

Diversity and distribution of the Palaearctic Cryptocephalini and Pachybrachini (Coleoptera: Chrysomelidae)

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Résumé

Parmi le total de 987 espèces de Cryptocephalini et Pachybrachini listées dans l'édition actuelle du catalogue des Coléoptères paléarctiques, d'Afrique du Nord, d'Asie et d'Europe, 79, 666 et 214 espèces ont été enregistrées respectivement. Du Paléarctique occidental et du Paléarctique oriental, 723 et 479 espèces ont été enregistrées respectivement. La diversité des Cryptocephalini et Pachybrachini diffère considérablement entre les subdivisions de la région paléarctique. La diversité est la plus faible dans l'Arctique avec 26 espèces. La richesse spécifique la plus élevée a été trouvée dans la région séthienne (désert) et un total de 507 espèces de Cryptocephalini (419 espèces) et de Pachybrachini (88 espèces) a été enregistré. Plus précisément, la sous-région méditerranéenne de la région hespérienne (forêt à feuilles persistantes) et la sous-région iranoturaniennne de la région séthienne (désert) sont riches en espèces avec respectivement 297 et 291 espèces. Le pays le plus riche en espèces est la Chine avec un total de 289 suivie de la Russie (avec des parties européennes et asiatiques) avec un total de 166 espèces et de la France et de l'Italie avec respectivement 143 et 142 espèces. Le pays avec le pourcentage le plus élevé (34%) d'espèces endémiques est le Népal et le plus grand nombre d'espèces endémiques se trouve au Kazakhstan (27 espèces) suivi par l'Espagne et l'Iran avec respectivement 26 et 25 espèces. La répartition géographique des genres et sous-genres de Cryptocephalini et Pachybrachini est compilée. Les espèces appartenant à la région Orientale sont discutées. 27 espèces sont considérées comme Orientales. Sur cette base, un total de 915 espèces paléarctiques de Cryptocephalini et Pachybrachini peut être estimé. Les espèces insulaires sont listées et la biogéographie insulaire est discutée.

Mots-clés : Chrysomèles, Cryptocephalinae, biodiversité, biogéographie, Afrique du Nord, Asie, Europe

Abstract

Among the total of 987 species of Cryptocephalini and Pachybrachini listed in the actual edition of the catalogue of Palaearctic Coleoptera, from North Africa, Asia and Europe 79, 666 and 214 species were recorded, respectively. From the Western Palaearctic and Eastern Palaearctic, 723 and 479 species were recorded, respectively. The diversity of Cryptocephalini and Pachybrachini differs considerably among the subdivisions of the Palaearctic region. Diversity is lowest in the Arctic, with 26 species. The highest species richness was found in the Sethian (desert) region, a total of 507 species of Cryptocephalini (419 species) and Pachybrachini (88 species) were recorded. Specifically, the Mediterranean subregion of the Hesperian (evergreen forest) region

and the Irano-Turanian subregion of the Sethian (desert) region are species-rich with 297 and 291 species, respectively. The most species-rich country is China with a total of 289 species, followed by Russia (with both European and Asian parts) with a total of 166 species and France and Italy with 143 and 142 species, respectively. The country with the highest percentage (34%) of endemic species is Nepal. The highest number of endemic species is found in Kazakhstan (27 species) followed by Spain and Iran with 26 and 25 species, respectively. The geographical distribution of the genera and subgenera of Cryptocephalini and Pachybrachini is compiled. Species belonging to the Oriental region are discussed. Seventy-two species are considered Oriental, based on this a total of 915 species of Palaearctic Cryptocephalini and Pachybrachini can be estimated. Species on islands are listed, and island biogeography is discussed.

Key words: Leaf beetles, Cryptocephalinae, biodiversity, biogeography, North Africa, Asia, Europe

INTRODUCTION

The Cryptocephalini and the Pachybrachini are two out of four tribes in the subfamily Cryptocephalinae (Gómez-Zurita & Cardoso, 2021). The adults are feeding on annual herbs, trees, or flowers, while the larvae of most species are feeding on leaf litter. The larvae carry a self-constructed case, for this reason the Cryptocephalinae are also called case-bearing leaf beetles (Erber, 1988).

The Region proposed by Wallace (1876) is widely accepted as a natural subdivision of the biosphere and was adopted in the respective chapters of the catalogue of Palaearctic Chrysomeloidea (Lopatin *et al.*, 2010; Schöller *et al.*, 2010) which included information on the distribution of the species. In the forthcoming new edition of the catalogue of Palaearctic Chrysomelidae (Bezděk & Sekerka, 2023, in press), a total of 988 species of Cryptocephalini and Pachybrachini are listed. However, the diversity and distribution of the Palaearctic Cryptocephalini and Pachybrachini was not reviewed previously. In the present publication, the information on geographical distribution in the new edition of the catalogue is analysed. Boundaries towards the Oriental and Afrotropical regions are discussed. Species on islands are listed, and island biogeography is treated for the first time for this group of leaf beetles.

MATERIALS AND METHODS

The Palaearctic region includes Africa north of the Sahara, Asia except for the part that is arbitrarily defined as belonging to the Oriental region, and Europe. For the catalogue of Palaearctic Coleoptera, the Oriental region was defined as areas south of the People's Republic of China and Taiwan, areas south of the Himalaya in India, the Philippines, Malaysia and Indonesia. Europe includes Russia west of the main ridge of the Ural Mountains, the Permsk Oblast, Bashkortostan Republic and Orenburskaya Oblast, and the small part of Kazakhstan west of the Ural River. The south-eastern boundaries are the political boundaries of Georgia, Azerbaijan, Kazakhstan, and the Caspian and Black seas. North Africa includes Morocco, Algeria, Tunisia, Libya and Egypt west of the Suez Canal, and the Canary Islands and Madeira. The boundaries of the Palaearctic region usually followed national boundaries for practical reasons (Löbl & Smetana, 2010). This concept was continued in the 2023 edition of the catalogue with little modifications in detail. China and India were subdivided according to Provinces. Russia was subdivided according to biogeographical criteria (Bezděk & Sekerka, 2023). A total of 140 areas

(states, provinces, biogeographical areas) were distinguished (North Africa: 8; Asia: 81; Europe: 51). Additionally, the occurrence on islands was listed separately.

RESULTS

A total of 988 species of Cryptocephalini and Pachybrachini are recorded in the catalogue. The numbers of species recorded from North Africa, Asia and Europe are 79, 666 and 214, respectively (**Figure 1**).

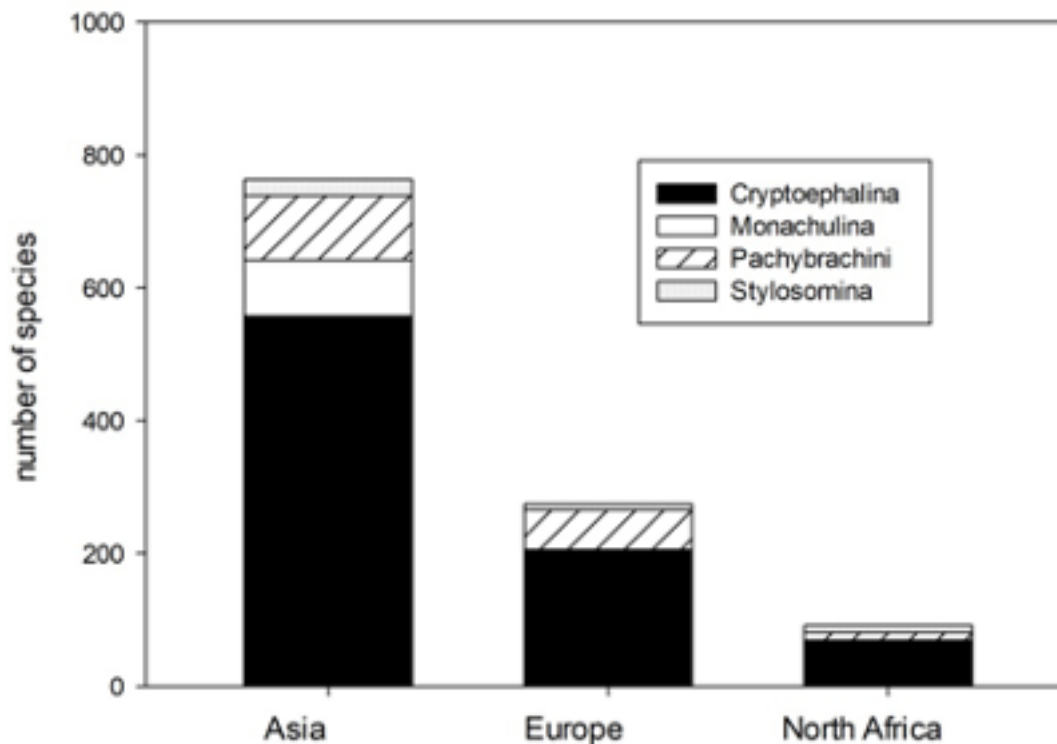


Fig. 1: Number of species of Pachybrachini and Cryptocephalini and its subtribes in the catalogue of Palaearctic Chrysomelidae in Asia, Europe and North Africa.

The three main parts of the Palaearctic Region differ considerably by their surface area, i.e. North Africa, Asia and Europe have 4,750,000 km², 44,580,000 km² and 10,530,000 km², respectively. If the number of species per m² is calculated, the numbers are 26.02 x 10⁻⁶ species per m², 19.36 x 10⁻⁶ species per m² and 20.63 x 10⁻⁶ species per m² for North Africa, Asia and Europe, respectively.

