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An overview of the Brazilian Chrysomelidae (Insecta: Coleoptera): the most species-rich beetle family in Brazil

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ABSTRACT. The leaf beetles (Chrysomelidae) are one of the most species-rich family of herbivorous beetles with about 45,000 species worldwide. Based on the contributions of chrysomelidologists to the Taxonomic Catalog of the Brazilian Fauna – CTFB, the family comprises 6,079 species in 562 genera of which 951 species are endemic to Brazil, standing out as the most diverse, representing 4.8% of the Brazilian fauna and 17.1% of the beetle species. Chrysomelidae has twelve subfamilies with nine reported to Brazil: Galerucinae, the richest with 1,916 species in 202 genera, followed by Cassidinae, Eumolpinae, Cryptocephalinae, Chrysomelinae, Bruchinae, Criocerinae, Lamprosomatinae and Sagrinae – this with only one species. Most of these subfamilies need urgent revision, since many species are poorly characterized, and polymorphism is frequent in some groups. The Czech couple Jan and Bohumila Bechyně were the researchers who described most species from Brazil. Furthermore, despite the increase of research on biology, natural history, host plants, genetics, ecology from 1980's much still need to be investigated to better known the Brazilian Chrysomelidae and probably many new species are yet to be discovered.

KEY WORDS. Brazilian fauna, CTFB, biodiversity, leaf beetles, phytophagous.

INTRODUCTION

Chrysomeloidea are one of the seven Coleoptera superfamilies of the Series Cucujiformia and are considered a sister-group of Curculionoidea; the two superfamilies constitute a clade informally known as Phytophaga, with more than 125,000 species (Haddad and McKenna 2016). With approximately 63,000 described extant species (Ślipiński et al. 2011), Chrysomeloidea include Cerambycidae, Disteniidae, Vesperidae, Orsodacnidae, Megalopodidae and

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Chrysomelidae (Bouchard et al. 2011, Reid 2014a, Haddad et al. 2018). All Chrysomeloidea families occur in Brazil (Monné 2012) and constitutes the most species rich superfamily representing 30% of the Brazilian Coleoptera fauna (Caron et al. 2024) and 8.5% of the Brazilian animal fauna (Boeger et al. 2024). Within the superfamily, Chrysomelidae (= leaf beetles) stand out as the most species rich, reaching 45,000 described species and estimated to include 55,000–60,000 species globally (Jolivet 2015), with the highest diversity in the tropics. The species are herbivorous with each subfamily showing a preference for a certain set of host plants or even parts of plants.

The internal classification of Chrysomelidae has undergone many changes throughout the years (for a more detailed discussion see Haddad and McKenna 2016). Some taxonomic groups have been constantly recovered as monophyletic in phylogenetic studies by different authors using different sets of characters such as mitochondrial and nuclear genes, adults and larval morphology and ecology (e.g., Crowson 1955, Kuschel and May 1990, Reid 1995, 2000, Chaboo 2007, Haddad and McKenna 2016, Nie et al. 2020, Douglas et al. 2023). Currently, twelve extant subfamilies are recognized in Chrysomelidae grouped in the following general relationships: a basal 'sagrine' clade, consisting of ((Bruchinae + Sagrinae) + (Criocerinae + Donaciinae)) which is sister to the 'eumolpinae' clade including (Cassidinae + (Eumolpinae + (Cryptocephalinae + Lamprosomatinae))) with Spilopyrinae (Nie et al. 2020) or Synetinae subtending this clade (Douglas et al. 2023), plus the 'chrysomeline' clade (Chrysomelinae + Galerucinae) (Reid 1995, Gómez-Zurita et al. 2008, Nie et al. 2020, Douglas et al. 2023). Among them Donaciinae, Synetinae and Spilopyrinae do not occur in Brazil.

Twenty-three years after the first synthesis of knowledge of the beetles of Neotropical region by Costa (2000), we provide an update of the Brazilian Chrysomelidae genera and species based on the Taxonomic Catalog of the Brazilian Fauna (or "Catálogo Taxonômico da Fauna do Brasil", hereafter shortened to its Portuguese abbreviation CTFB). The CTFB is an online open access database where renowned zoologists are working in an integrated way to generate the first valid species list of the Brazilian fauna. The database is constantly updated to include newly described species, corrections based on published nomenclatural acts and inclusion of new data about each of the species in the checklist.

In this overview, we present a summary of our current findings based on our efforts compiling the checklist, some background information on each of the subfamilies, the methods used to generate the new data included in the checklist, a discussion of the main authors who have contributed to our knowledge of the Brazilian Chrysomelidae fauna, and end with some considerations regarding the challenges faced towards expanding our understanding and expertise of the Chrysomelidae in Brazil. We hope that our efforts will contribute to improvement to the knowledge on Brazilian Chrysomelidae and that the set of data and references here presented serve as a source of information and inspiration for the study of this fascinating group.

MATERIAL AND METHODS

The first phase of the CTFB project aimed to generate a comprehensive, up-to-date list of all valid species reported to occur in Brazil. This information was compiled for Chrysomelidae by the international team of authors of this paper. Each expert compiled a checklist for their respective groups based on primary (original descriptions, revisions) and secondary (catalogs) taxonomic publications. Particular attention was given to verify previous secondary sources to avoid perpetuating prior mistakes and to ensure that the current valid taxon names were listed. The second phase of the CTFB project, which is ongoing and still largely missing for most Chrysomelidae species, will include additional taxonomic, ecological and biological information, such as geographic distribution, host plants, synonymies and bibliography.

Data for this paper was obtained from the Chrysomelidae section of the CTFB website (http://fauna.jbrj.gov.br/) (Linzmeier et al. 2023). The number of species, genera and researchers were accounted for using an Excel spreadsheet containing all Chrysomelidae data set available as of March 7th, 2023.

The classification adopted in the CTFB followed Bouchard et al. (2011). However, as tribes are not well established for all subfamilies, some modifications were adopted: Eumolpinae follows the traditional system as accepted by Seeno and Wilcox (1982) with inclusion of Megascelidini; for Chrysomelinae all major subtribes of Chrysomelini sensu Seeno and Wilcox (1982) are here treated as tribes; Lamprosomatinae includes the newly described tribe Cachiporrini (Chamorro and Konstantinov 2011); Cryptocephalinae follows Gómez-Zurita and Cardoso (2021) which recognize Clytrini, Cryptocephalini, Fulcidacini, Pachybrachini, and Mylassini; Galerucinae follows Viswajyothi and Clark (2022); Cassidinae follows Borowiec and Świetojańska 2014.

