

Revision of the *Ropalopus ungaricus/insubricus* group (Coleoptera: Cerambycidae: Callidiini) from the western Palaeartic region

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Received 1 May 2019; revised 26 September 2019; accepted for publication 30 October 2019

This paper revises the taxonomy and phylogeny of *Ropalopus* (Coleoptera: Cerambycidae: Callidiini) species belonging to the taxonomically intricate *Ropalopus ungaricus/insubricus* group from the western Palaeartic. Specimens from all taxa were studied and compared. The key characters, including the male terminalia, were examined by means of scanning electron microscopy. High-quality stacked photographs of the habitus of the specimens (dorsal, ventral) are presented. The phylogenetic analyses were based on 34 adult morphological characters. Both the strict and majority consensus trees revealed the monophyly of the revised group. Identification keys are provided for every taxon from this group, and their geographical distributions are also mapped. All European populations are reduced to subspecies of *Ropalopus ungaricus*. Additionally, a new subspecies from Greece, *Ropalopus ungaricus ossae* subsp. nov., is described and illustrated. A new synonymy for *Ropalopus insubricus fischeri* is proposed: *Callidium insubricum* = *Callidium fischeri*. *Ropalopus nataliyae*, which was described based on only a single female, is herein redescribed owing to the collection of abundant new material. Apart from geographical barriers, the main differentiating factor in this group is proved to be the elevation above sea level. Taxa of the *R. ungaricus/insubricus* group are therefore allopatric or, when parapatric, are isolated by elevation.

ADDITIONAL KEYWORDS: Europe – morphological phylogenetics – morphological systematics – new taxa – scanning electron microscopy – taxonomy.

INTRODUCTION

The term '*Ropalopus ungaricus/insubricus*' has been used in the literature by various authors (e.g. Sama, 2002; Sama & Rejzek, 2002) and it refers to established names of the following species from the subgenus *Ropalopus* Mulsant, 1839: *Ropalopus boreki* Rapuzzi, 2017; *Ropalopus hanae* Sama & Rejzek, 2002; *Ropalopus insubricus* (Germar, 1824) with three described subspecies [*Ropalopus insubricus fischeri* (Krynicky, 1829), *Ropalopus insubricus gallicus* Vartanis, 2018 and *Ropalopus insubricus insubricus*]; *Ropalopus lederi* (Ganglbauer, 1882); *Ropalopus nataliyae* Danilevsky & Skrylnik, 2014; *Ropalopus siculus* (Stierlin, 1864) and

Ropalopus ungaricus (Herbst, 1784). These taxa are connected by their ecological association with maples (*Acer* spp., Sapindaceae) and the metallic gloss of their elytra. All are mountain and submontane species that are distributed from central Germany to North Africa and from Spain to the western part of European Russia, the Caucasus and northern Iran.

The taxonomic system of this group always caused difficulties, and recently the situation has been complicated by the descriptions of new species (*R. boreki*) and subspecies (*R. insubricus gallicus*). Doubts on the distinctiveness of some species and the need for revision of this entire group have been previously noted by Sama (2002), who, besides indicating strictly morphological issues, reported on positive results in the interbreeding of three different taxa (*R. insubricus*, *R. siculus* and *R. ungaricus*) in laboratory conditions. Sláma (2018) shared this point of view and additionally included the recently (Rapuzzi, 2017) described taxon

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[Version of record, published online 3 March 2020;
<http://zoobank.org/urn:lsid:zoobank.org:pub:F7564C93-D0FA-4907-AC35-D3EF3BB2A151>]

R. boreki here. The situation of this group is complicated further by the fact that the type material of some of the taxa has been lost or destroyed (Sama, 2002). In turn, Švácha & Danilevsky (1988) emphasized the lack of good characters for identification between the larvae of a few European species. Further doubts concerning the distinctness of species in this group were shared by other cerambycid specialists (e.g. M. Danilevsky, 2018, and S. Ziarko, 2019, personal communications).

The recognition of the real taxonomic position within this group is also important from a biodiversity conservation point of view (Plewa *et al.*, 2018), especially in Europe and the Middle East. This is because these taxa are considered relicts of primeval forest ('Urwald') and are monophagous and endemic to European mountain forests (e.g. *R. ungaricus*; Kust, 2016; Kašák & Foit, 2018, respectively). Moreover, most were placed on several lists of endangered species, following the IUCN (2019) and the European Red List of saproxylic beetles (Nieto & Alexander, 2010). Therefore, without a generic revision and phylogeny, it is impossible to assess the estimated area of occupancy or current population trends of individual taxa correctly, in order to evaluate the category of threat and to ensure adequate protection for these beetles. Thus, the aim of this work is to clarify and establish a new taxonomy for this contentious group.

MATERIAL AND METHODS

EXAMINED SPECIMENS

Beetles were studied using an Olympus SZH10 Stereo Microscope at $\times 7$ – $\times 140$ magnification, and a PROLAB MSZ Stereo Microscope at $\times 7$ – $\times 90$ magnifications.

This study is based on the examination of ~220 specimens (Table 1), housed in the following collections: CAW, Collection of Adam Woźniak, Warsaw, Poland; CBB, Collection of Bartłomiej Bujnik, Elbląg, Poland; CCC, Collection of Christian Cocquempot, Plourin-les-Morlaix, France; CJS, Collection of Josef Steinhöfer, Geiersthal, Germany; CLKR, Collection of Lech Kruszelnicki, Siemianowice Śląskie, Poland; CMD, Collection of Michail Danilevsky, Moscow, Russia; CRP, Collection of Radosław Plewa, Sękocin Stary, Poland; CTW, Collection of Tomasz Wróbel, Malinowice, Poland; CWTS, Collection of Wojciech Szczepański, Siemianowice Śląskie, Poland; MIZ, Museum and Institute of Zoology Polish Academy of Sciences, Warsaw, Poland; MNHN, Muséum National d'Histoire Naturelle, Paris, France; MZCM, Museo Zoologico of Centro Musei delle Scienze Naturali e Fisiche Università di Napoli Federico II, Napoli, Italy; NHMW, Naturhistorisches Museum, Vienna, Austria; SDEI, Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany; USMB, Upper Silesian Museum, Bytom, Poland;

ZMB, Museum für Naturkunde – Leibniz Institute for Evolution and Biodiversity Science, Berlin, Germany; ZMMU, Zoological Museum of Moscow University, Moscow, Russia.

Other abbreviations used: BL, body length; BW, body width; HT, holotype.

The habitus of the further ~100 specimens that were depicted on professional websites and colour plates in publications by the following authors were also analysed: Sama (2002), Sama & Rejzek (2002), Danilevsky & Skrylnik (2014), Rapuzzi (2017), Sláma (2018), Vartanis (2018) and Hoskovec *et al.* (2019). Some of the localities that were posted on professional websites (<http://www.cerambyx.uoehb.cz>; <http://www.entomologiitaliani.net>; <https://www.zin.ru>; <https://www.naturamediterraneo.com>; <https://www.biolib.cz>; <http://www.hmyzfoto.cz>; <http://molbiol.ru>; <http://www.alsphotopage.com>; <http://insecterra.forumactif.com/>) were taken into consideration and presented (Table 1) only when combined with photographs, enabling accurate identification.

The type material of *R. hanae* (a single male specimen) is probably still preserved in Martin Rejzek's private collection. Our attempts to contact this collector have not brought any results. Therefore, this species is studied based on the detailed description and a photograph of the holotype, in addition to a photograph of a pair that was collected in Kastamonu (northern Turkey) by Nicole and Claude Auvray.

PROCEDURE FOR PREPARATION OF MALE TERMINALIA

To examine the sclerotized parts of the male terminalia, the specimens were relaxed in distilled water for 12–24 h at room temperature. Then, the genitalia and last abdominal segment were separated from the other abdominal structures using pins or forceps, without removing the rest of the abdomen. Separated genitalia were put into 10% KOH solution at room temperature for ~24–48 h.

SCANNING ELECTRON MICROSCOPE PHOTOGRAPHY

Scanning electron microscope (SEM) images were taken using a Hitachi S-3400N SEM at MIZ.

STACKING PHOTOGRAPHY

Photographs of the habitus were taken with a Canon EOS 50D digital camera equipped with a Canon 100 mm f/2.8 USM Macro lens and a Canon MP-E 65 mm f/2.8 1–5 \times lens. The images that were produced were stacked, aligned and combined using HELICON FOCUS software (www.heliconsoft.com).