The most species-rich country is China with a total of 289 species, followed by Russia (with both European and Asian parts) with a total of 166 species (**Table 1**).

These are followed by two European countries, i.e., France and Italy with 143 and 142 species, respectively. All countries with more than 49 species are given in Table 1.

While the ranking is identical for Cryptocephalini and Cryptocephalina for the top four countries, the subtribe Stylosomina is most species-rich in Kazakhstan followed by Spain and Uzbekistan.

The Monachulina were only recorded from China (68 species) and Nepal (10 species). The Pachybrachini are most species-rich in Spain followed by Italy, Kazakhstan, and Turkey.

Table 1: Diversity of Palaearctic Cryptocephalini and Pachybrachini per country (countries with more than 49 species only).

Country	Cryptocephalina	Monachulina	Pachybrachini	Stylosomina	Total
China	204	68	14	3	289
Russia	143	0	19	4	166
France	116	0	22	5	143
Italy	112	0	25	5	142
Spain	90	0	32	6	128
Kazakhstan	91	0	25	7	123
Turkey	81	0	25	3	107
Iran	77	0	17	1	95
Mongolia	67	0	18	4	89
Switzerland	70	0	7	1	78
Austria	68	0	7	1	76
Bulgaria	66	0	8	2	76
Croatia	62	0	11	3	76
Romania	66	0	9	1	76
Ukraine	62	0	6	3	71
Hungary	63	0	6	0	69
Czech Republic	63	0	5	0	68
Slovakia	63	0	5	0	68
Nepal	55	10	0	2	67
Azerbaijan	57	0	11	1	67
Germany	58	0	7	0	65
Bosnia-Herzegovina	55	0	8	1	64
Slovenia	55	0	8	0	63
Georgia	52	0	8	2	61
Poland	56	0	4	0	60
Greece	45	0	9	3	57
Morocco	42	0	9	5	55
Kirgistan	35	0	23	4	52
Serbia	45	0	6	1	52
Uzbekistan	35	0	24	6	51
Moldau	44	0	7	0	51
Algeria	38	0	12	5	50

Oriental species

The conventionally accepted Palaearctic-Oriental boundary inside China has an east-west orientation (see He *et al.*, 2017 and references therein). Potentially, the fauna of the following Chinese provinces belongs to the Oriental region: Anhui, Chongqing, Fujian, Guangdong, Guangxi, Guizhou, Hainan, Hubei, Hunan, Jiangxi, Yunnan, and Zhejiang. The number of species of Cryptocephalini in the catalogue occurring exclusively in one or more of these provinces is 72. Specifically, these are in the genera *Adiscus* (20 species), *Coenobius* (4 species), *Cryptocephalus* (*Burlinius*) (5 species), *Cryptocephalus* (*Cryptocephalus*) (37 species), *Cryptocephalus* (*Sopidus*) (1 species), *Isnus* (1 species) and *Melixanthus* (4 species). Among

these, 36 species are distributed in Yunnan only. No species of Pachybrachini was found yet in this area.

Afrotropical species

The Palaearctic-Afrotropical boundary is delimited by the south of the Sahara Desert, and eastwards including the South of the Arabian Peninsula (Kreft & Jetz, 2010). Most species found on the Arabian Peninsula are either endemic, or the distribution is extended towards the Middle East (Schöller, 2021a). Few species are also found in Western Africa. An exception is *Cryptocephalus barkeri* Jacobi 1901 from South Africa, which is known from a single specimen from Saudi Arabia but not from the areas in between and might have been translocated.

Palaearctic species

The catalogue lists eight genera in Cryptocephalini (with four, three and one genera in Cryptocephalina, Monachulina and Stylosomina, respectively), and one genus in Pachybrachini. The genera *Isnus* and *Dichachus* are not Palaearctic, therefore the Palaearctic region has six genera in Cryptocephalini (with three, two and one genera in Cryptocephalina, Monachulina and Stylosomina, respectively). Peculiar to the Palaearctic region is the genus *Jaxartiolus*.

If the 72 Oriental species and one Afrotropical species are excluded from the species listed in the catalogue, a total of 915 species of Palaearctic Cryptocephalini and Pachybrachini can be estimated. Based on the above, the numbers of Palaearctic species are 59, 666, 34 and 156 in Monachulina, Cryptocephalina, Stylosomina and Pachybrachini, respectively. The number of Palaearctic species in Asia calculated is 594, with 59, 511, 24 and 97 in Monachulina, Cryptocephalina, Stylosomina and Pachybrachini, respectively.

Most Palaearctic species do not occur outside the region. Specifically, this applies to 77 species (7.8 %). *Diachus auratus* (Fabricius 1801) can also be found in the Neotropical, Nearctic, Afrotropical and Oriental regions. Six species of *Cryptocephalus* and *Isnus biseriatus* (Chapuis 1877) are shared with the Afrotropical region. *Cryptocephalus moraei* (Linné 1758) was imported to the Nearctic region. A total of 67 species (6.8 % of the 988 species in the catalogue) do also occur in the Oriental region.

The Palaearctic region can be divided into the Eastern Palaearctic and the Western Palaearctic with the Yenisey River as a natural boundary between the two halves, which approximates to 90 degrees (de Lattin, 1967).

Western Palaearctic

From the Western Palaearctic, 723 species were recorded. The top most widely distributed species, i.e. with the largest number of areas are *Cryptocephalus (Cryptocephalus) bipunctatus bipunctatus* (Linné 1758) (51 areas), *C. (Burlinius) ocellatus* (Drapiez 1819) (51 areas), *C. (Cryptocephalus) moraei* (50 areas), *C. (Cryptocephalus) sericeus* (Linné 1758) (48 areas), *C. (Burlinius) fulvus fulvus* Goeze 1777 (47 areas), *C. (Cryptocephalus) parvulus* Müller 1776 (46 areas), *C. (Burlinius) labiatus* (Linné 1761) (46 areas), *C. (Homalopus) coryli* (Linné 1758) (44 areas), *C. (Burlinius) bilineatus* (Linné 1767) (43 areas), and *C. (Cryptocephalus) nitidus* (Linné 1758), *C. (Cryptocephalus) sexpunctatus sexpunctatus* (Linné 1758), *C. (Burlinius) elegantulus* Gravenhorst 1807 and *C. (Cryptocephalus) anticus* Suffrian 1848 (40 areas each).

Eastern Palaearctic

From the Eastern Palaearctic, 479 species were recorded. The most widely distributed species, i.e. with more than 15 areas are *Cryptocephalus (Burlinius) exiguus amicus* Baly 1873 and *C. (Burlinius) confusus* Suffrian 1854 (19 areas each), *C. (Sopidus) koltzei* Weise 1887 (17 areas), *C. (Cryptocephalus) parvulus* (16 areas), *C. (Burlinius) nigrofasciatus* Jacoby 1885 (16 areas), *C. (Cryptocephalus) regalis regalis* Gebler 1830 (15 areas) and *C. (Cryptocephalus) hyacinthinus* Suffrian 1860 (15 areas).

In the following, the biodiversity of Cryptocephalini and Pachybrachini in the main divisions of the Palaearctic region (after Emeljanov, 1974, **Figure 2**) is given.



Fig. 2: Main divisions of the Palaearctic region (after Emeljanov, 1974, simplified).

I = Arctic (Circumpolar Tundra) region, II = Taiga (Euro-Siberian) region, III = European (nemoral) region, IV = Stenopean (nemoral) region, V = Hesperian (evergreen forest) region [Va = Macaronesian subregion, Vb = Mediterranean subregion], VI = Orthrian (evergreen forest) region, VII = Scythian (steppe) region [VIIa = West Scythian subregion, VIIb = East Scythian subregion], VIII = Sethian (desert) region [VIIIa = Saharo-Arabian subregion, VIIIb = Irano-Turanian subregion, VIIIc = Central Asian subregion].

Arctic (Circumpolar Tundra) region

In the northernmost and coldest part of the Palaearctic, Cryptocephalini and Pachybrachini can be found in the tundra areas of Chukotka (Chernov *et al.*, 2014) and the Southern part of Norway. These are 25 species of *Cryptocephalus* and one species of *Pachybrachis*. Few species of Chrysomelidae are truly arctic, among them no Cryptocephalini and Pachybrachini (Silfverberg, 1994). However, some Cryptocephalini reach the arctic although their main range lies further south. *Cryptocephalus (Cryptocephalus) krutovskyi* Jakobson 1900 is distributed from North-West Siberia and Altai to the Ussuri river, Sachalin and Japan, and reaches the Arctic at the lower Ob River. *Pachybrachis amurensis* Medvedev 1973 ranges from Western Mongolia to the Amur River and to Chukotka, where it reaches the Arctic (Medvedev & Korotyaev, 1980). The species reaching the arctic represent 2.5% of the diversity of the two tribes.

Taiga (Euro-Siberian) region

From the taiga, 122 and 13 species of Cryptocephalini and Pachybrachini were recorded, respectively (**Table 2**). The species most widely distributed in the Taiga are *Cryptocephalus (Burlinius) bilineatus*, *C. (Burlinius) elegantulus*, *C. (Burlinius) frontalis* Marsham 1802, *C. (Burlinius) pallifrons* Gyllenhal 1813, *C. (Cryptocephalus) parvulus*, *C. (Cryptocephalus) nitidulus* Fabricius 1787, *C. (Cryptocephalus) sericeus*, *C. (Cryptocephalus) sexpunctatus*

sexpunctatus, *Cryptocephalus (Homalopus) coryli* and *Pachybrachis hieroglyphicus* Laicharting 1781.