RESULTS AND DISCUSSION

Among the Brazilian fauna, Chrysomelidae stand out as the most diverse family with 6,079 species and 562 genera, representing 4.8% of the entire fauna (Boeger et al. 2024) and 17.1% of the beetle diversity (Caron et al. 2024). Galerucinae are the most species rich subfamily with 1,916 recorded species in 144 genera, followed by Cassidinae with 1,477 species in 140 genera (Table 1, Fig. 1). These subfamilies together represent 55.8% of the Brazilian leaf beetle species. The most speciose Brazilian leaf beetle genus is *Chlamisus* Rafinesque, 1815 with 222 species, which represents 30.4% of the species of Cryptocephalinae. In addition to this, the following genera are very diverse having more than 100 species: *Platyphora* Gistel, 1857 with 175 species, *Diabrotica* Chevrolat, 1837 with 149 species, *Lema* Fabricius, 1798 with 132 species, *Charidotis* Boheman, 1854 with 130 species and *Stolas* Billberg, 1820 with 102 species. The Brazilian Criocerinae fauna consist of only three genera, with *Lema* representing 97% of the species in this subfamily. Also, in Lamprosomatinae, *Lamprosoma* Kirby, 1818 represents 85.5% of the species; and in Bruchinae *Acanthoscelides* Schilsky, 1905 and *Amblycerus* Thunberg, 1815 compose together 45.4% of bruchine species. In Eumolpinae the most species rich genus is *Colaspis* Fabricius, 1801 with 78 species, followed by *Metazyonycha* Chevrolat, 1836 with 69 species, that together represents 15.4% of the eumolpine'species in Brazil.

Similar efforts to count and catalog beetle and leaf beetle species have been done in other Latin American countries. In Mexico, 2,141 species and 298 genera of leaf beetles (not included Bruchinae; excluding numbers of "Megalopodinae") were recorded (Ordóñez-Reséndiz et al. 2014) where Galerucinae (825 species; 138 genera), Cryptocephalinae (348 species; 26 genera) and Cassidinae (333 species; 67 genera) stand out as the most species rich subfamilies. In Chile, the Chrysomelidae diversity (168 species; 78 genera) represents less than 5% of beetle species with Staphylinidae and Tenebrionidae as the most diverse families (Elgueta 2000). The Peruvian Chrysomelidae fauna is composed of 1,767 species and 278 genera with Galerucinae as the most diverse (640 species; 129 genera) (Chaboo and Clark 2015, Chaboo and Flowers 2015a, 2015b, Chaboo and Morse 2015, Chaboo and Schmitt 2015, Chaboo and Staines 2015, Furth et al. 2015, Chaboo and Schöller 2016). Also, in Nicaragua at least 550 chrysomelid species have been recorded (Maes and Staines 1991, Maes and Gómez-Zurita 2016, Maes et al. 2016a, 2016b, Gómez-Zurita and Maes 2022) while in El Salvador 420 species (Roie et al. 2019), and in Argentina 979 species in 258 genera of leaf beetles have been recorded (Cabrera and Roig-Juñent 1998). These data emphasize the Chrysomelidae megadiversity found in Brazil and begins to present a better and more comprehensive overview of the diversity of this family in Latin America, especially in the Neotropical region, which have many unique habitats that must harbor many species yet to be discovered. Furthermore, it is necessary to produce an integrated and updated catalog of Neotropical Chrysomelidae since species lists are available to some countries, and probably many species are shared.

Costa (2000) recognized Chrysomelidae as the most species-rich Neotropical beetle family and the second richest family in Brazil with 4,362 species after Curculionidae (5,041 species). Since then, the total number of chrysomelid species and genera from Brazil has increased by 28.2% and

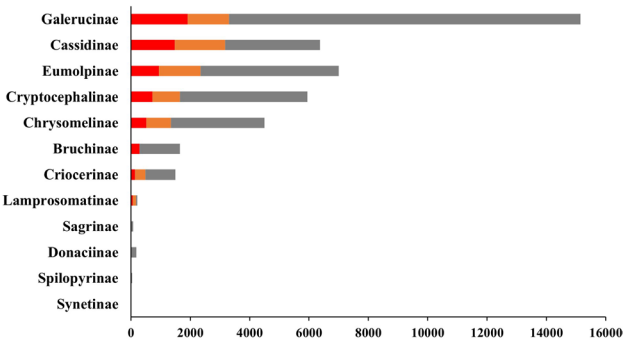

Figure 1. Diversity of subfamilies of Chrysomelidae. Bar colors indicate regional diversity as follows: World fauna (grey), Neotropical fauna (orange), and Brazilian fauna (red).

Table 1. Species diversity of Chrysomelidae subfamilies. All numbers with exception of Bruchinae and Galerucinae are based on the unpublished database of world Chrysomelidae (Sekerka, unpubl. data), which is incomplete for several Old World subfamilies so numbers here are approximate.

Subfamilies	World fauna	Neotropical fauna	Brazilian fauna
Bruchinae	1,650		293
Cassidinae	6,376	3,173	1,477
Chrysomelinae	~ 4,500	1,341	519
Criocerinae	1,497	481	136
Cryptocephalinae	5,952	1,652	729
Donaciinae	176	1	-
Eumolpinae	~ 7,000	2,344	947
Galerucinae	15,145		1,916
Lamprosomatinae	213	166	62
Sagrinae	72	2	1
Spilopyrinae	39	5	–
Synetinae	10	–	–

36.6%, respectively (see dataset about Brazilian Coleoptera fauna in Caron et al. 2024). This does not only represent new taxonomic descriptions, but the inclusion in the database of many taxonomic Chrysomelidae papers not included in Costa (2000), such as those published by Bechyně's (see the Bechyně's bibliography in Seeno et al. 1976).

