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Research Article

Forty years of ground-beetle sampling in Crete. A major contribution to the Carabidae (Coleoptera, Adephaga) fauna of Crete (Greece)

Christoforos Pavlou[1*], Giannis Bolanakis[1,2*], Ljubitsa Kardaki[2], Apostolos Trichas[2]

1 *Department of Biology, University of Crete, Heraklion, Crete, Greece*

2 *Natural History Museum of Crete, University of Crete, Heraklion, Crete, Greece*

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Corresponding author: Giannis Bolanakis (bolanakisjohn@hotmail.com)

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Abstract

Carabidae (Coleoptera, Adephaga) are one of the most diverse and widely studied beetle families. Crete along with its satellite islets is a Mediterranean biodiversity hotspot that hosts a unique faunistic assemblage. In this work, we present the first part of our findings regarding the ground beetles of Crete after almost 40 years of continuous research. We report 24 species new to the Cretan biodiversity, while also comment on the distributions of rare or problematic species. Spatial and ecological data are provided for all the 29 species discussed. Most of the species recorded for the first time in Crete are linked to wetlands and, more specifically, coastal saline habitats. Therefore, issues concerning their conservation have risen, due to the pressure of the economic development of the Cretan coastline. The genera *Anaulacus* W.S. Macleay, 1825 and *Paranchus* Lindroth, 1974, as well as the species *Anaulacus ruficornis* (Chaudoir, 1850) and *Paranchus albipes* (Fabricius, 1796), are noted in this study as new taxa for the Greek fauna. Genus *Anaulacus* is also new for the fauna of the Balkan Peninsula. *Sirdenus grayii* (Wollaston, 1862) is cited with its first specified record from Greece.

Key Words

Aegean, Chrysi islet, coastal wetlands, Mediterranean

Introduction

Ground beetles (Carabidae) are one of the largest [including over 40,000 described species (Bouchard et al. 2017)] and most adequately studied (Kotze et al. 2011) beetle families. Their high numbers (both in terms of diversity and abundance) and their popularity amongst professional and amateur entomologists have produced large data compilations across space and time. Carabidae are common in many different habitats (Arndt et al. 2011), they are easily sampled, especially through pitfall trapping (Lemieux and Lindberg 1999) and display an impressive assemblage of qualitative and quantitative functional traits. Therefore, they are the central focus of numerous ecological studies and, also, they are widely used as bioindicators (Rainio and Niemelä 2003; Pearce and Venier 2006; Kotze et al. 2011; but see also Koivula (2011) as a critique).

The carabid research in Greece dates back to the beginning of 19th century, when Brullé – during the "Expédition scientifique de Morée" in 1829 – produced a detailed report for the Peloponnesian carabid fauna (amongst other insects) (Brullé 1932). Other scientists and naturalists continued Brullé's work, carrying out expeditions in the recently freed state of Greece in combination with local efforts that

* These authors contributed equally to this study.

followed the establishment of a Natural History Museum and University in Athens (Anastasiou et al. 2018). The German, Theodor Heinrich Hermann von Heldreich, (3 March 1822 – 7 September 1902), who served as a director of the National Garden of Athens for over 50 years, organised samplings in many areas including Crete, during the period 1858–1872 (Anastasiou et al. 2018). A landmark study regarding the Carabid fauna of Greece and Crete is the one of Schaum (1857), utilising material collected from various expeditions and naturalists (e.g. those of Zebe (1853) (Schaum 1857)). With this material, many species of prominent carabid beetles were reported from Crete for the first time (e.g. *Scarites buparius* (Forster, 1771), *Calosoma maderae* (Fabricius, 1775), *Apotomus rufithorax* Pecchioli, 1837, *Chlaenius festivus* (Panzer, 1796) and others). Another seminal study is that of von Oertzen (1886), compiling a massive amount of data in an exhaustive report for the Greek beetle fauna.

From a faunistic point of view, Apfelbeck's (1904) study is perhaps the second most authoritative study focusing on a holistic assessment of the Greek Carabidae, until the most recent one by Arndt et al. (2011). Between these landmark scientific efforts, most of the literature produced was of smaller scope, focusing on specific taxa, ecological groups or regions (e.g. Csiki (1914); Mařan (1934); Jeanne and Battoni (1988); Trichas (1996)). The study of Arndt et al. (2011) is a modern, updated catalogue of the Greek ground beetles after the careful research of the existing bibliography and the utilisation of specimen series from natural history museums and private collections all over Europe. Thus, it represents an updated point of reference to be compared with any future research on Greek Carabidae. After the foundation of the University of Crete (1974) and the Natural History Museum of Crete (NHMC) that followed (1981), numerous sampling efforts have yielded a voluminous dataset of the Cretan Carabidae. From the late 80s, there has been an almost uninterrupted sampling in Crete (majorly by pitfall trapping), focusing primarily on Carabidae, Tenebrionidae, Arachnids, Centipedes, Scorpions and other ground living arthropods.

Crete is the fifth largest Mediterranean island (following Sicily, Sardinia, Cyprus and Corsica), the largest Greek island (8,400 km^2) and it is located at the southernmost frontier of the Aegean Archipelago. The gradual isolation of Crete began with the formation of the Mid-Aegean Trench 12–9 Mya ((Dermitzakis and Papanikolaou 1981) but also see Papadopoulou et al. (2010) for the footprint of this split in the Aegean fauna), followed by the end of the Messinian salinity crisis at the end of Miocene (5.96–5.33 Mya, Krijgsman et al. (1999)). The re-opening of the Gibraltar strait transformed the Mediterranean Basin to a deep sea, making the isolation of Crete from its neighbouring areas more steep. Moreover, it led to the formation of Cretan palaeoislands during the Pliocene (Fassoulas 2018), which were conjoined to what is known as the today's shape of Crete during the Pleistocene (2.4 Mya); followed by the Cretan orogenesis (1.7 Mya) (Fassoulas 2018). Despite the reduction of the sea level during the glacial maxima of the Quaternary, Crete remained isolated from Cyclades and Peloponnesus, as the Cretan Sea is much deeper (Schule 1993).

The Cretan landscape is highly mountainous, defined by large and high mountain ranges extending from west to east, three of them exceeding 2,000 m of altitude. These mountains create a steep climatic variation from west to east, with aridity increasing from west to east and from north to south. Additionally, the harsh relief of Crete shaped by montane areas, gorges and caves contributes to an acute habitat heterogeneity. The main island is also surrounded by about 36 larger or smaller offshore islets. Crete is covered mostly by phrygana and maquis. Additionally, Pine forests in central and east Crete (*Pinus brutia*), Cypress forests in west Crete (*Cupressus sempervirens*) and patches of Oak (mainly kermes oak – *Quercus coccifera*). The coastline is irregular forming peninsulas, gulfs and deltas. The latter together with small stream and creeks estuaries form a diverse coastal wetland system.

Crete has undergone intensive human influence, with a long history of human presence (at least 8,000 years (Legakis et al. 1993; Poulakakis et al. 2014)). The upsurge in tourism, agriculture intensification and the urbanisation are still shaping the contemporary assemblages of the Cretan biota and, naturally, the ground beetles do not pose an exception. For example, intensive grazing on the mountains of Crete, one of the oldest human activities on the island (Rackham and Moody 1996), may have a negative footprint on the Carabidae assemblages of the Cretan shrublands (Kaltsas et al. 2013). Additionally, it appears that urban areas have been increased by 16.8% in the lowlands of Crete during the span of twenty years (1998–2018) (Bolanakis et al. 2024).

Crete's faunistic composition is strongly influenced by European and Asian (near-East and/or middle-East) elements. Besides its property as a biogeographical "sink" between Europe and Asia, the island owes an important part of its biodiversity to *in situ* speciation (Gittenberger 1991; Trigas et al. 2013; Assing 2019; Trichas et al. 2020; Willemse et al. 2023) driven by its complex geological history and its diverse milieu of different habitats.

The main objective of this study is to present new records of identified Carabid species and genera for the island of Crete (and its satellite islets) compiled throughout a sampling period of almost 40 years. Moreover, grounded on the annotated list of Arndt et al. (2011), we establish the presence of some species in Crete with detailed data and also comment on strange distributions of rare and/or problematic species.

Materials and methods

Samplings

Specimen collection was part of a 40-year sampling period that was carried out by the Natural History Museum of the University of Crete. The surveys included both pitfall trapping and hand collection that were performed by NHMC research staff and several students of the University of Crete (Trichas et al. 2008). These surveys were part of BSc, MSc and PhD studies, as well as several research projects and environmental monitoring programmes (Trichas et al.

2008). They aimed mostly at the epigeal fauna of Crete and the main research goals of these studies were the description of diversity, phenology and biogeography of several ground-dwelling beetle families (Carabidae, Tenebrionidae, Staphylinidae, etc.) (Trichas et al. 2008). After the mid-1990s, Gnaphosidae and other ground spider families were also studied, while, in the late 2000s, chilopods, diplopods and isopods were added in the list. Details on sampling protocols (operation time of traps, dates, number of traps, trap dimensions, chemicals etc.) and trap efficiency are discussed extensively in the following publications: Trichas et al. (2008); Kaltsas and Simaiakis (2012); Kaltsas et al. (2013); Salata et al. (2020).

During these surveys, arthropod sampling occurred in many different habitats across all of Crete and its surrounding islets. Sampling sites were located within areas with phrygana, maquis, montane vegetation or with mosaic formations including various types of vegetation (e.g. Kaltsas et al. (2013); Salata et al. (2020)). Additionally, sampling was performed at several wetlands (e.g. estuaries, rivers, dams, saline lakes, mountainous temporary ponds), pine forests (*Pinus brutia*), sand dunes and mountain peaks. Vegetation in phrygana was mostly comprised of *Sarcopoterium spinosum*, *Thymbra capitata*, *Genista acanthoclada*, *Calicotome villosa*, *Phlomis* spp., *Cistus* spp., *Euphorbia acanthothamnos* and *Ballota pseudodictamnus* (Kaltsas et al. 2013; Salata et al. 2020). Maquis vegetation included mostly *Pistacia lentiscus*, *Juniperus phoenicea*, *Quercus coccifera*, *Arbutus unedo*, *Ceratonia siliqua* and *Euphorbia dendroides* (Kaltsas et al. 2013; Salata et al. 2020). Vegetation in wetlands was mostly comprised of *Arthrocnemum* spp., *Salicornia* spp., *Juncus* spp. and *Phragmites* spp., while, in sand dunes, *Pancratium maritimum*, *Ammophila* spp., *Elytrigia* spp., *Euphorbia* spp., *Eryngium* spp. and *Anthemis* spp. were amongst the present plant species.