European (nemoral) region

In the European (nemoral) region a total of 199 species of *Cryptocephalini* (168 species) and *Pachybrachini* (31 species) were recorded. The most widely distributed species here are *C. (Burlinius) fulvus fulvus* (40 areas), *C. (Cryptocephalus) moraei* (36 areas), *C. (Cryptocephalus) bipunctatus bipunctatus* (34 areas), *C. (Cryptocephalus) nitidus* (32 areas), *C. (Cryptocephalus) sericeus* (31 areas), *Cryptocephalus (Homalopus) coryli*, *C. (Cryptocephalus) parvulus* and *C. (Burlinius) labiatus* (30 areas, respectively), *C. (Cryptocephalus) hypochaeridis* (Linné 1758) and *C. (Burlinius) ocellatus* (28 areas each), and *C. (Cryptocephalus) sexpunctatus sexpunctatus* and *C. (Burlinius) bilineatus* (27 areas each).

Stenopean (nemoral) region

In the Stenopean (nemoral) region, a total of 101 species of *Cryptocephalini* (92 species) and *Pachybrachini* (9 species) were recorded.

The most widely distributed species here are *Cryptocephalus (Burlinius) exiguus amicus* (11 areas), *C. (Burlinius) confusus* (10 areas), *C. (Cryptocephalus) parvulus* (9 areas), *C. (Sopidus) koltzei* (8 areas), *C. (Sopidus) semenowi* Weise 1889, *C. (Cryptocephalus) regalis regalis*, *C. (Burlinius) nigrofasciatus* (7 areas, respectively), *C. (Cryptocephalus) hyacinthinus*, *C. (Cryptocephalus) ochroloma* Gebler 1830, *C. (Cryptocephalus) sexpunctatus sexpunctatus* and *Pachybrachis (Pachybrachis) ochropygus* Solsky 1871 (6 areas each).

Hesperian (evergreen forest) region

The Hesperian region is subdivided into the Mediterranean subregion (297 species of *Cryptocephalini* and *Pachybrachini*) and the Macaronesian subregion (5 species of *Cryptocephalini*).

Mediterranean subregion

Among the most widely distributed species in the Mediterranean subregion are some which are widespread in the whole western Palaearctic region, like *Cryptocephalus (Burlinius) ocellatus* and *C. (Burlinius) fulvus fulvus* (13 areas in the Mediterranean subregion each), *C. (Burlinius) pygmaeus vittula* Suffrian 1848, *C. (Cryptocephalus) anticus* Suffrian 1848, *C. (Cryptocephalus) bipunctatus bipunctatus*, *C. (Cryptocephalus) parvulus* and *C. (Cryptocephalus) moraei* (10 areas each).

More characteristics for the Mediterranean subregion are *Cryptocephalus (Burlinius) macellus* Suffrian 1860 (13 areas), *Stylosomus (Stylosomus) tamarisci* Herrich-Schäffer 1836 (11 areas), *C. (Cryptocephalus) rugicollis rugicollis* Olivier 1792, *C. (Cryptocephalus) trimaculatus* Rossi 1790 and *C. (Burlinius) connexus* Olivier 1808 (10 areas each).

Some species form subspecies in the Western and Eastern Mediterranean, respectively. Examples are *C. (Cryptocephalus) rugicollis rugicollis* and *C. (Cryptocephalus) rugicollis sexnotatus* Fabricius 1792 or *C. (Cryptocephalus) violaceus scaffaiolus* Burlini 1961 and *C. (Cryptocephalus) violaceus violaceus* Laicharting 1781.

Macaronesian subregion

The diversity is low with 5 species only. All four *Cryptocephalus* species are in the subgenus *Burlinius*. The only species which is present on all islands is *C. gounellei* Pic 1922. The fifth species is *Stylosomus* (*Stylosomus*) *biplagiatus* Wollaston, 1864.

Orthrian (evergreen forest) region

The estimated number of species for the Orthrian (evergreen forest) region is 201. The species are in the genera *Adiscus* (29 species), *Coenobius* (18 species), *Cryptocephalus* (*Burlinius*) (16 species), *Cryptocephalus* (*Cryptocephalus*) (122 species), *Cryptocephalus* (*Sopidus*) (1 species), *Isnus* (1 species), *Melixanthus* (11 species) and *Stylosomus* (*Stylosomus*) (3 species). The most widely distributed species here are *Cryptocephalus* (*Cryptocephalus*) *guttifer* Suffrian 1854 (6 areas), *C. (Cryptocephalus) suavis* Duvivier 1892 and *C. (Cryptocephalus) trifasciatus* Fabricius 1787 (5 areas each), *C. (Cryptocephalus) deficiens* Suffrian 1854, *C. (Cryptocephalus) exsulans* Suffrian 1854, *C. (Cryptocephalus) luteosignatus* Pic 1922, *C. (Cryptocephalus) sannio* Kollar & Redtenbacher 1844, *C. (Cryptocephalus) triangularis triangularis* Hope 1831, *C. (Cryptocephalus) tricinctus* Kollar & Redtenbacher 1844 and *Coenobius fulvipes* Baly 1877 (**Figure 3q**) (with 4 areas, respectively).

Scythian (steppe) region

In the Scythian region, a total of 237 species of Cryptocephalini (190 species) and Pachybrachini (47 species) were recorded. The most widely distributed species here are *Cryptocephalus* (*Homalopus*) *coryli* and *C. (Burlinius) bilineatus* (7 areas each), *P. (Pachybrachis) scriptidorsum* Marseul 1874, *Cryptocephalus* (*Sopidus*) *bohemi* Drapiez 1819, *Cryptocephalus* (*Sopidus*) *apicalis* Gebler 1830, *C. (Cryptocephalus) virens* Suffrian 1847, *C. (Cryptocephalus) sericeus*, *C. (Cryptocephalus) laetus* Fabricius 1792, *C. (Cryptocephalus) flavipes* Fabricius 1781, *C. (Cryptocephalus) cordiger* (Linné 1758), *C. (Burlinius) ocellatus*, *C. (Burlinius) labiatus* and *C. (Burlinius) elegantulus* (with 6 areas, respectively).

In the West Scythian subregion, a total of 175 species of Cryptocephalini (142 species) and Pachybrachini (33 species) were recorded. The most widely distributed species here are *Cryptocephalus* (*Burlinius*) *ocellatus*, *C. (Sopidus) apicalis* and (*Homalopus*) *coryli* (with 6 areas, respectively).

In the East Scythian subregion, a total of 97 species of Cryptocephalini (79 species) and Pachybrachini (18 species) were recorded. The most widely distributed species here are *Cryptocephalus* (*Sopidus*) *altaicus* Harold 1872 and *C. (Sopidus) koltzei* (with 3 areas, respectively).

Sethian (desert) region

In the Sethian (desert) region, a total of 507 species of Cryptocephalini (419 species) and Pachybrachini (88 species) were recorded. The most widely distributed species here are *Melixanthus melanocephalus* Suffrian 1857 (12 areas), *Pachybrachis* (*Pachybrachis*) *glycirrhizae* Olivier 1808 (11 areas), *P. (Pachybrachis) scripticollis* Faldermann 1837, *P. (Pachybrachis) nigropunctatus* Suffrian 1854 and *Cryptocephalus* (*Sopidus*) *tamaricis* Solsky 1867 (8 areas each), *C. (Sopidus) undulatus* Suffrian 1854, *C. (Cryptocephalus) anticus*, *C. (Burlinius) connexus* (7 areas each), *C. (Burlinius) dilutellus* Jacobson 1901, *C. (Cryptocephalus) petraeus* Suffrian 1854, *C. (Cryptocephalus) semiargenteus* Reitter 1894, *C. (Homalopus) tarsalis tarsalis*

Weise 1887, *P. (Pachybrachis) scriptidorsum* and *Stylosomus (Microsomus) weberi* Reitter 1905 (with 6 areas, respectively).

In the Saharo-Arabian subregion, a total of 140 species of Cryptocephalini (119 species) and Pachybrachini (21 species) were recorded. The most widely distributed species here are *Melixanthus melanocephalus* (9 areas), *C. (Cryptocephalus) petraeus* (6 areas) and *Pachybrachis (Pachybrachis) glycirrhizae*, *Stylosomus (Stylosomus) tamarisci* and *C. (Cryptocephalus) dumonti* Peyerimhoff 1924 (with 5 areas, respectively).

In the Irano-Turanian subregion, a total of 291 species of Cryptocephalini (225 species) and Pachybrachini (66 species) were recorded. The most widely distributed species here are *Cryptocephalus (Sopidus) undulatus* (7 areas), *C. (Sopidus) tamaricis*, *C. (Cryptocephalus) semiargenteus*, *C. (Burlinius) dilutellus*, *Stylosomus (Microsomus) weberi*, *Pachybrachis (Pachybrachis) glycirrhizae* and *P. (Pachybrachis) nigropunctatus* (with 6 areas, respectively).

In the Central Asian subregion, a total of 132 species of Cryptocephalini (121 species) and Pachybrachini (11 species) were recorded. The most widely distributed species here are *Cryptocephalus (Cryptocephalus) regalis regalis* (5 areas), *Pachybrachis (Pachybrachis) scriptidorsum*, *Stylosomus (Stylosomus) submetallicus* Chen 1941 and *Adiscus variabilis* (Jacoby 1890) (with 4 areas, respectively).