The study of Brazilian Chrysomelidae fauna started with Linnaeus in 1758 with the description of 17 species. Since then the second half of the 19th century (1851–1900) was the period with most species described, totalizing 2,224 species, and the two most prolific decades were 1950 and 1850, with 987 and 917 species described, respectively (Fig. 2). Most of the Brazilian leaf beetles were described by non-Brazilian scientists. Of the approximately 140 scientists that have described Brazilian Chrysomelidae species, the Czech couple Jan Karel Bechyně (1920–1973) and Bohumila Špringlová Bechyně (1924–2003) stand out as the most prolific, together having described 1,293 species (21.2%). Of these, 76.4% are authored only by J. Bechyně, while the remainder are coauthored with B. Bechyně or authored only by her. The couple lived in Brazil from 1960 to 1963 working in the Museu Emilio Goeldi, in Belém, Pará. While living in Belém, they sampled and studied thousands of specimens that are now deposited in this institution (Overal and Gorayeb 1981). Following the Bechyněs, the ten most prolific authors were the Swedish scientist Carl Henrik Boheman (1796–1868) (546 species), the British Joseph Sugar Baly (1816–1890) (376 species), the British Hamlet Clark (1823–1867) (303 species), the German Julius Weise (1844–1925) (274 species), the British Martin Jacoby (1842–1907) (257 species), the French Jean Théodore Lacordaire (1801–1870) (255 species), the Swedish Carl Stål (1862–1865) (255 species), the German Eduard Suffrian (1805–1876) (238 species), the French Maurice Pic (1866–1957) (237 species) and the French Édouard Lefèvre (1839–1894) (212 species), together totalizing more 48.6% of the species described. The American Doris Holmes Blake (1892–1978) was the first woman to describe any Brazilian Chrysomelidae species. She studied Galerucinae and Eumolpinae, and described 29 species from Brazil (Blake 1950, 1952, 1955, 1966). Her papers are usually well illustrated facilitating species identification, and her types are mainly deposited at National Museum of Natural History of the Smithsonian Institution. Nowadays, the Brazilian Bruchinae expert Cibele Stramare Ribeiro-Costa (1962–) together with her students and collaborators, has described the most Brazilian leaf beetles, totaling 53 species.

The description of new Chrysomelidae species has decreased considerably since 1970 (Fig. 2). However, since then, the number of Brazilians working on the family has increased, with new species described by 20 researchers. Additionally, the number of species described in collaboration with both foreign and other Brazilian researchers has increased, and new lines of research and collaboration have been established, many focusing on the following topics: ecological studies (e.g., Linzmeier and Ribeiro-Costa 2009, 2012, 2013, Bouzan et al. 2015, Macedo et al. 2017, Teles et al. 2020), genetics (e.g., Vasconcellos-Neto 1988, Almeida et al. 2009, Mello et al. 2014, Azambuja et al. 2020, Vidal et al. 2023), behavior (e.g., Macedo et al. 1998, Flinte and Macedo 2004, Nogueira-de-Sá et al. 2005, Medeiros and Boligon 2007, Chaboo et al. 2014, Flinte et al. 2017), description of immatures stages and life history (e.g., Duckett and Casari 2002, Moura and Duckett 2002, Fernandes and Buzzi 2007, Linzmeier et al. 2007, Świętojańska and Medeiros 2007, Casari and Teixeira 2008, 2010, 2011, Antonio et al. 2022, Świętojańska and Linzmeier 2024), and host plant association (e.g., Buzzi 1994, Nogueira-de-Sá and Vasconcellos-Neto 2003a, Flinte et al. 2009b). Baseline data on these topics for the New World chrysomelid fauna, including Brazil were published in the book series "Biology of Chrysomelidae" (Jolivet et al. 1988, 1994, Jolivet and Cox 1996a, 1996b, 1996c, Furth 2003), followed by the series "Research on Chrysomelidae" with nine volumes published since 2008 (Jolivet et al. 2008, 2009, 2011, 2013, 2015, 2016, Chaboo and Schmitt 2017, 2023, Schmitt et al. 2019).

Furthermore, towards the end of 20th century, some of Brazil's most recognized postgraduate programs related to entomology were implemented and became well-established, such as those at Universidade Federal do Paraná (UFPR), Curitiba (Graduate Program in Biological Sciences – Entomology), Universidade Federal do Rio de Janeiro (UFRJ), Rio de Janeiro (Graduate Program in Biological Sciences – Zoology), Universidade de São Paulo (USP), São Paulo (Graduate Program in Zoology), Universidade Estadual de Campinas (UNICAMP), Campinas (Graduate Program in Ecology) and Universidade de São Paulo (USP/RP), Ribeirão Preto (Graduate Program in Entomology). This contributed to the training of a new generations of Brazilian researchers and to considerable improvement of chrysomelid knowledge in the region. Associated with this, important collections that have considerable chrysomelid holdings have significantly supported these studies. Among them are Coleção Entomológica Padre Jesus Santiago Moure (DZUP-UFPR), Curitiba, Paraná; Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo, São Paulo; Museu Paraense Emílio Goeldi (MPEG), Belém, Pará;

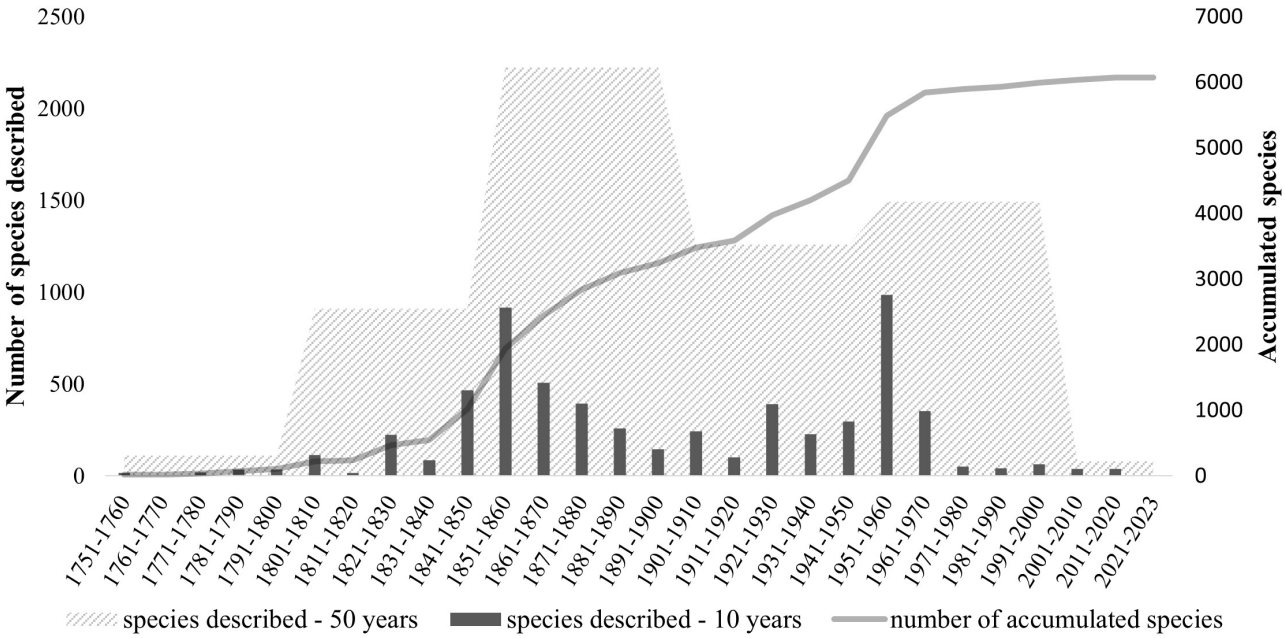

Figure 2. Number of Chrysomelidae described over the years.

