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A revision of the genus *Cholovocera* Victor, 1838 (Coleoptera: Endomychidae)

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Abstract. We revise all the species of the genus *Cholovocera* Victor, 1838 (Coleoptera: Endomychidae), with descriptions, illustrations and complete synonymies, based on the examination of 1878 specimens of *Cholovocera* and a few beetles of other genera, collected by the senior author and from museum collections, including primary types. We recognise eight valid species, resurrecting three species from synonymy, sinking three as new junior synonyms, and describing a new species. Geographic distributions and a key for the identification of all the species are also given. Species which have been incorrectly associated with *Cholovocera* are listed and discussed.

Keywords. *Cholovocera*, Coleoptera, Endomychidae, revision, myrmecophily.

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Introduction

The species of the genus *Cholovocera* Victor, 1838 are minute myrmecophilous beetles belonging to the coleopterous family Endomychidae. Notwithstanding their small size and subterranean way of life in close relationship with ants, *Cholovocera* beetles have been frequently collected by many entomologists, who have studied and recorded them in many publications (e.g., Tomaszewska 2000, 2010; Shockley *et al.* 2009a; Rücker 2018, 2020). However, the genus concept and which species are included in it have not yet been completely clarified, with conflicting opinions regarding generic allocations and species delimitations. The main reason for the lack of unequivocal species recognition has been the use of external characters, such as colour, size and surface punctation, which are variable within species and not clearly different among species.

The genus *Cholovocera* and one species, *Ch. formicaria*, were described by Victor (1838) from the Caucasus Region. A second species, *Ch. punctata*, was described by Märkel (1845) from the Mediterranean

Basin, characterised by a heavier punctation than that of *Ch. formicaria*. Since then, all specimens with a dense punctation were identified as *Ch. punctata*, and further new species were differentiated by having intermediate external characters of dubious taxonomic value. Assessing internal morphological features to distinguish species, such as male and female genitalia, began in the 20th century, but only partially. For example, male parameres have not been described in detail yet, and female spermathecae have not been used at all. The result has been a great deal of misidentifications, both in publications and in museum collections. Therefore, we believe that a complete taxonomic revision of all taxa associated with *Cholovocera* is necessary to clarify the status and number of species which belong to this genus, as well as other nominal species which have been incorrectly placed in *Cholovocera*.

In this paper, we propose a new taxonomic arrangement that will allow the differentiation and identification of the eight species of *Cholovocera* which we recognise as valid. To achieve such arrangement, we have:

1. revised all relevant literature pertinent to *Cholovocera*, regarding taxonomy, morphology, biology, ecology, distributions and synonymies;
2. made a detailed study of the external and internal morphology, with particular attention to the genitalia of both sexes;
3. determined which characters have taxonomic value to define the genus and the species;
4. proposed new synonymies and resurrected species hitherto regarded as junior synonyms, based on our newly defined species concept;
5. given updated geographic distributions and ant-beetle associations for all species;
6. included a key for the identification of adults of all the species (except for the male of *Ch. afghana*);
7. listed and discussed species which, according to our definition of the genus, have been incorrectly associated with *Cholovocera*.

Material and methods

A total of 1878 specimens of *Cholovocera* and some of other genera were examined dry mounted, except where otherwise indicated. A great number of beetles of both sexes were dissected to examine their appendices and genitalia in detail. For that purpose, dry specimens were rehydrated for about 12 hours. Male genitalia were extracted in situ, if possible, trying to maintain intact the abdominal segments. Female abdomens were completely sectioned from the rest of the body. Dissected genitalia were treated with hot 10% solution of KOH for a few minutes. The macerated pieces were washed with distilled water, and mounted temporarily in lactic acid on cavity slides for their examination under the microscope. Female genitalia were left in lactic acid for two to three days to allow the distension of the spermatheca. Whole specimens, abdominal sclerites, antennae, and legs were treated in the same way and mounted temporarily in Hoyer's medium. After their examination, all dissected structures were glued on the mounting card of the original specimen, with the male genitalia on the right side and the female genitalia in the centre behind the remaining parts of the beetle. This standard procedure allows an easy identification of the sex of each specimen, and rapid finding of dissected parts.

Body measurements were made with an ocular micrometre under a stereoscopic microscope, and measurements of dissected parts using a micrometre slide under a compound microscope. Line drawings were prepared with the aid of a camera lucida attached to a Nikon Eclipse E600 microscope. Habitus photographs were taken with a Nikon DS-U2 unit camera attached to a Leica MZ9S stereomicroscope, assembled using the CombineZP freeware program, and subsequently processed with Adobe Photoshop 5.0. Distribution maps were taken from Bright Blue Marble Next Gen (Visible Earth Project, NASA) downloaded from https://visibleearth.nasa.gov/images/74042/may-blue-marble-next-generation/74062l with modifications made using Adobe Photoshop 5.0.

In the material examined, label data may have added comments, locality remarks and translations from other languages into English. These additions are placed in squared brackets ([ ]).

Abbreviations used in figures

aa = tentorial anterior arms
bp = aedeagal basal piece
co = spermathecal cornu
da = tentorial dorsal arms
ed = aedeagal ejaculatory duct
el = elytron
ep = epipleuron
fl = femoral line
fo = aedeagal foramen
hp = hypomeron
hw = hindwing
la = laminatentorium
ml = aedeagal median lobe
ms = mesosternum
mt = metasternum
no = spermathecal nodulus
pa = tentorial posterior arms
pe = perithecium of thallus
pg = proctiger
pm = paramere
pp = paraproct
pr = pronotum
ps = prosternal process
ra = spermathecal ramus
sc = scutellum
sd = spermathecal duct
sg = spermathecal gland
sk = stalk of thallus
sr = aedeagal sclerotised ring
st = stylus
V1–V5 = visible sternites
va = valvifer
vp = ventral pits

Abbreviations for repository institutions of the material examined and the names of people in charge of such collections, who kindly made their specimens available for our study:

BMNH = The Natural History Museum, London, United Kingdom (Data Portal: Museum's Research and Collections Data)
CDUM = J.A. Delgado Collection, Universidad de Murcia, Murcia, Spain
CMUS = Univerzitet Sv. Kiril i Metodij [Saints Cyril and Methodius University], Skopje, North Macedonia (V. Krpach)
CNHM = Hrvatski Prirodoslovni Muzej [Croatian Natural History Museum], Zagreb, Croatia (V. Mičetić)
HNHM = Magyar Természettudományi Múzeum [Hungarian Natural History Museum], Budapest, Hungary (O. Merkl)

MCNM = Museo Nacional de Ciencias Naturales [National Museum of Natural Sciences], Madrid, Spain (M. París)
MCVR = Museo Civico di Storia Naturale [Civic Museum of Natural History], Verona, Italy (L. Latella & R. Salmaso)
MFNB = Museum für Naturkunde [Museum of Natural History], Berlin, Germany (B. Jaeger)
MHNG = Muséum d'Histoire Naturelle [Museum of Natural History], Genève, Switzerland (G. Cuccodoro)
MNHS = Prirodoslovni Muzej [Museum of Natural History], Split, Croatia (B. Kokan)
MZLU = Biological Museum, Lunds Universitet, Lund, Sweden (C. Fägerström)
NHMB = Naturhistorisches Museum [Museum of Natural History], Basel, Switzerland (M. Borer)
NHMW = Naturhistorisches Museum [Museum of Natural History], Wien, Austria (M. Jäch)
NKME = Naturkundemuseum Erfurt, [Museum of Natural History Erfurt] Erfurt, Germany (M. Hartmann)
NMPC = Národní Muzeum [National Museum], Prague, Czech Republic (J. Hájek)
SDEI = Senckenberg Deutsches Entomologisches Institut [Senckenberg German Entomological Institute], Müncheberg, Germany (M. Schröeder & L. Behne)
SFUN = Senckenberg Forschungsinstitut und Naturkundemuseum [Senckenberg Research Institute and Museum of Natural History], Frankfurt am Main, Germany (A. Hastenpflug-Vesmanis)
SMNH = Prirodoslovni Muzej Slovenije [Slovenian Museum of Natural History], Ljubljana, Slovenia (T. Trilar)
SMTD = Staatliches Museum für Tierkunde [State Museum of Zoology], Dresden, Germany (K-D. Klass & O. Jaeger)
SNSB = Staatliche Naturwissenschaftliche Sammlungen Bayerns [State Natural Science Collections of Bavaria], München, Germany (D. & M. Balke)
ZFMK = Zoologisches Forschungsmuseum Alexander Koenig [Zoological Research Museum Alexander Koenig], Bonn, Germany (D. Ahrens)
ZMUM = Zoologicheskiy muzey Moskovskogo gosudarstvennogo universiteta imeni M.V. Lomonosova [Zoological Museum of Lomonosov State University], Moscow, Russia (A.A. Gusakov).

Results

Family Endomychidae Leach, 1815

Papers by Tomaszewska (2000, 2010) deal with the morphology, phylogeny, classification and history of this family. Traditionally, Merophysiinae and Endomychidae were treated as separate families which together with Coccinellidae and other minor families formed the Cerylonid series of the Superfamily Cucujoidea (Crowson 1955). However, recent molecular research by Robertson *et al.* (2015) showed that Cucujoidea is not monophyletic, and the family Endomychidae was redefined. The subfamilies Eupsilobiinae, Mycetaeinae and Anamorphinae were excluded from Endomychidae, being elevated to family level. Endomychidae is currently included in the superfamily Coccinelloidea, close to Coccinellidae (Kovář 1973; Robertson *et al.* 2015; Zhang *et al.* 2018).

Subfamily Merophysiinae Seidlitz, 1872

Members of this subfamily are small, ranging from one to three millimetres, and are defined by (1) absence of adult cephalic corpotentorium, (2) adult labial palpomere 2 oval or inflated, and (3) absence of larval stemmata (Tomaszewska 2010). Recent molecular studies support the monophyly of this subfamily (Robertson *et al.* 2015). Shockley *et al.* (2009b) gave the more recent generic classification within Merophysiinae, comprising 12 genera and more than 100 species, with the greatest species diversity in the Old World. Nevertheless, Rücker (2018, 2020) maintains the view that this subfamily should be regarded as a family.

Taxonomy

Class Insecta Linnaeus, 1758
Order Coleoptera Linnaeus, 1758
Superfamily Coccinelloidea Latreille, 1807
Family Endomychidae Leach, 1815
Subfamily Merophysiinae Seidlitz, 1872

Genus ***Cholovocera*** Victor, 1838

Cholovocera Victor, 1838: 177, pl. 3 fig. b.

Choluocera – Kraatz 1858: 140. Unnecessary replacement name.
Coluocera – Gemminger & Harold 1868: 905. Unjustified emendation.
Colovocera – Belon 1879: 185. Misspelling.

Type species

Cholovocera formicaria Victor, 1838 (by monotypy).

Remarks concerning authorship

Victor Ivanovich de Motschulsky (1810–1871) published papers under two names: "Victor, T." and "Motschulsky, V. de" (also spelt "Motchoulsky"). However, various authors in many publications cited his name incorrectly, usually "Motschulsky" instead of "Victor". In the case of *Cholovocera*, we agree with Sherborn (1926: 2483) and Jäch *et al.* (2016) in that "Victor" is the correct name of the author, and not "Motschulsky" as given in many publications.

Taxonomic history

The description of *Cholovocera* by Victor (1838) is accurate, except where he incorrectly described as bifid the last tarsomere of all legs. However, he correctly illustrated that tarsomere in his fig. b1. Conversely, although not mentioned in the text, his fig. b shows the length of all ventrites shorter than the metasternum, which is incorrect (Fig. 1), and his fig. b3 shows ten antennomeres when, in fact, there are only eight (Fig. 2C). Erichson (1845: 125) included *Cholovocera* in the Coccinellidae, Redtenbacher (1858: 380, 1874: 411) and Reitter (1875: 301) redescribed the genus, repeating the incorrect number of ten antennomeres, an error corrected to eight by Schaufuss (1876a: 394) and confirmed by Reitter (1877: 2). Des Gozis (1881: 142) translated Reitter's (1875) paper into French, adding references and comments on morphology, correcting the number of antennomeres to eight, and including keys for the identification of genera and species. Both Ganglbauer (1899: 821) and Belon (1902: 5) redescribed *Cholovocera* again, reviewing the confusion about the number of antennomeres, and Belon (1902) added a list of known species and their distribution.

Rücker (1980: 142) published the first comprehensive revision of *Cholovocera*, comprising six species with their geographic distribution and a dichotomous key for their identification, including illustrations of male genitalia. Shockley *et al.* (2009b: 64), in their checklist of the world species of Endomychidae, listed the species of *Cholovocera* which they recognised as valid, including some junior synonyms (see below under Species included in *Cholovocera*). Recently, Rücker (2018), in his revision of the western Palearctic Merophysiidae, published a key to the genera of that family, including *Cholovocera*, as well as descriptions, illustrations and a key to identify the species he placed in this genus. As will be shown below, our concept of a valid species of *Cholovocera* differs greatly from that of Rücker (2018: 568).

Species included in Cholovocera

Shockley *et al.* (2009b: 65) listed nine species in *Cholovocera*, including one which we consider to be a new junior synonym (*Ch. major*) and two which we do not regard as belonging to *Cholovocera* (*Coluocera beloni* Wasmann, 1899 and "*Cholovocera*" *brevicornis* Johnson, 1977). Further, Shockley *et al.* (2009b: 65) regarded as junior synonyms two species which we consider valid: *Ch. formiceticola* (Rosenhauer, 1856) and *Ch. gallica* (Schaufuss, 1876). Considering the ten species included in *Cholovocera* by Rücker (2020: 34), we only agree with five of them. We do not recognise two species from the Neotropical Region (*Pseudevolocera atomarioides* Champion, 1913 and *Coluocera ecitonis* Wasmann, 1890) and one from Afghanistan ("*Ch*". *brevicornis*) as belonging to *Cholovocera*, and we regard *Co. formicaria major* Reitter, 1887 and *Co. punctata sardoa* Reitter, 1911 as new junior synonyms. Furthermore, we consider as valid, three species which were listed by Rücker (2020: 34) as junior synonyms: *Ch. balcanica* (Karaman, 1936), *Ch. formiceticola* and *Ch. gallica*. Finally, we found that *Co. fleischeri* Reitter, 1902 is a new junior synonym of *Ch. gallica,* and we describe one new species.

In conclusion, from our examination and study of 1878 specimens of *Cholovocera*, including types, we recognise eight valid species in *Cholovocera*: one new to science, three with new status and three junior synonyms, as follows:

Cholovocera formicaria Victor, 1838
Cholovocera subterranea Motchoulsky, 1845
Coluocera formicaria v. *major* Reitter, 1887. **Syn. nov.**
Cholovocera punctata Märkel, 1845
Coluocera punctata sardoa Reitter, 1911. **Syn. nov.**
Cholovocera formiceticola (Rosenhauer, 1856). New status
Cholovocera attae (Kraatz, 1858)
Cholovocera gallica (Schaufuss, 1876). New status
Coluocera fleischeri Reitter, 1902. **Syn. nov.**
Cholovocera balcanica (Karaman, 1936). New status
Cholovocera afghana Johnson, 1977
Cholovocera occulta Delgado & Palma sp. nov.

Generic descriptions

Adults, both sexes

Considering the morphological similarity among all the species of *Cholovocera*, this generic description includes diagnostic characters which will not be repeated in the species descriptions, but which will be mentioned only when they are diagnostic for species differentiation.

Total length, average 1.30 mm (range 1.20–1.60 mm). Body elliptical and dorsally convex, reddish-brown, with shiny smooth surface, finely punctured and slightly pubescent; setation decumbent and more evident ventrally (Fig. 1).

Head. Rounded, slightly shorter basally and retracted into prothorax behind eye level (Fig. 3A). Eyes reduced to a single, prominent facet, protected by a lateral rim (Figs 1A, 3A, 24E). Antennae short, securiform, about 1/3 longer than head, eight-segmented: scape geniculate, antennomeres 1 and 2 long, 3 to 6 isodiametric, and terminal antennomere forming a subtriangular club, depressed dorsoventrally (Fig. 2C). Antennae inserted ventrally, and basally concealed by projections of frons, with the possibility of retracting in a ventral depression of the prothorax (Fig. 1B: hp). Fronto-clypeal ridge strongly curved laterally; clypeus transverse, flat. Epipharynx with well-developed tormae (Fig. 2B). Labrum not visible from above, punctured, disc covered by sparse setae; anterior margin almost devoid of setae and

lateral borders with a row of moderately long, recurved setae (Fig. 2A). Mandibles asymmetrical: right mandible with a semi-membranous, well-developed prostheca, several sclerotised teeth on its apical tip and some fringed sclerotised projections on the remainder of its external margin; penicillus well-developed (Fig. 2F). Left mandible with mola narrow, curved, without sclerotised teeth, with long, slender trichomes on its external margin, bearing a brush-like penicillus (Fig. 2E). Maxillae with a terminal palpomere as long as next two palpomeres combined, subcylindrical, rounded at apex and with many distal sensilla. Galea moderately broad, approximately three times as wide as the lacinia, with long broad apical spines and a developed subapical seta. Lacinia elongate, with some mesal spines (Fig. 2D). Labium with palpomere 1 slightly larger than palpomere 2, cylindrical, only moderately inflated; terminal palpomere subtriangular, with a row of sensilla at apex (Fig. 2G). Mentum transverse, with a middle large, triangular area finely punctured, disc covered with short and sparse setae (Fig. 2G). Prementum globose, membranous, with the sides of the ligula slightly lobulated (Fig. 2G). Hypopharynx lobulated distally (Fig. 2H). Tentorium (Fig. 3A–B) connected with base of head capsule by two inconspicuous posterior ventral pits (Fig. 3A: vp); with anterior arms well developed (Fig. 3A–B: aa); distal ends of anterior arms divergent, basal areas expanded and fused forming a laminatentorium (Fig. 3A: la); dorsal arms short (Figs 3A: da, 3B: da); posterior arms wide (Figs 3A: pa, 3B: pa); corpotentorium absent.

Thorax. Pronotum transverse, widest at base (Fig. 1A: pr); pronotal disc convex; surface coarsely and sparsely punctured; base of pronotum with a pair of small, dark, rounded shallow cavities; anterior margin sinuous with slightly produced, blunt angles; posterior angles obtuse, lateral margins sharply carinated (Fig. 1A). Prosternal process shaped as an hourglass (Figs 1B, 4), well developed and

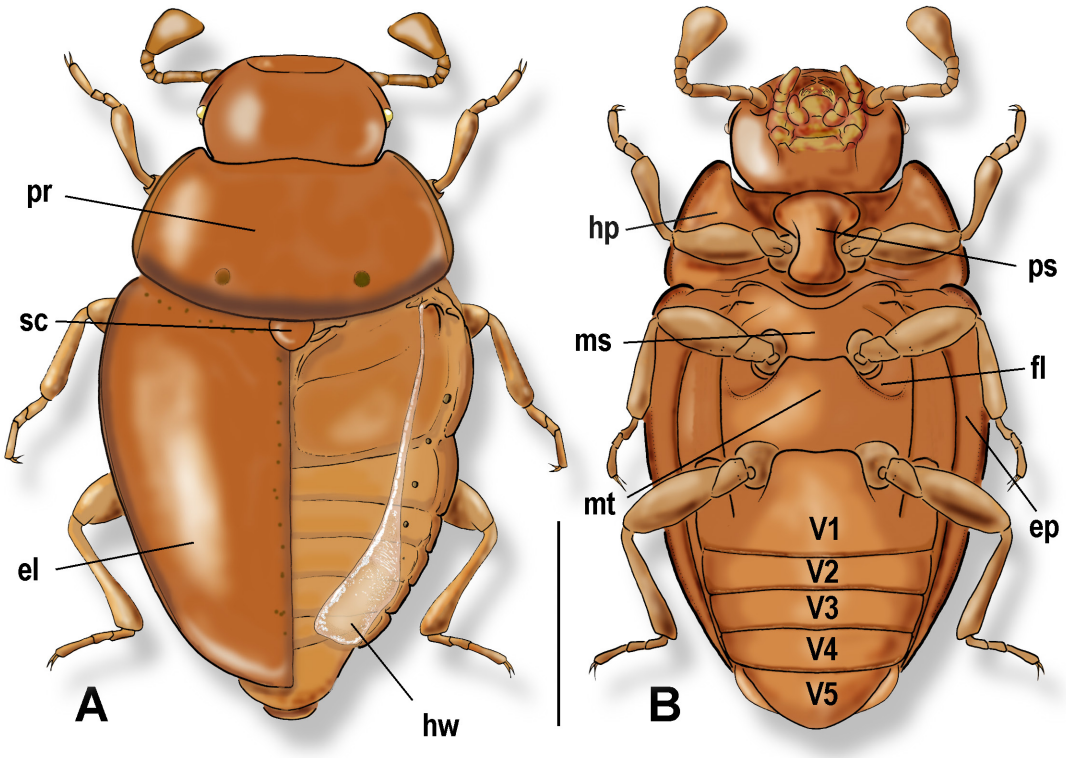

Fig. 1. General aspect of a stylised female of *Cholovocera* Victor, 1838. **A**. Dorsal view. **B**. Ventral view. Abbreviations: see Material and methods. Scale bar = 0.5 mm.

separating the precoxae; in natural position, the prosternal process extends anteriorly concealing the base of the head (Fig. 1B). Hypomeron wide, with a pair of cavities, where the distal antennomeres can be retracted (Fig. 1B: hp). Scutellum visible, subtriangular, with rounded vertices (Fig. 1A: sc). Mesosternun with an anterior depression which accommodates the posterior border of the prosternal process (Fig. 1B: ms). Elytra oval, convex, finely punctured (Fig. 1A: el); epipleuron broad at base, narrowing towards apex, incomplete apically (Fig. 1B: ep). Hind wings highly reduced, narrow basally, without any trace of venation and with a subquadrate distal portion (Figs 1A: hw, 3C). Metasternum transverse (Fig. 1B: mt); femoral lines distinct, complete (Fig. 1B: fl). Legs compressed dorsoventrally: coxae circular in outline; trochanters broad and stout; femora sparsely setose; tibiae setose on the distal half, with an apical fringe of stout setae, and variable across species, from short, stout with straight sides to long, slender with sinuous sides; tarsi tri-segmented: tarsomeres elongate; claws simple; empodium (pretarsus) well developed, globose basally and pointed distally (Fig. 1I).

Abdomen. With five visible ventrites (Fig. 1B): ventrite 1 as long as ventrites 2 and 3 together; femoral lines obsolete; ventrites 2–4 equal in length; ventrite 5 slightly longer, with expanded lateral margins and rounded distal margin in females (Fig. 5A), but weakly depressed and slightly emarginated or truncated in males (Fig. 6A).

Male terminalia. The morphology of the terminalia is similar in all species: tergite 8 is formed by two plates, one external well sclerotised, covered by short setae, and one internal membranous (Fig. 6C). Sternite 8 is a much shorter transverse piece, well sclerotised and with a brush of long setae on its distal margin (Fig. 6E). Tergite 9 is formed by two hemitergites, without setae and closely associated with the proctiger (tergite 10 of some authors) (Fig. 6B–F). In addition, there is a Y-shaped spiculum gastrale (Fig. 6D).

Aedeagus. Formed of two fused pieces: a basal piece or phallobase (Fig. 3D: bp) and a median lobe or penis (Fig. 3D: ml), with only one dorsal paramere (Fig. 3D: pm). The basal piece is spherical or oval in ventral view, in some specimens slightly elongated in lateral view; it is lightly sclerotised with very thin walls, and with a very wide lumen where an entwined ejaculatory duct can be seen through transparent walls (Fig. 3D: ed). The duct emerges through a basal foramen (Fig. 3D: fo), circular or oval surrounded by a sclerotised ring, on the ventro-distal side of the basal piece (Fig. 3D: sr); the foramen is a useful reference to observe the aedeagus in an uniform standard position allowing comparisons among species and avoiding differences due to orientation.

The median lobe is an asymmetrical piece in ventral view, well sclerotised, dorso-laterally flattened and of variable size among species: relatively short with a wide base in some species, or much longer than wide and medially sinuous in others; in both cases it tapers towards its apex and bends to the right side in ventral view (Fig. 3D: ml). The morphology of the median lobe is constant within species and of good taxonomic value.

The paramere is formed of two parts: one basal, laminar, lightly sclerotised, partially surrounding the median and basal sections of the median lobe, and another part distal, conical and slightly elongated; the distal section is much more sclerotised with two areas separated by a narrow, dorsal, clear band, each area carrying several setae; the basal part has two short setae, but the distal part has a variable number of setae, between two to eight (Fig. 3D: pm). Only *Ch. formiceticola*, lacks these distal setae.

The morphology of the distal section of the aedeagus is constant within species and can be used as a useful diagnostic character among species.

Female terminalia. The ovipositor is formed by a pair of gonocoxites (Fig. 5B: va, st) articulated with the paraprocts or laterotergites (Fig. 5C: pp); the gonocoxites are dorsally covered by the proctiger

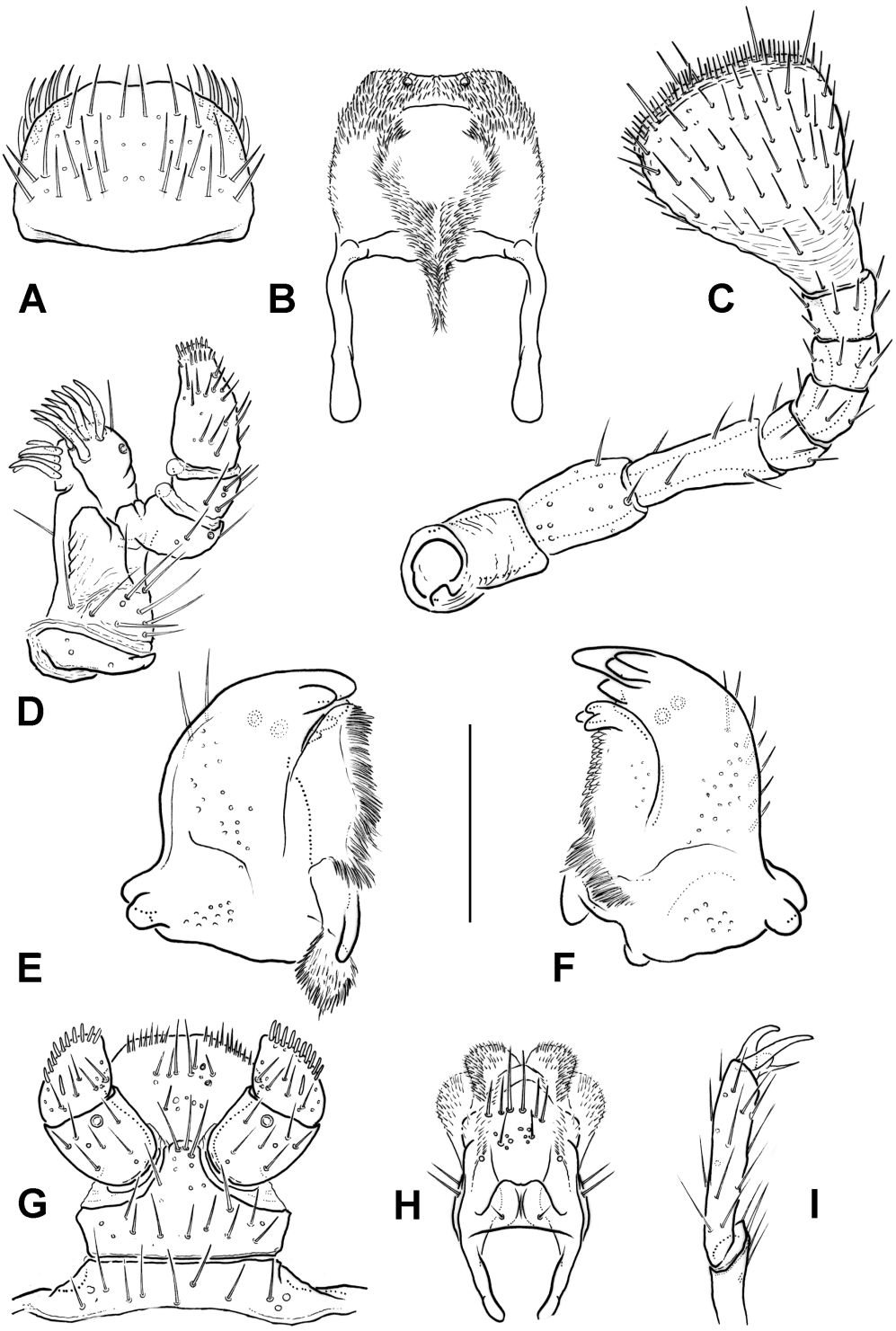

Fig. 2. Mouth parts, antenna and distal metatarsomere of *Cholovocera formiceticola* (Rosenhauer, 1856). **A**. Labrum, dorsal view. **B**. Epypharynx, ventral view. **C**. Left antenna, ventral view. **D**. Left maxilla, ventral view. **E**. Left mandible, dorsal view. **F**. Right mandible, dorsal view. **G**. Labium, ventral view. **H**. Hypopharynx, ventral view. **I**. Distal metatarsomere, dorsolateral view. Scale bar = 0.1 mm.

(tergite 10 of some authors) (Figs 5B: pg, 5E) just above the anus, and are formed by two sections: one proximal, the valvifer (Fig. 5B: va) and one distal, the stylus (Fig. 5B: st); the valvifer carries several distal setae, and shows slight variation across species, mainly in its width, but we do not consider it of taxonomic value; the stylus has a pair of long distal setae, but it does not vary morphologically among species. Both valvifer and stylus are dorsally covered by tergite 8 (Fig. 5C), which has a rounded margin and a row of marginal short setae, and ventrally covered by sternite 8 (Fig. 5D). Our detailed study of the female ovipositor has shown that it is not a diagnostic character to differentiate species.

The spermatheca is a relatively simple organ in most species of Coleoptera, formed by three main parts: the reservoir, the duct and the accessory gland. De Marzo (2008) described five main types of spermathecae in beetles, depending on the absence or relative development of one of those parts. In *Cholovocera*, the spermatheca (Fig. 7) has the main three parts and is similar to those of species of the

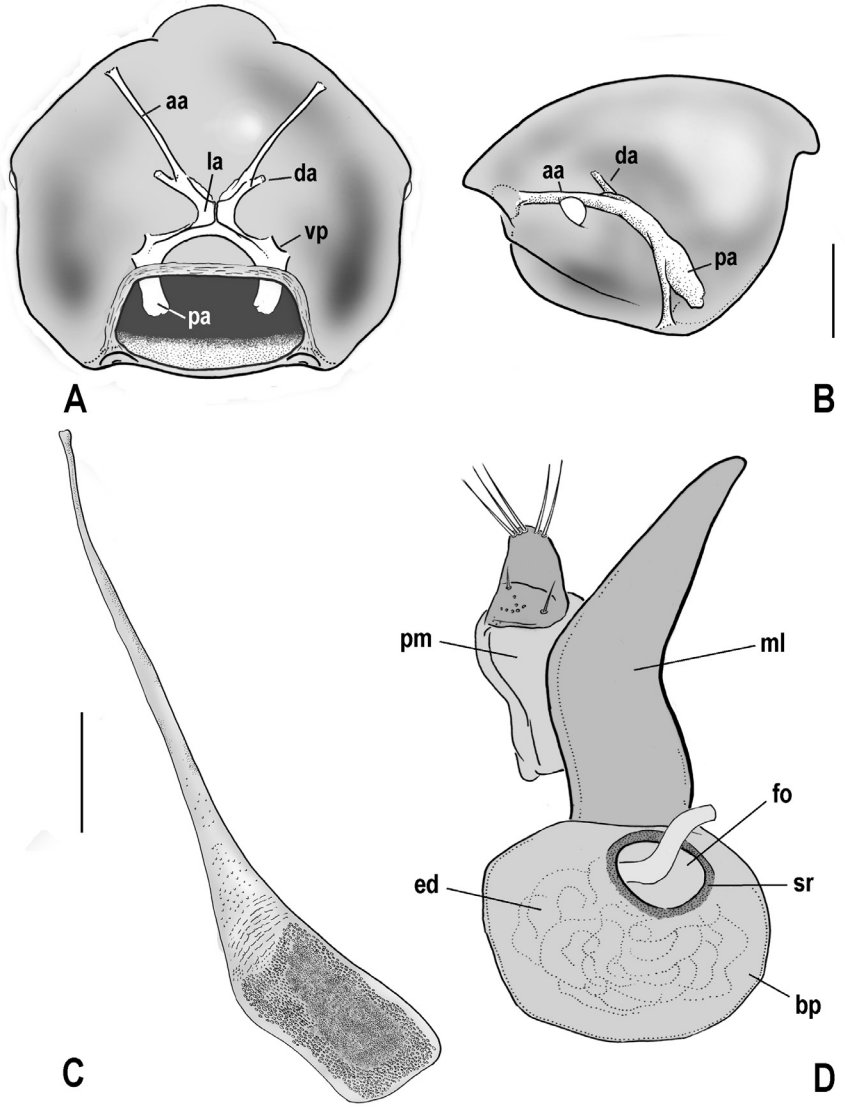

Fig. 3. Head. **A**. Tentorium, ventral view. **B**. Tentorium, lateral view. **C**. Hind wing of *Cholovocera formiceticola* (Rosenhauer, 1856). **D**. Stylised aedeagus, ventral view. Abbreviations: see Material and methods. Scale bars = 0.1 mm.

family Coccinellidae (De Marzo 2008). The spermathecal duct is a simple, short tube (Fig. 7D: sd), which connects the spermathecal reservoir with the bursa copulatrix; the spermathecal reservoir is T-shaped with thin, soft walls, formed by a distal area called the cornu (Fig. 7D: co), slightly more sclerotised with variable morphology in different species, and a proximal area called the ramus (Fig. 7D: ra), usually sacciform, with wrinkled walls allowing considerable dilation; the basal branch of the reservoir is the nodulus (Fig. 7D: no), which connects to the spermathecal duct. This is the region of the spermatheca with most morphological variability among the species of *Cholovocera* (Fig. 7). The nodulus has two parts which vary in shape, thickness and length: one distal, narrower, joining with the spermathecal duct; another proximal, wider, attached to the ramus. Between the nodulus and the ramus is the spermathecal gland (Fig. 7D: sg), a long, narrow sac of uniform morphology among all the species.

Preimaginal stages

Lawrence (1991) and Tomaszewska (2000, 2010) contributed data on larvae of Endomychidae in general, but the only information on preimaginal stages of species of *Cholovocera* was published by Silvestri (1912), who described the egg, larva and pupa in detail. Silvestri (1912) described the egg as white, sub-elliptical, 0.546 mm long and 0.351 mm wide, with a smooth surface, but slightly reticulated when observed at high magnification. The larva is elongated, slightly depressed dorsoventrally and tapering towards both ends, measuring approximately 2.3 mm long in the last instar. The head, darker than the body, has convex sides without stemmata (synapomorphy for the subfamily), and very short antennae. The mandibles are subtriangular short, robust, with curved anterior facies, a tricuspid apex and a developed mola, without prostheca. The maxillae and labia are short and robust. The thorax wider than the head, with short, thick legs. Silvestri (1912) also included a figure showing the dorsal and ventral views of the larva, with details of the cephalic capsule, its appendices, plus the legs. Furthermore, Silvestri (1912) briefly described the chaetotaxy of some body parts, in particular the dorsal abdominal setae, clearly capitate, and the ventral abdominal setae not capitate. In addition, Silvestri (1912) described the pupa as whitish, 1.35 mm long, with a figure showing it in dorsal and ventral views.