A few stacked photographs presented in our colour plates were taken from the website [hmyzfoto.cz](http://www.hmyzfoto.cz) (www.hmyzfoto.cz) with the consent of the authors. They

Table 1. List of material studied (taxon, origin and collection)

Taxon name	Country	Locality	Collection
<i>Ropalopus hanae</i>	Turkey	Buğlan Geçidi Pass <i>Kastamonu</i>	n/a n/a
<i>Ropalopus lederi</i>	Russia	Adygeia reg. <i>Apsheironsk</i> Novorossiysk	CLKR, CTW n/a NHMW (lectotype, herein designated)
<i>Ropalopus nataliyae</i>	Iran	Khoshyeylāq <i>Māzandarān</i>	CMD (holotype) , CBB, CLKR, CWTS CLKR
<i>Ropalopus ungaricus boreki</i>	Greece	Lakonia, Oityllo	CJS
<i>Ropalopus ungaricus gallicus</i>	France	Aiguines <i>Ailefroide</i> <i>Castellane</i> <i>Puy-Saint-Vincent</i> <i>Rocher de la Fenêtre</i> <i>Vosges</i>	CAW, CLKR, CTW, CWTS CRP, CTW n/a CTW n/a n/a
<i>Ropalopus ungaricus insubricus</i>	?Austria (probably) Bulgaria Croatia	No data <i>Ropotamo</i> <i>Istria</i> Karlobag Klenovica Krk Island Kvarner Gulf <i>Mount Velika Javornica</i> Senj Stinica, Velebit Mountains Šušanj, Velebit Mountains Vrbnik <i>Zavala</i>	MIZ n/a n/a CLKR, CWTS CBB, CTW CRP CTW n/a CLKR, CTW CBB CAW, CLKR, CRP, CTW, CWTS CRP n/a
	Hungary	Vértes Mountains no data	CLKR MIZ
	Italy	Aurisina	CJS
	Romania	<i>Eşelnița, Iron Gates National Park</i>	n/a
	Russia	<i>Bakhilova Polyana</i> <i>Samara</i> <i>Voronezh, Tellerman forest</i>	CMD ZMMU ZMMU
	Serbia	<i>Tekija</i>	n/a
	Slovakia	Nová Bana	CAW
	Turkey	<i>Istanbul, Belgrad Forest</i>	n/a
	Ukraine	<i>Kharkov</i> (type locality of <i>Callidium fischeri</i>) <i>Sokolówka</i> <i>Odessa</i> Śniatyn <i>Svyatogorsk</i> <i>Tatyanovka</i>	ZMMU n/a n/a MIZ n/a CMD

Table 1. Continued

Taxon name	Country	Locality	Collection
<i>Ropalopus ungaricus ossae</i>	Greece	<i>Kalabaka</i> Spilia, Mount Ossa Stomio, Mount Ossa	n/a CJS CCC (Holotype), CAW, CLKR
<i>Ropalopus ungaricus siculus</i>	Italy	Piano Zucchi, Madonie Mountains <i>Nebrodi</i> Sicily	CBB, CLKR, CRP, CTW n/a SDEI (lectotype)
<i>Ropalopus ungaricus ungaricus</i>	Austria	Plansee	CTW
	?Bosnia and Herzegovina (prob.)	Dalmatia	USMB
	Czech Republic	<i>Hostýnské vrchy Mountains</i>	n/a
		Svor, Lusatian Mountains	CAW, CRP, CTW
		<i>Vidly</i>	n/a
	France	Saint-Étienne-de-Tinée	MNHN (<i>R. vogti</i>)
		Saint-Pierre-de-Chartreuse	CCC
	Germany	<i>Vosges</i>	ZMMU
		Bad Hindelang	MIZ
		<i>Bad Oberdorf</i>	ZMMU
	Italy	Ruhpolding	MIZ
		<i>Monte Lupone</i>	n/a
		Monte Vergine	MZCM (<i>R. annulus</i>)
	Montenegro	<i>Pescasseroli</i>	n/a
		<i>San Giacomo d'Entracque</i>	n/a
		<i>Serrone</i>	n/a
		<i>Val Cimoliana</i>	n/a
		Biogradsko Jezero	CJS
	Poland	Bielice, Bialskie Mountains	CAW, CLKR
		<i>Dukla Pass</i>	n/a
		Galizien	MIZ
	Romania	<i>Mount Jaworne</i>	n/a
		Banat	ZMB (Lectotype, herein designated)
<i>Colibița</i>		n/a	
Slovakia	Donovaly	CAW, CBB, CLKR, CTW	
	Martin	CBB, CRP	
	<i>Martinské hole</i>	n/a	
	Mount Vihorlat	CRP	
	Staré Hory	CLKR, CTW	
	Turecká	CBB	
	Valentová, Mount Velka Fatra	CBB, CLKR, CRP	
Ukraine	<i>Burkut</i>	n/a	

Bold text: type locality; italic text: specimens not available, studied based on photographs from professional sources only. n/a, Not applicable.

were obtained in different conditions (www.hmyzfoto.cz/actual.en.html) and are marked accordingly in the figure description.

ANALYSES OF PHYLOGENY

Morphological characters for phylogenetic analyses were prepared in Nexus Data Editor (Page, 2001). The matrix contains 34 characters involving the

morphology of the head, pronotum, elytra, ventral side of the body and genitalia. *Ropalopus hanae* was included, although some of the characters were unknown because they could not be studied on the pictures. *Phymatodes testaceus* (Linnaeus, 1758) and *Ropalopus clavipes* (Fabricius, 1775) were chosen as outgroup taxa to include closely related species belonging to the same tribe (Callidiini Kirby, 1837) as the analysed group. A list of the characters and their

Table 2. List of morphological characters used for the phylogenetic analysis

1	Average body length: (0) small; (1) medium; (2) large
2	Microsculpture of body: (0) barely striate; (1) clearly striate
3	Length of antennae in males (predominantly): (0) shorter than elytra; (1) as long as elytra; (2) slightly longer than elytra; (3) clearly longer than elytra
4	Shape of antennal joints: (0) cylindrical; (1) expanded towards apex (triangular)
5	Thickness of antennae: (0) slender; (1) robust
6	Pubescence on first antennal joint: (0) sparse and long; (1) sparse and short
7	Ratio of second antennal joint: (0) as long as wide (almost spherical); (1) slightly longer than wide (more triangular); (2) clearly longer than wide (ratio 1:1.2–1.3)
8	Longitudinal furrow on head between eyes: (0) absent; (1) present
9	Pronotal coloration: (0) black or blackish; (1) orange
10	Shape of pronotum in males: (0) relatively narrow, hexagonal, evenly tapering towards anterior and posterior margin; (1) clearly wider than long, hexagonal, evenly tapering towards anterior and posterior margin; (2) wide, raised at base then cordate, unevenly tapering towards anterior and posterior margin; (3) clearly rounded on sides but usually wider than long; (4) almost round
11	Punctuation in central part of pronotum: (0) absent or scarce and barely marked; (1) scarce and slightly marked, often with wrinkles; (2) dense and clearly visible, absent only in a small area in middle; (3) dense and clearly visible, without unpunctured area; (4) deep and wide, unevenly scattered over entire surface
12	Pubescence of pronotum: (0) mainly on sides; (1) additionally with single hairs near central part; (2) distinct, long and dense, almost on entire surface; (3) distinct and dense evenly distributed on entire surface
13	Distinguished stains with deep rough punctuation on sides of pronotum in males: (0) absent; (1) present
14	Range of distinguished stains with deeper punctuation on each side of pronotum in males: (0) rather uniform, almost merged at anterior and posterior margin; (1) narrow and irregular, never about to merge into each other; (2) narrow and irregular, seemingly homogeneous and less visible owing to connection with remaining densely punctate or rugose area in central part of pronotum
15	Elytral coloration: (0) metallic green or bluish; (1) blue or orange; (2) black
16	Lustre of elytra: (0) matt; (1) glossy, non-metallic; (2) slight metallic, less visible; (3) strong metallic, clearly visible
17	Scutellum shape: (0) always rounded, wider than long; (1) usually triangular, longer than wide
18	Longitudinal wrinkles on basal part of elytra: (0) absent; (1) present
19	Intensity of longitudinal wrinkles on basal part of elytra: (0) moderately wrinkled; (1) strongly wrinkled
20	Sculpture of basal part of elytra: (0) none or barely noticeable; (1) slight; (2) moderate; (3) pronounced
21	Elytral hair depressions: (0) microscopic, barely noticeable; (1) narrow and shallow; (2) wide and deep with clear border
22	Pubescence on basal part of elytra: (0) short and sparse, mainly on shoulders; (1) moderately long and sparse; (2) short and denser; (3) moderately long and dense; (4) long and dense
23	Pubescence on lower part of elytra: (0) sparse; (1) moderate; (2) dense
24	Pubescence on ventral side of body: (0) sparse, barely noticeable; (1) white and dense (especially around prosternum); (2) yellowish and dense, especially around prosternum; (3) long, dense and yellowish on whole surface; (4) white and sparse
25	Prosternal margin: (0) flat and indistinct; (1) guttered but thin; (2) pronounced, guttered and thick
26	Prosternal punctuation in males: (0) regular, fine and dense; (1) irregular, scattered, wide and shallow; (2) composed of individual small points
27	Shape of prosternal process: (0) wide and rounded, sometimes bifurcate; (1) narrow and rounded, sometimes bifurcate; (2) triangular and sharpened; (3) triangular but short
28	Mesosternal process: (0) narrow, (1) wide
29	Coloration of legs: (0) black or brown; (1) orange
30	Lobes of protarsomere 3: (0) short, wide, blunt and cordate; (1) slightly longer, more slender and blunt; (2) long, slim and sharper
31	Shape of external margin of lateral lobe: (0) straight; (1) convex; (2) concave
32	Shape of distinguished margin of phallobase roof: (0) with deep concave in middle; (1) clearly concave in middle; (2) slightly concave in middle; (3) almost straight, only with small depression in middle
33	Relative width of parameres to length: (0) narrow; (1) wide; (2) very wide
34	Width of median lobe: (0) narrow; (1) wide

states is provided in Table 2, and the character matrix is in the Supporting Information (Table S1). The data matrix in Nexus format is available in the Supporting Information (Appendix S1).