Coleção Entomológica do Museu de Ciências Naturais do Rio Grande do Sul (MCNZ), Porto Alegre, Rio Grande do Sul; and Museu Nacional do Rio de Janeiro (MNRJ), Rio de Janeiro, Rio de Janeiro. Regrettably, MNRJ, which was one of the largest and most representative collections in Latin America burned down during the fire on September 2, 2019. The entire Coleoptera collection was completely destroyed with a handful of exceptions, which include the several Chlamisinae types and other leaf beetles and weevil specimens on loan with Maria Lourdes Chamorro.

Hereafter, information on each Chrysomelidae subfamily recorded from Brazil is presented and discussed. A summary of the main aspects of each subfamily can be found in the Chrysomelidae section of Leschen and Beutel (2014).

Bruchinae

Bruchinae Latreille, 1802, stand out mainly because of its exclusive larval feeding habit. During the developmental time, a larva may consume one or more seeds, and this behavior can cause serious damage compromising future plant generations. Most of the seeds consumed are legumes (Fabaceae), with some of them also included in the human diet as beans, peas, etc, with high nutritional content (Ribeiro-Costa and Almeida 2012). Their feeding preferences make this group of a great economic importance, with some species considered pests of stored grains or field crops, while others are used as biological control agents of weeds (Briano et al. 2002). In Brazil *Zabrotes subfasciatus* (Boheman, 1833), *Acanthoscelides obtectus* (Say, 1831) and *Callosobruchus maculatus* (Fabricius, 1775) are the main bean (*Phaseolus vulgaris* L. (Fabaceae)) pests (Ribeiro-Costa et al. 2007, Ribeiro-Costa and Almeida 2012), and *Sennius* species consume many *Senna*, *Cassia* and *Chamaecrista* species (Silva et al. 2003, Linzmeier et al. 2004, Viana and Ribeiro-Costa 2013). Other species of economic importance include those associated with palms, with *Pachymerus nucleorum* (Fabricius, 1792) considered a pest of commercially grown palms in Brazil (Garcia et al. 1980, Andrade et al. 2013, Silva et al. 2020). In contrast, adults feed on pollen and/or nectar, but the pest species in stored grain conditions do not require to eat as adults. Bruchines also have been the subject of studies on evolutionary patterns of host-plant use (Kergoat et al. 2011, 2015, Manfio et al. 2016) and only data collected from hosts of larvae are used for this purpose.

Composed of more than 1,650 species worldwide distributed mainly in tropical regions (Morse 2014), Bruchinae are classified into six tribes and 65 genera; most of the tribes have been suggested to be paraphyletic based on molecular studies (Kergoat et al. 2008, 2015). Of the total number of bruchine species, 293 in 25 genera are recorded to occur in Brazil, representing approximately 17% of the world fauna. However, we believe a much higher number of species occurs

in Brazil. The endophagous habit of the group, developing inside fruits that require specific collecting methods, probably is one reason for the low record of bruchine species collected in Brazil.

Two genera stand out as the most diverse in Brazil, *Acanthoscelides* (Bruchini) and *Amblycerus* (Amblycerini) with 70 and 63 Brazilian species, respectively. A catalog of the Brazilian species of *Amblycerus* was published by Ribeiro-Costa et al. (2018) with the aim of stimulating new studies on this genus, which still has many Brazilian species to be described and is in need of phylogenetic analyses based on a wider taxon sampling. On the other hand, while *Acanthoscelides* is the most diverse genus in the group, many species remain poorly studied.

Many scientists have described Brazilian bruchines, but three stand out as the most prolific: the French Maurice Pic (82 species), the Brazilian Cibele Stramare Ribeiro-Costa (53 species; 25 with co-authors) and the American John Mark Kingsolver (1925–2013) (37 species; 11 with co-authors). Other researchers worth mentioning who have significantly contributed to our understanding of Brazilian bruchines are the American Clarence Dan Johnson (1931–2005) and the Argentinian Arturo Luis Teràn (1932–2016). Bruchines are one of the few chrysomelid subfamilies with a published world catalog (Udayagiri and Wadhi 1989), an overview of world genera (Borowiec 1987), as well as a complex treatment of the Nearctic fauna (Kingsolver 2004), and a subject of a book chapter (Ribeiro-Costa and Almeida 2012). Aspects of the natural history of Brazilian species have been recently investigated by Linzmeier et al. (2004), Sari and Ribeiro-Costa (2005), Grenha et al. (2008), Rodrigues et al. (2012), and Sousa-Lopes et al. (2019).

Sagrinae

Sagrinae Leach, 1815 have only one species in Brazil – *Megamerus alvarengai* Monrós, 1956, restricted to Rio Grande do Norte. Little is known about its biology (Monrós 1956a). Morphologically it is most similar to the Malagasy genus *Prionesthis* Lacordaire, 1845 (formerly known as *Rhagiosoma* Chapuis, 1878) rather than to Australian *Megamerus* MacLeay, 1827 (Sekerka 2007, Sekerka and Voisin 2014). This subfamily contains presently 72 species classified in 13 genera and four tribes worldwide. The subfamily has a mainly palaeotropical distribution, with the center of diversity in Australia. The Neotropical fauna is very poor and only two species of Megamerini are recorded so far; the diversity of this tribe is mainly in Australia and Madagascar. The other Neotropical species, *Atalasis sagroides* Lacordaire, 1845, is so far known only from Northern and Central Argentina but it is very likely present also in SE Brazil (Mato Grosso do Sul and Paraná) since these two regions share similar habitats. This species is associated with various Malvaceae and is one of a few among Sagrinae with known biology and described larva (Monrós 1943, 1955). Genera of Sagrinae were revised by the Argentinean Francisco de Asís Monrós (1922–1958), who also established the tribal system (Monrós 1960).

Criocerinae

Criocerinae Latreille, 1807 are a moderately large subfamily containing almost 1,500 described species worldwide classified into three tribes and 22 genera with the majority of species contained in four genera: *Lema* Fabricius, 1798 (ca. 900 spp.), *Lilioceris* Reitter, 1913 (ca. 140 spp.), *Oulema* Des Gozis, 1886 (128 spp.), and *Crioceris* Müller, 1764 (61 spp.) (Vencl and Leschen 2014). The remaining genera are not as speciose, containing no more than 20 species and five are monotypic. *Lema* is divided into five subgenera, which are restricted geographically to either the New or Old World.