Morphological species identification

All carabid beetles were morphologically identified using established identification keys (Trautner and Geigenmüller 1987; Arndt et al. 2011) and articles on species descriptions or revisions. The identification was accomplished via examination of several taxonomic characters, as they were described in the above-mentioned identification keys. In many cases, the species identification was verified via examination of male genitalia.

Results

Cicindelinae Latreille, 1802: Megacephalini Laporte, 1834

1. *Grammognatha euphratica* Latreille & Dejean, 1822

Fig. 1

Habitat and general distribution. *Grammognatha euphratica* has a wide distribution extending from Morocco and southern Spain over northern Africa, parts of the eastern Mediterranean, Arabia and Central Asia as far as Pakistan and northern India (Cassola 1981; Franzen 2001). The species is found in salt marsh and salt meadow habitats, mainly active at hours of twilight (Trautner and Geigenmüller 1987; Arndt et al. 2011) or night (Cassola et al. 2014). Within the eastern Mediterranean, more or less recent distribution data exist from Cyprus, Turkey, Israel and Egypt (Franzen 2001; Şekeroğlu and Aydin 2002; Austin et al. 2008), while recently, the beetle has been discovered on the island of Sant'Antioco in Italy (Cassola et al. 2014). In Greece, it is also present on the island of Rhodes ((Horn 1910) without exact locality); however, this occurrence has not been reconfirmed by the latest known surveys of Wiesner (1990, 1994). The only known locality on Crete until the present study was that of Palaiokastron, in east Crete (Cassola 1981).

Material examined. • Heraklion: Aposelemis River, 35.280642°N, 25.358629°E, 131 m elev., 1.VI.1989, handpicking, 1 spm, leg. Trichas A. (NHMC); • Aposelemis River mouth 35.335003°N, 25.330901°E, 28.V.2015–30.VII.2015, pitfall traps, 9 spms, leg. Pavlou Chr. (NHMC); • same data, but 30.VII.2015–27.XI.2015, 2 spms; • Kouremenos Beach wetland, 35.204385°N, 26.271490°E, 13.IV.2022–10.VI.2022, pitfall traps, 4 spms, leg. Bolanakis G. (NHMC); • same data, but 13.IV.2022, handpicking, 1 spm, leg. Pavlou Chr. (NHMC); • Chrysi isl., Vages Beach, salt-lake, 34.874799°N, 25.728071°E, 23.III.2023–13.VII.2023, pitfall traps, 2 spms, leg. Bolanakis G. (NHMC).

Comments. Cassola (1981) was the first author to report *Grammognatha euphratica* from Crete ("Palaiokastron", east Crete or Palaikastro/Palekastro – not to be confused with the tautonym in central Crete). Both this record and the ones from Rhodes (Cassola 1973) needed confirmation according to Franzen (2001) and Arndt et al. (2011). For example, the record from Rhodes was never recovered during the surveys of Wiesner in 1990 and 1994 (Franzen 2001). In essence, the records presented here are the first of this rare and fragmentarily distributed beetle from Crete in four decades. We confirm the species' presence in Crete and also expand its distribution in a southern satellite islet of Crete, Chrysi. All our records are from salt-lakes and are confined in the central-east part of the island. Moreover, the Aposelemis specimens represent the westernmost findings of this species on Crete, pointing to an eastern origin of the species' dispersal.

Carabinae Latreille, 1802: Carabini Latreille, 1802

2. *Calosoma* (s.str.) *inquisitor* (Linnaeus, 1758)

Fig. 2A

Habitat and general distribution. *Calosoma inquisitor* has a wide distribution in Europe, North Africa, Anatolia, Middle and Far East (Häckel 2017). It is a forest dwelling species, frequently spotted to prey on caterpillars in trees and bushes (Trautner and Geigenmüller 1987; Arndt et al. 2011).

Figure 1. *Grammognatha euphratica* in its natural habitat.

Material examined. • Heraklion: Rouvas Forest by the monastery, 35.169894°N, 24.922200°E, 1100 m elev., 6. V.1990–27.XI.1990, pitfall traps, 3 spms, leg. Trichas A. (NHMC); • Psiloritis, Nida plateau SW slopes, 35.196594°N, 24.821603°E, 1762 m elev., 13.I.1991, 1 spm, handpicking, leg. Trichas A. (NHMC); • Rethymnon: Psiloritis, Akolita plateau in sub-alpine phrygana, 35.198692°N, 24.793800°E, 1900 m elev., 6.V.1990–13.I.1991, pitfall traps, 9 spms, leg. Trichas A. (NHMC); • Psiloritis, Akolita plateau, 35.197291°N, 24.791999°E, 1900 m elev., 14.IV.2000–2.VII.2000, 120 spms, pitfall traps, leg. Chatzaki M. (NHMC); • same data, but: 31.X.2000–12.VI.2001, 70 spms; same data, but: 35.209192°N, 24.792997°E, 2213 m elev., 16 spms.

Comments. Csiki (1914), summarising all previous classic works on Cretan Coleoptera fauna in his "Fauna Coleopterorum Insulae Cretae", reported only *C. sycophanta* (Linnaeus, 1758) and *C. maderae* from Crete. *Calosoma inquisitor* (Linnaeus, 1758) is reported from Crete for the first time by Breuning (1927), from specimens deposited in the collections of the Natural History Museum of Vienna ("Mus. Vindob."). Later on, Jeannel (1941) listed again *C. inquisitor* in Crete ("Crète et îles de la mer Égée") without any further details, most probably based on Breuning's references. Trichas (1996), provided fresh *C. inquisitor* specimens from Ida Mt., including also the above references as valid, in his doctoral dissertation of South Aegean Archipelago ground-dwelling beetles. More recently, Arndt et al. (2011) also listed *C. sycophanta* and *C. maderae* on Crete, but excluded *C. inquisitor* from the island. Finally, *C. inquisitor* is included in the appendix of Kaltsas et al. (2013), albeit this is an ecological work, so the species references could easily be overlooked when compiling faunal records. Moreover, as no other (specimen based) records for this taxon in Crete have been presented in the international literature between 1927–2013, this is the first detailed cataloguing of *C. inquisitor* on the island for almost a century. Clearly, *C. inquisitor* forms robust populations in the mountain of Psiloritis (Ida Mt.), especially on higher altitudes, found both in forests and mountain shrublands. Additionally, although there are dozens of specimens of *C. sycophanta* in the NHMC collections, from almost all larger Cretan Mountain massifs (Ida, Dikti, Thrypti – except Lefka Ori Mts. where only *C. maderae* have been observed twice, see below), *C. inquisitor* seems to be confined only on the central Cretan massif (Ida).

3. *Calosoma* (*Campalita*) *maderae* (Fabricius, 1775)

Fig. 2B

General distribution. *Calosoma maderae* has a wide distribution in Europe, North Africa and Near and Middle East (Häckel 2017).

Material examined. • Chania: Chora Sfakion, 35.201518°N, 24.138031°E, 40 m elev., 16.V.2019, handpicking, 1 spm, leg. Alexandrakis G. (NHMC); • Lefka Ori, Niato plateau, 35.29416°N, 24.14765°E, 1226 m elev., pitfall traps, 20.VI.2019–31.VII.2019, 1 spm, leg. Bolanakis G. (NHMC).

Comments. The taxonomic status of this species and its close relatives is ambiguous, with a wide discussion of the species/subspecies rank amongst the different taxa (see Roeschke (1900); Breuning (1927); Jeannel (1941)). Herein, we follow Bruschi (2010) who suggests a lumping approach for the different taxa of the *C. maderae* group, as well as the inclusion of

C. auropunctatum as a synonym of *C. maderae s. str.* (https://www.calosomas.com/Campalita/cal_maderae.html).

The first record of *C. maderae* in Crete is that of Schaum (1857), from material collected by Zebe. Zebe also managed to collect *C. maderae* from the island of Syros "Syra" at the same time (Schaum 1857). Apfelbeck (1904) cites these references and adds two more, both from the volcanic island of Milos. Herein, we report new specimens of *C. maderae* from Crete for the first time in more than 150 years. This is indicative of its rarity, which is both distributional (until now the only known localities of the species in Crete are confined on Lefka Ori mountain massif) and in terms of abundance (only two specimens), in contrast to the other two *Calosoma* spp. of Crete which exhibit far greater abundances (and a broad distribution in *C. sycophanta* case). The species was found in a mountain shrubland (Niato plateau) with *Berberis cretica* and *Quercus coccifera*, as well as to an urban environment (Chora Sfakion), near the sea level.

4. *Carabus* (*Pachystus*) *graecus trojanus* Dejean, 1826

Fig. 2C

Habitat and general distribution. *Carabus graecus trojanus* is endemic to Greece (Arndt et al. 2011). The subspecies, as the other members of *C. graecus* Dejean, 1826, live in a broader range of habitats, found in phrygana, maquis, urban areas and forests.

Material examined. • Heraklion: Heraklion Port, 35.343391°N, 25.153453°E, 1 m elev., 9.X.1989, hand-picking, 1 spm, leg. Trichas A. (NHMC).

Comments. Turin et al. (2003) repeatedly mentioned that *C. g. trojanus* occurs in Crete (although in p. 48, they mark Crete with "?"). Trichas (1996) mentioned that the original record of *C. g. trojanus* in Crete by Cecconi (1895) from Chania (as *C. trojanus*) was most likely erroneous. Nevertheless, Trichas (1996) himself found one specimen of *C. g. trojanus* in Heraklion port, which he reported, that differs clearly from the Karpathos island subspecies, i.e. *C. t. oertzeni* Ganglbauer, 1888 – now considered also as a separate subspecies of *C. graecus* (Häckel, 2017). Thus, *C. g. trojanus* has been recorded at least twice from Crete in the span of a century. Given the extremely high abundances of the endemic *Carabus* (*Procrustes*) *banonii* Dejean, 1830 throughout the island (thousands of specimens in the NHMC collections) in almost all habitats; and the systematic and continuous samplings with pitfall traps from the late 80s till today, we believe that the records of *C. g. trojanus* in Crete derive from random and not stable dispersal incidents (anthropochorous). The absence of a second *Carabus* lineage in Crete is an interesting biogeographical problem, since Crete is large enough to host more than one *Carabus* species, whereas other, much smaller islands host two or more species (e.g. Kythira, Karpathos, Rhodes (Trichas 1996)).

