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This contribution is published to honor Prof. Vladimir Chikatunov, a scientist, a colleague and a friend, on the occasion of his 80th birthday.

The Caterpillar Hunter Beetles *Calosoma* Weber (Coleoptera: Carabidae) in the southern Levant

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ABSTRACT

Eight species of the ground beetle genus *Calosoma* are reported from the southern Levant (Egypt (Sinai), Israel, Jordan) and adjacent areas in Egypt, Iraq, Lebanon, Saudi Arabia, and Syria. The reports of one species were probably due to mislabelling. An illustrated identification key for the species in the region is provided. The current state of knowledge on ecological traits (e.g. dispersal power, phenology and prey) and distribution range, especially in the southern Levant, of the treated *Calosoma* species is summarized. Additional information about taxonomy and identification of the species is also provided.

We dedicate this work to Vladimir Chikatunov, a curator of the Coleoptera Collection of the Steinhardt Museum of Natural History, Tel Aviv University, Israel, on the occasion of his 80th birthday. He supported us in many different ways in our work with carabids from Israel and neighbouring countries. Some of us particularly remember the excellent excursions he led to the Negev and the Golan Heights.

KEYWORDS: Coleoptera, Carabidae, Carabini, ground beetles, identification key, species traits, taxonomy, Palaearctic, climate change, poleward shift.

INTRODUCTION

The ground beetles of the genus *Calosoma* Weber, 1801 are among the most popular insects (Scherney 1959; Thiele 1977). Both adults and larvae are voracious predators, especially on caterpillars in forests, steppes and arable fields. Several *Calosoma* species are effective control agents of some moth pests (Burgess 1911*a*;

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Burgess & Collins 1915; Weseloh 1985*b*; Kimberling 2004). Some *Calosoma* species are known to form population outbreaks when conditions are favourable; these are noticed very well by general public and are covered in the media (e.g., TOI 2019; Baladi 2020). Despite ecological importance and ecosystem services provided by the *Calosoma* species, our knowledge about this beetle group in the southern Levant is still limited (e.g. Borzatti von Lowenstern 1987; Gobbi 1995). To advance both faunistic and ecological research, we here present a species identification key and summarize the known distribution, species traits, natural history and habitat selection of the *Calosoma* species of the Levant.

MATERIALS AND METHODS

The delineation of the study area, measurements, photography, species traits (dispersal power, phenology) and habitat selection were done as described in Assmann *et al.* (2012, 2015*a*, *b*, 2018). We prepared the photos with the microscope and camera mentioned in the previously cited publications or with a Lumix GX 80 and a Leica Macro-Elmarit 45 mm. Stacking (of up to about 100 layers) was done with the *Picolay* software (www.picolay.de).

This study is based on the examination of specimens (i) observed and/or collected during field trips of the authors in Israel, Jordan and Egypt (between 2004 and 2019), (ii) collected in context of ecological surveys (e.g. Buse *et al.* 2010), and/or (iii) stored in entomological collections (including historical collections). Records of species were critically compiled from available literature (e.g. Breuning 1927, 1928*a*, *b*; Jeannel 1940, 1941–1942; Casale *et al.* 1982; Bandinelli 1984; Borzatti von Lowenstern 1987; Gobbi 1995; Roggeman 1995; El-Akkad *et al.* 1998; Deuve 2004; Franzen 2006; Bruschi 2013). We studied approximately 300 *Calosoma* individuals from the southern Levant, but material from Lebanon and Syria is very limited.

Acronyms of collections:

CAB – Working collection Assmann, Asendorf (formerly Bleckede) (part of ZSM; including wet collection, material in almost absolute ethanol in freezers at -20 or -80 °C);
COQ – Working collection Orbach, Qiryat Tiv'on (to be transferred to SMNHTAU);
CWGB – Working collection Wrase, Gusow-Platkow (part of ZSM);
SMNHTAU – Steinhardt Museum of Natural History, Tel Aviv University, Israel;
ZSM – Zoological State Collection Munich (Zoologische Staatssammlung München), München, Germany.

Transliterated names of localities in Israel follow the *Israel Touring Map and List of settlements* published by the Survey of Israel (2009). The most recent transliterated Hebrew names are given followed by alternative, old or erroneously cited names in brackets, for example: Be'er Menuha [Bir Maliha]. Regional subdivision of Israel follows Theodor (1975), with changes made by Ionescu and Eyer (2016).

TAXONOMY

Delineation of the genus Calosoma

Nomenclature and classification of the taxa of the subtribe Calosomatina are not stable at both the (sub-) generic and the species level (e.g. Obydov 2002; Arndt & Trautner 2006; Bousquet *et al.* 2003; Lorenz 2005; Arndt *et al.* 2011; Bruschi 2013; Häckel 2017; Toussaint & Gillett 2018). Particularly, the phylogenetic studies of Toussaint and Gillet (2018) reveal that the subgenera or genera established by many authors (Breuning 1927, 1928*a*, *b*; Jeannel 1940; Bruschi 2013) are polyphyletic. Therefore, we follow the current *Palaearctic Catalogue* (Häckel 2017) and accept the taxon *Calosoma* Weber, 1801 as a genus and refrain from subdividing it into subgenera or further genera.

Identification key to the *Calosoma* species from the southern Levant

Eight *Calosoma* species are recorded from the southern Levant; these can be easily identified by the following combination of characters: (1) no white spots of hairs or other brightened pattern, (2) longer than 15 mm, (3) procoxa open (Bousquet 2010: 60, fig. 23), (4) metacoxae contiguous along midline (Müller-Motzfeld 2006: 7, fig. 4b), (5) mandibles wrinkled (Fig. 1A), and (6) very short second antennomere (Fig. 1A). The species of the genus *Calosoma* are easily separated from *Carabus* spp. by the last two character states (cf. Assmann *et al.* 2008) (Fig. 1B).

1 Elytra rounded laterally (in dorsal view), dorsally convex, at least at basal third (in lateral view), shoulders rounded. Elytral sculpture strongly reduced to small grains. Brachypterous, hindwings reduced (beetles unable to fly). Colour black with slight blue hue. 19–25 mm. Fig. 4 .....*ewersmanni* (Chaudoir, 1850)

– Elytra straight laterally, subparallel or elytral sides slightly diverging subapically (in dorsal view), shoulders well developed; dorsally flattened, at least at basal

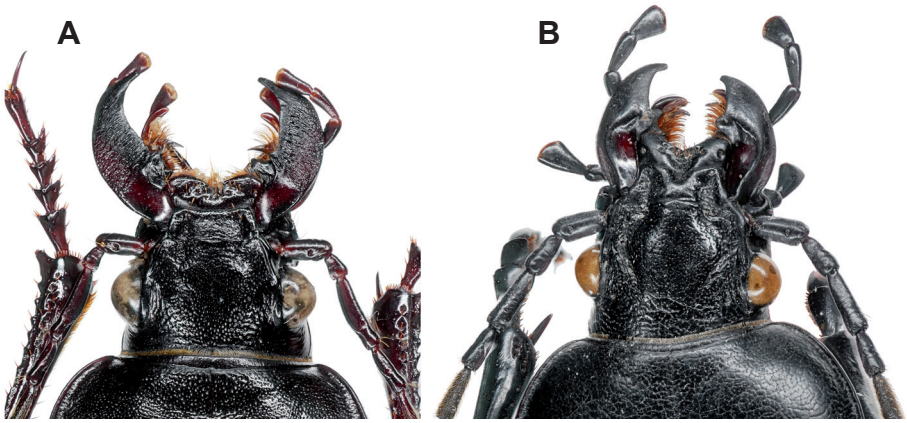

Fig. 1: Head of *Calosoma* and *Carabus* spp.: (A) *Calosoma algiricum*, Kebili (Tunisia), mandibles wrinkled, antennal segment 3 about 3× as long as segment 2; (B) *Carabus syrus*, Mt Meron (Israel), mandibles not wrinkled, antennal segment 3 less than twice as long as segment 2.

