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Cholevinae (Coleoptera: Leiodidae) of the Sierra de Guadarrama National Park, Spain: occurrence in the MSS of a siliceous landscape

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ABSTRACT

In siliceous landscapes, study of the mesovoid shallow substratum (MSS) provides interesting species records. The Cholevinae Kirby, 1837 are normally found in the forest litter, and they also are a constant element in underground habitats. However, their knowledge is totally lacking in relation to the underground realm of Sierra de Guadarrama National Park (Spain). Over the period of a year, the MSS of this mountain range was prospected to acquire first insights into the Cholevinae species established in this habitat. The prior literature was reviewed to establish an initial checklist of the Cholevinae species in the National Park, and distributional maps of the captured species were provided for the area. Twelve species of Cholevinae were captured, five of which are new records for the National Park, four for the province of Segovia, and one for the province of Madrid. All the species present wide Iberian ranges, except *Choleva* (*Choleva*) *cisteloides* (Frölich, 1799), whose new record notably expands its known distribution range. Ten species had been identified in subterranean habitats before, six of which have been previously reported in the MSS. The species accumulation curve built for the observed species richness showed that the inventory was not complete. Finally, the collection of *Choleva* (*Cholevopsis*) *punctata* Brisout, 1866 facilitated detailed study of the taxonomic characters used for the identification of *Choleva* (*C.*) *punctata* and *Choleva* (*C.*) *securiformis* Blas, 1980, allowing us to propose the synonymisation of *C. (C.) securiformis* n. syn. into *C. (C.) punctata*. This study highlights the importance of investigating hidden habitats, such as the MSS in siliceous landscapes, so as to uncover the previously unknown biodiversity, even in protected natural areas supposedly well studied.

KEY WORDS

Cholevinae,
Iberian Peninsula,
MSS,
siliceous landscapes,
subterranean habitat,
species distributions,
stone debris,
new synonymy.

RÉSUMÉ

Les Cholevinae (Coleoptera: Leiodidae) du Parc national de la Sierra de Guadarrama, Espagne : occurrence dans le MSS d'un paysage siliceux.

Dans les paysages siliceux, l'étude du milieu souterrain superficiel (MSS) fournit des signalisations intéressantes d'espèces. Les Cholevinae Kirby, 1837 se trouvent normalement dans la litière forestière et sont également un élément constant des habitats souterrains. Cependant, ils sont totalement méconnus dans le domaine souterrain du Parc national de la Sierra de Guadarrama (Espagne). Pendant un an, le MSS de cette chaîne de montagnes a été prospecté afin d'acquérir les premières informations sur les espèces de Cholevinae établies dans cet habitat. L'examen de la littérature a permis d'établir un inventaire préliminaire des espèces de Cholevinae dans le Parc national, et des cartes de répartition des espèces capturées sont fournies pour la zone. Douze espèces de Cholevinae ont été capturées, dont cinq sont de nouvelles signalisations pour le Parc national, quatre pour Segovia et une pour Madrid. Toutes les espèces présentent une vaste aire de répartition ibérique, à l'exception de *Choleva (Choleva) cisteloides* (Frölich, 1799), dont le nouveau signallement élargit notablement son aire de répartition connue. Dix espèces avaient été identifiées auparavant dans des habitats souterrains, dont six avaient déjà été signalées dans le MSS. La courbe d'accumulation des espèces construite pour la richesse en espèces observées montre que l'inventaire n'est pas complet. Enfin, la collecte de *Choleva (Cholevopsis) punctata* Brisout, 1866 a facilité l'étude détaillée des caractères taxonomiques utilisés pour l'identification des sous-espèces *Choleva (C.) punctata* et *Choleva (C.) securiformis*, ce qui nous permet de proposer la mise en synonymie de *C. (C.) securiformis* n. syn. avec *C. (C.) punctata*. Cette étude souligne l'importance d'étudier les habitats cachés, tels que le MSS dans les paysages siliceux, afin de découvrir la biodiversité jusqu'alors inconnue, même dans les zones naturelles protégées réputées bien étudiées.

MOTS CLÉS

Cholevinae,
péninsule ibérique,
MSS,
paysages siliceux,
habitat souterrain,
répartition des espèces,
débris de pierre,
synonymie nouvelle.

INTRODUCTION

The mesovoid shallow substratum (MSS) was described by Juberthie *et al.* (1980, 1981) and Ueno (1980, 1981) as a habitat formed by the subterranean tridimensional network of fissures and interstices that can be found immediately below the edaphic horizon (if it exists) and that connects the soil and the surface to the deep subterranean realm. Thus, the MSS is considered to be an ecotonal habitat located between the external environment and the deepest subterranean horizons (Moseley 2010). Organic materials and energy flow through the MSS (Gers 1998), while the interchange of fauna between the subterranean and endogean environments also occurs there (Giachino & Vailati 2017). The MSS is characterized by particular abiotic conditions, such as the complete absence of light, a saturated humid atmosphere during a greater part of the year, and the buffering of thermal fluctuations with respect to the surface, while still maintaining daily and seasonal cycles (Pipan *et al.* 2011). The MSS can be classified into four main categories based on the lithological processes from which they originate, namely the colluvial, alluvial, bedrock, and volcanic MSS (see the review in Mammola *et al.* 2016). The colluvial MSS will be investigated in the present study. It typically results from the erosion of rock walls and the subsequent deposition of rock fragments forming sloped surfaces (Juberthie *et al.* 1980), or from the actions of glaciers originating the typical moraine deposits (Juberthie 1983).

In siliceous landscapes, in which karstic phenomena do not operate and hence the caves that can typically be found in limestone substrates do not develop (Juberthie *et al.* 1980), the MSS offers a refuge to fauna with a tendency toward a hypogean life. Thus, it is common to find in the MSS a fauna

that shows morphological, behavioral or physiological adaptations for subterranean life (troglaphiles and troglobionts *sensu* Sket 2008; Mammola *et al.* 2016). However, there is also a fauna that has accidentally accessed this environment (troglonexes) from epigeal populations. Despite the logistical difficulties associated with the study of the MSS, the exploration of this habitat generally offers interesting species records (e.g., Gilgado *et al.* 2014, 2015a, c; Ortuño *et al.* 2014b, 2017; Carles-Tolrà *et al.* 2018), and it tends to reveal taxonomic novelties (e.g. Barranco *et al.* 2013; Ortuño *et al.* 2014a; Gilgado *et al.* 2015b, c, 2017; Baquero *et al.* 2017; Sendra *et al.* 2017; Akkari *et al.* 2018; for an extensive list of references, see Mammola *et al.* 2016). However, the verification of the regular presence within the MSS of some species considered to be exclusively epigeal proposes important changes with regard to ecological knowledge concerning such species (Ortuño *et al.* 2019).

The subfamily Cholevinae Kirby, 1837 (a subfamily of Leiodidae Fleming, 1821 *sensu* Lawrence & Newton 1982; Newton 1998) is a taxon notorious for its presence within the natural spaces of the soil and subsoil. With more than 1980 species having been described worldwide (Lievers & Schilthuizen 2010), it is the most diverse subfamily of Leiodidae (de Jong *et al.* 2014). During the last two centuries, and especially in the last few decades, the studies devoted to this group in the Ibero-Balearic region have substantially increased, so at present the Cholevinae of this region is a relatively well-known group (Salgado *et al.* 2008, Fresneda & Salgado 2016). One reason for the growing research interest in this subfamily concerns the high number of species with endogean or hypogean habits as well as their remarkable degree of endemism in not particularly extensive areas (Juberthie & Decu 1998).

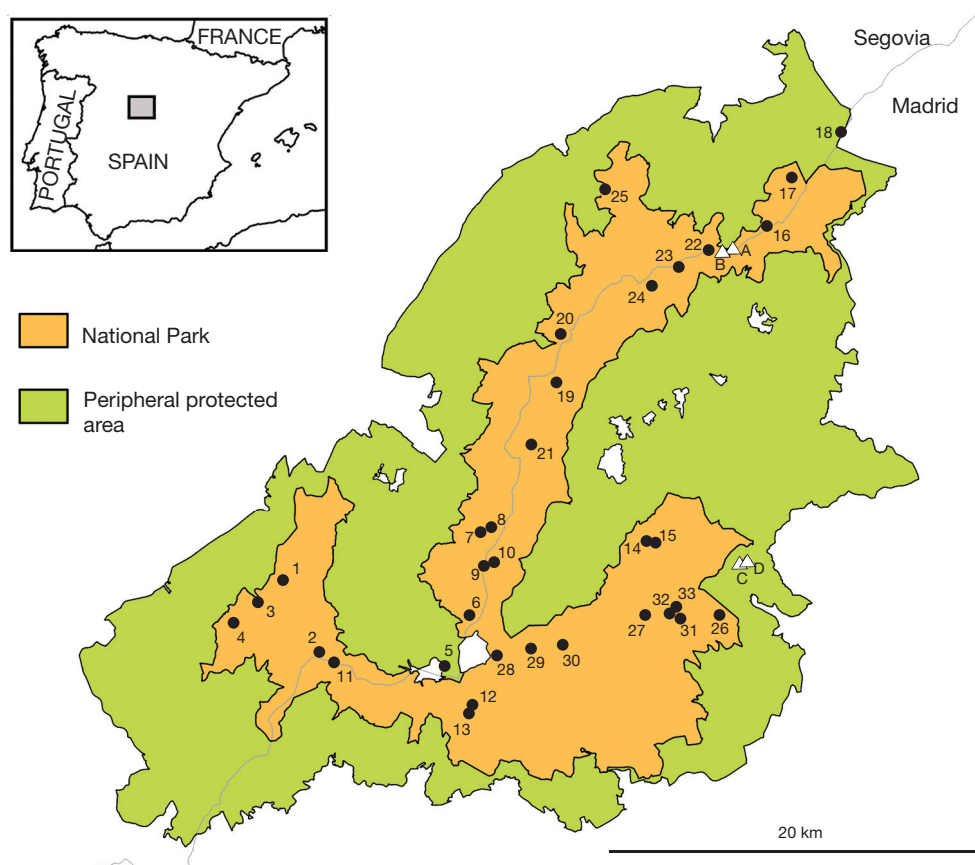


FIG. 1. — Locations of the 33 scree slopes and four talus that were sampled in the Sierra de Guadarrama National Park and in the surrounding area. Symbols: ●, subterranean sampling devices (SSDs); Δ, talus pitfall traps (TSPs).

Although the majority of Cholevinæ underground sampling has been conducted in caves (see references in Salgado *et al.* 2008), since the discovery of the MSS, Cholevinæ sampling has been extended to other subterranean spaces (Decu *et al.* 2005; Nitzu *et al.* 2006, 2010, 2014; Rendoš *et al.* 2012; Ortuño *et al.* 2013; Langourov *et al.* 2014; Jiménez-Valverde *et al.* 2015; Mammola *et al.* 2017).

The main objective of the present study is to inventory the species of Cholevinæ that occur in the siliceous MSS of the Sierra de Guadarrama National Park, Spain. Importantly, and due to the taxonomic nature of the study, a problem arises with regard to the validity of *Choleva* (*Cholevopsis*) *punctata securiformis* Blas, 1980, which is solved by proposing its synonymy with the monotypic species.

MATERIAL AND METHODS

STUDY AREA

The study area is located in the Sierra de Guadarrama National Park (Iberian Peninsula). This recently created National Park (BOE 2013) is located in the Central System mountain range, between the provinces of Madrid and Segovia (Fig. 1). The National Park covers an expanse of 33960 hectares (BOE 2013), and it is surrounded by a peripheral protected area (PPA) of

some 62687 hectares (<https://www.parquenacionalsierraguadarrama.es/en/regulations/zoning>). The National Park shows different lithologies, although orthogneiss and metamorphic quartz-feldspathic rocks represent the predominant formations (Vialeto *et al.* 1987). The fragmentation of these rocks and the subsequent movement of the rocky materials by glacial action in the past, as well as the fragmentation by weathering, have led to the formation of colluvial scree slopes typical of montane areas (Sanz 1986). The climate can be mainly categorized as cold continental Mediterranean, since it has a short, dry, and chilly summer season and a long, cold winter (<https://www.parquenacionalsierraguadarrama.es/en/nature/climate>). Precipitation in the highest elevations occurs frequently in the form of snow, which forms a layer that lasts all winter and for part of the spring season (Salazar Rincón & Vía García 2003).

SAMPLING

Thirty-three scree slopes (sampled by means of vertical access) were selected from across the Sierra de Guadarrama National Park with the intention of covering the majority of the geographical area (Figs 1; 2A, B). Two scree slopes covered with pine forest (*Pinus sylvestris*), with horizontal access for sampling available via a talus, were also selected (Figs 1; 2C, D; Table 1). Most of the sampled sites were located within the National Park, although a few were within the PPA (see

TABLE 1. — Location of the traps. Provinces: **S**, Segovia; **M**, Madrid.

Ssd	(Province) Toponymy	Utm (10 × 10 km)	Geographical coordinates	Altitude (m asl.)	Sampling Period	
SSD-1	(S) Cancho del Río Peces	30TVL02	40°49'47.42"N, 4°5'18.95"W	1606	20.V.2015	21.IX.2016
SSD-1 (0.5 m)						
SSD-2	(S) Corrales de la Majada Minguete	30TVL11	40°47'45.00"N, 4°3'57.98"W	1818	20.V.2015	21.IX.2016
SSD-2 (0.5 m)						
SSD-3	(S) Mujer Muerta	30TVL01	40°49'7.57"N, 4°6'14.31"W	1622	21.V.2015	21.IX.2016
SSD-3 (0.5 m)						
SSD-4	(S) Majada Conejo	30TVL01	40°48'34.99"N, 4°7'6.45"W	1685	21.V.2015	21.IX.2016
SSD-4 (0.5 m)						
SSD-5	(S) Arroyo Seco	30TVL11	40°47'22.26"N, 3°59'16.05"W	1923	27.V.2015	22.IX.2016
SSD-6	(S) La Pedriza	30TVL11	40°48'52.12"N, 3°58'20.87"W	1787	27.V.2015	22.IX.2016
SSD-7	(S) Majada Hambrienta	30TVL12	40°51'12.19"N, 3°57'59.95"W	1994	2.VI.2015	21.IX.2016
SSD-8	(S) Majada Aranguez	30TVL12	40°51'20.00"N, 3°57'35.65"W	2071	2.VI.2015	22.IX.2016
SSD-9	(M) Dos Hermanas	30TVL12	40°50'14.60"N, 3°57'50.33"W	2208	3.VI.2015	22.IX.2016
SSD-10	(M) Hoya de la Laguna Grande	30TVL12	40°50'22.35"N, 3°57'31.01"W	2049	3.VI.2015	22.IX.2016
SSD-11	(M) Cerro Ventoso	30TVL11	40°47'28.36"N, 4°3'22.64"W	1876	9.VI.2015	21.IX.2016
SSD-12	(M) Collado del Piornal	30TVL11	40°46'17.26"N, 3°58'16.14"W	2102	9.VI.2015	14.X.2016
SSD-13	(M) Cuerda de la Buitrera – Cuerda de los Almorchones	30TVL11	40°46'6.74"N, 3°58'20.51"W	2113	10.VI.2015	14.X.2016
SSD-14	(M) El Purgatorio	30TVL22	40°50'58.83"N, 3°51'37.83"W	1406	18.VI.2015	28.IX.2016
SSD-15	(M) Hueco de los Ángeles	30TVL22	40°50'58.59"N, 3°51'45.24"W	1375	18.VI.2015	28.IX.2016
SSD-16	(S) Las Revueltas – Los Horcos	30TVL33	0°48'51.94"N, 3°58'20.94"W	1956	23.VI.2015	29.IX.2016
SSD-17	(S) Peña del Buitre	30TVL34	41°1'16.88"N, 3°46'36.03"W	1976	23.VI.2015	29.IX.2016
SSD-18	(S) Los Loberos	30TVL34	41°2'36.37"N, 3°44'45.10"W	1885	23.VI.2015	29.IX.2016
SSD-19	(M) La Gelecha . La Flecha	30TVL23	40°55'25.95"N, 3°55'16.92"W	1866	24.VI.2015	29.IX.2016
SSD-20	(S) Cerro de Navahonda	30TVL23	40°56'49.73"N, 3°55'6.23"W	1937	24.VI.2015	29.IX.2016
SSD-21	(M) El Paredón	30TVL22	40°53'40.48"N, 3°56'10.13"W	1891	24.VI.2015	29.IX.2016
SSD-22	(S) Alto del Puerto	30TVL33	40°59'12.52"N, 3°49'39.29"W	1995	24.VI.2015	22.IX.2016
SSD-23	(M) Circo del Pico Nevero	30TVL23	40°58'42.11"N, 3°50'44.00"W	2144	25.VI.2015	22.IX.2016
SSD-24	(M) Peñacabra	30TVL23	40°58'10.66"N, 3°51'42.44"W	2042	25.VI.2015	6.X.2016
SSD-25	(S) Arroyo del Charco - La Cepa	30TVL24	41°0'54.08"N, 3°53'31.92"W	1731	2.VII.2015	6.X.2016
SSD-26	(M) La Najarra - Cuatro Calles	30TVL31	40°48'57.05"N, 3°49'8.03"W	1890	2.VII.2015	28.IX.2016
SSD-27	(M) Bailanderos	30TVL21	40°48'53.80"N, 3°51'49.95"W	2101	2.VII.2015	28.IX.2016
SSD-28	(M) Collado de Valdemartín	30TVL11	40°47'43.48"N, 3°57'20.81"W	2156	3.VII.2015	14.X.2016
SSD-29	(M) Cabeza de Hierro Mayor – Cabeza de Hierro Menor	30TVL21	40°47'54.79"N, 3°56'6.45"W	2301	3.VII.2015	14.X.2016
SSD-30	(M) Collado de Peña Vaqueros (Loma de Pandasco)	30TVL21	40°48'2.32"N, 3°54'58.07"W	2233	3.VII.2015	14.X.2016
SSD-31	(M) Collado de la Najarra	30TVL21	40°48'49.43"N, 3°50'35.18"W	1946	9.VII.2015	6.X.2016
SSD-32	(M) Arroyo de La Najarra	30TVL21	40°48'59.57"N, 3°50'51.76"W	1948	9.VII.2015	28.IX.2016
SSD-33	(M) Arroyo de La Najarra	30TVL21	40°49'3.43"N, 3°50'46.59"W	1819	9.VII.2015	28.IX.2016
TSP-A	(S) Puerto de Navafria	30TVL33	40°59'12.92"N, 3°48'51.60"W	1780	24.VI.2015	22.IX.2016
TSP-B	(S) Puerto de Navafria	30TVL33	40°59'12.84"N, 3°48'52.57"W	1780	24.VI.2015	13.VI.2016
TSP-C	(M) Arroyo Reajo Cazado	30TVL32	40°50'28.98"N, 3°48'11.31"W	1538	30.10.2015	5.IV.2017
TSP-D	(M) Arroyo Reajo Cazado	30TVL32	40°50'27.89"N, 3°48'12.46"W	1520	30.10.2015	5.IV.2017

Fig. 1). The sampling was mainly performed using subterranean sampling devices (SSD) similar to those used in other MSS surveys conducted in Iberian enclaves (Barranco *et al.* 2013; Ortuño *et al.* 2013, 2014a; Gilgado *et al.* 2014; Jiménez-Valverde *et al.* 2015). Briefly, these devices consist of a pitfall trap located at the bottom of a buried PVC cylinder one metre long (Fig. 2B). In the case of four scree slopes (locations 1-4, see Fig. 1; Table 1), double SSDs (1 m and 0.5 m deep) were installed. A full description of the traps, which were specifically designed to collect species inhabiting the MSS, can be found in Baquero *et al.* (2017). Furthermore, four talus slope pitfall traps (TSPs: A-D, see Figs 1; 2D; Table 1) similar to those used by Giachino & Vailati (2010), which contained the same type of preservative and bait as the SSDs, were installed in the MSS in two different localities. To do this, two horizontal holes of approximately 80 cm long were dug and, once the pitfall traps were placed inside, the holes were closed.