Brachininae Bonelli, 1810: Brachinini Bonelli, 1810

5. *Brachinus* (s.str.) *plagiatus* Reiche, 1868

Figs 2D, 5A

Habitat and general distribution. *Brachinus plagiatus* is a Turano-Mediterranean species (Hrdlička 2017). The species is associated with saline fields and marshes (Nyilas 1994), but also freshwater lakes and ponds (Austin et al. 2008).

Material examined. Heraklion: • Almyros estuary, salt-marsh, 35.338506°N, 25.061404°E, 2 m elev., 3.V.2012–3.VI.2013, pitfall traps, 1 spm, leg. Aspradaki E. (NHMC); • same data, but in phrygana.

Comments. *Brachinus plagiatus* was recorded for the first time from Greece (Corfu, Attiki, Aetoloakarnania and Zakynthos) by von Oertzen (1886) as *B. bombarda*. Peloponnese (Tayget, Nauplio) was later on added in the Greek distribution of the species (Apfelbeck 1904). To our knowledge, this is the first record of this species in Crete. The species was found in a saline environment in the marsh formed by the delta of Almyros estuary. The species' distribution in Crete requires further investigation. Whether this is a recent dispersal or an old relictual presence, is unclear.

5. *Brachinus* (s.str.) *psophia* Audinet-Serville, 1821

Figs 2E, 5B

Habitat and general distribution. *Brachinus psophia* has a wide distribution over Europe, North Africa to the Far East (Arndt et al. 2011). It is a hygrophilous, wetland species, that is also common in croplands (Drmić et al. 2016; Lemic et al. 2017).

Material examined. • Chania: Falassarna wetland, 35.479700°N, 23.575000°E, 2 m elev., 15.V.2015–9.VII.2015, pitfall traps, 20 spms, leg. Pavlou Chr. (NHMC); • same location data, but: 9.VII.2015–2.XI.2015, 7 spms

Comments. *Brachinus psophia* was recorded for the first time from Greece (Corfu, Aetoloakarnania, Peloponnese) by Apfelbeck (1904). Arndt et al. (2011) accept this species for Greece (Ionian islands, Greek mainland and Peloponnese). The extant literature suggests that this is the first record of *B. psophia* in Crete. The species was only found in Falassarna Bay indicating a dispersal event from a western locality, perhaps Peloponnese. Dispersals from western areas confined in the west coastline of Crete are also recovered for other Carabidae species (e.g. *Scarites procerus eurytus* Fischer von Waldheim, 1828) and other taxa (e.g. *Tentyria grossa* Besser, 1832, Tenebrionidae (Trichas 1996)). The species was found in a coastal salt-marsh.

Scaritinae Bonelli, 1810: Clivinini Rafinesque, 1815

6. *Clivina* (s.str.) *ypsilon* Dejean & Boisduval, 1829

Fig. 2F

Habitat and general distribution. *Clivina ypsilon* has a wide distribution in Europe, North Africa, Near and

Middle East (Balkenohl 2017). The species occurs in saline, surface waters (Trautner and Geigenmüller 1987; Arndt et al. 2011)

Material examined. • Chania: Kournas Lake, north bank, 35.336232°N, 24.274637°E, 8.III.2018–15.V.2018, pitfall traps, 1 spm, leg. Amyntas A. (NHMC); • Heraklion: Almyros Estuary, salt-marsh, 35.338506°N, 25.061404°E, 2 m a.s.l, 28.XI.2012–30.V.2013, pitfall traps, 2 spms, leg. Aspradaki E. (NHMC).

Comments. *Clivina ypsilon* was noted for the first time in Greece by von Oertzen (1886). Apfelbeck (1904) reports again the species providing two localities (Phaleron, in Attica and Thessaly Province). Arndt et al. (2011) accept this species for Greece, but only for the Greek mainland. This constitutes the first documentation of *C. ypsilon* in Crete. The species was found in two quite different habitats, i.e., in a salt-marsh and in the sandy banks of a freshwater lake (Kournas).

Scaritinae Bonelli, 1810: Scaritini Bonelli, 1810

7. *Scarites* (s.str.) *procerus eurytus* Fischer von Waldheim, 1828

Fig. 2H

Habitat and general distribution. *Scarites p. eurytus* has a wide Turano-Mediterranean distribution (Balkenohl 2017). The species occurs in swamp habitats (Arndt et al. 2011).

Material examined. • Chania: Falassarna wetland, 35.479700°N, 23.575000°E, 2 m elev., 15.V.2015–9.VII.2015, pitfall traps, 18 spms, leg. Pavlou Chr. (NHMC).

Comments. The species is known from the Greek Mainland and the Aegean (Arndt et al. 2011). More specifically the species was reported for the first time in Greece by von Oertzen (1886) from Andros and Naxos, while the records from the Greek mainland are more recent (Arndt et al. 2011). To our knowledge, this is the first record from Crete. A larger population was spotted in Falassarna Bay, west of Chania. The habitat consists of a small coastal salt-marsh inside a sand-dune system and fits the description given by Arndt et al. (2011) (swampy habitats) for the species' suitable habitat. It is one of the few areas in Crete combining a marsh habitat with a sand dune system. This could explain the absence of this species in other parts of the island (albeit the extensive research in marshes and coastal deltas). Another explanation could be that the observed population is a result of a dispersal from a western region, something that has been also observed for other beetles found in the west coastline of Crete (Trichas 1996). We consider this scenario less plausible since *S. p. eurytus* has a wide distribution in all the areas surrounding Crete, although, a stochastic dispersal event from the west cannot be excluded. The species is not yet recorded from Peloponnese, but our record encourages more research regarding the species' distribution in the southern parts of Greek Mainland. The aggressive touristic development in the wider area of Falassarna Bay and especially around the coastline could pose a serious threat for the species' population in Crete, even leading to extirpation events.

8. *Scarites* (*Scallophorites*) *buparius* (Forster, 1771)

Fig. 2I

Habitat and general distribution. *Scarites buparius* has a Mediterranean distribution, occurring in south Europe and North Africa (Balkenohl 2017). The species is found in coastal sand habitats (Arndt et a. 2017).

Materials examined. • Chania: Platanias, Platanias River mouth 35.336232°N, 24.274637°E, 1 m elev., 28.V.2021–4.VIII.2021, pitfall traps, 1 spm, leg Bolanakis G. (NHMC).

Comments. *Scarites buparius* was first mentioned from Crete in 1857 as *S. pyracmon* (Schaum 1857) from specimens collected by Zebe during his expedition to the island in 1853. This record seems to be the source for all the following references (von Oertzen 1886; Apfelbeck 1904; Csiki 1914; Arndt et al. 2011). In all these references, there is no locality given for the species in Crete. Schaum (1857) described the habitat where Zebe found the specimens, but no precise locality name was given. In this study, we report the first detailed locality for the species in Crete, a coastal wetland that fits perfectly with the habitat described by Schaum (1857) and Arndt et al. (2011). Moreover, we provide concrete data for the species' existence in Crete for the first time after one and a half centuries. Despite *S. buparius* being a typical Mediterranean species and the exhaustive samplings that we carried out in the coastal wetlands of Crete, we only managed to obtain one specimen, indicative of the species rarity in the island. Further research is required in order to clarify the species' distribution in Crete. Unfortunately, when we revisited the small delta where the species was found, the sandy coast had been pressed and cleared to be exploited for recreational activities. Wood and plant debris, as well as stones have been dumped in the small dune where the species was found and we did not manage to find any new specimens. Therefore, further sampling effort is required in order to reconfirm the presence of the *S. buparius* in Platanias River mouth.

Trechinae Bonelli, 1810: Pogonini Laporte, 1834

9. *Sirdenus* (*Syrdenopsis*) *grayii* (Wollaston, 1862)

Figs 2G, 5C

Habitat and general distribution. *S. grayii* is an Afrotropical-Mediterranean species, mainly found in Cyprus, North Africa and Near East, but also southern Europe (Austin et al. 2008; Bousquet 2017b). The species dwells in saline wetlands (Austin et al. 2008), burrowing in endogean galleries (Saulleda 1985; Machado 1992).