Species richness of Cryptocephalini is highest in the Sethian region and the Hesperian region with 419 and 228 species, respectively. The Pachybrachini are most species-rich in the Sethian region and the Mediterranean subregion with 88 and 74 species, respectively (**Table 2**).

Table 2: Diversity of Cryptocephalini and Pachybrachini in the main divisions of the Palaearctic region (see Fig. 2).

Divisions	Cryptocephalini	Pachybrachini	Total
Arctic	25	1	26
Taiga	122	13	135
European	168	31	199
Stenopean	92	9	101
Hesperian	228	74	302
Macaronesian	5	0	5
Mediterranean	223	74	297
Orthrian	201	0	201
Scythian	190	47	237
West Scythian	142	33	175
East Scythian	79	18	97
Sethian	419	88	507
Saharo-Arabian	119	21	140
Irano-Turanian	225	66	291
Central Asian	121	11	132

Geographical distribution of the genera and subgenera of *Cryptocephalini* and *Pachybrachini*

Genus *Cryptocephalus* Geoffroy 1762

subgenus *Bertiellus* Lopatin 1977

The subgenus *Bertiellus* was erected for four species from Afghanistan. Beside the original descriptions, no information on these species is available. In **Figure 3a** external morphological characters are illustrated for the first time, i.e., the relatively short antenna, elytra with sparse setae and the expanded tibiae with an apical row of spines.

subgenus *Burlinius* Lopatin 1965

The subgenus comprises 141 species and subspecies. Almost all (134 species) are Palaearctic in distribution. One species was found in Yemen (Sana'a, Wadi Dhar, 29.V.1987, specimen not determinable) and another in Ethiopia. Five species are in the Oriental area of China (**Figures 3b, c**).

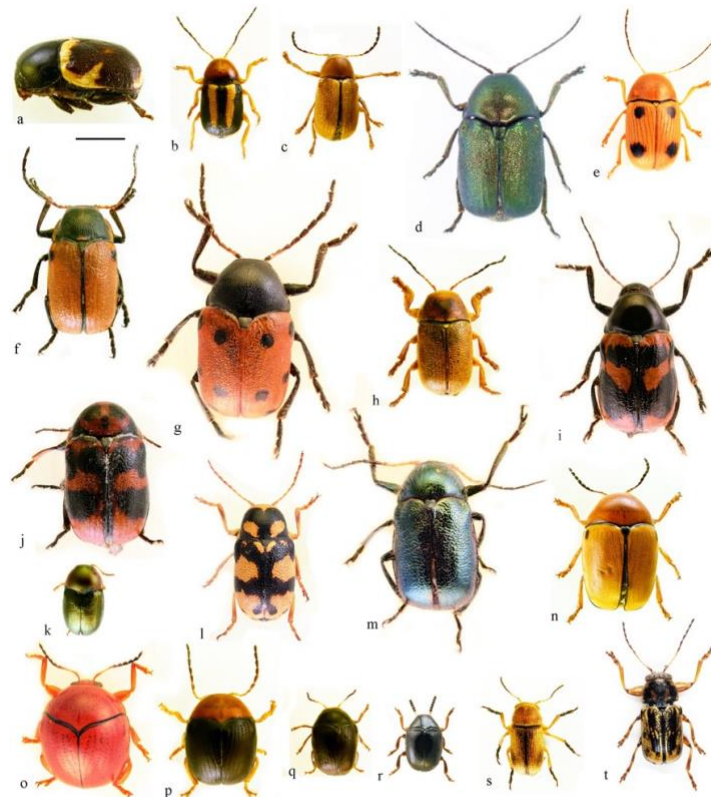


Fig. 3: Representatives of Palaearctic *Cryptocephalini* and *Pachybrachini*: a) *Cryptocephalus* (*Bertiellus*) *lopatini* Medvedev 1978, b) *C. (Burlinius)* *presuturalis* Pic 1907, c) *C. (Burlinius)* *flabellatus* Schöller 2009, d) *C. (Cryptocephalus)* *sericeus* (Linné 1758), e) *C. (Cryptocephalus)* *nigronotatus* Bryant 1954, f) *C. (Cryptocephalus)* *distinguendus* Schneider 1792, g) *C. (Cryptocephalus)* *pexicollis* Suffrian 1847, h) *C. (Disopus)* *pini pini* (Linné 1758), i) *C. (Homalopus)* *tarsalis tarsalis* Weise 1887, j) *C. (Lamellosus)* *laevicollis* Gebler 1830, k) *Diachus auratus* (Fabricius 1801), l) *C. (Sopidus)* *manchuricus* Gressit & Kimoto 1961, m) *C. (Protophysus)* *euchirus* Kraatz 1879, n) *Melixanthus assamensis* (Jacoby 1908), o) *Adiscus mouhoti* (Baly 1877), p) *Adiscus lewisii* (Baly 1873), q) *Coenobius fulvipes* Baly 1877, r) *Isnus yunnanus* Schöller 2021, s) *Stylosomus (Stylosomus)* *tamarisci* Herrich-Schäffer 1836, t) *Pachybrachis (Pachybrachis)* *pallidulus* Suffrian 1852.

subgenus *Cryptocephalus* Geoffroy 1762

For the nominate subgenus, 385 species are listed in the catalogue. The number of species restricted to the Oriental part of China is 37, i.e. the number of Palearctic species and subspecies of *Cryptocephalus* is 348. These are distributed from Portugal to Japan. Within the nominate subgenus, a number of species-groups were suggested (e.g. Weise, 1882; Schöller, 2021a). However, much more studies are required on species-groups and their distribution (**Figures 3d-g**).

subgenus *Disopus* Chevrolat 1836

Five species and subspecies only are in this subgenus, these are distributed from Portugal to Japan. *Cryptocephalus pini pini* Linnaeus 1758 is of economic importance as a pest of pine plantations in some areas of its areal (**Figure 3h**).

subgenus *Homalopus* Chevrolat 1837

In this subgenus, 27 species and subspecies are placed. In Asia and Europe, 12 and 16 species were recorded, respectively. One species, *C. coryli* Linnaeus 1758, is widely distributed and the only species in the Taiga. Otherwise the subgenus is especially species-rich in the European (nemoral) and Mediterranean regions with 12 and 15 species, respectively (**Figure 3i**).

subgenus *Lamellosus* Tomov 1979

The subgenus *Lamellosus* was erected for two species only, i.e., *C. angorensis* Pic 1908 from Turkey and *C. laevicollis* Gebler 1830 (**Figure 3j**) distributed from Germany in the West to Southern Siberia in the East.

subgenus *Protophysus* Chevrolat 1836

The subgenus *Protophysus* was erected for five species and subspecies from Europe and Asia, distributed from Spain via Iran to Mongolia (**Figure 3m**).

subgenus *Sopidus* Jacobson 1901

In the subgenus *Sopidus* (= *Asionus* Lopatin 1988), 119 species are placed. In Asia, Europe and North Africa, 113, 20 and 3 species were recorded, respectively. The subgenus is especially diverse in Central Asia, Russia and China (**Figure 3l**). Most species-rich is the Sethian (desert) region (82 species), followed by the Scythian (steppe) region (66 species), European (nemoral) region (21 species), Taiga (20 species), Stenopean (nemoral) region (11 species), Mediterranean subregion (7 species), and Orthrian (evergreen forest) region (1 species).

Genus *Diachus* LeConte 1881

The genus *Diachus* is originally Neotropical. The species *Diachus auratus* (Fabricius 1801), a pest of sweet potato and other agricultural crops, was introduced to Asia and other biogeographical regions (**Figure 3k**).

Genus *Jaxartiolus* Jacobson 1922

The genus *Jaxartiolus* was erected for three species from Central Asia and China (Gansu). Beside the original descriptions, little information is available.

Genus *Melixanthus* Suffrian 1854

In the catalogue, 21 species of *Melixanthus* are listed. Four species are Oriental, i.e., there are 17 Palaearctic species. *Melixanthus melanocephalus* Suffrian 1857 and similar species are widely distributed in Northern Africa and the Middle East, and another 13 species were recorded from China (**Figure 3n**).

The genus *Melixanthus* was originally described by monotypy for a species from Borneo. Already in his original description, Suffrian (1854) discussed the lack of specific characters to distinguish *Cryptocephalus* from *Melixanthus*. Some following authors placed all species with appendiculate or toothed tarsal claws in *Melixanthus* based on this character alone and included species in the subgenus *Anteriscus* Weise of *Cryptocephalus* as well. However, this leads most likely to a polyphyletic grouping. *Anteriscus* Weise was synonymised with *Cryptocephalus* (Schöller, 2021a). The second frequently mentioned character for *Melixanthus* are short and widened antennae. However, there is a continuum between short and widened and long and slender antennae in various *Cryptocephalina*. Future studies are needed to solve the question of generic affiliation of the species currently listed in *Melixanthus*.

Genus *Adiscus* Gistel 1857

For the genus *Adiscus*, 53 species are listed in the catalogue, 20 of which are Oriental. Most of the 33 Palaearctic species are distributed in China (Duan & Zhou, 2022), the others in Northern India and Nepal (**Figures 3o, p**). The Orthrian (evergreen forest), Sethian (desert) and Stenopean (nemoral) regions have 29, 13 and 4 species, respectively.