The sampling period ran from 20 May 2015 to 14 October 2016 (except for TSP-C and TSP-D, for which the sampling period ran from 30 October 2016 to 5 April 2017), with three collection moments: 1) during the autumn period; 2) during the last month of spring and the first month of summer; and 3) again during the autumn period (except for TSP-C and TSP-D).

The biological samples were transported to the laboratory. The adult Cholevinidae specimens were separated from the rest of the material and stored in vials filled in 70% ethanol slightly acidulated with acetic acid. The species nomenclature used in this study follows that used by Fresneda & Salgado (2016), while the specimens were identified to the species level using Salgado *et al.* (2008) and Fresneda *et al.* (2019). Specimens are deposited at the Department of Life Sciences, Faculty of Sciences, University of Alcalá, Alcalá de Henares, Madrid, Spain (V. M. Ortuño's collection) and at the Muséum national d'Histoire naturelle, Paris, France.



FIG. 2. — Sampled habitats and sampling devices: **A**, a typical scree slope; **B**, placement of a subterranean sampling device (SSD); **C**, a talus on a scree slope; **D**, placement of a talus slope pitfall traps (TSP).

DISTRIBUTION OF THE SPECIES

The chorotype classification proposed by Vigna Taglianti *et al.* (1992) was used to classify each species based on the information available via Fauna Europaea (Jong *et al.* 2014) and the Cholevinae Iberian catalogue (Fresneda & Salgado 2016). New species records for the Sierra de Guadarrama National Park, Segovia, or Madrid, were checked using the literature records from before 2020. Furthermore, the literature concerning the captured species was reviewed to check whether the species had previously been reported in the MSS. Using data records from the literature, a checklist of Cholevinae for the Sierra de Guadarrama National Park was compiled. The records were referred to the Iberian 10 × 10 km Universal Transversal Mercator (UTM) grid. Those records that only offered a toponym were assigned to the most probable UTM cell, and a few imprecise records that could not be assigned to a UTM cell were discarded.

ASSESSMENT OF THE INVENTORY COMPLETENESS

To evaluate the completeness of the inventory, a species accumulation curve was constructed using the 33 SSDs of one metre long. The curve was built using the analytical approach based on the Bernoulli product model for sample-based rarefaction proposed by Colwell *et al.* (2012). Six non-parametric species richness estimators were also calculated, namely Chao1, Chao2, first-order Jackknife (Jack1), second-order Jackknife (Jack2), ICE, and ACE (Colwell & Coddington 1994). All the calculations were performed using EstimateS version 9.1.0 software (Colwell 2013).

STUDY OF *CHOLEVA* (*CHOLEVOPSIS*) *PUNCTATA* MATERIAL

The taxonomic study of *Choleva* (*Cholevopsis*) *punctata* Brisout, 1866 required a comparative analysis of the qualitative and quantitative morphological characters. To evalu-

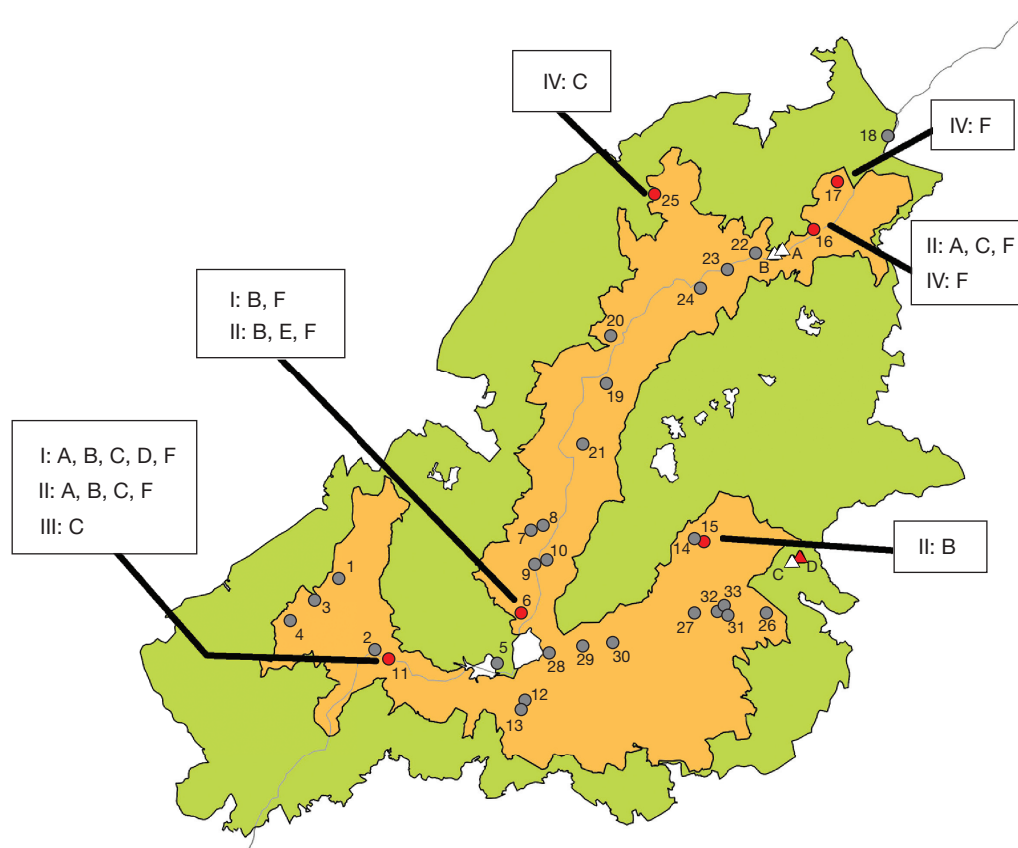


FIG. 3. — Distribution of *Choleva (Cholevopsis) punctata* Brisout, 1866 in the MSS of the Sierra de Guadarrama National Park. Legends and symbols: ● subterranean sampling devices (SSDs); Δ, talus pitfall traps (TSP); ● and ▲ presence of *C. (C.) punctata*. The combination of the different manifestations of the aedeagus with the different morphologies of the metatrochanter is shown for each SSD following the classification of Figs 6; 7.

ate the intrapopulation variability of the characters under study, all the male adults (96 specimens) from all SSDs and the female adults from SSD-11 (48 specimens) were analyzed in detail. First, the male specimens were dissected, the aedeagi were extracted, and microscopic preparations were made by placing them on acetate sheets with dimethyl hydantoin formaldehyde (DMHF) to which chloral hydrate was added. Second, the aedeagi were categorized according to the disposition (extroversion) of the various parts of the inner sac with respect to the median lobe. Third, the morphological variability of the trochanters was categorized. Finally, the diversity in the expression of all these male characters was photographed using a stereomicroscope (LEICA EZ4D). The interpopulation variability was analyzed by these characters in the adults obtained between different localities (see Fig. 3). Ten female specimens were randomly selected for the genitalia study, for which the dissection, digestion, staining, and preparation protocol proposed by Ortuño *et al.* (1992, 2003, 2005) was followed. The maximum width of the pronotum (PWmax), the middle width of the pronotum (PWmid), and the pronotum length (PL) were measured in all the specimens. To test for significant differences between males and females in terms of the three morphological measures, three Welch's t-tests were performed.

ABBREVIATIONS AND CONVENTIONS

bur	bursa copulatrix;
ex.exx	adult specimen;
gcox	gonocoxite;
gscov	gonosubcoxite;
ltg	laterotergite;
mtg	metatergite;
ovi	odd oviduct;
spe	spermatheca;
spg	spermathecal gland;
vag	vagina.

Deposit

Coll. V. M. O.	V. M. Ortuño's collection, Department of Life Sciences, Faculty of Sciences, University of Alcalá, Alcalá de Henares, Madrid;
MNHN	Muséum national d'Histoire naturelle, Paris.

RESULTS

In total, 4266 adult specimens of Cholevinae pertaining to 12 species were collected, with two of the species being present only in the TSPs (Appendix 1). At the same time, 994 larva specimens of Cholevinae were collected, but they have not been included in this work due to the impossibility of identifying them at a specific or generic level.

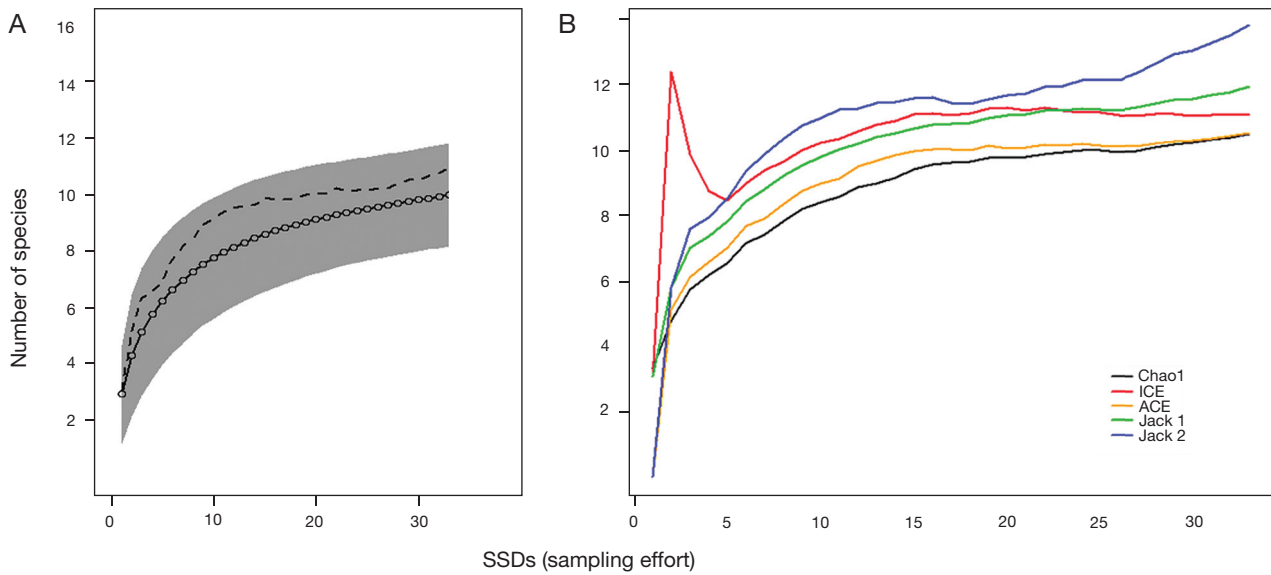


FIG. 4. — Species accumulation curves for the complete inventory of the Sierra de Guadarrama National Park: **A**, sample-based species accumulation curve using the subterranean sampling devices (SSDs) as effort units (empty circles); 95% confidence interval as grey bands, and Chao2 curve (stripped line); **B**, non-parametric richness estimators.

SUMMARY OF RESULTS

All the species, without taking into account the rare or casual species, showed adults with maximum activity during the summer-autumn period, while their abundance decreased considerably during the rest of the year (Appendix 1). The exception to this was *C. (C.) cisteloides* (Frolich, 1799), which was only observed during the second sampling (September–November 2015 to May–July 2016). *Speonemadus angusticollis* (Kraatz, 1870), with 1915 specimens, and *C. fuscus fuscus* (Panzer, 1794), with 1770 specimens, were the two most abundant species. *Attumbra josephinae josephinae* (Saulcy, 1862), with one specimen, and *C. (A.) marqueti* Fairmaire, 1857, with two specimens, were the rarest species (Appendix 1).

The two most abundant species in this study, together with *Sepeonemadus vandalitiae* (Heyden, 1870) and *P. (P.) tenuicornis tenuicornis* (Rosenhauer, 1856) (Appendix 1), were also the most widely distributed across the study area (Appendix 2). The remaining of the species showed more limited distributions (Appendices 1; 2). All the species present wide Iberian ranges (Fresneda & Salgado 2016), and only *C. (C.) cisteloides* notably expands its known distribution range. Additionally, *C. (C.) cisteloides* is the only species not previously recorded in the province of Madrid. Four species are new records for the province of Segovia, while five species are new additions to the checklist for the Sierra de Guadarrama National Park, whose inventory of Cholevinæ hence increases from 13 to 18 species (Fig. 3). Three species are endemic to the Iberian region, namely *S. clathratus*, *S. angusticollis*, and *C. (C.) punctata*, and they coexist in the MSS with other species that have a wider biogeographical category. None of the species found can be considered hypogean, although with the exception of *A. josephinae* and *C. (A.) marqueti*, the rest of the species (83.33%) had previously been reported in subterranean

habitats, four of them in caves (33.3%), one in the MSS (8.33%), and five in both habitats (41.6%).

The species accumulation curve ended before reaching the asymptote (Fig. 4A), which indicates that the inventory was not complete, although the steepness of the sample-based curve – as well as of the Chao2 curve – was not notable. With regard to the non-parametric estimators, some of the curves showed a greater tendency toward stabilisation (ICE and ACE) than others (Jack1 and Jack2) (Fig. 4A, B). The estimated degree of completeness of the inventory ranged from 72.35% to 100% (estimated number of species: Jack2 = 13.82, Jack1 = 11.94, Chao2 = 10.97, ICE = 11.07, ACE = 10.51, Chao1 = 10.00).

SYSTEMATIC ACCOUNT

Family LEIODIDAE Fleming, 1821
Subfamily CHOLEVINAE Kirby, 1837
Tribe Anemadini (Hatch, 1928)
Genus *Speonemadus* Jeannel, 1922

Speonemadus angusticollis (Kraatz, 1870)
(Fig. 5A)

Choleva angusticollis Kraatz, 1870: 90.

Catops angusticollis – Marseul 1884: 69.

Anemadus angusticollis – Reitter 1885: 60.

Speonemadus angusticollis – Jeannel 1936: 220.

TYPE LOCALITY. — Spain: Córdoba (Kraatz 1870).

DISTRIBUTION. — (IBER) Iberian endemism, distributed in the southern half of the Iberian Peninsula.

MATERIAL COLLECTED. — 1814 exx.

Spain • 65 exx; SSD-1; 17.IX.2015; coll. V. M. O. • 1 ex; same locality; 24.V.2016; coll. V. M. O. • 7 exx; same locality; 21.IX.2016; coll. V. M. O. • 17 exx; SSD-3; 17.9.2015; coll. V. M. O. • 1 ex; same locality; 26.V.2016; coll. V. M. O. • 7 exx; same locality; 21.IX.2016; coll. V. M. O. • 16 exx; SSD-4; 17.IX.2015; coll. V. M. O. • 7 exx; same locality; 26.V.2016; coll. V. M. O. • 11 exx; same locality; 21.IX.2016; coll. V. M. O. • 57 exx; SSD-5; 22.IX.2015; coll. V. M. O. • 2 exx; same locality; 24.V.2016; coll. V. M. O. • 19 exx; same locality; 22.IX.2016; coll. V. M. O. • 5 exx; SSD-6; 22.IX.2015; coll. V. M. O. • 4 exx; same locality; 24.V.2016; coll. V. M. O. • 4 exx; same locality; 22.IX.2016; coll. V. M. O. • 29 exx; SSD-7; 17.IX.2015; coll. V. M. O. • 1 ex; same locality; 28.VI.2016; coll. V. M. O. • 10 exx; same locality; 21.IX.2016; coll. V. M. O. • 11 exx; SSD-8; 17.IX.2015; coll. V. M. O. • 1 ex; same locality; 28.VI.2016; coll. V. M. O. • 12 exx; same locality; 22.IX.2016; coll. V. M. O. • 11 exx; SSD-9; 5.X.2015; coll. V. M. O. • 20 exx; same locality; 22.IX.2016; coll. V. M. O. • 11 exx; SSD-11; 17.IX.2015; coll. V. M. O. • 2 exx; SSD-13; 14.X.2016; coll. V. M. O. • 1 ex; SSD-14; 2.VI.2016; coll. V. M. O. • 3 exx; SSD-17; 29.IX.2016; coll. V. M. O. • 2 exx; SSD-19; 6.X.2015; coll. V. M. O. • 25 exx; SSD-20; 6.X.2015; coll. V. M. O. • 3 exx; same locality; 9.VI.2016; coll. V. M. O. • 43 exx; same locality; 29.IX.2016; coll. V. M. O. • 14 exx; SSD-21; 6.X.2015; coll. V. M. O. • 4 exx; same locality; 29.IX.2016; coll. V. M. O. • 161 exx; SSD-23; 6.X.2015; coll. V. M. O. • 7 exx; same locality; 22.IX.2016; coll. V. M. O. • 320 exx; SSD-24; 22.X.2015; coll. V. M. O. • 4 exx; same locality; 9.VI.2016; coll. V. M. O. • 172 exx; same locality; 6.X.2016; coll. V. M. O. • 23 exx; SSD-30; 6.XI.2015; coll. V. M. O. • 48 exx; same locality; 13.VII.2016; coll. V. M. O. • 20 exx; same locality; 14.X.2016; coll. V. M. O. • 1 ex; SSD-31; 22.X.2015; coll. V. M. O. • 1 ex; same locality; 8.VII.2016; coll. V. M. O. • 5 exx; same locality; 6.X.2016; coll. V. M. O. • 1 ex; SSD-32; 22.X.2015; coll. V. M. O. • 16 exx; SSD-33; 22.X.2015; coll. V. M. O. • 3 exx; same locality; 8.VII.2016; coll. V. M. O. • 1 ex; same locality; 28.IX.2016; coll. V. M. O. • 225 exx; TSP-A; 22.IX.2015; coll. V. M. O. • 20 exx; same locality and date; MNHN • 41 exx; same locality; 13.VI.2016; coll. V. M. O. • 329 exx; same locality; 22.IX.2016; coll. V. M. O.