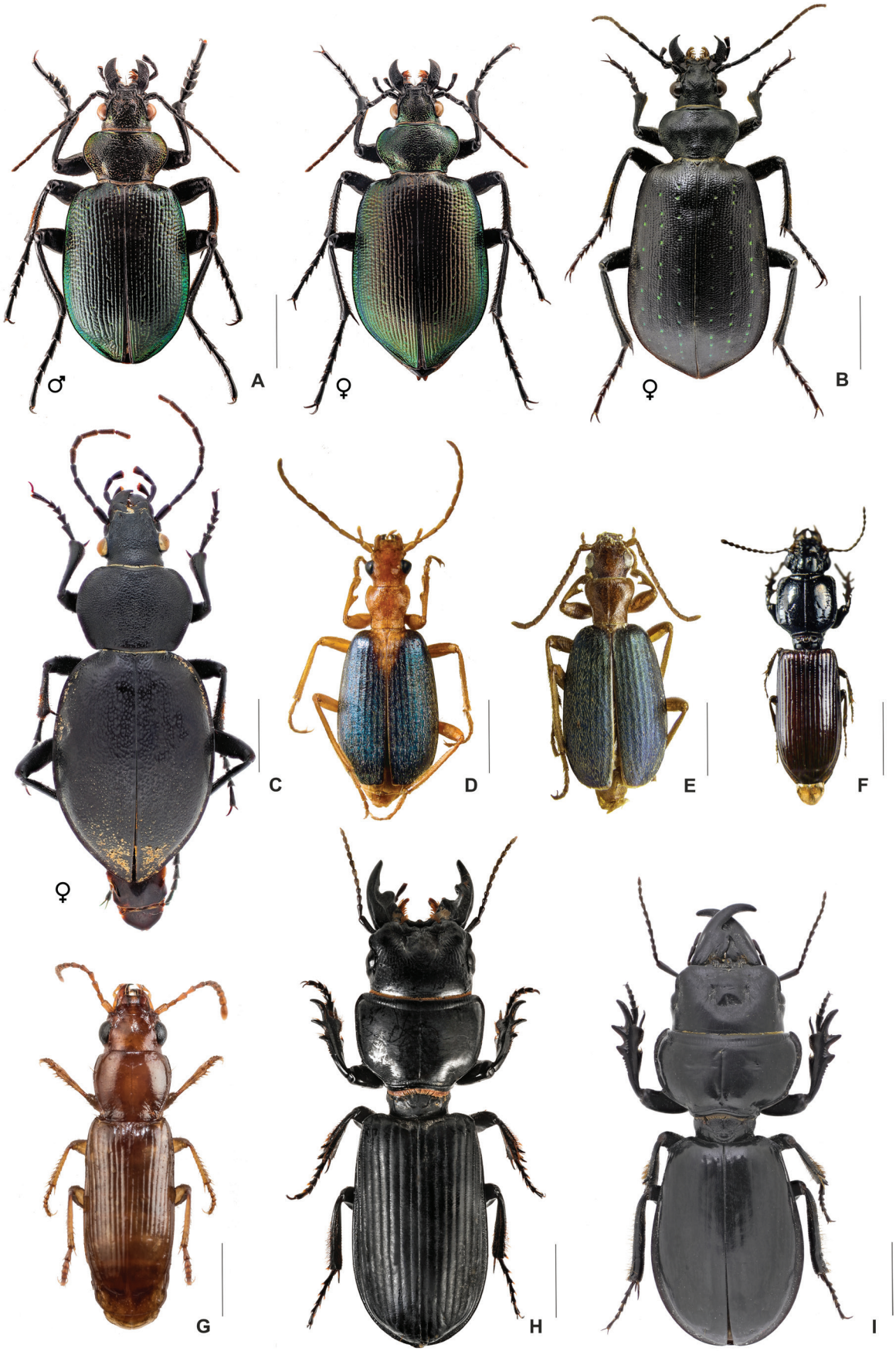

Figure 2. A. *Calosoma inquisitor*; **B.** *Calosoma maderae*; **C.** *Carabus graecus trojanus*; **D.** *Brachinus plagiatus*; **E.** *Brachinus psophia*; **F.** *Clivia ypsilon*; **G.** *Sirdenus grayii*; **H.** *Scarites eurytus*; **I.** *Scarites buparius.* Scale bars: 5.5 mm (**A**); 7.75 mm (**B**); 5 mm (**C**); 3 mm (**D**); 2.5 mm (**E**); 1.75 mm (**F**); 1.1 mm (**G**); 6.4 mm (**H**); 6.8 mm (**I**).

Material examined. • Lasithi: Xerokampos salt-lake (phrygana) 35.050979°N, 26.240301°E, 2 m elev., 5.VIII.2015–26.XI.2015, pitfall traps, 1 spm, leg. Pavlou Chr. (NHMC); • Chrysi isl., Vages Beach salt-lake, 34.874799°N, 25.728071°E, 1 m elev., 23.III.2023–13.VII.2023, pitfall traps, 62 spms, leg. Bolanakis G. (NHMC).

Comments. The genus *Sirdenus* was mentioned for a first time in Greece in Arndt et al. (2011) by a specimen of *S. filliformis* from "Griechenland, Attica", deposited in the collection of Museum für Naturkunde, Berlin. Arndt et al. (2011) were critical of the validity of this specimen. Thus, our record is the first concrete record of *S. grayii* in Crete and consequently Greece, confirming the presence of the genus in Greece. Naturally, the species was first discovered in a salt-lake (the largest of Crete) at the easternmost coastline of the island (Xerokampos), by a single specimen in 2015. However, we re-sampled this locality many times and never managed to re-collect this species. According to Matalin and Makarov (2008), *S. grayii* is a rare species, difficult to encounter. In 2023, we found a large population of *S. grayii* (62 specimens) in Chrysi, a southern satellite islet of Crete. The species was found in a small, temporary salt-lake, near a southern beach of the islet. The species has not been spotted in other salt lakes and marshes in the west, central and north parts of Crete (e.g. Falassarna, Almyros, Tympaki). The current known distribution of the species in Crete indicates an eastern origin, echoing the biogeographical remarks of Koch (1948) for a dispersal path as such.

Harpalinae Bonelli, 1810: Chlaeniini Brullé, 1834

10. *Chlaenius* (*Epomis*) *dejeanii* (Dejean, 1831)

Fig. 3A

Habitat and general distribution. *Chlaenius dejeanii* is an East European-Mediterranean species with its distribution reaching Middle East (e.g. Syria, Iraq) (Arndt et al. 2011; Kirschenhofer 2017).

Material examined. • Heraklion: Aposelemis, Sfentyli Dam, 35.234204°N, 25.420799°E, 211 m elev., 24.III.2017–25.IV.2017, pitfall traps, 1 spm, leg. Amyntas A. (NHMC); • same data but 25.IV.2017–30.V.2017, 1 spm; • same data, but 30.V.2017–19.X.2017, 21 spms; • Tympaki, salt-lake, 35.075001°N, 24.745918°E, 2 m elev., 15.IV.2022–2.VI.2022, pitfall traps, 4 spms, leg. Bolanakis G. (NHMC); • same data, but 2.VI.2022–4.VII.2022, 2 spms; • same data, but 15.IV.2022, handpicking, 1 spm; • Lasithi: Bramiana artificial lake, 35.043096°N, 25.706700°E, 76 m elev., 4.I.1999–3.III.1999, pitfall traps, 1 spm, leg. Papadimitrakis M. (NHMC); • same data, but 3.III.1999–4.V.1999, 13 spms; • same data, but 4.V.1999–22. VII.1999, 13 spms.

Comments. *Chlaenius dejeanii* is a prominent and scarce (Austin et al. 2008) carabid that was first reported from Greece by Schaum (1857) from Peloponnese ("Morea") and Athens. Apfelbeck (1904) expanded the distribution of the species beyond the Greek mainland in the Ionian islands, by the reporting of specimens from Corfu. This is the first time the species is recorded from Crete. Several populations were captured through pitfall trapping, in the central-east part of the island, from the north (e.g. Aposelemis) to the south (e.g. Tympaki). The species was found in natural (Tympaki) and artificial wetlands (Aposelemis, Bramiana), with different gradients of salinity.

Harpalinae Bonelli, 1810: Masoreini Chaudoir, 1871

11. *Anaulacus* (*Aephnidius*) *ruficornis* (Chaudoir, 1850)

Figs 3B, 5D

Habitat and general distribution. *A. ruficornis* occurs in Near and Middle East (Bousquet 2017a), barely reaching Europe, only from its north-eastern region bordering with Asia (e.g. south Russia) (Bousquet 2017a). This rare (Austin et al. 2008) species dwells in wetlands and coastal habitats with fresh or saline water (Assmann et al. 2015).

Material examined. • Chania: Frangokastello wetland, 35.184786°N, 24.227804°, 4 m elev., 23.IV.2017–8.VI.2017, pitfall traps, 4 spms, leg. Amyntas A. (NHMC).

Comments. This is the first record of the genus *Anaulacus* W.S. Macleay, 1825 from Greece, establishing its presence in the southern parts of Europe. Notably, *A. ruficornis* was found in the south-western part of Crete, while a more eastern locality would be more expected given the species' distribution. We should highlight that Egypt is excluded from the species' distribution in Bousquet (2017a), while it is included in Assmann et al. (2015) who cite an old reference (Alfieri 1976). More research is recommended in order to clarify whether the species also occurs in the Greek mainland and the Aegean, as well as to clarify its distribution in Crete.

12. *Masoreus* (s.str.) *aegyptiacus* Dejean, 1828

Fig. 3C

Habitat and general distribution. *Masoreus aegyptiacus* is an East-Mediterranean species (Bousquet 2017a). The species occurs in sand-dune habitats (Assmann et al. 2015).

Material examined. • Lasithi: Chrysi isl., north beach salt-lake, 34.878045°N, 25.697966°E, 1 m elev., 15.VI.1992, handpicking, 2 spms, leg. Lymberakis P. (NHMC); • Chrysi isl., Vages Beach, salt-lake, 34.874799°N, 25.728071°E, 1 m elev., 23.III.2023–13.VII.2023, pitfall traps, 39 spms, leg. Bolanakis G. (NHMC); • Koufonisi isl., near salt-marsh, 34.935084°N, 26.140310°E, 60 m elev., 16.XI.1997, handpicking, 2 spms, leg. Trichas, A. (NHMC); • Xerokampos sand dunes, 35.049891°N, 26.239803°E, 1 m elev., 1.IV.2015–31.V.2015, pitfall traps, 4 spms, leg. Kyriakouli Chr. (NHMC); • same data, but 31.V.205–5.VIII.2015.

Comments. The genus *Masoreus* Dejean, 1821 has been known from Greece since the 19th century (von Oertzen 1886) by the species *M. wetterhallii* (Gyllenhal, 1813). *Masoreus aegyptiacus* has only recently been

reported from Greece (Wrase 2009) by some specimens from Peloponnese. Arndt et al. (2011) include only Peloponnese in the species' distribution for Greece; thus, this is the first time the species is recorded from Crete. Till now, the species has been spotted in three localities, one in the eastern-most part of the island (Xerokampos) and two in a couple of south-eastern satellite islands of Crete (Chrysi and Koufonisi). This may indicate an eastern origin, which is to be expected given the species east-Mediterranean distribution (Bousquet 2017a). Assmann et al. (2015) report that this species prefers sand-dune habitats. In Crete, we observed a clear preference for coastal salt lakes/marshes, like those of Xerokampos and Chrysi.

Harpalinae Bonelli, 1810: Lebiini Bonelli, 1810

13. *Cymindis* (*Arrhostus*) *andreae* Ménétriés, 1832
Figs 3D, 5E

Habitat and general distribution. *Cymindis andreae* is an eastern species. The larger part of its range extents to Near and Middle East, while it is also known from North Africa (Egypt) and Eastern Europe (Kabak 2017).

Material examined. • Lasithi: Chrysi isl., north beach salt-lake, 34.878045°N, 25.697966°E, 1 m elev., 17.V.1994, handpicking, 3 spms, leg. Trichas A. (NHMC); • Chrysi isl., Vages Beach, salt-lake, 34.874799°N, 25.728071°E, 1 m elev., 23.III.2023–13.VII.2023, pitfall traps, 6 spms, leg. Bolanakis G. (NHMC).