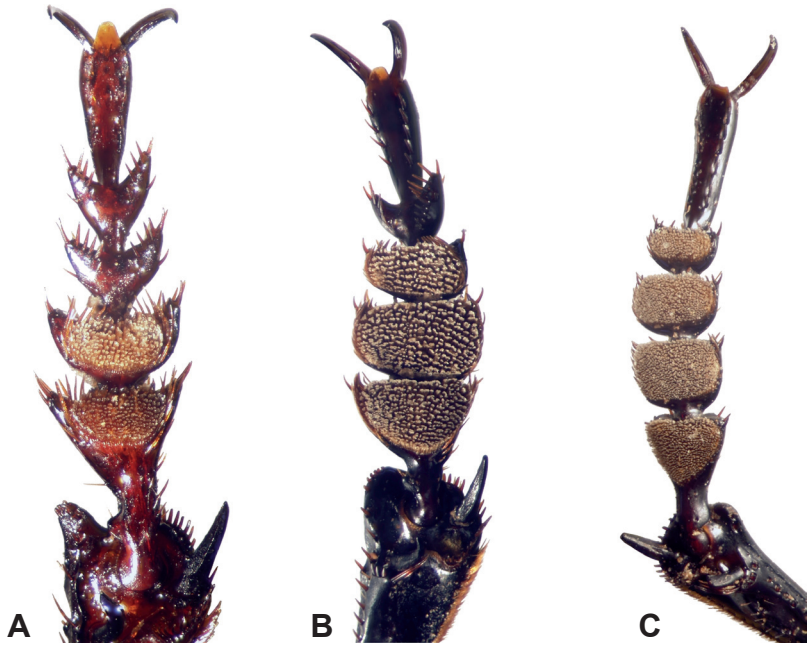

Fig. 2: *Calosoma* spp., lower side of male protarsi, 2 (A), 3 (B) and 4 (C) dilated segments with adhesive setae: (A) *C. algiricum*, Palmyra (Homs, Syria); (B) *C. maderae*, Canet-Plage (France); (C) *C. inquisitor*, Loevelingloh (Germany).

third. Elytral sculpture well developed with clearly visible striae, foveae (in primary striae), and intervals. Macropterous, hindwings well developed and beetles flight active. Colour variable, black to brassy green, shiny or matt 2

2 Lateral margin of pronotum obsolete at hind angles, not connected to basal margin; hind angles bent downwards, without seta..... 3
– Lateral margin of pronotum in contact to basal margin; in most species, hind angles less bent downwards and with seta (which, however, may be broken off)..... 4

3 Large species, longer than 23 mm. Male: 3 segments of protarsi dilated and with adhesive setae on lower side (as in Fig. 2B). Elytra with fine transverse lines between striae. 24–33 mm. Fig. 11 ..... *sycophanta* (Linnaeus, 1758)
– Smaller species, <23 mm. Male: 4 segments of protarsi dilated and with adhesive setae on lower side (Fig. 2C). Elytra with coarse transverse lines between striae. 16–22 mm. Fig. 8 ..... *inquisitor* (Linnaeus, 1758)

4 Male: Anterior side of mesotibia (and sometimes also of metatibia) at apical part with brush of reddish or brownish hairs (Fig. 3). Mesotibiae and metatibiae arcuate in males and strongly arcuate, metatibiae less arcuate in females..... 5
– Male: Anterior side of mesotibia without hair brush. Mesotibiae and metatibiae straight or slightly arcuate in both sexes 7

Fig. 3: *Calosoma maderae*, male; arrow points to the brush of brownish hairs at the apical end of the left middle tibia.

5 Male: 3 segments of protarsi dilated and with adhesive setae on lower side (Fig. 2B). Antennae longer (in females antennae proceed above first third of elytra). Hind angles of pronotum rounded or obtuse-angled. Elytra of most individuals with 3 rows of golden, greenish or bluish foveae. Elytral sculpture simple, between primary striae (those comprising foveae) only 3 further striae 6

– Male: 2 segments of protarsi dilated and with adhesive setae on lower side (Fig. 2A). Antennae short (in females antennae only reach base of elytra). Hind angles of pronotum acuminate. Elytra and entire body black or foveae and elytral margin greenish. Elytral sculpture different, between primary striae (those comprising foveae) 5 further striae. 27–35 mm. Fig. 4..... *algiricum* Géhin, 1885

6 Elytra brown or black with bronze or copper hue; elytral structure strongly developed (striae deep, punctated, intervals convex to keeled, transverse structure well developed and deep, interrupting striae). Pronotum wide (pronotum length/width >1.6). 20–30 mm. Fig. 5 ..... *chlorostictum* Dejean, 1831

– Elytra black, only margin and foveae bronze to green and with metallic hue, elytral sculpture differently developed, but weaker than in proceeding species. Pronotum smaller (pronotum length/width <1.6). 16–35 mm. Fig. 9..... ..... *maderae* (Fabricius, 1775)

7 Elytral sculpture with 3 (regular) intervals between primary striae (those comprising foveae), intervals convex, foveae pronounced. Upper side sometimes black, but mostly with metallic green, coppery or bronze hue, especially foveae. 15–22 mm (subsp. *deserticola* Semenov, 1897 up to 28 mm). Fig. 7 .... *imbricatum* Klug, 1832

– Elytral sculpture with 5 (more irregular) intervals between primary striae (those comprising foveae), intervals flattened, foveae fine. Upper side mostly black, but elytral foveae with metallic hue. 20–28 mm. Fig. 10 .....*olivieri* Dejean, 1831

Species accounts

Calosoma algiricum Géhin, 1885

(Figs 1A, 2A, 4)

Dispersal power: Macropterous, very active flyers; single records from vagrants of this desert species also from southern Europe (Sicily, Tuscany, Greece: Casale *et al.* 1982; Bandinelli 1984; Franzen 2006; Bruschi 2013).

Habitat: Desert habitats, especially oases (Breuning 1927*a*; Casale *et al.* 1982; Gourves 1997).

Phenology: Adults from March to June (Bruschi 2013), supported by label data of the specimens in SMNHTAU.

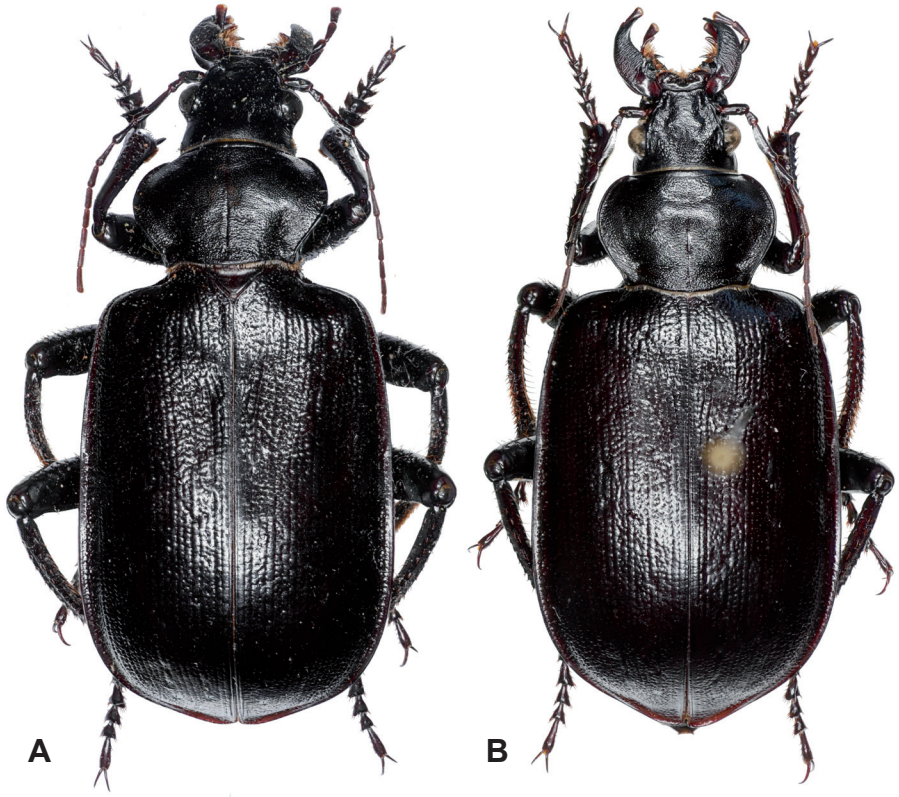

Fig. 4: *Calosoma algiricum*, habitus of (A) male, Kebili (Tunisia) and (B) female, and Boumzil (Morocco).

Material examined: Israel: *Upper Galilee*: 1♂ 1♀ Karmi'el, 29.v.2019, U. Shalom; *Lower Galilee*: 1♀ Qiryat Tiv'on, 22.iv.2001, E. Orbach; *Central Coastal Plain*: 1♂ Tel Aviv, Ramat Aviv, 5.v.1998, Y. Orion; *'Arava Valley*: 1♀ 'En Yotvata, 20.iii.2001, V. Kravchenko, I. Yarom; 1♀ 'En Yotvata, 14.iv.2004, U. Shanas, V. Chikatunov (SMNHTAU). **Syria:** 1♂ 1♀ Prov. Homs, env. Palmyra, 450 m, 14.iv.1988, de Freina (CAB).

Distribution range: From Morocco and Mauritania to Iran and Turkmenistan (Bruschi 2013; Häckel 2017).

Distribution in southern Levant: In Israel, there are single records from across the entire country (except for Har Hermon); it was previously recorded from 'En Gedi (Gobbi 1995). The species is also known in Jordan: Wadi Rum (Borzatti von Lowenstern 1987), Lebanon (only 1 specimen from Tripolis; most probably a vagrant) (Deuve 2004), and Syria (Bruschi 2013). Two specimens were collected in the Upper Galilee during the 2019 outbreak of *C. olivieri* (see below). *Calosoma algiricum* is a species restricted to deserts, therefore areas with the Mediterranean climate cannot be regarded as part of its regular distributional range.