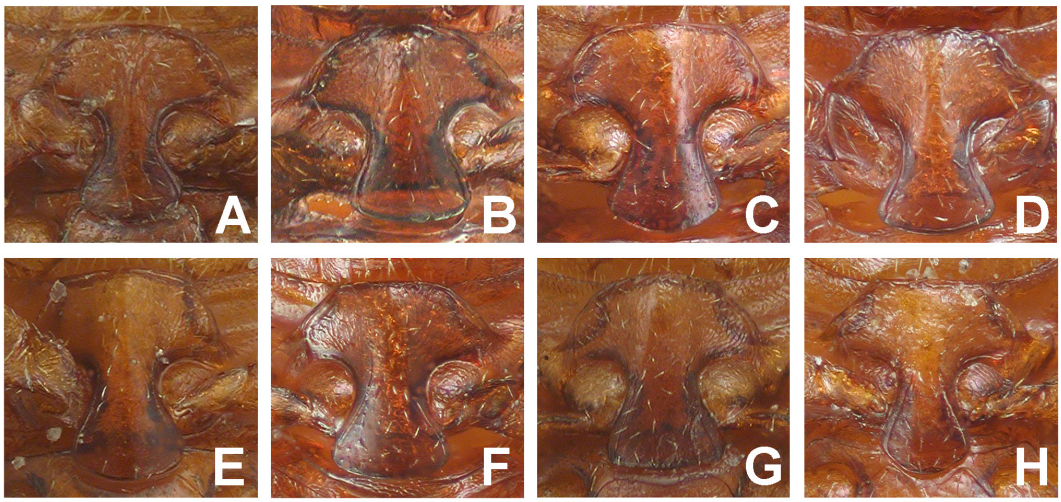

Fig. 4. Prosternal processes. **A**. *Cholovocera afghana* Johnson, 1977. **B**. *Ch. attae* (Kraatz, 1858). **C**. *Ch. balcánica* (Karaman, 1936). **D**. *Ch. gallica* (Schaufuss, 1876). **E**. *Ch. formicaria* Victor, 1838. **F**. *Ch. formiceticola* (Rosenhauer, 1856). **G**. *Ch. occulta* sp. nov. **H**. *Ch. punctata* (Märkel, 1845).

Biology

Feeding habits

Tomaszewska (2010) suggested that fungi is the principal food of the family Endomychidae. Skelley & Leschen (2002) mentioned spores and hyphae of microfungi as the food of species of Merophysiinae. However, Shockley *et al.* (2009b) expressed doubt about what food endomychid species feed on inside ant nests, suggesting that some tropical species may feed on the fungal gardens cultivated by the ants or just feed on adventive fungi growing inside the ant nest. Rücker (2018) adds to these theories, mentioning that the adult mouth parts of these beetles are compatible with mycophagy, and even with eating ant larvae.

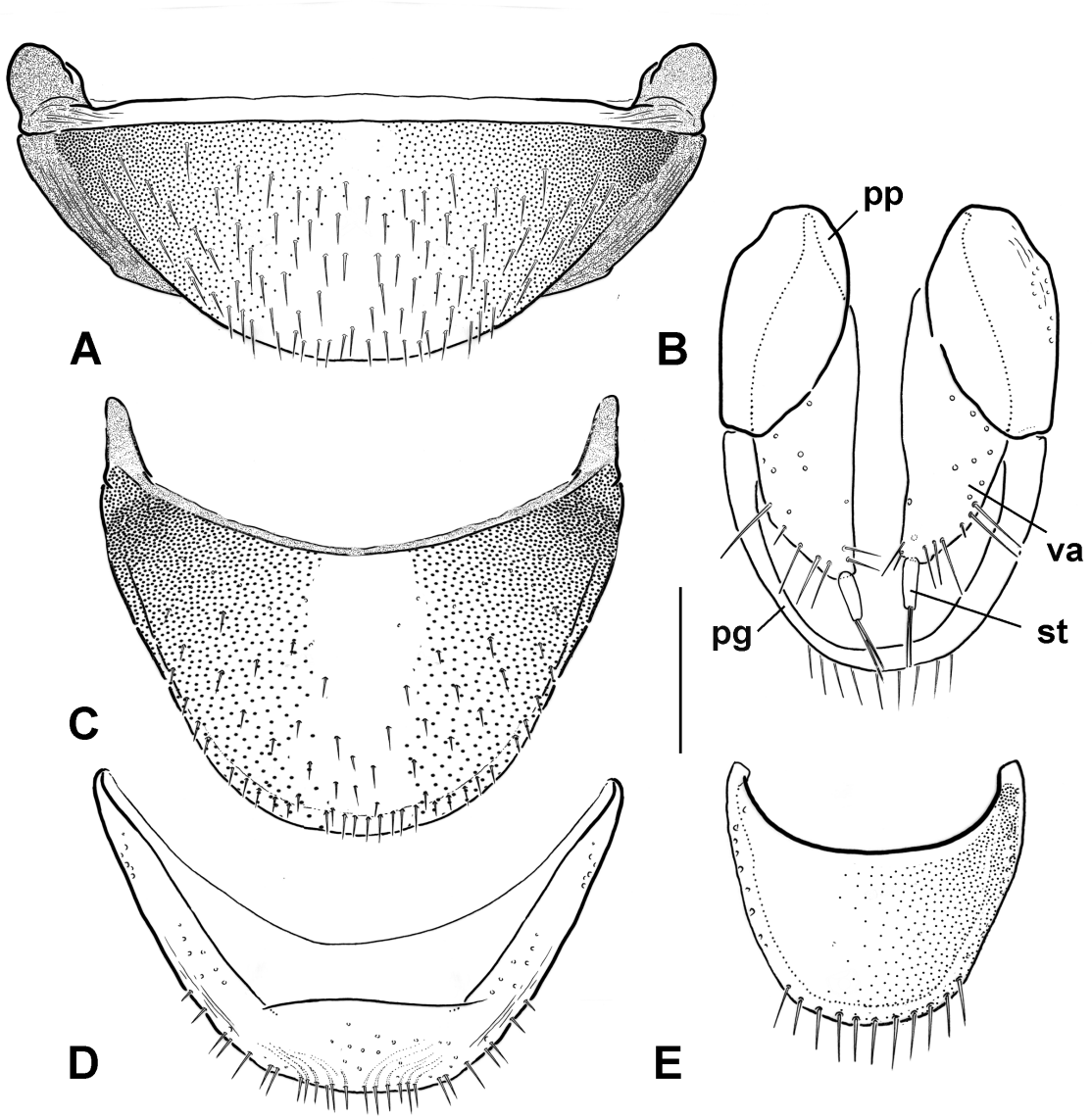

Fig. 5. Terminal abdominal segments of *Cholovocera formiceticola* (Rosenhauer, 1856), ♀. **A**. Last visible ventrite, ventral view. **B**. Gonocoxites, paraprocts and proctiger, ventral view. **C**. Tergite 8, dorsal view. **D**. Sternite 8, ventral view. **E**. Proctiger, dorsal view. Abbreviations: see Material and methods. Scale bar = 0.1 mm.

Following on the work by Silvestri (1912), Baroni-Urbani (1963) made an important contribution to the knowledge of the biology of *Cholovocera*, studying what he identified as *Ch. formicaria* from Ancona (Italy), but likely to have been *Ch. gallica*, the most frequently found species on mainland Italy (see below). Baroni-Urbani (1963) collected 148 beetles from one medium size colony of *Messor capitatus* (Latreille, 1798) and observed that they occupied food stores and cells where waste material accumulates, eating remains of seeds previously eaten by ants. Also, Baroni-Urbani (1963) observed that,

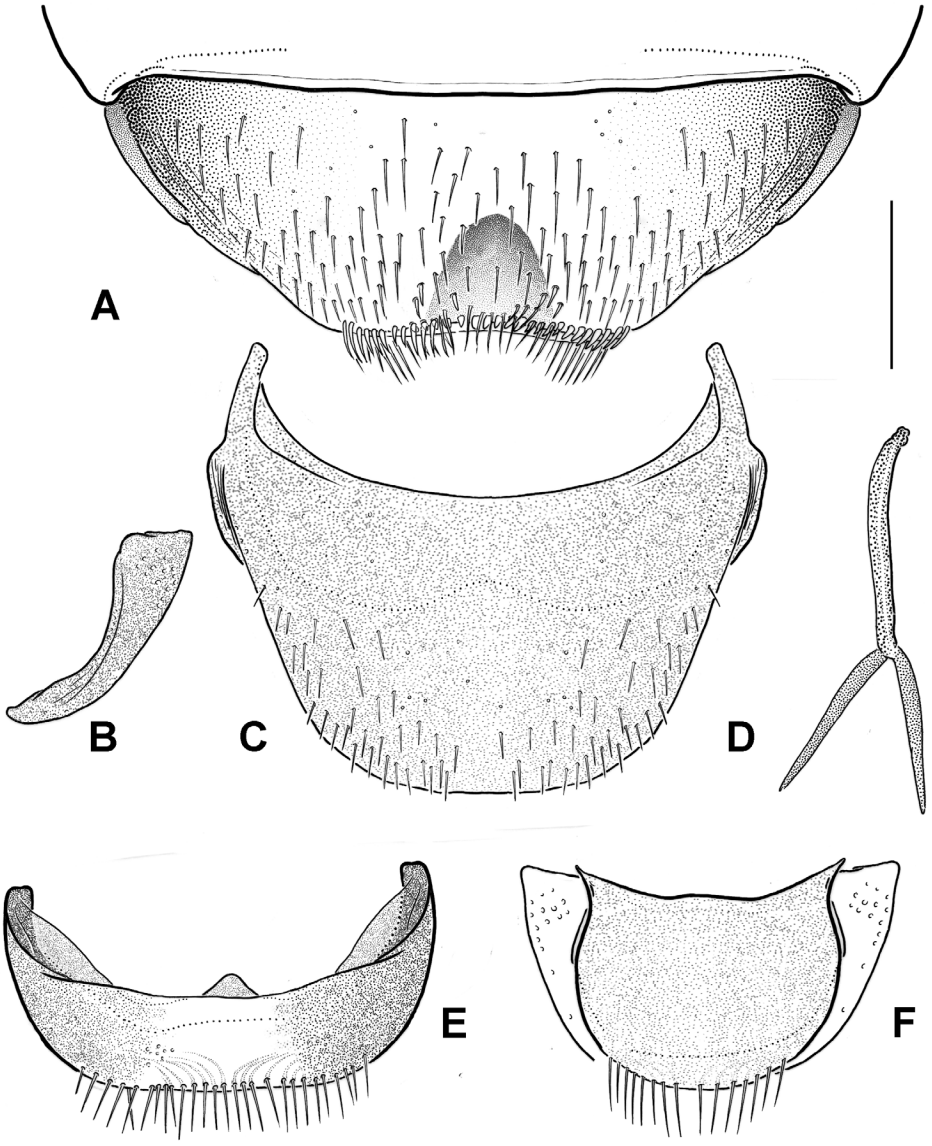

Fig. 6. Terminal abdominal segments of *Cholovocera formiceticola* (Rosenhauer, 1856), ♂. **A**. Last visible ventrite, ventral view. **B**. Left hemitergite, dorsal view. **C**. Tergite 8, dorsal view. **D**. Spiculum gastrale, ventral view. **E**. Sternite 8, ventral view. **F**. Hemitergites and proctiger, dorsal view. Scale bar = 0.1 mm.

occasionally, the beetles would feed on insect remains left by the ants, which they eat as complement to their granivorous diet; however, he did not observe any beetle consuming anything alive, neither ant eggs nor ant larvae, as they only fed on dead insects killed by the ants.

Our analysis of some beetle gut contents has shown a high proportion of unidentifiable vegetal remains (Fig. 8B), but also spores and hyphae (Fig. 8C–E) and some remains of arthropod cuticle (Fig. 8F). In conclusion, available data would indicate that the species of *Cholovocera* have followed the same pattern of other groups of myrmecophilous Coleoptera, initially fungivorous but adapted to a more varied diet, eclectic and opportunist, as discussed by Schigel (2012).

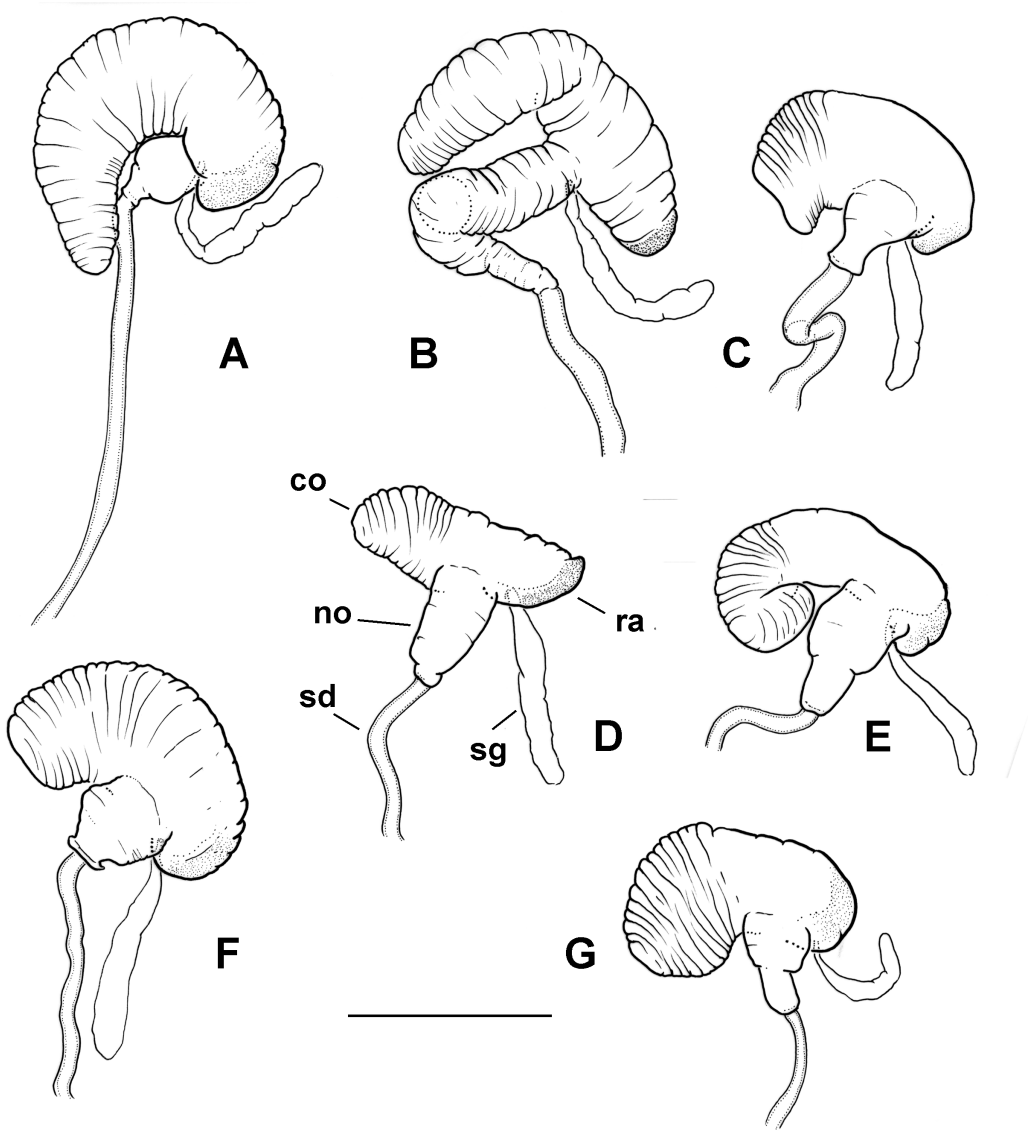

Fig. 7. Spermathecae, lateral view. **A**. *Cholovocera afghana* Johnson, 1977. **B**. *Ch. balcánica* (Karaman, 1936). **C**. *Ch. occulta* sp. nov. **D**. *Ch. gallica* (Schaufuss, 1876). **E**. *Ch. formicaria* Victor, 1838. **F**. *Ch. formiceticola* (Rosenhauer, 1856). **G**. *Ch. punctata* (Märkel, 1845). Abbreviations: See Material and methods. Scale bar = 0.1 mm.

Behaviour and myrmecophily

In his original description of the genus, Victor (1838) wrote that *Ch. formicaria* was a slow-moving species, but Lucas (1849) qualified as very agile a species (probably *Ch. punctata*) that he observed in Algeria. Again, Lucas (1874) regarded a species from southern France as agile. From our observations of *Ch. formiceticola* on external foraging tracks of *Messor barbarus* (Linnaeus, 1767), the beetles initially move slowly, but then increase their pace at irregular intervals. In contrast, our observations of *Ch. formiceticola* inside ant nests in the laboratory show that these beetles move slowly most of the time, as recorded by Victor (1838). However, if they are suddenly exposed to light, they seek refuge rapidly, this being a possible explanation of the observations by Lucas (1849, 1874).

Myrmecophily has been variously described, but Kistner's (1982) definition is one of several widely accepted. Myrmecophily can be present in four symbiotic types, according to the benefit received by the ants, in decreasing order: mutualism, commensalism, kleptoparasitism and parasitism. Species of *Cholovocera* are placed between commensalism and kleptoparasitism. Victor (1838) was the first to record the association between *Cholovocera* and ants, clearly shown by the name he chose for his new species: *Ch. formicaria*. Märkel (1845), while describing *Ch. punctata*, suspected its association with ants but he could not confirm it. Lucas (1849) and other early authors mentioned that the beetles were associated with ant nests or that they were collected under stones together with ants. Belon (1879) again drew attention to the myrmecophilous character of species of *Cholovocera*, assuming that these beetles lived in a "peaceful" relation with ants, and citing a case where he found specimens in abandoned ant nests. This observation indicates that *Cholovocera* beetles may survive in the nest without the presence of ants.

Krausse (1911) reported an experiment in which he placed a group of ants (*Messor barbarus*) in a small breeding container together with several myrmecophilous arthropods collected in Sardinia, i.e., beetles (including some *Ch. punctata*), termites, silverfish and isopods. On the following day, he observed that the ants had eaten all the silverfish, but not the remaining specimens. A further observation was that one specimen of *Ch. punctata* was on top of an isopod, which made Krausse (1911) suggest that these beetles may use other commensals to move inside the ant nest. In our opinion, that behaviour may have been an artefact resulting from the artificial nature of the environment where the experiment was performed.

Silvestri (1912) provided useful behavioural data based on his observation of hundreds of *Cholovocera* beetles, which he identified as "*Ch. formicaria*", from various localities in southern Italy, all associated with nests of species of *Messor* Forel, 1890. Judging from the localities cited by Silvestri (1912), we deduce that the species would have been *Ch. punctata* and/or *Ch. gallica*. Silvestri (1912) placed several adult beetles inside artificial ant nests, observing their behaviour for several months, from November 1910 to September 1911. He wrote that the beetles acclimatised very well to these conditions and that during the summer of 1911 there were eggs and larvae. Further, he commented that *Cholovocera* adults mostly lived inside chambers where the ants kept grains, but that they laid eggs in chambers with debris and/or grain infested by fungi, where eggs would hatch, larvae develop and pupate. Also, Silvestri (1912) commented that any interaction between beetles and ants was low. These observations largely agree with ours, also made from nests in the laboratory (Fig. 8A). According to Silvestri (1912), if a worker ant attempted to capture a beetle with its mandibles, the victim would manage to free itself, due to its robustness, smooth surface and elliptical shape; however, *Cholovocera* larvae were totally ignored by the ants.

Escherich (1917), possibly based on Silvestri's (1912) observations, qualified the genus *Cholovocera* as myrmecophilous in a synoecy, a strategy where ants are indifferent to their cohabiting beetles. Baroni-Urbani (1963) observed that the beetles avoided the ants as much as possible, moving carefully within the galleries from one food chamber to another and seeking refuge within wall cracks, while they were

not feeding. Baroni-Urbani (1963) also described a digging behaviour by the beetles, which used their heads and thorax as a shovel to dig and hide inside the substrate. According to Baroni-Urbani (1963), the ants appear to accept these beetles without attacking them, possibly because they are saprophagous inquilines which, in some way, assist by eliminating unwanted waste.

Our field observations agree with the above ones, i.e., *Cholovocera* beetles move over foraging tracks and around the entrance to the nest being completely ignored by the ants. However, we observed that some beetles introduced into ant nests held in the laboratory, are eaten by the ants few hours after being inside the nest, only sometimes surviving a few days. This scenario would indicate the beetles may have to first acquire the pheromone odour of the ant nest to survive inside it.

Some authors recorded the identity of ant hosts when publishing about *Cholovocera*. Wasmann (1894), Bernard (1968) and more recently Shockley *et al.* (2009b) included tables with limited data on *Cholovocera* myrmecophily, but without new records or comments. In general, published data indicate that species of *Cholovocera* are mainly associated with ant species of the subfamily Myrmicinae, especially of the genus *Messor* and, to a lesser extent, with those of *Aphaenogaster* Mayr, 1853, *Pheidole* Westwood, 1839 and *Tetramorium* Mayr, 1855 (Karaman 1964). Also, there are few records of associations with species of *Camponotus* Mayr, 1861 (Formicinae) (Donisthorpe 1927; Karaman 1964). From our study of museum collections and from our own collecting, we agree that ant species of the five genera mentioned above are the hosts of *Cholovocera* beetles, in the same order of abundance. *Cholovocera attae*, *Ch. formiceticola* and *Ch. occulta* sp. nov. are exclusively associated with species of *Messor*, as well as most of the specimens of *Ch. balcanica*, *Ch. gallica* and *Ch. punctata*. However, we found *Ch. formicaria* associated with only one species of *Tetramorium*, and the host of the sole specimen we examined of *Ch. afghana* was *Pheidole indica* Mayr, 1879.

Because of the dubious identifications of *Cholovocera* species in the literature, even in recent publications, we feel that giving a complete list or table of published ant host-beetle associations will be confusing rather than useful. However, under the treatment of each *Cholovocera* species, we discuss published erroneous ant host-beetle associations and establish what we believe are true associations.

Parasites, commensals and phoresy

Shockley *et al.* (2009a: 6) wrote that pathogens, such as bacteria of the genus *Wolbachia* Hertig, 1936, had not been recorded from any member of the family Endomychidae, but they mentioned records of an ectoparasitic fungus of the genus *Rickia* Cavara,1899 (order Laboulbeniales) infesting several species of Endomychidae in some Asian and African localities. However, no species of the subfamily Merophysiinae is mentioned as host of any parasite. Shockley *et al.* (2009a) failed to cite a paper by Santamaría (1995) where the species *Parvomyces merophysiae* (order Laboulbeniales) was newly described, parasitising specimens of the beetle *Merophysia formicaria* Lucas, 1852, from material collected at Lérida, in the northeast of the Iberian Peninsula.

During our examination of many specimens of *Cholovocera*, we found a few beetles of the species *Ch. formiceticola* from Lisbon (Portugal) with thalli of a fungus on their legs (Fig. 8G–H). The perithecium (Fig. 8H: pe) of these fungi was attached to the insect cuticle by a basal area or stalk (Fig. 8H: sk) and these structures are diagnostic for their identification. Although our specimens resemble *Parvomyces merophysiae*, a more detailed study is needed to confirm their identity, as they may represent an undescribed species (S. Santamaría pers. comm. February 2022).

Shockley *et al.* (2009a: 6) do not mention any endoparasite known to infest any endomychid species, they only list several yeast species as endosymbionts of eight endomychids but, again, no Merophysiinae is mentioned (Shockley *et al.* 2009a: Table 2). However, we found cysts of a protozoan in the Malpighian tubes (Fig. 8I) of four species of *Cholovocera*: *Ch. formiceticola* from southeastern Spain,

Ch. punctata and *Ch. gallica* from Sicily, and *Ch. formicaria* from Azerbaijan. All the cysts studied were morphologically similar: elliptical with rounded poles and refractive, measuring 9.5 µm long by 6 µm wide, and occupying almost the entire lumen of the Malpighian tubes (Fig. 8J). These cysts do not appear to affect other organs of the beetles, and we could not find them in other species present in the same ant nest, i.e., ants (*Messor barbarus*), springtails (Collembola) and silverfish (Zygentoma).

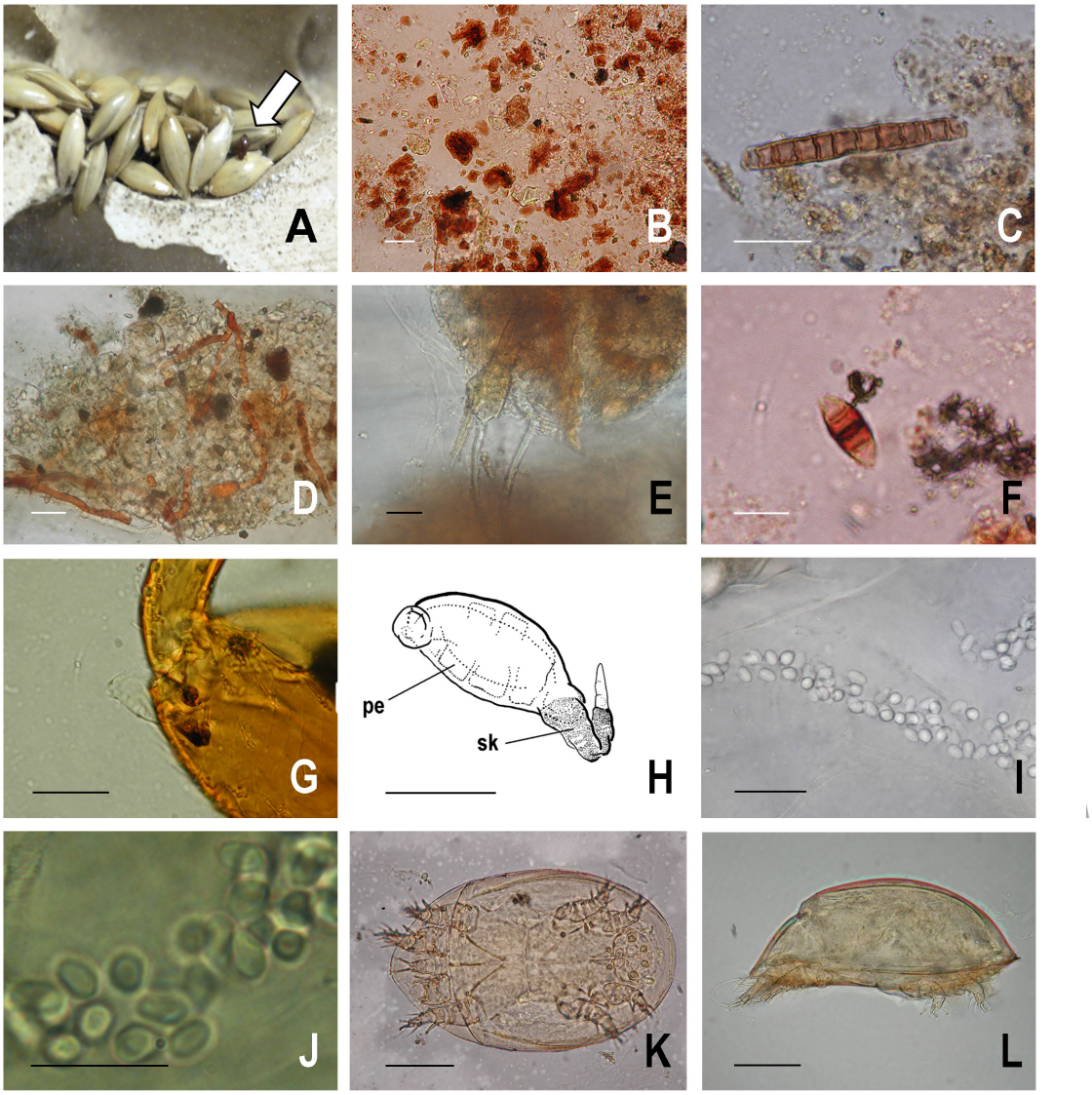

Fig. 8. *Cholovocera* Victor, 1838 feeding, parasites and commensals. **A.** Nest chamber of *Messor barbarus* (Linnaeus, 1767) with seeds and one specimen of *Ch. formiceticola* (Rosenhauer, 1856). **B.** Gut content: particulate material. **C–D.** Fungal spores. **E.** Hyphae. **F.** Arthropod remains. **G.** *Parvomyces* cf. *merophysiae* Santamaria, 1995 attached to a leg of *Ch. formiceticola* (Rosenhauer, 1856). **H.** Specimen of *Parvomyces* cf. *merophysiae* Santamaria, 1995. **I.** Malpighian tubules of *Ch. formiceticola* (Rosenhauer, 1856) with cyst of parasitic amoebae. **J.** Cysts enlarged. **K.** Rhizoglyphine mite, phoretic on *Ch. punctata* (Märkel, 1845), ventral view. **L.** Same mite, lateral view. Scale bars: A–F = 20 µm; G–L = 30 µm.

In an attempt to further identify this protozoan, we placed the internal organs of one beetle in a saline solution for approximately 15 hours, after which we observed that the cysts opened, producing an amoeboid phase, mobile but without pseudopods. These features suggest that it belongs to the Amoebozoa, a large group of protists, including some pathogenic species (C. Lange, pers. comm. May 2022). Lange & Lord (2012) reported that a few species of Amoebozoa invading the Malpighian tubes of insects are, placed in three genera: *Malpighiella* Minchin, 1910, *Malpighamoeba* Prell, 1926 and *Malamoeba* Taylor & King, 1937; however, we were unable to further identify our specimens. Lange & Lord (2012) wrote that the immature phase of these protozoans moves from the insect gut or the body cavity into the Malpighian tubes, completely occupying the lumen of the tubes as cysts. This feature agrees with our observations in species of *Cholovocera*.

Considering the large number of *Cholovocera* beetles that we examined for this revision, and the small number that we found with parasites or commensals, we agree with Shockley *et al.* (2009a) in that these symbionts are rare in species of Endomychidae.

Shockley *et al.* (2009a: 6) stated that phoresy on species of Endomychidae is rare compared to other beetle families of similar habits, and that the most frequent phoretics of endomychids are mites, mostly of the subfamily Rhizoglyphinae and, to a lesser extent, of the Uropodinae. On a specimen of *Ch. gallica* from Sicily, we found three deutonymphs of a mite belonging to the Rhizoglyphinae (Fig. 8K–L). According to Dr P. Klimov (pers. comm. 7 Feb. 2022), our mites may belong to one of three genera: *Sancasania* Oudemans, 1916, *Schwiebea* Oudemans, 1916, or *Rhizoglyphus* Clapadère, 1869, but a detailed examination is needed to achieve an identification.

Geographic distribution

The distribution of most species of *Cholovocera* is on the south-west of the Palearctic Region (Fig. 9), with a few populations north of the Black Sea, one species on the Caucasus Mountains and the Caspian Sea coast, and another species reaching Afghanistan (Fig. 9C). Seven species are distributed around the Mediterranean Sea (Fig. 9), agreeing with the chorologic distribution Turanic-Mediterranean, as proposed by Vigna-Taglianti *et al.* (1992). There are published citations of *Cholovocera* outside these areas but, as it will be discussed below, they refer to species which we do not regard as belonging to this genus.

Furthermore, due to a number of published misidentifications of species of *Cholovocera*, as mentioned in the Introduction above, current distributional data for the species of this genus are questionable. Even the more recent distributions given by Löbl & Smetana (2007), Shockley *et al.* (2009b), and Rücker (2020) must be critically revised. Therefore, under each species treatment below, we give a list of the specimens examined, include what we consider the correct distributional data, and discuss which specimens we regard as misidentifications and/or erroneous locality records.

According to the locality data associated with our material examined, we conclude that, where two or more *Cholovocera* species are sympatric (in north-eastern Spain, southern France, western Italy, Sardinia, Sicilia, northern Africa, Greece and Turkey), they are rarely found at exactly the same locality, and two species are seldom found in the same ant nest. We are aware of only two cases where two or more species of *Cholovocera* were recorded in the same ant nest: one is a report by Stalling (2019), who found several beetles of the species *Ch. attae* and *Ch. balcanica* (as *Ch. major*) inside an abandoned ant nest; the other is from our own examination of one female of *Ch. gallica* sharing the same ant nest with several specimens of *Ch. punctata* in Sicily. However, more often, species of *Cholovocera* may share an ant nest with other myrmecophilous beetles. Species of *Cholovocera* are frequently found with the tenebrionid *Oochrotus unicolor* Lucas, 1852 (Bargagli 1872; Parmentier *et al.* 2020), or with species of Merophysiidae. For example, *Ch. afghana* has been collected together with *Displotera beloni*

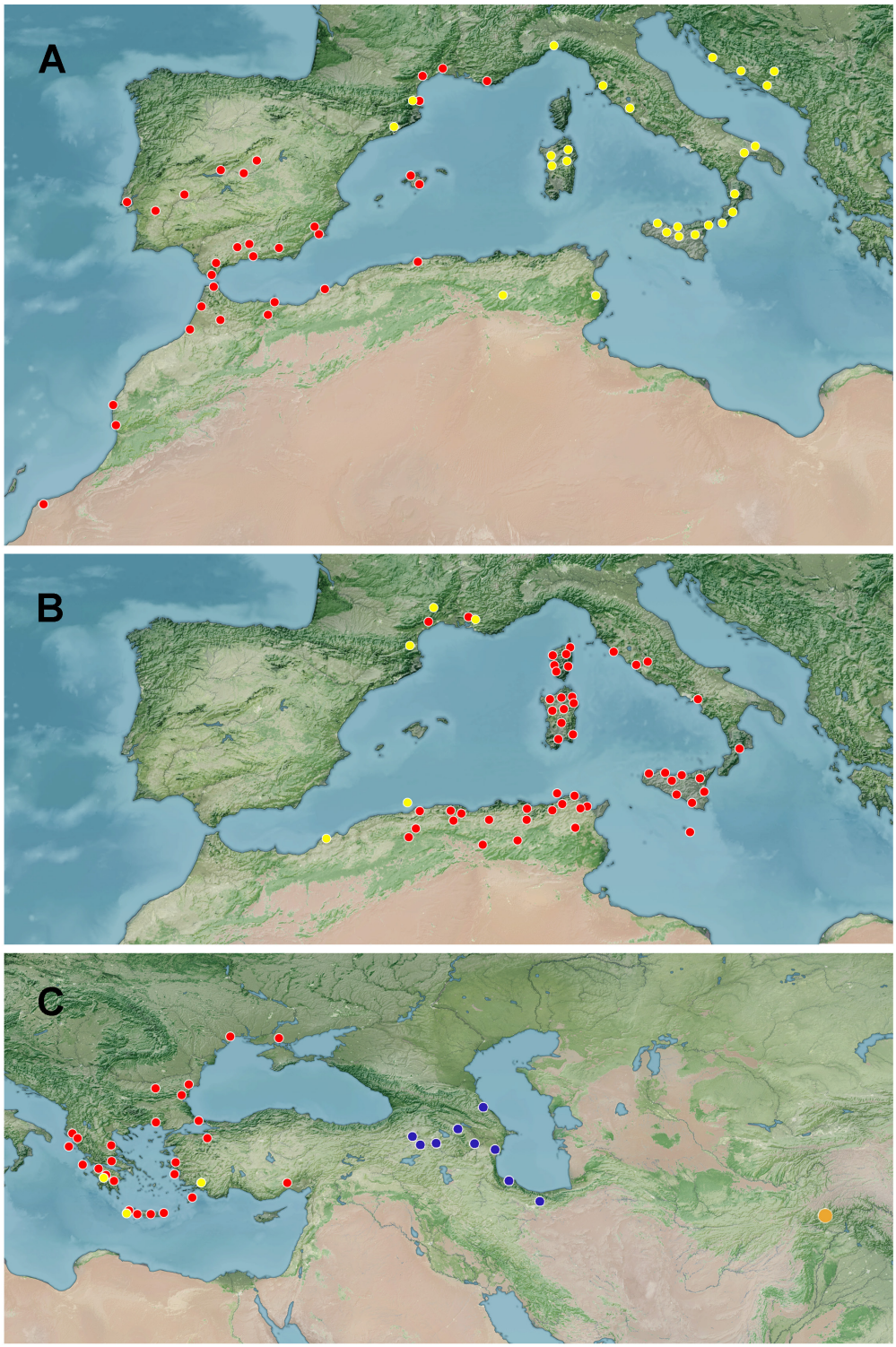

Fig. 9. Known geographical distribution of the species of *Cholovocera* Victor, 1838. **A**. *Ch. formiceticola* (Rosenhauer, 1856) (red dots) and *Ch. gallica* (Schaufuss, 1876) (yellow dots). **B**. *Ch. punctata* (Märkel, 1845) (red dots) and *Ch. occulta* sp. nov. (yellow dots). **C**. *Ch. balcanica* (Karaman, 1936) (red dots), *Ch. attae* (Kraatz, 1858) (yellow dots), *Ch. formicaria* (dark blue dots) and *Ch. afghana* Johnson, 1977 (orange dot).

