* Erichson, 1847 (13 spp.)
    - *Scatrichus* Génier and Kohlmann, 2003 (3 spp.)
    - *Silvinha* Vaz-de-Mello, 2008 (1 sp.)
    - *Trichillidium* Vaz-de-Mello, 2008 (4 spp.)
    - *Trichillum* Harold, 1868 (11 spp.)
  - ***incertae sedis* in Ateuchini (1 g., 5 spp.)**
    - *Agamopus* Bates, 1887 (5 spp.)
- **Coprini Leach, 1815 (1 g., 45 spp.)**
  - *Copris* Geoffroy, 1762 (45 spp.)
    - *Copris* s. str. (45 spp.)
- **Deltochilini Lacordaire, 1855 (20 gg., 457 spp.)**
  - *Anisocanthon* Martínez and Pereira, 1956 (4 spp.)
  - *Anomiopus* Westwood, 1842 (63 spp.)
  - *Atlantemolanum* González-Alvarado et al., 2019 (2 spp.)
  - *Boreocanthon* Halffter, 1958 (13 spp.)
  - *Canthon* Hoffmannsegg, 1817 (163 spp.)
    - *Canthon* s. str. (65 spp.)
    - *Canthon* (*Bajacanthon*) Halffter, 2022 (1 sp.)
    - *Canthon* (*Francmonrosia*) Pereira and Martínez, 1959 (6 spp.)
    - *Canthon* (*Glaphyrocanthon*) Martínez, 1948 (48 spp.)
    - *Canthon* (*Goniocanthon*) Pereira and Martínez, 1956 (3 spp.)
    - *Canthon* (*Nesocanthon*) Pereira and Martínez, 1956 (3 spp.)
    - *Canthon* (*Peltecanthon*) Pereira, 1953 (4 spp.)
    - *Canthon* (*Pseudepilissus*) Martínez, 1954 (14 spp.)
    - *Canthon* (*Trichocanthon*) Pereira and Martínez, 1959 (1 sp.)
    - *incertae sedis* in *Canthon* (18 spp.)
  - *Deltepilissus* Pereira, 1949 (2 spp.)
  - *Deltochilum* Eschscholtz, 1822 (114 spp.)
    - *Deltochilum* s. str. (7 spp.)
    - *Deltochilum* (*Aganhyboma*) Kolbe, 1893 (27 spp.)
    - *Deltochilum* (*Calhyboma*) Kolbe, 1893 (13 spp.)
    - *Deltochilum* (*Deltohyboma*) Lane, 1946 (50 spp.)
    - *Deltochilum* (*Euhyboma*) Paulian, 1938 (1 sp.)
    - *Deltochilum* (*Hybomidium*) Shipp, 1897 (13 spp.)
    - *Deltochilum* (*Parahyboma*) Paulian, 1938 (2 spp.)
    - *Deltochilum* (*Rubrohyboma*) Paulian, 1938 (1 sp.)
  - *Hansreia* Halffter and Martínez, 1977 (6 spp.)
  - *Holocanthon* Martínez and Pereira, 1956 (2 spp.)
  - *Malagoniella* Martínez, 1961 (9 spp.)
    - *Malagoniella* s. str. (4 spp.)
    - *Malagoniella* (*Megathopomima*) Martínez, 1961 (5 spp.)
  - *Megathopa* Eschscholtz, 1822 (2 spp.)
  - *Megathoposoma* Balthasar, 1939 (1 sp.)
  - *Melanocanthon* Halffter, 1958 (4 spp.)
  - *Pseudocanthon* Bates, 1887 (11 spp.)
  - *Scatonomus* Erichson, 1835 (11 spp.)
  - *Scybalocanthon* Martínez, 1948 (24 spp.)
  - *Scybalophagus* Martínez, 1953 (5 spp.)
  - *Sylvicanthon* Halffter and Martínez, 1977 (15 spp.)
  - *Tetraechma* Blanchard, 1841[1] (5 spp.)
  - *Xenocanthon* Martínez, 1952 (1 sp.)
- **Dichotomiini Pereira, 1954 (4 gg., 215 spp.)**
  - *Chalcocopris* Burmeister, 1846 (2 spp.)