This subfamily is mostly distributed in the tropics and subtropics and their diversity rapidly decreases towards the poles. The larvae and adults usually feed on open leaf surfaces, however, there are species known to have larvae that mine leaves or bore into stems. Exophagous larvae are eruciform and due to the vertically oriented anus, bear a characteristic fecal coating or shields formed of digestive wasted that can cover partially or totally the larva; the majority of species occurs mostly in disturbed secondary habitats, i.e. forest edges, stream banks and other open areas (Vencl et al. 2004). Host plants association in Criocerinae are relatively well known in comparison to other chrysomelid subfamilies, but the natural history is poorly known, except for some species considered pests (Schmitt 1988, Jolivet 1988). Criocerinae are primarily associated with monocotyledons. The most frequently utilized families are Commelinaceae, Liliales (mainly Liliaceae and Smilacaceae but also others), Dioscoreaceae, Poaceae, and nearly all families of Zingiberales; some species also colonized dicotyledons, mainly Solanaceae and, also Piperaceae and Basellaceae (Schmitt 1988, Vencl et al. 2004, Vencl and Leschen 2014).

New World Criocerinae fauna is rich and contains nearly 500 species, mainly belonging to the tribe Lemiini. Criocerini are represented by *Metopoceris* Heinze, 1931 (19 spp.), and a few species of *Lilioceris* and *Crioceris* that colonized the New World becoming pests, since these genera have the center of diversity in the Oriental Region, being widespread in the Old World (Vencl and Leschen 2014).

Neotropical criocerine species were intensively studied by F.A. Monrós, although he worked predominantly on the Argentinean fauna (e.g. Monrós 1956c). Monrós (1960) also published an overview of genera and catalog of species.

The Brazilian fauna of Criocerinae is represented by 136 species (27% of New World, and 9% of world fauna), most belonging to *Lema*. Three species belong to *Plectonycha* Lacordaire, 1845 and one to *Lilioceris*. Since the Brazilian fauna of Criocerinae has not been well studied we anticipate that many more species can be found in Brazil. Additionally, some species, specially of *Lema* are known only from the original description, which are mainly based on coloration and might be found to be only color forms of other species. Most of the Brazilian species (77.7%) were described by three authors: J.T. Lacordaire (51 species), M. Pic (36 species) and F. Monrós (18 species).

Cassidinae

Cassidinae Gyllenhal, 1813 are a large subfamily containing 6,376 species classified in 358 genera and 33 tribes (Sekerka, unpubl. data). The species are distributed worldwide with greater diversity in the Neotropics (Chaboo 2007, Borowiec and Świetojańska 2014, 2024). In general, Cassidinae are better studied than any other chrysomelid group as the subfamily has always had specialists working on it continuously since the 1850's. In the past, the group was considered as two separate subfamilies Cassidinae ("tortoise beetles" – cassidiforms) and Hispinae ("leaf-mining beetles" – hispidiforms) together forming the group Cryptostoma (e.g., Chapuis 1874, Crowson 1938, Monrós and Viana 1947). Already, early authors suggested similarity between the two subfamilies as some tribes were considered transitional, which generated several changes in their classification over the years (see Staines (2002) to a brief review of the classification history). However, since the first modern phylogenetic analyses of cassidines based on morphological data (Borowiec 1995), many authors have been proposing the placement of the taxa under the subfamily Cassidinae (Reid 1995, Lawrence and Newton 1995, Suzuki 1996, Chaboo 2007, Gómez-Zurita et al. 2008, Bocak et al. 2013). Internal classification of Cassidinae is quite stable and most tribes are supported by morphological data based on the larvae as well as adults (Borowiec 1995, Chaboo 2007).

Compared to other chrysomelid subfamilies, Cassidinae have much more diverse biology, life strategies, and larval and adult morphology known (Chaboo 2007). The larvae can be fully exophagous, hidden in narrow crevices of their host plant ("cryptic"), or mining inside leaves (Staines 2004, Chaboo 2007). There are two main trends, which can be observed: 1) early diverging hispidiform lineages are primarily associated with monocots, while cassidiforms are associated with eudicots; and 2) tribes with leaf mining larvae use many more plant families than those with exophagous larvae; Cassidiforms have eruciform larvae with caudal abdominal processes usually bearing exuvial or fecal shields, often combined, which are absent to most hispidiforms (Sekerka 2017).

The diversity of Cassidinae is almost equally divided between New and Old World. The New World has 3,173 species in 17 tribes with only the tribe Cassidini being shared between the two regions. Brazil has the highest diversity in the world, with 1,477 species, 826 of which are known only from Brazil. However, the number of truly endemic species is likely much lower, as research in neighboring countries has been limited, and some species are also found in other countries, such as Bolivia (Sekerka, unpubl. data). Most Brazilian taxa have not undergone taxonomic revision since their original description; therefore, a decrease in the number of species can be expected due to synonymy. On the other hand, Brazil likely still has numerous undescribed species, as cassidines (particularly hispine tribes) have cryptic lifestyles and require specific collection methods on their host plants.

The most prolific Cassidinae authors were C. H. Boheman (508 spp. ~ 34%), Franz Spaeth (1863–1946) (184 spp. ~ 12%), J. Weise (127 spp. ~ 8.5%), Erich Uhmann (1881–1968) (112 spp. ~ 7.5%), J. S. Baly and M. Pic (each 110 spp. ~ 7.4%). Together these authors described 77.9% of Brazilian Cassidinae fauna. A large amount of information is summarized and available online, including key to the world genera and photo gallery (to 'cassidines' see Borowiec and Świetojańska (2024); to 'hispines' see Staines (2015)). Brazilian Cassidinae have been widely studied in terms of ecological and biological aspects since the 1980's. Many species have been studied in terms of their natural history (e.g., Buzzi 1988, Nogueira-de-Sá and Trigo 2002, Nogueira-de-Sá and Vasconcellos-Neto 2003b, Flinte et al. 2009a, Chaboo et al. 2014, Albertoni and Casari 2017), immature stages (e.g., Świętojańska and Medeiros 2007, Fernandes and Buzzi 2007, Casari and Teixeira 2010), and host-plant association (e.g., Medeiros et al. 1996, Nogueira-de-Sá and Vasconcellos-Neto 2003a, Gomes et al. 2021).

Eumolpinae

Eumolpinae Hope, 1840 are one of the largest subfamilies within Chrysomelidae, containing roughly 7,000 described species in at least 500 genera (Jolivet et al. 2014).