Calosoma chlorostictum Dejean, 1831

(Fig. 5)

Dispersal power: Macropterous, flight active.

Habitat: Unknown in the Levant. In St Helena, Basilewsky (1972) reports this species from meadows at altitudes up to 1,400 m, where rain can fall in any season.

Phenology: Adults throughout the year (Bruschi 2013).

Distribution range: From St Helena and Cape Verde Islands through North Africa to Persian Gulf, southwards to South Africa and Madagascar (Bruschi 2013; Häckel 2017).

Distribution in southern Levant: Egypt (Sinai): northern region and Wadi El Arish (Mandl 1970; Alfieri 1976; Abdel-Dayem 2004), but El-Akkad *et al.* (1998) do not mention the taxon for Egypt.

Calosoma ewersmanni (Chaudoir, 1850)

(Fig. 6)

Dispersal power: Brachypterous.

Habitat: Steppe habitats at 1,200–1,700 m asl (Bruschi 2013).

Phenology: Unknown.

Material examined: There are two specimens in the SMNHTAU: 1♀ labelled "Palestine / F.S. Bodenheimer" [printed], "Papyrus, Nuphar, 5-7-[19]34" [handwritten], "Callisthenes / eversmanni / Det. G.E. Bryant" [handwritten/printed] and 1♂ "Hula / Palestine / on Nuphar / VII 1942 / leg. Shulov" [printed and handwritten], "locality certainly / erroneous!! Probably / Anatolia leg. Bodenheimer" [handwritten]) (Fig. 6). There is a suspicion that the specimens were mislabelled, since one of them was admittedly collected on *Nuphar*, which is a water plant (see also the comment under the Distribution range). However, the mention of papyrus and water-lily may rather refer to the habitat, where the beetles were collected.

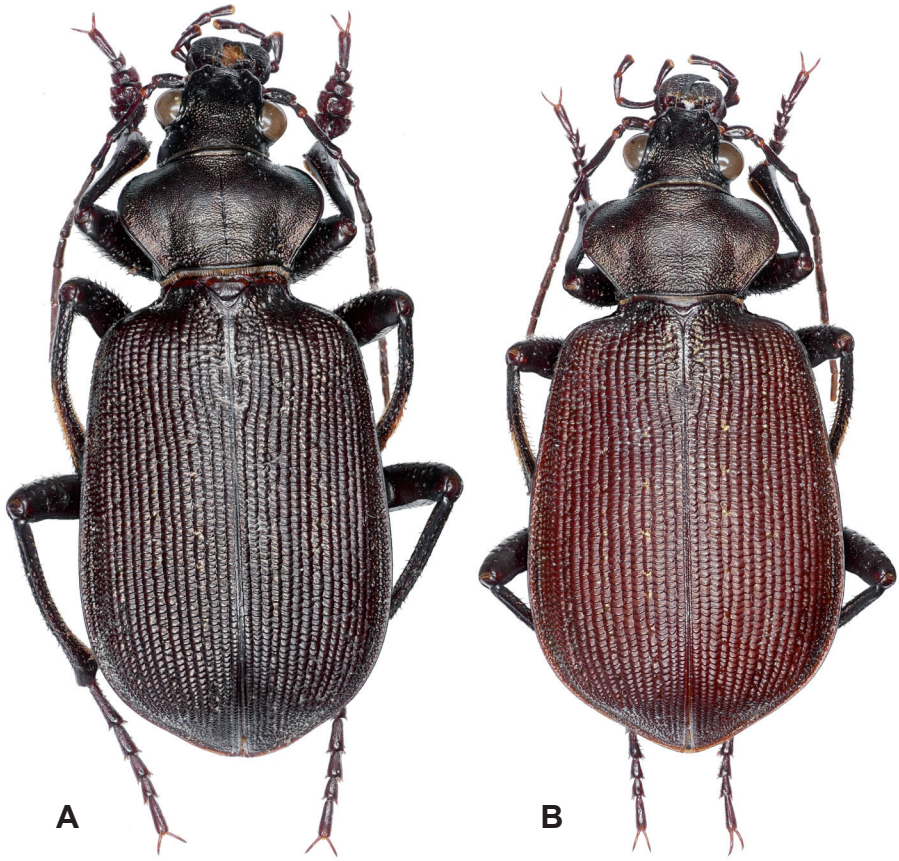

Fig. 5: *Calosoma chlorostictum*, habitus of male (a) and female (b), env. Voi (Kenya).

Distribution range: Obydov (2002) lists *C. ewersmanni* as endemic to Turkey. A record of this species in NE Iran (Ghahari *et al*. 2009) requires confirmation, and its penetration into North Israel seems doubtful at the moment.

Calosoma imbricatum Klug, 1832

(Fig. 7)

Dispersal power: Macropterous, flight active.

Habitat: Unknown.

Phenology: Adults throughout the year in Africa south of Sahara, and in January–March in Egypt (Alfieri 1976).

Material examined: Saudi Arabia: 2♂ 2♀ Riyadh Province, v.1982, K. O'Brien (CWGP, Wrase det.).

Fig. 6: *Calosoma ewersmanni*, male, habitus; specimen from the Hula Valley (SMNHTAU).

Distribution range: From Cape Verde Islands to Central Asia (Mongolia), southwards to South Africa (Felix 2009; Bruschi 2013; Häckel 2017), also in Egypt west of Nile (Alfieri 1976; Bruschi 2013).

Distribution in southern Levant: Sinai (El-Akkad *et al.* 1998). Ptashkovsky (2013) mentioned this species in the Upper Galilee, but we are unaware of any specimens of *C. imbricatum* from Israel, since no material has been found in the SMNHTAU, including the collection of the late Ptashkovsky, which was incorporated in the SMNHTAU.

Taxonomic notes: The species has two subspecies in the Palaearctic. The specimen from Djibouti (Fig. 7A) belongs to the nominate subspecies, which occurs also in Sinai and the Arabian Peninsula and eastwards to Iran. The subspecies *C. i. desertícola* Semenov, 1897 occurs from the Southern Russian Plain through Kazakhstan (Fig. 7B) and Turan (Kryzanovskij *et al.* 1995) and to the northern regions of Iran

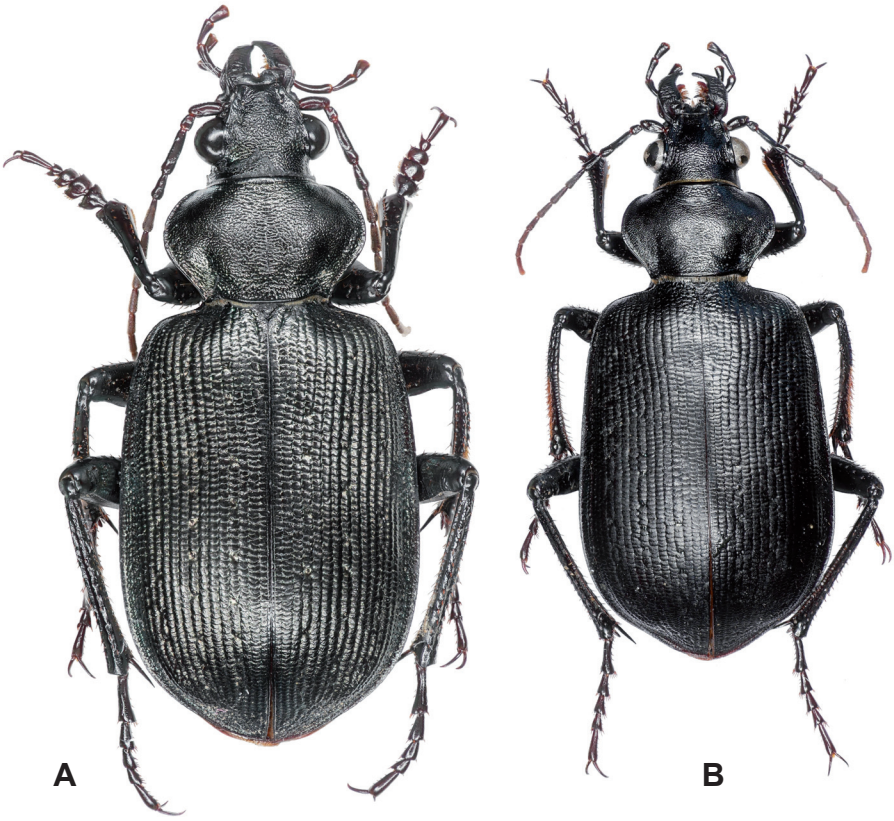

Fig. 7: *Calosoma imbricatum*, habitus of (A) male *C. imbricatum* s.str., Ambouli (Djibouti) and (B) female *C. i. deserticola*, Beyneu (Kazakhstan).