  - *Dichotomius* Hope, 1838 (200 spp.)
    - *Dichotomius* s. str. (74 spp.)
    - *Dichotomius* (*Cephagonus*) Luederwaldt, 1929 (40 spp.)
    - *Dichotomius* (*Homocanthonides*) Luederwaldt, 1929 (1 sp.)
    - *Dichotomius* (*Selenocopris*) Burmeister, 1846 (85 spp.)
  - *Holocephalus* Hope, 1838 (6 spp.)

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[1] Nunes and Vaz-de-Mello (2022) stated that the publication date of *Tetraechma* and its type species *T. sanguineomaculata* was February 1842. This is incorrect. These names were made available in plate 10 of Brullé & Blanchard's insect volume of d'Orbigny's series *Voyage dans l'Amérique méridionale*. The entire series was issued into 90 livraisons between 1835 and 1847, 32 of which corresponding to Brullé & Blanchard's volume (Evenhuis, 1997; Bousquet, 2016). Plate 10, authored by Blanchard alone, is part of livraison 54, whose precise publication date is still unknown. However, the Société Géologique de France recorded in the proceedings of its session from 08 November 1841 the receipt of copies of livraisons 51 to 54 from the French ministry of education ("ministre de l'instruction publique") (Anonymous, 1842). Plate 10, therefore, and the new names contained in it, must have been published before that date, not in February 1842 as Nunes and Vaz-de-Mello asserted. Following Articles 21.3 and 21.5 of the ICZN (1999), 08 November 1841 must be adopted as the publication date of *Tetraechma* and *T. sanguineomaculata* until the actual date – or an earlier record – is retrieved.

- *Isocopris* Pereira and Martínez, 1960 (7 spp.)

- **Eucraniini Burmeister, 1873 (4 gg., 14 spp.)**
    - *Anomiopsoides* Blackwelder, 1944 (4 spp.)
    - *Ennearabdus* Van Lansberge, 1874 (1 sp.)
    - *Eucranium* Brullé, 1838 (6 spp.)
    - *Glyphoderus* Westwood, 1838 (3 spp.)
- **Eurysternini Vulcano et al., 1961 (1 g., 53 spp.)**
    - *Eurysternus* Dalman, 1824 (53 spp.)
- **Oniticellini Kolbe, 1905 (4 gg., 7 spp.)**
  - **Attavicina Philips, 2016 (1 g., 1 sp.)**
    - *Attavicinus* Philips and Bell, 2008 (1 sp.)
  - **Liatongina Philips, 2016 (1 g., 2 spp.)**
    - *Liatongus* Reitter, 1893 (2 spp.)
  - **Oniticellina Kolbe, 1905 (2 gg., 4 spp.)**
    - *Anoplodrepanus* Simonis, 1981 (2 spp.)
    - *Euoniticellus* Janssens, 1953 (2 spp.)
- **Onitini Castelnau, 1840 (1 g., 1 sp.)**
    - *Onitis* Fabricius, 1798 (1 sp.)
- **Onthophagini Streubel, 1846 (3 gg., 229 spp.)**
    - *Digitonthophagus* Balthasar, 1959 (1 sp.)
    - *Hamonthophagus* Roggero et al., 2016 (2 spp.)
    - *Onthophagus* Latreille, 1802 (226 spp.)
      - *Onthophagus* s. str. (226 spp.)
- **Phanaeini Hope, 1838 (11 gg., 216 spp.)**
  - **Gromphadina Zunino, 1985 (2 gg., 8 spp.)**
    - *Gromphas* Brullé, 1838 (6 spp.)
    - *Oruscatus* Bates, 1870 (2 spp.)
  - **Phanaeina Kolbe, 1838 (9 gg., 208 spp.)**
    - *Bolbites* Harold, 1868 (1 sp.)
    - *Coprophanaeus* d'Olsoufieff, 1924 (50 spp.)
      - *Coprophanaeus* s. str. (38 spp.)
      - *Coprophanaeus* (*Megaphanaeus*) d'Olsoufieff, 1924 (4 spp.)
      - *Coprophanaeus* (*Metallophanaeus*) d'Olsoufieff, 1924 (8 spp.)