Parsimony analysis of morphological data was performed using TNT software (Goloboff *et al.*, 2008) using the traditional search approach (1000 replicates, 50 trees saved per replicate, Tree Bisection and Re-connection as the swapping algorithm). Characters were mapped on the majority and strict consensus trees using WinClada (Nixon, 2002).

DISTRIBUTION MAP

The distribution of species was illustrated using Quantum GIS (QGIS) 3.6.0 'Noosa', and the raster layer was downloaded from the Natural Earth webpage (www.naturalearthdata.com).

RESULTS

TAXONOMY

Detailed study of the morphology of specimens, representing all taxa from the discussed group, reveals close relationships between all European populations and significantly stronger dissimilarity of these with the taxa from the Caucasus and Near East. The results of this study are presented as both SEM and stacked colour plates (Figs 1–16) and in the Supporting Information (Figs S1–S6). Particular body parts illustrating the key characters are presented as follows: heads (Fig. 1; Supporting Information, Figs S1, S2), antennae (Supporting Information, Figs S3, S4), pronota (Figs 2, 3; Supporting Information, Fig. S5), elytra (basal parts, Figs 4, 5; apices, Fig. 6; lateral view, Fig. 7), protarsi (Fig. 8) and prosternal processes (Figs 9, 10). Additionally, male terminalia are shown, as follows: tegmens (Fig. 11), lateral lobes (Fig. 12), median lobes (Fig. 13) and pygidia (Supporting Information, Fig. S6). The general habitus of the beetles is also presented dorsally (Figs 14, 15) and ventrally (Fig. 16). The habitus of the type specimens of most of the taxa is depicted in Figure 17, and Figure 18 illustrates other peculiar specimens. The most important key characters are presented separately in Figure 19.

The present analysis shows that many of the characters used in the literature for distinguishing species from this group turn out to represent only individual or subspecific variability. Moreover, some of those traits can differ in strength, especially in the case of the European populations. For instance, pronotal punctation expands considerably from the sparsest (Fig. 2B, C), in the northern part of the range, to total, in case of the populations from the southern part of

the continent (Figs 2M–O, 3A). Elytral wrinkles, one of the main key characters for distinguishing the taxon *R. ungaricus*, is not constant and seems to vary, inter alia, with elevation (e.g. Fig. 4B, D). Moreover, the taxon *R. gallicus*, which was described as a subspecies of *R. insubricus*, also has coarse elytra, although to a lesser extent (Fig. 4F), whereas the nominative form always has a smooth elytra (Figs 4H–J, 5I–K). The shape of particular body parts (especially of the elytra), although often stable, may be highly variable, which makes this character of little use. A good example is provided by the females of the taxon *R. ungaricus*, in which the proportions of the length and width of the elytra vary greatly, even between specimens from the same area (Fig. 14A10–14). This is probably attributable to larval development and pupation taking place under the bark and inside the wood of still living trees, and therefore, the immature stages are subjected to different pressures which might affect the final shape of the pronotum and elytra. Furthermore, the colour of the body and, primarily, of the elytra can be completely different even in specimens from the same population. One example is the taxon *R. insubricus*, in which legs and antennae are usually completely black (e.g. Fig. 14C1–4), but they can be also brown (Fig. 14C5) or even reddish (Fig. 14C7). The colour of the elytra varies from light green (Fig. 14C9) through purely blue (Fig. 14C12) or purple (Fig. 14C13) to almost black (Fig. 14C4). Likewise, in *R. nataliyae* it varies from purely green (Fig. 15D5) through olive (Fig. 15D7) to blue (Fig. 15D4). Although the length of antennae is generally a useful character, it can also be variable in particular individuals of the same taxon and sex (e.g. Fig. 14A2 vs. A5, or C10 vs. C14). It is most likely to depend on prevailing conditions during larval development, and it might also relate to their thickness. These differences tend to be so significant that males are sometimes confused with females. Also, the number of antennomeres with a tooth on the inner side is not constant and is connected to individual variability. Another example is the prosternal process, which appears to be constant in some taxa, but when studying a longer series of individuals it proves to be inconsistent (Figs 9A vs. B, or 10K vs. L). A similar situation is observed in the male terminalia: although the shape of the tegmen and lateral lobes are rather stable in particular taxa (e.g. Figs 11F–I, 12F–I), their variability can be surprising in others (Fig. 12A–E). However, the shape of the median lobe (Fig. 13) and pygidia (Supporting Information, Fig. S6) seem to be taxonomically uninformative characters owing to their variability between taxa.

Based on the above information, several taxonomic and nomenclatural changes need to be considered. First of all, a hypothesis is proposed herein that all European populations of *Ropalopus* from this group

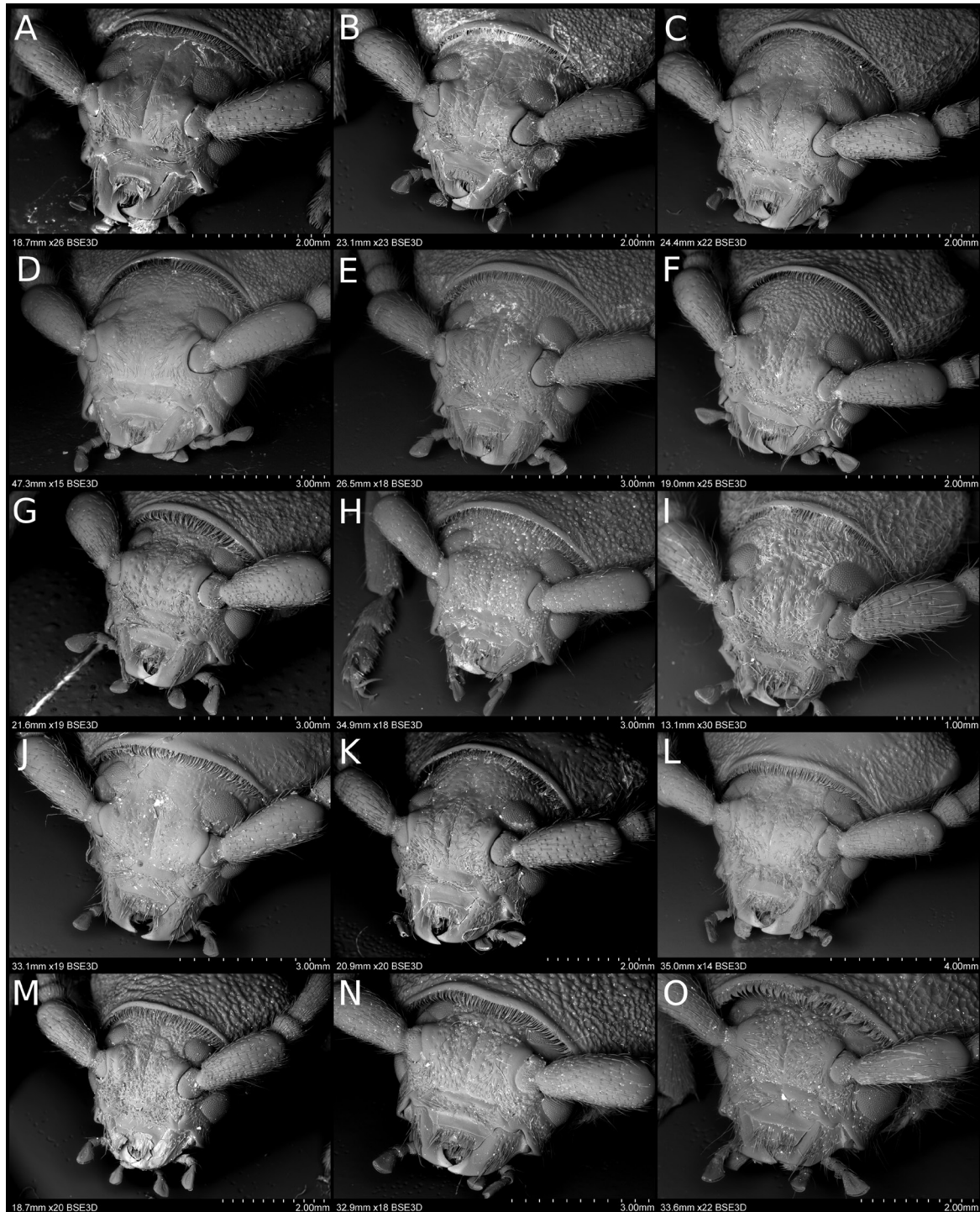


Figure 1. A–O, heads (front view): A–I, males; J–O, females. A, *Ropalopus ungaricus ungaricus*, Austria. B, C, *Ropalopus ungaricus gallicus*, France. D, *Ropalopus ungaricus insubricus*, Croatia. E, *Ropalopus ungaricus boreki*, Greece (Peloponnese). F, *Ropalopus ungaricus siculus*, Italy (Sicily). G, *Ropalopus ungaricus ossae*, Greece (Thessaly). H, *Ropalopus nataliyae*, Iran. I, *Ropalopus lederi*, Russia (north-west Caucasus). J, *Ropalopus ungaricus ungaricus*, Poland. K, *Ropalopus ungaricus gallicus*, France. L, *Ropalopus ungaricus insubricus*, Croatia. M, *Ropalopus ungaricus siculus*, Italy (Sicily). N, *Ropalopus ungaricus ossae*, Greece (Thessaly). O, *Ropalopus nataliyae*, Iran.