(Bruschi 2013). Both subspecies differ in the body size, coloration, proportions of the pronotum and elytra, the shape of the eyes, sculpture of the pronotum and elytra, etc. In Pakistan, a hybrid zone between both subspecies seems to occur (cf. Bruschi 2013). The specimens from Saudi Arabia are almost black (as *deserticola*), but otherwise show the morphological characters of the nominate subspecies.

Calosoma inquisitor (Linnaeus, 1758)

(Figs 2C, 8)

Dispersal power: Macropterous, flight active (e.g. Lindroth 1985, 1986; pers. obs.).

Habitat: An arboreal species of deciduous, mostly oak-dominated woodlands. In Central Europe and Scandinavia, the adults hunt during daytime and feed on geometrid and tortricid caterpillars (e.g. winter moth *Operophthera brumata*, oak leaf roller moth *Tortrix viridiana*). The larvae are ground dwellers (Lindroth 1945, 1985;

pers. obs.). In southern Europe, also in evergreen oak woodlands (e.g. *Quercus ilex*) (cf. Vigna-Taglianti 1993; Pisano & Delunas 1998; pers. obs.).

Phenology: In Central, northern and southern Europe reproduction in spring and early summer. Newly hatched beetles appear in autumn, adults hibernate. Beetles can live up to three years (Larsson 1939; Lindroth 1945, 1985).

Distribution range: From Scandinavia to southern Europe and north-western Africa (Morocco), eastwards to Iran (nominate subspecies) and East Siberia and China (*C.*

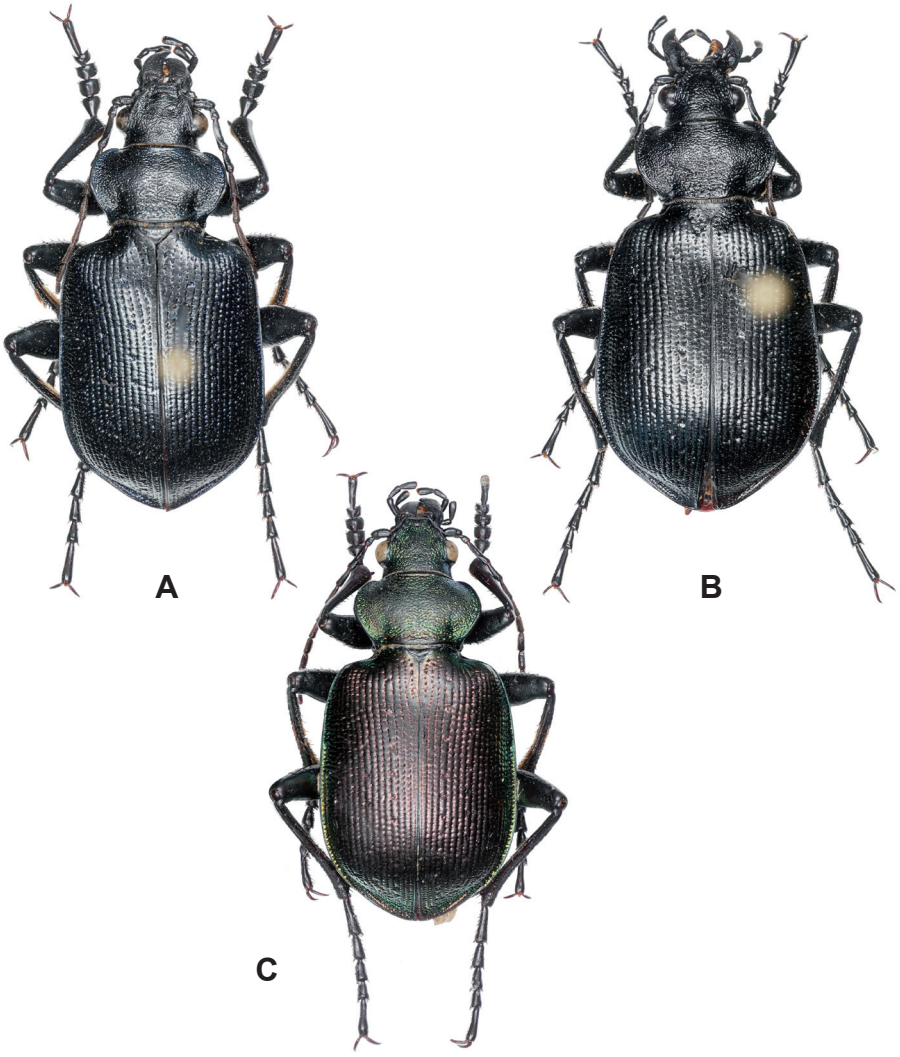

Fig. 8: *Calosoma inquisitor*, habitus: (A, B) male and female, Pindos Mountains (Greece); (C) male, Pülümür (Turkey).

i. cyanescens (Motschulsky, 1859)) (Breuning 1927; Bruschi 2013; Häckel 2017). Not recorded by Bousquet *et al.* (2003), Buschi (2013) and Häckel (2017) from most North African countries, Syria and Lebanon, but Breuning (1927) mentions the species also from Algeria and Tunisia.

Distribution range in southern Levant: Breuning (1927: 167) summarized records from Lebanon (Beirut and Anti-Lebanon Mountains). The subspecies *C. i. viridulum* Kraatz, 1877, now regarded as an older synonym of the nominate subspecies (Bruschi 2013), was described from Beirut. The Mt Hermon belongs to the Anti-Lebanon mountain range, and it is possible that the species occurs in Israel (Hermon, Golan Heights, Upper Galilee). The preferred oak-feeding moth species (see Habitat above) also occur in Israel and Lebanon.

Taxonomic notes: The variant with a copper-greenish hue (see Lindroth 1985) is the commonest in Central Europe and Scandinavia. This coloration is also used as a character state in many identification keys (Lindroth 1985; Arndt & Trautner 2006; Arndt *et al.* 2011). In south-eastern Europe and south-western Asia, there are also completely black beetles or those with a slightly bluish hue (Figs 8A, B). Beetles with a green hue or greenish front body and reddish elytra are known from the Levant and southern Turkey (Breuning 1927; Fig. 8C).

Conservation: The species is considered threatened in Central Europe (e.g. in Germany) (Schmidt *et al.* 2016; Nolte *et al.* 2017). The lack of records of recent decades from Lebanon is perhaps an indication of a decline of this species population in the southern Levant.

Calosoma maderae (Fabricius, 1775)

(Figs 2B, 3, 9)

Dispersal power: Macropterous, flight active (Lindroth 1945).

Habitat: Epigeic species of open habitats (arable fields, steppes, batha, wadis in the Mediterranean, dunes) (Lindroth 1985; Bruschi 2013, pers. obs. in Europe and in the Levant). In Israel, from the north (Mt Hermon, Golan Heights, Upper Galilee) to the steppe zone in northern Negev (e.g. Nature Reserve Pura, Ma'agar Yeroham), although the majority of the collected specimens is from the Mediterranean part of the country (pers. obs.; SMNHTAU). A similar climate niche is reported from Morocco, where the species occurs in the Mediterranean climate zone to the semi-arid steppe zone close to Marrakesh (Gourves 1997). In both Morocco and the southern Levant, *C. maderae* co-occurs with *C. olivieri*.

Phenology: Spring breeder with summer larvae. Adults hibernate and can live up to three years (Larsson 1939; Lindroth 1945, 1985).

Material examined (all SMNHTAU, if not stated otherwise): **Israel:** 1♀ 'Israel'; *Har Hermon*: 1♂ Har Hermon, 9.vi.1992, Shney-Dor?; 1♂ Har Hermon, 2200 m, 2.vi.1993, V. Chikatunov; 1♀ Har Hermon, 2000 m, 8.vi.1993, V. Chikatunov; 1♀ Har Hermon, Nahal Guveta, 1.5 km W Majdal Shams, 1250 m, 28.iv.1995, E. Orbach; *Hula Valley*: 1♀ Hula Valley, 17.iii.1969, M.P. Pener, Y. Ayal; 1♂ Dan,