(Wasmann, 1899) in Afghanistan (as "*Ch. brevicornis* Johnson, 1977", see below). In Spain, we found *Ch. formiceticola* sharing ant nests with species of *Merophysia* Lucas, 1852 and we have examined specimens of *Ch. attae* and *Reitteria escherichi* Wasmann, 1896 collected from the same ant nest in western Anatolia (see under material examined of *Ch. attae*).

Cholovocera formicaria Victor, 1838
Figs 4E, 7E, 9C, 11A, 12E, 13D, 14H–I, 15, 23A–B, 24A–B, 24F–G

Cholovocera formicaria Victor, 1838: 179, pl. III.

Colovocera formicaria – Belon 1879: 194.
Cholovocera subterranea – Motchoulsky 1845: 111.
Coluocera formicaria – Heyden *et al.* 1883: 80.
Coluocera formicaria v. *major* – Reitter 1887: 10. **Syn. nov.**
Cholovocera major – Rücker 2011a: 13, figs 18–20.

Differential diagnosis

Cholovocera formicaria is morphologically and geographically close to *Ch. afghana* and *Ch. balcanica*, but it can be distinguished from both species by the shape of the metatibiae. Those of *Ch. formicaria* are club-shaped and sinuous (Fig. 14H–I), but straight and gradually tapering in *Ch. afghana* (Fig. 14A), and much shorter and wide in *Ch. balcanica* (Fig. 14D–E).

Furthermore, the aedeagus and the paramere are useful characters to distinguish *Cholovocera formicaria* from *Ch. balcanica* and *Ch. gallica* (Fig. 15 against Figs 20–21).

Type material

Cholovocera formicaria: two female syntypes of *Ch. formicaria* (Figs 23A, 24A–B) held in Motschulsky's Collection at the University of Moscow (A.A. Gusakov pers. comm. May 2021) were not available for our examination. Instead, we have examined a male of *Ch. formicaria* from "Derbent" (Fig. 23B), the type locality, held in the Märkel Collection in SMTD (Dresden), which may have been part of Motschulsky's type series. However, considering its different labelling from the syntypes (Fig. 23A–B), we cannot be absolutely sure of its status. Nevertheless, it is an authenticated specimen of *Ch. formicaria*, which allows us to make a comparison between this species and the male syntype of *Ch. punctata* to conclude that they are different species. Victor (1838) also mentioned to have found *Ch. formicaria* in "Kahétie" (Georgia), but no specimen with such a label have been located.

Coluocera formicaria var. *major*: lectotype (male) and two paralectotypes (male and female) held in HNHM. The type locality given by Reitter (1887) is "Talish Gebiete" [Talish Region]. However, the label attached to the lectotype reads "Rasano" (see Rücker 2011a: fig. 18, bottom, left), which is located in the region of the Talish Mountains. According to the ICZN Code (1999), the type locality is what is written on the label associated with the type specimen, in this case "Rasano".

Syntypes, not examined

RUSSIA – **Dagestan** • 2 ♀♀; Derbent, "Litt. m. csp." [Caspian Sea region]; ZMUM.

Lectotype of *Coluocera formicaria* var. *major*

AZERBAIJAN – **Lankaran** • 1 ♂; "Caspi.–M.–Gebiet" [Caspian Sea region], Rasano [Ancient town in ruins, 15 km southwest of Lerik, 38°40′12.0″ N, 48°18'46.0″ E. See Lazarev (2017)]; Leder leg.; HNHM. Designated by Rücker's (2011a: 13).

Paralectotypes of *Coluocera formicaria* var. *major*

AZERBAIJAN – **Lankaran** • 2 ♂♂; "Caspi.–M.–Gebiet" [Caspian Sea area], Rasano; Leder leg.; [each specimen associated with a *Tetramorium* worker ant, det. X. Espadaler]; HNHM.

Notes

As it can be seen in Rücker 2011a (fig. 18), there is a label reading "Holotypus" attached to the specimen that Rücker designated as the lectotype. However, this specimen cannot be regarded as the holotype because it was not designated in the original description, which included more than one specimen, i.e., syntypes. Examining the handwriting of the Holotypus label, we conclude that it was added at a later date than the description by Reitter (1887).

The same comment given above under the lectotype, applies to the paralectotypes.

Additional material, non-types

RUSSIA – **Dagestan** • 1 ♀; Derbent; MCNM 198707 • 1 ♂, 1 ♀; Derbent; SMTD • TURKEY – **East Anatolia** • 2 ♀♀; Kars, Digor; 1650 m a.s.l.; 15 Jun. 1986; MHNG.

AZERBAIJAN – **Göygöl** • 1 ♂; "Caucasus, Helenendorf" [modern Göygöl]; Couřil leg.; NMPC • 1 ♂; "Caucasus", Helenendorf"; SMTD. – **Ganja** • 1 ♂, 1 ♀; "Caucasus, Elisabetpol" [modern Ganja]; SDEI 10850 to 10851 • 1 specimen; "Caucasus, Elisabetpol"; NHMW. – **Lankaran** • 1 ♂, 3 specimens; Leder leg.; NHMB • 1 ♀; Leder leg.; SDEI 11874 • 1 specimen; Leder leg.; MHNG • 2 ♂, 2 ♀; Leder leg.; NMPC • 1 ♂, 1 ♀; "Talyschgeb[er]g [Talish area], Transcaucas[us]."; Leder leg.; SDEI 11875–11876 • 2 ♂♂, 3 specimens; "Talyschgebg., Transcaucas."; Leder leg.; SFUN • 1 ♂; "Talyschgebg., Transcaucas."; Leder leg.; SMTD • 2 specimens; "Talyschgebg., Transcaucas."; Leder leg.; MFNB • 1 specimen; "Caspi.–M.–Gebiet, Rasano"; Leder leg.; SFUN. – **Ordubad** • 1 ♀, 1 specimen; "Caucasus, Araxesthal" [Arax River Valley]; Leder leg.; NMPC. – **Caucasus, no specific locality** • 2 ♂♂; "Kaukas"; Leder leg.; [18]86; SDEI 10842– 10843 • 1 ♂, 2 ♀♀; "Kaukas"; Leder leg.; SDEI 10847– 10849" • 1 ♀; "Kaukas"; Leder leg.; NMPC • 1 ♂; "Cauc. Sept."; NMPC • 1 specimen; "Kaukas"; Leder leg.; ZFMK • 1 ♂; "Kauka"; Leder leg.; ZFMK • 1 ♀; "Caucasus"; Leder leg.; MZLU 2020-001 • 1 specimen; "Kaukasus"; ZFMK • 2 ♀♀; "Caucasus"; SMTD • 1 specimen; "Kaukasus"; MFNB.

IRAN – **Guilan** • 1 ♂, 2 ♀♀; Chalus-Polzoghal; 29 Apr. 1970; Wittmer and Bothmer leg.; MHNB • 1 ♀; Bandar Pahlavi [modern Bandar-e Anzali]; 20 Aug. 1973; S. Vit leg.; "marais" [marshland]; MHNG. – **Mazandaran** • 1 ♂, 1 ♀; Dadu; NHMB – **Unknown localities** • 1 ♂; Nov. 1917; SDEI 10793 • 1 ♂, 1 ♀; MFNB.

Type locality

"Derbent, non loin de la mer Caspienne" [Derbent, not far from the Caspian Sea], Dagestan, Russia.

Description

Male as in Fig. 11A. Body length: 1.43 mm average, range 1.30–1.50 mm (N = 41, males and females). Shape of body elliptical, with the lateral margins of the pronotum continuous with those of the elytra, i.e., without an indentation. Elytral apex markedly acute. Terminal antennomeres subtriangular, with round angles (Figs 12E, 13D). Metatibiae as in Figs 14H and 14I, narrower in the proximal half and with sinuous margins, especially in the male. Prosternal process slightly keeled anteriorly, with a marked median constriction and rounded distally (Fig. 4E). Male last visible ventrite with a slight emargination and bordered by a brush of short setae.

Median lobe of aedeagus sinuous and narrow from the first third of its length in ventral view, tapering and acutely pointed distally (Fig. 15A). Aedeagus in lateral view as in Fig. 15C. Distal portion of

paramere long, subcylindrical, sinuous, with a round apex bearing a brush of many setae (Figs 15B, 15D). Spermathecal duct and spermathecal reservoir short; ramus long and curved distally, cornu round and nodulus moderately developed, smaller than cornu and ramus together (Fig. 7E).

Geographic distribution

The known distribution of *Cholovocera formicaria* is on the Caucasus Mountains and the Caspian Sea coast, extending from eastern Anatolia to north-eastern Iran (Fig. 9C). There is a record from Switzerland (Löbl & Smetana 2007; Shockley *et al.* 2009b; Rücker 2011b, 2020), which needs to be reviewed, but we regard it as almost certainly erroneous.

Host ants

Determining the identity of the species of ant hosting *Cholovocera formicaria* is not an easy task. The main problem is that the name "*Ch. formicaria*" has been incorrectly applied to almost all the other species of the genus for over 170 years (see Taxonomic history below). For example, Wasmann (1894: 133), Bernard (1968: 383) and Kistner (1982: 125), among many others, cited species of *Messor* as hosts of "*Ch. formicaria*", which are erroneous due to the misidentification of the beetles. Rücker (1980: 143) goes even further and incorrectly associates "*Ch. formicaria*" with *Messor barbarus*, *Aphaenogaster testaceopilosa* (Lucas, 1849) and *Pheidole megacephala* (Fabricius, 1793).

From literature reports and our own examination of specimens associated with ants, we were able to recognise two ant taxa correctly associated with *Ch. formicaria* in its true geographic distribution: (1) a species of *Tetramorium*, based on the identification of two worker ants collected with the paratypes of *Coluocera formicaria* var. *major* in the Talish Region, Azerbaijan (see above), and (2) *Messor structor* (Latreille, 1798) reported by Arakelian & Kalashian (1993: 51) from Armenia.

Junior synonyms

***Cholovocera subterranea* Motchoulsky, 1845**

Motchoulsky (1845: 111) described *Ch. subterranea* from "Daghestan", distinguishing it from *Ch. formicaria* by being slightly smaller, darker and brighter. Gemminger & Harold (1868: 905) and Schaufuss (1876b: 413) accepted *Ch. subterranea* as a good species, without further comment. However, Reitter (1877: 5) found that the differences given by Motchoulsky (1845) did not justify the recognition of *Ch. subterranea* as a different, valid species. We agree with Reitter (1877) in regarding *Ch. subterranea* as a junior synonym of *Ch. formicaria*.

Wasmann (1894: 133), still using the name *Ch. subterranea*, made a doubtful association of this beetle with a species of the ant genus *Aphaenogaster* Mayr, 1853, without giving any details or reference. More recently, Shockley *et al.* (2009b: 65) and Rücker (2009: 14; 2020: 34) accepted Reitter's (1877) synonymy but, without explanation, they erroneously name it as "*Merophysia subterranea* Motschulsky, 1845".

***Coluocera formicaria* var. *major* Reitter, 1887**

Reitter's (1887: 10) description of *Coluocera formicaria major* is very brief, only distinguishing it from the nominate subspecies by size. Leder (1886: 133) included this taxon in his catalogue, qualifying it as identical to *Ch. formicaria*, but larger. Heyden *et al.* (1883: 80) and Wasmann (1894: 133) included *Co. formicaria major* in their catalogues, indicating its location, but without an ant association. Escherich (1897) and Seidlitz (1898: 197) associated this subspecies with the ant *Messor structor* in his catalogue, but the correct identity of the beetles would have been *Ch. balcanica*. In his key to species of *Cholovocera*, Rücker (1980: 144, fig. 26) elevated this taxon to full species, but his interpretation of its type locality was erroneous, placing the Talish Region in "Angora", which is actually in Turkey.

Arakelian & Kalashian (1993: 51) cited *Co. f. major* from Armenia, around the city of Noubarashen, reporting 10 to 15 individuals inside nests of *Messor structor* from March to June. We have not examined these beetles, which are deposited in the Entomology Museum of the National Academy of Sciences of Armenia in Yereban, Armenia (G. Arakelian & M. Kalashian pers. comm. 2020). Several checklists and catalogues (i.e., Löbl & Smetana 2007: 557; Shockley *et al.* 2009b: 65; Rücker 2009: 14; 2011b; 2020: 34) still regarded *Co. f. major* as a full species and gave an erroneous geographical distribution, either by citing Turkey or by including several countries where this taxon does not occur, probably confusing it with the distribution of *Ch. balcanica* (see below).

Rücker (2018: 576, figs 1179–1180) described in detail what he believed to be "*Ch. major*", but his figure of the aedeagus clearly shows that it was *Ch. balcanica*, associated with *Messor barbarus* and *M. structor*. Stalling (2019: 13) also misidentified material of *Ch. balcanica* from the Dodecanese Islands (Greece) as "*Ch. major*", an error repeated by Lapeva-Gjonova & Rücker (2011: 6) and Lapeva-Gjonova (2013: 9) with specimens of *Ch. balcanica* from Bulgaria, associated with *M. structor*.

We have examined the holotype male and two paratypes (male and female) of *Co. f. major*, with type locality in Rasano (Talish Mountains), as well as over 20 males of *Ch. formicaria*. The body length of the holotype falls within the range measured for males of *Ch. formicaria*. Also, we have compared the morphology of the aedeagus of the holotype with those of *Ch. formicaria*. Although the distal tip of the median lobe of the aedeagus and the paramere are missing in the holotype (Fig. 24F–G), the remaining parts are identical to those of the many males of *Ch. formicaria*, which we have studied, also collected in the Talish Region (Fig. 15A, C). Furthermore, Rasano is located approximately 400 km south of Derbent, the type locality of *Ch. formicaria*. Therefore, we have no hesitation in placing *Coluocera formicaria major* as a new junior synonym of *Ch. formicaria*.

Erroneous synonymies

"*Cerylon lapidarium* Dejean"

This species has not been formally published, therefore it is not taxonomically available, i.e., it is a nomen nudum (A. Slipinski, pers. com. 2021). However, Belon (1879: 194) regarded it as a synonym of *Ch. formicaria*. Considering the morphology of species of *Cerylon* Latreille, 1802 (Cerylonidae), it is possible that the material studied by Belon (1879) belonged to a species of the genus *Merophysia*.

***Merophysia ragusae* Belon, 1895**

Rücker (2020: 34) regards *Merophysia ragusae* as a junior synonym of *Ch. formicaria*. This is an error considering that Belon (1895) clearly places *M. ragusae* from Sicily close to *Merophysia sicula* Kiesenwetter, 1872, and not to any species of *Cholovocera*. Furthermore, Rücker (2011a: 18) had already placed *Merophysia ragusae* as a junior synonym of *Merophysia formicaria* Lucas, 1852. It is apparent that Rücker (2020: 34) confused *Ch. formicaria* with *M. formicaria*.

Taxonomic history and remarks

Although Victor's (1838) description of *Cholovocera formicaria* is very brief, his illustrations allow an accurate identification of the taxon. However, as it will be discussed below, most of the records of *Ch. formicaria* published until recently proved to be incorrect, as well as geographic distributions and names of host ants given for *Ch. formicaria* in several checklists. Although there are many papers dealing with *Ch. formicaria*, there is a great deal of incorrect data repeated in them.

Märkel (1845: 255), while describing *Ch. punctata*, studied a specimen of *Ch. formicaria* from Russia, sent to him by Motschulsky (see Material examined, above). Lucas (1849: 553) reported "*Ch. formicaria*" from the margins of Lake Tonga (Algeria), on the border with Tunisia, but it was most likely *Ch. punctata*. Rosenhauer (1856: 355), while describing *Ch. formiceticola*, compared it with *Ch. formicaria* and

Ch. punctata. Redtenbacher (1858: 380; 1874: 411) discussed the differences between *Ch. formicaria* and *Ch. punctata*, in particular their elytral punctuation. Fairmaire (1859: 267) and Dieck (1870a: 399; 1871: 202) recorded "*Ch. formicaria*" from Corsica, but these were misidentifications of *Ch. punctata*. Saulcy (1862: 291) reported "*Ch. formicaria*" from Banyuls (Southern France, associated with *Messor capitatus* (Latreille, 1798)) but the correct identity of that material is uncertain because there are four species which occur in Southern France: *Ch. punctata*, *Ch. formiceticola*, *Ch. gallica* and *Ch. occulta* sp. nov. In their catalogue, Gemminger & Harold (1868: 905) gave the distribution of *Ch. formicaria* in "Grusia" (Georgia). Piccioli (1871: 304) recorded "*Ch. formicaria*" from Florence and Corsica, and Bargagli (1872: 100) from Sardinia; however, these records are likely to be misidentifications of *Ch. gallica* or *Ch. punctata*.

Schaufuss (1876a: 396, 400) commented about the morphology of *Ch. formicaria* and incorrectly regarded it as an endemic of Greece. André (1874: 226) associated *Ch. formicaria* with *Messor barbarus*, citing Saulcy (1862), who actually cited *Messor capitatus* (see above). Reitter (1877: 5) placed *Ch. gallica* as a junior synonym of *Ch. formicaria*, a status that we do not agree with. Belon (1879: 191) took a radical view, placing all five species of *Cholovocera* described until then, as junior synonyms of *Ch. formicaria*; however, Reitter (1882: 161) rejected such action claiming that *Ch. punctata* was a different species from *Ch. formicaria* because of its obvious punctuation, a position which was later accepted by Belon (1884a: 2; 1887: 216). Heyden *et al.* (1883: 80) incorrectly placed *Ch. formicaria* in southern Europe in their catalogue. Bolívar (1886: 51) recorded samples from Alicante and Algeciras (Spain), Morocco and Blidah (Algeria) as "*Ch. formicaria*"; we have studied a great part of this material which includes *Ch. formiceticola* (specimens from Spain and Morocco) and *Ch. punctata* (from Algeria). Similarly, Oertzen (1886: 201) recorded "*Ch. formicaria*" from Naxos (Greece), which were most likely *Ch. balcanica* or *Ch. attae*, Walker (1889: 377) reported it from Gibraltar and Tangier – actually *Ch. formiceticola* – and Gallois (1893: 18) cited it incorrectly from Nantes (France).

Wasmann (1894: 133) summarised published associations of what he regarded as "*Ch. formicaria*" with several species of ants: with *Messor barbarus* in eastern Pyrenees (from Saulcy 1862), in Gibraltar and Tangier (from Walker 1888) and in Tunisia (from Wasmann 1890); with a species of *Pheidole* in Andalusia, Spain (from Rosenhauer 1856), and with *Aphaenogaster testaceopilosa* in Menton, France (from Walker 1888). Even if the ant identities were correct, the beetles were certainly not *Ch. formicaria*.

Other reports of beetle samples misidentified as "*Ch. formicaria*" are:

Escherich & Emery (1897) cited it from "Brussa" (Bursa), associated with *Messor structor*, and from Angora (both localities in Anatolia, Turkey), but the correct identity of the beetles would have been *Ch. balcanica*; Escherich (1897) reported it from Anatolia again, but as "*Coluocera formicaria* var. *major*" and associated with *Messor barbarus*; Sahlberg (1903: 31) recorded a great number of specimens near Constantine (Algeria) associated with *Messor barbarus*, but we have examined material from this locality, which is *Ch. punctata*; Luigioni & Adelchi (1910: 69) recorded about 100 specimens under a rock in Lazio (Italia) in February, which we believe were *Ch. punctata* (see Material examined, below); Donisthorpe (1927: 9) collected specimens in Sicily, associated with "*Camponotus atlantis nylanderi* Emery, 1921", although this ant does occur in Sicily, the beetles were either *Ch. gallica* or *Ch. punctata*; Luigioni (1929: 528) reported material from Liguria, Toscana, Umbria, Lazio, Puglia, Calabria, Sardinia and Sicily (Italy), but the correct identity would have been *Ch. gallica* or *Ch. punctata*; Martínez de la Escalera (1914: 123) collected beetles from several localities in northern Morocco, which we have examined and identified as *Ch. formiceticola*; Angelini & Rücker (1999: 218) reported "*Ch. formicaria*" from Puglia, Calabria and Sicily, but it was most likely *Ch. punctata* or *Ch. gallica*, equally for Sabella & Sparacio's (2004: 498) report from Sicily, and for the listed record in Fadda *et al.* (2007: 70) from Provence (France), which may also refer to *Ch. occulta* sp. nov. and/or *Ch. formiceticola*.

Ponel (2011: 254) reported "*Ch. formicaria*" from Villeneuve à Fréjus, near Nice (France), but it may have been *Ch. punctata*, *Ch. gallica* or *Ch. occulta* sp. nov. Prieto-Manzanares (2018: 464) recorded "*Ch. formicaria*" in Barcelona (Spain), but it was either *Ch. formiceticola* or *Ch. gallica*. Parmentier *et al.* (2020: 589) reported "*Ch. formicaria*" from Córdoba (Spain) but, again, it was a misidentification of *Ch. formiceticola*.

Rücker (1980: 143) published a key for the identification of the six species which he recognised as belonging to *Cholovocera*, illustrating the median lobe of the aedeagus of all the species (Rücker 1980: 145, figs 21–26), including that of *Ch. formicaria*; however, the geographic distribution of this species is erroneous, and was repeated by Rücker (1983: 3).

Several recent checklists included *Ch. formicaria*, but repeated incorrect geographic distributions published previously (Rücker 2009: 14, 2008: 576, 2020: 34; Shockley *et al.* 2009b: 65). Finally, Rücker (2018: 576, figs 1183–1184) gave a detailed description of *Ch. formicaria*, including figures of the aedeagus; however, we believe these figures actually represent the aedeagus of *Ch. punctata* (Fig. 16).

Cholovocera punctata Märkel, 1845
Figs 4H, 7G, 9B, 11D, 12H, 13G, 14N–O, 16, 17, 23C–E, 24H–I, 25C, 25E

Cholovocera punctata Märkel, 1845: 255.

Colovocera formicaria – Belon 1879: 191 (in part).
Coluocera punctata sardoa – Reitter, 1911: 70. **Syn. nov.**
Colnocera [sic] *punctata sardoa* – Krausse 1913: 62.
Coluocera punctata ? n. sp.? – Krausse 1915: 120.
Cholovocera sardoa – Rücker 1980: 144, fig. 24.

Differential diagnosis

Cholovocera punctata can be distinguished from all other species in the genus by the shape of the terminal antennomeres, which are shaped like equilateral triangles (Figs 12H, 13G). Also, the aedeagus is characteristic (Fig. 16), but similar to that of *Ch. attae*. However, in lateral view, they clearly differ in shape (Figs 16C, 19C), as well as in the shape of the parameres (Figs 16B, 19B).

Furthermore, the aedeagus, the paramere and the spermatheca are useful characters to distinguish *Cholovocera punctata* from all other species in the genus.

Type material

Cholovocera punctata: the type material comprises two syntypes, collected in Sicily by J.W. Helfer, which Märkel (1845) examined and compared with one specimen of *Ch. formicaria* sent to him by V.I. Motschulsky. In order to locate and recognise the syntypes of *Ch. punctata*, we had to examine specimens from the Märkel Collection deposited in SMTD, and from the Helfer Collection held in NMPC. A male and female pair was found in SMTD labelled as "Sicilia – Coll. Märkel" (Fig. 23E) and mounted on card triangles (Fig. 23C, left). Also, five females mounted on the same kind of mounting cards (Fig. 23C, right) were located in NMPC, all of them with a single label, written by J.W. Helfer, reading "Monte Pellegrino, Palermo" (Fig. 23D). From the foregoing, we deduce that J.W. Helfer sent only two specimens to Märkel, which are the syntypes, keeping the others in his collection (see below). Märkel (1845) also examined a third specimen from the Germar Collection, which we were not able to locate.

Considering the great number of misidentifications of the species of *Cholovocera*, both in collections and in the literature, it is advisable to designate a lectotype from the syntypes of *Ch. punctata*, to give this name taxonomic stability (Article 74.7.3, ICZN 1999). We hereby designate the male syntype from the Märkel Collection deposited in SMTD, with label reading "Sicilia – Coll. Märkel", as the lectotype of *Cholovocera punctata* (Fig. 23C, left).

Coluocera punctata sardoa: The type series comprises the lectotype male, five paralectotypes held in HNHM, and twenty-four paralectotypes in SDEI (labelled as "syntypes"), all collected in "Assuni", Sardinia.

Lectotype (designated above)
ITALY – **Sicily** • 1 ♂, "Sicilia / Coll. Märkel"; SMTD.

Paralectotype
ITALY • 1 ♀; Sicily; SMTD.

Lectotype of *Coluocera punctata sardoa* (designated by Rucker 2011a: 13)
ITALY • 1 ♂; Sardinia, "Assuni"; Krausse leg.; HNHM.

Paralectotypes of *Coluocera punctata sardoa*
ITALY – **Sardinia** • 2 ♂♂, 3 ♀♀, 19 specimens; "Assuni"; Krausse leg.; SDEI: 11985–12004 and 12015–12018 [labelled as "syntypes"] • 5 specimens; "Assuni"; Krausse leg.; HNHM.

Notes
As it can be seen in Rücker 2011a (fig. 21), there is a label reading "Holotypus" attached to the specimen that Rucker designated as the lectotype. However, this specimen cannot be regarded as the holotype because it was not designated in the original description, which included more than one specimen, i.e., syntypes. Examining the handwriting of the Holotypus label, we conclude that it was added at a later date than the description by Reitter (1911).

The same comment given above under the lectotype, applies to the paralectotypes.

Additional material, non-types

FRANCE – **Laguedoc-Roussillon** • 1 ♂, 3 ♀♀; "Süd-Frankreich, Hérault"; NHMB – **Provence-Côte D'Azur** • 1 ♂, 7 specimens; Marseille; NHMB – **Corsica** • 5 specimens; "Umgeb." [environs] Porto-Vecchio; 22– 25 Apr. 1927; SFUN • 4 specimens; Porto Vecchio; MHNG • 2 specimens; "Meerstrand b [near beach] Porto-Vecchio"; 22–25 Apr. 1927; MFNB • 2 specimens; "Umgeb." [environs] Porto-Vecchio; 22–25 Apr. 1927; MFNB • 3 specimens; Ajaccio; A. Krausse leg.; SFUN • 1 specimen; Ajaccio; 6 Apr. 1911; A. Krausse leg.; NMPC • 1 ♀; Ajaccio; V. Budtz leg.; SMTD • 1 ♂; Ajaccio; SMTD • 2 specimens; Bastia; ZFMK • 9 specimens; Canvia; 24 Apr. 1973; S. Vit leg.; "ss. les pierres" [under stones]; MHNG • 4 specimens; "env." [environs] Propiano; 30 Apr. 1973; S. Vit leg.; "ss. une pierre" [under a stone], [three specimens associated with a *Pheidole* worker ant, the fourth with a *Messor* worker ant]; MHNG • 2 specimens; Piana; 20 Apr. 1973; S. Vit leg.; "ss. une pierre" [under a stone], [one specimen associated with a *Camponotus* worker ant. The other one with a *Lasius* worker ant]; MHNG • 2 specimens; "env." [environs] Sartène; 24 Apr. 1973; S. Vit leg.; "ss. une pierre" [under a stone], [each specimen associated with a *Pheidole* worker ant]; MHNG • 1 specimen; Ghisonaccia mer[idional]; 26 Apr. 1973; S. Vit leg.; MHNG • 1 specimen; Olmeto; 21 Apr. 1973; S. Vit leg.; "tronc enfoncé" [buried log]; MHNG – **Corsica, no specific locality** • 1 ♂, 1 specimen; SFUN • 2 ♂♂, 1 ♀, 5 specimens; ZFMK • 1 ♂; MCNM 198708 • 3 ♀♀; NMPC • 4 specimens; SMTD • 3 ♂♂, 7 ♀♀; SDEI 10776– 10777, 10790–10801, 10823 and 10844–10846 • 2 ♂♂, 2 ♀♀; Krausse leg.; NKME • 1 ♂; Miller leg.; NHMB • 1 ♂, 6 specimens; NHMB • 16 specimens; SMTD • 1 ♂, 3 ♀♀; MFNB – **France, no specific locality**

• 1 ♂; “Gallia Meridio”; NKME • 2 ♀♀; “Frankreich”; SFUN • 1 specimen; “gallia”; MFNB • 1 ♀; “Gall. Mer.”; MFNB.