Genus *Coenobius* Suffrian 1857

The genus *Coenobius* is species-rich both in the Afrotropical and the Oriental regions. In the catalogue, 30 species are listed, four of which are Oriental. Again, most of the 26 Palaearctic species are distributed in China and the others in Northern India and Nepal, with six species extending to Japan (**Figure 3q**). The Orthrian (evergreen forest) region has 18 species.

Genus *Isnus* Weise 1898

The genus *Isnus* is similar to *Coenobius* (with upper eye lobes separated, not touching as in *Coenobius*), and most species-rich in Africa. In the catalogue, there is the Afrotropical species *C. biseriatus* Chapuis 1877 which is extending its range to the Arabian Peninsula, and the Oriental species *C. yunnanus* Schöller 2021 (**Figure 3r**).

Genus *Stylosomus* Suffrian 1848

The genus *Stylosomus* is restricted to the Palaearctic region, 34 species and subspecies are listed in the catalogue. The subgenus *Microsomus* Burlini 1957 is distributed in Asia and Europe, the subgenus *Stylomicrus* Petitpierre & Alonso-Zarazaga 2000 and the nominate subgenus are distributed in Asia, Europe and Northern Africa (**Figure 3s**). The Sethian (desert) region, Mediterranean subregion, Scythian (steppe) region and European (nemoral) region have 22, 14, 7 and 7 species, respectively.

Genus *Pachybrachis* Chevrolat 1836

The genus *Pachybrachis* is distributed in the Neotropical, Nearctic and Palaearctic regions. In the catalogue, 156 Palaearctic species are listed. The subgenus *Chloropachys* Rey 1883 is distributed in the Iberian Peninsula and Northern Africa. The nominate subgenus is distributed from Portugal to Japan. The areal of some species is very small, e.g. *P. fraudolentus* Müller 1955 in a few

alpine valleys, *P. chafarinensis* on the small islands of Isla del Congreso or *P. sassii* Montagna 2011 on Giglio island (**Figure 3t**).

The Sethian (desert) region, Mediterranean subregion, Scythian (steppe) region, European (nemoral) region and Stenopean (nemoral) region have 88, 74, 47, 31 and 9 species, respectively.

Genus *Acolastus* Gerstaecker 1855

In the new catalogue, the genus *Acolastus* was included in the tribe Clytrini. It is especially diverse in the Afrotropical region and in Central Asia, 105 species are listed. The nominate subgenus and the subgenus *Lapsionus* are distributed all over North Africa and Asia. The subgenus *Anodontelytrus* Jacobson 1917 is distributed in the Middle East and North Africa. There are three Oriental species from Southern India and Sri Lanka (subgenus *Pachylanka* Medvedev 1989).

Endemism

The number of endemic species (= in one territory only) in the catalogue is 273, out of 988 species, i.e. 27.6%. There are 29 endemic species (36.71%) in North Africa (8 areas) and 48 endemic species (22.43%) in Europe (51 areas). In Asia (81 areas), a total of 319 species out of 666 species are endemic (47.90%). More than one third of the fauna is endemic in Nepal, Afghanistan and Kirgistan. More than 27% of the species are endemic in Spain, Tajikistan and Morocco (**Table 3**).

Table 3: Number of endemic species of Cryptocephalini and Pachybrachini per country

Country	Endemic	Total no° species	% endemic
Nepal	23	67	34.33%
Afghanistan	11	33	33.33%
Kirgistan	16	52	30.77%
Spain	26	90	28.89%
Tadjikistan	13	46	28.26%
Morocco	15	55	27.27%
Iran	25	95	26.32%
Kazachstan	27	123	21.95%
Mongolia	16	89	18.00%
Algeria	9	50	18.00%
Turkey	16	107	14.95%
Italy	13	112	11.61%
France	6	116	5.17%

Island biogeography

Eighty-five species are endemic to islands, i.e. 20 European species (**Table 4**), 59 Asian species (**Table 5**) and six North African species (**Table 6**). In Northern Africa, all endemic island species in the genus *Cryptocephalus* belong to the subgenus *Burlinius*. Fifty-nine species were recorded from one island only, and out of these, 39 from Taiwan (**Tables 7, 8**). Taiwan is the island with most species, followed by Sicily, Honshu, Corsica, Sardinia, Great Britain and Kyushu (**Table 9**). An example for an extremely local species is *Cryptocephalus (Burlinius) chafarinensis* which is known so far only from Isla del Congreso (Spain, Islas Chafarinas close to the coast of Morocco)

which has an area of 0.256 km² only or *Pachybrachis (Pachybrachis) sassii* Montagna 2011 living only on Giglio island, the latter with a surface of 23.80 km². Among the species with the most remote island distributions are *Cryptocephalus (Burlinius) crenatus* endemic to Madeira, *C. (Cryptocephalus) sokotrensis* Schöller 2014 endemic to Sokotra and *C. (Burlinius) kurentzovi* Medvedev 1966 endemic to the Kuriles islands (**Tables 5, 6**).

Table 4: European species of Cryptocephalini and Pachybrachini endemic to islands

Genus	Subgenus	Species	Country	Islands
<i>Cryptocephalus</i>	<i>Burlinius</i>	<i>alnicola</i> Costa 1884	France, Italy	Corsica, Sardinia
<i>Cryptocephalus</i>	<i>Burlinius</i>	<i>biondii</i> Sassi & Regalin 1998	France, Italy	Corsica, Sardinia, Capraia Isl.
<i>Cryptocephalus</i>	<i>Burlinius</i>	<i>cognatus</i> A. Costa 1886	France, Italy	Corsica, Sardinia
<i>Cryptocephalus</i>	<i>Burlinius</i>	<i>lostiai</i> Burlini 1951	France, Italy	Corsica, Sardinia
<i>Cryptocephalus</i>	<i>Burlinius</i>	<i>majoricensis</i> Fuente 1918	Spain	Balears: Cabrera, Dragonera, Formentera, Mallorca, Menorca
<i>Cryptocephalus</i>	<i>Burlinius</i>	<i>plantaris</i> Suffrian 1868	Italy, Madeira	Sicily, Madeira
<i>Cryptocephalus</i>	<i>Burlinius</i>	<i>pulchellus equiseti</i> Costa 1886	France, Italy	Corsica, Sardinia
<i>Cryptocephalus</i>	<i>Burlinius</i>	<i>tramuntanae</i> Petitpierre 1993	Spain	Balears: Mallorca
<i>Cryptocephalus</i>	<i>Cryptocephalus</i>	<i>creticus</i> Suffrian 1847	Greece	Crete
<i>Cryptocephalus</i>	<i>Cryptocephalus</i>	<i>hirticollis</i> Suffrian 1847	Italy	Egadi islands, Levano Marettimo, Sicily
<i>Pachybrachis</i>	<i>Pachybrachis</i>	<i>anoguttatus</i> Suffrian 1866	Italy, Spain	Sardinia, Balears: Mallorca, Menorca
<i>Pachybrachis</i>	<i>Pachybrachis</i>	<i>burlinii</i> Daccordi & Ruffo 1971	Italy	Pontine Isl.
<i>Pachybrachis</i>	<i>Pachybrachis</i>	<i>cinctus</i> Suffrian 1848	France, Italy	Corsica, Sardinia
<i>Pachybrachis</i>	<i>Pachybrachis</i>	<i>creticus</i> Weise 1886	Greece	Crete
<i>Pachybrachis</i>	<i>Pachybrachis</i>	<i>freyi</i> Burlini 1957	Greece	Ionian Isl.: Cephalonia
<i>Pachybrachis</i>	<i>Pachybrachis</i>	<i>osellai</i> Daccordi & Ruffo 1975	Italy	Levanzo and Marettimo in Egadi Isl.
<i>Pachybrachis</i>	<i>Pachybrachis</i>	<i>sassii</i> Montagna 2011	Italy	Giglio Isl.
<i>Pachybrachis</i>	<i>Pachybrachis</i>	<i>siculus</i> Weise 1891	Italy, Malta	Pantelleria Isl., Sicily, Malta
<i>Pachybrachis</i>	<i>Pachybrachis</i>	<i>testaceus</i> Perris 1866	France, Italy	Corsica, Sardinia, Sicily
<i>Stylosomus</i>	<i>Stylosomus</i>	<i>corsicus</i> Rey 1883	France, Italy	Corsica, Sardinia, Sicily

Table 5: Asian species of Palearctic Cryptocephalini and Pachybrachini endemic to islands (except for Taiwan)