They are the least studied and known subfamily of leaf beetles, with enigmatic classifications at tribal and generic levels that are not well stablished. The tribal classification has not been studied in detail since Chapuis' (1874) classification. As a result, many higher taxa are probably assemblages of phylogenetically unrelated species. Recent molecular data found Eumolpinae paraphyletic with respect to Cryptocephalinae and Cassidinae (Gómez-Zurita et al. 2007, 2008).

Adult eumolpines are usually exophagous, feeding on foliage, while larvae are external root feeders. They are associated with a wide range of host plants, but prefer eudicots. The Neotropical fauna of Eumolpinae is diverse, with approximately 2,400 species and subspecies currently recognized as valid. Brazil is home to 947 documented species. Species of *Megascelis* Sturm, 1826, *Colaspis* Fabricius, 1801 and *Myochrous* Erichson, 1847 have been reported causing considerable damage to agricultural crops, mainly soybean and corn, in Brazil. Many of these pests have been difficult to identify due to the lack of taxonomic revisions and information for the group (personal observation, AML).

Nearly half of the Brazilian species of Eumolpinae were described by Jan and Bohumila Bechyně (e.g., Bechyně 1949, 1953, 1954a, Bechyně and Bechyně 1964, 1968), who intensively studied Neotropical Eumolpinae. Despite their efforts, many descriptions are based on limited characters to delimit individual taxa. They also proposed numerous aberrations, which were later considered as infrasubspecific entities due to updates of the Code of Zoological Nomenclature (the infrasubspecific rank are not regulated by the Code (Article 1.3.4), since it is not considered an available name unless the provisions of Article 45.6 specify otherwise (ICZN 1999)). Thus, they started to use subspecies instead. The use of male and female genitalia has only been recently implemented to distinguish among species (Gómez-Zurita and Maes 2022) and are now considered to be fundamental morphological characters in Eumolpinae. Therefore, we expect that the current known diversity of eumolpines will increase with the examination of these features.

Cryptocephalinae

Cryptocephalinae Gyllenhal, 1813 currently include the Clytrini, Fulcidacini (formerly treated as subfamilies Clytrinae and Fulcidacinae), Cryptocephalini, Pachybrachini and Mylassini (Gómez-Zurita and Cardoso 2021), this last tribe absent in Brazil. The group comprises approximately 5,300 worldwide species in 127 genera (Chamorro 2014b), with 728 species recorded from Brazil. For the Neotropical region, a key to the genera of Argentinian Cryptocephalinae and Lamprosomatinae is given by Agrain et al. (2017), which is valid for most of the Brazilian genera. Also, the world host plant data for the subfamily was summarized by Agrain et al. (2024).

Cryptocephalinae and Lamprosomatinae (below) are collectively known as "Camptosomata" or "case-bearers," due to the peculiar habit of having their eggs, larvae, and pupae living in a fecal protective case (Agrain and Marvaldi 2009, Chaboo et al. 2016, and references therein). Adults of case-bearing chrysomelids feed on foliage of a variety of eudicots (Erber 1988, Agrain et al. 2024), but their larvae often depart from strict phytophagy, living on the ground, in leaf litter, feeding on dry vegetable material and detritus (Brown and Funk 2005, and references therein). One of the most interesting aspects of cryptocephaline biology is that some species have been documented to be closely associated with ants (Hymenoptera: Formicidae). Agrain et al. (2015) synthesized global literature on this topic, revealing that myrmecophilous cryptocephalines primarily live among formicine and myrmecines ants hosts. Myrmecophily is more common in the tribe Clytrini than in Cryptocephalini and Pachybrachini, but it has not been documented for Fulcidacini and Mylassini, or the closely related Lamprosomatinae.

Fulcidacini (i.e., the Chlamisinae/- ini of most studies) are a small group with approximately 500 species described worldwide in 11 genera (Chamorro-Lacayo and Konstantinov 2009, Chamorro 2014b). Most of their diversity is in the New World (ca. 450 species) and Brazil with 255 species (42.5% of world fauna) is the country with the richest species diversity. The group was intensively studied by F.A. Monrós, who also published a revision of fauna of the southern part of South America (Monrós 1952). Another prolific worker was the Brazilian Werner Carl August Bokermann (1929–1995), who published 20 papers devoted mainly to the Brazilian fauna (e.g., Bokermann 1961, 1962, 1964). Fulcidacini have the largest diversity in seasonally dry regions and are rather rare in wet tropics. Adult beetles as well as larvae are phytophagous. Larvae of many species feed on bark of young twigs of various woody plants similarly to Lamprosomatinae and build complicated portable cases, which often resembles morphological structures of their respective host plant. All Fulcidacini genera were reviewed, diagnosed, keyed, and illustrated by Chamorro-Lacayo and Konstantinov (2009). The biology and seasonality of *Fulcidax monstrosa* (Fabricius, 1798) were studied by Flinte and Macedo (2004).

Clytrini are a moderately large group containing 1,862 species worldwide. They are mostly associated with arid habitats, and have the largest diversity in Central Asia,

Africa and the southern part of South America (Chamorro 2014b). The New World fauna comprises currently 475 species with most of the diversity in seasonally dry regions of Argentina, Brazil and Bolivia. Currently, 153 species (8.2% of world diversity) are known to occur in Brazil and 108 of them are so far considered to be endemic to the country. The Neotropical fauna was intensively studied by F.A. Monrós, which resulted in the publication of a large monograph on Argentinean fauna (Monrós 1954) that also applies largely to Brazil. Another important researcher was Jacintho Guérin (Guérin 1943, 1944, 1945, 1949, 1952), who mostly studied the Brazilian fauna and described 21 species. Clytrini larvae are mostly saprophagous feeding on decomposing leaves in litter or on bark of twigs of various woody plants, some are myrmecophilous, while the adults usually eat the youngest tender leaves of their host plants (Erber 1988).

Cryptocephalini are a large group containing at least 3,500 described species worldwide. Neotropical Cryptocephalini are poorly known and have remained nearly untouched since Suffrian's (1863, 1866) monographs. The only other major worker was Martin Jacoby. Suffrian and Jacoby described 625 species of the 800 known Neotropical species. Brazil, with 148 species, has the largest diversity in the region, however, there is most likely a considerable number of undescribed species. Most of the Brazilian species have unknown distribution within the country and the only references are the original descriptions. Contrary to Fulcidacini and Clytrini, Cryptocephalini are very diverse in the wet tropics. Cryptocephalini larvae are mainly saprophagous, feeding on decomposing leaves in litter, and some species feed on fresh leaves; adults usually feed on the youngest tender leaves of their host plant, and many species are also found on flowers where they eat pollen and petals (Chamorro 2014b).