REMARK

First record for Segovia province. Previously reported in caves (see Fresneda & Salgado 2016), this is the first record in the MSS.

Speonemadus clathratus (Perris, 1864) (Fig. 5B)

Catops clathratus Perris, 1864: 281.

Anemadus clathratus – Uhagón 1890: 34.

Anemadus transversostriatus Reitter, 1885: 60 (*nec* Murray).

Hormosacus clathratus – Jeannel 1936: 214.

Speonemadus clathratus – Giachino & Vailati 1993: 197.

TYPE LOCALITY. — Spain: Navacerrada and Peñalara Sierra de Guadarrama (Perris 1864).

DISTRIBUTION. — (IBER) Iberian endemism, widespread in the Iberian Peninsula.

MATERIAL COLLECTED. — 21 exx.

Spain • 2 exx; TSP-A; 22.IX.2015; coll. V. M. O. • 4 exx; same locality; 13.VI.2016; MNHN • 3 exx; same locality; 22.IX.2016;

coll. V. M. O. • 4 exx; TSP-B; 22.IX.2015; coll. V. M. O. • 8 exx; same locality; 13.VI.2016; coll. V. M. O.

REMARKS

Previously reported in caves (see Fresneda & Salgado 2016), this is the first record in the MSS.

Speonemadus vandalitiae (Heyden, 1870) (Fig. 5C)

Catops vandalitiae Heyden, 1870: 97.

Ptomaphagus vandalitiae – Heyden 1883: 368.

Anemadus vandalitiae – Uhagón 1890: 32.

Hormosacus vandalitiae – Jeannel 1936: 214.

Hormosacus vandalitiae pyrenaeus Jeannel, 1936: 214.

Speonemadus vandalitiae – Giachino & Vailati 1993: 183.

TYPE LOCALITY. — Spain: Andalucía, Ronda, Sierra de la Nieve (Heyden 1870).

DISTRIBUTION. — (WMED) Present in French Atlantic Pyrenees, Sicily and North Africa. Wide distribution in the Iberian Peninsula and also present in the Balearic Islands.

MATERIAL COLLECTED. — 286 exx.

Spain • 1 ex; SSD-2 (0.5m); 21.IX.2016; coll. V. M. O. • 2 exx; SSD-1; 24.V.2016; coll. V. M. O. • 1 ex; same locality; 21.IX.2016; coll. V. M. O. • 1 ex; SSD-2; 21.IX.2016; coll. V. M. O. • 2 exx; SSD-3; 17.IX.2015; coll. V. M. O. • 1 ex; same locality; 26.V.2016; coll. V. M. O. • 2 exx; SSD-4; 17.IX.2015; coll. V. M. O. • 1 ex; same locality; 26.V.2016; coll. V. M. O. • 13 exx; same locality; 21.IX.2016; coll. V. M. O. • 15 exx; SSD-6; 22.IX.2015; coll. V. M. O. • 4 exx; same locality; 24.V.2016; coll. V. M. O. • 25 exx; same locality; 22.IX.2016; coll. V. M. O. • 1 ex; SSD-8; 28.VI.2016; coll. V. M. O. • 1 ex; SSD-11; 24.V.2016; coll. V. M. O. • 1 ex; same locality; 21.IX.2016; coll. V. M. O. • 1 ex; SSD-12; 26.V.2016; coll. V. M. O. • 12 exx; SSD-14; 2.VI.2016; coll. V. M. O. • 6 exx; SSD-15; 2.VI.2016; coll. V. M. O. • 14 exx; same locality; 28.IX.2016; coll. V. M. O. • 13 exx; SSD-16; 7.X.2015; MNHN • 2 exx; same locality; 2.VI.2016; MNHN • 50 exx; same locality; 29.IX.2016; coll. V. M. O. • 1 ex; SSD-17; 7.X.2015; coll. V. M. O. • 4 exx; same locality; 2.VI.2016; coll. V. M. O. • 1 ex; SSD-18; 2.VI.2016; coll. V. M. O. • 1 ex; SSD-20; 29.IX.2016; coll. V. M. O. • 1 ex; SSD-22; 22.IX.2015; coll. V. M. O. • 1 ex; same locality; 13.VI.2016; coll. V. M. O. • 3 exx; same locality; 22.IX.2016; coll. V. M. O. • 5 exx; SSD-23; 6.X.2015; coll. V. M. O. • 5 exx; same locality; 13.VI.2016; coll. V. M. O. • 2 exx; same locality; 22.IX.2016; coll. V. M. O. • 2 exx; SSD-25; 22.X.2015; coll. V. M. O. • 6 exx; same locality; 9.VI.2016; MNHN • 24 exx; TSP-A; 22.IX.2016; coll. V. M. O. • 1 ex; TSP-C; 13.VI.2016; coll. V. M. O. • 24 exx; same locality; 6.X.2016; coll. V. M. O. • 2 exx; same locality; 5.IV.2017; coll. V. M. O. • 1 ex; TSP-D; 13.VI.2016; coll. V. M. O. • 7 exx; same locality; 6.X.2016; coll. V. M. O.

REMARK

Previously reported in caves (see Fresneda & Salgado 2016) and the MSS (Fresneda *et al.* 2007; Sáez Bolaño & Blanco Villero 2010).



FIG. 5. — Habitus of Cholevinae Kirby, 1837 species captured in this study: **A**, *Speonemadus angusticollis* (Kraatz, 1870); **B**, *Speonemadus clathratus* (Perris, 1864); **C**, *Speonemadus vandalitiae* (Heyden, 1870); **D**, *Attumbra josephinae josephinae* (Saulcy, 1862); **E**, *Catops fuliginosus* Erichson, 1837; **F**, *Catops fuscus* (Panzer, 1794); **G**, *Catopsimorphus* (*Attiscurra*) *marqueti* Fairmaire, 1857; **H**, *Catopsimorphus* (*Weiratherella*) *rougeti* Saulcy, 1864; **I**, *Choleva* (*Choleva*) *cistelooides* (Frolich, 1799); **J**, *Choleva* (*Cholevopsis*) *punctata* Brisout, 1866; **K**, *Sciodrepoides watsoni watsoni* (Spence, 1815); **L**, *Ptomaphagus* (*Ptomaphagus*) *tenuicornis tenuicornis* (Rosenhauer, 1856). Scale bars: 1 mm.

Tribe Cholevini Kirby, 1837
Genus *Attumbra* Des Gozis, 1886

Attumbra josephinae josephinae
(Saulcy, 1862)
(Fig. 5D)

Catopsimorphus josephinae Saulcy, 1862: 286.

Attumbra josephinae – Des Gozis 1886: 17.

TYPE LOCALITY. — France: Pyrénées-Orientales, Port-Vendres (Saulcy 1862).

DISTRIBUTION. — (SOER) Known from France and Corsica Island. Present in distant locations in Spain.

MATERIAL COLLECTED. — 1 ex.
Spain • 1 ex; SSD-33; 22.X.2015; coll. V. M. O.

REMARK

First record for Sierra de Guadarrama National Park, also first record in the hypogean environment.

Genus *Catops* Paykull, 1798

Catops fuliginosus Erichson, 1837
(Fig. 5E)

Catops fuliginosus Erichson, 1837: 239.

Catops nigricans var. *minor* Kraatz, 1852: 429.

Catops cognatus Rey, 1889: 4.

Catops fuliginosus inermis Jeannel, 1934: 16.

Catops fuliginosus caucasicus Jeannel, 1936: 42.

Catops fuliginosus claudeli Coiffait, 1954: 115.

Catops mateui Coiffait, 1954: 23, 24.

Catops bonadonai Coiffait, 1954: 116.

Catops franzi Jeannel, 1961: 59.

TYPE LOCALITY. — Germany: “Mark Brandenburg” (Erichson 1837).

DISTRIBUTION. — (EURP) This species is wide extended throughout Europe and Asia Minor. It also has a wide Iberian distribution.

MATERIAL COLLECTED. — 5 exx.
Spain • 1 ex; SSD-12; 14.X.2016; coll. V. M. O. • 1 ex; SSD-14; 2.VI.2016; coll. V. M. O. • 2 exx; SSD-21; 29.IX.2016; MNHN • 1 ex; SSD-23; 13.VI.2016; coll. V. M. O.

REMARK

First record for Sierra de Guadarrama National Park. Previously reported in caves (see Fresneda & Salgado 2016) and the MSS (Fresneda *et al.* 2007, 2010; Sáez Bolaño & Blanco Villero 2010; Rendoš *et al.* 2012; Langourov *et al.* 2014; Mammola *et al.* 2017).

Catops fuscus fuscus (Panzer, 1794)
(Fig. 5F)

Helops fuscus Panzer, 1794: 1.

Catops sericeus Paykull, 1798: 342.

Catops rufescens Fabricius, 1801: 563.

Choleva festinans Spence, 1815: 145.

Choleva agilis Spence, 1815: 140.

Catops fuscus – Erichson 1837: 235.

TYPE LOCALITY. — Germany: Saxony, Dresden (Panzer 1794).

DISTRIBUTION. — (EURP) Species widely distributed in Europe, and North Africa, also present in Afghanistan. The distribution in the Iberian Peninsula is wide, although the species is unknown from the western part.

MATERIAL COLLECTED. — 1770 exx.

Spain • 2 exx; SSD-2 (0.5m); 17.IX.2015; coll. V. M. O. • 1 ex; same locality; 24.V.2016; coll. V. M. O. • 17 exx; same locality; 21.IX.2016; coll. V. M. O. • 1 ex; SSD-4 (0.5m); 26.V.2016; coll. V. M. O. • 1 ex; SSD-1; 17.IX.2015; coll. V. M. O. • 3 exx; 24.V.2016; same locality; coll. V. M. O. • 58 exx; SSD-2; 17.IX.2015; coll. V. M. O. • 10 exx; same locality; 24.V.2016; coll. V. M. O. • 45 exx; same locality; 21.IX.2016; coll. V. M. O. • 2 exx; SSD-3; 26.V.2016; coll. V. M. O. • 2 exx; same locality; 21.IX.2016; coll. V. M. O. • 47 exx; SSD-5; 22.IX.2015 9 exx; same locality; 24.V.2016 45 exx; same locality; 22.IX.2016; coll. V. M. O. • 12 exx; SSD-6; 22.IX.2015; coll. V. M. O. • 5 exx; same locality; 24.V.2016; coll. V. M. O. • 19 exx; same locality; 22.IX.2016; coll. V. M. O. • 16 exx; SSD-7; 17.IX.2015; coll. V. M. O. • 19 exx; same locality; 28.VI.2016; coll. V. M. O. • 9 exx; same locality; 21.IX.2016; coll. V. M. O. • 2 exx; SSD-8; 17.IX.2015; coll. V. M. O. • 2 exx; same locality; 28.VI.2016; coll. V. M. O. • 10 exx; same locality; 22.IX.2016; coll. V. M. O. • 1 ex; SSD-9; 5.X.2015; coll. V. M. O. • 2 exx; same locality; 28.VI.2016; coll. V. M. O. • 1 ex; SSD-10; 5.X.2015; coll. V. M. O. • 1 ex; same locality; 28.VI.2016; coll. V. M. O. • 2 exx; SSD-11; 17.IX.2015; coll. V. M. O. • 3 exx; same locality; 24.V.2016; coll. V. M. O. • 2 exx; SSD-12; 14.X.2016; coll. V. M. O. • 1 ex; SSD-13; 26.V.2016; coll. V. M. O. • 4 exx; SSD-14; 2.VI.2016; coll. V. M. O. • 1 ex; SSD-15; 2.VI.2016; coll. V. M. O. • 40 exx; SSD-16; 7.X.2015; coll. V. M. O. • 14 exx; same locality; 2.VI.2016; coll. V. M. O. • 21 exx; same locality; 29.IX.2016; coll. V. M. O. • 47 exx; SSD-17; 7.X.2015; coll. V. M. O. • 18 exx; same locality; 2.VI.2016; coll. V. M. O. • 42 exx; same locality; 29.IX.2016; coll. V. M. O. • 76 exx; SSD-18; 7.X.2015; coll. V. M. O. • 31 exx; same locality; 2.VI.2016; coll. V. M. O. • 25 exx; same locality; 29.IX.2016; coll. V. M. O. • 40 exx; SSD-19; 6.X.2015; coll. V. M. O. • 21 exx; same locality; 9.VI.2016; coll. V. M. O. • 7 exx; same locality; 29.IX.2016; coll. V. M. O. • 129 exx; SSD-20; 6.X.2015; coll. V. M. O. • 23 exx; same locality; 9.VI.2016; coll. V. M. O. • 67 exx; same locality; 29.IX.2016; coll. V. M. O. • 378 exx; SSD-21; 6.X.2015; coll. V. M. O. • 20 exx; same locality and date; MNHN • 83 exx; same locality; 9.VI.2016; coll. V. M. O. • 118 exx; same locality; 29.IX.2016; coll. V. M. O. • 21 exx; SSD-22; 22.IX.2015; coll. V. M. O. • 14 exx; same locality; 13.VI.2016; coll. V. M. O. • 34 exx; same locality; 22.IX.2016; coll. V. M. O. • 17 exx; SSD-23; 6.X.2015; coll. V. M. O. • 13 exx; same locality; 13.VI.2016; coll. V. M. O. • 14 exx; same locality; 22.IX.2016; coll. V. M. O. • 3 exx; SSD-24; 22.X.2015; coll. V. M. O. • 7 exx; SSD-25; 22.X.2015; coll. V. M. O. • 25 exx; same locality; 9.VI.2016; coll. V. M. O. • 4 exx; same locality; 6.X.2016; coll. V. M. O. • 1 ex; SSD-26; 8.VII.2016; coll. V. M. O. • 8 exx; SSD-28; 6.XI.2015; coll. V. M. O. • 1 ex; same locality; 14.X.2016;

coll. V. M. O. • 2 exx; SSD-29; 6.XI.2015; coll. V. M. O. • 1 ex; same locality; 14.X.2016; coll. V. M. O. • 2 exx; SSD-33; 22.X.2015; coll. V. M. O. • 2 exx; same locality; 8.VII.2016; coll. V. M. O. • 1 ex; TSP-A; 22.IX.2015; coll. V. M. O. • 5 exx; same locality; 13.VI.2016; coll. V. M. O. • 1 ex; same locality; 22.IX.2016; coll. V. M. O. • 2 exx; TSP-B; 13.VI.2016; coll. V. M. O. • 1 ex; TSP-C; 13.VI.2016; coll. V. M. O. • 12 exx; same locality; 6.X.2016; coll. V. M. O. • 11 exx; same locality; 5.IV.2017; coll. V. M. O. • 3 exx; TSP-D; 6.X.2016; coll. V. M. O.

REMARK

Previously reported in caves (see Fresneda & Salgado 2016) and MSS (Nitzu *et al.* 2006, 2010, 2014).

Genus *Catopsimorphus* Aubé, 1850
Subgenus *Attiscurra* Des Gozis, 1886

Catopsimorphus (Attiscurra) marqueti
Fairmaire, 1857
(Fig. 5G)

Catopsimorphus marqueti Fairmaire, 1857: 729.

Catopomorphus bicolor Kraatz, 1870: 12.

Catopomorphus marqueti – Reitter 1885: 48.

Attiscurra marqueti – Des Gozis 1886: 17.

Catopsimorphus bedeli Caillol, 1913: 8.

Catopsimorphus (Attiscurra) marqueti – Jeannel 1936: 321.

TYPE LOCALITY. — France: Probably from Hérault, Béziers (Fairmaire 1857).

DISTRIBUTION. — (WMED) Presence confirmed in the Iberian Peninsula with few and distant records, also present in southern France and Morocco.

MATERIAL COLLECTED. — 2 exx.

Spain • 1 ex; SSD-3; 26.V.2016; coll. V. M. O. • 1 ex; same locality; 21.IX.2016; coll. V. M. O.

REMARK

First record for Madrid and Segovia provinces, also first record in the hypogean environment.

Subgenus *Weiratherella* Jeannel, 1929

Catopsimorphus (Weiratherella) rougeti Saulcy, 1864
(Fig. 5H)

Catopsimorphus rougeti Saulcy, 1864: 653.