Comments. In Greece, *Cymindis andreae* is only known from the Aegean (Arndt et al. 2011). In fact, the only record of this species in Greece (Rhodes) dates back to 1935 (Schatzmayr 1935). This is the first record of *C. andreae* in Crete. The species was found in Chrysi islet in 1994 (northern salt-lake) (leg. Trichas) and recorded again in 2023 (leg. Bolanakis), in the southern salt-lake of Chrysi (Vages Beach). Since the southern/eastern coastal salt-lakes of Crete have been intensively sampled, the species presence in the island of Crete is unlikely, although more research is required. The species' origin is obscure. Crete is very poor in African taxa; thus, it is more likely that the species is an eastern dispersal, a common pattern for species restricted in the eastern parts of the island (or its eastern satellite islets) (Koch 1948; Trichas 1996). We confirm the presence of the species in Greece and encourage further research for this species in the eastern part of the Aegean.

14. *Cymindis* (s.str.) *ornata* Fischer von Waldheim, 1823
Fig. 3E

Habitat and general distribution. *Cymindis ornata* is a West Ponitc species (Kabak 2017). The species' habitat preferences vary. We have found it in river mouths and coastal phrygana, while Teofilova et al. (2015) note that the species occurs strictly in arid, open environments.

Material examined. • Heraklion: Aposelemis River mouth, 35.334994°N, 25.330875°, 1 m elev., 30.VII.2015–27.XI.2015, pitfall traps, 1 spm, leg. Pavlou Chr. (NHMC); • Rethymnon: Moni Preveli River, phrygana at the west slopes above the beach, 35.151797°N, 24.472496°, 22 m elev., 25.VI.1996–28.VIII.1996, pitfall traps, 1 spm, leg. Lymberakis P. (NHMC); • Petres River mouth, 35.350988°N, 24.358007°E, 1 m elev., 15.V.2015–9.VII.2015, pitfall trap, 2 spms, leg. Pavlou Chr. (NHMC).

Comments. *Cymindis ornata* is reported in Greece from the Greek mainland (excluding Peloponnese) and Aegean (Schatzmayr 1935; Arndt et al. 2011). To our knowledge, this is the first record of this species in Crete. It is common for Balkan species or genera to occur in Crete, although such species are usually restricted in the west part of the island (Trichas 1996). In this case, all the records are in the central Crete (both south and north).

15. *Trichis maculata* Klug 1832
Fig. 3F

Habitat and general distribution. *Trichis maculata* is a Turano-Mediterranean species (Kabak 2017). The species occurs in coastal saline habitats (Arndt et al. 2011).

Material examined. • Chrysi isl., Vages Beach, salt-lake, 34.874799°N, 25.728071°E, 1 m elev., 23.III.2023–13.VII.2023, pitfall traps, 6 spms, leg. Bolanakis G. (NHMC).

Comments. *Trichis maculata* has been reported from Greece by von Oertzen (1886) from Attiki. In his 1904 report, Apfelbeck also cites *T. maculata* from Attiki, attributing this information to Krüper. In addition to the record of Apfelbeck (1904), no further documentation pertaining to this species occurs for Greece. This is the first documentation of the genus in Greece for a period of 150 years and, moreover, this signifies the inaugural record of the species in Crete. *Trichis maculata* was found in a small salt-lake in the southern coast of Chrysi islet. The species occurs in North Africa and near East (Kabak 2017) and has not been found yet anywhere else in Crete. Further research is required in order to confirm whether the species is also present in other parts of Crete or Greece.

Harpalinae Bonelli, 1810: Harpalini Bonelli, 1810

16. *Anisodactylus* (*Pseudodichirius*) *intermedius* Dejean, 1829
Fig. 3G

Habitat and general distribution. *Anisodactylus intermedius* is a Turano-Mediterranean species (Arndt et al. 2011). The species is found in wetlands (Austin et al. 2008).

Material examined. • Chania: Falassarna wetland, 35.479700°N, 23.575000°E, 2 m elev., 9.VII.2015–2.XI.2015, pitfall traps, 1 spm, leg. Pavlou Chr. (NHMC).

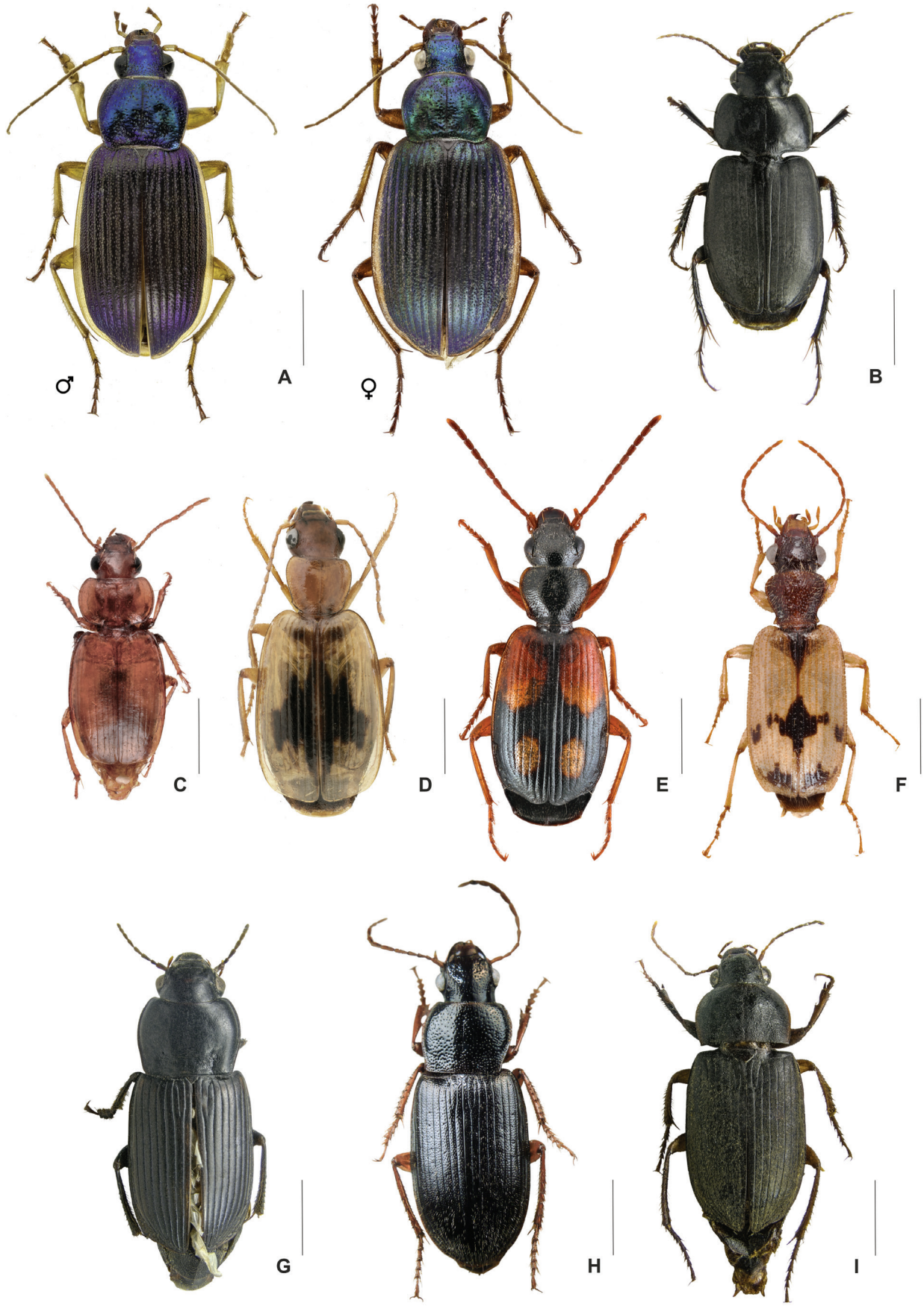

Figure 3. A. *Chlaenius dejeanii*; **B.** *Anaulacus ruficornis*; **C.** *Masoreus aegyptiacus*; **D.** *Cymindis andreae*; **E.** *Cymindis ornata*; **F.** *Trichis maculata*; **G.** *Anisodactylus intermedius*; **H.** *Ophonus puncticeps*; **I.** *Parophonus hirsutulus*. Scale bars: 4 mm (**A**); 1.75 mm (**B**); 1.75 mm (**C**); 2.55 mm (**D**); 2 mm (**E**); 1.8 mm (**F**); 3 mm (**G**); 2.2 mm (**H**); 2.1 mm (**I**).

Comments. *Anisodactylus intermedius* was reported for the first time in Greece by v. Oertzen (1886) from Corfu and the Greek mainland (Aetoloakarnania, Veluchi). Arndt et al. (2011) also report Peloponnese in the species' distribution. To our knowledge, this is the first time *A. intermedius* has been reported from Crete. The species was recorded from Falassarna, in the westernmost coast of the island. Despite the extensive sampling throughout Crete, the species remains known only from the Falassarna area. Hence, we assume that this may be a recent dispersal event from Peloponnese.

17. *Ophonus* (*Metophonus*) *puncticeps* Stephens, 1828

Figs 3H, 5F

Habitat and general distribution. *Ophonus puncticeps* has a Turano-Mediterranean distribution, extending into Europe, Near and Middle East, as well as North Africa (Morocco) (Kataev and Wrase 2017). The species has also been introduced in North America (Kataev and Wrase 2017). *Ophonus puncticeps* is an euryecous species, occurring in open fields and in anthropogenic areas (Lindroth 1968; Nováková and Šťastná 2014).

Material examined. • Heraklion: Almyros River near phrygana, 35.334000°N, 25.048799°E, 3 m elev., 3.VI.2012–1. VIII.2012, pitfall traps, 1 spm, leg. Aspradaki E. (NHMC); • Almyros River, in phrygana and cultivations, 35.333509°N, 25.048097°E, 2 m elev., 1.VIII.2012–28.XI.2012, pitfall traps, 2 spms, leg. Aspradaki E. (NHMC); • Aposelemis River, Sfentyli Dam, in a *Tamarix* grove near road, 35.237073°N, 25.421797°E, 218 m elev., 30.V.2017–19.X.2017, pitfall traps, 3 spms, leg. Amyntas A. (NHMC).