Species	Country	Islands
<i>lewisiai</i> Baly 1873	Japan	Awaji-jima, Honshu, Kōzu-shima, Kyushu, Shodo-shima, Shikoku
<i>nigrocastaneus</i> Chûjô 1954	Japan, Taiwan	Ishigaki, Iriomote, Taiwan
<i>kimotoi</i> Nakane 1963	Japan	Honshu
<i>kurentzovi</i> Medvedev 1966	Russia	Kuriles islands
<i>ejimai</i> Takizawa 1990	Japan	Danjo, Hirado, Iki, Kyushu
<i>honshuensis</i> Takizawa 2015	Japan	Honshu
<i>nigrorufus</i> Gressitt 1942	China	Hainan
<i>pseudofulvus</i> Medvedev 1973	Japan	Hokkaido, Honshu
<i>hainanicus</i> Gressitt 1942	China	Hainan
<i>instabilis</i> Baly 1873	Japan	Honshu, Kyushu, Shikoku
<i>loochooensis loochooensis</i> Chûjô 1935	Japan	Aka, Amami-Ōshima, Ishigaki, Kume-jima Isl, Nijjima, Okinawa main, Taketomi
<i>loochooensis miyakoensis</i> Kimoto 1974	Japan	Miyako
<i>ohnoi</i> Kimoto 1983	Japan, Taiwan	Honshu, Taiwan
<i>perelegans insulanus</i> Chûjô 1935	Japan	Ryukyu Archipelago
<i>perelegans perelegans</i> Baly 1873	Japan, Taiwan	Hachijo, Hokkaido, Honshu, Kyushu, Okinawa, Shikoku, Shimokoshiki, Shodo, Yaku, Taiwan
<i>perelegans yonaguniensis</i> Kimoto 1974	Japan	Ryukyu Archipelago, Yonaguni
<i>socotrensis</i> Schöller 2014	Yemen	Socotra
<i>babai</i> Chûjô 1959	Japan	Honshu
<i>scitulus</i> Baly 1873	Japan	Awaji Isl., Hokkaido, Honshu, Kōzushima Isl., Kyushu, Oki Isl., Shikoku, Shodo Isl.
<i>eruditus</i> Baly 1873	Japan	Hokkaido, Honshu, Kyushu, Oki Isl., Shikoku

Table 6: North African species of *Cryptocephalini* endemic to islands

Genus	Subgenus	Species	Country	Islands
<i>Cryptocephalus</i>	<i>Burlinius</i>	<i>crenatus</i> Wollaston 1854	Portugal	Madeira, Porto Santo
<i>Cryptocephalus</i>	<i>Burlinius</i>	<i>nitidicollis</i> Wollaston 1864	Spain	Gomera, Gran Canaria, Hierro, La Palma, Teneriffa
<i>Cryptocephalus</i>	<i>Burlinius</i>	<i>chafarinensis</i> Petitpierre 2007	Morocco	Islas Chafarinas: Isla del Congreso
<i>Cryptocephalus</i>	<i>Burlinius</i>	<i>puncticollis</i> Wollaston 1864	Spain	Gomera, Gran Canaria, Hierro, La Palma, Teneriffa
<i>Cryptocephalus</i>	<i>Burlinius</i>	<i>trapezicollis</i> Lindberg 1953	Spain	Gran Canaria, La Palma
<i>Stylosomus</i>	<i>Stylosomus</i>	<i>biplagiatus</i> Wollaston 1864	Spain	Fuerteventura

Table 7: Species of *Cryptocephalini* endemic to Taiwan: *Cryptocephalina*

Genus	Subgenus	Species
<i>Cryptocephalus</i>	<i>Burlinius</i>	<i>hohuanshanus</i> Kimoto 1996
<i>Cryptocephalus</i>	<i>Cryptocephalus</i>	<i>formosanus</i> Chûjô 1934
<i>Cryptocephalus</i>	<i>Cryptocephalus</i>	<i>hamifasciatus</i> Chûjô 1934
<i>Cryptocephalus</i>	<i>Cryptocephalus</i>	<i>hiro</i> Chûjô 1954
<i>Cryptocephalus</i>	<i>Cryptocephalus</i>	<i>kanoi</i> Chûjô 1954
<i>Cryptocephalus</i>	<i>Cryptocephalus</i>	<i>kiyoyamai</i> Kimoto 1974
<i>Cryptocephalus</i>	<i>Cryptocephalus</i>	<i>makii</i> Chûjô 1934
<i>Cryptocephalus</i>	<i>Cryptocephalus</i>	<i>mitchy</i> Chûjô 1954
<i>Cryptocephalus</i>	<i>Cryptocephalus</i>	<i>moya</i> Chûjô 1954
<i>Cryptocephalus</i>	<i>Cryptocephalus</i>	<i>nigronoticollis</i> Chûjô 1934
<i>Cryptocephalus</i>	<i>Cryptocephalus</i>	<i>nitidissimus</i> Chûjô 1934
<i>Cryptocephalus</i>	<i>Cryptocephalus</i>	<i>nitobei</i> Chûjô 1954
<i>Cryptocephalus</i>	<i>Cryptocephalus</i>	<i>ruri</i> Chûjô 1934
<i>Cryptocephalus</i>	<i>Cryptocephalus</i>	<i>sauteri</i> Chûjô 1934
<i>Cryptocephalus</i>	<i>Cryptocephalus</i>	<i>solus</i> Chûjô 1934
<i>Cryptocephalus</i>	<i>Cryptocephalus</i>	<i>tainanensis</i> Schöller 2010
<i>Cryptocephalus</i>	<i>Cryptocephalus</i>	<i>taiwanus</i> Chûjô 1934
<i>Melixanthus</i>	<i>Melixanthus</i>	<i>formosensis</i> Chûjô 1934
<i>Melixanthus</i>	<i>Melixanthus</i>	<i>tubu</i> Chûjô 1954

Table 8: Species of Cryptocephalini endemic to Taiwan: Monachulina

Genus	Species
<i>Adiscus</i>	<i>apicalis</i> Chûjô 1954
<i>Adiscus</i>	<i>arisanus</i> Chûjô 1954
<i>Adiscus</i>	<i>issikii</i> Chûjô 1954
<i>Adiscus</i>	<i>longicornis</i> Chûjô 1954
<i>Adiscus</i>	<i>matudai</i> Chûjô 1954
<i>Adiscus</i>	<i>mediofulvus</i> Chûjô 1954
<i>Adiscus</i>	<i>melanopterus</i> Chûjô 1954
<i>Adiscus</i>	<i>osawai</i> Kimoto 1987
<i>Adiscus</i>	<i>rufonigrus</i> Chûjô 1954
<i>Adiscus</i>	<i>sauteri</i> Chûjô 1938
<i>Adiscus</i>	<i>sungkangensis</i> Kimoto 1996
<i>Adiscus</i>	<i>taiwanus</i> Chûjô 1954
<i>Coenobius</i>	<i>babai</i> Chûjô 1963
<i>Coenobius</i>	<i>choanus</i> Schöller 1999
<i>Coenobius</i>	<i>chujoi</i> Aslam 1967
<i>Coenobius</i>	<i>endoi</i> Chûjô 1954
<i>Coenobius</i>	<i>flavescens</i> Chûjô 1954
<i>Coenobius</i>	<i>kaohsiungensis</i> Kimoto & Chu
<i>Coenobius</i>	<i>taiwanus</i> Chûjô 1954
<i>Coenobius</i>	<i>yosionis</i> Chûjô 1954

Table 9: Diversity of Palaearctic Cryptocephalini and Pachybrachini on islands (islands with more than 4 species only)

Island	Cryptocephalina	Monachulina	Pachybrachini	Stylosomina	Total
Taiwan	32	27	0	0	59
Sicily	21	0	9	3	33
Honshu	25	5	1	0	31
Corsica	24	0	4	2	30
Sardinia	17	0	4	3	24
Great Britain	23	0	0	0	23
Kyushu	17	5	1	0	23
Öland	21	0	0	0	21
Hokkaido	18	0	1	0	19
Sakhalin	16	0	1	0	18
Shikoku	12	1	1	0	14
Hainan	12	1	0	0	13
Mallorca	8	0	1	1	10
Rügen	7	0	0	0	7
Korfu	6	0	1	0	7
Cyprus	5	0	0	2	7
Gotland	6	0	0	0	6
Kuriles	6	0	0	0	6
Ireland	6	0	0	0	6
Bornholm	5	0	0	0	5
Crete	3	0	2	0	5
Elba	4	0	1	0	5
Malta	3	0	2	0	5
Pantelleria	3	0	1	1	5