ITALY – **Sardinia** • 3 specimens; Asuni; A.H. Krausse leg.; SMTD • 13 specimens; Asuni; Krausse leg.; SDEI: 12019 to 12031 • 25 specimens; Asuni; SDEI 11920–11922, 12033–12044 and 11920–11922 • 1 specimen; Asuni, Posta Senio; Krausse leg.; MFNB • 2 specimens; Asuni; NKME • 3 ♀♀, 8 specimens; Asuni; NMPC • 1 ♀; Asuni; A.H. Krausse leg; NMPC • 1 ♂, 11 specimens; Asuni; SFUN • 2 specimens; Asuni b. [near] Cagliari; 1916; J. Krasni leg.; SFUN • 47 specimens; Asuni; SMTD • 1 ♂, 49 specimens; Asuni; NHMB • 20 specimens; Asuni; Dr. Krausse leg.; NFNB • 1 specimen; Mount Turitas; NMPC • 6 specimens; Oristano; SMTD • 3 specimens; Oristano, NMPC • 1 ♀; Terranova [modern Olbia]; NMPC • 14 specimens; Sardinia; Cagliari; SMTD • 1 ♀; Golfo Aranci; A. Dodero leg.; NHMB • 1 ♂, 1 ♀; 4 km Notrhwest of Telti; 350 m a.s.l.; 12 Apr. 1992; J. Scheuern leg.; [one specimen associated with two *Messor* worker ants]; NKME • 2 specimens; Southwest of Macomer; 500 m a.s.l.; 13 Apr. 1992; J. Scheuern leg.; [each specimen associated with a *Messor* worker ant]; NKME • 2 ♂♂, 1 ♀; Sardina, Lago dei Coghinas; 160 m a.s.l.; 12 Apr. 1992; J. Scheuern leg.; [one specimen associated with a *Messo*r worker ant, other specimen associated with a *Camponotus* worker ant]; NKME • 24 specimens; Cagliari; SMTD • 1 specimen; Cagliari; A. Fiori leg.; MFNB • 1 specimen; Mount Sette Fratelli; SMTD • 1 ♂, 8 specimens; Sorgono; NHMB • 1 ♀, 1 specimen; Sorgono; SDEI 12032 and 11929 • 1 ♂, 5 specimens; Ozieri; NHMB • 2 specimens; Ozieri; A. Dodero leg.; NHMB • 4 specimens; Sardina, Sassari, Macomer; 13 Apr. 1952; SFUN • 2 ♂♂, 2 specimens; Maccomer; 24 May 1920; MFNB • 1 specimen; Golfo Aranci; A. Dodero leg; SFUN • 1 specimen; Golfo Aranci; SFUN • 1 specimen; Golfo Aranci; 9 Apr. 1977; S. Vit leg.; “ss. une pierre” [under a stone], [specimen associated with a *Camponotus* worker ant]; MHNG • 1 ♂, 2 ♀♀, 1 specimen; Alá dei Sardi; T. Derosas leg.; MCNM 197913–197916 • 1 ♂, 5 specimens; 12 km North of Dorcali; 250 m a.s.l.; 23 Apr. 1992; J. Scheuern leg.; [two specimens associated with an *Aphaenogaster* worker ant]; ZFMK • 2 specimens; Noth of Pattada; 450 m a.s.l.; 12 Apr. 1992; J. Scheuern leg.; [one specimen associated with four *Pheidole* worker ants]; ZFMK • 5 specimens; North of Pattada; 300 m a.s.l.; 12 Apr. 1992; J. Scheuern leg.; [each specimen associated with a *Messor* worker ant]; ZFMK • 4 specimens; South of Pattada; 300 m a.s.l.; 12 Apr. 1992; J. Scheuern leg.; [each specimen associated with a *Messor* worker ant]; NKME • 1 ♂, 2 specimens; North of San Vito; 50 m a.s.l.; 18 Apr. 1992; J. Scheuern leg.; [specimens associated with three *Pheidole* worker ants]; ZFMK • 15 specimens; Telti, Olbia; 9 Apr. 1977; S. Vit leg.; “ss. une pierre” [under a stone], [one specimen associated with a *Camponotus* worker ant]; MHNG • 2 specimens; “M”[ount]. Ferru; A. Dodero leg.; MFNB • 1 specimen; Seui; MFNB – **Sardinia, no specific locality** • 1 ♂, 17 specimens; J. Krausse leg.; NHMB • 4 specimens; SFUN • 2 ♀♀; Bruck leg.; SFUN • 1 specimen; ZFMK • 1 ♀; MCNM 198737 • 10 specimens; SDEI 12005–12014 • 1 specimen; Baudi leg.; SDEI 11938 • 1 specimen; SMTD • 1 ♀, 6 specimens; MFNB – **Sicily** • 3 specimens; Erica; 10 Dec. 1993; Sabella leg.; “Bosco misto” [mixed forest]; NMPC • 6 specimens; Calabria, Sambiase; May 1925; C. Minozzi leg.; [each specimen associated with a *Messor* worker ant]; SMTD • 1 specimen; Agricento, Valle dei Templi; 18 Mar. 2013; P. Hlavác leg.; Under rock, ant nest [specimen associated with a *Cataglyphis* worker ant]; NMPC • 12 specimens; Ficuzza; SDEI 12033–12044 • 2 ♂♂; Ficuzza; NHMB • 1 ♂, 7 specimens; Ficuzza; May 1895, Flach leg.; SFUN • 13 specimens; Ficuzza; 14 May 1912; Fiori leg.; MHNG • 3 ♂♂, 1 ♀; Ficuzza; 16 Mar 1942; NKME • 2 ♀♀; Ficuzza; 16 Mar. 1942; MFNB • 1 ♂, 5 specimens; Palermo, Ficuzza; 700–900 m a.s.l; 21–24 May 1996; F. Angelini leg.; MZLU • 1 ♂, 6 specimens; Ficuzza; NHMB • 21 specimens; Ficuzza; 5 Apr. 1925; Dr. Rambousek leg.; NMPC • 3 ♀♀; Palermo, Ficuzza; 700 m a.s.l.; 1–4 May 2000; “Bosco leccio” [oak forest], F. Angelini leg.; NMPC • 1 ♂, 6 specimens; Palermo, Marineo, L.[ake] Scanzano; 525 m a.s.l.; 9 Apr. 1993; F. Angelini leg.; MCVR • 1 ♂, 5 specimens; Palermo, Madonie, Road Castelbuono–Gerace, Pitorno; 30 Apr. 1996; Angelini leg.; MCVR • 1 ♂, 1 ♀, 1 specimen; Palermo, Lago di Piana degli Albanesi; 610 m a.s.l.; 21 May 1996; F. Angelini leg.; MCVR • 5 ♀♀; “G.” [environs] Palermo, Monti Pellegrino; 1852; Helger leg.; NMPC [Helfer Collection] • 1 ♂; Palermo; NHMB • 2 ♂♂, 2 ♀♀, 1 specimen; Palermo;

SDEI 11914–11919 • 1 ♂, 2 specimens; Palermo; SDEI 11912–11915 • 1 ♂; Palermo; E. Ragusa leg.; SFUN • 2 specimens; Palermo; 1906; O. Leonhard leg.; SMTD • 1 ♂, 2 specimens; Randazza; 6 May 1933; W. Liebmann leg.; SDEI 11972–11974 • 3 ♂♂, 2 ♀♀, 4 specimens; Catania; SDEI 11976–11984 • 5 specimens; Catania; SDEI 05764–05768 • 11 specimens; Catania; NMPC • 3 specimens; Catania; Prof. Lera leg.; MFNB • 1 specimen; Catania; MFNB • 1 ♂, 4 specimens; Catania; SDEI 11976–11980 • 1 ♂, 18 specimens; Gibilmanna; 800 m a.s.l.; 6 May 1982; T. Palm leg.; "Sten" [stone]; MZLU • 1 ♂, 2 specimens; Siracusa, Melilli; 100 m a.s.l.; 5 Apr. 1997; F. Angelini leg.; MCVR • 1 ♀; Trapani, Mount S. Giuliano; 24 Jan 1913; A. Dodero leg.; NHMB • 1 ♂, 2 specimens; Bertolia; SFUN • 4 specimens; Licata; ZFMK • 2 specimens; "M."[ount] Busambra; 16 May 1912; A. Fiori leg.; MHNG • 2 ♀; Calabria, Cimina; Paganeti leg.; NMPC – **Sicily, no specific locality** • 1 ♂; SDEI 11932 • 2 ♂♂; NHMB • 1 ♀; SFUN • 1 ♂, 1 ♀; Flach leg.; SFUN • 1 ♂, 1 ♀, 1 specimen; ZFMK • 1 ♂; "C. Rissen" leg.; SDEI 11941 • 4 specimens; Sicily; SMTD • 1 specimen; 21 Nov.; Füge leg.; SMTD • 1 specimen; NMPC – **Tuscany** • 1 ♂, 4 ♀♀; Mt. Argentario; May 1907; Dr. Stolz leg.; NHMW – **Lazio** • 1 ♂, 3 ♀♀, 3 specimens; Mte. Circeo; H. Franz leg.; NHMW • 1 specimen; Maccarese; 20 Feb. 1910; Luigioni leg.; MFNB • 1 ♀; Roma; 23 Apr. 1904; A. Fiori leg.; MFNB • 1 ♂, 1 ♀; Roma, Acilia; Castel.; Nov. 1931; MFNB – **Campania** • 1 ♀; Salerno, Pioppi; Nov. 1964; W. Liebmann leg.; MFNB – **Calabria** • 2 ♀♀; Alli; 24 Apr. [19?]84; MFNB.

MALTA – **Northern Region** • 2 ♀♀; Bidnija, NW Mosta; 1 Apr. 2002; Schuh and Mifsud leg.; NHMW.

ALGERIA – **Oran** • 1 ♂; Oran; NMPC – **Algiers** • 1 ♂; Quendef.; SDEI 10768 • 1 ♀; SDEI 11928 • 1 ♂, 10 specimens; Kabilie, Bou-Berak; L. Puel leg., NHMB • 1 ♂, 1 ♀; St Charles; NHMB • 1 ♂, 1 ♀; Biskra; May 1898; L. Vareilles leg.; NHMB • 2 ♂♂, 1 ♀; Philippeville [now Skikda]; May 1898; L. Vareilles leg.; [each specimen associated with a *Cataglyphis* worker ant]; NHMB • 1 ♂, 1 ♀; Constantine; Le Thierry leg.; MCNM 198706 • 5 ♀♀; Constantine; Sep 1957; ZFMK • 4 ♀♀; Blida; 19 Apr. 1896; L. Bleuse leg.; "dans detritus où ils se trouvent des fourmis" [in an ant refuse pile]; ZFMK • 1 ♂; "Bliad" [Blida?]; MCNM 198704 • 1 ♂; Lambèze [now Tazoult-Lambése]; Jun. 1885; L. Bleuse leg.; ZFMK • 1 ♂, 1 ♀, 9 specimens; Bone [now Annaba]; ZFMK • 1 specimen; Gorges de la Chiffa, Ruisseau des Singes; 280– 380 m a.s.l.; 4 May 1988; Besuchet, Löbl and Burckh. leg.; MHNG • 2 specimens; Djurdjura, 4 km Southwest of Tikjda; 1200 m a.s.l.; 7 May 1988; Besuchet, Löbl, Burckh. leg.; MHNG • 1 ♂, 2 ♀♀; G.[orge] de Kabylie, Djebel Bou-Berak; 350 m a.s.l.; 19 May 1988; Besuchet, Löbl and Burckh. leg.; MHNG • 3 ♂, 7 specimens; G.[orge] de Kabylie, Adekar; 900 m a.s.l.; 15 May 1988; Besuchet, Löbl and Burckh. leg.; MHNG • 1 specimen; G. de Kabylie, L'Arbatache sur El Kseur; 300–400 m a.s.l.; 18. May 1988; Besuchet, Löbl and Burckh. leg.; MHNG • 4 specimens; G.[orge] de Kabylie, 9 km East of Yakouren; 930 m a.s.l.; 13 May 1988; Besuchet, Löbl and Burckh. leg.; MHNG • 3 ♀♀; MFNB • 1 ♂, 2 ♀♀, 33 specimens; Laverdure; 30 Apr–14 May 1927; Mařan leg.; [six specimens associated with a *Tetramorium* worker ant, and an additional label: "*Tetramorium* sp.; P. Werner det. 2016"]; NMPC • 7 specimens; Batna; NMPC – **Algeria, no specific locality** • 1 ♂; Algier; NHMB • 1 ♂; Doufou leg.; MFNB.

TUNISIA – **Bizerte** • 2 ♀♀; Bordj Djedid; SFUN • 1 ♂, 1 ♀; Tabarka, Cap Negro; 17 Mar. 1984; H. Meybohm leg.; NHMW • 1 specimen; Belif, "prés" [near] Cap Negro; 5 Apr 1962; Cl. Besuchet leg.; MHNG • 1 ♂; Teskraia bei Bizerte; 16 Mar. 1984; H. Meybohm leg.; NHMW • 2 ♂♂, 2 ♀♀; Galita I[sland]; H. Franz leg.; NHMW • 1 ♀; Monts de la Mejerda, Fôret Quedzen, ca. 20 km Southeast of Ain Draham; 26 Jan. 2004; Lebenbauer leg.; NHMW – **Jendouba** • 2 ♂♂; Umg. Ain Draham; 18 Mar. 1984; H. Meybohm leg.; NHMW • 1 ♂, 13 specimens; Ain Draham; 10 Mar. 1925; Dr. Rambousek leg.; NMPC • 3 specimens; Ain Draham; 16–18. Apr. 1927; Mařan leg.; NMPC • 1 ♀; Ain Drahan; B. v. Bodemeyer leg.; SDEI 11975 – **Tunis** • 1 specimen; Souk El Arba; NMPC • 1 ♀; Dijedid; NMPC • 3 specimens; Dr Normand leg.; NMPC • 1 specimen; Belvedere; 3 Mar. 1962; Cl. Besuchet leg.; MHNG • 1 specimen; Oued Mitiane près de Tunis; 26 Mar. 1962; Cl. Besuchet leg.; MHNG • 3 ♂♂;

Hanman-El-Def [for Hamman-Lif]; 10. Jul. 1914; CNHM – **Kef** • 1 specimen; Le kef; Dr Normand leg.; NMPC – **Kairouan** • 1 ♂, 7 specimens; Ain Jioula; 26 Mar. 1984; leg. H. Meybohm; NHMW – **Tunisia, no specific locality** • 1 ♂, 1 ♀; "Tunis"; 8 Nov. [18?]85; ZFMK • 1 specimen; "Tunis"; NMPC.

Type locality

"in Sicilien" [Sicily], Italy.

Description

Male as in Fig. 11D. Body length: 1.40 mm average, range 1.30–1.50 mm (N = 49, males and females). Shape of body subelliptical, pronotum almost rectangular, with angular lateral margins. Elytral apex rounded. Terminal antennomeres triangular, equilateral, in both sexes. Metatibiae as in Fig. 14N, O, narrower in the proximal half and with almost straight margins. Prosternal process slightly keeled anteriorly, with a marked median constriction and distally rhomboidal (Fig. 4H). Male last visible ventrite with a marked emargination and bordered by a brush of long setae.

Median lobe of aedeagus short, subrectangular in the first third of its length and distally oblique, tapering with a round apex in ventral view (Fig. 16A). Aedeagus in lateral view as in Fig. 16C. Distal portion of paramere long, conical, with a pointed apex bearing a brush of setae of variable number (Fig. 16B–C). The parameral apex and the number of apical setae show a clinal variation in shape and number respectively (Fig. 17A–F). Specimens from North Africa and central Italy have a parallel-sided, rounded apex with five or six setae (Fig. 17A–B). The apex gradually tapers, becoming more triangular and pointed, with a decreasing number of setae in more northern European populations (Fig. 17C–F). Both the spermathecal duct and the spermathecal reservoir are short; ramus short, round and globose distally, cornu round, and nodulus weakly developed, much smaller than cornu and ramus together (Fig. 7G).

Geographic distribution

The known distribution of *Cholovocera punctata* is typically Mediterranean, extending from southern France in the northwest, to Corsica, Sardinia, the west coast of continental Italy and Sicily in the east, and Algeria and Tunisia in the south (Fig. 9B).

Host ants

Sahlberg (1903: 31) reported specimens of *Ch. punctata* associated with *Messor barbarus* in Lake El Bahira (Algeria) and in Hamman-Lif (Tunisia); considering that we have examined three males of *Ch. punctata* from Hamman-Lif (see above), we consider this association to be most likely correct. Confirmation of that association can be found in Krausse (1911), who found *Ch. punctata* (as *Co. punctata sardoa*) associated with *Messor barbarus* in Sardinia, and both species do occur in this island. Rücker (2018) associated *Ch. punctata* with the ant genera *Messor* and *Atta*; however, the genus *Atta* is exclusively Neotropical in distribution, making it impossible to be associated with a beetle of Mediterranean distribution!

Besides its association with *Messor barbarus*, we were able to recognise another six ant genera associated with *Ch. punctata* in its geographic distribution (see Material examined above), as follows: (1) *Pheidole* in Corsica and Sardinia, (2) *Camponotus* in southern France and Sardinia, (3) *Cataglyphis* in Sardinia and Algeria, (4) *Lasius* in Corsica, (5) *Aphaenogaster* in Sardinia, and (6) *Tetramorium* in Algeria. Among all the species of *Cholovocera*, *Ch. punctata* has the greatest range of associations with ant taxa, especially in Sardinia, where it has been recorded with species of five different ant genera.

Junior synonym

***Coluocera punctata sardoa* Reitter, 1911**

Reitter (1911: 70) described *Co. punctata sardoa* from specimens collected in "Assuni", Sardinia, provided by A.H. Krausse, distinguishing it from nominate *Ch. punctata* by external features, such as being slightly longer, more punctured and lacking two dark spots on the base of the pronotum. Krausse (1911: 148, 1913: 62, 1915: 120, 1917: 51) recorded *Co. p. sardoa* in Sardinia, adding Sorgono as a new locality for it. Seidlitz (1912: 67) included *Co. p. sardoa* in his list of Coleoptera described until 1911.

Rücker (1980: 144) raised this taxon to full species, including it in an identification key, with a figure of the median lobe of the aedeagus; however, Rücker's (1980: 145, figs 24–25) illustrations of the median lobes of *Ch. sardoa* and *Ch. punctata* appear different because they are presented in different orientations. Döbler (1987: 16) reported the presence of 24 "syntypes" (in fact, paratypes) de *Co. p. sardoa* in the collection of the SDEI. Subsequent catalogues and checklists include *Ch. sardoa* as a valid taxon and endemic to Sardinia (Löbl & Smetana 2007: 557; Rücker 2009: 14, 2011b, 2018: 579, 2020: 34; Shockley *et al.* 2009b: 65).

We have examined the holotype male of *Co. punctata sardoa* and compared it with many males of *Ch. punctata* from the type locality, without finding any significant morphological difference that would justify the separation of this species into two subspecies. The terminal antennomere of the holotype is identical to that of *Ch. punctata*, and its aedeagus, although partially broken in the basal piece (Fig. 24H–I), is otherwise like those of several males of *Ch. punctata*, which we have studied (Fig. 16). Therefore, we have no hesitation in placing *Coluocera punctata sardoa* as a new junior synonym of *Ch. punctata.*

Taxonomic history and remarks

Märkel's (1845: 255) description of *Cholovocera punctata* is in Latin and brief, qualifying it as "elongate, oval, convex, reddish-yellow, punctured, with elytral apex attenuated, and habitat in Sicily", but he emphasized the main difference from *Ch. formicaria* being the abundance of punctures on the entire surface of the body; also, Märkel (1845) implied a possible association with ants but could not confirm it. Erichson (1845: 125) and Ragusa (1873: 176) cited *Ch. punctata* in Sicily again; Redtenbacher (1858: 380, 1874: 411) mentioned its punctation as the main difference with *Ch. formicaria*, and Fairmaire & Coquerel (1860: 170) published an illustration of the mouth parts of *Ch. punctata*. In their catalogue, Gemminger & Harold (1868: 905) mentioned Sicily as the distribution of *Ch. punctata*. Piccioli (1871: 304) and Bargagli (1872: 100) reported *Ch. punctata* from Sardinia for the first time. Schaufuss (1876a: 396) commented on the morphology of *Ch. punctata*; Reitter (1875: 302) gave a brief description of *Ch. punctata*, and later sank *Ch. formiceticola* as a junior synonym of it (Reitter (1877: 5). Belon (1879: 191) proposed to sink *Ch. punctata* under *Ch. formicaria*, but Reitter (1882: 161) disagreed with Belon (1879) alluding to the denser punctuation of *Ch. punctata*. Then, Belon (1884a: 2, 1887: 216) gave other characters to separate *Ch. punctata* from *Ch. formicaria*. The catalogue of European beetles by Heyden *et al.* (1883: 80) gave the distribution of *Ch. punctata* as Sicily and Sardinia only, but Riggio (1885: 31) added a new locality for this species in the Island of Ustica, 100 km north of Sicily, and Heyden (1886: 38) recorded it in Algeria. Ciofalo (1886: 188) recorded it in Termini Imerese, northern Sicily. However, the catalogue published by Wasmann (1894: 133) only mentioned Sicily as the distribution of *Ch. punctata*.

Ganglbauer (1899: 821) and Belon (1902: 5) published redescriptions of *Ch. punctata* and its distribution, while Vitale (1904: 75) commented that this beetle is very rare in Messina (East Sicily). Luigioni & Adelchi (1910: 70, 1913: 152) recorded a few specimens in moist soil under *Eucalyptus* trees near Rome and others in Sicily, respectively. In his catalogue of Italian Coleoptera, Luigioni (1929: 528) mentioned Liguria, Toscana, Capri Island, Lazio, Campania, Calabria and Sicily, as localities for *Ch. punctata*; we have examined specimens from Lazio, Calabria and Sicily which confirm Luigioni's (1929) records.

Martínez de la Escalera (1914: 123) reported "*Ch. punctata*" from several localities in northern Morocco, but the correct identification of the beetles would have been *Ch. formiceticola*. In his catalogue, Sainte-Claire Deville (1914: 255) suggested that *Ch. punctata* occurs in western Mediterranean islands, while *Ch. formicaria* lives in southern France, but the latter statement is incorrect. Rücker (1980: 144) included *Ch. punctata* in his key for the identification of *Cholovocera* species, illustrating the median lobe of the aedeagus (Rücker 1980: 145, fig. 25); also, he gave the geographic distribution of this species as: France, Spain, Corsica, Sardinia, Sicily, Algeria and Tunisia, which was repeated by Rücker (1983: 4). We agree with that distribution except for Spain, where we have not found any record of *Ch. punctata* (Fig. 9B). Angelini & Rücker (1999: 218) reported *Ch. punctata* from Basilicata (southern Italy) and Sicily.

Catalogues and checklists which include *Ch. punctata* have been published by Löbl & Smetana (2007: 557), Rücker (2009: 14), Shockley *et al.* (2009b: 65) and Rücker (2011b, 2018: 576, 2020: 34); all these papers gave the geographic distribution as: southern France, Corsica, Italy, Sardinia, Sicily, Hungary, Spain, Switzerland, Algeria and Tunisia. Our examination of many specimens shows that these localities are mostly correct, except for Spain, Hungary and Switzerland. Records from Spain are most likely of *Ch. formiceticola* (see below), but those from Hungary and Switzerland are not supported by specimens; therefore, they need to be confirmed. Rücker (2018: 576, figs 1181–1182) gave a detailed description of *Ch. punctata*, including a figure of the aedeagus; however, we believe these figures actually represent the aedeagus of *Ch. formicaria* (Fig. 15).

Cholovocera formiceticola (Rosenhauer, 1856) new status
Figs 2, 3C, 4F, 5–6, 7F, 8A, 9A, 11B, 12F, 13E, 14J–K, 18, 23F–G, 24E, 25D

Choluocera formiceticola Rosenhauer, 1856: 355.

Cholovocera formiceticola – Gemminger & Harold 1868: 905.
Coluocera formcieticola – Schaufuss 1876a: 400.
Coluocera formicaria – Reitter 1875: 301 (in part).
Colovocera formicaria – Belon 1879: 191 (in part).
Cholovocera punctata – Shockley *et al.* 2009b: 65 (in part).

Differential diagnosis

Cholovocera formiceticola is morphologically and geographically close to *Ch. gallica*, but these species can be separated by the shape of the pronotum and of the metatibiae (Fig. 14F–G against Fig. 14J–K). Also, *Ch. formiceticola* is geographically close to *Ch. punctata*, but they can be distinguished by the shape of the terminal antennomeres (Fig. 12F, H against Fig. 13E, G).

Furthermore, the aedeagus and the paramere are useful characters to distinguish *Cholovocera formiceticola* from all other species in the genus (Fig. 18).

Type material

Cholovocera formiceticola: the collections of Wilhelm D. Rosenhauer were sold by his family to several European institutions upon his death (Katter 1881). The beetle collection, which was the base of his 1856 book *Die Thiere Andalusiens*, was mostly acquired by the *Muséum national d'histoire naturelle* in Paris, via R. Oberthür (Cambefort 2006: 282; Bousquet 2016: 450). However, no specimen of *Cholovocera* from the Rosenhauer Collection could be found in that museum (A. Taghavian pers. comm. Dec. 2019). Alternatively, M. Balke found two male specimens from the Rosenhauer Collection in the SNSB (Berlin) labelled as *Choluocera formiceticola* and collected in "Spanien". As we could not

locate any more specimens from the type series, despite enquiries made to several European museums, we believe that these two beetles are the only extant syntypes of this species.

Considering the great number of misidentifications of the species of *Cholovocera*, both in collections and literature, it is advisable to designate a lectotype from the syntypes of *Ch. formiceticola*, to give this name taxonomic stability (Article 74.7.3, ICZN 1999). We hereby designate one syntype male from the Rosenhauer Collection deposited in SNSB, with label reading: "*Choluocera formiceticola* Rosenh. Spanien." as the lectotype of *Cholovocera formiceticola* (Fig. 23F–G). The other syntype male, without a label, becomes a paralectotype.

Lectotype

SPAIN • 1 ♂; "Spanien"; [Rosenhauer Collection], SNSB. Designated above.

Paralectotype

COUNTRY UNKNOWN • 1 ♂; without label; [Rosenhauer Collection], SNSB.

Additional material, non-types

FRANCE – **Languedoc-Rousillon** • 1 ♂, 13 ♀♀; "Pyr. Or." [eastern Pyrenees], Banyuls; Cl. Besuchet leg.; 25 Apr. 1953; "pierre avec fourmis" [stone with ants], two specimens with a *Messor* worker ant; MHNG • 2 ♀♀; "Pyrenäen" [Pyrenees], Collioure; SFUN.

PORTUGAL – **Lisbon** • 2 ♂♂, 4 ♀♀, 8 specimens; Apr.–May 1910; A. Schatzmayr leg.; SDEI 10804–10806 and 10829–10836 • 2 specimens; 1919; Schatzmayr leg.; NHMB • 1 specimen; 1910; SFUN • 1 specimen; "Schakm." leg.; SMTD • 2 specimens; 1910; MNHS – **Evora** • 1 specimen; 1910; SFUN • 3 specimens; 1910; MNHS.

SPAIN – **Castilla and León** • 1 ♂, 4 specimens; Avila, Candeleda; 30 Mar. 1929; MCNM 198721–198725 – **Madrid** • 7 specimens; Madrid; ZFMK • 15 specimens; Madrid; MCNM 198703, 198728, 198730–198731 • 2 specimens; Madrid; 1872; "En el retiro, bajo piedras, con hormigas" [At the Retiro Park, under stones, with ants]; MCNM 198729 – **Castilla and La Mancha** • 7 specimens; Toledo, Malpica [Malpica de Tajo]; MCNM 198736 – **Extremadura** • 1 ♂, 1 ♀; Badajoz; P. Seiler leg.; NHMB • 2 specimens; Badajoz; NHMB • 1 specimen; Badajoz; Bleuse leg.; ZFMK • 2 specimens; Badajoz; ZFMK • 13 specimens; Badajoz; MCNM 198726 – **Murcia** • 2 specimens; Cartagena; MCNM 198720 • 1 specimen; Cartagena; Simon leg.; NMPC • 1 ♂, 7 ♀♀ [four females in alcohol]; Murcia, La Alcayna, Rambla de las Monjas; 38º05′26.3″ N, 1º10′10.7″ W; 7 Jun. 2018; J. Delgado leg.; CDUM • 1 ♀; Murcia, La Alcayna, Rambla de las Monjas; 38º05′27.3″ N, 1º10′12.3″ W; 10 Apr. 2018; J.A. Delgado leg.; CDUM • 1 ♀ [in alcohol]; Murcia, La Alcayna, Rambla de las Monjas; 38º05′27.3″ N, 1º10′12.3″ W; 31 May 2021; J.A. Delgado leg.; [at the entry of an ant nest]; CDUM • 9 ♀♀; Murcia, Molina de Segura, La Alcayna, Rambla de las Monjas; 38º05′27.3″ N, 1º10′12.3″ W; 7 Jun 2018; J.A. Delgado leg.; [in ant nest]; CDUM – **Andalusia** • 2 specimens; Cadiz, Villaluenga del Rosario; 2 May 1960; Cl. Besuchet leg.; MHNG • 2 ♀♀; Tarifa; 22 Jan. 2005; Lebenbauer and Egger leg.; NHMW • 3 specimens; Cadiz, Los Barrios; Cl. Besuchet leg.; 22 Apr. 1960; MHNG • 1 ♂, 3 specimens; Cadiz, Cortijo Salomón; MCNM 198059 and 198063–198064 • 1 ♂, 6 specimens; Cadiz, San Roque, Cortijo Salomón; 20 Jan. 1990; De Ferrer leg.; MCNM 198058 and 198060–198062 • 5 specimens; Cadiz, Algeciras; Apr. 1901; Escalera leg.; MCNM 198709–198713 • 1 specimen; Cadiz, Algeciras; Apr. 1901; Escalera leg.; ZFMK • 7 specimens; Cadiz, Algeciras; MCNM 198693 and 198714–198717 • 1 specimen; Algeciras, Dieck leg.; MCNM 198732 • 3 specimens; Algeciras; Arias leg.; MCNM 198733–198735 • 7 specimens; Algeciras; NHMW • 1 specimen; Algeciras; SFUN • 2 ♂♂, 3 ♀♀; Algeciras; SDEI 10819, 11924–11926 and 11944 • 3 specimens; Algeciras; NHMB • 1 specimen; Srra [Range] Carbonera; MCNM 198719 • 18 specimens; Cordoba; SMTD • 2 ♂♂, 12 ♀♀; Cordoba; NMPC • 19 specimens; Malaga,

Nerja; 19–30 Apr. 1987; Scheuern leg.; "Macchia" [Machis], [each specimen associated with a *Messo*r worker ant]; ZFMK • 4 specimens; Gaucin; Jan. 1970; "Fourmilière" [Ant nest]; MCNM 198738 • 1 ♀, 1 specimen; Colmenar; 7 May 2017; Ernst leg.; NMPC • 1 ♂; Sierra Nevada, 10 km Southeast of Orgiva, "Bco." [Gorge] de las Cuevas de Camacho; 500 m a.s.l.; Scheuern leg.; ZFMK • 1 specimen; Granada; NHMB • 1 specimen; Mt. [Mount, most likely refers to Sierra Nevada] Granada; SMTD • 4 specimens; Sierra Nevada; V. Heyden leg.; SFUN – **Andalusia, no specific locality** • 1 ♂, 1 ♀; NHMB • 3 specimens; ZFMK, • 5 specimens; SFUN – **Balearic Islands** • 1 ♂; Manacor; MCNM 198718 • 1 ♀; Miramar; MFNB – **Melilla [Northern Africa]** • 2 ♀♀, 1 specimen; Nov. 1908; Arias leg.; MCNM 197992–197994 – **Spain, no specific locality** • 2 specimens; "Hispania"; SFUN • 2 specimens; "Spanien"; SFUN • 4 specimens; "Hispania"; MFNB.

MOROCCO – **Tangier-Tétouan** • 1 ♂, 85 specimens; Tangier; M. Escalera leg.; MCNM 197922–197949 and 197950–197952 • 14 specimens; Tangier; M. Escalera leg.; MCNM 197995–198006 and 198008 • 1 specimen; Tangier; Sep. 1957; ZFMK • 4 specimens; Tangier; E. Vaucher leg.; Sep. 1957; ZFMK • 1 specimen; Tangier, Herrmann leg.; NHMW • 3 specimens; Tangier; MHNG • 1 ♀; Tangier, 1899; NMPC • 1 ♀; Tangier; NMPC • 1 ♂, 2 ♀♀; Bani-Msuar [Beni Mesauar, near Tetouan]; M. Escalera leg.; MCNM 197921 • 1 ♂, 2 ♀♀; Cas. Blnc. [Casablanca]; NKME • 1 ♂, 2 ♀♀, 1 specimen; F. Taourirt; 20 Mar. 1923; E. Handschin leg.; B.? "Ameisen" [With ants]; NHMB – **Fez-Meknes** • 1 specimen; "Maroc, prés de [near] Meknes"; 24 Apr. 1961; Munard leg.; MHNG • 1 ♂, 3 ♀♀; Moyen Atlas, Azrou, Ito env.; 33º54.759′ E, 005º32.884′ W; 1440 m a.s.l.; 9 May 2009; Hlaváč, leg.; Under rocks on open meadow; NMPC • 2 ♀♀; Moyen Atlas, Azrou, Forêt de Cedres; 33º43.490′ E, 5º18.418′ W; 1600 m a.s.l.; 9 May 2009; Hlaváč leg.; under stone in forest; NMPC – **Souss-Massa** • 1 ♂; Agadir; 16–29 Jan. 1976; T. Palm leg.; "hos myror" [among ants]; MZLU 2020-006 – **Rabat** • 1 ♂; Rabat; NHMB • 2 ♀♀; Ouimes [Oulmés], El Harcha "nördl." [north of]; H. Franz leg.; NHMW • 1 specimen; O.[ued] Beth entre Aïn-el Orma et Khemisset; 24 May 1961; Munard leg.; MHNG – **Marrakech-Safí** • 1 ♀; Mogador; Nov. 1905; Escalera leg.; MCNM 197991 – **Laâyoune-Sakia El Hamra** • 3 ♀♀; "Algérie" [error for Morocco], Tarfaïa; NHMB – **Morocco, no specific locality** • 1 ♂, 1 ♀; "Marocco"; SFUN • 1 ♂; "Marocco"; SDEI 10828 • 2 ♂♂, 1 ♀; "Marokko"; SDEI 10825–10827 • 2 specimens; "Maroc"; Gambey leg.; ZFMK • 6 specimens; "Maroc"; MHNG.

ALGERIA – **Oran** • 1 ♂, 2 ♀♀; Oran; SDEI 11911 and 10779–10780 • 2 ♀♀; Oran; SFUN – **Algier** • 1 ♂; Laverdure; C. De Barros leg.; SMTD.

Type locality

"Algeciras, Malaga, Estepona und Ronda" [Andalusia], Spain.

Description

Male as in Fig. 11B. Body length: 1.34 mm average, range 1.30–1.50 mm (N = 54, males and females). Shape of body elliptical, with the lateral margins of the pronotum continuous with those of the elytra, i.e., without an indentation. Elytral apex rounded. Terminal antennomeres subtriangular, with round angles (Figs 12F, 13E). Metatibiae as in Fig. 14J–K. Prosternal process slightly keeled anteriorly, with a slight median constriction and triangular distally (Fig. 4F). Male last visible ventrite with a marked emargination and bordered by a brush of long setae.

Median lobe of aedeagus in ventral view, wide, subconical, short, with a pointed apex and slightly serrated on its right side (Fig. 18A). Aedeagus in lateral view as in Fig. 18C. Distal portion of paramere very short, wide and conical, with only two short subapical setae (Fig. 18B, D). Spermathecal duct short and reservoir c-shaped; ramus long and curved distally, cornu round and nodulus short and wide (Fig. 7F).

Geographic distribution

The known distribution of *Cholovocera formiceticola* is western Mediterranean, extending from southern France in the northeast to the Balearic Islands, and from continental Spain to Algeria, and Morocco in the south, reaching the Atlantic coast (Fig. 9A).

Host ants

Rosenhauer (1856: 355) associated *Cholovocera formiceticola* with "*Oecophthora pusilla* Heer, 1852" (now *Pheidole megacephala*) in several locations of Andalusia (Spain). The presence of *Ph. megacephala* in Andalusia is doubtful; although myrmecologists cannot rule out the possibility that it was established in the Iberian Peninsula, it has not been found in the last 100 years despite intense search (Espadaler & Collingwood 2001: 260). Most likely, the ant that Rosenhauer (1856: 355) referred to was *Pheidole pallidula* (Nylander, 1849), an abundant species in southern Spain (Martínez-Ibáñez & Espadaler-Gelabert 1986: 1026; Bernard 1968: 153).

Our examination of specimens of *Ch. formiceticola* showed two records, each associated with an unidentified species of *Messor*, in southern France and in Andalusia respectively.

Taxonomic history and remarks

Rosenhauer's (1856: 355) original description of *Cholovocera formiceticola* is long and detailed, but he only dealt with external morphology and mouth-parts, which are not sufficient to reliably separate species within *Cholovocera*. In their catalogue, Gemminger & Harold (1868: 905) correctly cited Spain as the geographic distribution of *Ch. formiceticola*, but Piccioli (1871: 304) cited Sardinia in error, probably referring to *Ch. punctata* or *Ch. gallica*. Schaufuss (1876a: 400) gave the distribution of *Ch. formiceticola* as Spain, Balearic Islands, Corsica, Sardinia and Algeria; according to our data, Corsica and Sardinia are incorrect, most likely referring to *Ch. punctata* or *Ch. gallica*. Dieck (1870b: 173) reported specimens from Algeciras (Andalusia, Spain), and Verdiani-Bandi (1874: 149) from Tuscany (Italy), but the latter is, again, a likely an error for *Ch. gallica* or *Ch. punctata*.

Reitter (1875: 301) discussed the external similarity of *Ch. formiceticola* with *Ch. attae*, but he synonymised both species under *Ch. formicaria*, a synonymy accepted by Heyden *et al.* (1883: 80) in their catalogue. Dieck (1888: 41) reported *Ch. formiceticola* from Tangier, a new locality, and Fauvel (1890: 338) resurrected it from the synonymy in his rectification of Heyden *et al.* (1883) catalogue. However, over a century later, Rücker (2009: 14) synonymised *Ch. formiceticola* under *Ch. punctata* in his checklist, a status which was accepted by Shockley *et al.* (2009b: 65) and Rücker (2020: 34).

As shown above, our examination of many specimens of *Ch. formicaria*, *Ch. punctata* and *Ch. formiceticola*, including type material, showed that *Ch. formiceticola* is a distinct species, which we herewith resurrect as a valid taxon.

Cholovocera attae (Kraatz, 1858)
Figs 4B, 9C, 10B, 12B, 13A, 14B–C, 19

Choluocera Attae Kraatz, 1858: 140.

Coluocera attae – Gemminger & Harold 1868: 905.
Colovocera Attae – Lucas 1874: 239.
Coluocera formicaria – Reitter 1875: 301 (in part).
Colovocera formicaria – Belon 1879: 192 (in part).
Colnocera [sic] *attae* – Walker 1888: 181.