Catopsimorphus (Weiratherella) rougeti – Jeannel 1936: 318.

TYPE LOCALITY. — France: Pyrénées-Orientales, Collioure and Port-Vendres (Saulcy 1864).

DISTRIBUTION. — (SOER) Known from France and Italy. Present in the southern half of the Iberian Peninsula, with two exclusive records close to the coast in Barcelona.

MATERIAL COLLECTED. — 5 exx.

Spain • 1 ex; SSD-23; 6.X.2015; coll. V. M. O. • 1 ex; same locality; 13.VI.2016; coll. V. M. O. • 2 exx; SSD-25; 9.VI.2016; MNHN • 1 ex; SSD-26; 8.VII.2016; coll. V. M. O.

REMARK

First record for Segovia province and Sierra de Guadarrama National Park. Reported previously in the MSS (Jiménez-Valverde *et al.* 2015).

Genus *Choleva* Latreille, 1797
Subgenus *Choleva*

Choleva (Choleva) cisteloides cisteloides
(Frölich, 1799)
(Fig. 5I)

Luperus cisteloides Frölich, 1799: 25.

Choleva oblonga Spence, 1815: 138.

Choleva humeralis Brullé, 1832: 162.

Catops castaneus Sturm, 1839: 9.

Choleva tournieri Pic, 1922: 22.

Choleva (Choleva) cisteloides – Reitter 1885: 42.

TYPE LOCALITY. — No data. Probably Germany (Frölich 1799).

DISTRIBUTION. — (EURP) Limited to Western Europe and Turkey. Known from various locations in the northern half of the Iberian Peninsula.

MATERIAL COLLECTED. — 13 exx.

Spain • 1 ex; SSD-1; 24.V.2016; coll. V. M. O. • 1 ex; SSD-22; 13.VI.2016; coll. V. M. O. • 4 exx; SSD-23; 13.VI.2016; coll. V. M. O. • 5 exx, same locality and date; MNHN • 2 exx; SSD-26; 8.VII.2016; coll. V. M. O.

REMARK

The captures of this study are the first records of this species in the Central System of the Iberian Peninsula, thus this is the first record for Madrid and Segovia provinces and Sierra de Guadarrama National Park. Previously reported in caves (see Fresneda & Salgado 2016), this is the first record in the MSS.

Subgenus *Cholevopsis* Jeannel, 1922

Choleva (Cholevopsis) punctata Brisout, 1866
(Fig. 5J)

Choleva punctata Brisout, 1866: 364.

Choleva (Cholevopsis) punctata – Jeannel 1923: 51.

TYPE LOCALITY. — Spain: Cantabria, Reinosa (Brisout de Barneville 1866).

DISTRIBUTION. — (IBER) Species known from France and from numerous localities in the northern half of the Iberian Peninsula.

TABLE 2. — Biometry and qualitative characters of the *Choleva* (*C.*) *punctata* Brisout, 1866 adults. Abbreviations and symbols: **ID**, identifier of specimen (**M**, male; **F**, female), **SSD**, subterranean sampling device, **AED**, manifestation of the aedeagus (see Fig. 8); **PWmid**, pronotum width in the midpoint; **PWmax**, maximum width of the pronotum; **PL**, pronotum length; **Pmid**, **PWmid.PL** (see Fig. 8); **Pmax**, **PWmax.PL**; **TR**, metatrochanter type (see Fig. 7); *, unit of measurement, millimetres.

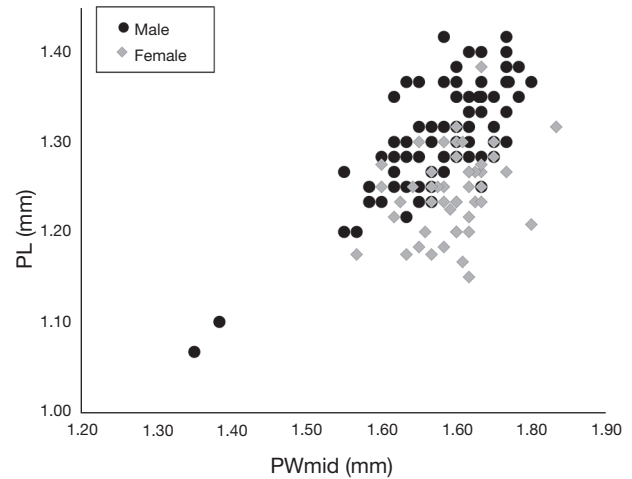
ID	SSD	AED	PWmid = (PWmax)*	PL*	Pmid = (Pmax)	TR
M1	6	I	1.38	1.10	1.26	b
M2	6	I	1.62	1.27	1.28	f
M3	6	I	1.55	1.27	1.22	f
M4	6	I	1.62	1.25	1.29	f
M5	6	I	1.63	1.28	1.27	f
M6	6	I	1.58	1.25	1.27	f
M7	6	I	1.55	1.20	1.29	f
M8	6	I	1.68	1.32	1.28	f
M9	6	I	1.70	1.28	1.32	f
M10	6	I	1.60	1.23	1.30	f
M11	6	I	1.58	1.23	1.28	f
M12	6	I	1.73	1.25	1.39	f
M13	6	I	1.57	1.20	1.31	f
M14	6	I	1.63	1.22	1.34	f
M15	6	I	1.68	1.32	1.28	f
M16	6	I	1.38	1.10	1.26	f
M17	11	I	1.68	1.27	1.33	c
M18	11	I	1.73	1.40	1.24	b
M19	11	I	1.75	1.28	1.36	c
M20	11	I	1.70	1.35	1.26	c
M21	11	I	1.70	1.35	1.26	c
M22	11	I	1.62	1.35	1.20	b
M23	11	I	1.62	1.28	1.26	c
M24	11	I	1.77	1.38	1.28	c
M25	11	I	1.72	1.33	1.29	c
M26	11	I	1.75	1.35	1.30	c
M27	11	I	1.77	1.40	1.26	c
M28	11	I	1.80	1.37	1.32	c
M29	11	I	1.73	1.25	1.39	b
M30	11	I	1.72	1.32	1.30	a
M31	11	I	1.67	1.30	1.28	c
M32	11	I	1.73	1.28	1.35	c
M33	11	I	1.70	1.32	1.29	c
M34	11	I	1.72	1.32	1.30	c
M35	11	I	1.70	1.30	1.31	b
M36	11	I	1.72	1.33	1.29	c
M37	11	I	1.55	1.20	1.29	c
M38	11	I	1.72	1.40	1.23	c
M39	11	I	1.77	1.33	1.33	a
M40	11	I	1.70	1.35	1.26	c
M41	11	I	1.77	1.37	1.29	c
M42	11	I	1.78	1.35	1.32	b
M43	11	I	1.77	1.42	1.25	b
M44	11	I	1.67	1.32	1.27	c
M45	11	I	1.72	1.32	1.30	b
M46	11	I	1.65	1.32	1.25	d
M47	11	I	1.72	1.32	1.30	b
M48	11	I	1.73	1.37	1.27	b
M49	11	I	1.63	1.30	1.26	b
M50	11	I	1.73	1.33	1.30	c
M51	11	I	1.68	1.42	1.19	c
M52	11	I	1.77	1.37	1.29	b
M53	11	I	1.73	1.35	1.28	c
M54	11	I	1.62	1.30	1.24	d
M55	11	I	1.72	1.35	1.27	f
M56	11	I	1.72	1.28	1.34	f
M57	11	I	1.72	1.30	1.32	f
M58	6	I	1.63	1.25	1.31	f
M59	6	II	1.77	1.37	1.29	e
M60	6	II	1.58	1.23	1.28	f
M61	6	II	1.67	1.23	1.35	f
M62	6	II	1.73	1.35	1.28	f
M63	6	II	1.67	1.23	1.35	f
M64	6	II	1.60	1.28	1.25	f

Table 2. — Continuation.

ID	SSD	AED	PWmid = (PWmax)*	PL*	Pmid = (Pmax)	TR
M65	6	II	1.63	1.28	1.27	f
M66	6	II	1.65	1.23	1.34	f
M67	6	II	1.35	1.07	1.27	f
M68	11	II	1.70	1.37	1.24	b
M69	11	II	1.77	1.37	1.29	c
M70	11	II	1.68	1.32	1.28	c
M71	11	II	1.70	1.35	1.26	a
M72	11	II	1.68	1.28	1.31	c
M73	11	II	1.72	1.32	1.30	c
M74	11	II	1.73	1.33	1.30	c
M75	11	II	1.73	1.28	1.35	b
M76	11	II	1.68	1.28	1.31	b
M77	11	II	1.65	1.37	1.21	c
M78	11	II	1.77	1.37	1.29	c
M79	11	II	1.75	1.30	1.35	b
M80	11	II	1.70	1.32	1.29	f
M81	11	II	1.77±(1.78)	1.37	1.29±(1.30)	f
M82	11	II	1.73±(1.75)	1.35	1.28±(1.30)	f
M83	15	II	1.63	1.37	1.20	b
M84	16	II	1.65	1.28	1.29	c
M85	16	II	1.65	1.25	1.32	f
M86	16	II	1.70	1.35	1.26	f
M87	16	II	1.77	1.30	1.36	f
M88	16	II	1.63	1.25	1.31	a
M89	11	III	1.70	1.38	1.23	c
M90	16	IV	1.75	1.32	1.33	f
M91	16	IV	1.67	1.27	1.32	f
M92	25	IV	1.70	1.32	1.29	c
M93	17	IV	1.62	1.27	1.28	f
M94	6	—	1.67	1.25	1.33	—
M95	11	—	1.78	1.38	1.29	a
M96	11	—	1.68	1.37	1.23	c
F1	11	—	1.67	1.27	1.32	—
F2	11	—	1.73	1.27	1.37	—
F3	11	—	1.72	1.25	1.37	—
F4	11	—	1.75	1.30	1.35	—
F5	11	—	1.72	1.22	1.41	—
F6	11	—	1.67	1.27	1.32	—
F7	11	—	1.75	1.28	1.36	—
F8	11	—	1.72	1.15	1.49	—
F9	11	—	1.70	1.20	1.42	—
F10	11	—	1.72	1.20	1.43	—
F11	11	—	1.80	1.21	1.49	—
F12	11	—	1.57	1.18	1.33	—
F13	11	—	1.68	1.23	1.36	—
F14	11	—	1.68	1.25	1.35	—
F15	11	—	1.72	1.27	1.36	—
F16	11	—	1.70	1.23	1.38	—
F17	11	—	1.77	1.27	1.39	—
F18	11	—	1.60	1.25	1.28	—
F19	11	—	1.70	1.32	1.29	—
F20	11	—	1.73	1.38	1.25	—
F21	11	—	1.68	1.25	1.34	—
F22	11	—	1.73	1.25	1.39	—
F23	11	—	1.70	1.30	1.31	—
F24	11	—	1.70	1.20	1.42	—
F25	11	—	1.69	1.23	1.38	—
F26	11	—	1.68	1.18	1.42	—
F27	11	—	1.70	1.28	1.32	—
F28	11	—	1.73	1.23	1.40	—
F29	11	—	1.65	1.30	1.27	—
F30	11	—	1.67	1.25	1.33	—
F31	11	—	1.66	1.20	1.38	—
F32	11	—	1.71	1.30	1.31	—
F33	11	—	1.70	1.23	1.38	—
F34	11	—	1.62	1.22	1.33	—
F35	11	—	1.67	1.23	1.35	—
F36	11	—	1.73	1.27	1.36	—
F37	11	—	1.71	1.17	1.46	—

Table 2. — Continuation.

ID	SSD	AED	PWmid = (PWmax)*	PL*	Pmid = (Pmax)	TR
F38	11	—	1.73	1.23	1.41	—
F39	11	—	1.73	1.28	1.36	—
F40	11	—	1.63	1.18	1.39	—
F41	11	—	1.67	1.18	1.42	—
F42	11	—	1.72	1.27	1.36	—
F43	11	—	1.60	1.28	1.25	—
F44	11	—	1.63	1.23	1.32	—
F45	11	—	1.65	1.18	1.39	—
F46	11	—	1.68	1.30	1.29	—
F47	11	—	1.83	1.32	1.39	—
F48	11	—	1.64	1.25	1.31	—

Fig. 6. — Relation between the pronotum width (PWmid) and the pronotum length (PL) of both sexes of *Choleva (Cholevopsis) punctata* Brisout, 1866.

MATERIAL COLLECTED. — 212 exx (96 males and 116 females).

Spain • 11 exx; SSD-6; 22.IX.2015; coll. V. M. O. • 13 exx; same locality and date; MNHN • 3 exx; same locality; 24.V.2016; coll. V. M. O. • 16 exx; same locality; 22.IX.2016; coll. V. M. O. • 19 exx; same locality and date; MNHN • 101 exx; SSD-11; 17.IX.2015; coll. V. M. O. • 3 exx; same locality; 24.V.2016; coll. V. M. O. • 9 exx; same locality; 21.IX.2016; coll. V. M. O. • 1 exx; SSD-15; 28.IX.2016; coll. V. M. O. • 16 exx; SSD-16; 7.X.2015; coll. V. M. O. • 6 exx; same locality; 2.VI.2016; coll. V. M. O. • 9 exx; same locality; 29.IX.2016; coll. V. M. O. • 2 exx; SSD-17; 29.IX.2016; coll. V. M. O. • 2 exx; SSD-25; 9.VI.2016; coll. V. M. O. • 1 ex; TSP-D; 6.X.2016; coll. V. M. O.

REMARK

First record for Segovia province. Previously reported in caves (see Fresneda & Salgado 2016), this is the first record in the MSS.

TAXONOMIC STUDY

The validity of the taxa *Choleva (Cholevopsis) punctata securiformis* Blas, 1980 was questioned based on the study of key morphological characters. The data are presented and discussed in the following paragraph. The conclusions are presented at the end of discussion of this paper.

The biometric study was performed on all male individuals and 48 females from SSD-11. In only two male specimens did the PWmax fail to coincide with the PWmid, with the PWmax being displaced 0.11 mm from the midpoint of the pronotum to the anterior region (Table 2). Three male specimens were found to be particularly small (see Fig. 6 and Table 2), and they were not considered for further analysis. There were no significant differences in the PWmid between the male (mean $\pm$ SD, 1.69 ± 0.06) and female (1.69 ± 0.05) ($t = -0.47$, p -value = 0.637) specimens, although there were significant differences in the PL between the males (1.31 ± 0.05) and females (1.25 ± 0.05) ($t = 7.56$, p -value < 0.001).

Studying the 96 male specimens revealed great variability in terms of the morphology of the metatrochanters. The internal and external angles of the metatrochanter appear with different expressions (Fig. 7A-C), while a medial spine appears on

the inner side of the metatrochanter with a variable degree of development (Fig. 7D-F).

The analysis of the aedeagus allows for the observation of different expressions of extroversion in the sclerotized parts of the internal sac, with the manifestations of the aedeagus I-state and II-state being predominant (Fig. 8). The diversity of the manifestations of the aedeagus did not indicate any relationship with one or more morphological expressions of the metatrochanters (Fig. 3).

The female genitalia in this species shows the following morphological characters (Fig. 9). The external genitalia (i.e., genital shield) is formed by an IX metatergite (IX mtg), IX laterotergites (IX ltg), and dimerous IX gonopods formed by an IX gonocoxite (IX gcox) and an IX gonosubcoxite (IX gscox) (Fig. 9D, E); the IX mtg is longer than it is wide, with a convex anterior border and slightly concave posterior border (in the standard anatomical position) (Fig. 9C); the IX gscox is lateroventral to the IX gcox, it is globe-shaped and it has a single thorn-shaped ventral seta (Fig. 9D, E); the IX gcox is oval and globose (Fig. 9), and it is articulated with a gonostyle that shows two thorn-shaped setae; a thick seta emerges from the middle of the gonostyle, while the other setae, which are thinner and shorter, emerge from the lateral of the gonostyle (Fig. 9E). The internal genitalia (i.e., spermathecal complex) is completely membranous; tubular-shaped; the wide vagina leads perpendicularly to the bursa copulatrix with a sacciform dorsal end (Fig. 9A); the bursa is a third larger than the vagina; the spermatheca is sacciform and hyaline (Fig. 9A, D); the spermathecal gland has a spermatheca-like appearance, albeit slightly smaller (Fig. 9A, D); the thin spermathecal duct is inserted into the middle of the bursa copulatrix (Fig. 9A, D); the odd oviduct makes contact with the ventral end of the bursa copulatrix (Fig. 9A, D); and from here it extends toward the anterior region. (Fig. 9A, B, D).