Comments. *Ophonus puncticeps* is reported in Greece from the Greek mainland (excluding Peloponnese), Ionian islands and the Aegean (Arndt et al. 2011). To our knowledge, this is the first time *O. puncticeps* has been reported from Crete. *Ophonus puncticeps* is a good disperser (e.g. it has been introduced and expanding in the USA (Larsen 2013)), thus it is not surprising that it also occurs in Crete, given its current distribution in Greece. Both localities, where the species was found, are located in the north part of central Crete, in rivers that form small deltas and have artificial dams.

18. *Parophonus* (*Ophonomimus*) *hirsutulus* (Dejean, 1829)

Figs 3I, 5H

Habitat and general distribution. *Parophonus hirsutulus* has a Turano-Mediterranean distribution (Kataev and Wrase 2017).

Material examined. • Rethymno: Petres River mouth, 35.351030°N, 24.358000°E, 2 m elev., 15.V.2015–9. VII.2015, pitfall traps, 9 spms, leg. Pavlou Chr. (NHMC); • same data, but 9.VII.2015–2.XI.2015, 30 spms; • Amari, Potamon Dam, 35.275710°N, 24.581507°E, 206 m elev., 4.IV.2017, handpicking, 1 spm, leg. Amyntas A. (NHMC); • same data, but 8.VI.2017, 2 spms, leg. Pavlou Chr. (NHMC); • same data, but 8.VI.2017–17.X.2017, pitfall traps, 1 spm, leg. Amyntas A. (NHMC).

Comments. *Parophonus hirsutulus* has a Turano-Mediterranean distribution (Kataev and Wrase 2017). In Greece, the species has been reported from the Greek mainland and Peloponnese (Apfelbeck 1904; Arndt et al. 2011). This is the first record of *P. hirsutulus* from Crete. The species appears to be restricted in central Crete.

20. *Dicheirotrichus* (s.str.) *obsoletus* (Dejean, 1829)

Figs 4A, 5G

Habitat and general distribution. *D. obsoletus* has a Mediterranean distribution (Jaeger and Kataev 2017). The species occurs in saline coastal habitats (Austin et al. 2008; Arndt et al. 2011).

Material examined. • Heraklion: Almyros River, salt-marsh, 35.339104°N, 25.061201°E, 1 m elev., 3.V.2012–3.VI.2012, pitfall traps 2 spms, leg. Aspradaki E. (NHMC); • same data, but 1.VIII.2012–28.XI.2012, 3 spms; • same data, but 28.XI.2012–30.V.2013, 1 spm; • Aposelemis River mouth, 35.335000°N, 25.330891°E, 1 m elev., 6.XI.2014–5.12.2014, pitfall traps, 2 spms, leg. Pavlou Chr. (NHMC); • same data, but 30.VII.2015–27. XI.2015, 4 ind; • Tympaki, Kokkinos Pyrgos, salt-marsh, 35.074700°N, 24.746101°E, 1 m elev., 9.XII.2021, handpicking, 1 spm, leg. Bolanakis G. (NHMC).

Comments. *Dicheirotrichus obsoletus* is reported from the Greek mainland (including Peloponnese) and the Aegean (Arndt et al. 2011). This is the first time *D. obsoletus* is reported from Crete. It is important to note that, in addition to *D. punicus* (see below), this also constitutes the first documentation of the genus *Dicheirotrichus* on the island of Crete. *Dicheirotrichus obsoletus* has been collected from central Crete, both in north and south coastal saline wetlands and marshes.

21. *Dicheirotrichus* (*Pelagophilus*) *punicus* Bedel, 1899

Fig. 4B

Habitat and general distribution. *Dicheirotrichus punicus* has an circum-Mediterranean distribution (Jaeger and Kataev 2017). The species occurs in saline coastal habitats (Austin et al. 2008; Arndt et al. 2011).

Material examined. • Lasithi: Chrysi isl., Vages Beach, salt-lake, 34.874799°N, 25.728071°E, 1 m elev., 23.III.2023–13.VII.2023, pitfall traps, 2 spms, leg. Bolanakis G. (NHMC).

Comments. *Dicheirotrichus punicus* was first recorded in Greece by Apfelbeck (1904) from Kyklades (Naxos). To our knowledge, this is the first record of the species in Crete. Moreover, it is the first time the species has been recorded in Greece in more than one century

(Arndt et al. 2011). Its geographical distribution in the Aegean Archipelago requires further research. The species was found in a salt-lake at Chrysi islet. In contrast to *D. obsoletus*, the species has not been recorded in the Cretan island yet, although it may occur in southern/eastern saline wetlands.

Harpalinae Bonelli, 1810: Platynini Bonelli, 1810

22. *Agonum* (*Europhilus*) *thoreyi* Dejean, 1828
Fig. 4C

Habitat and general distribution. *Agonum thoreyi* is a Holarctic species (Arndt et al. 2011). The species is stenotopic in reeds (Arndt et al. 2011).

Material examine. • Rethymnon: Petres River mouth, 35.351030°N, 24.358000°E, 2 m elev., 9.VII.2015–2.XI.2015, 1 spm, leg. Pavlou Chr (NHMC).

Comments. *Agonum thoreyi* is a widespread, cosmopolitan species that has been reported from Greece for a first time by Schmidt and Liebherr (2009), while this is the first record of *A. thoreyi* in Crete. The species was found in a northern small river mouth near a sand dune system that is regularly crowded for recreational activities.

23. *Agonum* (*Olisares*) *viridicupreum* (Goeze, 1777)
Fig. 4D

Habitat and general distribution. *Agonum viridicupreum* has a wide distribution in West Palaearctic (Arndt et al. 2011). The species prefers open wet habitats with warm temperatures (meadows, open wetlands, fens and floodplains) (Arndt et al. 2011; Drees et al. 2011). It exhibits some tolerance to saline environments (Arndt et al. 2011) and has fluctuations in its range, driven by climate change (Drees et al. 2011).

Material examined. • Heraklion: Dikti Mountain, Omalos Viannou plateau, in a temporary wetland, 35.072394°N, 25.450799°E, 1334 m elev., 16.X.2014, handpicking, 1 spm, leg. Pavlou Chr. (NHMC); • same data, but 16.X.2014–8.12.2014, 974 spms; • same data, but 9.V.2015–23.VII.2015, 87 spms.

Comments. *Agonum viridicupreum* is reported in Greece from the Greek mainland (excluding Peloponnese) and Ionian islands (Arndt et al. 2011), but no further records exist of *A. viridicupreum* in Crete. The species was found in a temporary pond with grass and wetland vegetation (*Juncus* spp. etc.), on a mountain plateau (Omalos Viannou, Dikti Mountain). Perimetrical to the pond, the plateau forms a mixed dehesa-like forest with *Quercus coccifera*, *Crataegus* and *Acer*. This combination of a wet meadow in a warm environment fits the description of the species' habitat provided by Drees et al. (2011) who also stress the species' tendency to expand its range towards the northern areas of Palaearctic. Based on the attention given to the southern limits of *A. viridicupreum*'s distribution by Drees et al. (2011), our records could be useful for a better understanding of the species' range expansion-contraction dynamics.

24. *Paranchus albipes* (Fabricius, 1796)
Fig. 4E

Habitat and general distribution. *Paranchus albipes* is a Euro-Mediterranean species, also occurring in Turkey (Schmidt 2017). It is a montane species (Arndt et al. 2011) that dwells in different types of shadow banks (Serrano 1988).

Material examined. • Heraklion: Agia Irini temporary stream with *Platanus orientalis* veteran trees, 35.279550°N, 25.165032°E, 140 m elev., 26.V.2016–8.V.2016, pitfall traps, 13 spms, leg. Vlachopoulos N. (NHMC).

Comments. To our knowledge, this is the first detailed record of *P. albipes* in Crete and Greece. Schmidt (2017) does not include Greece in the species' distribution, while Arndt et al. (2011) include it in their key for the Greek ground beetles, but omit it from the catalogue provided. The species was found in a small, thick riparian forest. This is also the first record of the genus *Paranchus* in Greece and Crete.

Harpalinae Bonelli, 1810: Pterostichini Bonelli, 1810

25. *Pterostichus* (*Argutor*) *cursor* (Dejean, 1828)
Fig. 4F

Habitat and general distribution. *Pterostichus cursor* is distributed in central-southern Europe, Siberia, Near and Middle East (Arndt et al. 2011). It occurs in freshwater reed-beds (Austin et al. 2008).

Material examined. • Chania: Agya Lake, 35.360704°N, 24.251689°E, 5 m elev., pitfall traps, 5 spms, leg. Amyntas A. (NHMC); • Rethymno: Amari, Potamon Dam, 35.275710°N, 24.581507°E, 206 m elev., 4.IV.2017–8.v.2017, pitfall traps, 3 spms., leg. Amyntas A. (NHMC).

Comments. *Pterostichus cursor* is reported in Greece from the Greek mainland and Peloponnese (Arndt et al. 2011). This is the first record of *P. cursor* in Crete. The species was spotted in artificial wetlands, in western and central-west Crete. In the sampling sites, there were plenty of reeds, fitting the species' habitat preferences.

26. *Pterostichus* (*Pseudomaseus*) *anthracinus* (Illiger, 1798)
Figs 4G, 5I

Habitat and general distribution. *Pterostichus anthracinus* is a West Palaearctic species (Arndt et al. 2011). It prefers habitats that combine warm and wet conditions (Kolesnikov and Karyaman 2019) like floodplains and forest stream banks (Lindroth 1992).