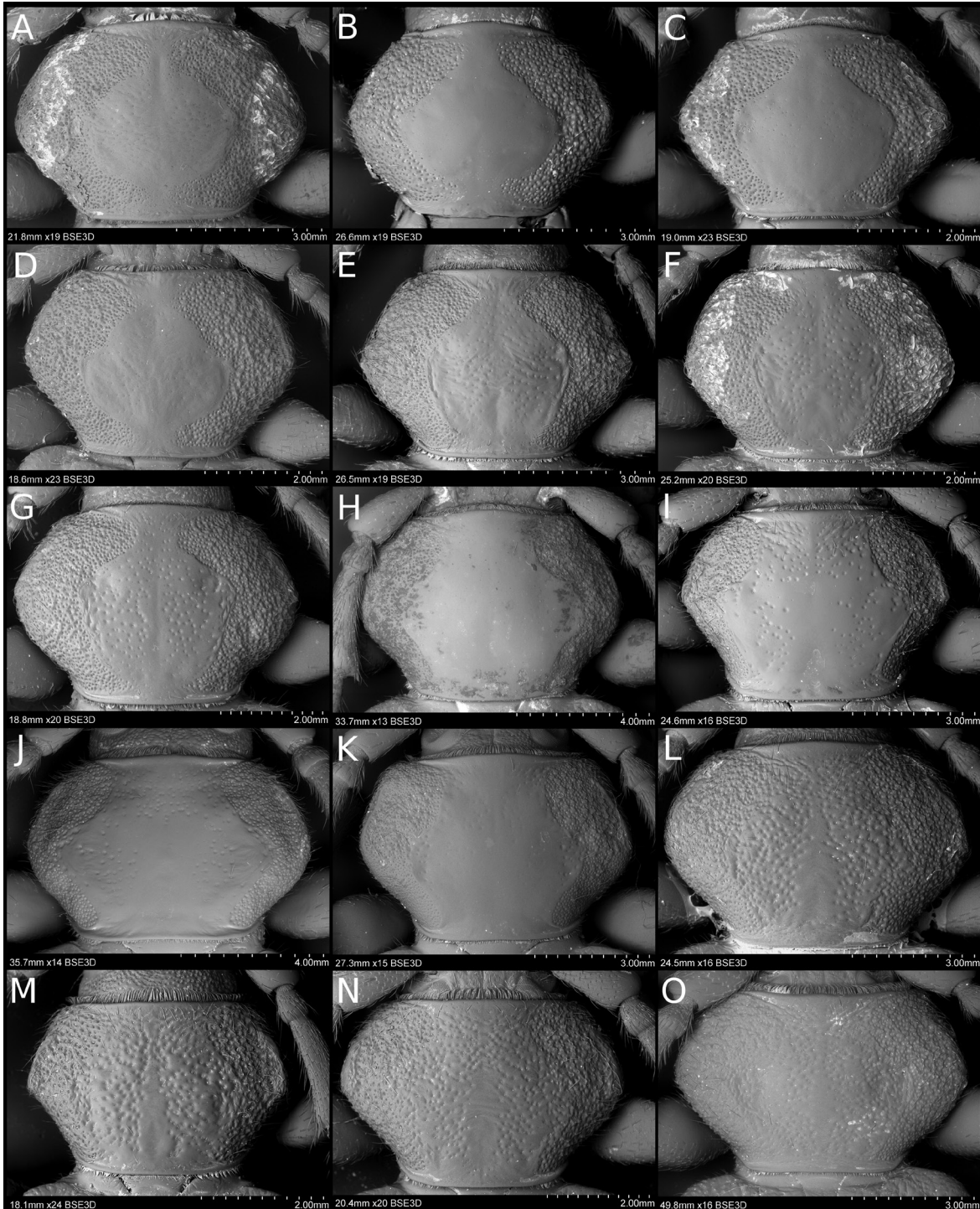


Figure 2. A–O, pronota, males. A–D, *Ropalopus ungaricus ungaricus*, Slovakia, Poland, Austria and Montenegro, respectively. E–G, *Ropalopus ungaricus gallicus*, France. H–K, *Ropalopus ungaricus insubricus*, Croatia. L, *Ropalopus ungaricus boreki*, Greece (Peloponnese). M, N, *Ropalopus ungaricus siculus*, Italy (Sicily). O, *Ropalopus ungaricus ossae*, Greece (Thessaly).

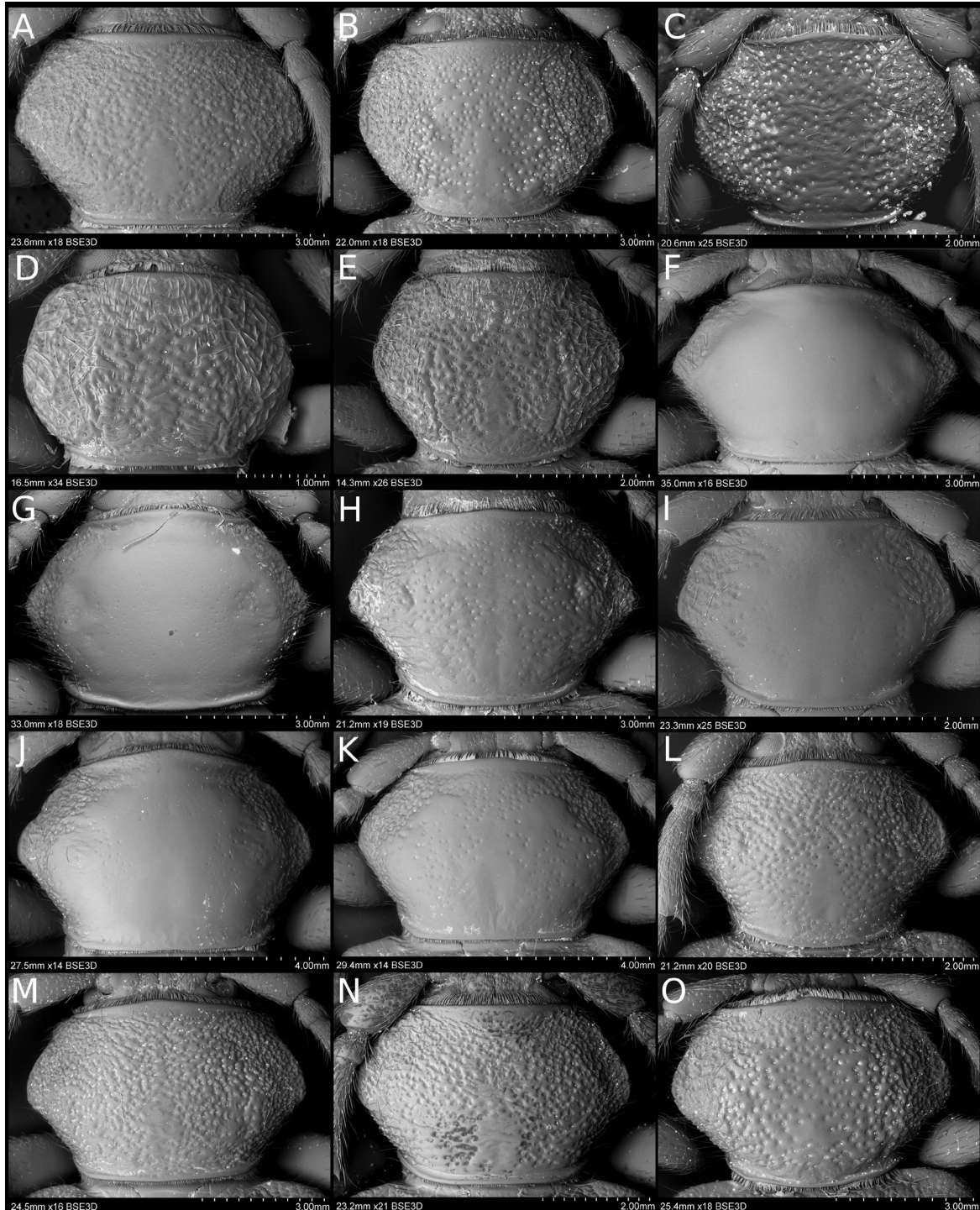


Figure 3. A–O, pronota: A–E, males; F–O, females. A, *Ropalopus ungaricus ossae*, Greece (Thessaly). B, C, *Ropalopus nataliyae*, Iran. D, E, *Ropalopus lederi*, Russia (north-west Caucasus). F, G, *Ropalopus ungaricus ungaricus*, Slovakia. H, *Ropalopus ungaricus gallicus*, France. I–K, *Ropalopus ungaricus insubricus*, Slovakia, Croatia and Croatia, respectively. L, *Ropalopus ungaricus siculus*, Italy (Sicily). M, N, *Ropalopus ungaricus ossae*, Greece (Thessaly). O, *Ropalopus nataliyae*, Iran.