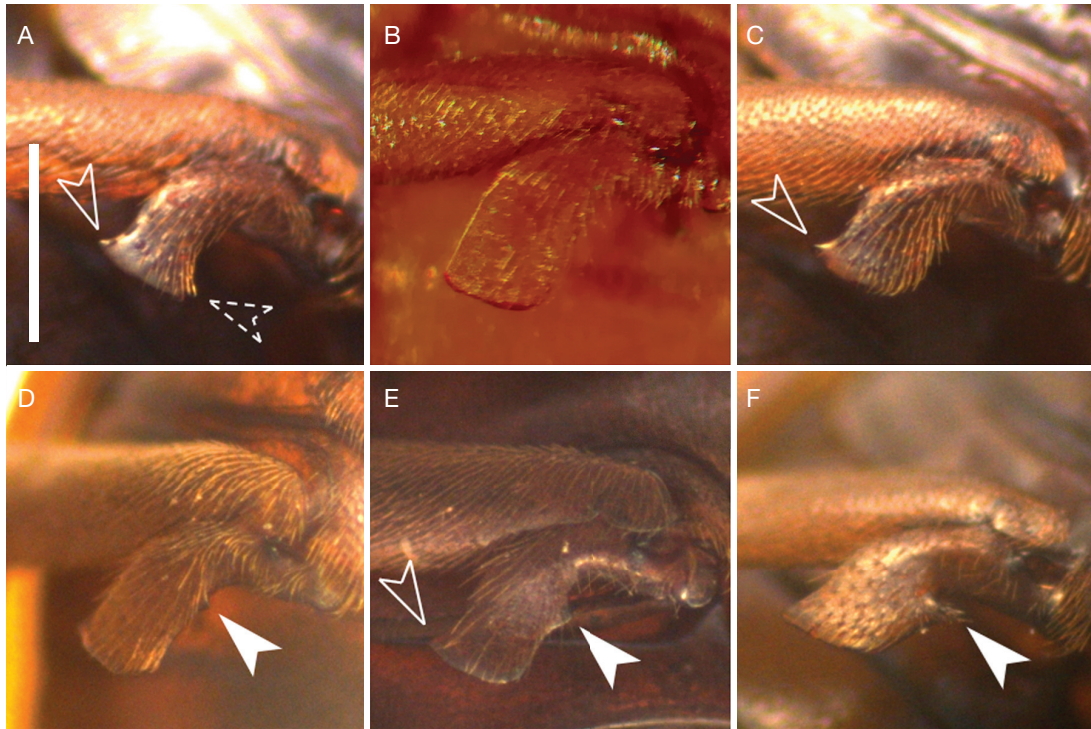


FIG. 8. — The morphological diversity of the *Choleva* (*Cholevopsis*) *punctata* Brisout, 1866 metatrochanter from Sierra de Guadarrama: **A-F**, external spiny angle (hollow arrow with continuous contour), inner spiny angle (hollow arrow with discontinuous contour), and medial spine (solid arrow). Scale bar: 1 mm.



FIG. 7. — Different states of evagination of the inner sac with respect to the median lobe of the aedeagus of *Choleva* (*Cholevopsis*) *punctata* Brisout, 1866. Categorized in columns (I-IV states) and in rows. Abbreviations: **lat**, lateral view; **v**, ventral view. Scale bars: 1 mm.

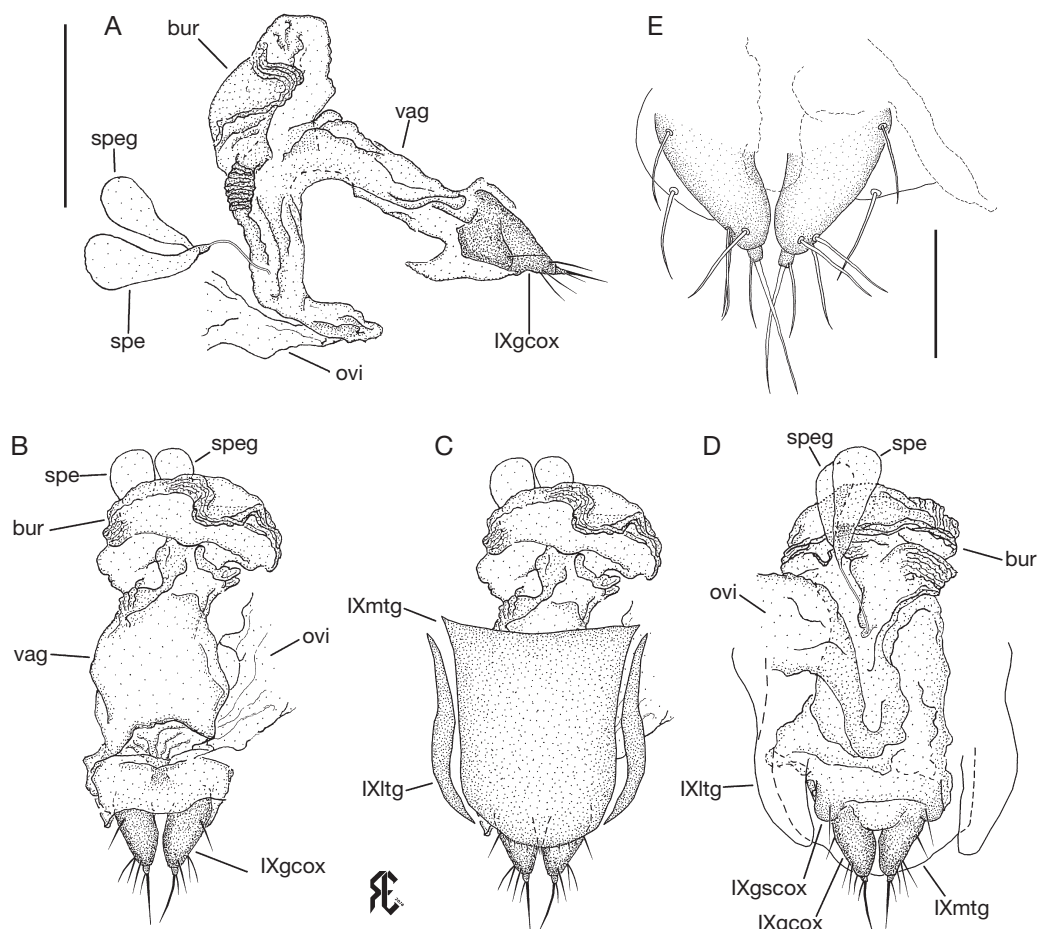


FIG. 9. — Female genitalia of *Choleva (Cholevopsis) punctata* Brisout, 1866: **A**, left lateral vision; **B** dorsal vision without IX ltg and IX mtg; **C**, dorsal vision with complete genital shield; **D**, ventral vision; **E**, detail of the female genital armor. Scale bars: A, D, 0.5 mm; E, 0.2 mm. Abbreviations: see Material and methods. The abbreviations associated with the genital shield are those used by Deuve (1993).

Genus *Sciodrepoides* Hatch, 1933

Sciodrepoides watsoni watsoni (Spence, 1815) (Fig. 5K)

Choleva watsoni Spence, 1815: 156.

Ptomaphagus watsoni – Stephens 1829a: 7; 1829b: 72.

Catopomorphus curticornis Fairmaire, 1877: 65.

Sciodrepa rugulosa Thomson, 1884: 1034.

Catops (Catops) watsoni – Bugnion 1890: 145.

Choleva horniana Blanchard, 1915: 294.

Sciodrepoides watsoni – Jeannel 1934: 5.

TYPE LOCALITY. — United Kingdom (Spence 1815).

DISTRIBUTION. — (ASER) Species with a wide European distribution. Unknown from the western of the Iberian Peninsula.

MATERIAL COLLECTED. — 3 exx.

Spain • 2 exx; TSP-A; 13.VI.2016; coll. V. M. O. • 1 exx; same locality and date; MNHN.

REMARK

Reported previously in caves (see Fresneda & Salgado 2016) and the MSS (Fresneda *et al.* 2007, 2010; Langourov *et al.* 2014; Mammola *et al.* 2017).

Tribe Ptomaphagini Jeannel, 1911
Genus *Ptomaphagus* Hellwig, 1795
Subgenus *Ptomaphagus* Hellwig, 1795

Ptomaphagus (Ptomaphagus) tenuicornis tenuicornis (Rosenhauer, 1856) (Fig. 5L)

Catops tenuicornis Rosenhauer, 1856: 61.

Ptomaphagus (Ptomaphagus) tenuicornis – Jeannel 1936: 89.

TYPE LOCALITY. — Spain: Cádiz, Algeciras (Rosenhauer, 1856).

DISTRIBUTION. — (SOER) Known from France. Species of wide Iberian distribution.

MATERIAL COLLECTED. — 160 exx.

Spain • 4 exx; SSD-1 (0.5m); 21.IX.2016; coll. V. M. O. • 1 ex; SSD-2 (0.5m); 21.IX.2016; coll. V. M. O. • 7 exx; SSD-4 (0.5m); 26.V.2016; coll. V. M. O. • 2 exx; SSD-1; 17.IX.2015; coll. V. M. O. • 2 exx; SSD-2; 21.IX.2016; coll. V. M. O. • 1 ex; SSD-3; 17.IX.2015; coll. V. M. O. • 4 exx; same locality; 26.V.2016; coll. V. M. O. • 6 exx; same locality; 21.IX.2016; coll. V. M. O. • 5 exx; SSD-4; 17.IX.2015; MNHN • 9 exx; same locality; 26.V.2016; coll. V. M. O. • 18 exx; same locality and date; MNHN • 11 exx; same locality; 21.IX.2016; coll. V. M. O. • 1 ex; SSD-6; 22.IX.2015; coll. V. M. O. • 1 ex; same locality; 22.IX.2016; coll. V. M. O. • 19 exx; SSD-11; 17.IX.2015; coll. V. M. O. • 1 ex; same locality; 24.V.2016; coll. V. M. O. • 19 exx; same locality; 21.IX.2016; coll. V. M. O. • 1 ex; SSD-15; 5.X.2015; coll. V. M. O. • 3 exx; same locality; 2.VI.2016; MNHN • 1 ex; same locality; 28.IX.2016; coll. V. M. O. • 1 ex; SSD-16; 29.IX.2016; coll. V. M. O. • 1 ex; SSD-18; 29.IX.2016; coll. V. M. O. • 1 ex; SSD-26; 8.VII.2016; coll. V. M. O. • 1 ex; SSD-31; 8.VII.2016; coll. V. M. O. • 1 ex; TSP-A; 22.IX.2015; coll. V. M. O. • 7 exx; same locality; 13.VI.2016; coll. V. M. O. • 11 exx; same locality; 22.IX.2016; coll. V. M. O. • 1 ex; TSP-C; 13.VI.2016; coll. V. M. O. • 11 exx; same locality; 6.X.2016; coll. V. M. O. • 9 exx; TSP-D; 6.X.2016; coll. V. M. O.

REMARK

Reported previously in caves (see Fresneda & Salgado 2016) and the MSS (Fresneda *et al.* 2007; Sáez Bolaño & Blanco Villero 2010).

DISCUSSION

Cholevinae species are mainly epigeal, although they show strong lucifugous and hygrophilous behaviors (Salgado *et al.* 2008). Thus, many Cholevinae species inhabit dark and damp habitats such as the fallen-leaf layer and soil burrows in the forest floor. Darkness and high humidity are shared properties with the hypogean domain. In fact, many Cholevinae species can be found in caves and in the MSS (Nitzu *et al.* 2006, 2010; Fresneda *et al.* 2007, 2010; Sáez Bolaño & Blanco Villero 2010; Langourov *et al.* 2014; Mammola *et al.* 2017). This is because the MSS is a subterranean habitat that is in close contact with the surface and the deepest hypogean environments (Delay & Juberthie 1981; Racovitza 1983; Růžicka 1993; Juberthie 2000; Giachino & Vailati 2010). The majority of species captured in this study had already been collected in underground environments in previous studies, mainly in caves (see Fresneda & Salgado 2016, and the references therein). In high-mountain regions, the extreme weather conditions force a large part of the fauna to take shelter (Ledesma *et al.* 2020). Undoubtedly, an increase or decrease in the temperature cause a deepening of the fauna, with the possible displacement of epigeal and endogean species into subterranean environment (Giachino & Vailati 2017; Ledesma *et al.* 2020). Therefore, due to the absence of caves in siliceous landscapes, the MSS plays a fundamental role at this altitude, providing refuge for the type of fauna that temporally moves from the epigeal to the hypogean environment, thereby shielding such fauna from the inclemency of the surface conditions.

Obtaining reliable faunistic inventories in the MSS is generally quite a difficult task (Jiménez-Valverde *et al.* 2015). Despite the relatively low diversity of the group, this study

is no exception. We know that at least 18 Cholevinae species can be found in the Sierra de Guadarrama. The 33 one-metre SSDs collected ten species, so we are almost half way toward the last reliable inventory. As the accumulation curve is not too steep at the end, it means that the addition of species to the inventory would be a very slow process and would involve a lot of effort. The highest value yielded by the non-parametric estimations is 14 from Jack2, although its curve shows that it has not stabilized, so the predictions are clearly a lower bound. Another two species were captured by only the TSPs (*S. clathratus* and *S. watsoni watsoni*), which suggests that the use of complementary methods in addition to SSDs could help to collect additional species.

Some species of Cholevinae, such as *C. fuscus fuscus*, *C. (C.) punctata*, *S. angusticollis*, and *S. vandallitiae*, were represented in the MSS of the National Park with high abundance throughout the sampling period (Appendix 1). Taking into account the fact that they had also previously been reported from the MSS in other enclaves, this suggests that they are not simply anecdotal species within the underground compartment, but rather that they find accommodation in this environment. All of them have occasionally been collected in prior studies conducted in the surroundings of the National Park (Appendix 3), and they have been reported in both epigeal and hypogean environments (Fresneda & Salgado 2016), which suggests that these species exhibit a wider ecological valence than the exclusively epigeal or hypogean species. Although the conditions are favorable for the development of strictly hypogean fauna (troglodionts), we found no evidence of any species of Cholevinae with these habits; however, it has previously been established that a troglodiont Leptodirini Lacordaire, 1854, namely *Quaestus (Quasticulus) cisnerosi cisnerosi* (Pérez-Arcas, 1872), lives in the limestone caves near the Central System (Fresneda & Salgado 2016).

Attumbra josephinae josephinae and *C. (A.) marqueti* have both occasionally been found in clayey cracks, and their myrmecophile behavior has been reported. Given the trend of both species to appear in an edaphic environment (Jeannel 1936; Uhagón 1898), it is not surprising that they are rarely found in the MSS and should hence be described as anecdotal. Nonetheless, their occurrence in this medium is interesting, since the presence of these exogenous elements makes clear the connection between the MSS and the higher soil layers, and it emphasizes its role as a transitional habitat between the surface and deeper horizons (Moseley 2010).

THE STATUS OF *C. (C.) SECURIFORMIS*

In her review study of the Iberian *Choleva*, Blas (1980a) described *C. (C.) securiformis*, a new species for science, based on a single male individual collected in El Ventorrillo (Sierra de Guadarrama). Indicating a close proximity to *C. (C.) punctata*, three taxonomic characters were defined for its identification: 1) the slight difference in the location of the maximum width of the pronotum, which for *C. (C.) securiformis* is on the midpoint and for *C. (C.) punctata* is slightly anterior; 2) the morphology of the male metatrochanter, which differs in *C. (C.) securiformis* due to it possessing a marked tooth on

the inner border that is not present in *C. (C.) punctata*; and 3) the morphology of the aedeagus, which is noticeably different in both species. Decades later, after studying numerous specimens of *C. (C.) punctata*, Salgado *et al.* (2004) observed wide variability in the morphology of male trochanters. Due to this observation, they considered that the identified differences only justified the separation of both entities at the sub-specific level in *C. (C.) punctata punctata* and *C. (C.) punctata securiformis*, and they restricted the differential characters to the difference in the location of the maximum width of the pronotum and in the slight differences in the aedeagi.

The study of specimens of *C. (C.) punctata* obtained from the Sierra de Guadarrama National Park has allowed to reconsider the taxonomic status of the two subspecies. First, it is confirmed that the form of the male metatrochanter is a hypervariable intraspecific character, so it cannot be used as a taxonomic difference (Salgado *et al.* 2004). Second, the two manifestations of the aedeagus (ascribable to *C. punctata* and *C. securiformis*), described by Blas (1980a), and then later interpreted by Salgado *et al.* (2008) as similar forms with slight differences, were both observed in the specimens of *C. (C.) punctata* captured in the MSS of the Sierra de Guadarrama National Park. These manifestations, which corresponded to I-state and II-state, respectively (Fig. 8), also showed intermediate expressions, which indicate the displacement of the sclerotized parts of the inner sac to the apical end. These parts can show also extroverted expressions (III-state and IV-state). This eversion gradient of the inner sac was observed in males from the same locality as well as from different localities (Fig. 3; Table 2). Therefore, there are no anatomical differences in the aedeagi, since the differences observed are actually an artifact generated by the different degrees of evagination of the parts of the inner sac of the middle lobe, which does not allow for taxonomic separation beyond the specific level. Third, with regard to the last character indicated by Blas (1980a), namely the situation of the maximum width of the pronotum (PW_{max}), the majority of studied specimens (98.57%) exhibited this maximum at the midpoint, that is, as Blas assigned it to *C. (C.) punctata securiformis*. Only two specimens (M81 and M82) presented a PW_{max} that deviated 0.11 mm from the center to the anterior region of the pronotum; however, these two specimens manifested aedeagi with the inner sac of the medium lobe not being evaginated (Table 2) as would correspond to *C. (C.) punctata punctata*. The appearance of individuals with the maximum width of the pronotum (PW_{max}) located at the midpoint (PW_{max} = PW_{mid}) and others with the PW_{max} displaced to the anterior region (PW_{max} ≠ PW_{mid}) suggests that it does not represent a robust taxonomic character. Finally, the anatomy of the female genitalia, which is here described for the first time for this species, does not show differences between two or more syntopic taxa within the *C. (C.) punctata* complex.

When a taxon is described from a single individual, the lack of one of the two sexes, as well as ignorance of the variability of the taxon characters, produce a high risk of generating a synonym. Once it has been made clear why the evaluated taxonomic characters that discriminate, a priori, the two subspecies of *C. (C.) punctata* are invalid, it can be confirmed

that these characters are part of the variability of the species *C. (C.) punctata*. Moreover, we cannot assume that there are two syntopic subspecies in the same ecological niche in a natural way. On the contrary, an allopatric-type distribution would be expected. Therefore, we conclude that it is actually the same taxon (i.e., a monotypic species). In light of all the above, we propose the following synonymisation: *C. (C.) securiformis* n. syn. under *C. (C.) punctata*.

This series of results highlights the importance of studying a neglected habitat, such as the MSS, so as to improve our knowledge regarding the biodiversity harbored in very diverse terrestrial places, including natural protected areas in siliceous landscapes.