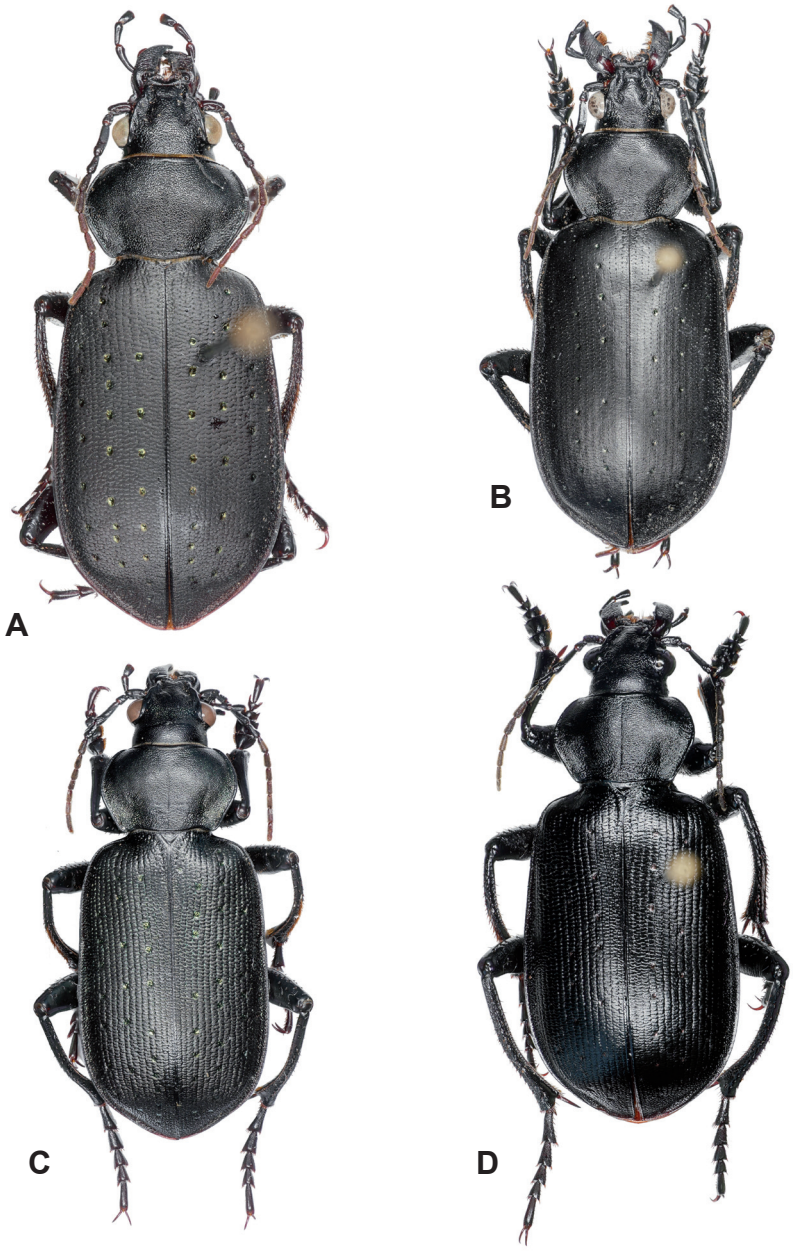

Fig. 9: *Calosoma maderae* ssp., habitus: (A) *auropunctatum*, Laaersberg, Vienna (Austria); (B) *maderae s.str.*, Canet-Plage (France); (C) *dsungaricum*, Orenburg Region (Russia); (D) specimen from Nature Reserve Pura (Israel), most probably from a transition zone between *dsungaricum* and *maderae* and/or *auropunctatum*.

26.iv.1974, E. Horovitz; 1♀ Dan, 30.iv.1974, E. Horovitz; 1♂ Dan, 16.vi.1974, E. Horovitz; 1♂ Dan, cotton field, vi.1979, E. Tzhori; 1♂ Hula Nature Reserve, 9.iv.1987, G. Muller; 1♀ Sede Nehemya [Huliyyot], 28.iii.1957; 1♀ Sede Nehemya, 16.iv.1960, Z. Shoham; 1♂ Sede Nehemya, 23.iv.1960, Z. Shoham; 2♀ Sede Nehemya, 2.ii.1962, 3.vii.1962; 1♀ Sede Nehemya, 1.vi.1968, H. Bytinski-Salz, light; 2♂ Sede Nehemya, 20.vi.1968, H. Bytinski-Salz, light; 1♂ Sede Nehemya, 20.iv.1967, Z. Shoham; 2♂ 1♀ Sede Nehemya, 15.v.1969, Z. Shoham; 1♂ 1♀ Sede Nehemya, Hawat Ramatayyim, 4.vi.1969, Z. Shoham, light trap; 3♂ Sede Nehemya, 8.vi.1972, Z. Shoham; *Upper Galilee*: 1♀ Ziv'on, meadow, 23.iv.2011, Th. Assmann (CAB); *Northern Coastal Plain*: 1♂ Nahsholim, sea coast, 19.v.2012, A. Orlov; 1♂ Kefar Glikson, 29.vii.1959; 1♂ Binyamina, 1.v.1965, M. Kaufshtein; *Central Coastal Plain*: 1♂ Kefar Vitkin, 18.iii.1940, A. Shulov; 1♀ Shefayyim, 4.iii.1990, E. Orbach; 1♂ Hod haSharon, 14.v.1993, A. Traub; 1♂ Hod haSharon, 1996, A. Traub; 1♀ Hod haSharon, 21.iii.1998, A. Traub; 1♂ Tel Aviv, xii.1960, Z. Ilan; *Southern Coastal Plain*: 1♀ Giv'at Brenner, 19.vii.1970, D. Gerling, light trap; 1♂ Neta'im, 8.vii.1972, Ch. Levinson; *Judean Foothills*: 1♂ 'Adullam, 3.iv.2003, U. Columbus, T. Levanony; *Judean Hills*: 1♂ Yerushalayim [Jerusalem], ii.1956; 1♀ Zur Hadassa, 31.iii.2001, Y. Mandelik; *Northern Negev*: 1♀ 1♂ Pura Nature Reserve, 210 m, 31.472°N 34.774°E, 1–18.iv.2010, C. Drees, pitfall (1♂ in CAB); 1♀ Gevulot, vii.2018, M. Zaytzov-Raz; 1♀ Hazerim, 16.v.1992, E. Orbach; 1♂ Be'er Sheva', 7.iv.2015, A. Orlov; *Central Negev*: 1♀ Ma'agar Yeroham, 450 m, 30.9833°N 34.8833°E, 8–20.v.2010, C. Drees, pitfall.

Observation records: 1♀ *Golan Heights*: Ya'ar Odem, Jubat el-Kabira, 24.iv.2011, Th. Assmann.

Distribution range: From Macaronesian Islands, Morocco and Portugal eastwards to India (incl. the Himalayas) and Central Asia, northwards to southern Scandinavia and southwards to the North and East Africa (Austin *et al.* 2008; Bruschi 2013).

Distribution range in southern Levant: Widespread, mostly in regions with the Mediterranean climate: Egypt (El-Akkad *et al.* 1998; Häckel 2017), although Alfieri (1976) mentioned that the species was wrongly reported from Egypt; Israel (from Upper Galilee to northern Negev: Bodenheimer 1937; pers. obs., SMNHTAU); Jordan (Bruschi 2013: Zarqa; Madaba: pers. obs.); Lebanon (Häckel 2017); and Syria (Bruschi 2013).

Taxonomic notes: Numerous taxa are now ranked as subspecies or older synonyms of *maderae* (Häckel 2017). Particularly, *C. m. auropunctatum* (Herbst, 1748) has been treated very controversially by numerous authors: as a junior synonym of *C. m. maderae* (Bruschi 2013; Cavazzuti 2017; Häckel 2017), as an independent species of its own (Jeannel 1940, 1941–1942; Casale *et al.* 1982; Forel & Leplat 2001; Arndt & Trautner 2006; Coulon *et al.* 2011), or as a subspecies (Breuning 1927; Lindroth 1985; Maguerre 2016) with some similarities to *C. m. dsungaricum* Gebler, 1833. Toussaint and Gillett (2018) reveal strong differences of mitochondrial and nuclear DNA sequences between the nominative subspecies and *auropunctatum*. The scale of variation at the given loci is comparable to some interspecific differences within the genus *Calosoma*. The molecular clock dates splitting of the two linages (*maderae s.str.* and *auropunctatum*) back to a few million years ago. Therefore, a revision (including molecular data) is needed to solve the taxonomic conundrum in this group. Genetic and phenotypic differences between *maderae s.str.* and *auropunctatum* prompt a separate discussion of the latter below. Häckel (2017) lists both *C. m. maderae* and *C. m. dsungaricum* from Cyprus and Syria, but only *maderae s.str.* for Egypt, Israel, Jordan and Lebanon. In fact, beetles from the southern Levant show moderately convex distinctly transversely wrinkled elytral

intervals. In *maderae s.str.*, the elytral intervals are nearly completely flattened and wrinkles are indistinct; in *auropunctatum*, the intervals are flat, but distinctly transversely wrinkled; in *dsungaricum*, the elytral intervals are strongly convex and distinctly transversely wrinkled (Fig. 7). The beetles from the southern Levant show an intermediate phenotype between *auropunctatum* or *maderae s.str.*, on one hand, and *dsungaricum*, on the other hand. Therefore, it is possible that the populations in the southern Levant represent a hybrid zone between two (or more?) subspecies. Bruschi (2013) indicates a contact zone between *maderae s.str.* and *dsungaricum* west of the southern Levant and classifies the beetles from the southern Levant as *dsungaricum*.

Calosoma olivieri Dejean, 1831

(Fig. 10)

Dispersal power: Macropterous, active flyer, attracted to light.