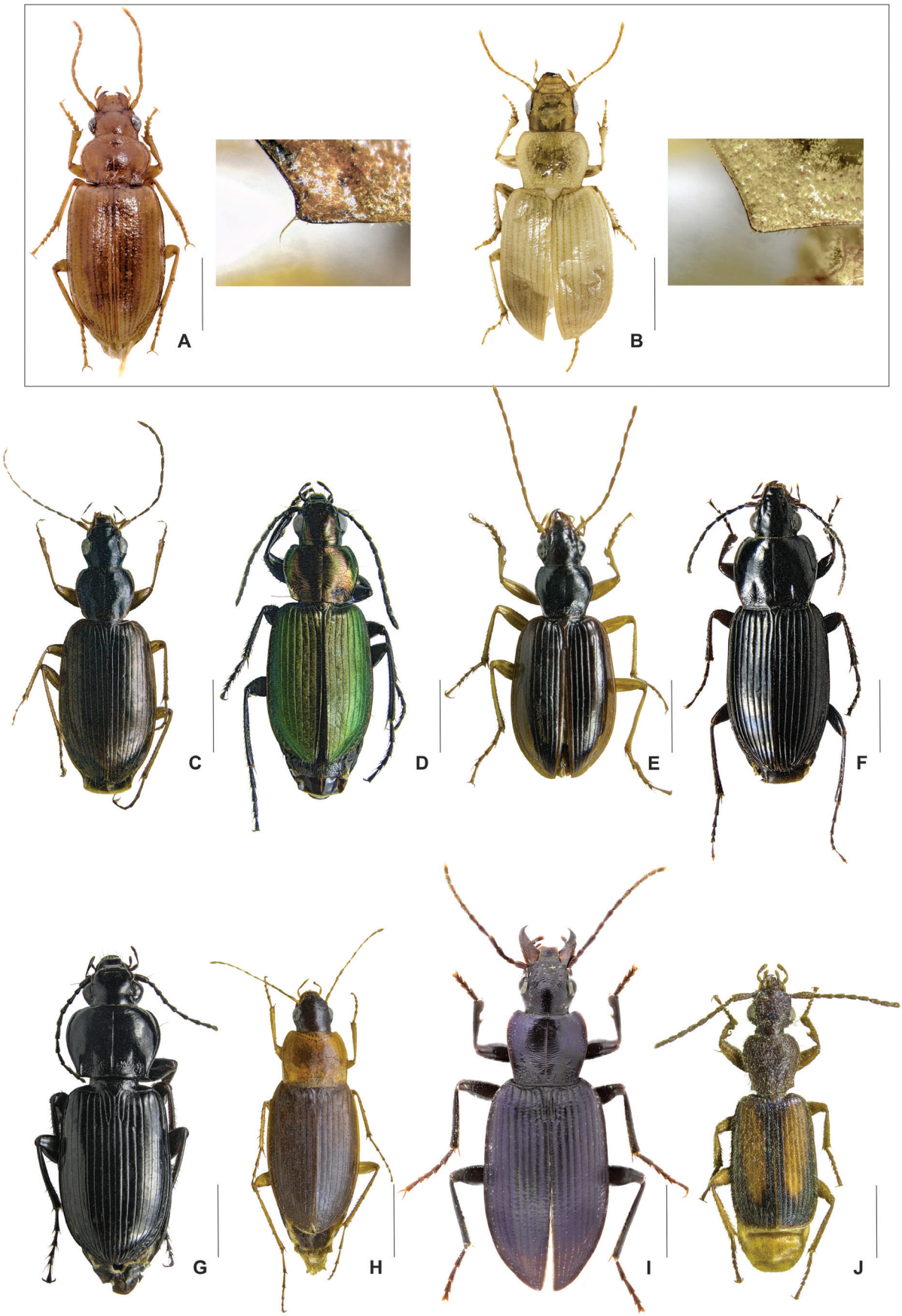

Figure 4. A. *Dicheirotrichus obsoletus*; **B.** *Dicheirotrichus punicus*; **C.** *Agonum thoreyi*; **D.** *Agonum viridicupreum*; **E.** *Paranchus albipes*; **F.** *Pterostichus cursor*; **G.** *Pterostichus anthracinus*; **H.** *Calathus cinctus*; **I.** *Laemostenus venustus*; **J.** *Polistichus connexus*. Scale bars: 2 mm (**A**); 1.9 mm (**B**); 2.2 mm (**C**); 2.1 mm (**D**); 2.3 mm (**E**); 2.1 mm (**F**); 2.7 mm (**G**); 2.2 mm (**H**); 3.4 mm (**I**); 2.2 mm (**J**).

Material examined. • Chania Agya Lake, 35.360704°N, 24.251689°E, 5 m elev., 10.IV.2017–8.V.2017, pitfall traps, 13 spms, leg. Amyntas A. (NHMC); • same data, but 8.V.2017, handpicking, 8 spms, leg. Pavlou Chr. (NHMC); • same data, but 8.V.2017–8.VI.2017, pitfall traps, 7 spms, leg. Amyntas A.

Comments. *Pterostichus anthracinus* is known from the Greek mainland, Peloponnese and the Aegean (von Oertzen 1886; Apfelbeck 1904; Arndt et al. 2011). To our knowledge, this is the first time *P. anthracinus* has been reported from Crete. It was only recorded from one locality (Agya Lake). Unfortunately, we observed intense human intervention (construction of various artificial structures mainly for recreational activities) near the sampling site. Given that Agya Lake is an artificial lake, it is uncertain whether *P. anthracinus* is a relatively novel species of the Cretan Carabid fauna. More research regarding its distribution in the island is needed.

Harpalinae Bonelli, 1810: Sphodrini Laporte, 1834

27. *Calathus* (*Neocalathus*) *cinctus* Motschulsky, 1850

Figs 4H, 5J

Habitat and general distribution. *Calathus cinctus* has a wide distribution in Europe and Near East (Arndt et al. 2011). The species prefers open habitats, with sparse vegetation (Brigić et al. 2016).

Material examined. • Lasithi: Moni Toplou, phrygana, 35.236595°N, 26.227372°E, 170 m elev., 11.XII.1993, handpicking, 1 spm, leg. Trichas A. (NHMC); • Koufonisi isl., northern beach, 34.945326°N, 26.141217°E, 2 m elev., 1.XI.1997–16.I.1998, pitfall traps, 1 spm, leg. Trichas A. (NHMC); • Xerokampos salt-lake, 35.049107°N, 26.236602°E, 1 m elev., 1.IV.2015–31.V.2015, pitfall traps, 2 spms, leg. Pavlou Chr. (NHMC); • Xerokampos phrygana, 35.050610°N, 26.240080°E, 2 m elev., 5.VIII.2015–26.XI.2015, pitfall traps, 4 spms, leg. Pavlou Chr. (NHMC); • Bramiana Dam, 35.049097°N, 25.696204°E, 88 m elev., 19.X.2017–13.XII.2017, pitfall traps, 1 spm, leg. Amyntas A. (NHMC); • same data, but 13.XII.2017–15.III.2018, 6 spms; • Bramiana Dam, in phrygana vegetation, 35.048798°N, 25.697588°E; 72 m elev., 13.XII.2017–15.III.2018, pitfall traps, 10 spms, leg. Amyntas A. (NHMC); • Kouremenos wetland, 35.204399°N, 26.271505°E, 1 m elev., 13.IV.2022–10.VI.2022, pitfall traps, 2 spms, leg. Bolanakis G. (NHMC).

Comments. *Calathus cinctus* is known in Greece from Greek mainland, Peloponnese and the Aegean (Arndt et al. 2011). To our knowledge, this is the first time *C. cinctus* has been reported from Crete. The species has been found mainly in coastal saline wetlands (Kouremenos, Xerokampos), but also in inland artificial dams (Bramiana) and phrygana vegetation (Moni Toplou). It appears to be sympatric with the closely related species *C. mollis*. *Calathus cinctus* is restricted to east Crete, not crossing the isthmus of Ierapetra, which may indicate an eastern origin.

28. *Laemostenus* (s.str.) *venustus* (Dejean, 1828)

Fig. 4I

Habitat and general distribution. *Laemostenus venustus* is a Euro-Mediterranean species that dwells in forests (especially of *Q. coccifera* and *P. orientalis*) (Austin et al. 2008).

Material examined. • Rethymno: Rouvas Forest, 35.169897°N, 24.922200°E, 1100 m elev., 20.II.1990–6.V.1990, pitfall traps, 1 spm, leg. Trichas A. (NHMC); • Lochria, in *Quercus coccifera* dehesa-like forest, 35.17640°N 24.77780°E, 980 m elev., 24.V.2019–2.VII.2019, pitfall traps, 1 spm leg. G. Bolanakis (NHMC).

Comments. *Laemostenus venustus* is known in Greece from the Greek mainland and Peloponnese (von Oertzen 1886; Apfelbeck 1904; Arndt et al. 2011). This is the first record of *L. venustus* reported from Crete. The species has been recorded only from two localities. Specifically, it has been recorded in Rouvas Forest (a shadowed riparian forest with large, veteran plane trees and kermes oaks). The original record dates back to 1990 (Trichas 1996). After several re-samples with pitfall traps, we managed to find one more specimen in 2018, in Lochria, a dehesa-like shrubland with old kermes oaks. Therefore, *L. venustus* appears to be a rare species in Crete, with a restricted distribution around Ida mountain.

Harpalinae Bonelli, 1810: Zuphiini Bonelli, 1810

29. *Polistichus connexus* (Geoffroy, 1785)

Fig. 4J

Habitat and general distribution. *Polistichus connexus* has a wide distribution in Europe, North Africa, Near and Middle East (Huber and Marggi 2017). The species occurs in open habitats, often in artificial areas (Holec et al. 2019).

Material examined. • Heraklion: Almyros Estuary, salt-marsh, 35.338503°N, 25.061403°E, 1 m elev., 3.V.2012–3.VI.2012, pitfall traps, 4 spms, leg. Aspradaki E (NHMC); • same data, but 3.VI.2012–1.VIII.2012, 1 spm; • Lasithi: Lasithi plateau, moni Vidiani, 35.182902°N, 25.462299°E, 816 m elev., 13.XII.1997, handpicking, 1 spm, leg. Mylonas M. (NHMC).

Comments. *Polistichus connexus* is known from the Greek mainland and Peloponnese (Arndt et al. 2011) and this is the first time the species has been reported from Crete. It has been found in two different habitats (a coastal salt-marsh and a humid mountain plateau with shrublands, dehesa-like forests and cultivations).