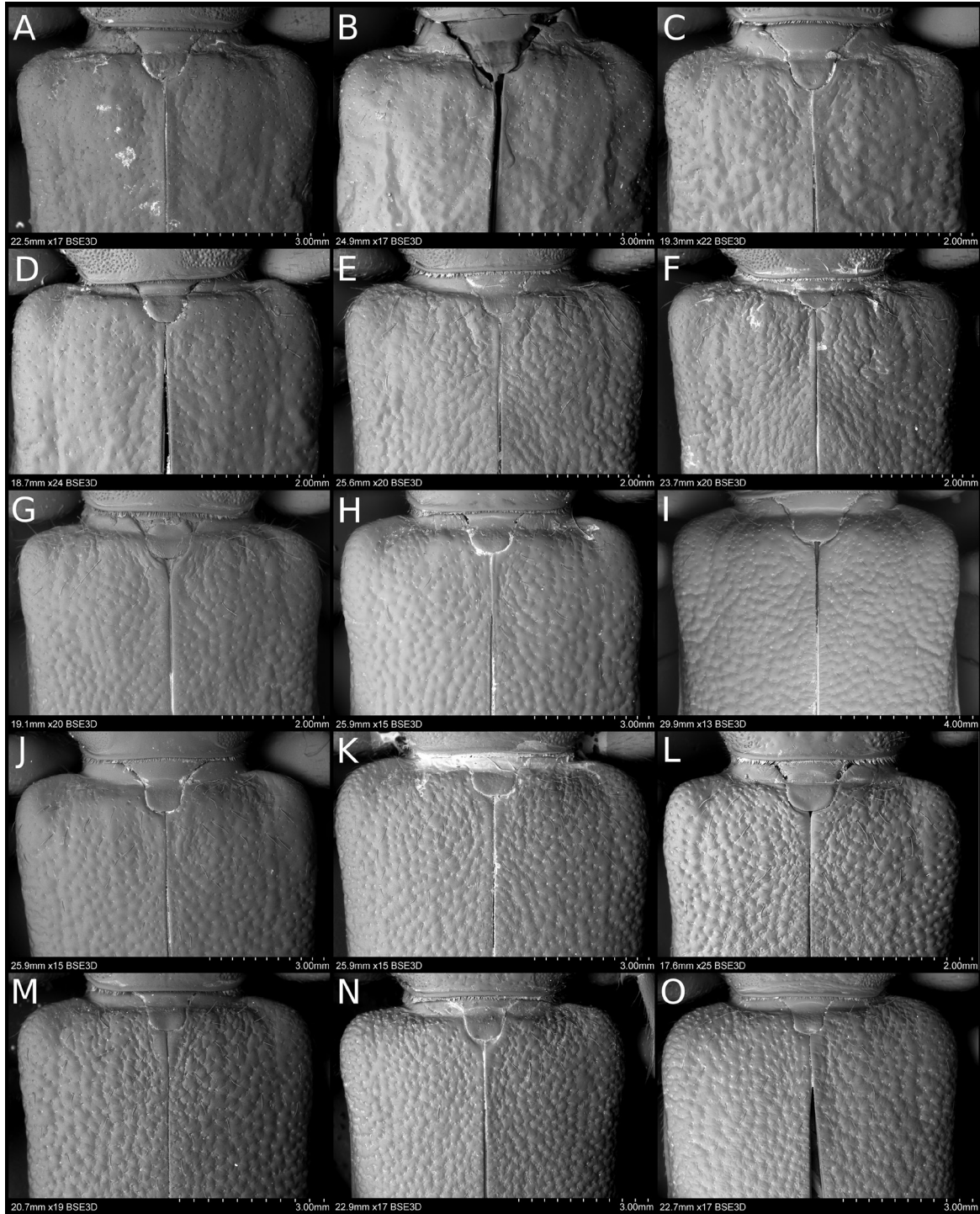


Figure 4. A–O, elytra (basal part), males. A–D, *Ropalopus ungaricus ungaricus*, Slovakia, Poland, Austria and Montenegro, respectively. E–G, *Ropalopus ungaricus gallicus*, France. H–J, *Ropalopus ungaricus insubricus*, Croatia. K, *Ropalopus ungaricus boreki*, Greece (Peloponnese). L, M, *Ropalopus ungaricus siculus*, Italy (Sicily). N, O, *Ropalopus ungaricus ossae*, Greece (Thessaly).

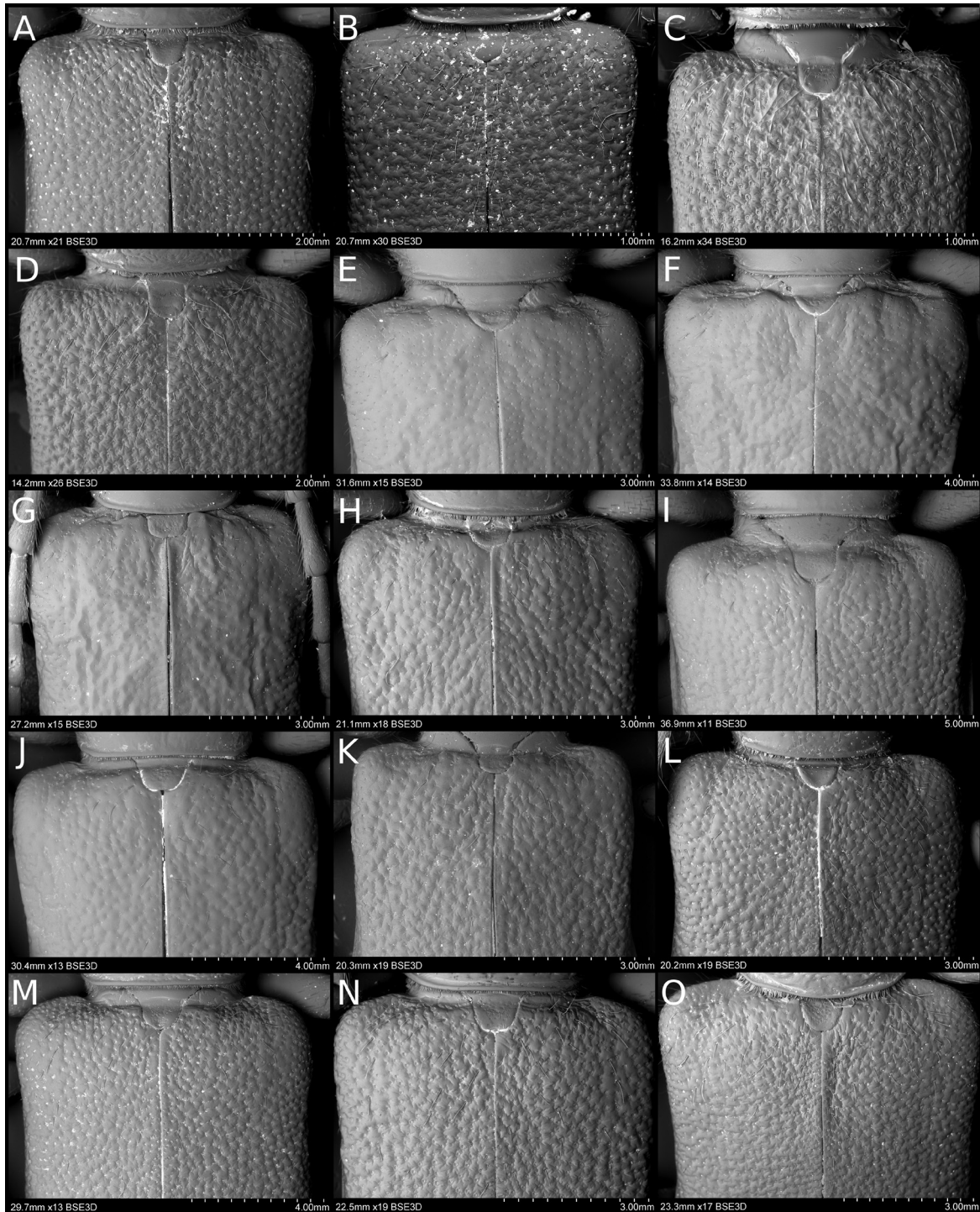


Figure 5. A–O, elytra (basal part): A–D, males; E–O, females. A, B, *Ropalopus nataliyae*, Iran. C, D, *Ropalopus lederi*, Russia (north-west Caucasus). E–G, *Ropalopus ungaricus ungaricus*, Slovakia. H, *Ropalopus ungaricus gallicus*, France. I–K, *Ropalopus ungaricus insubricus*, Slovakia, Croatia and Croatia, respectively. L, *Ropalopus ungaricus siculus*, Italy (Sicily). M, N, *Ropalopus ungaricus ossae*, Greece (Thessaly). O, *R. nataliyae*, Iran.