Pachybrachini are most diverse in the Neotropical region (Chamorro 2013, 2014b). The monophyly of the tribe is currently supported by molecular data (Gómez-Zurita and Cardoso 2021) and on a combination of the presence (or absence) of morphological features present in other tribes (Chamorro 2013). A total of 172 species in four genera are present in Brazil. Almost 70% of the species in the subfamily were described by E. Suffrian (237 species), J.T. Lacordaire (151 species), F.A. Monrós (76 species), and W.C.A. Bokermann (40 species).

Lamprosomatinae

Lamprosomatinae Lacordaire, 1848 are a small subfamily containing 213 species classified in four tribes and 14 genera (Chamorro 2014a). Most of the diversity is in the tribe Lamprosomatini and *Lamprosoma* Lacordaire, 1848 is the largest genus with 133 species. Cachiporrini and Sphaerocharini are monotypic, known only from Brazil, and Neochlamysini have two genera (Chamorro and Konstantinov 2011, Chamorro 2014a). Lamprosomatinae are morphologically quite uniform and share many characters with Cryptocephalinae in the Camptosoma clade (e.g., Reid 1995, 2000, Gómez-Zurita and Cardoso 2021). Larvae are eruciform and build portable fecal enclosures. Larvae and adults are phytophagous usually on bark or thick leaf veins of various woody plants similarly as many Fulcidacini. *Lamprosoma azureum* Germar, 1824, which is associated with the Brazilian native strawberry guava (*Psidium cattleianum*) (Caxambú and Almeida 1999) was studied as a potential biocontrol of this plant introduced in Hawaii. However, as it consumes other myrtaceous species it was not recommended (Wikler et al. 2000).

Lamprosomatinae are distributed mainly in tropics with the center of diversity in the Neotropics, where 166 species occur. They were intensively studied by F.A. Monrós who revised the genera and established the higher classification of the group (Monrós 1956b). Phylogenetic relationships among genera and tribes were tested by Chamorro and Konstantinov (2011) based on morphological characters. Currently, 62 species, representing 31% of world fauna, are reported from Brazil. Thus, Brazil is the country with the highest diversity of Lamprosomatinae in the world. Despite Monros' intensive study of the group, there has been no comprehensive species revision since Lacordaire's (1848) monograph. Lacordaire described 53% of lamprosomatine species and Monrós described an additional 18%.

Chrysomelinae

Chrysomelinae Latreille, 1802 are a large subfamily with about 4,500 described species and subspecies (Reid 2014b). Traditionally two tribes are recognized, Timarchini and Chrysomelini; Chrysomelini are divided into numerous subtribes and even lower taxonomic categories (i.e., Seeno and Wilcox 1982). Based on recent molecular studies, the position of Timarchini is not fully resolved which have been recovered as sister to the chrysomeline clade (Nie et al. 2020). Timarchini was also found as sister to remaining Chrysomelinae and Galerucinae or as sister to subtribe Chrysomelina (Gómez-Zurita et al. 2008). The latter study also supports monophyly of at least two other subtribes of Chrysomelinae, supporting the phylogeny by Takizawa (1976) which was based on larval characters, and also, suggest that Timarchini

should be considered a separate subfamily. Phylogenetic studies based on adult morphological characters have not been attempted so far, probably because Chrysomelini adults are rather uniform. This is also reflected at genus level as many genera are subdivided into numerous subgenera with considerable numbers of transitional taxa.

Chrysomelinae have eruciform exophagous larvae. The majority of species are associated with eudicots, particularly Solanaceae in the New World (Jolivet 1988, Medeiros and Vasconcellos-Neto 1994). Chrysomelinae have worldwide distribution with some species reaching the Arctic Region. In contrast to other chrysomelids, most of their diversity is in temperate and drier subtropical areas. Nevertheless, the Neotropical fauna is species rich and currently includes about 1,400 species and subspecies, 519 of these occuring in Brazil. Neotropical chrysomelines were studied extensively by two authors who lived 100 years apart: Carl Stål and Jan Bechyně. Stål (1862–1865)'s monograph on New World Chrysomelinae serves as the main reference for recognition of species today. Bechyně's studies (e.g., Bechyně 1954b, 1958, Bechyně and Bechyně 1969) on the Neotropical fauna built on Stål's work and described numerous species. However, Bechyně often only used a poor set of characters to delimit individual taxa and therefore many subspecies might be invalid and may represent polymorphism or local variation. Stål and Bechyně are responsible for describing 375 (69%) Brazilian species and subspecies. The distribution of many chrysomeline species remain poorly known and are based on primary description only. The most species rich genus in Brazil is *Platyphora* Gistel, 1857 with 176 species and subspecies representing approximately 39% of the diversity of the genus worldwide. Recently, an illustrated catalog of the Chrysomelinae types housed in Northern Brazil collections and an illustrated key to the Brazilian genera were published (Sampaio and Fonseca 2023, Sampaio et al. 2024). Studies on host plant association, biology, seasonal patterns of Brazilian species have significantly advanced our knowledge of Brazilian Chrysomelinae (e.g., Medeiros and Vasconcellos-Neto 1994, Vasconcellos-Neto and Jolivet 1994, Macedo et al. 1998, Flinte et al. 2017).

Galerucinae

Galerucinae Latreille, 1802 are the most diverse group of Chrysomelidae with approximately 15,000 species worldwide, with the greatest diversity in tropical regions (Nadein and Bezděk 2014, Nie et al. 2017b). In Brazil, 1,916 species in 202 genera, representing 31.5% of the Chrysomelidae fauna, are registered.

The relationship of Galerucinae s. str. ('true' galerucines) and Alticini/Alticinae is an active research area since they were considered traditionally as distinct subfamilies (Seeno and Wilcox 1982, Furth and Suzuki 1998). This classification was based mainly on the metafemoral spring, which gives to alticines the jumping ability (and the name "flea beetles"). However, Ge et al. (2011) evaluated this structure as susceptible to rapid diversification and convergent evolution. The question of whether Alticinae are a subfamily distinct from Galerucinae within the Chrysomelidae has been explored using morphological, molecular and larval characters with studies by Furth and Suzuki (1998), Biondi and D'Alessandro (2010), Ge et al. (2012) and Nie et al. (2020) recovering a monophyletic Alticinae, whereas Lingafelter and Konstantinov (1999), Gómez-Zurita et al. (2008), Nadein and Bezděk (2014), Nie et al. (2017a) and Douglas et al. (2023) recover alticines as a tribe of Galerucinae.