Cholovocera attae – Rücker 1980: 143, fig. 22 — Audisio *et al.* 1995: 9.

Differential diagnosis

Cholovocera attae and *Ch. occulta* sp. nov. are the smallest species in the genus. Size and short wide legs would separate *Ch. attae* from its sympatric *Ch. balcanica*. However, the most useful character to distinguish *Ch. attae* from *Ch. balcanica* and from all the other species is the morphology of the aedeagus (Fig. 19).

Type material

Cholovocera attae: lectotype male and paralectotype female in the Kraatz Collection, held in SDEI.

Lectotype of *Colovocera attae*
GREECE • 1 ♂; "Graecia"; Kraatz Collection; SDEI 11869. Designated by Rucker (2011a: 13).

Paralectotype of *Colovocera attae*
GREECE • 1 ♀; "Graecia"; Kraatz Collection; SDEI 11870.

Notes
As it can be seen in Rücker 2011a (fig. 12), there is a label reading "Holotypus" attached to the specimen that Rücker designated as the lectotype. However, this specimen cannot be regarded as the holotype because it was not designated in the original description, which included more than one specimen, i.e., syntypes. Examining the printed Holotypus label, we conclude that it was added at a later date than the description by Kraatz (1858).

The same comment given below under the lectotype, applies to the paralectotype.

Additional material, non-types

GREECE – **Peloponnese** • 2 ♂♂, 1 ♀; Menalon mts., 5 km E. Vitina; 37º40′46.5″ N, 22º14′52.7″ E; 1380 m a.s.l.; 10 May 2013; Schuh leg.; "Almweide" [Mountain meadow], [one specimen associated with a *Messor* worker ant]; NHMW – **Crete** • 1 ♂; West Crete, Vai-Itanos; 13 Apr. 1984; H. Fülscher leg.; NHMW • 4 ♂♂, 1 ♀; West Crete, Levka Ori, r[oa]d. Hania to Omalos, 2.5 km NNE of Omalos; 1150 m a.s.l.; 2 Jun. 2010; Schuh leg.; NHMW • 2 ♂♂; Crete; NMPC.

TURKEY – **Western Anatolia, Aegean** • 1 ♂, 2 ♀♀; Muğla, Göcek; 2 May 1975; Besuchet and Löbl leg.; MHNG.

***Reitteria escherichi* Wasmann, 1896**
TURKEY – **Western Anatolia, Aegean** • 1 ♂, 1 ♀; Muğla, Göcek; 2 May 1975; Besuchet and Löbl leg.; MHNG.

Type locality

"Griechenland", Greece.

Description

Male as in Fig. 10B. Body length: 1.36 mm average, range 1.20–1.40 mm (N = 10, males and females). Shape of body oval, with the lateral margins of the pronotum slightly widened anteriorly. Elytral apex rounded. Terminal antennomere subtriangular, with round angles (Figs 12B, 13A). Metatibiae relatively short, as in Fig. 14B–C. Prosternal process slightly keeled anteriorly, with a marked median constriction and subquadrangular distally (Fig. 4B). Male last visible ventrite with a slight emargination and bordered by a brush of short setae.

Median lobe of aedeagus curved towards the right in ventral view, tapering to a pointed apex (Fig. 19A). Aedeagus in lateral view as in Fig. 19C. Distal portion of paramere conical, with five or six long apical setae (Fig. 19B–C). The spermatheca was not dissected because of the small number of females available for study.

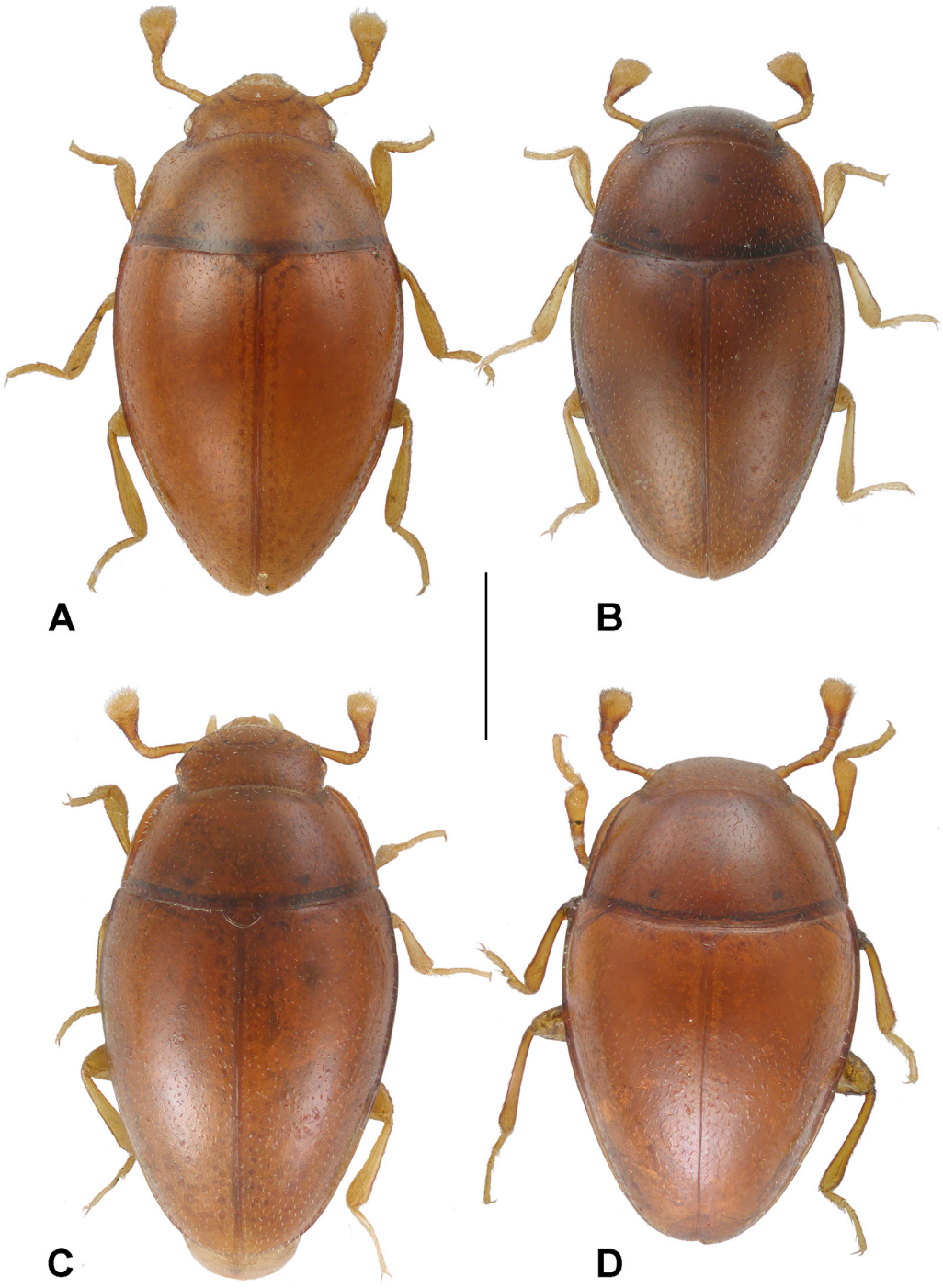

Fig. 10. Habitus, dorsal view. **A**. *Cholovocera afghana* Johnson, 1977, ♀. **B**. *Ch. attae* (Kraatz, 1858), ♂. **C**. *Ch. balcanica* (Karaman, 1936), ♂. **D**. *Ch. gallica* (Schaufuss, 1876), ♂. Scale bar = 0.5 mm.

Geographic distribution

The known distribution of *Cholovocera attae* is in Greece (Peloponnese, Crete) and western Turkey (Fig. 9C). However, the few available records of this species may not represent its total distributional range.

Host ants

Smith (1874) cited studies by Moggridge (1873), who collected *Ch. attae* in nests of *Messor ibericus* Santschi, 1925 (as *Atta structor*) in Menton (southern France). *Messor ibericus* is the only species of the *Messor structor* complex present in that region (Steiner *et al.* 2018). However, according to our present knowledge, the beetles could not have been *Ch. attae***,** but *Ch. punctata*, *Ch. gallica* or *Ch. occulta* sp. nov. Subsequent authors perpetuated the incorrect identifications of both beetles and ants (e.g., Lucas 1874; Rücker 1980; Angelini & Rücker 1999). However, Rücker (2018: 576) correctly associated *Ch. attae* with *Messor*.

At present, it is not possible to know the species of ant associated with *Cholovocera attae* in Greece. We have examined one beetle preserved together with an ant worker of the genus *Messor* but, considering the large number of species of this genus living in Greece and the lack of good descriptions, we cannot identify it to species (X. Espadaler pers. comm. 13 Mar. 2021).

Taxonomic history and remarks

Kraatz's (1858: 140) description of *Cholovocera attae* is brief, but he accurately distinguished it from both *Ch. punctata* and *Ch. formiceticola* by its body shape and size. In their catalogue, Gemminger & Harold (1868: 905) gave the distribution of *Ch. attae* as Greece, and Schaufuss (1876a: 396) made comments about its morphology. Reitter (1875: 301) examined the type of *Ch. attae* and found it similar to *Ch. formiceticola*, but he listed both *Ch. attae* and *Ch. formiceticola* as junior synonyms of *Ch. formicaria*, an action accepted by Heyden *et al.* (1883: 80) in their catalogue. Walker (1888: 181, 1892: 248) reported "*Ch. attae*" from Gibraltar, but it was most likely *Ch. formiceticola*, and Fauvel (1890: 338) resurrected *Ch. attae* as a valid taxon. A report by Wasmann (1890: 298) in Tunisia was most likely of *Ch. punctata* or *Ch. gallica*. Bodemeyer (1900: 24) recorded "*Ch. attae*" in "Karakeuy" (Istanbul), but we have examined some of Bodemeyer's material and have identified it as *Ch. balcanica*. Reitter (1902: 5) compared the morphology of *Ch. attae* with that of *C. gallica*.

Rücker (1980: 144) included *Ch. attae* in his key for the identification of *Cholovocera* species, illustrating the median lobe of the aedeagus (Rücker 1980: 145, fig. 22); also, he gave the geographic distribution of this species as: southern Europe, Greece and northern Africa, probably taken from previous publications, and associated it with *Messor barbarus* and *M. structor*. Later, Rücker (1983: 4) reported *Ch. attae* from southern Hungary, including a habitus figure with metatibiae equal to those of *Ch. balcanica*, and an illustration of the distal part of the aedeagus (Rücker 1983: 5, fig. f), which also matches that of *Ch. balcanica*. Actually, Rücker's (1983) figure f, labelled as *Ch. attae*, represents the same species as his figure e, labelled as *Ch. balcanica*, but both shown in different orientations.

Döbler (1987: 14) recorded two "syntypes" of *Ch. attae* in the SDEI collection, although one of them had a label reading "Holotypus" (see Rücker 2011a: fig. 12). Audisio *et al.* (1995: 9) and Angelini & Rücker (1999: 218) cited Italy as the location of *Ch. attae*, again an error by confusing this species with *Ch. punctata*. We have examined over 30 specimens collected by F. Angelini in Sicily, which we have identified as *Ch. punctata* (see Material examined above).

Sár *et al.* (2004: 331) expressed doubt about the record of *Ch. attae* in Rücker (1983) from Hungary, commenting that some records and specimens found in museum collections labelled as from "Hungary", may have originated from territories which once were part of the Austro-Hungarian Empire, such as

Serbia, Romania and nearby countries. Therefore, we believe that, unless specimens are re-examined, reports from those countries should be considered doubtful, probably referring to *Ch. balcanica*.

Several subsequent catalogues and checklists gave large geographic distributions for *Ch. attae*, including France, Greece, Italy, Hungary, Serbia, Montenegro, Algeria, Morocco and Tunisia, which we regard as erroneous, except for Greece (Löbl & Smetana 2007: 557; Rücker 2009: 14, 2011b; Shockley *et al.* 2009b: 65). However, Rücker (2018: 576, 2020: 34) restricted that distribution to only Crete and Rhodes, which is partially correct. Also, Rücker (2018: 576, fig. 1187) gave a detailed description of *Ch. attae*, including a figure of the aedeagus in lateral view. Finally, Stalling (2019: 13) reported the island of Kos (Dodecanese Islands) as a new locality for *Ch. attae* in Greece.

Cholovocera gallica (Schaufuss, 1876) new status
Figs 4D, 7D, 9A, 10D, 12D, 13C, 14F–G, 20, 25A–B

Coluocera gallica Schaufuss, 1876a: 398.

Colovocera formicaria – Belon 1879: 192 (in part).
Coluocera fleischeri Reitter, 1902: 5. **Syn. nov.**
Cholovocera fleischeri Reitter [sic] – Rücker 1980: 144, fig. 23 — Audisio *et al.* 1995: 9.

Differential diagnosis

Cholovocera gallica is morphologically and geographically close to *Ch. formiceticola*, but these species can be separated by the shape of the pronotum (Fig. 10D against Fig. 11B) and of the metatibiae (Fig. 14F–G against Fig. 14J–K). Furthermore, *Cholovocera gallica* can be distinguished from all other species by having a bulbous pronotum with a wide anterior margin (Fig. 10D), and large, subtriangular terminal antennomeres (Figs 12D, 13C).

Also, the shape of the aedeagus and paramere (Fig. 20), as well as of the spermatheca (Fig. 7D), are useful characters to distinguish *Cholovocera gallica* from all other species in the genus.

Type material

Cholovocera gallica: as far as we know, the type material was not examined by any author after the original description of *Ch. gallica*. In our opinion, that may be the reason for the species having been synonymised and not re-evaluated until now. Dr Bernd Jaeger found two syntypes, one male and one female, in the Schaufuss Collection held at MFNB, which he kindly made available for examination.

Considering the great number of misidentifications of the species of *Cholovocera*, both in collections and literature, and the fact that the syntypes of *Ch. gallica* belong to two species, it is advisable to designate a lectotype to give this name taxonomic stability (Article 74.7.3, ICZN 1999). We hereby designate the syntype male from the Schaufuss Collection deposited in MFNB, with labels reading: "*Cholovocera formicaria* Motsch., Gall merid" and "Syntype *Coluocera gallica* Schaufuss, 1876, labelled by MFNB 2021" as the lectotype of *Cholovocera gallica* (Fig. 25A). The syntype female becomes a paralectotype (Fig. 25B), but it is a misidentified specimen of *Ch. punctata*.

Coluocera fleischeri: lectotype male and four paralectotypes held in HNHM.

Lectotype of *Coluocera gallica*
FRANCE – 1 ♂; "*Gallia meridional*"; [Schaufuss Collection], MFNB. Designated below.

Paralectotype of *Coluocera gallica*
FRANCE – 1 ♀; "*Gallia meridional*"; [Schaufuss Collection], MFNB. Reidentified as *Ch. punctata.*

Lectotype of *Coluocera fleischeri* (designated by Rücker (2011a: 13)
CROATIA – **Dubrovnik-Neretva** • 1 ♂; "Dalmatia, Metkovic"; HMHN.

Paralectotypes of *Coluocera fleischeri*
CROATIA – **Dubrovnik-Neretva** • 2 ♂, 2 ♀; "Dalmatia, Metkovic"; HMHN.

Notes
As can be seen in Rücker 2011a (fig. 17), there is a label reading "Holotypus" attached to the specimen that Rücker designated as the lectotype. However, this specimen cannot be regarded as the holotype because it was not designated in the original description, which included more than one specimen, i.e., syntypes. Examining the handwriting of the Holotypus label, we conclude that it was added at a later date than the description by Reitter (1902).

Additional material, non-types

SPAIN – **Catalonia** • 1 ♂, 2 ♀♀, 10 specimens; B[arcelona], Bellaterra; 25 Aug. 1980; X. Espadaler leg.; "nid [nest] *Messor barbarus*"; MHNG.

FRANCE – **Languedoc-Rousillon** • 1 ♂; Collioure; Gambey leg.; ZFMK • 1 ♂; "P.O." [Pyrénées-Orientales], Collioure; MHNG • 1 ♀; "Pyr. O" [Pyrénées-Orientales], Collioure; Dr Normand leg. [associated with a *Messor* worker ant labelled: "*Messor* sp., P. Werner det. 2016"]; NMPC • 1 ♂; Agde; MHNG.

ITALY – **Liguria** • 2 ♀♀; Genova; Nov. 1892; A. Solari leg.; MFNB – **Sardinia** • 1 ♂, 1 ♀; North of Bolóntana; 850 m a.s.l.; 13 Apr. 1992; J. Scheuern leg. [one specimen associated with a *Messor* worker ant, the second with a *Camponotus* worker ant] NKME • 1 ♂, 1 ♀; 8 km Northeast of Lula; 250 m a.s.l.; J. Scheuern leg. [one specimen associated with three *Messor* worker ants]; NKME • 1 ♂; S.of Teresa; Jun. 1968; Palm leg.; MZLU 2020-065 • 1 ♀; Lago Baratz; 23 May 1995; F. Angelini leg.; MCVR • 1 ♀; MCNM 303883 • 1 ♂; Nuoro, Altopiano della Campeda; 580 m a.s.l.; 18 May 2006; Starke leg.; NHMW • **Sicily** • 1 ♀; Palermo, Ficuzza; 700 m a.s.l.; 1–4 May 2000; F. Angelini leg.; "Bosco leccio" [oak forest]; NMPC • 1 ♂; Palermo; NHMB • 1 ♂, 1 specimen; Ficuzza; 16. Mar. 1942; SMTD • 1 ♂, 1 ♀; Ficuzza; 16 Mar. 1942; NKME • 1 ♀; Ficuzza; 16 Mar. 1942; MFNB • 26 specimens; Ficuzza; 1906; O. Leonhard leg.; SDEI 11948–11955 • 3 ♂♂, 4 ♀♀; Randazzo; 6 May 1933; W. Liebemann leg. [one specimen associated with a *Messor* worker ant]; SDEI 10860–10866 • 1 ♂; Messina; 1906; O. Leonhard leg.; SDEI 11940 • 1 ♂; Scanzano, Palermo, Marineo; 525 m as.l.; 9 Apr. 1993; F. Angelini leg.; MZLU 2020-002 • 8 specimens; Palermo, "N. Ti" [North of] Madonie, "dint." [inside the city of] Isnello; 700 m a.s.l.; 9 Jun. 1991; F. Angelini leg.; MCVR • 1 ♂; Campofelice; 28 Apr. 1980; T. Palm leg.; MZLU 2020/009 • 3 specimens; Erica; 10 Dec. 1993; Sabella leg.; "Bosco misto" [mixed forest]; NMPC • 6 specimens; Mount Sfaracavallo; 4 Apr. 1925; Dr Rambousek leg.; NMPC – **Sicily, no specific locality** • 3 ♂♂; SDEI 11927 and 11934–11935 • 1 ♂; NHMB • 1 specimen; Sicily; SFUN – **Tuscany** • 3 ♀♀; SMNH • 1 ♂; Bertolini leg.; MFNB – **Lazio** • 1 ♂, 3 specimens; Maccarese; P. Luigioni leg.; SFUN • 2 ♂♂, 4 ♀♀; Maccarese; P. Luigioni leg.; MFNB • 1 ♀; Roma, Maccarese; 26 Feb. 1911; P. Luigioni leg.; MFNB – **Calabria** • 1 ♂; Antonimina; 1905; SDEI 11909 • 1 ♂; Antonimina; 1905; Paganetti leg.; SDEI 11908 • 1 ♂; Antonimina; 1905; Paganeti leg.; NMPC • 1 ♂; Gerace; Paganetti leg.; SDEI 10856 • 1 ♂, 12 specimens; Gerace; Paganetti leg.; NMPC • 1 specimen; Gerace; Paganetti leg.; SMTD • 6 specimens; Aspromonte, San Luca; 200 m a.s.l.; 28 Apr. 2002; F. Angelini leg.; "Prato" [meadow]; MZLU 2020-003 • 1 ♂, 6 specimens; Aspromonte, Africo; 50 m a.s.l.; 14 Apr. 1997; F. Angelini leg.; "Prato" [meadow], MCVR • 1 ♂, 5 specimens; Sambiase; May 1920; C. Minozzi leg.; [each specimen

associated with a *Messor* worker ant]; NHMB – **Puglia** • 1 ♂, 2 ♀♀; Murgia, San Basilio; Paganetti leg.; SDEI 10818 and 10840–10841• 1 ♂; Murgia, San Basilio; NHMB • 1 ♂, 3 specimens; Bari; Nov. 1984; L. De Marzo leg.; MCVR • 1 ♂, 3 specimens; Rutiglieno; Nov. 1991; L. De Marzo leg.; MCVR – **Italy, no specific locality** • 1 ♂, 1 ♀; Italia, NMPC.

ALGERIA – **Algier** • 1 ♂; Lambèze [modern Tazoult]; Jun. 1885; L. Bleuse leg.; ZFMK.

TUNISIA – **Mahdia** • 1 ♂, 1 specimen; Tunisia, El Djem; 2 Apr. 1925; Dr Rambousek leg.; "fourm." [ants or ant nest]; NMPC.

CROATIA – **Zadar** • 1 ♂, 1 ♀; "D"[almatia], Diklo; Jul. 1913; Novak leg.; NHMB • 1 ♀; "D"[almatia], Diklo; 7 Jul. 1913; CNHM • 1 specimen; "D"[almatia], Diklo; Jul. 1913; Novak leg.; MNHS • 1 ♂; "D"[almatia], Diklo; Jul. 1913; Novak leg.; MFNB • 1 specimen; "D"[almatia], Zara; Novak leg.; MNHS • **Split** • 1 ♂; "D"[almatia]; Novak leg.; 15 Apr. 1928; [associated with a *Tetramorium* worker ant]; SFUN • 1 specimen; Salona; Karaman leg.; MNHS – **Dubrovnik-Neretva** • 6 specimens; "Dalmatia, Ragusa" [modern Dubrovnik]; Dr Fleischer leg.; NMPC • 1 ♂, 3 ♀♀; "Dalmatia", Metkovic; SDEI 05781 and 11910 • 1 ♂; "Dalmatia", Metkovic; SFUN • 1 ♀; "Dalmatia" Metkovic; Formanek leg.; NHMB.

BOSNIA AND HERZEGOVINA – **Herzegovina-Neretva** • 1 ♂, 1 specimen; Herzegowina, Jablanica; SFUN.

Type locality

"Südfrankreich" [*Gallia meridional*], Southern France.

Description

Male as in Fig. 10D. Body length: 1.33 mm average, range 1.30–1.50 mm (N = 23, males and females). Shape of body oval, pronotum wide and dorsally bulbous, with rounded elytral apex. Terminal antennomeres large, subtriangular. Metatibiae long and narrow, with sinuous margins (Fig. 14F–G). Prosternal process markedly keeled anteriorly, with a wide median constriction and subtriangular distally (Fig. 4D). Male last visible ventrite with a slight emargination and bordered by a brush of long setae.

Median lobe of aedeagus in ventral view tapering markedly in its distal third, with a round tip (Fig. 20A). Aedeagus in lateral view as in Fig. 20C. Distal portion of paramere short, quadrangular, with an irregular tip (Fig. 20B), bearing five medium setae (Fig. 20A–B). Spermathecal duct short and reservoir straight; ramus short and rounded, cornu short and nodulus long and conical (Fig. 7D).

Geographic distribution

The known distribution of *Cholovocera gallica* is the central Mediterranean, extending from the Balkans in the east to Catalonia in the west, and from northern Italy to Algeria and Tunisia in the south (Fig. 9A).

Host ants

There is almost no published information about the ants associated with *Cholovocera gallica*. Rücker (1980, 1983, 2018) mentioned unidentified species of the genus "*Atta*" as hosts of *Ch. fleischeri* (now *Ch. gallica*). However, species of *Atta* live exclusively in the Neotropical Region, and therefore cannot be hosts of this beetle species. Lundberg *et al.* (1987: 123) reported *Ch. fleischeri* from a large nest of *Camponotus* in Sicily.

Our examination of *Ch. gallica* material preserved with ant specimens showed the following associations: (1) with an unidentified species of *Messor* in southern France, in Andalusia, in Sardinia and in Sicily; (2)

with *Messor barbarus* (det. X. Espadaler) in Spain; (3) with an unidentified species of *Camponotus* in Sardinia; (4) with an unidentified species of *Tetramorium* in Croatia.

Junior synonym

***Coluocera fleischeri* Reitter, 1902**

Reitter (1902: 5) described *Co. fleischeri* from specimens collected near Metkovic, Dalmatia (Croatia). Rücker (1980: 144) included *Ch. fleischeri* in his key for the identification of *Cholovocera* species, illustrating the median lobe of the aedeagus (Rücker 1980: 145, fig. 23); also, he gave the geographic distribution of this species as Dalmatia, Yugoslavia. Further, Rücker (1983: 4–5) added Herzegovina to the distribution and included a figure of a partial aedeagus. Lundberg *et al.* (1987: 123) reported *Ch. fleischeri* from Sicily. Audisio *et al.* (1995: 9) mentioned *Ch. fleischeri* in Italy, and Angelini & Rücker (1999: 218) in Puglia y Basilicata (Italy), but both records were based on the same material collected by F. Angelini in association with "ants", without an identification. An additional locality was reported by Lo Cascio *et al.* (2006: 325) who recorded *Ch. fleischeri* in Lipari Island (Aeolian Islands, north of Sicily, Italy). Subsequent catalogues and checklists increased the geographic distributions of *Ch. fleischeri* even more, adding Macedonia (Löbl & Smetana (2007: 557), Malta, Montenegro and Serbia (Shockley *et al.* (2009b: 65), Hungary (Rücker 2011b), and Corsica and Tunisia (Rücker 2020: 34). Although we have not seen material of *Ch. fleischeri* (as *Ch. gallica*) from Corsica, Malta, Macedonia, Montenegro and Serbia, we cannot rule out the possibility that this beetle occurs in those localities. However, we believe that the record from Hungary needs confirmation as it is unlikely to be correct. Finally, Rücker (2018: 578, figs 1188–1189) gave a detailed description of *Ch. fleischeri*, including a figure of the aedeagus in lateral and ventral views.

Notwithstanding the many reports of this species as *Ch. fleischeri*, we have examined its holotype male and compared it with many males of *Ch. gallica*, including the lectotype, without finding any significant morphological difference that would justify the separation of these species. Therefore, we have no hesitation in placing *Coluocera fleischeri* as a new junior synonym of *Ch. gallica.*

Taxonomic history and remarks

Schaufuss (1876a: 398) described *Cholovocera gallica* from southern France in great detail, comparing it with material from Corsica (Fig. 25C), the Balearic Islands (Fig. 25D), Algeria (Fig. 25E) and Sardinia. Although his identifications of those specimens were not all correct, our study showed that he had *Ch. punctata* and *Ch. formiceticola* for comparison. However, one year later, Reitter (1877: 5) placed *Ch. gallica* as a junior synonym of *Ch. formicaria*, a status which was accepted by Belon (1879: 192), and a number of subsequent catalogues, such as those by Heyden *et al.* (1883: 80), Rücker (2009: 14), Shockley *et al.* (2009b: 65) and Rücker (2020: 34). Other authors, with the exception of Löbl & Smetana (2007: 557), did not mention *Ch. gallica* at all, but recorded and listed *Ch. fleischeri* instead.

However, from our examination of the lectotype of *Ch. gallica* and many other samples from a wide geographical area (Fig. 9A), we believe that *Ch. gallica* is a distinct species, which we herewith resurrect as a valid taxon.

Cholovocera balcanica (Karaman, 1936) new status
Figs 4C, 7B, 9C, 10C, 12C, 13B, 14D–E, 21, 23H, 24F–G

Reitteria balcanica Karaman, 1936: 131, figs a–f.

"*Cholovocera major*" – Rücker 2011a: 12. Non *Coluocera formicaria* v. *major* Reitter, 1887.

Differential diagnosis

Cholovocera balcanica is sympatric with *Ch. attae*, but they can be distinguished by the larger size and longer legs of the former species. Furthermore, *Ch. balcanica* can be clearly separated from *Ch. attae* and from all other species in the genus by the morphology of the median lobe of the aedeagus, and the paramere (Fig. 21). The spermatheca of *Ch. balcanica* is also diagnostic, in particular because of its large nodulus (Fig. 7B).

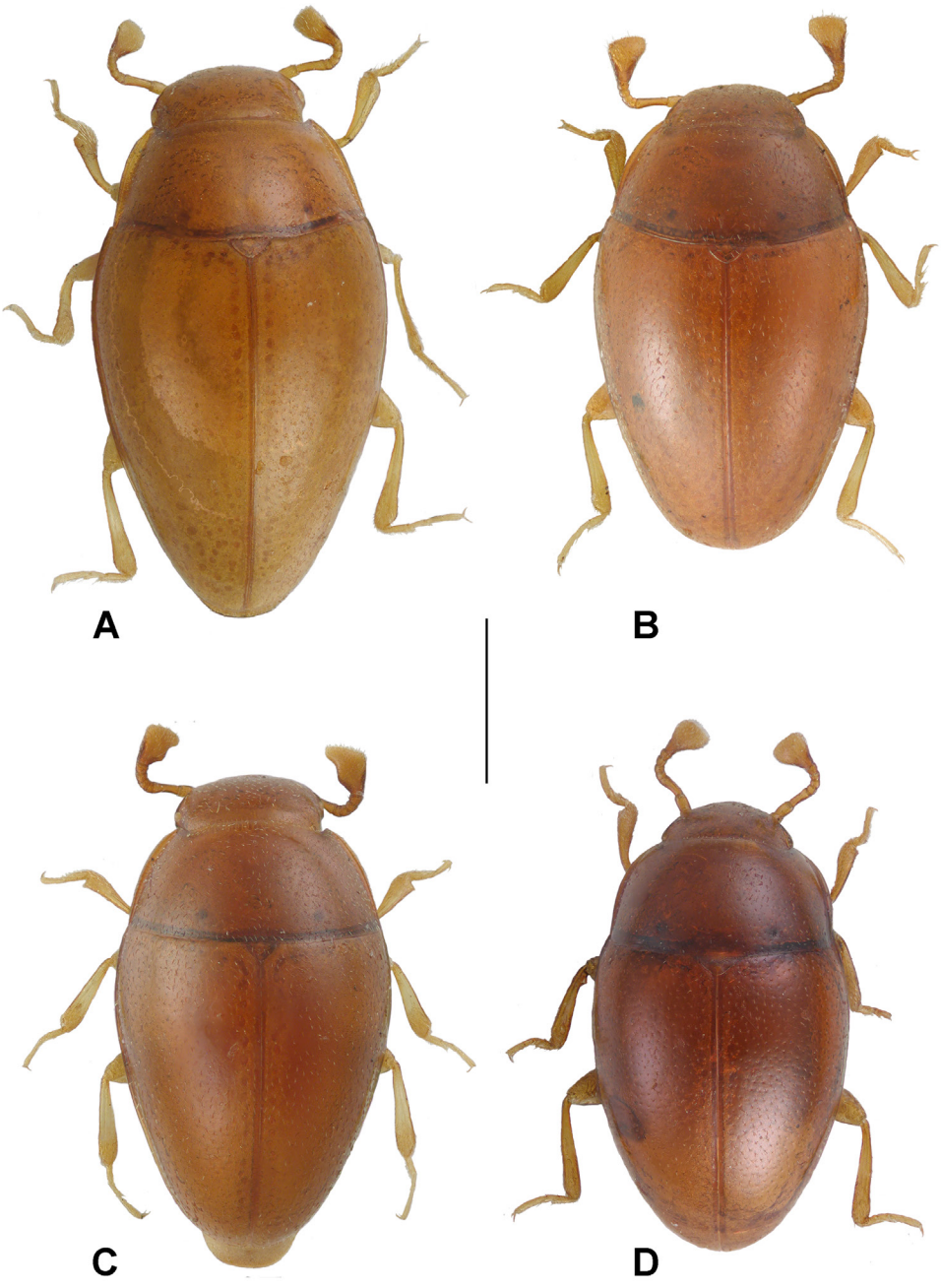

Fig. 11. Male habitus, dorsal view. **A**. *Cholovocera formicaria* Victor, 1838. **B**. *Ch. formiceticola* (Rosenhauer, 1856). **C**. *Ch. occulta* sp. nov., paratype. **D**. *Ch. punctata* (Märkel, 1845). Scale bar = 0.5 mm.

Type material

Cholovocera balcanica: Karaman (1936) examined 18 specimens (syntypes) from two localities for her description of *Reitteria balcanica*. However, only five of them have been located in the collection of the Faculty of Agricultural Science and Food, Saints Cyril and Methodius University (CMUS) in Skopje, Republic of North Macedonia (Fig. 23H). Furthermore, in the collection of the Senckenberg German Entomological Institute (SFUN), there are five specimens from Skopje identified as "*Reitteria balcanica*" which may be syntypes but, as their labels do not include a date, their status cannot be confirmed. Alternatively, these five beetles (see Material examined, non types below) may be part of the samples collected after 1936 and reported by Karaman (1964: 33).

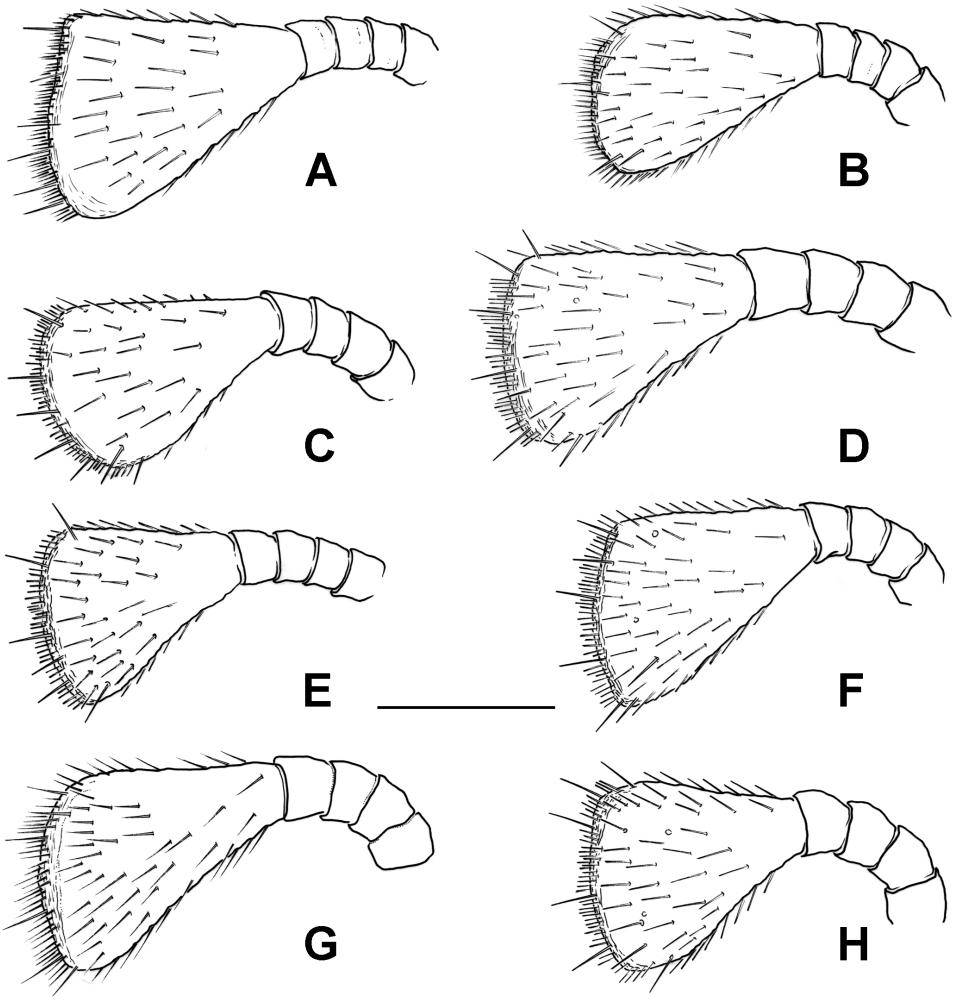

Fig. 12. Terminal female antennomeres. **A**. *Cholovocera afghana* Johnson, 1977. **B**. *Ch. attae* (Kraatz, 1858). **C**. *Ch. balcánica* (Karaman, 1936). **D**. *Ch. gallica* (Schaufuss, 1876). **E**. *Ch. formicaria* Victor, 1838. **F**. *Ch. formiceticola* (Rosenhauer, 1856). **G**. *Ch. occulta* sp. nov. **H**. *Ch. punctata* (Märkel, 1845). Scale bar = 0.1 mm.