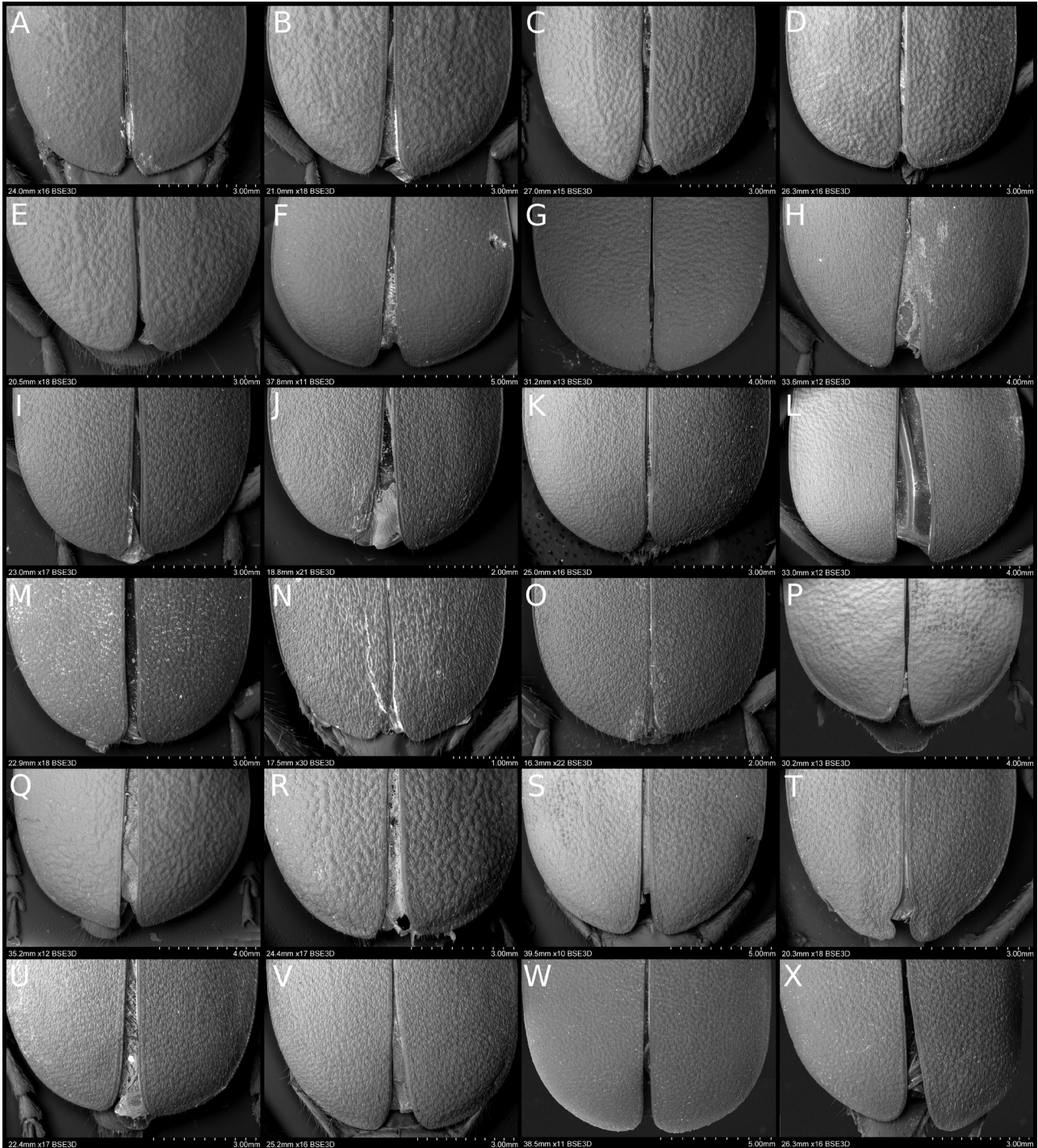


Figure 6. A–X, elytra (apices): A–O, males; P–X, females. A, B, *Ropalopus ungaricus ungaricus*, Slovakia and Austria, respectively. C–E, *Ropalopus ungaricus gallicus*, France. F, G, *Ropalopus ungaricus insubricus*, Croatia. H, *Ropalopus ungaricus boreki*, Greece (Peloponnese). I, J, *Ropalopus ungaricus siculus*, Italy (Sicily). K, L, *Ropalopus ungaricus ossae*, Greece (Thessaly). M, *Ropalopus nataliyae*, Iran. N, O, *Ropalopus lederi*, Russia (north-west Caucasus). P, Q, *Ropalopus ungaricus ungaricus*, Poland and Slovakia, respectively. R, *Ropalopus ungaricus gallicus*, France. S, T, *Ropalopus ungaricus insubricus*, Croatia. U, *Ropalopus ungaricus siculus*, Italy (Sicily). V, W, *Ropalopus ungaricus ossae*, Greece (Thessaly). X, *Ropalopus nataliyae*, Iran.

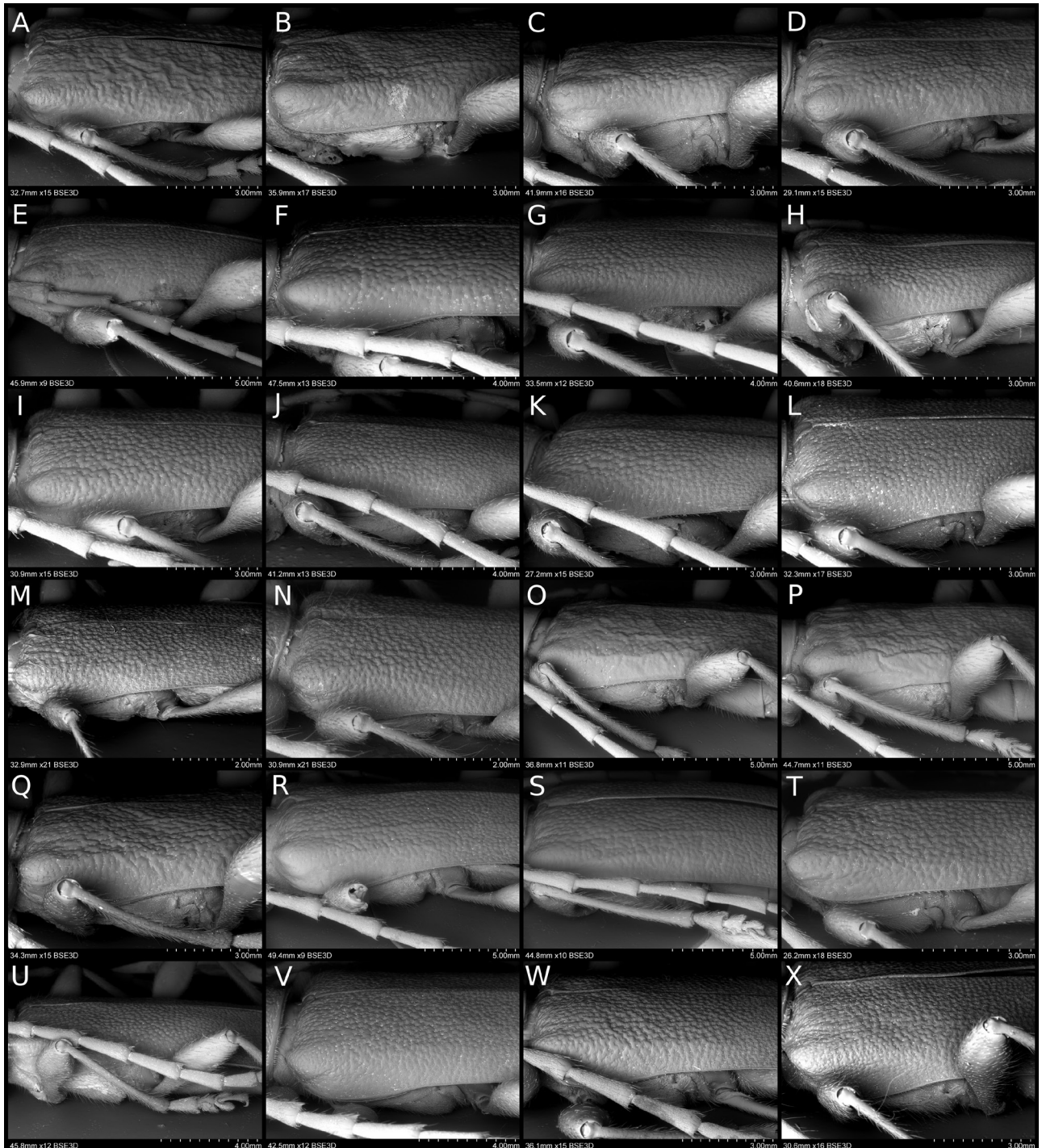


Figure 7. A–X, elytra (lateral view): A–N, males; O–X, females. A, *Ropalopus ungaricus ungaricus*, Austria. B–D, *Ropalopus ungaricus gallicus*, France. E, F, *Ropalopus ungaricus insubricus*, Croatia. G, *Ropalopus ungaricus boreki*, Greece (Peloponnese). H, I, *Ropalopus ungaricus siculus*, Italy (Sicily). J, K, *Ropalopus ungaricus ossae*, Greece (Thessaly). L, *Ropalopus nataliyae*, Iran. M, N, *Ropalopus lederi*, Russia (north-west Caucasus). O, P, *Ropalopus ungaricus ungaricus*, Poland and Slovakia, respectively. Q, *Ropalopus ungaricus gallicus*, France. R–T, *Ropalopus ungaricus insubricus*, Croatia, Croatia and Slovakia, respectively. U, *Ropalopus ungaricus siculus*, Italy (Sicily). V, W, *Ropalopus ungaricus ossae*, Greece (Thessaly). X, *Ropalopus nataliyae*, Iran.