Nie et al. (2017b) summarized that Galerucinae s. str. has 7,145 species (7,132 recent, 13 fossils) and 192 subspecies from 543 genera (542 recent, 1 fossil); Viswajyothi and Clark (2022) updated this number to 544 genera and 7,318 species. Galerucinae s. str. does not have cosmopolitan genera and in the Neotropical region there are 98 recorded genera – 52 of them endemic (Viswajyothi and Clark 2022); this group consists of five tribes: Oidini, Hylaspini, Galerucini, Metacyclini and Luperini – the last three occurring in Brazil, totaling 503 species included in 58 genera. Luperini includes the most species-rich genera of the Neotropical Region: *Diabrotica* Chevrolat, 1836 with 370 species (138 of these occur in Brazil), *Isotes* Weise, 1922 with 181 species (38 Brazilian taxa), *Acalymma* Barber, 1947 with 72 species (13 species listed for Brazil), and *Paranapiacaba* Bechyně, 1958 with 58 species (20 recorded for Brazil) (Nie et al. 2017b). The main authors that described Brazilian taxa were the same of Alticini except Gerard Scherer (see below), with addition of Frederick C. Bowditch (1853–1825), Doris H. Blake, Jan K. Bechyně and John Avery Wilcox (1921–2003). Wilcox (e.g., 1971, 1972, 1973, 1975) published the catalog of world Galerucinae s. str. species known.

The tribe Alticini comprises about 10,000 species and over 601 genera worldwide (Douglas et al. 2023). Alticines, or flea-beetles, are mostly represented by small or medium-sized leaf beetles distributed worldwide (with exceptions of Antarctica and some oceanic islands), reaching its highest diversity in the Neotropical Region (Damaška 2017). They are generally recognized by the enlarged hind femora containing the metafemoral spring. The adults and larvae are herbivorous, and most of them show host plant

specialization being mono- or oligophagous (Jolivet 1988).

The Brazilian Alticini fauna is composed of 1,413 species across 144 genera. The main researchers on this group in Brazil were Jan Bechyně and Bohumila Bechyně whit together described 43.9% of the species and 41.1% of the Alticini genera. Hamlet Clark also was an important researcher, having described 31 genera and 246 species (17.4%). Other significant contributors include Martin Jacoby with 126 described species, Joseph S. Baly with 64 species, Edgar Harold (1830–1886) described 63 species, and Gerard Scherer (1929–2012) who described 50 species in the 1960s (Scherer 1960), and published the only key to Neotropical Alticini genera (Scherer 1962, 1983). These seven authors are responsible for describing 82.8% of the Brazilian Alticini fauna. The most recently described Alticini species have been discovered by sampling moss and leaf litter, habitats that had never been investigated before in Brazil (Linzmeier and Konstantinov 2009, Oliveira et al. 2021). More recently, several studies on ecology (Linzmeier et al. 2006, Rech and Linzmeier 2019), natural history and biology of Alticini have been published (e.g., Del-Claro 1991, Linzmeier et al. 2007, Begha et al. 2021, Antonio et al. 2022). However, much still remains to be explored for this taxon and all other chrysomelid groups.

Final considerations

Brazil, covering 8,510,000 square kilometers and encompassing six biomes hosts a significant portion of the world's Chrysomelidae fauna. Despite Blackwelder's catalog of all the New world taxa (Blackwelder 1946), a comprehensive checklist of Brazilian Chrysomelidae, compiled by international experts has never been done before. This step is essential and necessary for advancing our knowledge of the group. Here we presented the results of this long-awaited goal. Armed with the knowledge of Chrysomelidae genera and species occurring in Brazil, we can now begin to build on this solid foundation. The CTFB project serves as a backbone, allowing us to further expand our understanding of the Brazilian Chrysomelidae fauna. This includes the discovery of new taxa, digitization of types specimens, taxonomic revisions, and a deeper understanding of their biology, ecology, distribution, life history, evolutionary history and their potential to be pestiferous or beneficial organisms.

Among the subfamilies reported to occur in Brazil, Galerucinae (one of the least studied in the country), and Cassidinae (the best studied) are the most species-rich, together representing more than 55% of the family. Large portions of these species have poorly known distribution within Brazil and are still known only from their original descriptions, which are often insufficiently detailed and sometimes based on coloration rather than a reliable set of diagnostic characters for identification. As a consequence, many Brazilian genera across nearly all subfamilies require revision. The most problematic groups include those in the Alticini and Eumolpinae, as well as large genera such as *Chlamisus*, *Lema*, *Acanthoscelides*, *Megascelis*, and others that have never been revised. Consequently, many taxa currently considered valid need to be re-examined and their status re-evaluated, which will undoubtedly lead to significant changes in the number of known chrysomelid species and genera in Brazil. However, the shortage of taxonomists remains important obstacles to achieve these goals.

Many scientists have contributed to our understanding of the Chrysomelidae fauna in Brazil. Among them, Jan and Bohumila Bechyně stand out as important authors, particularly regarding to the Brazilian Galerucinae, Chrysomelinae and Eumolpinae. Both Jan and Bohumila Bechyně described many new species and new genera, but they also left many puzzles to be solved, particularly concerning intraspecific categories (i.e., aberrations and subspecies). For Neotropical Galerucinae (and possibly also in Chrysomelinae and Eumolpinae), it is important to consider the following aspects regarding taxa described by Jan Bechyně and deposited in Brazilian collections (Museu Paraense Emílio Goeldi, Belém, PA; Museu de Zoologia da Universidade de São Paulo, São Paulo, SP; Museu Anchieta, Porto Alegre, RS): (1) many species were subdivided and labeled as an aberration (ab.), a term that refers to an invalid infrasubspecific taxonomic entity (some of Bechyně's papers also include identification keys for aberrations); (2) specimens that were named and labeled as types, but which were never formally described (nomina nuda not listed by Seeno et al. 1976). The taxa labeled as new should be re-examined and properly described if they are truly distinct, and the status of aberrations should be evaluated to determine whether they represent merely color variations or if they represent distinct, valid taxa.

Since the last decades of the 20th century the number of new species described from Brazil has significantly decreased. Instead, studies on biology, genetics, host plant association, ecology, behavior and immature description increased making the Brazilian Chrysomelidae fauna one of the best-studied in the World. However, considering the great Brazilian chrysomelid diversity, many species still need to have the mentioned aspects investigated. Furthermore, it is still necessary to continue to explore additional aspects of Chrysomelidae, such as a better understanding

of pest species, many belonging to Eumolpinae, Alticini and Criocerinae, investigating non-traditional habitats such as moss and leaf litter, expanding our efforts in exploring habitats or regions under sampled, and encouraging new students to embrace the taxonomic challenges necessary to address these and other unanswered questions. Thus, the megadiverse Brazilian Chrysomelidae remains a challenge!

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