Syntypes and voucher specimens of *Reitteria balcanica*, not examined*

NORTH MACEDONIA – **Skopje** • 3 syntypes; Vodno; 7 Jun. 1936; "Mravinjak" [ant nest]; CMUS, 245. • 2 specimens; Vodno; 7 Jun. 1936; CMUS, C164 • 1 specimen; Rasce; 5 Feb. 1959; "Mravinjak" [ant nest]; CMUS, 277 • 1 specimen; Stip; 17 Apr. 1960; [associated with an ant labelled as: "*Camponotus ligniperdus*, Det. Zora Karaman"]; CMUS • 1 specimen: Skopska Crna Gora [Black Mountain of Skopje]; 10 Jun. 1960; CMUS (Fig. 23H).

* Despite our request to loan the above eight specimens from CMUS, we were not able to examine them. However, we believe it is important to record them here, including their photograph, kindly provided by Vladimir Krpach (CMUS).

Additional material, non-types

NORTH MACEDONIA – **Skopje** • 1 ♂, 4 ♀♀; "Serbia, S. Makedonia", Skopje; [one specimen associated with a *Camponotus* worker ant]; SFUN.

ALBANIA – **Vlora** • 2 ♂♂, 1 ♀; "M.E." [Mount] Tartarit; Jun. 1932; Bischoff leg.; MHNB • 1 ♀; "M.E." [Mount] Tartarit; Jun. 1932; Bischoff leg.; MFNB – **Gjirikaster** • 1 ♀; Albania mer. [idional], Tepelene; May 1931; Winkler leg.; [associated with a *Messor* worker ant]; MHNG.

BULGARIA – **Dobrich** • 1 specimen; Albena; 31 Jan. 1990; Batelka leg.; NMPC • 6 specimens; Albena; 14 Sep. 1990; Batelka leg.; NMPC – **Lovech** • 1 ♂; Tirnowa [modern Veliko-Tarnovo]; May 1994; Flach leg.; SMTD • 4 ♀♀; Tirnowa [modern Veliko-Tarnovo]; May 1994; Flach leg.; SFUN – **Burgas** • 1 ♂, 1 ♀; Karabajir, Rumel; 3 Apr. 1909; Rambousek leg.; SDEI 10773–10769 • 1 ♂, 10 specimens; Karabajir, Rumel; 3 Apr. 1909; Rambousek leg.; [three specimens, each associated with a *Messor* worker ant labelled as: "*Messor structor* (Latreille) P. Werner det. 2016"]; NMPC • 3 ♀♀**;** Burgas; Mar. 1909; Rambousek leg.; [two specimens, each associated with a *Messor* worker ant]; SDEI 10770 and 10774–10775 • 3 ♂♂, 2 ♀♀; Flach leg.; SDEI 10854–10855 and 10782–10784 • 1 ♂, 18 specimens; Burgas; May 1895; Flach leg.; SMTD • 1 specimen; Burgas; May 1895; Flach leg.; SFUN • 1 specimen; Burgas; Flach leg.; SFUN • 1 ♂, 19 specimens; Burgas; May 1894; Flach leg.; SFUN • 1 ♂, 1 ♀; Burgas, May 1894; Flach leg.; NMPC • 1 specimen; Burgas; NMPC • 2 specimens; Burgas; Rambousek leg.; [associated with a *Messor* worker ant]; NMPC • 2 specimens; Burgas "maritime"; Apr. 1909; F. Rambousek leg.; NMPC • 1 specimen; Rumel, Bačkovo; 11 May 1909; Rambousek leg.; [associated with a *Messor* worker ant, labelled as: "*Messor structor* (Latreille) P. Werner det. 2016"]; NMPC • 4 specimens; Bulgaria Oriental, Zeitinburun [Mount Zeytin Burnu]; Apr. 1933; "Mař Táb." [Mařan and Táborský leg.]; NMPC • 1 ♂, 4 specimens; Bulg. Mac.; Jun. 1933; "Mař Táb." [Mařan and Táborský leg.]; NMPC • 1 specimen; Burgas; Rambousek leg.; MNHS • 5 specimens; Bulgaria or.[iental], Bozurec; Ernest leg.; NMPC.

GREECE – **Corfu** • 2 ♂♂; S. Corfu, Paxos, 2 km NW of Galos; 17 Apr. 1981; Scheuern leg.; "Oliven hain" [olive grove]; [one specimen assocaited with a *Messor* worker ant]; ZFMK • 1 ♀; Corfu monats., Paleaskastritza; 10 Apr. 1972; V. Mahnert leg.; MHNG – **Tessaly** • 1 ♂, 1 ♀, 16 specimens; Pelion; MHNB – **Ionian Islands** • 3 ♀♀; Cephalonia, Argostoli; NHMB • 1 ♂; Cephalonia; Paganetti leg.; SMTD • 1 ♂; Cephalonia; Paganetti leg.; NMPC – **Central Greece** • 1 ♂, 2 ♀♀; Parnassos; SDEI 10790–10791 and 10856 • 2 ♂♂, 1 ♀, 3 specimens; "Balkan Parnass."; 1903; Paganetti leg.; SMTD • 1 ♂; "Parnass"; Paganetti leg.; NMPC – **Attica** • 1 ♀; Greece, Atica; SMTD – **Peloponnese** • 5 ♂♂, 9 ♀♀, 25 specimens; Ahaïa, Erimanthos–Geb., Kaletzi; 37°57′04″ N, 21°46′17″ W; 1100 m a.s.l.; 23 Apr. 1998; Zerche leg.; "Tannenwald oberh.[alb]" [above fir forest],; [each specimen associated with a *Messor* worker ant]; SDEI 11792–11816 and 11877–11907 • 1 ♂, 2 specimens; Ahaïa, surroundings of Panahaiko, near Ano Kastrisi; 38º15′54″ N, 21º50′42″ W; 900 m a.s.l.; 28 Mar. 1997; L. Zerche leg.; "unter Steinen" [under stones]; [each specimen associated with a *Messor* worker ant]; SDEI 11807 and 11811–10815 • 1 ♂, 11 specimens; Kalavyrta, Morea; MHNB • 2 ♀; Nauplia; SFUN • 1 ♂, 1 specimen;

Nauplia; Mar. 1890; Hänel leg.; SMTD • 1 ♀; Ilia, Erymanthos mts, 1.5 km NNW of Orini; 1290–1370 m a.s.l.; 9 May 2013; Schuh leg.; NHMW – **Thrace** • 2 ♂♂, 13 specimens; "Alexandrupolis"; 2 May 1937; Bartoň leg.; NMPC – **Crete** • 2 ♂♂, 17 specimens; Omalos, Lefka Ora; 27 May–1 Jun. 1980; Brodský and Bílý leg; NMPC • 2 ♂♂; Omalos, Lefka Ori Mts; 3 Jun. 1984; Bílý leg.; NMPC • 1 ♀; NW Crete, Dikti Oros, Limnakaro; 35º08′08″ N, 25º29′00″ E; 1170 m a.s.l.; 7 Apr. 2012; V. Assing leg.; *Messor* nest; NMPC • 2 ♀♀; Crete, Lasithi Geb. [iet] [surroundings of]; MFNB • 3 ♂♂, 5 ♀♀, 10 specimens; East Crete, Lasithi Plateau, road Kaminaki–Embaros, Mesovouni Pass; 1150 m a.s.l.; 5 Jun. 2010; Schuh leg.; NHMW • 1 ♂; Crete; NMPC – **Sporades Islands** • 4 ♂♂, 2 ♀♀; Samos, "val. des Rossignols" [Nightingale valley], "sous" [near] Manolates; 100 m a.s.l.; 17 May 1985; Besuchet leg.; MHNG • 2 ♀♀; South Sporades, Karpathos; V. Oertzen leg.; MFNB – **Dodecanese** • 2 ♂♂, 1 ♀; Rhodas, Ebonas; 15 Apr. 1977; Cl. Besuchet leg.; MHNG – **Greece, no specific locality** • 1 ♀; Greece; 1901; Sabel leg.; SFUN • 1 ♂, 2 specimens; Greece; SMTD • 1 ♂, 1 ♀; Greece; SMTD.

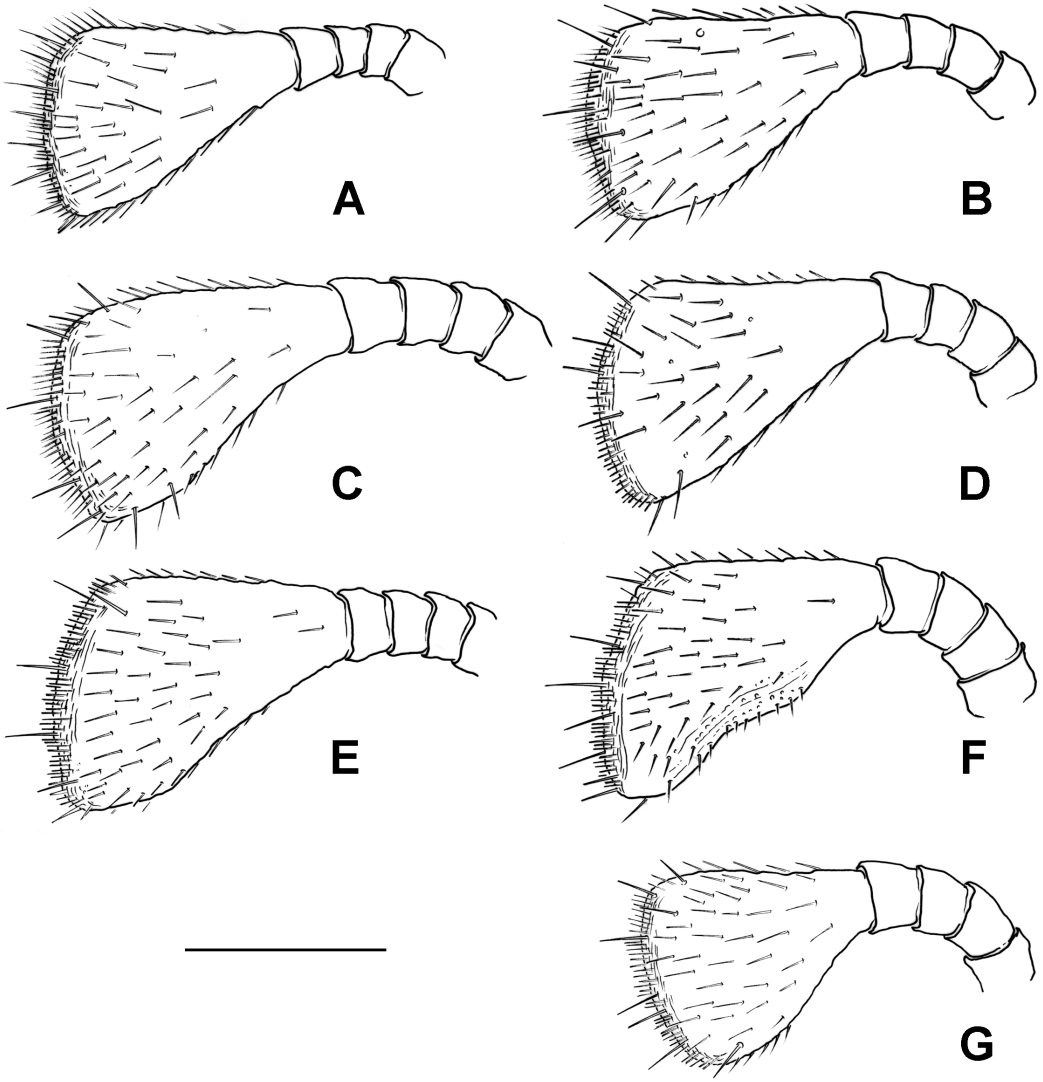

Fig. 13. Terminal male antennomeres. **A**. *Cholovocera attae* (Kraatz, 1858). **B**. *Ch. balcánica* (Karaman, 1936). **C**. *Ch. gallica* (Schaufuss, 1876). **D**. *Ch. formicaria* Victor, 1838. **E**. *Ch. formiceticola* (Rosenhauer, 1856). **F**. *Ch. occulta* sp. nov. **G**. *Ch. punctata* (Märkel, 1845). Scale bar = 0.1 mm.

TURKEY – **Marmara** • 1 ♂; "Asia minor", Karakeuy; V. Vodemeyer leg. [for Bodemeyer]; [associated with two *Messor* worker ants]; SFUN • 1 ♂; Bursa; 1 Apr. 1917; [associated with a *Messor* worker ant]; SMTD – **Western Anatolia, Aegean** • 1 ♀; Smyrna, SMNH • 1 ♀; Smyrna; NMPC • 1 ♀; Smyrna; MFNB • 2 ♀♀; Ephesus; J. Sahlb[erg]. leg.; HMHN • 1 ♀; Ephesus; J. Salhb[erg]. Leg.; SFUN – **Mediterranean** • 1 ♀; Mersin, 10[sic] km NW of Silifke; 27 Apr. 1978; Besuchet and Löbl leg.; MHNG.

UKRAINE • 1 ♀; Odesa; Dr Lgocki leg.; SMTD • 1 ♀; Kherson; 17 Apr. 1941; Lasovko leg.; NHMW.

Description

Male as in Fig. 10C. Body length: 1.40 mm average, range 1.30–1.50 mm (N = 30, males and females). Shape of body elliptical, with the lateral margins of the pronotum continuous with those of the elytra, i.e., without an indentation. Elytral apex pointed. Terminal antennomeres subtriangular, sexually dimorphic (Figs 12C, 13B). Metatibiae with straight margins, diverging distally (Fig. 14D–E). Prosternal process slightly keeled anteriorly, with a slight median constriction and distally rhomboidal (Fig. 4C). Male last visible ventrite with a slight emargination and bordered by a brush of short setae.

Median lobe of aedeagus long and sinuous in ventral view, tapering and acutely pointed distally (Fig. 21A). Aedeagus in lateral view as in Fig. 21C. Distal portion of paramere long, conical, with a round apex bearing a brush of many long setae in ventral view (Fig. 21B), but polygonal in lateral view (Fig. 21D). Spermathecal duct short, spermathecal reservoir long and T-shaped; ramus long and curved distally, cornu round and nodulus greatly developed, almost as long as cornu and ramus together (Fig. 7B).

Type localities

"Schlucht von Topolka bei Veles, Vodno-Berg bei Skoplje" [Canyon of Topolka near Veles, and Vodno near Skopje], Republic of North Macedonia.

Geographic distribution

The known distribution of *Cholovocera balcanica* extends from the Balkan Peninsula in the west to eastern Turkey, and from the northern Black Sea coast and the Crimean Peninsula in the north to Crete and other Greek islands in the south (Fig. 9C).

Host ants

Karaman (1964: 33) reported that the specimens from Mount Vodno, the type locality of *Ch. balcanica*, were collected in nests of *Tetramorium caespitum* (Linnaeus, 1758). Also, Karaman (1964: 33) recorded *Ch. balcanica* in nests of *T. caespitum* and *Camponotus ligniperda* (Latreille, 1802) from Skopska Crna gora (Black Mountain, near Skopje) and Rasce (near Skopje), but associated with *Messor* in Stip (E. of Macedonia) and around Mostar (Bosnia and Herzegovina).

Our examination of *Ch. balcanica* material preserved with ants showed that it is frequently found with species of *Messor* in Albania and Greece, and with *Messor structor* (det. P. Werner) in Bulgaria. The association with *Camponotus ligniperda* given by Karaman (1964) needs confirmation of the species, although the genus is correct. We have examined one specimen from North Macedonia identified by Zatia Karaman (see above) and we agree that it belongs to *Camponotus*.

Taxonomic history and remarks

The original description of *Reitteria balcanica* by Karaman (1936: 131, figs a–f) is well illustrated, including figures of an antenna, two metatibiae, the aedeagus and habitus in dorsal and ventral views; these illustrations agree with the same characters of the material we have examined and identified as *Cholovocera balcanica*. Karaman (1964: 33) published new locality records from the Balkans, based on

additional samples collected after her 1936 paper and from her examination of museum collections; these records were Skopska Crna Gora (Black Mountain, near Skopje), Rasce (near Skopje), Stip (Eastern Macedonia) and around Mostar (Bosnia and Herzegovina). Also, Karaman (1964: 33) mentioned to have studied many specimens from Spalato (Split, Croatia) deposited in the collection of the Institute of Crop Protection of Belgrade (now Institute for Plant Protection and Environment). This large collection was later divided between the Natural History Museum in Zagreb (I. Toševski, pers. comm. 17 Jun.

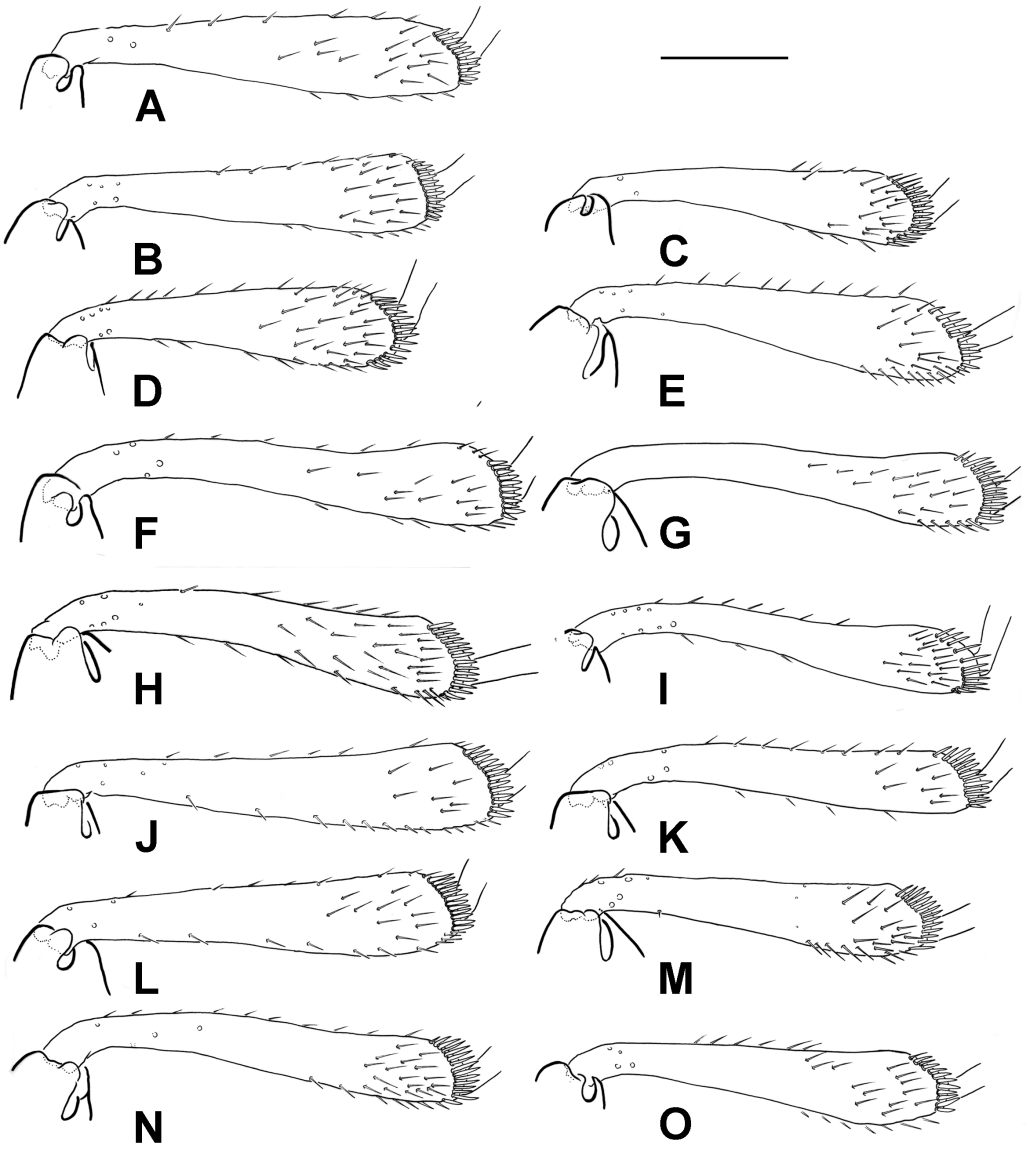

Fig. 14. Metatibiae. **A**. *Cholovocera afghana* Johnson, 1977, ♀. **B**. *Ch. attae* (Kraatz, 1858), ♀. **C**. *Ch. attae* (Kraatz, 1858), ♂. **D**. *Ch. balcanica* (Karaman, 1936), ♀. **E**. *Ch. balcanica* (Karaman, 1936), ♂. **F**. *Ch. gallica* (Schaufuss, 1876), ♀. **G**. *Ch. gallica* (Schaufuss, 1876), ♂. **H**. *Ch. formicaria* Victor, 1838, ♀. **I**. *Ch. formicaria* Victor, 1838, ♂. **J**. *Ch. formiceticola* (Rosenhauer, 1856), ♀. **K**. *Ch. formiceticola* (Rosenhauer, 1856), ♂. **L**. *Ch. occulta* sp. nov., ♀. **M**. *Ch. occulta* sp. nov., ♂. **N**. *Ch. punctata* (Märkel, 1845), ♀. **O**. *Ch. punctata* (Märkel, 1845), ♂. Scale bar = 0.1 mm.

2021) and the Museum of Natural History in Split (V. Mičetić, pers. comm. 3 Sep. 2021). However, despite our enquiries, Karaman's specimens have not been located.

Without examining the types of *Reitteria balcanica*, Rücker (2011a: 12) placed this species as a junior synonym of *Cholovocera major*. Apparently, Rücker (2011a: 13) missed the similarity between *Ch. major* and *Ch. formicaria* (see synonymy above) and, instead, he associated *Ch. major* with *Ch. balcanica* based on the morphology of the aedeagus, and on an earlier misinterpretation of type localities, as follows: Rücker (1980: 144) gave the type locality of *Ch. major* as "Angora (Talysch-Gebiet)"; however, "Angora" is situated in Anatolia (Turkey), and not in the Talish Region, which is located in the south of the Caucasus in Azerbaijan. Thus, Rücker (2011a: 12) believed that *Ch. major* and *Ch. balcanica* were sympatric and synonymised them. This synonymy was maintained by Rücker (2020: 34) in his latest checklist. Although we do not agree with the placement of *Reitteria balcanica* as a junior synonym of *Ch. major* as proposed by Rücker (2011a: 12), we agree that it belongs to the genus *Cholovocera*.

From our examination of five specimens from the type locality and many other samples from six countries (see Material examined) we conclude that *Cholovocera balcanica* is a distinct species, which we herewith resurrect as a valid taxon.

Cholovocera afghana Johnson, 1977
Figs 4A, 7A, 9C, 10A, 12A, 14a

Cholovocera afghana Johnson, 1977: 123.

Differential diagnosis

The female of *Cholovocera afghana* may be distinguished from females of other species in the genus by the combination of these characters: prosternal process, metatibiae and spermatheca. The shape of the prosternal process is not unique, but a comparison with the others would assist in an identification (Fig. 4A); the metatibiae (Fig. 14A) are closest to those of *Ch. balcanica* (Fig. 14D) and *Ch. occulta* sp. nov. (Fig. 14L) but distinguishable; and the spermatheca is diagnostic by having a long spermathecal duct, a large c-shaped spermathecal reservoir and a short, round nodulus (Fig. 7A).

However, a complete differential diagnosis of *Ch. afghana* will be achieved when a male is found and properly described.

Type material

Cholovocera afghana: holotype female in the J. Klapperich Collection held in ZFMK. Johnson (1977: 123) wrote that the type material was collected by J. Klapperich together with many other beetles in Afghanistan, during 1953–1954. Also, Johnson (1977: 123) mentioned that part of the material he studied would be deposited in the Hungarian Natural History Museum (Budapest, Hungary) and part would remain in the J. Klapperich Collection. The holotype of *Ch. afghana* was in the latter part, which was later acquired by the Zoologisches Forschungsmuseum Alexander Koenig (Bonn, Germany) (Ulmen *et al.* 2010: 16), where Klapperich worked as a technician between 1935 and 1952. We assume that the paratype was deposited in Budapest but, despite our enquiries requesting it for our examination, we have not been able to do so.

Holotype

AFGHANISTAN – **Nuristan** • 1 ♀; "Afghanistan, Nuristan, Bashgutal"; 1100 m a.s.l.; 14 Apr. 1953; J. Klapperich leg.; [associated with a worker ant of *Pheidole indica*, det. X. Espadaler]; ZFMK – COL 1000130.

Type locality

"Eastern Afghanistan, Prov. Nengrahar: Nuristan, Bashgultal".

Description

Male

Unknown.

Female as in Fig. 10A

Body length: 1.57 mm (N = 1, female). Shape of body elliptical, with the lateral margins of the pronotum continuous with those of the elytra, i.e., without an indentation. Elytral apex acute. Terminal antennomere large, subtriangular, as in Fig. 12A. Metatibiae with straight margins diverging distally (Fig. 14A). Prosternal process slightly keeled on its entire length, with a marked median constriction and rounded distally (Fig. 4A).

Spermathecal duct very long and spermathecal reservoir c-shaped; ramus long and tapering distally; cornu round distally and nodulus short and round (Fig. 7A).

Geographic distribution

The known distribution of *Cholovocera afghana* is in eastern Afghanistan, comprising the type locality only (Fig. 9C).

Host ants

Johnson (1977: 124) only mentioned an "ant host". However, from our examination of the holotype, which is associated with a worker ant, one host species is *Pheidole indica*.

Taxonomic history and remarks

Johnson's (1977: 123) original description of *Cholovocera afghana* is brief and without any definite character to distinguish it from the other species in the genus. Furthermore, Johnson (1977: 123) did not state the sex of either the holotype or the paratype, implying that he did not dissect them, as the external morphology of males and female of *Cholovocera* is very similar.

As far as we know, no other author has examined the type material or has reported other specimens of this species. Several catalogues and checklists have just listed it as valid species from Afghanistan (Löbl & Smetana 2007: 557; Rücker 2009: 14, 2020: 34; Shockley *et al.* 2009b: 65). Ulmen *et al.* (2010: 16) catalogued all the types of Coleoptera held in ZFMK, including the holotype of *Ch. afghana*.

The known geographic distribution of *Ch. afghana* is far from both the Mediterranean Basin and the distribution of its geographically closest species, *Ch. formicaria* (Fig. 9C). This apparently anomalous distribution would indicate that there may be more populations of *Cholovocera* between the ranges of these two species, including potentially new, yet undescribed species.

Cholovocera occulta sp. nov.

urn:lsid:zoobank.org:act:5315A058-8EAE-4B9E-AA2E-934DDAF70DF5

Figs 4G, 7C, 9B, 11C, 12G, 13F, 14L–M, 22

Differential diagnosis

The male of *Cholovocera occulta* Delgado & Palma sp. nov. can be easily distinguished from all the other species in the genus by the unique morphology of the terminal antennomere (Fig. 13F). Also, the

aedeagus and the paramere are diagnostic, especially to separate *Ch. occulta* sp. nov. from the externally more similar species, such as *Ch. punctata* and *Ch. attae* (Fig. 22 against Figs 16, 19).

The spermatheca of *Ch. occulta* sp. nov. is diagnostic, in particular its truncated ramus, the bent cornu, and a nodulus shaped like an inverted amphora (Fig. 7C).

Etymology

The species epithet '*occulta*' (Latin for 'hidden') refers to the fact that this species has remained undescribed and unnamed, despite being available for study in several well-known European museums during many years. The name also alludes to the lifestyle of these beetles, hidden inside ant nests.

Type material examined

Cholovocera occulta sp. nov.: we designate as type material a holotype male and eight paratypes, one male and seven females, deposited in two museums in Germany (see below).

Holotype

ALGERIA • 1 ♂; Oran; MFNB.

Paratypes

ALGERIA • 7 ♀♀; Oran; MFNB • 1 ♂; Oran; SMTD.

Additional material examined, non types

FRANCE – **Languedoc-Rousillon** • 2 ♂♂, 1 ♀; "P.O." [Pyrénées-Orientales], Collioure; Liveillé leg.; MHNG – **Provence-Côte D'azur** • 1 ♂; Toulon; SDEI 10821 • 1 ♂; Toulon; 20 Apr. 1945; V. Barbier leg.; "En nombre, sous une grosse pierre, prés de l'entrée d'un nid de Messor, follés du fortification" [In great numbers, under a stone, near the entry of a nest of *Messor*, fortification walls]; MHNG • 1 ♂; France, Gard, St. Gilles, Le grand Bois; 27 Mar. 1978; Kiener leg.; [associated with a *Messor barbarus* worker ant]; MHNG • 1 ♂; Gallia Toulon; MHNG – **France, no specific locality** • 1 ♂, 1 ♀; "gall. mer"; SDEI 10852–10853 • 1 ♀; "mer."; SDEI 10822 • 1 ♀; "Galia mer."; SMTD • 1 ♂, 8 ♀♀; "gallia"; MFNB.

ALGERIA – **Algier** • 1 ♂, 1 ♀; ZFMK • 1 ♂, 1 ♀; NMPC • 1 ♀; MFNB – **Algeria, no specific locality** • 4 ♂♂, 1 ♀; "Algerie"; NHMB.

CZECH REPUBLIC – **Parduvice** • 1 ♀; "Vysoká"; NMPC – **Moravian-Silesia** • 1 ♂, 1 ♀; "Gnojnik (Siles.)"; A. Hetschko; NMPC.

Note

The localities associated with the last three specimens are placed far outside the range of the other material of *Ch. occulta* sp. nov., as well as all other species of *Cholovocera*. We agree with the curator of the National Museum of the Czech Republic (NMPC) in that the data given on the labels are most likely incorrect (J. Hájek, pers. comm. 8 Oct. 2021).

Type locality

Oran, Algeria.

Description

Male as in Fig. 11C. Body length 1.33 mm average, range 1.30–1.40 mm (n = 11, males and females). Shape of body oval, with the lateral margins of the pronotum continuous with those of the elytra, i.e., without an indentation. Elytral apex moderately acute. Terminal antennomeres sexually dimorphic: that

of the male with a sinuous internal margin (Fig. 13F), but the female with a straight internal margin (Fig. 12G). Metatibiae as in Fig. 14L–M, narrower in the proximal half and with curved margins, especially in the male. Prosternal process keeled anteriorly, with a wide median constriction and triangular distally (Fig. 4G). Male last visible ventrite with a marked emargination and bordered by a brush of long setae.

Median lobe of aedeagus subrectangular, with an acutely pointed triangular apex in ventral view (Fig. 22A). Aedeagus in lateral view as in Fig. 22C. Distal portion of paramere short, triangular, pointed, with two short setae (Fig. 22A–B). Spermathecal duct short and spermathecal reservoir c-shaped; ramus short and truncated distally, cornu sharply bent and nodulus moderately developed, shaped like an inverted amphora (Fig. 7C).

Geographic distribution

The known distribution of *Cholovocera occulta* sp. nov. extends from the Mediterranean coast of France in the north, to the Mediterranean coast of Algeria in the south.

Host ants

Our examination of two samples of *Ch. occulta* sp. nov. preserved with ants showed that it is associated with a species of *Messor*, most likely *M. barbarus*, in Southern France.

Remarks

Although at first we found it surprising that a clearly different species of *Cholovocera* could remain undescribed for such a long time, we believe the reason for that may have been the fact that all the specimens we examined needed to be remounted to expose their legs and antennae hidden under the body. Once the antennae of the males were uncovered, we soon realised we had a different, undescribed and unnamed species in front of us.

Considering that we only have five detailed locality records, it is difficult to ascertain the total geographic distribution of *Ch. occulta* sp. nov., but we expect that more samples will be found, which will enlarge the present known distribution.