Habitat: An epigeic species in deserts (wadis with sparse vegetation), semi-arid steppes, dunes, also on arable fields (e.g. Madaba in Jordan) and between greenhouses (e.g. Be'er Milka in Israel).

Biology: A polyphagous predator, probably with a predilection for caterpillars (unpubl. data), also preys on *Schistocerca gregaria* (Jeannel 1940). The beetles are usually rare, but may occasionally appear in large numbers, so the general public becomes aware of the beetles, especially when they are attracted by light like it happened in 2019 in Israel (TOI 2019), Lebanon, Syria (Baladi 2019), northwards up to northern Syria and northern Iraq (Reuter pers. obs.). *Calosoma olivieri* occurs together with *C. maderae* only in habitats with semi-arid steppe climate. This corresponds to the habitat selection and distribution of both species in Morocco (Gourves 1997).

The 2019 outbreak spread over the entire Levant (Cyprus, Syria, Lebanon, Israel, Jordan) and the Arabian Peninsula (Saudi Arabia, Oman, Yemen), and lasted from the end of April to June. Swarms of beetles appeared at both day and night. Hundreds to thousands of beetles were flying and running everywhere in Israel, particularly in the south, while in the Arabian Peninsula, the beetles were so numerous, that their bodies covered roads and streets with such a thick black layer that required special cleaning efforts. The beetles did not cause any damage; however, members of general public complained of being attacked by beetles, bitten or "stinged". Wandering beetles entered everywhere, causing panic on agricultural farms, in industrial zones, hospitals etc. Some beetles entered into containers with fresh produce dispatched to Europe, were intercepted by the customs in the European ports of entry and nearly caused cancelation of the Israeli agricultural export. During 2020, i.e. after the outbreak, only a single specimen was collected by A.L.L. Friedman in the Central Negev.

Phenology: Adults active from February to June, but mainly in March and April.

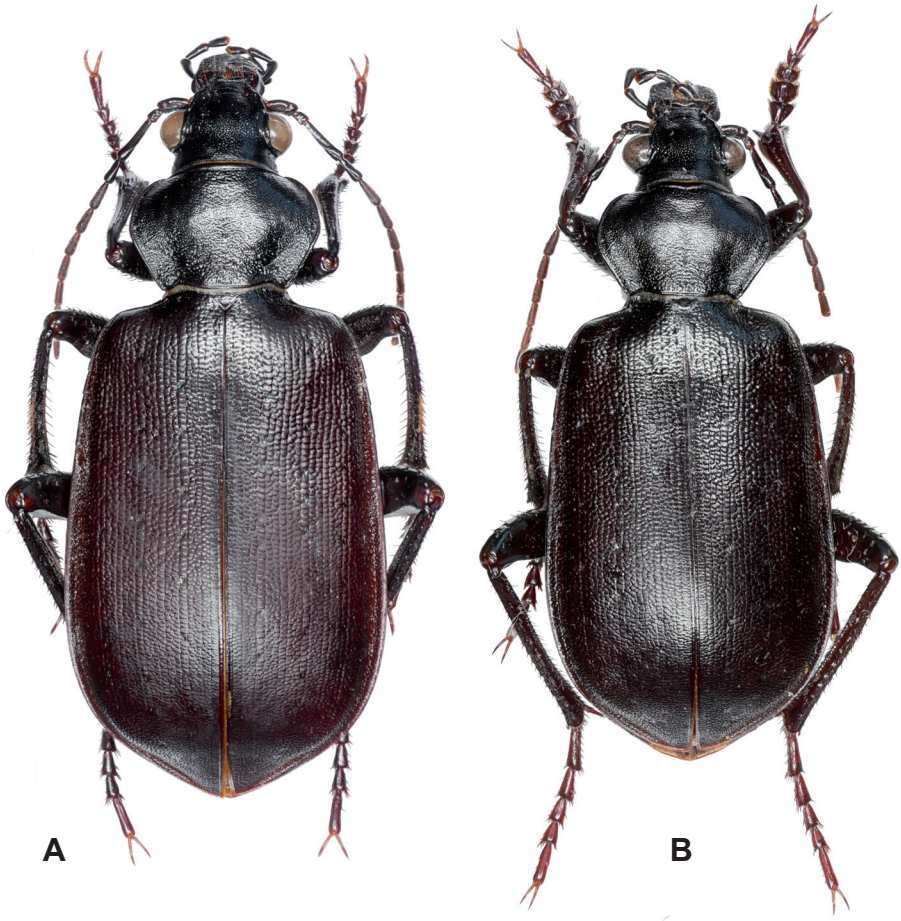

Fig. 10: *Calosoma olivieri*, habitus of female (A) and male (B), Shurjestan, Fars (Iran).

Material examined: Egypt: 1 ex., Sinai, Santa Katarina, 31.v.1975, H. Bytinski-Salz; 1♀ Sinai, Jebel Ahmar, 3 km S St Katherine, 23.iii.1975, B. Ben-Ya'aqov (SMNHTAU); 1♂ Cairo Governorate, El Maadi, 19.iv.1994, W. Ullrich (CWGP, Heinz/Wrase det.). **Iraq:** 1♂ Al Anbar Governorate, Western Desert, Wádí al Hazimi, 4–7.iv.1979, J. Macek (CWGP, Heinz det.). **Israel:** *Har Hermon*: 2♂ 1♀ Majdal Shams, 18.v.2001, V. Kravchenko, light trap; 5♀ Majdal Shams, 20.v.2001, V. Kravchenko, light trap; *Golan Heights*: 3♂ Merom Golan, 12.vi.2000, V. Chikatunov; *Upper Galilee*: 1♂ Har Kefir [Mt Kfir], 950 m, 7.v.1998, E. Orbach; 1♀ Birya, 11.iii.2009, E. Rotholz; *Lower Galilee*: 1♀ Kefar haHoresh, 8.iv.1987, Y. Dorchin; 2♀ Kokhav haYarden, 27.iii.2001, V. Chikatunov; *Carmel Ridge*: 1♂ Har Carmel, Haifa, Ahuza, 5.v.1998, E. Orbach; *Northern Coastal Plain*: 1♂ Qiryat Hayyim, 27.vii.2001, Y. Ptashkovsky, light, 1♂ 16.vii.2002, Y. Ptashkovsky, light; 1♂ 3♀ Ma'agan Mikha'el, 4.v.1998, A. Freidberg; *Hula Valley*: 1♀ Dan, cotton field, vi.1979, E. Tzhori; 6♂ 5♀ Kefar Szold, 5.v.1998, R. Ortal; 1♀ Ne'ot Mordekhay, 16.vii.1973, D. Furth, 1♀ 6.viii.1973, A. Schwartz; 1♀ Sede Nehemya, 19.ii.1963, Z. Shoham; 1♂ Sede Nehemya, 14.iii.1963, Z. Shoham; 1♀ Sede Nehemya, 30.v.1964, Z. Shoham; 1♂ Sede Nehemya, 5.vi.1969, Z. Shoham; *Central Coastal Plain*: 1♀ Netanya, South, Hof haSharon, 13.iv.2015, A. Orlov; 1♂ Apolonia, between coastal rocks, during strong storm, 15.iv.1957;