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REFERENCES

- AKKARI N., GILGADO J. D., ORTUÑO V. M. & ENGHOF H. 2018. — Out of the dark void: *Ommatoiulus longicornis* n. sp., a new julid from Spain (Diplopoda, Julida) with notes on some troglobiomorphic traits in millipedes. *Zootaxa* 4420: 415-429. <https://doi.org/10.11646/zootaxa.4420.3.7>
- BAQUERO E., LEDESMA E., GILGADO J. D., ORTUÑO V. M. & JORDANA R. 2017. — Distinctive Collembola communities in the Mesovoid Shallow Substratum: First data for the Sierra de Guadarrama National Park (Central Spain) and a description of two new species of *Orchesella* (Entomobryidae). *PLoS ONE* 12: e018925. <https://doi.org/10.1371/journal.pone.0189205>
- BARRANCO P., GILGADO J. D. & ORTUÑO V. M. 2013. — A new mute species of the genus *Nemobius* Serville (Orthoptera, Gryllidae, Nemobiinae) discovered in colluvial, stony debris in the Iberian Peninsula: A biological, phenological and biometric study. *Zootaxa* 3691 (2): 201-219. <https://doi.org/10.11646/zootaxa.3691.2.1>
- BLANCHARD F. 1915. — Two new Silphids (Col.). *Entomological News* 26: 294. <https://www.biodiversitylibrary.org/page/26320152>

- BLAS M. 1977. — Contribución al conocimiento de los Anemadinae de la Península Ibérica. (Col. Catopidae). *Comunicacions 6e Simposium d'Espeleologia: Biospeleologia, Terrassa*: 125-130.
- BLAS M. 1978. — Sobre una especie poco conocida de Choleva Latreille (1796). (Col. Catopidae). *Speleon* 24: 69-71.
- BLAS M. 1979. — Contribución al conocimiento de los Catopidae (excepto la subfam. Bathysciinae) de la Península Ibérica (Coleoptera Staphylinioidea). Universidad de Barcelona, Tesis Doctoral (inédita), 361 p.
- BLAS M. 1980a. — El género *Choleva* Latreille, 1796 en la Península Ibérica (Col. Catopidae). *Mémoires de Biospéologie* 7: 127-139.
- BLAS M. 1980b. — El género *Nargus* Thomson, 1867 en la Península Ibérica. (Col. Catopidae). *Publicaciones del Departamento de Zoología de la Universidad de Barcelona* 5: 69-77.
- BOE. 2013. — Ley 7.2013, de 25 de junio, de declaración del Parque Nacional de la Sierra de Guadarrama. *Boletín Oficial del Estado* 152: 47795-47852.
- BRISOUT DE BARNEVILLE C. 1866. — Coléoptères nouveaux trouvés en Espagne pendant l'excursion de la Société en 1865. *Annales de la Société entomologique de France*, 4^e série 6: 355-426.
- BRULLÉ A. G. 1832. — Expédition scientifique de Morée. Section des sciences physiques. Tome 3, 1^{re} partie, Zoologie, deuxième section. Des animaux articulés. Paris, 400 p. <https://gallica.bnf.fr/ark:/12148/btv1b8626687z>
- BUGNION E. 1890. — Introduction à la faune entomologique du Valais, in FAVRE E. (ed.), *Faune des Coléoptères du Valais et des régions limitrophes*. Imprimerie Zurcher & Furrer, Zurich: 9-44.
- CARLES-TOLRÁ M., TINAUT A., GILGADO J. D. & ORTUÑO V. M. 2018. — Presence of *Crumomyia glacialis* (Meigen, 1830) (Diptera: Sphaeroceridae) in the Sierra Nevada and Sierra de Guadarrama National Parks (Spain): first record from the Iberian Peninsula, and evidence of its presence in the Mesovoid Shallow Substratum. *Boletín de la Sociedad Entomológica Aragonesa* 63: 182-186.
- COIFFAIT H. 1954. — Catopidés récoltés en Andalousie. Description de trois formes nouvelles. *Notes biospéologiques* 9 (1): 21-24.
- COLWELL R. K. 2013. — *EstimateS: Statistical Estimation of Species Richness and Shared Species from Samples. Version 9. User's Guide and application*. Available from: <http://viceroy.eeb.uconn.edu/estimates>
- COLWELL R. K. & CODDINGTON J. A. 1994. — Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society B: Biological Sciences* 345 (1311): 101-118. <https://doi.org/10.1098.rstb.1994.0091>
- COLWELL R. K., CHAO A., GOTELLI N. J., LIN S. Y., MAO C. X., CHAZDON R. L. & LONGINO J. T. 2012. — Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. *Journal of Plant Ecology* 5 (1): 3-21. <https://doi.org/10.1093/jpe.rtr044>
- DECU V., JUBERTHIE C. & GHEORGHIU V. 2005. — Researches on the mesovoid shallow substratum (MSS) from Romania. *Travaux de l'Institut de Spéologie "Emile Racovitza"* 53-54: 193-26.
- DELAY B. & JUBERTHIE C. 1981. — Les problèmes d'introduction d'énergie dans le milieu souterrain superficiel. *Mémoires de Biospéologie* 8: 45-52.
- DES GOZIS M. 1886. — *Recherche de l'espèce typique de quelques anciens genres. Rectifications synonymiques et notes diverses*. Imprimerie Herbin, Montluçon, 36 p. <https://www.biodiversitylibrary.org/page/43206984>
- DEUVE T. 1993. — L'abdomen et les genitalia des femelles de Coléoptères Adephaga. *Mémoires du Muséum d'Histoire naturelle de Paris* 155: 1-184.
- ERICHSON W. F. 1837. — *Die Käfer der Mark Brandenburg*. Berlin, 384 p.
- ESPAÑOL F. 1948. — Resultados de una campaña biospeleológica realizada en la región media occidental de Navarra durante la segunda quincena de IX-1947. Coleópteros. *Eos* 24: 233-245.
- FABRICIUS J. C. 1801. — *Systema eleutheratorum secundum ordines, genera, species: adiectis synonymis, locis, observationibus, descriptionibus. Tomus II*. Impensis Bibliopolii Academici Novi, Kiliae, 1-687; 1-94.
- FAIRMAIRE L. 1857. — *Miscellanea entomologica*. Deuxième partie (1). *Annales de la Société entomologique de France*, 3^e série 5: 725-745.
- FAIRMAIRE L. 1877. — *Catopomorphus curticornis*. *Annales de la Société entomologique de France*, 5^{ème} série 7 (Séance du 11 Avril 1877): 65-67.
- FRESNEDA J. & SALGADO J. M. 2016. — Catálogo de los coleópteros Leiodidae Cholevinae Kirby, 1837 de la península ibérica e Islas Baleares. *Monografies del Museu de Ciències Naturals* 7: 1-38.
- FRESNEDA J., CÁRDENAS A. M., CASTRO A., LENCINA J. L., LÓPEZ-COLÓN J. I. & BAENA M. 2007. — Nuevos datos de los Cholevinae en la Península Ibérica (Coleoptera). *Boletín de la Asociación española de Entomología* 31 (3-4): 187-214.
- FRESNEDA J., BORDEAU C. & FAILLE A. 2010. — Sobre la presencia de *Catops subfuscus* Kellner, 1846 en los Pirineos (Coleoptera, Leiodidae, Cholevinae, Catopini). *Arxius de Miscel·lània Zoològica* 8: 9-14.
- FRESNEDA J., FAILLE A., FERY H. & RIBERA I. 2019. — A molecular phylogeny of Speonemadus Jeannel, 1922 with description of two new species from Morocco (Coleoptera: Leiodidae: Cholevinae: Anemadini). *Zootaxa* 4543 (1): 1-36. <https://doi.org/10.11646/zootaxa.4543.1.1>
- FRÖLICH J. A. 1799. — I. Einige neue Gattungen und Arten von Käfern. *Der Naturforscher* 28: 1-65.
- FUENTE J. M. DE LA 1925. — Catálogo sistemático-geográfico de los Coleópteros observados en la Península Ibérica, Pirineos propiamente dichos y Baleares. *Boletín de la Real Sociedad Entomológica de España* 7(2-3) [1924]: 93-117.
- GERS C. 1998. — Diversity of energy fluxes and interactions between arthropod communities: from Soil to Cave. *Acta Oecologica* 19: 205-213. [https://doi.org/10.1016/S1146-609X\(98\)80025-8](https://doi.org/10.1016/S1146-609X(98)80025-8)
- GIACHINO P. M. & VAILATI D. 1993. — *Revisione degli Anemadini*. Museo Civico di Scienze Naturali di Brescia. Monografie di "Natura Bresciana" 18, Brescia, 314 p.
- GIACHINO P. M. & VAILATI D. 2010. — *The Subterranean Environment: hypogean life, concepts and collecting techniques*. World Biodiversity Association onlus, Verona, 132 p.
- GIACHINO P. M. & VAILATI D. 2017. — Considerations on biological and terminological aspects of the subterranean and endogean environments: diversity, correlations and faunistic interchange. *Accademia Nazionale Italiana di Entomologia* 65: 157-166.
- GILGADO J. D., LEDESMA E., CUESTA E., ARRECHEA E., ZAPATA DE LA VEGA J. L., SÁNCHEZ-RUIZ A. & ORTUÑO V. M. 2014. — *Dima asoi* Pérez Arcas 1872 (Coleoptera: Elateridae): from montane to hypogean life. An example of exaptations to the subterranean environment? *Annales de la Société entomologique de France (N.S.)* 50 (3-4): 264-271. <https://doi.org/10.1080.00379271.2014.981421>
- GILGADO J. D., ENGHOF H. & ORTUÑO V. M. 2015a. — The hypogean Iberian genus *Typhlopsychrosoma* Mauriès, 1982 (Diplopoda, Chordeumatida, Vandeumatidae): distribution map, key to species, first record in a Mesovoid Shallow Substratum (MSS) and detailed iconography of *T. baeticaense* (Mauriès, 2013). *Zootaxa* 3937 (2): 337-346. <https://doi.org/10.11646.zootaxa.3937.2.5>
- GILGADO J. D., ENGHOF H., TINAUT A., MAURIÈS J.-P. & ORTUÑO V. M. 2015b. — Sierra Nevada (Granada, Spain): a high-altitude biogeographical crossroads for millipedes (Diplopoda), with first data on its MSS fauna and description of a new species of the genus *Ceratophys* Ribaut, 1920 (Chordeumatida: Opisthocheiridae). *Zootaxa* 4044 (3): 391-410. <https://doi.org/10.11646.zootaxa.4044.3.4>
- GILGADO J. D., ENGHOF H., TINAUT A., MAURIÈS J.-P. & ORTUÑO V. M. 2017. — A new genus and species of Haplobainosomatidae (Diplopoda: Chordeumatida) from the MSS of the Sierra de Guadarrama National Park, central Spain. *Zootaxa* 4347 (3): 492-510. <https://doi.org/10.11646.zootaxa.4347.3.4>
- HEYDEN L. VON 1870. — *Entomologische Reise nach dem südlichen Spanien der Sierra Guadarrama und Sierra Morena, Portugal und den Cantabrischen Gebirgen*. Berlin, 218 p. + 2 Tafeln

- HEYDEN L. VON 1883. — Zwei neue Käfer von Creta. *Deutsche entomologische Zeitschrift* 27 (2): 368. <https://www.deutsche-digitale-bibliothek.de/item/BJQKO6ASAPCDNU3ANVC2EDTJUT7KOFXY>
- JEANNEL R. 1922. — Silphidae Catopinae (Coléoptères) (deuxième série) avec une étude phylogénique et paléogéographique de la sous-famille. *Archives de Zoologie expérimentale et générale* 61 (1): 1-98.
- JEANNEL R. 1923. — Révision des *Choleva* Latreille pour servir à l'histoire du peuplement de l'Europe. *L'Abeille* 32: 1-160.
- JEANNEL R. 1934. — Les *Catops* de France. *Revue française d'Entomologie* 1 (1): 2-24.
- JEANNEL R. 1936. — *Monographie des Catopidae*. (Mémoires du Muséum national d'Histoire naturelle – Nouvelle Série (1935-1950): 1-433.
- JEANNEL R. 1961. — Un Catops nouveau d'Espagne. *Revue française d'Entomologie* 28 (2): 59-60.
- JIMÉNEZ-VALVERDE A., GILGADO J. D., SENDRA A., PÉREZ-SUÁREZ G., HERRERO-BORGOÑÓN J. J. & ORTUÑO V. M. 2015. — Exceptional Invertebrate Diversity in a Scree Slope in Eastern Spain. *Journal of Insect Conservation* 19 (4): 713-728. <https://doi.org/10.1007/s10841-015-9794-1>
- JONG DE Y., VERBEEK M., MICHELSEN V., BJØRN P. P., LOS W., STEEMAN F., BAILLY N., BASIRE C., CHYLARECKI P., STLOUKAL E., HAGEDORN G., WETZEL F. T., GLÖCKLER F., KROUPA A., KORB G., HOFFMANN A., HÄUSER C., KOHLBECKER A., MÜLLER A., GÜNTSCH A., STOEY P. & PENEV L. 2014. — Fauna Europaea - all European animal species on the web. *Biodiversity Data Journal* 2: e4034. <https://doi.org/10.3897/BDJ.2.e4034>
- JUBERTHIE C. 1983. — Le milieu souterrain: étendue et composition. *Mémoires de Biospéologie* 10: 17-65.
- JUBERTHIE C. 2000. — The diversity of the karstic and pseudokarstic hypogean habitats in the world, in WILKENS H., CULVER D. C. & HUMPHREYS W. F. (ed.), *Subterranean Ecosystems (Ecosystems of the World 30)*. Elsevier, Amsterdam: 17-39.
- JUBERTHIE C., DELAY B. & BOUILLON M. 1980. — Extension du milieu souterrain en zone non-calcaire: description d'un nouveau milieu et de son peuplement par les coléoptères troglobies. *Mémoires de Biospéologie* 7: 19-52.
- JUBERTHIE C., BOUILLON M. & DELAY B. 1981. — Sur l'existence du milieu souterrain superficiel en zone calcaire. *Mémoires de Biospéologie* 8: 77-93.
- JUBERTHIE C. & DECU V. 1998. — *Encyclopedia Biospeologica. Tome II*. Société de Biospéologie, Moulis and Bucarest.
- KRAATZ G. 1852. — Revision der europäischen Arten der Gattung Catops. *Stettiner entomologische Zeitung* 13: 397-408, 428-445.
- KRAATZ G. 1870. — In HEYDEN L. VON. (ed.) *Entomologische Reise nach dem südlichen Spanien der Sierra Guadarrama und Sierra Morena, Portugal und den Cantabrischen Gebirgen*. Berlin, 218 p. + 2 Tafeln.
- LANGOUROV M., LAZAROV S., STOEY P., GUÉORGUEV B., DELTSHEV C., PETROV B., ANDREEV S., SIMOV N., BEKCHIEV R., ANTONOVA V., LJUBOMIROV T., DEDOV I. & GEORGIEV D. 2014. — New and interesting records of the MSS and cave fauna of Vitosha Mt., Bulgaria. *Proceedings of Balkan Speleological Conference Sofia*: 66-76.
- LAWRENCE J. F. & NEWTON A. F. JR. 1982. — Evolution and classification of beetles. *The Annual Review of Ecology, Evolution, and Systematics* 13: 261-290.
- LEDESMA E., JIMÉNEZ-VALVERDE A., BAQUERO E., JORDANA R., DE CASTRO A. & ORTUÑO V. M. 2020. — Arthropod biodiversity patterns point to the Mesovoid Shallow Substratum (MSS) as a climate refugium. *Zoology* 141: 125771. <https://doi.org/10.1016/j.zool.2020.125771>
- LIEVERS R. & SCHILTHUIZEN M. 2010. — Cholevinae of the World. Available from: <http://cholevidae.myspecies.info/en> (accessed 5.11.2018)
- MAMMOLA S., GIACHINO P. M., PIANO E., JONES A., BARBERIS M., BADINO G. & ISAIA M. 2016. — Ecology and sampling techniques of an understudied subterranean habitat: the Milieu Souterrain Superficiel (MSS). *The Science of Nature* 103: 88. <https://doi.org/10.107.s0011>
- MAMMOLA S., PIANO E., GIACHINO P. M., ISAIA M. 2017. — An ecological survey of the invertebrate community at the epigean, hypogean interface. *Subterranean Biology* 24: 27-52. <https://doi.org/10.3897/subtbiol.24.21585>
- MARSEUL S. DE 1884. — Précis des genres et espèces de la tribu des Silphales de l'ancien-monde. *L'Abeille* 22: 1-204.
- MITÉCO. — Red de Parques Nacionales. Sierra de Guadarrama: ficha técnica. Available from: <https://www.miteco.gob.es/es-red-parques-nacionales.nuestros-parques.guadarrama.ficha-tecnica.default.aspx> (accessed 4.2019)
- MOSELEY M. 2010. — Are all caves ecotones? *Cave and Karst Science* 36 (2009): 53-58.
- NEWTON A. F. 1998. — Phylogenetic problems, current classification and generic catalogue of world Leiodidae (including Cholevinae). *Proceedings of a Symposium XX International Congress of Entomology* 41-178.
- NITZU E., NAE A. & POPA I. 206. — Eco-faunistic study on the invertebrate fauna (Araneae, Collembola and Coleoptera) from the Vârghis Gorge Natural Reserve (Eastern Carpathians, Romania), with special note on the micro-refugial role of the subterranean habitats. *Travaux de l'Institut de Spéologie "Émile Racovitza"* 45: 31-50.
- NITZU E., NAE A., GIURGINCA A. & POPA I. 2010. — Invertebrate communities from the mesovoid shallow substratum of the carpatho-euxinic area: eco-faunistic and zoogeographic analysis. *Travaux de l'Institut de Spéologie "Émile Racovitza"* 49: 41-79.
- NITZU E., NAE A., BÂNCILĂ R., POPA I., GIURGINCA A. & PLĂIAȘU R. 2014. — Scree habitats: ecological function, species conservation and spatial-temporal variation in the arthropod community. *Systematics and Biodiversity* 12 (1): 65-75. <https://doi.org/10.1080/14772000.2013.878766>
- NOVOA F. 1975. — Los Carabidae de la Sierra de Guadarrama. I. Inventario de especies y biogeografía. *Boletín de la Real Sociedad Española de Historia Natural: Sección Biológica* 73: 99-147.
- ORTUÑO V. M., OUTERELO R. & ALONSO J. 1992. — Estudio taxonómico comparativo de las especies ibéricas de *Chlaenius* Reiter, 1908 (Coleoptera, Caraboidea, Callistidae). *Boletín de la Real Sociedad Española de Historia Natural: Sección Biológica* 88: 147-163.
- ORTUÑO V. M., SERRANO J., ANDÚJAR A. & LENCINA J. L. 2003. — The female genitalia of the genus *Zabrus* (Coleoptera: Carabidae: Zabrinini). I. The general structure and the subgenera *Zabrus*, *Euryzabrus*, *Platyzabrus* and *Epomidozabrus*. *European Journal of Entomology* 100: 115-121.
- ORTUÑO V. M., SENDRA A., MONTAGUD S. & TERUEL S. 2005. — Systématique et biologie d'une espèce paléoenémique hypogée de la péninsule Ibérique: *Ildobates neboti* Español, 1966 (Coleoptera: Carabidae: Dryptinae). *Annales de la Société entomologique de France (N.S.)* 40 (2004): 459-475.
- ORTUÑO V. M., GILGADO J. D., JIMÉNEZ-VALVERDE A., SENDRA A., PÉREZ-SUÁREZ G. & HERRERO-BORGOÑÓN J. J. 2013. — The "Alluvial Mesovoid Shallow Substratum", a new subterranean habitat. *PLoS ONE* 8: e76311. <https://doi.org/10.1371/journal.pone.0076311>
- ORTUÑO V. M., CUESTA E., GILGADO J. D. & LEDESMA E. 2014a. — A new hypogean *Trechus* Clairville (Coleoptera, Carabidae, Trechini) discovered in a non-calcareous Superficial Subterranean Habitat of the Iberian System (Central Spain). *Zootaxa* 3802 (3): 359-372. <https://doi.org/10.11646/zootaxa.3802.3.5>
- ORTUÑO V. M., GILGADO J. D. & TINAUT A. 2014b. — Subterranean Ants: The Case of *Aphaenogaster cardenai* (Hymenoptera: Formicidae). *Journal of Insect Science* 14 (212): 1-7. <https://doi.org/10.1093/jisesa.ieu074>
- ORTUÑO V. M., LEDESMA E., GILGADO J. D., VEGUILLAS L. & BARRANCO P. 2017. — On the distribution and autoecology of *Trechus fulvus* Dejean, 1831. *Boletín de la Sociedad Entomológica Aragonesa* 60: 195-26.
- ORTUÑO V. M., LEDESMA E., JIMÉNEZ-VALVERDE A. & PÉREZ-SUÁREZ G. 2019. — Studies of the Mesovoid Shallow Substratum can change the accepted autecology of species: the case of ground