Keys for the identification of the species of Cholovocera, adults only (except male of Ch. afghana, unknown)

1. Last visible ventrite with apical margin truncated or emarginated, bearing a brush of marginal setae, and a slight triangular depression proximal to the emargination (Fig. 6A)..... 2 (males)
– Last visible ventrite with apical margin rounded, not emarginated, and without such depression (Fig. 5A) ..... 8 (females)

2. Aedeagus with short median lobe, not longer than the basal piece (Figs 16, 18) 3
– Aedeagus with long median lobe, longer than the basal piece (Figs 15, 19–22) 4

3. Median lobe of aedeagus with a rounded apex, curved to the right in ventral view (Fig. 16A). Paramere with an elongated apex bearing a variable number of long apical setae (Figs 16B, 17). Pronotum with lateral margins as in Fig. 11D. Terminal antennomere shaped as an equilateral triangle (Fig. 13G) ..... ***Cholovocera punctata*** Märkel, 1838
– Median lobe of aedeagus with a pointed apex, not curved to the right in ventral view (Fig. 18A). Paramere with a very short apex bearing two short subapical setae (Fig. 18B, 18D). Pronotum with lateral margins as in Fig. 11B. Terminal antennomere not shaped as an equilateral triangle (Fig. 13E)..... ***Cholovocera formiceticola*** (Rosenhauer, 1856)

4. Length of median lobe of aedeagus less than twice the length of the basal piece in ventral view (Figs 19, 22) 5
– Length of median lobe of aedeagus more than twice the length of the basal piece in ventral view (Figs 15, 20, 21) 6

5. Median lobe of aedeagus subrectangular, with a short acutely-pointed triangular apex in ventral view (Fig. 22A). Paramere with a short, triangular, pointed apex, bearing two short setae (Fig. 22B). Terminal antennomere with a sinuous internal margin (Fig. 13F) ..... ***Cholovocera occulta*** Delgado & Palma sp. nov.
– Median lobe of aedeagus subrectangular only on its basal half, with a long, tapering, pointed and curved to the right apex in ventral view (Fig. 19A). Paramere with a short, trapezoidal apex, bearing several long setae (Fig. 19B). Terminal antennomere with a straight internal margin (Fig. 13A) ..... ***Cholovocera attae*** (Kraatz, 1858)

6. Median lobe of aedeagus tapering markedly in its distal third, with a round tip in ventral view (Fig. 20A). Paramere with a short, quadrangular apex, with an irregular tip bearing five medium setae (Fig. 20A–B) ..... ***Cholovocera gallica*** (Schaufuss, 1876)
– Median lobe of aedeagus tapering in its distal two-thirds in ventral view (Figs 15A, 21A). Paramere with a longer than wide apex, bearing several medium setae (Figs 15B, 21B) 7

7. Median lobe of aedeagus tapering gradually, with a pointed tip in ventral view (Fig. 15A), and sinuous in lateral view (Fig. 15C). Paramere with a conical, curved and acute apex (Fig. 15B, D) ... ***Cholovocera formicaria*** Victor, 1838
– Median lobe of aedeagus tapering abruptly, with a round tip in ventral view (Fig. 21A), and curved in lateral view (Fig. 21C). Paramere with a trapezoidal round, not curved, apex (Fig. 21B, D) ..... ***Cholovocera balcanica*** (Karaman, 1936)

8. Metatibiae long, with curved and sinuous margins (Fig. 14F, H, N) 9
– Metatibiae long or short, with straight margins 11

9. Metatibiae as in Fig. 14H. Spermatheca as in Fig. 7E. Terminal antennomere as in Fig. 12E ..... ***Cholovocera formicaria*** Victor, 1838
– Metatibiae as in Fig. 14F or 14N. Spermatheca as in Fig. 7D, G. Terminal antennomere as in Fig. 12D or 12H 10

10. Metatibiae as in Fig. 14F. Spermatheca as in Fig. 7D. Terminal antennomere as in Fig. 12D. Prosternal process as in Fig. 4D ..... ***Cholovocera gallica*** (Schaufuss, 1876)
– Metatibiae as in Fig.14N. Spermatheca as in Fig. 7G. Terminal antennomere as in Fig. 12H. Prosternal process as in Fig. 4H ..... ***Cholovocera punctata*** Märkel, 1845

11. Metatibiae short, as in Fig. 14B, D 12
– Metatibiae long, as in Fig. 14A, J, L 13

12. Metatibiae as in Fig. 14B. Habitus as in Fig. 10B, with round elytral apex. Prosternal process as in Fig. 4B. Spermatheca unknown ..... ***Cholovocera attae*** (Kraatz, 1858)
– Metatibiae as in Fig. 14D. Habitus as in Fig. 10C, with pointed elytral apex. Prosternal process as in Fig. 4C. Spermatheca as in Fig. 7B ..... ***Cholovocera balcanica*** (Karaman, 1936)

13. Total body length more than 1.55 mm. Spermatheca as in Fig. 7A. Prosternal process as in Fig. 4A ..... ***Cholovocera afghana*** Johnson, 1977

– Total body length less than 1.55 mm. Spermatheca as in Fig. 7C or 7F. Prosternal process as in Fig. 4F or 4G..... 14

14. Spermatheca as in Fig. 7C. Prosternal process as in Fig. 4G ..... ***Cholovocera occulta*** sp. nov.
– Spermatheca as in Fig. 7F. Prosternal process as in Fig. 4F.....
..... ***Cholovocera formiceticola*** (Rosenhauer, 1856)

Species included in Cholovocera, which we regard as belonging to other genera

Besides the eight species belonging to the genus *Cholovocera* described above, there are six other beetle species that have either been described in this genus or transferred to it, but which we do not consider to be members of *Cholovocera*. In our opinion, the morphological characters of these six species do not fit our definition of *Cholovocera*, and some of them occur in regions far outside the geographic range of this genus.

Cholovocera maderae Wollaston, 1854

This taxon has a convoluted history regarding both its generic placement and its original geographic distribution. It was described from a single specimen, collected in the island of Madeira, in the North Atlantic Ocean. In the original description, Wollaston (1854: 180) wrote that it differed from the other two members of *Cholovocera* by its larger size ("Long. corp. lin. 7/8"), no punctuation, a more rounded outline, and described the eyes as "prominent", "being composed of merely few large facets, set widely apart upon a convex surface". Firstly, the given body length would be equivalent to 1.86 mm, a much longer measurement that the longest species of *Cholovocera* (see above); secondly, the multifaceted eye is not a generic feature of *Cholovocera*, which has only one facet, protected by a lateral rim (Fig. 24E).

"*Cholovocera*" *maderae* has been recorded from several localities around the world, always associated with the longhorn crazy ant, *Paratrechina longicornis* (Latreille, 1802), a pantropical invasive species, which appears to be responsible for the wide distribution of the beetle, but both have an unknown geographic origin.

Dajoz (1975: 200) transferred *Cholovocera maderae* to the genus *Displotera* Reitter, 1887, erected for the species *Displotera simoni* Reitter, 1887 from Addah, in the old British Gold Coast (present Ivory Coast) in western Africa. Also, Dajoz (1975) regarded *D. simoni* as a junior synonym of *D. maderae* and included two other species in *Displotera*: *D. beloni* (Wasmann, 1899) from north-eastern India, and *D. grandis* Dajoz, 1975 from Sri Lanka, because these three species had six facets on each ocular area. Thus, Dajoz (1975) implied that this genus had an Asiatic origin, but with a cosmopolitan member. Although Reitter (1887) did not mention any association of *D. simoni* with ants, *Paratrechina longicornis* does occur in Ivory Coast.

According to Wasmann (1905: 385), most of the localities where the species *P. longicornis* and "*Ch.*" *maderae* had been recorded together (Madeira, Trinidad and Pará in northern Brazil) were anthropogenic, on the sea coast, and connected with commerce. In contrast, the only places where this ant and beetle have been collected together in natural environments were located in India and Southeast Asia. Over one hundred years later, Wetterer (2008: 142) referred to further records of *P. longicornis* with "*Coluocera*" *maderae* in anthropogenic habitats of Myanmar (as Burma), Taiwan, Haiti, Galápagos Islands and Hawaii, which agreed with Wasmann's (1905) hypothesis that both the host-ant and the beetle have been dispersed by human activity. Wetterer (2008: 138) also referred to the ant cricket *Myrmecophilus americanus* Saussure, 1877, another insect closely associated with *P. longicornis*, as widespread in India and Southeast Asia, but known from other parts of the world only in coastal areas along major old trade

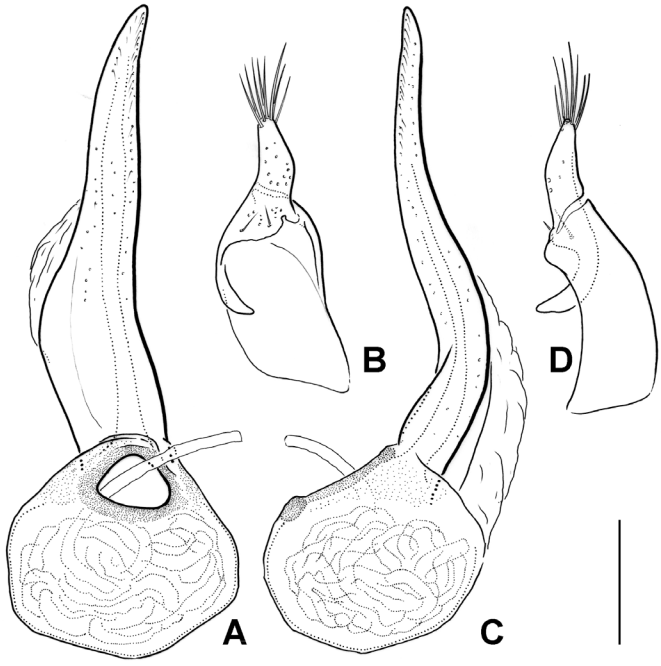

Fig. 15. Aedeagus and paramere of *Cholovocera formicaria* Victor, 1838. Male from type locality (Derbent). **A**–**B**. Ventral views. **C**–**D**. Lateral views. Scale bar = 0.1mm.

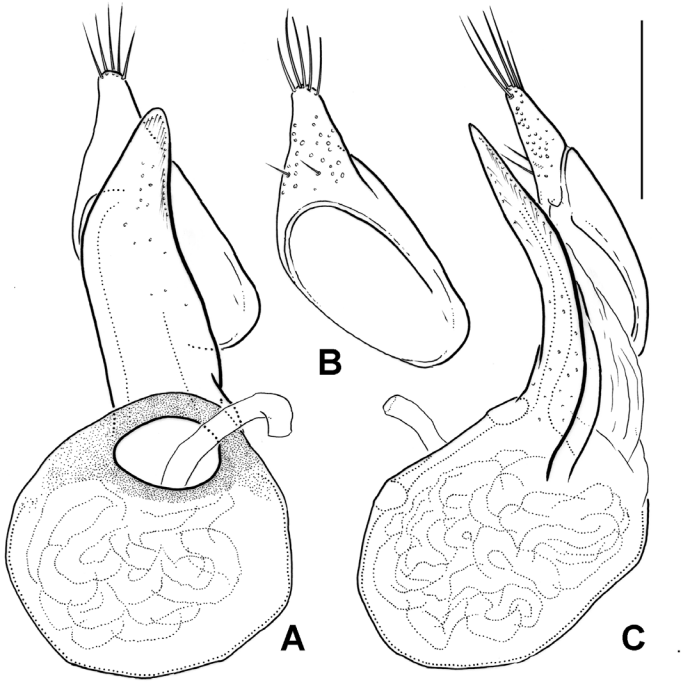

Fig. 16. Aedeagus and paramere of *Cholovocera punctata* (Märkel, 1845). Lectotype (Sicily). **A**–**B**. Ventral views. **C**. Lateral view. Scale bar = 0.1 mm.

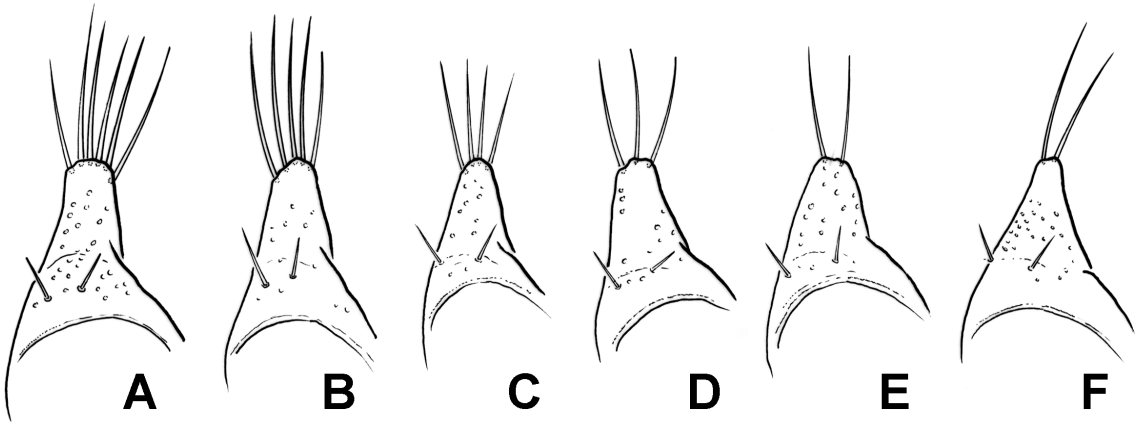

Fig. 17. Distal portions of parameres of *Cholovocera punctata* (Märkel, 1845) from various localities. **A**. Philippeville (Algeria). **B**. Monte Argentario (Central Italy). **C**. Palermo (Sicily). **D**. Corsica. **E**. Herault (Southern France). **F**. Marseille (Southern France).

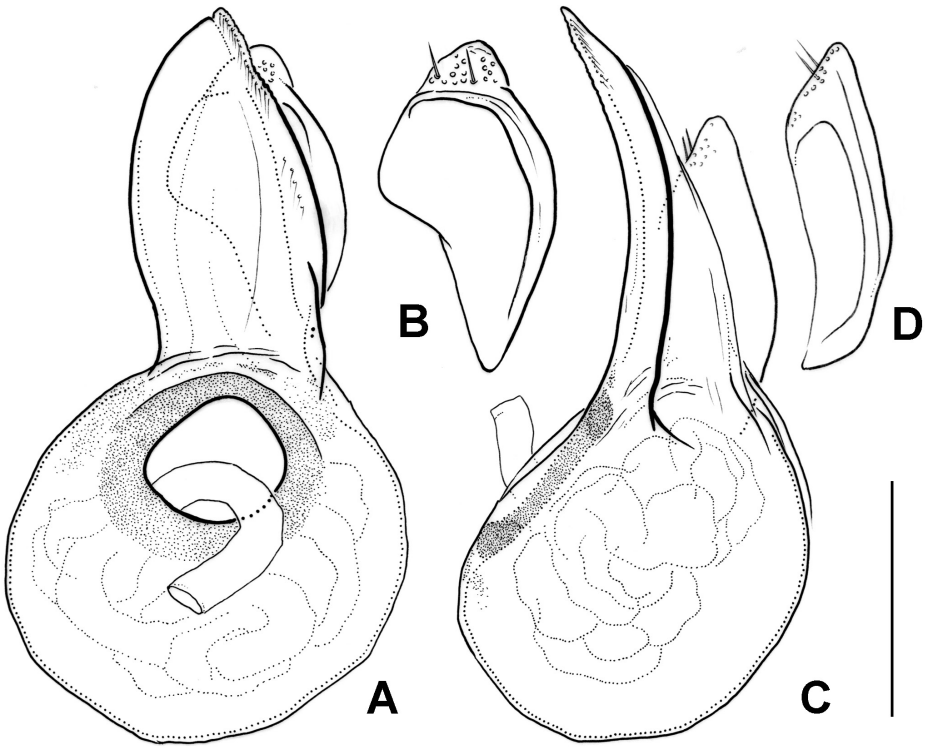

Fig. 18. Aedeagus and paramere of *Cholovocera formiceticola* (Rosenhauer, 1856). Lectotype (Spain). **A**–**B**. Ventral views. **C**–**D**. Lateral views. Scale bar = 0.1 mm.

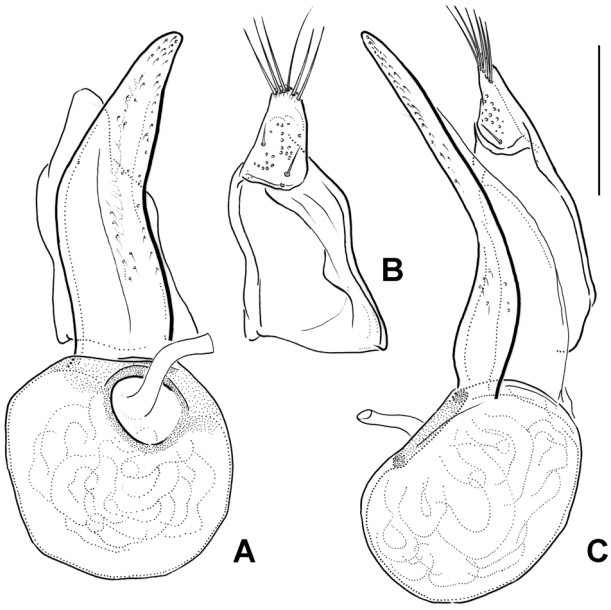

Fig. 19. Aedeagus and paramere of *Cholovocera attae* (Kraatz, 1858) (Greece). **A**–**B**. Ventral views. **C**. Lateral view.. Scale bar = 0.1 mm.

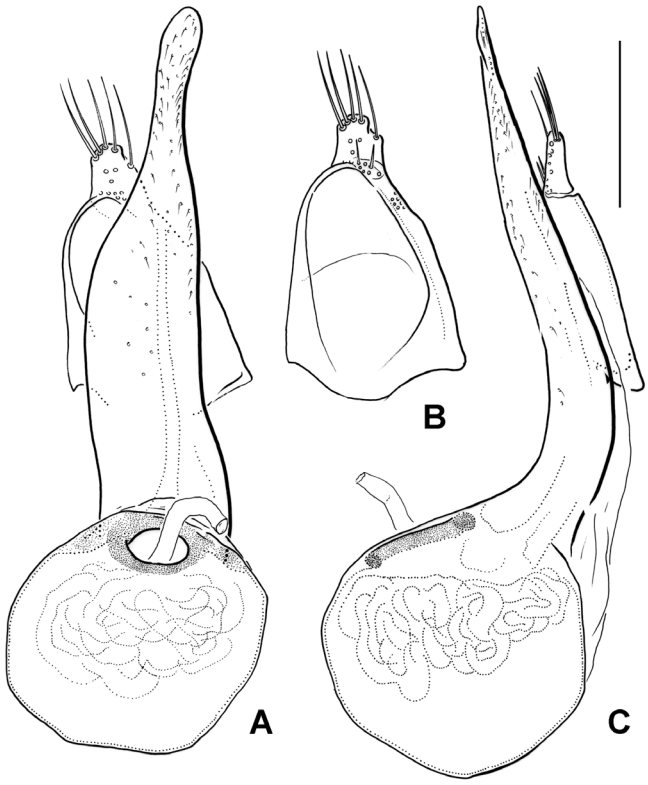

Fig. 20. Aedeagus and paramere of *Cholovocera gallica* (Schaufuss, 1876). Lectotype (Southern France). **A**–**B**. Ventral views. **C**. Lateral view. Scale bar = 0.1 mm.

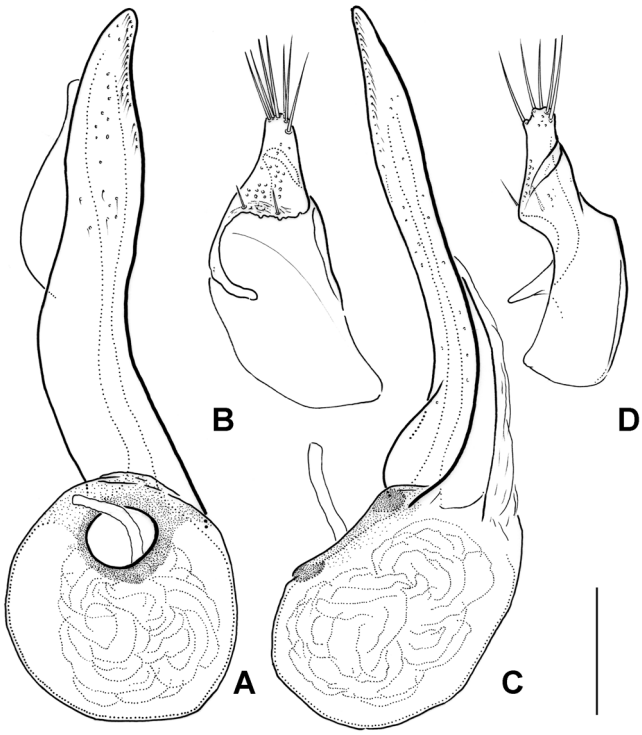

Fig. 21. Aedeagus and paramere of *Cholovocera balcanica* (Karaman, 1936). Male from type locality (Skopje). **A**–**B**. Ventral views. **C**–**D**. Lateral views. Scale bar = 0.1 mm.

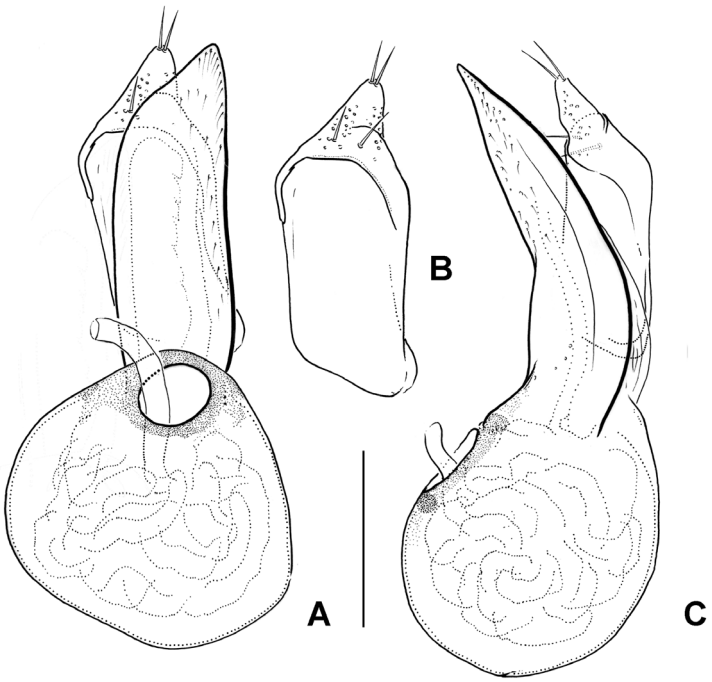

Fig. 22. Aedeagus and paramere of *Cholovocera occulta* sp. nov., holotype (Oran). **A**–**B**. Ventral views. **C**. Lateral view. Scale bar = 0.1 mm.

routes. The conclusion was that the most likely origin of the ant-host and its two symbionts was the Indomalayan Region (Wetterer & Hugel 2008, 2014; Wetterer 2015).

Kistner (1982: 124) studied the association between *P. longicornis* and "*Ch*." *maderae* in Hawaii, observing that if the ant nest was disturbed, the workers moved not only their larvae to a secure place, but the beetles as well. Furthermore, Kistner (1982) referred to a groove in the elytral epipleura of the beetles, where the ants' mandibles would fit to facilitate carrying them. No such intimate ant-beetle association is found between any species of *Cholovocera* and their ant hosts.

Shockley *et al.* (2009b: 65) placed *Displotera* as a new junior synonym of "*Cholovocerida"* Belon, 1884b (an unjustified emendation of *Colovocerida* Belon, 1884b), including "*Ch*." *maderae* together with two Neotropical species: "*Cholovocerida*" *unicurva* Belon, 1884b from Chile and "*Cholovocerida*" *ecitonis* (Wasmann, 1890) from Brazil. We disagree with Shockley *et al.* (2009b: 65) in both actions: in our opinion *Displotera* is not a junior synonym of *Colovocerida* but a valid genus of Indomalayan distribution, and "*Ch*." *maderae* does not belong in *Colovocerida*, because this genus appears restricted to the Neotropics.

In conclusion, from the morphological, distributional and biological evidence given above, we agree with Dajoz (1975: 200) that "*Cholovocera*" *maderae* should be placed in the genus *Displotera*, and referred to as *Displotera maderae* (Wollaston, 1854).

Coluocera ecitonis Wasmann, 1890

Wasmann (1890: 302) described *Coluocera ecitonis* from specimens collected in a nest of "*Eciton omnivorum* Koll." in Rio de Janeiro, Brazil. Belon (1897: 118, 1900: 141) expressed doubts regarding the generic position of this beetle species in *Cholovocera* [as *Colovocera*] because it had several ocelli, a different pronotum and lacked a scutellum, features not shared with typical *Cholovocera*. However, Belon (1897, 1900) did not transfer *Co. ecitonis* to any other genus.

Shockley *et al.* (2009b: 65) transferred *Coluocera ecitonis* to the genus "*Cholovocerida*" Belon, 1884, a position which we agree with, but it should be referred to as *Colovocerida ecitonis* (Wasmann, 1890).

Colovocera oculata Belon, 1891

Belon (1891: 878) described *Colovocera oculata* from 10 specimens collected in Mandalay (Myanmar), associated with *Paratrechina longicornis*. However, Belon (1897: 117) regarded his species as a junior synonym of "*Co*." *maderae*, a position he maintained in a later paper (Belon 1900: 140). Considering the type locality and the ant-host association of *Co. oculata*, we believe that Belon (1897, 1900) was most likely correct in synonymising these two species names.

Regardless of that synonymy, Belon (1891) described *Co. oculata* as having five or six ocelli in the ocular area, a confirmation that it cannot be included in Cholovocera, as we have defined it.

Coluocera beloni Wasmann, 1899

Wasmann (1899: 160) described *Coluocera beloni* from several specimens collected in Sangamner (Ahmednagar, India), associated with the ant *Pheidole sulcaticeps* Roger, 1863. In the original description, Wasmann (1899) gave the length of *Co. beloni* as 1.2 mm and described the ocular area as having several ocelli. As stated above, Dajoz (1975: 200) transferred *Co. beloni* to the genus *Displotera*.

Considering the lack of a proper taxonomic revision of the species placed in *Displotera*, we agree with Dajoz (1975) in naming this species as *Displotera beloni* (Wasmann, 1899).

Pseudevolocera atomarioides Champion, 1913

In his checklist of the Latridiidae and Merophysiinae of the world, Rücker (2020: 34) included a species from Guatemala, which he named as *"Cholovocera atomarioides* Champion, 1913". Considering that on the following page of the same checklist, Rücker (2020: 35) listed *Pseudevolocera atomarioides* Champion, 1913, with exactly the same location, we believe that it was an involuntary error to associate this species with the genus *Cholovocera*, a generic combination not found in any other publication.

Cholovocera brevicornis Johnson, 1977

Johnson (1977: 123) described two new species which he placed in the genus *Cholovocera*, both with exactly the same collecting data, i.e., locality, altitude, date and collector. The first species was *Cholovocera afghana* Johnson, 1977, which we have dealt with in detail above. Johnson (1977: 124) named his second species as *Cholovocera brevicornis*. We have examined the holotypes of both these species and concluded that, while *Ch. afghana* is a valid taxon and correctly placed in the genus *Cholovocera*, "*Cholovocera*" *brevicornis* not only belongs to another genus but is also a junior synonym.

The brief description of "*Ch.*" *brevicornis* includes the following features: length as 1.25 mm, colour reddish-yellow, eyes twice as long as broad, short antennae, shape of pronotum, fine punctuation, width as 0.72 mm, and last visible sternite not impressed. The host is given only as "ant".

Our study of the holotype of "*Ch.*" *brevicornis* revealed that it had six ocelli on each ocular area (Fig. 24D), while all the other species of *Cholovocera* have only one (Fig. 24E); this diagnostic generic character, in addition to its small size, its general habitus (Fig. 24C) and its association with ants of the genus *Pheidole*, indicate that it belongs to the genus *Displotera*. Furthermore, our detailed comparison of non-sexual features of the holotype of "*Ch.*" *brevicornis* against two female syntypes of *D. beloni* showed that they belong to the same taxon. Therefore, we propose that *Cholovocera brevicornis* Johnson, 1977 should be regarded as a junior synonym of *Displotera beloni* (Wasmann, 1899).

Material examined

Syntypes of *Displotera beloni*

INDIA – **Maharashtra** • 1 ♀; Ahmednagar, Wallon; Heim leg.; [associated with a *Pheidole* worker ant, labelled as: "*Pheidole poonensis* For. [Forel]"]; SDEI 12049 • 1 ♀; Ahmednagar, Wallon; Heim leg.; [associated with a worker ant labelled as "*Pheidole poonensis* For. [Forel]"]; SDEI 12050.

Holotype

AFGHANISTAN – **Nuristan** • 1 ♂; "Afghanistan, Nuristan, Bashgutal"; 1100 m a.s.l.; 14 Apr. 1953; J. Klapperich leg.; [with a *Pheidole indica* worker ant, X. Espadaler det.]; ZFMK COL–1000131.

Discussion

This taxonomic revision of the species belonging to the genus *Cholovocera* began as a simple attempt to identify specimens collected by the first author in southern Spain, as part of a study of the parasites and commensals associated with the ant *Messor barbarus* (e.g., Delgado *et al.* 2020). The absence of reliable identification sources soon became apparent due to contradictions and perpetuation of errors among the papers dealing with *Cholovocera*, published during the last 50 years. We believe that the widespread confusion in the identification of samples from many localities was due to two main factors: (1) not

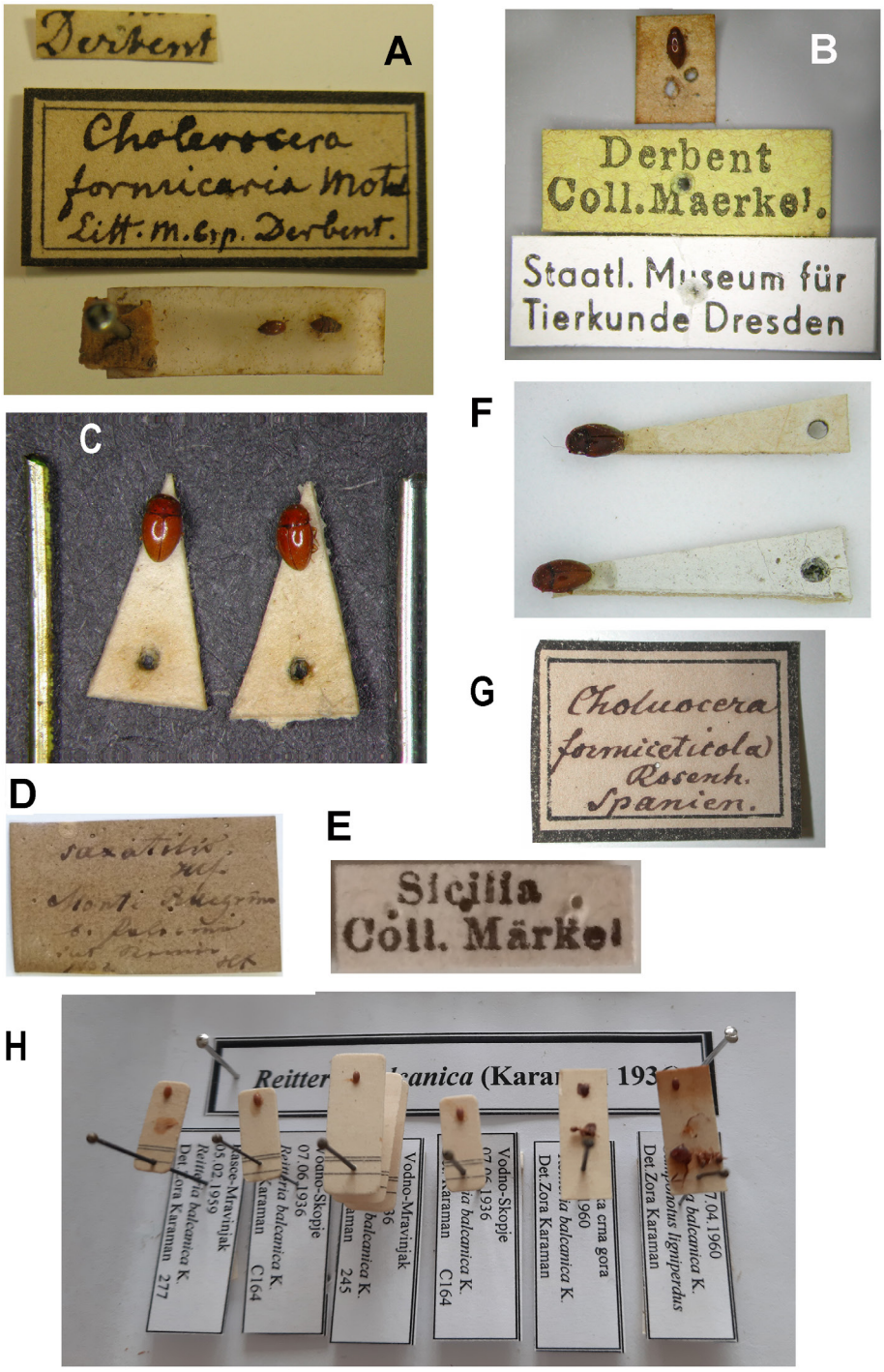

Fig. 23. Types and relevant specimens of species of *Cholovocera* Victor, 1838. **A**. Syntypes of *Ch. formicaria* Victor, 1838 on original Motchoulsky's mounting card (courtesy of A.A. Gusakov). **B**. Male specimen of *Ch. formicaria* Victor, 1838 from the type locality. **C**. Lectotype of *Ch. punctata* (Märkel, 1845) on left, and a specimen from the J.W. Helfer's Collection (NMPC) on right, showing identical pins and mounting cards. **D**. Single label attached to five females of *Ch. punctata* (Märkel, 1845) from the Helfer Collection. **E**. Label of *Ch. punctata* (Märkel, 1845) lectotype. **F**. Lectotype (above) and paralectotype (below) of *Ch. formiceticola* (Rosenhauer, 1856). **G**. Label of lectotype of *Ch. formiceticola* (Rosenhauer, 1856). **H**. Five syntypes of *Ch. balcanica* (Karaman, 1936), from left: second, third and fourth pins (courtesy of V. Krpach).

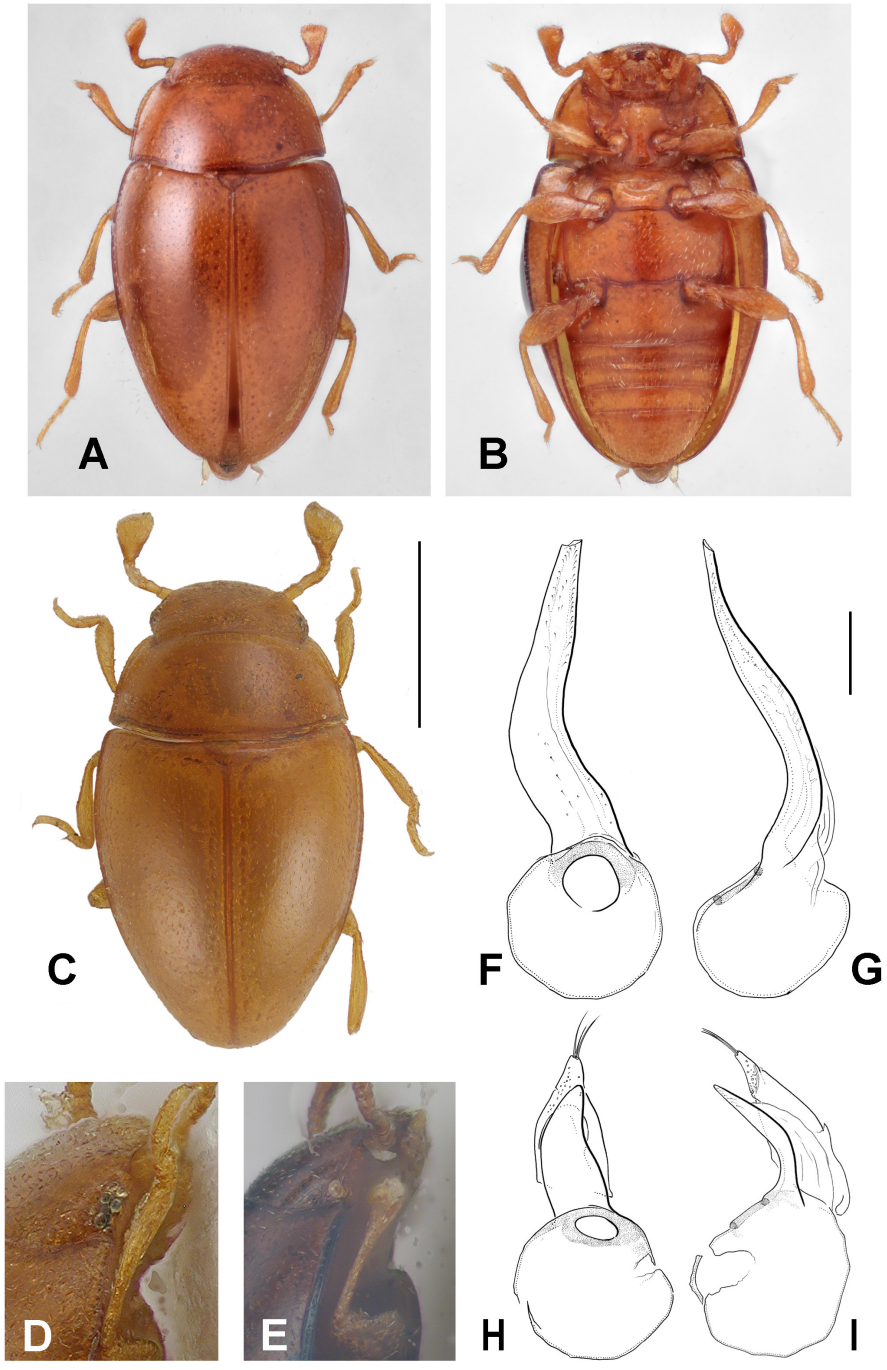

Fig. 24. A. A syntype of *Cholovocera formicaria* Victor, 1838, dorsal view (courtesy of K.V. Makarov). **B**. Same specimen, ventral view (courtesy of K.V. Makarov). **C**. Holotype of *Ch. brevicornis* Johnson, 1977 (= *Displotera beloni* (Wasmann, 1899)), dorsal view. **D**. Same specimen, ocular area, lateral view. **E**. Ocular area of *Ch. formiceticola* (Rosenhauer, 1856) (Lisbon), lateral view. **F**. Aedeagus of *Ch. formicaria major*, lectotype, ventral view. **G**. Same specimen, lateral view. **H**. Aedeagus of *Co punctata sardoa*, lectotype, ventral view. **I**. Same specimen, lateral view. Scale bars: A–C = 0.5 mm; D–I = 0.1 mm.

examining the type series of the nominal species and (2) dissecting very few or no specimens at all, thus missing the diagnostic morphology of both male and female genitalia.