1♀ Bet Berl, 20.i.1967, M. Tzaba'; 2♂ 1♀ Hod haSharon, 5.v.1998, A. Traub, 1♂ 6.v.1998, A. Traub, 1♀ x.1991, A. Traub; 1♂ Tel Aviv, 3.v.1971, H. Bytinski-Salz; 2♂ 3♀ Tel Aviv, Ramat Aviv, 5.v.1998, Y. Orion; *Judean Hills*: 1♂ 1♀ Zur Hadassa, 28.iv.2001, V. Kravchenko, light trap; 1♂ Yerushalayim [Jerusalem], 29.i.1956, 1♀ 15.?.1956; 1♂ 1♀ Yerushalayim, center, 23.iv.2007, A. Orlov, night, under halogen lamp; 1♀ Yerushalayim, Gilo, 23.iv.2005, A. Orlov, soil trap, 1♂ 30.iv.2014, A. Orlov, evening, under street lamp; *Dead Sea Area*: 1♂ 'Enot Zuqim, 30.iii.1987, G. Muller; 1♀ Nahal Qumeran, 22.iii.1993, V. Chikatunov; 2♂ 'En Gedi, 28.ii.2003, V. Kravchenko, V. Chikatunov, light trap; 1♂ 'En Boqeq, 4.ii.1981, A. Freidberg; 1♂ Be'er Mash'abim [Bir Asluj], 19.ii.1971, Y. Yefenof; 1♂ Judean Desert, 6.iii.1972, Y. Yefenov; *Judean Desert*: 1♂ Judean Desert, 25.v.2002, V. Kravchenko; 1♂ Nahal Perat [Wadi Kelt], 23.iv.2003, V. Kravchenko, V. Chikatunov, light trap; 1 ex., Nahal Perat [Wadi Kelt], St. George Monastery, 29.iii.2012, Th. Assmann (CAB); 1♀ Mar Saba, 23.iv.2003, V. Kravchenko, V. Chikatunov, light trap; *Northern Negev*: 1♂ Lahav, 14.v.1964, Kamon; 2♂ Hazerim, iv.1988, E. Orbach; 1♂ Hazerim, 20.iii.1988, E. Orbach; *Central Negev*: 1♂ Ma'agar Yeroham, 1.iv.2014, L. Friedman; 1♂ Retamim, 5.vi.2003, 23.iv.2003, V. Kravchenko, V. Chikatunov, light trap; 1♀ 'En Zin, 27.ii.2001, V. Chikatunov; 1♀ Sede Boqer, 14.iv.2003, R. Hoffman; 1♀ Sede Boqer, 13.v.2006, I. Shtirberg; 1♂ Nahal Nafha; 1♂ Nahal Nafha [Wadi Nafh], 1.iv.1945, J. Wahrman; 1♀ Nahal Zin [Wadi Abyad], 24.iii.1952, J. Wahrman; 1♀ Borot Loz, 930 m, 23.ii.2020, L. Friedman; 'Ezuz, 1♂ 1♀ 5.vi.2003, 23.iv.2003, V. Kravchenko, V. Chikatunov, light trap, 1♀ 15.iii.2007, V. Kravchenko, light trap, 1♂ 23.iii.2007, V. Kravchenko, light trap; 1♂ 1♀ Upper Nahal Nizzana, 1.iv.1997, B. Krasnov; 1♀ Mizpe Ramon, 21.iii.2001, R. Hoffman; 1♂ Makhtesh Ramon [Machtesh Rimon], 18.iv.1968, D. Gerling; *Southern Negev*: 1♂ Nahal 'Amram, 23.iv.1962, J. Wahrman; 1♀ Elat, 23.v.1962, J. Wahrman; 1♀ Elat, 13.iv.1998, L. Fishelsohn; *Arava Valley*: 2♀ 'Iddan, "Voice of America" fields, 14.iv.1999, V. Kravchenko, I. Yarom, light trap; 1♂ Hazeva, 9.iii.1979, D. Furth; 1♀ Hazeva, 13.iv.1998, V. Kravchenko; 1♂ Hazeva Field School, 9.v.1998, E. Ashkenazi, Malaise trap; 1♀ Hazeva Nature Reserve, wadi, -170 m, 9–23.iv.2010, C. Drees; 1♀ Shezaf Nature Reserve, 14.iv.1999, v. Kravchenko, I. Yarom, light trap; 1♀ Shezaf Nature Reserve, 26.i.2001, V. Kravchenko, light trap; 1♂ Be'er Menuha [Bir Maliha], 20.iii.1953, J. Wahrman; 1♂ 1♀ Gerofit, 7.i.2004, D. Utchitel, V. Chikatunov; 1♀ Gerofit, 11.i.2004, E. Topel, V. Chikatunov; 1♂ 1♀ Gerofit, 24.iii.2007, V. Kravchenko, light trap; 1♂ 'En Yotvata [Ein Radian], 24.iv.1957, L. Fishelsohn; 1♀ 'En Yotvata, 20.iii.2001, V. Kravchenko, I. Yarom, light trap; 1♂ 1♀ 'En Yotvata, 17.iv.2004, U. Shanas, V. Chikatunov; 1♀ Elifaz, iii–vi.2003, E. Topel, V. Chikatunov; 2♂ Timna', 3.iv.1997, V. Chikatunov; 1♀ Be'er Ora [Ora], 3.iv.1997, V. Chikatunov (all SMNHTAU). **Syria:** 1♀ Homs Governorate, Palmyra, fields of ruins, 24.iv.1996, L. Behne (CWGP, Wrase det.).

Observation data: Israel: Numerous specimens were seen by Th. Assmann, mainly in the *Eastern Northern Negev Sand Dunes*: Ya'ar Ramat Beqa', 17.iii.2013, iii.2018, Shunera Sands, 19.iii.2013, Shivta, iii.2018, Be'er Milka, iii.2018, 'Agur Sand, iii.2018, and in the *Central Negev*: Sede Boqer, iii.2018, Mizpe Ramon, iii.2018. **Jordan:** Al-Azraq-Lodge, 12.iii.2013, Th. Assmann (CAB); Wadi Rum, Touristique Village, 14.iii.2013, Th. Assmann.

Records during the outbreak in 2019: Israel: *Har Hermon*: 1♂ 1♀ Har Hermon, Geva'ot haQerav, 2070 m, 1.v.2019, T. Marcus; 2♂ Har Hermon, 1600 m, 14.iv.2019, G. Sinaiko; *Hula Valley*: 1♂ HaGosherim, Rt. 99, Nahal Senir, 14.iv.2019, G. Sinaiko; *Upper Galilee*: 4♂ 4♀ Karmi'el, 29.v.2019, U. Shalom; 1♂ 2♀ Mahanayim, gas station, 1.v.2019, T. Marcus; *Northern Coastal Plain*: 6♂ 7♀ Baqa el Gharbiya, 29.iv.2019, U. Shalom; *Samaria*: 1♂ Qedumim, 30.iv.2019, L. Friedman; *Jordan Valley*: 6♂ 4♀ Gadot, 29.iv.19, R. Shafir; *Central Coastal Plain*: 2♂ Netanya, 15.v.2019, O.T. Netanel; 1♀ Giv'atayim, 29.iv.2019, E. Morgulis; 1♂ 1♀ Bat Yam, 29.iv.2019, A. Weinstein; *Judean Hills*: 2♂ 4♀ Bet Shemesh, 28.iv.2019, U. Shalom; 8♂ 8♀ Yerushalayim [Jerusalem], Mahane Yehuda Market, Bet Alliance, 29.iv.2019, T. Marcus; *Dead Sea Area*: 1♀ 'En Gedi, 1.v.2019, D. David; *Northern Negev*: 3♂ 2♀ Ne'ot Hovav, 29.iv.2019, I. Ornan. **Jordan:** 1♂ Tutun, 12.ii.1999, I. Yarom, light; 1♂ Southern 'Arava Valley, 25.ii.2004, U. Shanas, V. Chikatunov (SMNHTAU); American University Madaba, iii.2013, Th. Assmann (CAB); Madaba Governorate, Madaba, American University env. S Madaba, ca 780 m, 31°39.056'N 35°47.664'E (field edges/perennial ruderal herbs/under stones/plants), 19.iii.2016, Wrase, Laser [01] (2♂ 1♀ CWGP, Wrase/Häckel det.); same data, but 31.iii.2016 (1♂ CWGP, Wrase det.; 1 ex. Th. Assmann, CAB).

Distribution range: From Azores and Cape Verde Islands to Pakistan, southwards to Mauretania and Oman, northwards to south-eastern Spain and Sicily (Bruschi

2013). The records from Sicily probably reflect immigration events from populations of the desert belt in the south.

Distribution range in southern Levant: Egypt (incl. Sinai), Israel, Jordan, Lebanon, Syria (Chikatunov *et al.* 2006; Bruschi 2013; Häckel 2017; Nasir & Katbeh-Bader 2017). In Israel, the species occurs throughout the country, from Mt Hermon to Elat, but more common in the southern, eremic part of Israel (Judean Desert, Dead Sea Area, the Arava Valley and the Negev Desert). It is unclear if records from northern Israel represent reproduction habitats or migrants from the south.

Taxonomic notes: Beetles from our material from Egypt, Israel, Jordan, Syria and Iraq are almost black, with only small foveae on the elytra having mostly a metallic hue (chiefly blue or green). Beetles from the Arabian Peninsula may also have a general metallic hue on the elytra (see Felix 2009: fig. 11).

Calosoma sycophanta (Linné, 1758)

(Fig. 11)

Dispersal power: Macropterous, flight active (Lindroth 1985, 1986). In Israel known from light trapping at middle altitudes of Mt Hermon.

Habitat and natural history: Both larvae and adults are arboreal in deciduous and coniferous woodlands, abundant especially during caterpillar outbreaks (Burgess & Collins 1917; Trautner 2017). In Israel, the species prefers stands with oak species (especially *Quercus libani*, *Q. cerris* and *Q. boisieri*). In Jordan, the two known specimens came from an oak forest close to Jarash (Nasir & Katbeh-Bader 2017), where *Quercus calliprinos* occurs. Basic life history and ecology aspects of *C. sycophanta*, including a life span up to 4 years, are described by Burgess (1911*a*, *b*), Burgess & Collins (1915, 1917) and Nolte (1938). The species is favoured by outbreaks of gypsy moth (*Lymantria dispar*) and makes a substantial impact on gypsy moth population density, at least in North America (Bess 1961; Campbell 1975; Weseloh 1985*a*, *b*, 1988, 1990). In Turkey, *C. sycophanta* beetles feed on numerous moth species, including pine processionary moth (*Thaumetopoea pityocampa*), and may regulate outbreaks of moth species (Kanat & Mol 2008, and references therein) and are used as biocontrol agents (Kanat & Özbolat 2006).