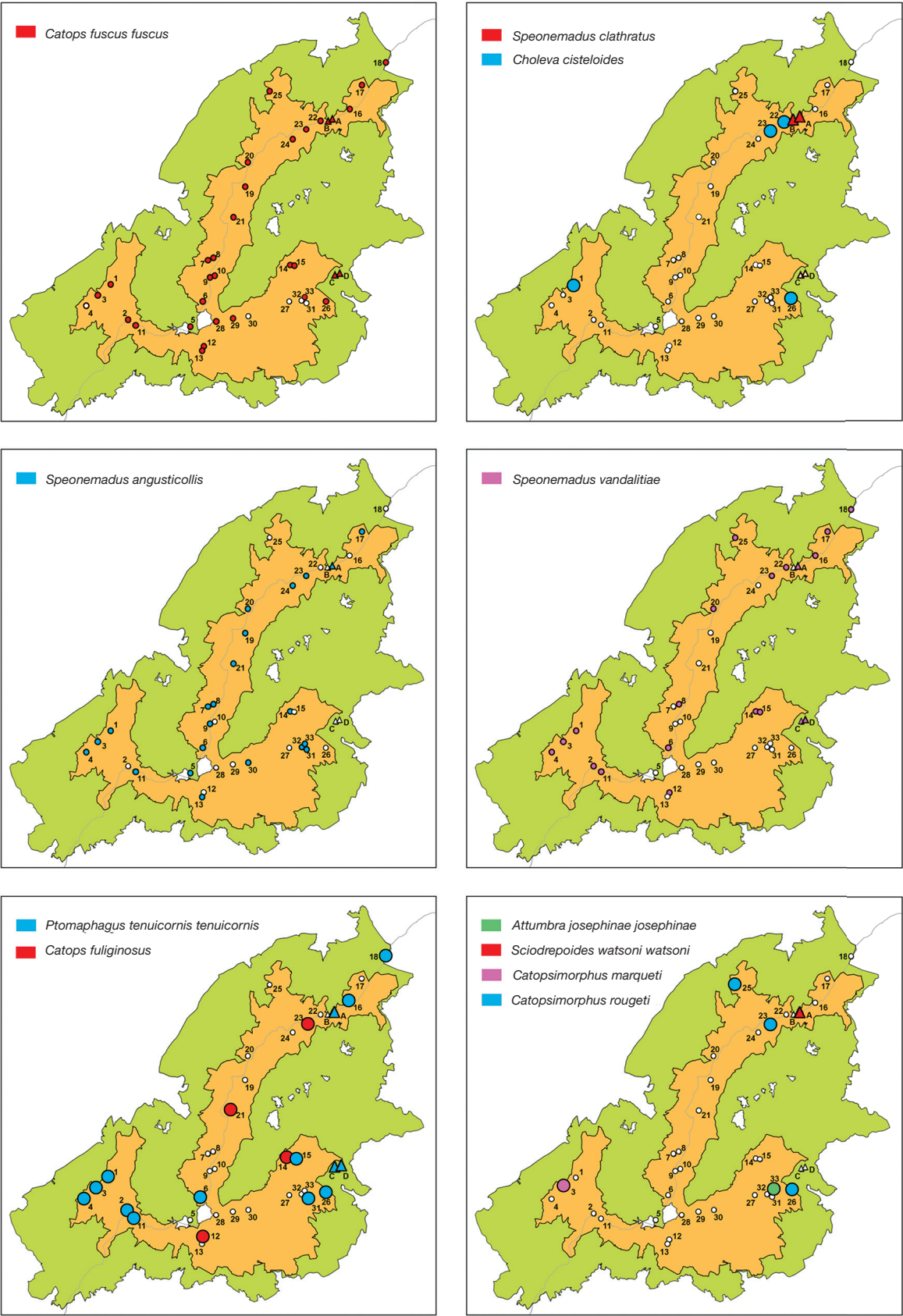
- beetles (Coleoptera: Carabidae) in the Sierra de Guadarrama National Park (Spain). *Animal Biodiversity and Conservation* 42 (2): 213-226. <https://doi.org/10.32800/abc.2019.42.0213>
- PANZER G. W. 1794. — *Fauna insectorum germanicae initia oder Deutschlands Insekten*. Nurnberg, pars 8 & pars 18.
- PAYKULL G. 1798. — *Fauna Svecica Insecta*. Litteris Joh. F. Edman, Reg. Acad. Typogr. Upsaliae: 1-360. <https://doi.org/10.5962/bhl.title.120338>
- PERREAU M. 2000. — Catalogue des Coléoptères Leiodidae Cholevinae et Platypsyllinae. *Mémoires de la Société entomologique de France* 4: 1-460.
- PERRIS E. 1864. — Description de quelques espèces nouvelles de Coléoptères et notes diverses. *Annales de la Société entomologique de France* 33: 273-310.
- PIC M. 1922. — Notes diverses, descriptions et diagnoses (Suite.). *L'Echange* 38 (408): 21-23. <https://www.biodiversitylibrary.org/page/57924549>
- PIPAN T., LÓPEZ H., OROMÍ P., POLAK S. & CULVER D. C. 2011. — Temperature variation and the presence of troglobionts in terrestrial shallow subterranean habitats. *Journal of Natural History* 45: 257-273. <https://doi.org/10.1080.00222933.2010.523797>
- PNSG NO YEAR. — Clima de la Sierra de Guadarrama. Sierra de Guadarrama. Parque Nacional. Ministerio de Agricultura y Pesca, Alimentación y Medio Ambiente – Comunidad de Madrid – Junta de Castilla y León. <https://www.parquenacionalsierraguadarrama.es/es/naturaleza/clima/116-clima> (accessed 30.4.2018)
- RACOVITZA G. 1983. — Sur les relations dynamiques entre le milieu souterrain superficiel et le milieu cavernicole. *Mémoires de Biospéologie* 10: 85-89.
- REITTER E. 1885. — Bestimmungs-Tabellen der europäischen Coleopteren, 12 Necrophaga. *Verhandlungen des naturforschenden Vereines in Brünn* 23 (1884): 3-122. <https://www.biodiversitylibrary.org/page/16396320>
- RENDOŠ M., MOCK A. & JÁSZAY T. 2012. — Spatial and temporal dynamics of invertebrates dwelling karstic mesovoid shallow substratum of Sivec National Nature Reserve (Slovakia), with emphasis on Coleoptera. *Biologia* 67 (6): 1143-1151. <https://doi.org/10.2478.s11756-012-0113-y>
- REY C. 1889. — Remarques en passant. Famille des Catopides. *L'Echange* (49): 4-5. <https://www.biodiversitylibrary.org/page/36676237>
- ROSENHAUER W. G. 1856. — *Die Thiere Andalusiens nach dem Resultate einer Reise zusammengestellt, nebst den Beschreibungen von 249 neuen oder bis jetzt noch unbeschriebenen GatTUNgen und Arten*. Erlangen, viii + 429 p. <https://doi.org/10.5962/bhl.title.66016>
- RŮŽIČKA V. 1993. — Stony debris ecosystems-sources of landscape diversity. *Ekologia (Bratislava)* 12 (3): 291-298.
- SÁEZ BOLAÑO J. & BLANCO VILLERO J. M. 2010. — Los colévidos epigeos (Coleoptera, Leiodidae, Cholevinae) de la Sierra de Tudía (Badajoz, Extremadura, España). *Boletín de la Sociedad Entomológica Aragonesa* 47: 357-361.
- SALAZAR RINCÓN A. & VÍA GARCÍA M. 2003. — *Características climáticas de la vertiente madrileña de la Sierra de Guadarrama*. Centro de Investigaciones Ambientales de la Comunidad de Madrid “Fernando González Bernáldez”, Soto del Real, Madrid.
- SALGADO J. M., BLAS M. & FRESNEDA J. 2004. — Nuevos datos sobre el género *Choleva* Latreille, 1796 en la Península Ibérica con la descripción de una nueva especie (Coleoptera: Cholevidae). *Elytron* 17-18: 47-71.
- SALGADO J. M., BLAS M. & FRESNEDA J. 2008. — *Fauna Ibérica, vol. 31. Coleoptera: Cholevidae*. Editorial CSIC, Madrid, Spain.
- SANZ C. 1986. — Periglacialismo en montaña: la Sierra de Guadarrama, in MARTÍNEZ DE PISÓN E. (ed.). *Atlas de Geomorfología*. Alianza editorial, Madrid: 239-254.
- SAULCY M. F. 1862. — Observations sur les genres *Choleva*, *Catops* et *Catopsimorphus* et remarques sur le nouveau catalogue de Mr. Schaum suivies de la description de deux nouveaux genres et de quatre nouvelles espèces de Coléoptères propres à la faune de France. *Annales de la Société entomologique de France, 4e série* 2: 281-291.
- SAULCY M. F. 1864. — Description de quatre nouvelles espèces de Coléoptères propres à la faune française et remarques sur quelques autres espèces. *Annales de la Société entomologique de France, 4e série* 3 (1863): 653-658.
- SENDRA A., JIMÉNEZ-VALVERDE A., GILGADO J. D., LEDESMA E., BAQUERO E., PÉREZ-SUÁREZ G., CUESTA E., HERRERO-BORGOÑÓN J. J., JORDANA R., TINAUT A., BARRANCO P. & ORTUÑO V. M. 2017. — Diplurans of subsurface terrestrial habitats in the Iberian Peninsula, with a new species description (Diplura: Campodeidae). *Zootaxa* 4291: 61-80. <https://doi.org/10.11646/zootaxa.4291.1.4>
- SPENCE W. 1815. — A monograph of the British Species of the Genus *Choleva*. *Transactions of the Linnean Society of London* 11: 123-160.
- SERRANO J., LENCINA J. L. & ANDÚJAR A. 2003. — Distribution patterns of Iberian Carabidae (Insecta, Coleoptera). *Graellsia* 59: 129-153.
- SKET B. 2008. — Can we agree on an ecological classification of subterranean animals? *Journal of Natural History* 42 (21-22): 1549-1563. <https://doi.org/10.1080.00222930801995762>
- STEPHENS J. F. 1829a. — *The Nomenclature of British Insects; being a compendious list of such species as are contained in the systematic catalogue or British insects, and forming a guide to their classification, &c.* Baldwin and Cradock, London, 68 p. <https://doi.org/10.5962/bhl.title.51800>
- STEPHENS J. F. 1829b. — *A systematic catalogue of british insects: being an attempt to arrange all the hitherto discovered indigenous insects in accordance with their natural affinities. Containing also the references to every english writer on entomology, and to the principal foreign authors. With all the published british genera to the present time.* Baldwin and Cradock, London, xxxiv + 388 p.
- STURM J. 1839. — *Deutschlands Fauna in Abbildung nach der Natur mit Beschreibungen, V. Abtheilung. Die Insecten. Vierzehntes Bändchen. Käfer. Deutschlands Insecten, XIV. Bändchen. Käfer.* Nürnberg, 119 p., 16 illuminirten Aufertafeln. <https://doi.org/10.5962/t.173057>
- THOMSON C. G. 1884. — *Opuscula Entomologica. Tomus decimus.* Typis expressit haquinius Ohlsson, Lundae: 937-1656. <https://www.biodiversitylibrary.org/page/9665811>
- UHAGÓN S. 1890. — Ensayo sobre las especies españolas del grupo “Cholevae”. *Anales de la Sociedad española de Historia natural* 19: 15-96.
- UHAGÓN S. 1898. — Adiciones a mi “Ensayo sobre las especies españolas del grupo *Cholevae*”. *Anales de la Sociedad Española de Historia Natural* 7 (2): 117-126.
- UENO S.-I. 1980. — The anophthalmic trechine beetles of the group of *Trechiana obshimai*. *Bulletin of the National Museum of Nature and Science, Series A* 6: 195-274.
- UENO S.-I. 1981. — New anophthalmic *Trechiana* (Coleoptera, Trechinae) from northern Shikoku, Japan. *Journal of Speleological Society of Japan* 6: 11-18.
- VIALETTE Y., CASQUET C., FÜSTER J. M., IBARROLA E., NAVIDAD M., PEINADO M. & VILLASECA C. 1987. — Geochronological study of orthogneisses from the Sierra de Guadarrama (Spanish Central System). *Neues Jahrbuch für Mineralogie - Abhandlungen* 10: 465-479.
- VIGNA TAGLIANTI A., AUDISIO P. A., BELFIORE C., BIONDI M., BOLOGNA M. A., CARPANETO G. M., BIASE A., FELICI S., PIATTELLA E., RACHELI T., ZAPPAROLI M. & ZOIA S. 1992. — Riflessioni di gruppo sui corotipi fondamentali della fauna W-paleartica ed in particolare italiana. *Biogeographia - The Journal of Integrative Biogeography* 16: 159-179. <https://doi.org/10.21426.B616110375>

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APPENDIX 1. — Abundance species $\times$ sampling sites matrices for the Cholevinae in the MSS of the Sierra de Guadarrama National Park, one matrix for the total data and four for each sampling period.