Therefore, to obtain the correct identity of the Spanish material, we had to examine and dissect hundreds of specimens, including primary types, from many European collections, as well as to acquire and

Fig. 25. Specimens of *Cholovocera* Victor, 1838 from the Schaufuss Collection. **A**. Syntype (now lectotype) of *Ch. gallica* (Schaufuss, 1876) from Southern France. **B**. Misidentified syntype (now a paralectotype) of *Ch. gallica* from Southern France (actually a female of *Ch. punctata* (Märkel, 1845)). **C**. Specimen of *Ch. punctata* from Corsica. **D**. Specimen of *Ch. formiceticola* (Rosenhauer, 1856) from the Balearic Islands. **E**. Specimen of *Ch. punctata* from Algeria.

evaluate all the available literature, a task that allowed us to produce this revision, which includes a key for the identification of the eight species we recognised as belonging to *Cholovocera*.

We hope that this paper will facilitate the identification of the genus and its species, will encourage future workers to study internal morphology, and will assist in establishing the correct associations of these beetles with their host ants. We anticipate that new species may be found, especially in more eastern areas, between Turkey and Afghanistan.

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References

André E. 1874. Description des fourmis d'Europe pour servir à l'étude des insectes myrmécophiles. *Revue et Magasin de Zoologie pure et appliquée* 3 (2): 152–235.

Angelini F. & Rücker H.W. 1999. Contributo alla conoscenza dei Merophysiidae e Lathridiidae dell'Italia meridionale e della Sicilia (Coleoptera). *Memorie della Società Entomologica Italiana* 77: 213–240.

Arakelian G. & Kalashian M. 1993. Fauna of Armenia: the beetles (Coleoptera) living in association with ants (Hymenoptera, Formicidae). *Biologicheski Zhurnal Armenii* 46 (2): 50–52 [In Russian].

Audisio P., Canepari C., De Biase A., Poggi R., Ratti E. & Zampetti M.F. 1995. Coleoptera Polyphaga XI (Clavicornia II). *In*: Minelli A., Ruffo S. & La Posta S. (eds) *Checklist delle specie della fauna italiana* 56: 1–19. Calderini, Bologna.

Bargagli P. 1872. Materiali per la fauna entomologica dell'isola di Sardegna, coleotteri. *Bullettino della Società entomologica italiana* 4 (1): 97–104.

Baroni-Urbani C. 1963. Contributo alla conoscenza etologica della *Coluocera formicaria* Motsch. coleottero mirmecofilo sinechete gregario (*Lathridiidae*). *Bollettino di Zoologia Agraria e di Bachicoltura* 5: 95–100.

Belon M.-J. 1879. Famille des Lathridiens, 1re partie. *In*: Mulsant E. (ed.) Histoire naturelle des coléoptères de France. *Annales de la Société linnéenne de Lyon*, *n.s*. 26: 157–365.

Belon M.-J. 1884a. Supplément à la monographie des Lathridiens de France. *In*: Mulsant E. (ed.) *Histoire naturelle des Coléoptères de France. Famille des Lathridiens* 10: 1–17. Pritat Ainè. Lyon.

Belon M.-J. 1884b. Description d'un Coléoptère nouveau du Chili. *Annales de la Société entomologique de Belgique* 28: clxiii–clxv [pagination given in Roman numerals].

Belon M.-J. 1887. Lathridiens nouveaux ou peu connus. *Revue d'Entomologie* 6: 215–229.

Belon M.-J. 1891. Viaggio di Leonardo Fea in Birmania e regioni vicine XXXVIII. Lathridiidae. *Annali del Museo civico di storia naturale di Genova*. Serie 2. 10: 877–880 [1890].

Belon M.-J. 1895. Nouvelle contribution à l'étude des Lathridiens. *Annales de la Société entomologique de Belgique* 39: 75–105.

Belon M.-J. 1897. Essai de classification générale des Lathridiidae avec le catalogue systematique et alphabétique de toutes les espèces du globe. *Revue d'Entomologie* 16: 105–221.

Belon M.-J. 1900. Récapitulation des Lathridiidae de l'Amérique méridionale. *Annales de la Société linnéenne de Lyon* (*N.S.*) 46: 137–192 [1899].

Belon M.-J. 1902. Coleoptera, Clavicornia, Fam. Lathridiidae. *In*: Wytsman P. (ed.) *Genera Insectorum:* Fasc. 9: 1–40. M.P. Wytsman, Bruxelles.

Bernard F. 1968. *Les Fourmis* (*Hymenoptera, Formicidae*) *d'Europe occidentale et septentrionale*. Masson, Paris.

Bodemeyer E. von 1900. *Quer durch Klein-Asien in den Bulgar-Dagh. Eine naturwissenschaftliche Studien-reise*. Druck und Verlags-Aktien Gesellschaft vormals Dölter, Emmendingen.

Bolívar I. 1886. Nota sobre los coleópteros recogidos en España y Norte de África. *Actas de la Sociedad Española de Historia Natural* 15: 48–55.

Bousquet Y. 2016. Litteratura Coleopterologica (1758–1900): a guide to selected books related to the taxonomy of Coleoptera with publication dates and notes. *ZooKeys* 583: 1–776. https://doi.org/10.3897/zookeys.583.7084

Cambefort Y. 2006. *Des Coléoptères, des Collections et des Hommes*. Muséum national d'histoire naturelle, Paris. https://doi.org/10.4000/books.mnhn.2265

Ciofalo S. 1886. Catalogo dei Coleotteri dei dintorni di Termini Imerese. *Atti della Accademia gioenia di scienze naturali in Catania* 19: 181–209.

Crowson R.A. 1955. *The Natural Classification of the Families of Coleoptera*. Nathaniel Lloyd, London.

Dajoz R. 1975. Coleoptera: Lathridiidae de Ceylan. *Entomologica Scandinavia Supplement* 4: 199–207.

Delgado J.A., Disney R.H.L. & Palma R.L. 2020. The ant host of *Razorfemora zaragozae* and some observations of their relationships under natural conditions. *Bulletin of Insectology* 73 (2): 193–200.

De Marzo L. 2008. Biodiversità della spermateca nei coleotteri. *Atti dell'Academia Nazionale Italiana di Entomologia*, *Rendiconti* 56: 69–96.

Des Gozis M. 1881. Révision des Latridiidae d'Europe par Edmond Reitter. Accompagnée de généralités sur l'histoire, les mœurs, la distribution géographique, la bibliographie de cette tribu avec addition des espèces extra européennes de l'ancien-monde. *L'Abeille: Journal d'Entomologie* 18 (6): 1–178.

Dieck G. 1870a. Ein entomologischer Ausflug in die Berge Süd-Corsica's. *Berliner Entomologische Zeitschrift* 14: 397–404.

Dieck G. 1870b. Eine entomologische Winter campagne in Spanien. *Berliner Entomologische Zeitschrift* 14: 145–180.

Dieck G. 1871. Coleotteri raccolti in Corsica. *Bullettino della Società entomologica Italiana* 3 (2): 201–204.

Dieck G. 1888. An entomological winter campaign in Spain and North Africa. *The Entomologists* 21: 38–43.

Döbler H. 1987. Katalog der in den Sammlungen der Abteilung Taxonomie der Insekten des Institutes für Pflanzenschutzforschung, Bereich Eberswalde (ehemals Deutsches Entomologisches Institut), aufbewahrten Typen – XXVI. *Nova Supplementa Entomologica* 3: 4– 96.

Donisthorpe H. 1927. The Ants (Formicidae), and some Myrmecophiles, of Sicily. *The Entomologist's Record* 38: 161–165.

Erichson W.F. 1845. Bericht über die wissenschaftlichen Leistungen in der Naturgeschichte der Insecten, Arachniden, Crustaceen und Entomostraceen während des Jahres 1844. *Archiv für Naturgeschichte* 11 (1–2): 67–181.

Escherich K. 1897. Zoologische Ergebnisse einer von Dr. K. Escherich und Dr. L. Kathariner nach Central-Kleinasien unternommen Reise. IV. Theil. Coleopteren. Unter Mitwirkung von E. Brenske, L. Ganglbauer, Dr. L. von Heyden, E. Wasmann und J. Weise. *Stettiner Entomologische Zeitschrift* 58 (1–3): 3–69.

Escherich K. 1917. *Die Ameise. Schilderung ihrer Lebensweise*. Friedr. Vieweg & Sohn, Braunschweig.

Escherich K. & Emery C. 1897. Zur kenntniss der myrmecophilen kleinasiens. I. Coleopteren. *Wiener Entomologische Zeitung* 16 (9): 229 –239.

Espadaler X. & Collingwood C.A. 2001. Transferred ants in the Iberian Peninsula (Hymenoptera, Formicidae). *Nouvelle Revue d'Entomologie* (*N.S.*) 17 (3): 257–263 [2000].

Fadda S., Orgeas J., Ponel P., Henry F., Buisson É. & Dutoit T. 2007. Conséquences de l'arrêt d'un pâturage séculaire sur les communautés de coléoptères terricoles de pelouses sèches. *Ecologia Mediterranea* 33: 53–71. https://doi.org/10.3406/ecmed.2007.1408

Fairmaire L. 1859. Liste des insectes récoltés en Corse par Ph. Lareynie. *Annales de la Société entomologique de France* 7: 266–269

Fairmaire L. & Coquerel C. 1860. Essai sur les coléoptères de Barbarie. Deuxième partie. *Annales de la Société entomologique de France* 8 (1–2): 145–176.

Fauvel A. 1890. Rectifications au catalogus coleopterorum Europae et Caucasi. *Revue d'Entomologie* 9: 330–344.

Gallois M.J. 1893. Catalogue des Coléoptères de Maine-et-Loire. *Bulletin de la Société des Sciences naturelles de l'Ouest de la France* 3 (2): 17–19.

Ganglbauer L. 1899. *Die Käfer von Mitteleuropa. Band 3* (*1*): *Familienpeihe Staphylinoidea. 2. Theil: Scydmaenidae, Silphidae, Clambidae, Leptinidae, Platypsyllidae, Corylophidae, Sphaeriidae,*

Trichopterygidae, Hydroscaphidae, Scaphidiidae, Histeridae. Druck und Verlag von Carl Geruld's Sohn, Wien.

Gemminger M. & Harold B. de 1868. *Catalogus coleopterorum hucusque descriptorum synonymicus et systematicus. Tom. III. Histeridae, Phalacridae, Nitidulidae, Trogositidae, Colydidae, Rhysodidae, Cucujidae, Cryptophagidae, Derodontidae, Latrididae, Othnidae, Mycetophagidae, Thorictidae, Dermestidae, Byrrhidae, Georyssidae, Parnidae, Heteroceridae, Lucanidae*. Sumptu E.H. Gummi, Monachii, Paris, London.

Heyden L. von. 1886. Zusammenstellung der von Herrn Dr. med. W. Kobelt von seiner Reise in den Provinzen Alger und Constantine, sowie von Tunis mitgebrachten Coleopteren. *Bericht über die Senckenbergische Naturforschende Gesellschaft in Frankfurt am Main* 1885–1886: 35–57.

Heyden L. von, Reitter E. & Weise J. 1883. *Catalogus coleopterorum Europae et Caucasi. 3*th *ed.* Libraria Nicolai, Berlin.

ICZN 1999. *International Code of Zoological Nomenclature* (*4*th *ed.*). The International Trust for Zoological Nomenclature, London.

Jäch M.A., Kodada J., Broje M., Shepar W.D. & Čiampor F. Jr. 2016. *World Catalogue of Insects, Volume: 14: Elmidae and Protelmidae* (*Coleoptera*). Brill Publishers, Leiden/Boston. https://doi.org/10.1163/9789004291775

Johnson C. 1977. Beiträge zur Kenntnis der fauna Afghanistans. Merophysiidae and Lathriidae, Coleoptera. *Acta Musei Moraviae* 62: 123–132.

Karaman Z. v. 1936. Ein balkanischer Vertreter des Koleopteren-Genus *Reitteria*, Reit. *balcanica* n. sp. *Glasnik* (*Bulletin*) *de la Société scientifique de Skopje* 17: 131–133.

Karaman Z. 1964. Nouvelle espèce de *Bathyscidius* de Sibérie orientale, et remarques sur l'expansion de l'espèce myrmicophylle (sic!) *Reitteria balcanica* Karaman. *Bulletin de la Société entomologique de Mulhouse* 1964: 30–33.

Katter F. 1881. Nekrolog. Wilhelm Gottlieb Rosenhauer. *Entomologische Nachrichten* 7 (1): 231–232.

Kistner D.H. 1982. The social insects' bestiary. *In*: Hermann H.R. (ed.) *Social Insects. Vol. 3*: 124–127. Academic Press, New York.

Kovář I. 1973. Taxonomy and morphology of adults. *In*: Hodek I. (ed.) *Biology of Coccinellidae*: 36–53. Dr. W. Junk N.V., The Hague. https://doi.org/10.1007/978-94-010-2712-0

Kraatz G. 1858. Beitrag zur Käferfauna Griechenlands. Staphylinidae (Schlufs), Trichopterygia, Histeridae, Phalacridae, Nitidularia, Trogositarii, Colydii, Cucujidae, Cryptophagidae, Thorictidae, Mycetophagidae, Dermestini, Byrrhii. *Berliner Entomologische Zeitschrift* 2: 123–148.

Krausse A.H. 1911. Beiträge zur Kenntnis der Insekten-fauna Sardiniens. *Entomologische Rundschau* 28 (19): 147–150.

Krausse A. 1913. Bei Sorgono im Gennargentugebirge auf Sardinien gesammelte Coleopteren. *Archiv für Naturgeschichte* 79 (1): 59–64.

Krausse A. 1915. Zoologische Notizen von Sardinien (nebst Verzeichnis bisheriger Arbeiten des Verfassers). *Archiv für Naturgeschichte* 81 (2): 120–128.

Krausse A. 1917. Hexapodologische Notizen. *Archiv für Naturgeschichte* 83 (6): 49–55.

Lange C.E. & Lord J. 2012. Chapter 10: Protistan entomopathogens. *In*: Vega F. & Kaya H. (eds) *Insect Pathology*. 2nd edition: 367–394. Academic Press, San Diego. https://doi.org/10.1016/B978-0-12-384984-7.00010-5

Lapeva-Gjonova, A. 2013. Ant-associated beetle fauna in Bulgaria: A review and new data. *Psyche* 2013: 1–14. Article ID 242037. https://doi.org/10.1155/2013/242037

Lapeva-Gjonova A. & Rücker W.H. 2011. Latridiidae and Endomychidae beetles (Coleoptera) from ant nests in Bulgaria. *Latridiidae* 8: 5–8.

Latreille P.A. 1807. *Genera Crustaceorum et Insectorum secundum ordinem naturalem in familias disposita, iconibus exemplisque plurimus explicata*. *Volume 3*. A. Koenig, Parisiis et Argentorati.

Lawrence J.F. 1991. Endomychidae (Cucujoidea) (Including Merophysiidae, Mycetaeidae). *In*: Stehr F.W. (ed.) *Immature Insects. Vol. 2*: 482–485. Kendall/Hunt Publishing Company, Dubuque.

Lazarev M.A. 2017. A new subspecies of *Dorcadion* (*Cribridorcadion*) *talyschense* Ganglbauer, 1884 from Iran (Coleoptera, Cerambycidae). *Humanity Space. International almanac* 6 (5): 878–888.

Leach W.E. 1815. Endomychidae. Entomology. *In*: Brewster D. (ed.) *The Edinburgh Encyclopaedia*. *Vol. 9*: 57–172.

Leder H. 1886. Die Coleopteren des Talysch-Gebietes, 1. *In*: Radde G. (ed.) *Die Fauna und Flora des südwestlichen Caspi-Gebietes*: 89–235. F.A. Brockhaus, Leipzig.

Löbl I. & Smetana A. 2007. *Catalogue of Palaearctic Coleoptera, vol. 4: Elateroidea, Derodontoidea, Bostrichoidea, Lymexyloidea, Cleroidea and Cucujoidea*. Apollo Books, Stenstrup. https://doi.org/10.1163/9789004260894

Lo Cascio P., Cecchi B., Abbazzi P. & Arnone M. 2006. A contribution to the knowledge of the Coleoptera of the Aeolian Islands (*Insecta Coleoptera*). *Il Naturalista Siciliano n.s.* 30 (2): 315–341.

Lucas H. 1849. *Exploration scientifique de l'Algérie pendant les années 1840, 1841, 1842. Zoologie: Animaux articulés: Vol. 2: Insectes*. Imprimerie Nationale, Paris.

Lucas H. 1874. Note. Séance 25 Novembre 1874. *Annales de la Société entomologique de France* (*Bulletin des Séances et Bulletin bibliographique*) 5 (4): 239.

Luigioni P. 1929. I Coleotteri d'Italia. Catalogo sinonimico-topografico-bibliografico. *Memorie della Pontificia Accademia delle Scienze, I Nuovi Lincei* 13 (2): 1–1159.

Luigioni P. & Adelchi T. 1910. Coleotteri del Lazio non citati come tali nel «catalogo dei coleotteri d'Italia», *Bollettino della Società entomologica italiana* 42 (1–4): 43–93.

Luigioni P. & Adelchi T. 1913. Una settimana in Sicilia. *Bollettino della Società entomologica italiana* 44 (1–4): 148–167.

Lundberg S., Palm T. & Trottestam O. 1987. Skalbaggsstudier, på Siciliens nordkust. II. Gräsmark, flodmynningar, havsstrand m. m. [Coleoptera from the northern Sicilian coast. II. Grassland, river-mouths, sea shores etc.]. *Entomologisk tidskrift* 108 (4): 123–129.

Märkel F. 1845. Beiträge zur Kenntniss der unter Ameisen lebenden Insekten. *Zeitschrift für die Entomologie* 5: 193–271 [1844].

Martínez de la Escalera M. 1914. Los Coleópteros de Marruecos. *Trabajos del Museo Nacional de Ciencias Naturales. Serie Zoológica* 2: 1–553.

Martínez-Ibáñez M.D. & Espadaler-Gelabert X. 1986. Revisión de las hormigas ibéricas de la colección M. Medina y nuevos datos de distribución (Hymenoptera, Formicidae). *Actas de las VIII Jornadas de la Asociación Española de Entomología* 1986: 1022–1034.

Moggridge J.T. 1873. *Harvesting Ants and Trap-door Spiders*. Lovell Reeve & Co., London.

Motchoulsky V. de 1845. Remarques sur la collection de coléoptères russes. *Bulletin de la Société impériale des Naturalistes de Moscou* 18 (1): 3–127.

Oertzen E. von. 1886. Verzeichniss der Coleopteren Griechenlands und Cretas. *Berliner Entomologische Zeitschrift* 30 (2): 189–291.

Parmentier T., Gaju-Ricart M., Wenseleer T. & Molero-Baltanás R. 2020. Strategies of the beetle *Oochrotus unicolor* (Tenebrionidae) thriving in the waste dumps of seed-harvesting *Messor* ants (Formicidae). *Ecological Entomology* 45: 583–593. https://doi.org/10.1111/een.12832

Piccioli F. 1871. Rivista dei coleotteri spettanti alla fauna sotterranea recentemente scoperti in Italia e descrizione di due nuove specie anottalme. *Bullettino della Società entomologica italiana* 2 (4): 301–305.

Ponel P. 2011. Chapitre 5. Analyses entomologiques (coléoptères). *In*: Excoffon P. (ed.) *Ville et Campagne de Fréjus romaine. Bibliothèque d'Archéologie méditerranéenne et africaine:* 245–256. Errance, Aix-en-Provence. https://doi.org/10.4000/books.pccj.1205

Prieto-Manzanares M. 2018. Els coleòpters del delta del Llobregat. Aproximació històrica i noves aportacions. *In*: Germain i Otzet J. & Pino i Vilalta J. (eds) *Els sistemes naturals del delta del Llobregat. Treballs de la Institució Catalana d'Història Natural,* 19: 407–482. Institut d'Estudis Catalans, Barcelona.

Ragusa E. 1873. Escursioni fatte sul monte Pellegrino presso Palermo. *Bollettino della Società entomologica italiana* 5: 170–179.

Redtenbacher L. 1858. *Fauna Austriaca. Die Käfer*. Carl Herold's Son, Wien.

Redtenbacher L. 1874. *Fauna Austriaca. Die Käfer, Vol 1*. Carl Herold's Son, Wien.

Reitter E. 1875. Revision der europäischen Lathridiidae. *Entomologische Zeitung* 36: 297–340.

Reitter E. 1877. Ueber *Merophysia* Luc., *Coluocera* Motsch. und *Reitteria* Leder. *Mittheilungen des Münchener Entomologischen Vereins* 1877: 1–6.

Reitter E. 1882. Neuere literatur. *Deutsche entomologische Zeitschrift* 26: 161–165.

Reitter E. 1887. *Bestimmungs-Tabellen der europäischen Coleopteren. III Helft. II Auflage. Enthaltend die Familien: Scaphidiidae, Lathridiidae und Dermestidae*. E. Reitter, Mödling.

Reitter E. 1902. Neue und seltene Coleopteren, gesammelt im Jahre 1901, in der Herzegowina, in Dalmatien und Bosnien. *Wiener Entomologische Zeitung* 21: 1–9.

Reitter E. 1911. *Coluocera punctata* Märk. Subsp. *sardoa* nov. *Wiener Entomologische Zeitung* 30 (1): 70.

Riggio G. 1885. Materiali per una fauna entomológica dell' isola d' Ustica. Prima contribuzione. *Il Naturalista Siciliano* 5 (2): 25–31, 52–56, 85–91.

Robertson J.A., Ślipiński A., Moulton M., Shockley F.W., Giorgi A., Lord N.P., Mckenna D.D., Tomaszewska W., Forrester J., Miller K.B., Whiting M.F. & Mchugh J.V. 2015. Phylogeny and classification of Cucujoidea and the recognition of a new superfamily Coccinelloidea (Coleoptera: Cucujiformia). *Systematic Entomology* 40: 745–778. https://doi.org/10.1111/syen.12138

Rosenhauer W.G. 1856. *Die Thiere Andalusiens nach dem Resultaten einer Reise zusammengestellt nebst den Beschreibungen von 249 neuen oder bis jetzt noch unbeshcreibenen Gattungen und Arten*. T. Blaesing, Erlangen.

Rücker H.W. 1980. Bestimmungstabelle der *Merophysiidae* des Mittelmeerraumes und der angrenzenden Gebiete (Coleoptera: *Merophysiidae*). *Entomologische Blätter* 75 (3): 141–154.

Rücker W.H. 1983. Különbözõ csápú bogarak VI. – Diversicornia VI. Bunkóscsápú bogarak VII. – Clavicornia VII. *In*: Zoltán K. (ed.) *Magyarország Állatvilága* (*Fauna Hungariae*) 8 (3): 1–73. Akadémiai Kiadó, Budapest.

Rücker W.H. 2009. Checklist Latridiidae & Merophysiinae of the World. *Latridiidae und Merophysiinae* 9: 1–15.

Rücker W.H. 2011a. Ergebnisse von Typenstudien der Gattungen *Metophthalmus* Motschulsky, 1850 (Coleoptera: Latridiidae), *Cholovocera* Motschulsky, 1838, *Reitteria* Leder, 1872, *Merophysia* Lucas, 1852 (Endomychidae: Merophysiinae) und *Holoparamecus* Curtis, 1833 (Endomychidae: Holoparamecinae). *Latridiidae – Mitteilungsblatt für Systematik und Taxonomie der Latridiidae* 8: 11–20.

Rücker W.H. 2011b. Fauna Europaea: Coleoptera, Endomychidae: Merophysiinae. *Fauna Europaea* ver. 2017.06 http://www.faunaeur.org

Rücker W.H. 2018. *Latridiidae und Merophysiidae der West-Paläarktis*. Selbstverlag Wolfgang H. Rücker, Neuwied.

Rücker W.H. 2020. Checkliste der Latridiidae & Merophysiidae der Welt. *Latridiidae und Merophysiinae* 22: 1–40.

Sabella G. & Sparacio I. 2004. Il ruolo dei parchi siciliani nella conservazione di taxa di insetti di particolare interesse naturalistico (Insecta Coleoptera et Lepidoptera Rhopalocera). *Il Naturalista Siciliano, n.s.* 28 (1): 477–508.

Sahlberg J. 1903. Coleoptera Numido-Punica mensibus Martio, Aprili et Majo 1899 in Tunisia et Algeria orientali collecta. *Öfversigt af Finska vetenskaps-societetens förhandlingar* 45 (19): 1–70.

Sainte-Claire Deville J. 1914. *Catalogue critique des Coléoptères de la Corse*. Imprimerie Adeline, G. Poisson et G^{in}, Successeurs, Caen.

Santamaría S. 1995. *Parvomyces*, a new genus of Laboulbeniales from Spain. *Mycological Research* 99 (9): 1071–1077. https://doi.org/10.1016/S0953-7562(09)80775-2

Sár J., Dudás G. & Merkl O. 2004. A hangyász álböde (*Pleganophorus bispinosus* Hampe, 1855) Magyarországon (Coleoptera: Endomychidae). *Somogyi Múzeumok Közleményei* 16: 329–332.

Saulcy F. de 1862. Observations sur les genres *Choleva*, *Catops* et *Catopsimorphus* et remarques sur le nouveau catalogue de M. Schaum suivies de la description de deux nouveaux genres et de quatre nouvelles espèces de coléoptères propres à la faune française. *Annales de la Société entomologique de France* 2: 281–291.

Schaufuss L.W. 1876a. Ueber *Merophysia* Luc., *Coluocera* Mtsch. und *Reitteria* Led. *Nunquam otiosus* 2: 393–400.

Schaufuss L.W. 1876b. Nachtrag zu *Merophysia* etc. *Nunquam otiosus* 2: 412–414.

Schigel D.S. 2012. Fungivory and host associations of Coleoptera: a bibliography and review of research approaches. *Mycology* 3 (4): 258–272. https://doi.org/10.1080/21501203.2012.741078

Seidlitz G. 1872. *Fauna Baltica. Die Käfer* (*Coleoptera*) *der Ostseeprovinzen Russlands*. Druck und Verlag von H. Laakmann, Dorpat.

Seidlitz G. 1898. Bericht über die wissenschaftlichen Leistungen im Gebiete der Entomologie während des Jahres 1897, Coleoptera. *Archiv für Naturgeschichte* 64 (2): 68–320.

Seidlitz G. 1912. Coleoptera für 1911. *Archiv für Naturgeschichte* 78 (5): 25–326.

Sherborn C.D. 1926. *Index animalium sive index nominum quae ab a.d. MDCCLVIII generibus et speciebus animalium imposita sunt.* 2 (10). British Museum, London.

Shockley F.W., Tomaszewska K.W. & McHugh J.V. 2009a. Review of the natural history of the handsome fungus beetles (Coleoptera: Cucujoidea: Endomychidae). *Insecta Mundi* 72: 1–24.

Shockley F.W., Tomaszewska K.W. & McHugh J.V. 2009b. An annotated checklist of the handsome fungus beetles of the world (Coleoptera: Cucujoidea: Endomychidae). *Zootaxa* 1999: 1–113. https://doi.org/10.11646/zootaxa.1999.1.1

Silvestri F. 1912. Contribuzioni alla conoscenza dei mirmecofili. II. Di alcuni mirmecofili dell'Italia meridionale e della Sicilia. *Bollettino del Laboratorio di Zoologia Generale e Agraria* 6: 221–245.

Skelley P.E. & Leschen R.A.B. 2002. Endomychidae Leach 1815. *In*: Arnett R.H. Jr., Thomas M.C., Skelley P.E. & Frank J.H. (eds) *American Beetles. 2. Polyphaga: Scarabaeoidea through Curculionoidea*: 366–370. CRC Press, Boca Raton.

Smith F. 1874. Letter, Entomological Society Feb. 16. *Societies and Academies. Nature* 9: 354.

Stalling T. 2019. Aktuelle funde einiger Merophysiinae und eine neue Wirtsameise von *Reitteria escherichi* Wasmann, 1896 von der insel Kos, Griechenland (Coleoptera: Merophysiidae). *Folia Latridiidae et Merophysiidae* 2: 11–13.

Steiner F.M., Csősz S., Markó B., Gamisch A., Rinnhofer L., Folterbauer C., Hammerle S., Stauffer C., Arthofer W. & Schlick-Steiner B.C. 2018. Turning one into five: Integrative taxonomy uncovers complex evolution of cryptic species in the harvester ant *Messor* "*structor*". *Molecular Phylogenetics and Evolution* 127: 387–404. https://doi.org/10.1016/j.ympev.2018.04.005

Tomaszewska W. 2000. Morphology, phylogeny and classification of adult Endomychidae (Coleoptera: Cucujoidea). *Annales Zoologici* 50 (4): 449–558.

Tomaszewska W. 2010. 10.32. Endomychidae Leach, 1815. *In*: Leschen R.A.B., Beutel R.G. & Lawrence J.F. (eds) *Coleoptera, Beetles. Volume 2: Morphology and Systematics* (*Elateroidea, Bostrichiformia, Cucujiformia Partim*): 442–454. Walter de Gruyter, Berlin/New York. https://doi.org/10.1515/9783110911213.442

Ulmen K., Newzella R., Hubweber L., Schmitt M., Klug T. & Ahrens D. 2010. Contribution to a catalogue of types preserved in the collection of Zoologisches Forschungsmuseum Alexander Koenig (ZFMK): Coleoptera: 1. Checklist of taxa. *Bonn Zoological Bulletin* 58: 5–48.

Verdiani-Bandi L. 1874. Caccie ed escursioni. *Bullettino della Società entomologica italiana* 6: 148–151.

Victor T. 1838. Coléoptères du Caucase et des Provinces transcaucasiennes recueillis et décrits. *Bulletin de la Société impériale des Naturalistes de Moscou* 11 (2): 175–188.

Vigna-Taglianti A., Audisio P.A., Belfiore C., Biondi M., Bologna M.A., Carpaneto G.M., De Biase A., De Felici S., Piattella E., Racheli T., Zapparoli M. & Zoia S. 1992. Rifflesioni di grupo sui corotipi fondamentali della fauna W-paleartica ed in particolare italiana. *Biogeographia* 16: 159–179.

Vitale F. 1904. I Coleotteri Messinesi. *Rivista italiana di scienze naturali, Bolletino del Naturalista* 24 (8): 74–76.

Walker J.J. 1888. A year's insect-hunting at Gibraltar. *Entomologist's Monthly Magazine* 24: 175–187.

Walker J.J. 1889. Notes on ant's-nest beetles at Gibraltar and Tangier, with special reference to the *Histeridae*. *Entomologist's Monthly Magazine* 25: 374–378.

Walker J.J. 1892. A year's insect-hunting at Gibraltar III. *The Mediterranean Naturalist* 2: 248–249.

Wasmann E. 1890. Verzeichniss der von Dr. August Forel (Zürich) in Süd-Tunesien und Ost-Algerien gesammelten Ameisen-Gäste. *Deutsche Entomologische Zeitschrift* 2: 297–304.

Wasmann E. 1894. *Kritisches Verzeichnis der myrmekophilen und termitophilen Arthropoden. Mit Angabe der Lebenweise und mit Beschreibung neuer Arten*. Dames, Berlin.

Wasmann E. 1899. Neue Termitophilen und Myrmecophilen aus Indien. *Deutsche Entomologische Zeitschrift* 1: 145–180.

Wasmann E. 1905. Zur Lebensweise einiger in- und ausländischen Ameisengäste. *Zeitschrift für wissenschaftliche insektenbiologie* 1 (7): 384–390.

Wetterer J.K. 2008. Worldwide spread of the longhorn crazy ant, *Paratrechina longicornis* (Hymenoptera: Formicidae). *Myrmeological News* 11: 137–149.

Wetterer J.K. 2015. Geographic origin and spread of cosmopolitan ants (Hymenoptera: Formicidae). *Halteres* 6: 66–78.

Wetterer J.K. & Hugel S. 2008. Worldwide spread of the ant cricket *Myrmecophilus americanus*, a symbiont of the longhorn crazy ant, *Paratrechina longicornis*. *Sociobiology* 52 (1): 157–165.

Wetterer J.K. & Hugel S. 2014. First North American records of the Old World ant cricket *Myrmecophilus americanus* (Orthoptera, Myrmecophilidae). *Florida Entomologist* 97 (1): 126–129. https://doi.org/10.1653/024.097.0117

Wollaston T.V. 1854. *Insecta Maderensia*; *Being an Account of the Insects of the Islands of the Madeiran Group*. John van Voorst, London.

Zhang S.-Q., Che L.-H., Li Y., Dan L., Pang H., Ślipiński A. & Zhang P. 2018. Evolutionary history of Coleoptera revealed by extensive sampling of genes and species. *Nature Communications* 9 (1): 205. https://doi.org/10.1038/s41467-017-02644-4

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