    - *Dendropaemon* Perty, 1830 (41 spp.)
      - *Dendropaemon* s. str. (9 spp.)
      - *Dendropaemon* (*Coprophanaeoides*) Edmonds, 1972 (10 spp.)
      - *Dendropaemon* (*Crassipaemon*) Cupello and Génier, 2017 (4 spp.)
      - *Dendropaemon* (*Enicotarsus*) Castelnau, 1831 (1 sp.)
      - *Dendropaemon* (*Eurypodea*) Klages, 1906 (2 spp.)
      - *Dendropaemon* (*Glaphyropaemon*) Génier and Arnaud, 2016 (3 spp.)
      - *Dendropaemon* (*Nigropaemon*) Génier and Arnaud, 2016 (1 sp.)
      - *Dendropaemon* (*Paradendropaemon*) Edmonds, 1972 (2 spp.)
      - *Dendropaemon* (*Rutilopaemon*) Génier and Arnaud, 2016 (1 sp.)
      - *Dendropaemon* (*Streblopaemon*) Génier and Arnaud, 2016 (1 sp.)
      - *Dendropaemon* (*Sulcopaemon*) Génier and Arnaud, 2016 (6 spp.)
      - *Dendropaemon* (*Titthopaemon*) Génier and Arnaud, 2016 (1 sp.)
    - *Diabroctis* Gistel, 1857 (5 spp.)
    - *Homalotarsus* Janseens, 1932 (1 sp.)
    - *Megatharsis* Waterhouse, 1891 (1 sp.)
    - *Oxysternon* Castelnau, 1840 (11 sp.)
      - *Oxysternon* s. str. (8 spp.)
      - *Oxysternon* (*Mioxysternon*) Edmonds, 1972 (3 spp.)
    - *Phanaeus* MacLeay, 1819 (83 spp.)
      - *Phanaeus* s. str. (49 spp.)
      - *Phanaeus* (*Notiophanaeus*) Edmonds, 1994 (34 spp.)
    - *Sulcophanaeus* d'Olsoufieff, 1924 (15 spp.)
- **Sisyphini Mulsant, 1842 (1 g., 2 spp.)**
    - *Sisyphus* Latreille, 1807 (2 sp.)
- ***incertae sedis* in Scarabaeinae (19 gg., 443 spp.)**
    - *Bdelyropsis* Vulcano et al., 1960 (3 spp.)
    - *Bdelyrus* Harold, 1869 (27 spp.)
    - *Canthidium* Erichson, 1847 (178 spp.)
      - *Canthidium* s. str. (80 spp.)
      - *Canthidium* (*Neocanthidium*) Martínez et al., 1964 (70 spp.)
      - *incertae sedis* in *Canthidium* (28 spp.)
    - *Canthochilum* Chapin, 1934 (24 spp.)
    - *Canthonella* Chapin, 1930 (17 spp.)
    - *Canthonidia* Paulian, 1938 (1 sp.)
    - *Canthotrypes* Paulian, 1939 (1 sp.)
    - *Cryptocanthon* Balthasar, 1942 (43 spp.)
    - *Eudinopus* Burmeister, 1840 (1 sp.)
    - *Homocopris* Burmeister, 1846 (4 spp.)
    - *Isacanthon* Pacheco and Vaz-de-Mello, 2019 (1 sp.)
    - *Ontherus* Erichson, 1847 (60 spp.)
      - *Ontherus* s. str. (34 spp.)
      - *Ontherus* (*Caelontherus*) Génier, 1996 (24 spp.)
      - *Ontherus* (*Planontherus*) Génier, 1996 (2 spp.)
    - *Paracanthon* Balthasar, 1938 (15 spp.)
    - *Paracryptocanthon* Howden and Cook, 2002 (2 spp.)
    - *Sinapisoma* Boucomont, 1928 (1 sp.)
    - *Streblopus* Van Lansberge, 1874 (2 spp.)
    - *Tesserodoniella* Vaz-de-Mello and Halffter, 2006 (2 spp.)
    - *Uroxys* Westwood, 1842 (59 spp.)
    - *Zonocopris* Arrow, 1932 (2 spp.)