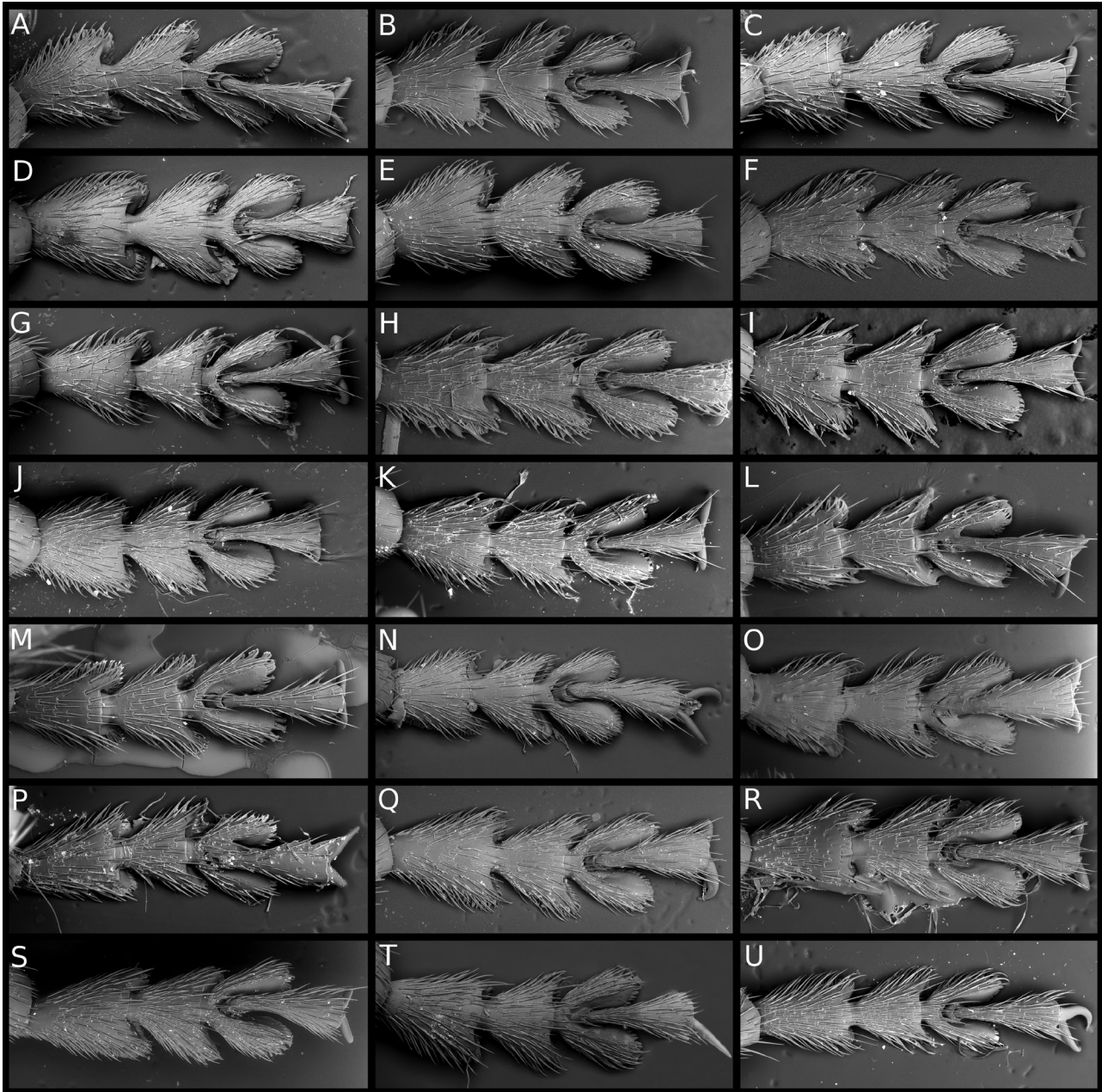


Figure 8. A–U, protarsi: A–M, males; N–U, females. A, *Ropalopus ungaricus ungaricus*, Austria. B, C, *Ropalopus ungaricus gallicus*, France. D, E, *Ropalopus ungaricus insubricus*, Croatia. F, *Ropalopus ungaricus boreki*, Greece (Peloponnese). G, H, *Ropalopus ungaricus siculus*, Italy (Sicily). I, J, *Ropalopus ungaricus ossae*, Greece (Thessaly). K, L, *Ropalopus nataliyae*, Iran. M, *Ropalopus lederi*, Russia (north-west Caucasus). N, O, *Ropalopus ungaricus ungaricus*, Poland and Slovakia, respectively. P, *Ropalopus ungaricus gallicus*, France. Q, *Ropalopus ungaricus insubricus*, Croatia. R, *Ropalopus ungaricus siculus*, Italy (Sicily). S, T, *Ropalopus ungaricus ossae*, Greece (Thessaly). U, *Ropalopus nataliyae*, Iran.

are only subspecies of one species, namely *Ropalopus ungaricus* (Herbst, 1784), and thus several taxa are moved to subspecies level: *Ropalopus ungaricus boreki* Rapuzzi, 2017 stat. nov., *Ropalopus ungaricus gallicus* Vartanis, 2018, *Ropalopus ungaricus insubricus*

(Germar, 1824) stat. nov., *Ropalopus ungaricus siculus* (Stierlin, 1864) stat. nov. and *Ropalopus ungaricus ungaricus*. Additionally, a new subspecies from the region of Thessaly (Greece), *Ropalopus ungaricus ossae* subsp. nov., is described below. *Ropalopus hanae* from

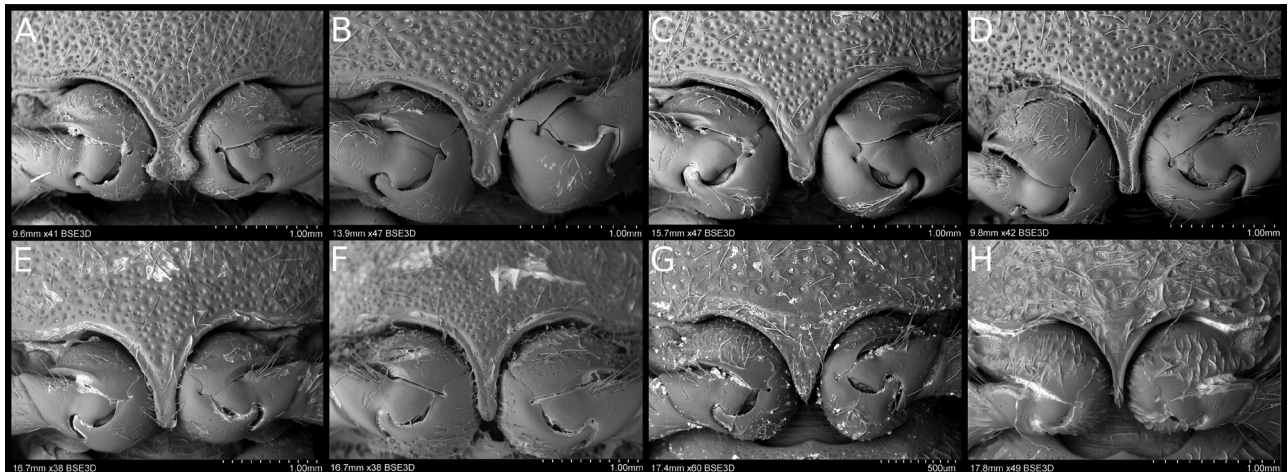


Figure 9. A–H, prosternal processes, males. A, B, *Ropalopus ungaricus ungaricus*, Austria and Poland, respectively. C, *Ropalopus ungaricus gallicus*, France. D, *Ropalopus ungaricus insubricus*, Croatia. E, *Ropalopus ungaricus siculus*, Italy (Sicily). F, *Ropalopus ungaricus ossae*, Greece (Thessaly). G, *Ropalopus nataliyae*, Iran. H, *Ropalopus lederi*, Russia (north-west Caucasus).