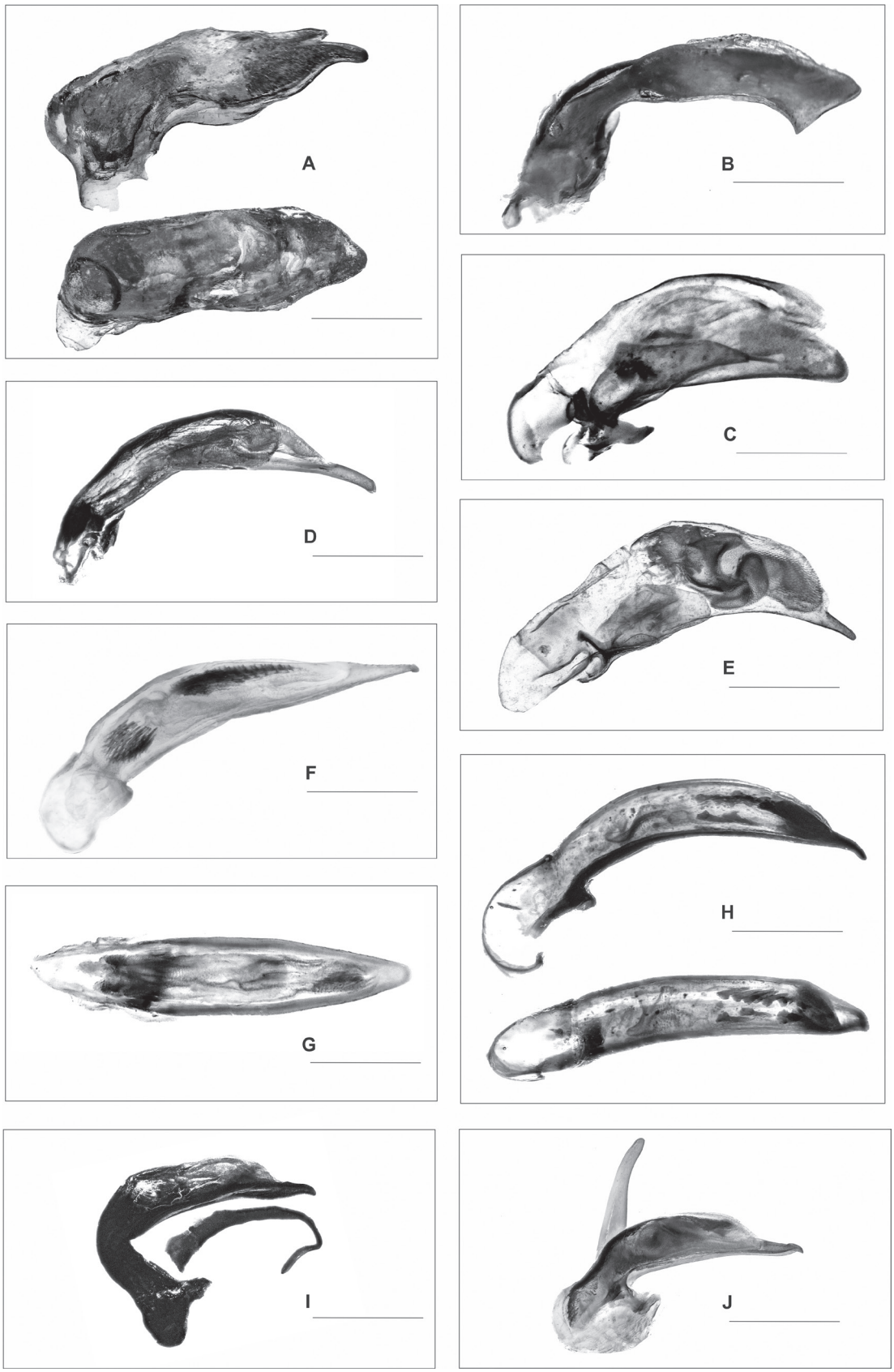

Figure 5. Aedeagii. **A.** *Brachinus plagiatus*; **B.** *Brachinus psophia*; **C.** *Sirdenus grayii*; **D.** *Anaulacus ruficornis*; **E.** *Cymindis andrae*; **F.** *Ophonus puncticeps*; **G.** *Dicheirotrichus obsoletus*; **H.** *Parophonus hirsutulus*; **I.** *Pterostichus anthracinus*; **J.** *Calathus cinctus*. Scale bars: 0.53 mm (**A**); 0.41 mm (**B**); 0.28 mm (**C**); 0.72 mm (**D**); 0.49 mm (**E**); 0.61 mm (**F**); 0.47 mm (**G**); 0.56 mm (**H**); 1.17 mm (**I**); 0.63 mm (**J**).

Discussion

After almost two centuries of Coleopterological research, Crete remains a fruitful ground for new faunistic and taxonomic discoveries in Carabidae (e.g. Giachino and Vailati (2023)). In this study, we aggregated the data after more than 40 years of sampling efforts in Crete (primarily with pitfall traps) and, based on the study of Arndt et al. (2011) that provides an updated frame for the ground beetle fauna of Greece, we introduce 24 new species for Crete. Moreover, we confirm the presence of four species with detailed data and, finally, we comment on the doubtful presence of *Carabus graecus trojanus*. Three of the species recorded here (*Anaulacus ruficornis*, *Sirdenus grayii* and *Paranchus albipes*) are recorded with concrete data for the first time in the Greek carabid fauna. Two genera, *Anaulacus* and *Paranchus*, are new for Greek fauna. The former genus is also new for the Balkan Peninsula. Arndt et al. (2011) listed 962 carabid taxa (including species and subspecies) for Greece, 219 (23%) of them being endemic. Interestingly, only 27 of the endemics (see Chapter 5 of Arndt et al. (2011) and the recent literature) are Cretan endemics, which correspond to only 12.2% of the Greek endemic carabid fauna. According to the data presented in Arndt et al. (2011), Crete hosts 26.5% (255 species) of the Greek ground beetles. With the addition of the new records presented in our study and the removal of *C. g. trojanus*, Crete's ground beetle fauna increases to 277 species, that is 279 species with the inclusion of two recently-described species (*Iason assingi* Giachino & Vailati, 2023 and *Duvalius augusti* Casale, Giachino, Vailati, 2021) (29.00% of the Greek Carabidae).

Crete's endemism in Carabidae fluctuates around 9%. This percentage is admittedly small when compared with other groups (e.g. land snails (~ 47% Vardinoyannis et al. (2018)). This is not surprising given the hygrophilic/mesophilic nature of Carabidae. Crete has a dry climate and is dominated by arid phrygana, maquis and olive grove cultivations. Hence, most of the Cretan endemic Carabidae are species of xerophilic to mid-mesophilic preferences (e.g. *Carabus banonii*; *Calathus oertzeni*; *Tapinopterus creticus*; *Zabrus oertzeni*) or subterranean nature (*Duvalius* spp., *Iason* spp.). Endemics aside, the highest Carabidae diversity is found in wetlands. Most of Crete's natural wetlands that are suitable for Carabidae, are small riparian habitats, streams or creeks in gorges that lack permanent waterbodies or a soft substrate. Moreover, there are also river mouths/small deltas, coastal wetlands and salt-lakes/marshes, while a significant number of artificial lakes, dams and estuaries, have been built through the last 30 years to combat drought and irrigation problems. All the above biotopes drive the shaping of an impressive – yet poor in endemics – Carabidae assemblage of Crete.

Out of the 24 new species for Crete reported here, 17 (70.8%) of them are closely or even strictly related to wetlands. Even though we do not have concrete information regarding the places visited by coleopterologists in their entomological excursions in Crete, it is safe to assume that the most well-sampled habitats were the dominant ones (i.e. lowland and montane shrublands). Most of the naturalists that visited Crete in the 19th and the first half of the 20th century collected material mainly from montane areas (Omalos Plateau, Nida Plateau), touristic destinations and lowland shrublands. Thus, it is expected that most of the material examined originated from these habitats. Nevertheless, there are reports on wetland species in Crete, dating back to the 19th century (Schaum 1857). Therefore, it can be said that there was at least some sampling effort in wetland habitats in the early days of carabid research in Crete. Due to drought and water scarcity, local institutions and government authorities have built dams and artificial lakes through the years. Many of the carabid species recorded in our study were reported from artificial lakes or dams (e.g. Agya Lake, Bramiana Dam, Potamon Dam, Aposelemis Dam). These new (compared to the natural) waterbodies could have acted as stepping stones for the expansion of many Carabidae species and the formation of early-stage carabid communities.

Given the presence of these species in vulnerable habitats such as coastal wetlands (Fattorini 2008; Janssen et al. 2016; Newton et al. 2020), plenty of conservation challenges arise. Coastal saline wetlands are continuously pressured by aggressive tourism expansion, urbanisation and agriculture. One of the most typical human interventions in coastal habitats is the stamping and clearance (removal of debris) of the beach or the draining of salt-lakes/marshes for eye-pleasing purposes. For example, in the Platanias River mouth (where we spotted *Scarites buparius*), the coastline was stamped, cleared and the dune part of the river mouth (where the pitfall traps have been placed) was covered with debris and rubbish. The coastal saline wetlands are of special interest since they are scarce in Crete and yet they yielded 37.5% (nine species) of the new species recorded here.

With Crete being in the middle of three continents, the biogeographical connotations for the species introduced in the Cretan fauna could be rather interesting. Dispersal paths from east and west, phenomena of filtering through geographical barriers or climatic gradients can all be thoroughly investigated. The formation and the evolution of the Carabidae assemblages can also be scrutinised by utilising the different ages of the artificial estuaries and reservoirs, in comparison with the natural wetland and shrubland ground beetle communities. For species, such as *Agonum viridicupreum*, its discovery in Crete could be proved crucial for the investigation of its range dynamics as a function of climate change, since it appears that the species is susceptible to the footprint of the latter (Drees et al. 2011).

Conclusively, it appears that Crete provides a fruitful ground for carabid research in a plethora of different disciplines (ecology, taxonomy, faunistics, conservation etc.). Most crucial for such scientific efforts should be an adequate and updated species catalogue. Our study contributed to this subject by recording 24 new species to

the Crete carabid fauna and confirming the presence or the absence of some others. However, further faunistic research in Crete is needed to investigate various carabid taxa. For example, the genus *Bembidion* comprises of many small hygrophilic/mesophilic predators, that are found along running or standing waters (Maddison 2012). Consequently, further research focused on the Cretan wetlands, especially small creeks and riparian streams that have been neglected from our sampling effort will contribute to a more complete catalogue of the Cretan *Bembidion* spp.

Conclusions

Our findings contribute to the update of the Cretan Carabid fauna to 279 species. Most of the new additions to the Carabid fauna are closely or strictly related to wetlands. Therefore, further sampling effort in wetland habitats could be important to verify or even find more new species for Crete and perhaps for Greece. Additionally, considering the continuous economic and touristic development of the island (mostly the coastline), several wetland species may be in need for an update of their conservation status.

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