	Species	Sample 1 (May~Jul2015;Sept-Nov2015)																																	Sample 2 (Sept-Nov2015;May-Jul2016)																																	Sample 3 (May-Jul2016;Sept-Oct2016)																																	Sample 4 (Oct2016;Apr2017)																																
		SSD-1 (0.5 m)	SSD-2 (0.5 m)	SSD-3 (0.5 m)	SSD-4 (0.5 m)	SSD-5	SSD-6	SSD-7	SSD-8	SSD-9	SSD-10	SSD-11	SSD-12	SSD-13	SSD-14	SSD-15	SSD-16	SSD-17	SSD-18	SSD-19	SSD-20	SSD-21	SSD-22	SSD-23	SSD-24	SSD-25	SSD-26	SSD-27	SSD-28	SSD-29	SSD-30	SSD-31	SSD-32	SSD-33	TP-A	TP-B	TP-C	TP-D	TOTAL																																																																																														
	<i>Speonemadus angusticollis</i>	0	0	0	73	0	25	34	78	13	40	24	31	0	1	0	2	1	0	0	3	0	2	71	18	0	168	496	0	0	0	0	0	91	7	1	20	615	0	0	0	1814																																																																																											
	<i>Speonemadus clathratus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	12	0	0	21																																																																																														
	<i>Speonemadus vandalliae</i>	0	1	0	0	3	1	3	16	0	44	0	1	0	0	2	1	0	12	20	65	5	1	0	1	0	5	12	0	8	0	0	0	0	0	0	24	0	27	8	260																																																																																												
	<i>Attumbra josephinae josephinae</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1																																																																																														
	<i>Catops fuliginosus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5																																																																																														
	<i>Catops fuscus fuscus</i>	0	20	0	1	4	113	4	0	101	46	14	3	2	5	2	1	4	1	75	107	132	68	219	599	70	44	3	36	1	0	8	3	0	0	4	7	2	24	3	1770																																																																																												
	<i>Catopsisomorphus (Atticurra) marqueti</i>	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2																																																																																														
	<i>Catopsisomorphus (Weiratherella) rougeti</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5																																																																																														
	<i>Choleva (Choleva) cisteloides</i>	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13																																																																																														
	<i>Choleva (Cholevoopsis) punctata</i>	0	0	0	0	0	0	0	0	62	0	0	0	0	0	0	0	1	31	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	212																																																																																													
	<i>Scioldropoides watsoni watsoni</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	3																																																																																														
	<i>Ptomaphagus (Ptomaphagus) tenuicornis</i>	4	1	0	7	2	2	11	43	0	2	0	0	0	0	39	0	0	5	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	19	0	12	9	160																																																																																													
	TOTAL	4	22	0	8	83	116	45	93	179	167	84	39	34	2	160	4	3	18	27	172	117	134	70	291	619	76	236	499	48	5	0	8	3	91	8	1	25	677	14	63	21	4266																																																																																										
	Sample 1 (May~Jul2015;Sept-Nov2015)																																																																																																																																				
	<i>Speonemadus angusticollis</i>	0	0	0	0	65	0	17	16	57	5	29	11	11	0	1	0	0	0	0	0	0	0	2	25	14	0	161	320	0	0	0	0	0	23	1	16	245	0	-	-	1020																																																																																											
	<i>Speonemadus clathratus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	4	-	-	6																																																																																													
	<i>Speonemadus vandalliae</i>	0	0	0	0	0	2	0	15	0	0	0	0	0	0	0	13	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	41																																																																																												
	<i>Attumbra josephinae josephinae</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	-	-	1																																																																																													
	<i>Catops fuscus fuscus</i>	0	2	0	0	1	58	0	47	12	16	2	1	1	2	0	0	0	40	47	76	40	129	398	21	17	3	7	0	0	0	7	2	0	0	2	1	0	-	-	932																																																																																												
	<i>Catopsisomorphus (Weiratherella) rougeti</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	1																																																																																													
	<i>Choleva (Cholevoopsis) punctata</i>	0	0	0	0	0	0	0	0	0	24	0	0	0	0	101	0	0	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	141																																																																																												
	<i>Ptomaphagus (Ptomaphagus) tenuicornis</i>	0	0	0	0	2	0	1	5	0	1	0	0	0	0	19	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	-	-	30																																																																																												
	Sample 2 (Sept-Nov2015;May-Jul2016)																																																																																																																																				
	<i>Speonemadus angusticollis</i>	0	0	0	1	0	1	7	2	4	1	1	0	0	0	0	0	1	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	48	1	0	3	41	0	0	0	118																																																																																											
	<i>Speonemadus clathratus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	8	0	0	12																																																																																													
	<i>Speonemadus vandalliae</i>	0	0	0	2	1	1	4	0	1	0	4	0	1	0	1	0	12	6	2	4	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	50																																																																																													
	<i>Catops fuliginosus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2																																																																																														
	<i>Catops fuscus fuscus</i>	0	1	0	3	10	2	0	9	5	19	2	2	1	3	0	1	4	14	18	31	21	23	83	15	13	0	25	1	0	0	0	0	0	0	2	5	2	1	0	318																																																																																												
	<i>Catopsisomorphus (Atticurra) marqueti</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1																																																																																													
	<i>Catopsisomorphus (Weiratherella) rougeti</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4																																																																																														
	<i>Choleva (Choleva) cisteloides</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13																																																																																														
	<i>Choleva (Cholevoopsis) punctata</i>	0	0	0	0	0	0	0	0	3	0	0	0	0	3	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14																																																																																														
	<i>Scioldropoides watsoni watsoni</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3																																																																																														
	<i>Ptomaphagus (Ptomaphagus) tenuicornis</i>	0	0	0	7	0	0	4	27	0	0	0	0	0	1	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0	1	0	52																																																																																												
	Sample 3 (May-Jul2016;Sept-Oct2016)																																																																																																																																				
	<i>Speonemadus angusticollis</i>	0	0	0	7	0	0	7	11	19	4	10	12	20	0	0	0	2	0	0	0	3	0	0	43	4	0	7	172	0	0	0	0	0	20	5	0	1	329	0	0	0	676																																																																																										
	<i>Speonemadus clathratus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	3																																																																																													
	<i>Speonemadus vandalliae</i>	0	1	0	0	1	0	13	0	25	0	0	0	0	0	0	0	14	50	0	0	0	1	0	3	2	0	0	0	0	0	0	0	0	0	24	0	24	0	7	167																																																																																												
	<i>Catops fuliginosus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3																																																																																												
	<i>Catops fuscus fuscus</i>	0	17	0	0	45	2	0	45	29	9	10	0	0	0	2	0	0	21	42	25	7	67	118	34	14	0	4	0	0	0	0	1	0	0	0	0	1	0	12	3	509																																																																																											
	<i>Catopsisomorphus (Atticurra) marqueti</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1																																																																																													
	<i>Choleva (Cholevoopsis) punctata</i>	0	0	0	0	0	0	0	0	0	35	0	0	0	0	9	0	0	1	9	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	57																																																																																											
	<i>Ptomaphagus (Ptomaphagus) tenuicornis</i>	4	1	0	0	0	2	6	11	0	1	0	0	0	0	19	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	0	11	9	78																																																																																												
	Sample 4 (Oct2016;Apr2017)																																																																																																																																				
	<i>Speonemadus vandalliae</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	0	2																																																																																												
	<i>Catops fuscus fuscus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-																																																																																																									

APPENDIX 2. — Distribution maps of all the Cholevinae species collected in the MSS of the Sierra de Guadarrama National Park, except for *Choleva* (*Cholevopsis*) *punctata* Brisout, 1866.



APPENDIX 3. — Cholevinæ species present in the Sierra de Guadarrama National Park. The reference list and the UTM 10 × 10 km cells are provided.

Species	Province	Locality/Toponymy	UTM	Reference
<i>Speonemadus angusticollis</i>	Madrid	Navacerrada	30TVL10	Uhagón 1890 1898; Jeannel 1922, 1936; Fuente 1925
		Puerto de Cotos, Dos Hermanas	30TVL12	this study
		Cerro Ventoso, Siete Picos	30TVL11	this study
		Entre Cuerda de la Buitrera y Cuerda de los Almorchones, La Maliciosa	30TVL11	this study
		El Purgatorio, Altos de la Morcuera	30TVL22	this study
		La Gelecha - La Flecha, Montes Carpetanos	30TVL23	this study
		El Paredón, Montes Carpetanos	30TVL22	this study
		Circo del Pico Nevero, Montes Carpetanos	30TVL23	this study
		Peñacabra, Montes Carpetanos	30TVL23	this study
		Loma de Pandasco, Cuerda Larga	30TVL21	this study
	Segovia	Canchal del Collado de la Najarra, Cuerda Larga	30TVL21	this study
		Cabecera del Arroyo de La Najarra, Cuerda Larga	30TVL21	this study
		Canchal en la cabecera del Arroyo de La Najarra	30TVL21	this study
		Cancho del Río Peces, Mujer Muerta	30TVL02	this study
		Canchal Umbría de la Mujer Muerta	30TVL01	this study
		Canchal de las Víboras, Mujer Muerta	30TVL01	this study
		Canchal del Arroyo Seco, Puerto de Navacerrada	30TVL11	this study
		Canchal La Pedriza, Puerto de Los Cotos	30TVL11	this study
		Canchal de la Majada Hambrienta, Peñalara	30TVL12	this study
		Canchal de la Majada Aranguez, Peñalara	30TVL12	this study
		Canchal de la Peña del Buitre, Montes Carpetanos	30TVL34	this study
		Canchal del Cerro de Navahonda, Montes Carpetanos	30TVL23	this study
		Refugio Puerto de Navafria	30TVL33	this study
<i>Speonemadus clathratus</i>	Madrid	Cercedilla	30TVL11	Blas 1977
		El Paular	30TVL22	Uhagón 1898; Blas 1977, 1979
		El Ventorrillo	30TVL11	Blas 1977, 1979
		Navacerrada, Peñalara	?	Perris 1864; Uhagón 1890; Fuente 1925; Jeannel 1936; Español 1948; Blas 1977, 1979
	Segovia	La Granja de San Ildefonso	30TVL12	Blas 1977, 1979; Giachino & Vailati 1993; CFL; Fresneda <i>et al.</i> 2007; Uhagón 1890
		Valsaín	30TVL12	Uhagón 1890; Blas 1977, 1979
		Refugio Puerto de Navafria	30TVL33	this study
<i>Speonemadus vandaltiae</i>	Madrid	Cercedilla	30TVL11	Blas 1977, 1979
		El Paular	30TVL22	Blas 1977, 1979
		Miraflores, entre Miraflores y el Puerto de la Morcuera	30TVL31	CFL; Fresneda <i>et al.</i> 2007
		Navacerrada	30TVL10	Uhagón 1890
		Cerro Ventoso, Siete Picos	30TVL11	this study
		Canchal Collado del Piornal, La Maliciosa	30TVL11	this study
		El Purgatorio, Altos de la Morcuera	30TVL22	this study
		Hueco de los Ángeles, Altos de la Morcuera	30TVL22	this study
		Circo del Pico Nevero, Montes Carpetanos	30TVL23	this study
		Arroyo de Reajo Cazado, Miraflores de la Sierra	30TVL32	this study
	Segovia	La Granja de San Ildefonso	30TVL12	Jeannel 1936; Blas 1977, 1979; Uhagón 1890
		Cancho del Río Peces, Mujer Muerta	30TVL02	this study
		Corrales de la Majada Minguete, Monton de Trigo	30TVL11	this study
		Canchal Umbría de la Mujer Muerta	30TVL01	this study
		Canchal de las Víboras, Mujer Muerta	30TVL01	this study
		Canchal La Pedriza, Puerto de Los Cotos	30TVL11	this study
		Canchal de la Majada Aranguez, Peñalara	30TVL12	this study
		Canchal Las Revueltas - Los Horcos, Montes Carpetanos	30TVL33	this study
		Canchal de la Peña del Buitre, Montes Carpetanos	30TVL34	this study
		Canchal de Los Loberos, Montes Carpetanos	30TVL34	this study
		Canchal del Cerro de Navahonda, Montes Carpetanos	30TVL23	this study
		Canchal del Alto del Puerto, Montes Carpetanos	30TVL33	this study
		Canchal del Arroyo del Charco (La Cepa), Montes Carpetanos	30TVL24	this study
		Refugio Puerto de Navafria	30TVL33	this study
<i>Attumbra josephinae josephinae</i>	Madrid	Cabecera del Arroyo de La Najarra, Cuerda Larga	30TVL21	this study

Appendix 3. — Continuation.

Species	Province	Locality/Toponymy	UTM	Reference
<i>Catops coracinus</i>	Madrid	Rascafría	30TVL22	Uhagón 1898
<i>Catops fuliginosus</i>	Madrid	Canchal Collado del Piornal, La Maliciosa	30TVL11	this study
		El Purgatorio, Altos de la Morcuera	30TVL22	this study
		El Paredón, Montes Carpetanos	30TVL22	this study
		Circo del Pico Nevero, Montes Carpetanos	30TVL23	this study
<i>Catops fuscus fuscus</i>	Madrid	Cercedilla	30TVL11	Jeannel 1936; Blas 1979
		Lozoya	30TVL33	Blas 1979
		Cueva del Cabo del Río, Lozoya	30TVL33	Jeannel 1936; Blas 1979
		Puerto de Cotos, Dos Hermanas	30TVL12	this study
		Hoya de la Laguna Grande, Peñalara	30TVL12	this study
		Cerro Ventoso, Siete Picos	30TVL11	this study
		Canchal Collado del Piornal, La Maliciosa	30TVL11	this study
		Entre Cuerda de la Buitrera y Cuerda de los Almorchones, La Maliciosa	30TVL11	this study
		El Purgatorio, Altos de la Morcuera	30TVL22	this study
		Hueco de los Ángeles, Altos de la Morcuera	30TVL22	this study
		La Gelecha - La Flecha, Montes Carpetanos	30TVL23	this study
		El Paredón, Montes Carpetanos	30TVL22	this study
		Circo del Pico Nevero, Montes Carpetanos	30TVL23	this study
		Peñacabra, Montes Carpetanos	30TVL23	this study
		Entre La Najarra y Cuatro Calles, Montes Carpetanos	30TVL31	this study
		Collado de Valdemartín, Cuerda Larga	30TVL11	this study
		Entre Cabeza de Hierro Mayor y Menor, Cuerda Larga	30TVL21	this study
		Canchal en la cabecera del Arroyo de La Najarra, Cuerda Larga	30TVL21	this study
	Segovia	Arroyo de Reajo Cazado, Miraflores de la Sierra	30TVL32	this study
		Valsain	30TVL12	Uhagón 1890; Fuente 1925
		Cancho del Río Peces, Mujer Muerta	30TVL02	this study
		Corrales de la Majada Minguete, Monton de Trigo	30TVL11	this study
		Canchal Umbría de la Mujer Muerta	30TVL01	this study
		Canchal de las Víboras, Mujer Muerta	30TVL01	this study
		Canchal del Arroyo Seco, Puerto de Navacerrada	30TVL11	this study
		Canchal La Pedriza, Puerto de Los Cotos	30TVL11	this study
		Canchal de la Majada Hambrienta, Peñalara	30TVL12	this study
		Canchal de la Majada Aranguez, Peñalara	30TVL12	this study
		Canchal Las Revueltas - Los Horcos, Montes Carpetanos	30TVL33	this study
		Canchal de la Peña del Buitre, Montes Carpetanos	30TVL34	this study
		Canchal de Los Loberos, Montes Carpetanos	30TVL34	this study
		Canchal del Cerro de Navahonda, Montes Carpetanos	30TVL23	this study
		Canchal del Alto del Puerto, Montes Carpetanos	30TVL33	this study
		Canchal del Arroyo del Charco (La Cepa), Montes Carpetanos	30TVL24	this study
		Refugio Puerto de Navafria	30TVL33	this study
<i>Catops grandicollis</i>	Segovia	La Granja de San Ildefonso	30TVL12	Uhagón 1890; Fuente 1925; Blas 1979
<i>Catops kirbyi</i>	Segovia	La Granja de San Ildefonso	30TVL12	Jeannel 1936; Blas 1979
<i>Catops nigricans</i>	Madrid	El Paular	30TVL22	Uhagón 1898
		Lozoya	30TVL33	Jeannel 1936; Blas 1979
<i>Catopsimorphus (Attiscurra) marqueti</i>	Segovia	Canchal Umbría de la Mujer Muerta	30TVL01	this study
<i>Catopsimorphus (Weiratherella) rougeti</i>	Madrid	Circo del Pico Nevero, Montes Carpetanos	30TVL23	this study
		Entre La Najarra y Cuatro Calles, Montes Carpetanos	30TVL31	this study
	Segovia	Canchal del Arroyo del Charco (La Cepa), Montes Carpetanos	30TVL24	this study
<i>Choleva (Choleva) cisteloides</i>	Madrid	Circo del Pico Nevero, Montes Carpetanos	30TVL23	this study
		Entre La Najarra y Cuatro Calles, Montes Carpetanos	30TVL31	this study
	Segovia	Cancho del Río Peces, Mujer Muerta	30TVL02	this study
		Canchal del Alto del Puerto, Montes Carpetanos	30TVL33	this study

Appendix 3. — Continuation.

Species	Province	Locality/Toponymy	UTM	Reference
<i>Choleva (Cholevopsis) punctata</i>	Madrid	El Ventorrillo	30TVL11	MZB; Blas 1979, 1980a; Perreau 2000; Salgado <i>et al.</i> 2004
		Puerto de Navacerrada	30TVL11	Uhagón 1890; Fuente 1925; Jeannel 1923 1936; Blas 1978, 1979, 1980a
	Segovia	Cerro Ventoso, Siete Picos	30TVL11	this study
		Hueco de los Ángeles, Altos de la Morcuera	30TVL22	this study
		Arroyo de Reajo Cazado, Miraflores de la Sierra	30TVL32	this study
		Canchal La Pedriza, Puerto de Los Cotos	30TVL11	this study
		Canchal Las Revueltas - Los Horcos, Montes Carpetanos	30TVL33	this study
		Canchal de la Peña del Buitre, Montes Carpetanos	30TVL34	this study
		Canchal del Arroyo del Charco (La Cepa), Montes Carpetanos	30TVL24	this study
<i>Nargus (Demochrus) brunneus</i>	Segovia	La Granja de San Ildefonso	30TVL12	Uhagón 1890; Jeannel 1936; Blas 1979, 1980b
<i>Sciodrepoides watsoni watsoni</i>	Madrid	Cercedilla	30TVL11	Blas 1979
		Navacerrada	30TVL10	Uhagón 1890; Jeannel 1936; Blas 1979
	Segovia	La Granja San Ildefonso	30TVL12	Uhagón 1890
		Valsain	30TVL12	Blas 1979
		Refugio Puerto de Navafria	30TVL33	this study
<i>Ptomaphagus (Ptomophagus) sericatus</i>	Madrid	Navacerrada	30TVL10	Uhagón 1890; Fuente 1925
<i>Ptomaphagus (Ptomophagus) tenuicornis tenuicornis</i>	Madrid	Navacerrada	30TVL10	Blas 1979
		Cerro Ventoso, Siete Picos	30TVL11	this study
		Hueco de los Ángeles, Altos de la Morcuera	30TVL22	this study
		Entre La Najarra y Cuatro Calles, Montes Carpetanos	30TVL31	this study
		Canchal en la cabecera del Arroyo de La Najarra	30TVL21	this study
	Segovia	Arroyo de Reajo Cazado, Miraflores de la Sierra	30TVL32	this study
		La Granja de San Ildefonso	30TVL12	Blas 1979
		Cancho del Río Peces, Mujer Muerta	30TVL02	this study
		Corrales de la Majada Minguete, Monton de Trigo	30TVL11	this study
		Canchal Umbría de la Mujer Muerta	30TVL01	this study
		Canchal de las Víboras, Mujer Muerta	30TVL01	this study
		Canchal La Pedriza, Puerto de Los Cotos	30TVL11	this study
		Canchal Las Revueltas - Los Horcos, Montes Carpetanos	30TVL33	this study
		Canchal de Los Loberos, Montes Carpetanos	30TVL34	this study
		Refugio Puerto de Navafria	30TVL33	this study