Phenology: In Europe and North America, a spring and early summer breeder with larvae during late spring and summer, adults hibernate (Burgess 1911*a*; Lindroth 1985, 1986). In Israel, observed and collected from April to June, mainly in May.

Material examined: Syria or **Lebanon:** 1♂ 'Syria, Reitter'. **Israel:** 1♂ 'Palaestina', Reitter; *Har Hermon*: Har Hermon: 1♀ 2200 m, 2.vi.1993, V. Chikatunov, 1 ex. (elytra), 2100 m, 17.v.2009, L. Friedman; Har Hermon, 2000 m: 1♂ 10.vi.1977, Y. Hadar, 1♀ 10.vi.1992, R. Kasher, 1♂ 1♀ 25.v.1996, R. Hoffman, 1♀ 12.vi.1996, A. Freidberg, 1♂ 15.v.2001, D. Simon; Har Hermon: 1♀ 1800 m, 12.vi.2003, L. Friedman, 1♀ 1600 m, 17.v.2001, R. Hoffman, 1♂ 1500 m, 21.v.1992, R. Kasher, 1♂ 1500 m, 30.v.1992, E. Oren; 1♀ Majdal Shams, 18.v.2001, V. Kravchenko; 1♂ 1♀ 'Syrien, Kaifa' [N Israel, probably Galilee], Reitter (all SMNHTAU); *Carmel Ridge*: Haifa, Mt Carmel, 11.vi.2012, B. Orbach (COQ).

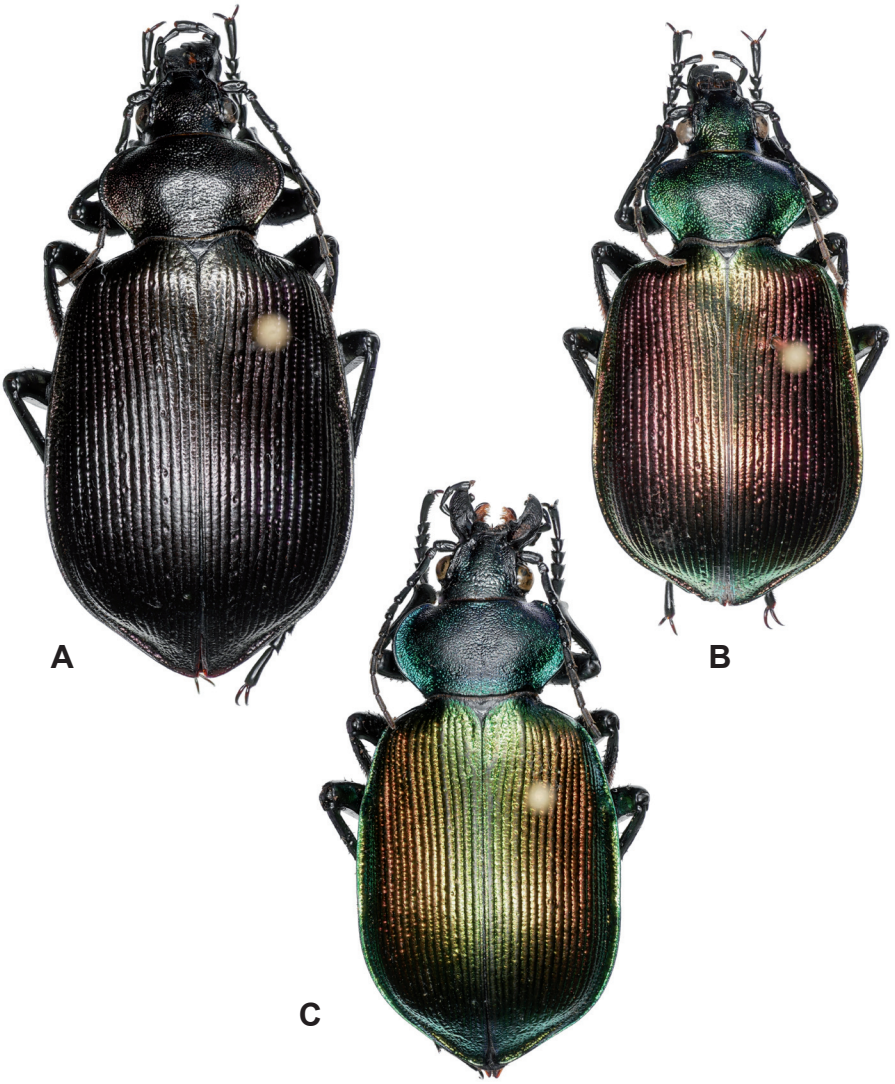

Fig. 11: *Calosoma sycophanta*, females, habitus from (A) Fethiye (Turkey), (B) Vrontamas (Greece) and (C) Taza (Morocco)

Distribution range: From Mauretania to Central Asia, northwards to Central Europe (Germany, Poland; records from Scandinavia and Britain are interpreted as accidental visitors; Lindroth 1974, 1985, 1986; Luff 2007), southwards to North Africa (Mediterranean climate zone) (Bruschi 2013; Häckel 2017). West Siberia is considered a recent range expansion (Stolbov *et al.* 2018). As an antagonist of *Ly-*

mantria dispar (Burgess 1911*a*), the beetle has been successfully introduced to North America, where its distribution range is still expanding (Schaefer *et al.* 1999).

Distribution range in southern Levant: Egypt (after Häckel 2017, but no records given by Alfieri (1976) and Abdel-Dayem (2004)), Jordan (Nasir & Katbeh-Bader 2017), Israel (only known from Carmel Mountains and Mt Hermon; Ptashkovsky (2013) also reports this species but there are no records in his collection), Syria (Bruschi 2013).

Conservation: In Central Europe, the species is threatened and its population is significantly waning (Luka *et al.* 2009; Schmidt *et al.* 2016). A similar decline has also been observed at least in the south-western part of the distribution range (pers. obs. in Spain and Italy). A strong sensitivity of beetles towards some pesticides may be the reason for the population drops (cf. Görn 2019).

DIS\CUSSION

The *Calosoma* fauna of the Levant has certainly not been exhaustively studied yet. This is illustrated not least by the few records of some species, both in literature and in the studied collections. However, we can identify trends in the frequency of records for the two commonest caterpillar hunting beetle species, *C. maderae* and *C. olivieri*. Both species are known from the Levant for a long time (Schatzmayr 1936), especially from Israel (Bodenheimer 1937). We know 27 records of *C. maderae* before 2000 and only 9 after 1999. For *C. olivieri*, the number of records are 44 and 59 (each site is only counted once per year and species, the single record from Iraq is excluded) before 2000 and after 1999, respectively. While the number of records of *C. maderae* has dropped after the turn of the century, those of *C. olivieri* has increased. Even when the 2019 records are excluded, there are significantly more records from the year 2000 and afterwards for *C. olivieri* (44) than for *C. maderae* (9).

We hypothesize that the changes in the frequencies of records may be influenced by climate change (cf. Shohami *et al.* 2011) or other drivers (e.g. increasing land-use of deserts and dunes). The highly mobile and flight-active caterpillar hunting beetles are likely to react faster to such changes than many other organisms. *Calosoma maderae s.l.* occupies a predominantly Mediterranean-temperate climate niche, and it presumably shows a poleward shift or a decreasing trend in population density at the edge of its distribution range (Brandmayr & Pizzolotto 2016; but cf. Hampe & Petit 2005). Another flight-active ground beetle, *Agonum viridicupreum* (Goeze, 1777), does not show a poleward shift of its distribution range in the southern Levant (Drees *et al.* 2011). *Calosoma olivieri* is rather characterized as a species of desert and semi-arid steppe habitats (see literature cited in species accounts). However, at least the latter species can be found all over Israel, esp. during the last years. This range extension fulfils the assumption of a poleward shift of the leading edge of the distribution range.

Such interpretation of collection data, as we present them here, can undoubtedly be criticized, since the study intensity can vary over the decades and regions under consideration. However, statistical tools have been recently employed to consider such biases in data analysis (Isaac *et al.* 2014; Bowler *et al.* 2020). Furthermore, there is an option to conduct long-term studies with pitfall traps (Brooks *et al.* 2012; Homburg *et al.* 2019; Hallmann *et al.* 2020). Thus, trends in changes of population densities and distribution ranges can be better documented.

Moreover, it also seems important to work on larvae of *Calosoma* species. They can easily be found, and those of *Calosoma maderae* and *C. olivieri* have been known for more than a century (Mayet 1887). Evidence of the larval and teneral specimens can be used to show whether the species in question develop in the relevant sites. This makes it easier to distinguish indigenous populations from migrating individuals, which are well known for many *Calosoma* species (see species accounts). This information helps to understand how Middle Eastern ground beetles react to the global change conditions.

ACKNOWLEDGEMENTS

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