Table 10: Species of *Cryptocephalini* recorded from six islands or more

Species	No. islands	Islands
<i>Cryptocephalus (Burlinius) fulvus fulvus</i> Goeze 1777	35	Korčula, Rab (CR) Anholt, Bornholm, Læsø (DE) Corsica, L'Île de Groix, L'Île-d'Yeu (FR) Isle of Wight (GB) Borkum, Fehmarn, Föhr, Hiddensee, Juist, Langeoog, Norderney, Rügen, Spiekeroog, Vilm (GE) Cephalonia, Korfu, Psathoura, Rhodes, Samos, Skiathos (GR) Aeolian Isl., Elba, Pantelleria, Sardinia, Sicily (IT) Ibiza, Formentera, Illas Cíes (SP) Gotland, Öland (SV)
<i>Coenobius obscuripennis</i> Chûjô 1935	15	Amami-oshima, Honshu, Iriomote, Ishigaki-jima, Kouri-jima, Kyushu, Miyako-shima, Okinawa-jima, Okinoerabu-jima, Ryukyu Archipelago, Shikoku, Tokara-Retto, Toku-no-shima, Yabuchi-shima, Yaku-shima, Yonaguni (JA)
<i>Cryptocephalus (Cryptocephalus) moraei</i> Linnaeus 1758	14	Bornholm (DE) Corsica (FR) Hiddensee, Langeoog, Rügen (GE) Alonnisos, Euboea, Korfu, Skiathos, Skopelos (GR) Sicily (IT) Ibiza (SP) Gotland, Öland (SV)
<i>Diachus auratus</i> Fabricius 1801	13	Aguni-jima, Ikei-jima, Kourishima, Minami-daito, Miyako, Okinawa main Isl., Ryukyu Archipelago, Senaga-shima, Sesoko-jima, Tonaki-jima, Tsuken-jima, Yoronshima (JA) Taiwan
<i>Cryptocephalus (Burlinius) macellus</i> Suffrian 1860	13	Corsica (FR) Crete, Cephalonia, Euboea, Naxos, Rhodes, Skiathos (GR) Aeolian Isl., Pontine Isl., Pantelleria Isl., Sardinia, Sicily (IT) Mallorca (SP)
<i>Cryptocephalus (Cryptocephalus) parvulus</i> O. F. Müller 1776	12	Corsica (FR) Rügen (GE) Sardinia (IT) Gotland, Öland (SV) Awaji Isl., Hokkaido, Honshu, Kyushu, Shikoku, Kurile Isl. (JA) Sakhalin (RU)
<i>Cryptocephalus (Cryptocephalus) hyacinthinus</i> Suffrian 1860	11	Zhoushan Isl. (CH) Awaji Isl., Goto Isl., Honshu, Iki-No Isl., Kyushu, Oki Isl., Shikoku, Shodo Isl., Tsushima Isl. (JA) Yeongheungdo Isl. (SC)
<i>Cryptocephalus (Burlinius) exiguus amicus</i> Baly 1873	11	Hokkaido, Honshu, Kyushu, Oki Isl., Rishiri Isl., Shikoku (JA) Jeju-Do (SC) Furugelm, Kuriles Isl., Popov, Sakhalin (RU)
<i>Cryptocephalus (Burlinius) rufipes</i> Goeze 1777	10	Grand Cavallo, Petit Cavallo, Tazrout (AG) L'Île de Groix, L'Île-d'Yeu (FR) Jersey (GB) Borkum, Langeoog, Spiekeroog (GE) Illas Cíes (SP)
<i>Cryptocephalus (Cryptocephalus) luridipennis signaticeps</i> Baly 1873	9	Awaji Isl., Hokkaido, Honshu, Kōzu-shima Isl., Kyushu, Oki Isl., Shikoku, Shodo Isl., Tobi Isl., Tsushima Isl. (JA)
<i>Cryptocephalus (Cryptocephalus) perelegans perelegans</i> Baly 1873	9	Hachijo, Hokkaido, Honshu, Kyushu, Okinawa, Shikoku, Shimokoshiki, Shodo, Yaku (JA)
<i>Coenobius piceus</i> Baly 1873	9	Hachijo-shima, Honshu, Kyushu, Miyake-shima, Oki-no, Oshima, Shikoku, Tane-ga-jima, Tsushima (JA)
<i>Cryptocephalus (Burlinius) labiatus</i> Linnaeus 1761	9	Rab (CR) Bornholm (DE) Rügen (GE) Korfu (GR) Sardinia, Sicilia (IT) Gotland, Öland (SV) Sakhalin (RU)

<i>Cryptocephalus (Burlinius) pusillus</i> Fabricius 1777	9	Bornholm (DE) Isle of Wight (GB) Hiddensee, Langeoog, Norderney, Rügen, Sylt, Vilm (GE) Öland (SV)
<i>Cryptocephalus (Burlinius) confusus</i> Suffrian 1854	8	Honshu, Awaji, Kōzu, Kyushu, Shōdo, Shikoku, Tsushima (JA) Sakhalin (RU)
<i>Melixanthus scitulus</i> Baly 1873	8	Awaji, Hokkaido, Honshu, Kōzushima, Kyushu, Oki, Shikoku, Shodo (JA)
<i>Cryptocephalus (Burlinius) gounellei</i> Pic 1922	7	Fuerteventura, Gomera, Gran Canaria, Hierro, La Palma, Lanzarote, Teneriffa (SP)
<i>Cryptocephalus (Cryptocephalus) loochooensis loochooensis</i> Chûjō 1935	7	Aka, Amami-Ōshima, Ishigaki, Kume-jima, Niijima, Okinawa main Isl., Taketomi (JA)
<i>Cryptocephalus (Cryptocephalus) sexpunctatus sexpunctatus</i> (Linnaeus 1758)	7	Gotland, Öland (SV) Hokkaido, Honshu, Kuriles, Shikoku (JA) Sakhalin (RU)
<i>Cryptocephalus (Cryptocephalus) bipunctatus bipunctatus</i> (Linnaeus 1758)	7	Mljet (CR) Bornholm (DE) Rügen (GR) Korfu (GR) Elba (IT) Gotland, Öland (SV)
<i>Cryptocephalus (Burlinius) fulvus fuscolineatus</i> Chûjō 1940	7	Honshu, Kyushu, Shikoku, Tsuno (JA) Kuriles Isl., Popov, Sakhalin (RU)
<i>Cryptocephalus (Cryptocephalus) nobilis</i> Kraatz 1879	6	Honshu, Kōzu-shima, Kyushu, Oki, Shikoku, Shodo (JA)
<i>Cryptocephalus (Cryptocephalus) nitidulus</i> Fabricius 1787	6	Öland (SV) Hokkaido, Rebun-to, Rishiri (JA) Sakhalin (RU)
<i>Cryptocephalus (Cryptocephalus) tetradecaspilotus</i> Baly 1873	6	Awaji-jima, Honshu, Kyushu, Oki, Shikoku (JA) Jeju-Do (SC)
<i>Adiscus lewisii</i> Baly 1873	6	Awaji-jima, Honshu, Kōzu-shima, Kyushu, Shodo-shima, Shikoku (JA)
<i>Coenobius piceipes</i> Gressitt 1942	6	Hachijo-shima, Honshu, Kyushu, Oki, Shikoku, Tsushima (JA)
<i>Coenobius sulcicollis</i> Baly 1873	6	Hirado, Honshu, Kyushu, Shikoku, Shodo-jima, Tsushima (JA)

CH=China, CR=Croatia, DE=Denmark, FR=France, GB=Great Britain, GE=Germany, GR=Greece, IT=Italy, JA=Japan, RU=Russia, SC=South Korea, SP=Spain, SV=Sweden

Among the species which are not endemic to islands, few occur on many islands (**Table 10**). The most widely distributed species on islands is *Cryptocephalus (Burlinius) fulvus fulvus* which was recorded from 35 islands (**Figure 4**). Another example is *C. (Burlinius) macellus* which was recorded, beside its mainland distribution, on Mediterranean islands only (**Figure 5**). This species

is more thermophilous compared to *C. (Burlinius) fulvus fulvus*. In Germany, its northernmost distribution is the state of Saxony-Anhalt. It does not reach the islands of the Baltic Sea.

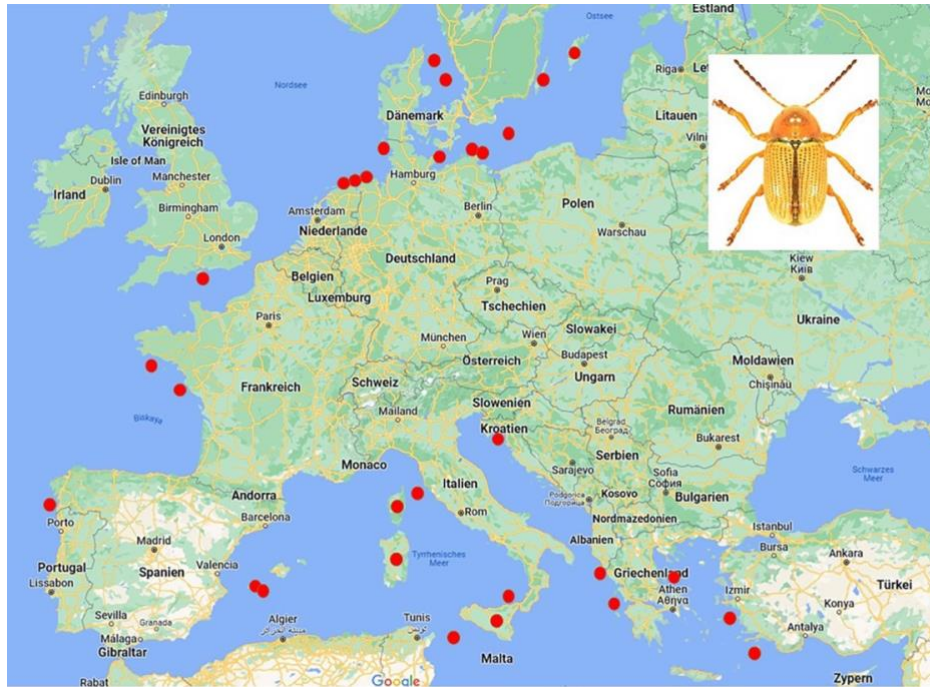


Fig. 4: Island distribution of *Cryptoccephalus (Burlinius) fulvus fulvus* (mainland distribution not shown).



Fig. 5: Island distribution of *Cryptoccephalus (Burlinius) macellus* (mainland distribution not shown).

There are a number of assumptions in island biogeography which were tested with the data on Cryptocephalini and Pachybrachini. Generally, more animals live on large islands compared to small islands. In this study, a significant correlation of number of species and island surface area was found (nonlinear regression, $P < 0.005$, $R = 0.458$) (**Figure 6**).

The general pattern is for species richness to increase from polar to tropical regions (Willig & Presley, 2013). There is a tendency of decrease of number of species of Cryptocephalini and Pachybrachini on islands with increase in latitude (**Figure 7**). However, this correlation is not significant (nonlinear regression, $P < 0.170$, $R = 0.311$).

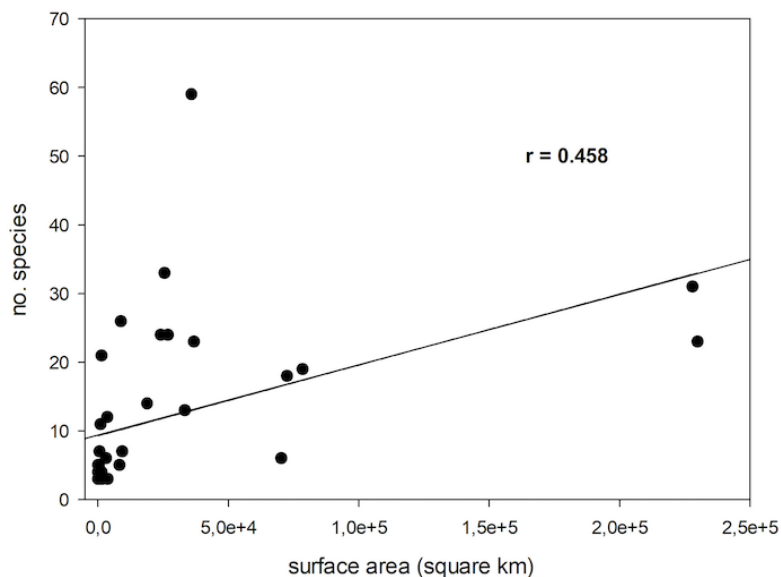


Fig. 6: Number of species of Cryptocephalini and Pachybrachini depending on Palaeartic Island surface area.

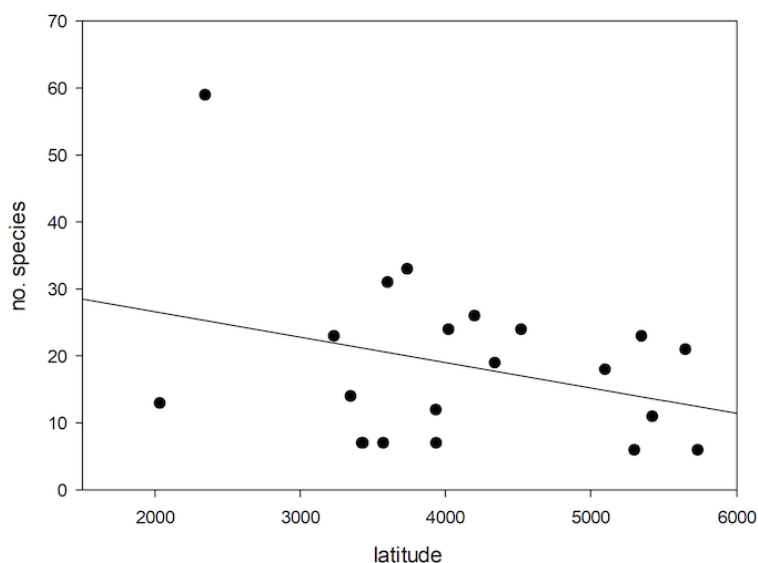


Fig.7: Number of Palaeartic species of Cryptocephalini and Pachybrachini depending on island latitude.

DISCUSSION

How precisely the current distribution of a species is known obviously depends on the existence of studies in the various territories in the Palaearctic. Fortunately, the knowledge on Cryptocephalinae diversity and distribution is comparatively good. For major geographical areas, the fauna was reviewed. Examples are Afghanistan (Medvedev, 1978), the Arabian peninsula (Medvedev, 1996), Central Asia and Kazakhstan (Lopatin, 1977), Central Europe (Schmitt *et al.*, 2014), China (Gressitt & Kimoto, 1961), Eastern Europe (Lopatin *et al.*, 2004), the Iberian Peninsula (Petitpierre, 2000), Iran (Schöller & Nasserzadeh, 2010), Korea (Cho & An, 2020), Mongolia (Medvedev, 1982), Morocco (Kocher, 1958), Nepal (Medvedev & Sprecher-Uebersax, 1997), Northern Europe (Silfverberg, 2010), Balkan (Gruev, 2005), Siberia and the Russian Far East (Medvedev, 1973) and Turkey (Sassi & Kismali, 2000).

Warchalowski (2000) published identification keys for most of the area treated here and additional information on China is available in Gressitt & Kimoto (1961). However, these works were published over a long period of time. Even though several more recent publications are available (e.g., Duan & Zhou, 2022; Schöller, 2021b), the fact a total of about 100 new country records were published in the course of the preparation of the catalogue (Schöller, 2020; Bezděk & Sekerka, 2023) shows there are still gaps in knowledge. Especially for China, many new findings can be expected.

The similar values for the number of species per square meter for North Africa, Asia and Europe despite the considerable differences in size of these areas may be a result of an increase of diversity from the temperate regions to the subtropical regions in the Palaearctic. In a large part of Northern Europe and especially the north of Asia, few or even no records of Cryptocephalini exist. Species numbers are declining from the most southern main divisions of the Palaearctic region towards the Arctic region, i.e. from 507 species to 26 species. This is in accordance with the general pattern of species richness of animals depending on latitude with an increase from polar to tropical regions (Willig & Presley, 2013). Continental, wet winter and dry winter climates vegetation types are less favourable for the establishment of Cryptocephalini and Pachybrachini populations. Cryptocephalini and Pachybrachini are typically absent in polar vegetation types like tundra and perpetual frost. Even though ecological factors like e.g. polyphagy and case-bearing in larve are probable causes for the observed pattern in Cryptocephalini and Pachybrachini, evolutionary, historical and stochastic processes have to be considered in future studies as well. The following factors were hypothesised to enable the Cryptocephalini to colonise semi-desert and desert environments and diversify there: the rectal apparatus enables adults to retain water from faeces, and the egg- and larval cases protect eggs and larvae physically from desiccation. Moreover, the latter protect the immatures from general predators like ants which are predominant in semi-desert and desert environments (Schöller, 1995).

A great belt of Northern hemisphere deserts occurs from North Africa to North Western China. In the eastern parts of Asian deserts, Cryptocephalini and Pachybrachini are the most species-rich group among the leaf beetles. Cryptocephalini, Clytrini, Pachybrachini and Eumolpinae dominate this fauna because they are better adapted to xeric environments because their larvae are case-bearing or soil-dwelling. They are mesophilous insects, however, some species of *Cryptocephalus* and *Pachybrachis* are active not only in spring but also in summer (*C. curtissimus*, *C. kiritschenkiellus*, *C. rubi*, *C. rufofasciatus*, *C. semiargenteus*) (Lopatin, 1999).

The genus *Jaxartiolus* is endemic here. On the species-level, diversity is declining from West to East in deserts of Central and Middle Asia: 32 and 16 species of Cryptocephalini and Pachybrachini, respectively, in the Western part versus 9 and 6 species in the Eastern part (Lopatin, 1999).

Recent studies suggested that the Palaearctic-Oriental boundary inside China has a stronger south-north orientation rather than the conventionally accepted east-west orientation (see He *et al.* (2017) and references therein). Konstantinov *et al.* (2009) stated the southern border of the Palaearctic in East Asia is nearly impossible to define, particularly in China. As the fauna of all the Chinese provinces was considered in the catalogue, the composition of Palaearctic and Oriental species can be analysed again in the future in case new findings on the Palaearctic-Oriental boundary emerge.

Islands

Both ecological and geographical factors must be considered in analysing species distribution (Rossaro, 1995). Even though Cryptocephalini are phytophagous beetles, the geographical distribution of host plants is not necessarily a major factor for the present distribution. The larvae of most species are phyto-saprophagous and the adults of most species are oligophagous or polyphagous (Schöller, 1996).

Cryptocephalus (*Burlinius*) species are comparatively small, which might ease distribution by air currents. However, North-African species endemic to islands might also be relicts of formerly more widely distributed species. One species within this subgenus, *C. (Burlinius) fulvus fulvus* is the species colonizing the highest number of islands, i.e. 35 (**Table 10**). This species is developing in dune vegetation (Schöller, pers. obs.), which is an important pre-adaptation for building up stable populations in the new environments and the colonization of islands.

In this study, a correlation of species number and island surface, but no correlation with distance from the closest continental mass was found for Cryptocephalini and Pachybrachini. One reason might be, most Palaearctic islands are only five to 10 km away from the closest continental mass and few are more than 100 km away. Muscarella & Baragona (2017) did find a correlation of species number and island surface, too, but no correlation with distance from the closest continental mass as well when studying all organisms from the Sicilian islands.

Only 15 species were recorded from Taiwan and other areas, compared to 39 endemic Taiwanese species. There are only two species which occur in Taiwan as well as in Nepal (*Cryptocephalus trifasciatus*) or the far east of Russia (*C. tetradecaspilotus*) and can be considered as Palaearctic. The remaining 13 species being common with Japan or continental China are distributed there in the subtropical parts of the countries, e.g. the Ryukyu Archipelago of Japan or Yunnan and other southern provinces of China. This data suggests a radiation of Cryptocephalini species on Taiwan complemented by a number of Oriental mainland species. Consequently, the fauna of Taiwan has to be considered oriental.

The identification of hotspots of diversity and information on extinction threat, endemism or rarity are important for conservation strategies (Biondi *et al.*, 2013). Concerning the responsibility for conservation, Table 2 provides an overview on countries with a high percentage of endemic species. Cryptocephalini and Pachybrachini should be included in conservation projects in these areas.

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