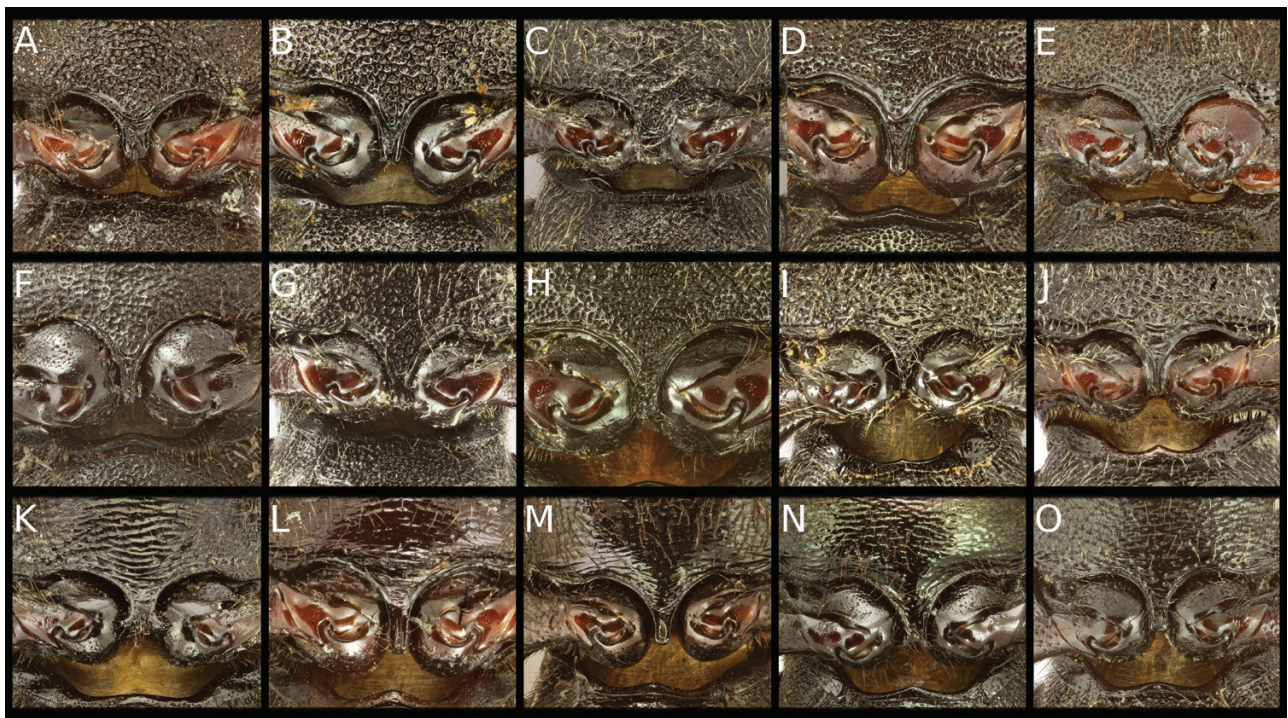


Figure 10. A–O, prosternal processes: A–J, males; K–O, females. A, B, *Ropalopus ungaricus ungaricus*, Czech Republic and Poland, respectively. C, *Ropalopus ungaricus gallicus*, France. D, E, *Ropalopus ungaricus insubricus*, Croatia and Ukraine, respectively. F, *Ropalopus ungaricus boreki*, Greece (Peloponnese). G, *Ropalopus ungaricus siculus*, Italy (Sicily). H, *Ropalopus ungaricus ossae*, Greece (Thessaly). I, *Ropalopus nataliyae*, Iran. J, *Ropalopus lederi*, Russia (north-west Caucasus). K, L, *Ropalopus ungaricus ungaricus*, Poland and Slovakia, respectively. M, N, *Ropalopus ungaricus insubricus*, Hungary and Croatia, respectively. O, *Ropalopus ungaricus ossae*, Greece (Thessaly).

Turkey, *R. lederi* from the Caucasus and *R. nataliyae* from Iran are treated as separate species. Moreover, a new synonymy of a former subspecies, *Ropalopus*

insubricus fischeri (Krynicky, 1829), is proposed: *Callidium insubricum* = *Callidium fischeri* syn. nov. The reason behind this proposal is the lack of any

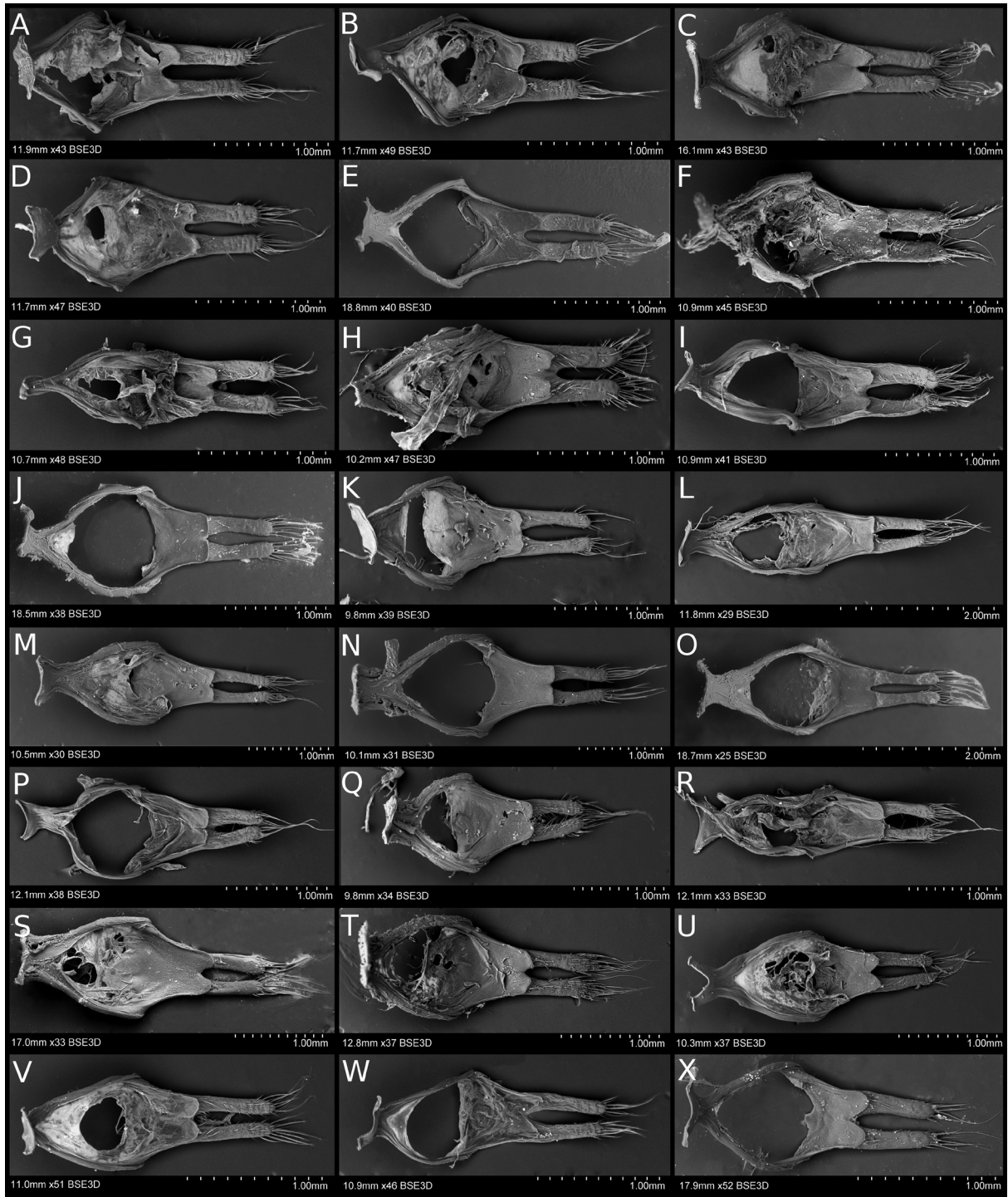


Figure 11. A–X, phallobases with parameres. A–E, *Ropalopus ungaricus ungaricus*, Slovakia, Slovakia, Poland, Austria and Montenegro, respectively. F–I, *Ropalopus ungaricus gallicus*, France. J–N, *Ropalopus ungaricus insubricus*, Italy, Croatia, Croatia, Croatia and Croatia, respectively. O, *Ropalopus ungaricus boreki*, Greece (Peloponnese). P–R, *Ropalopus ungaricus siculus*, Italy (Sicily). S, T, *Ropalopus ungaricus ossae*, Greece (Thessaly). U, V, *Ropalopus nataliyae*, Iran. W, X, *Ropalopus lederi*, Russia (north-west Caucasus).

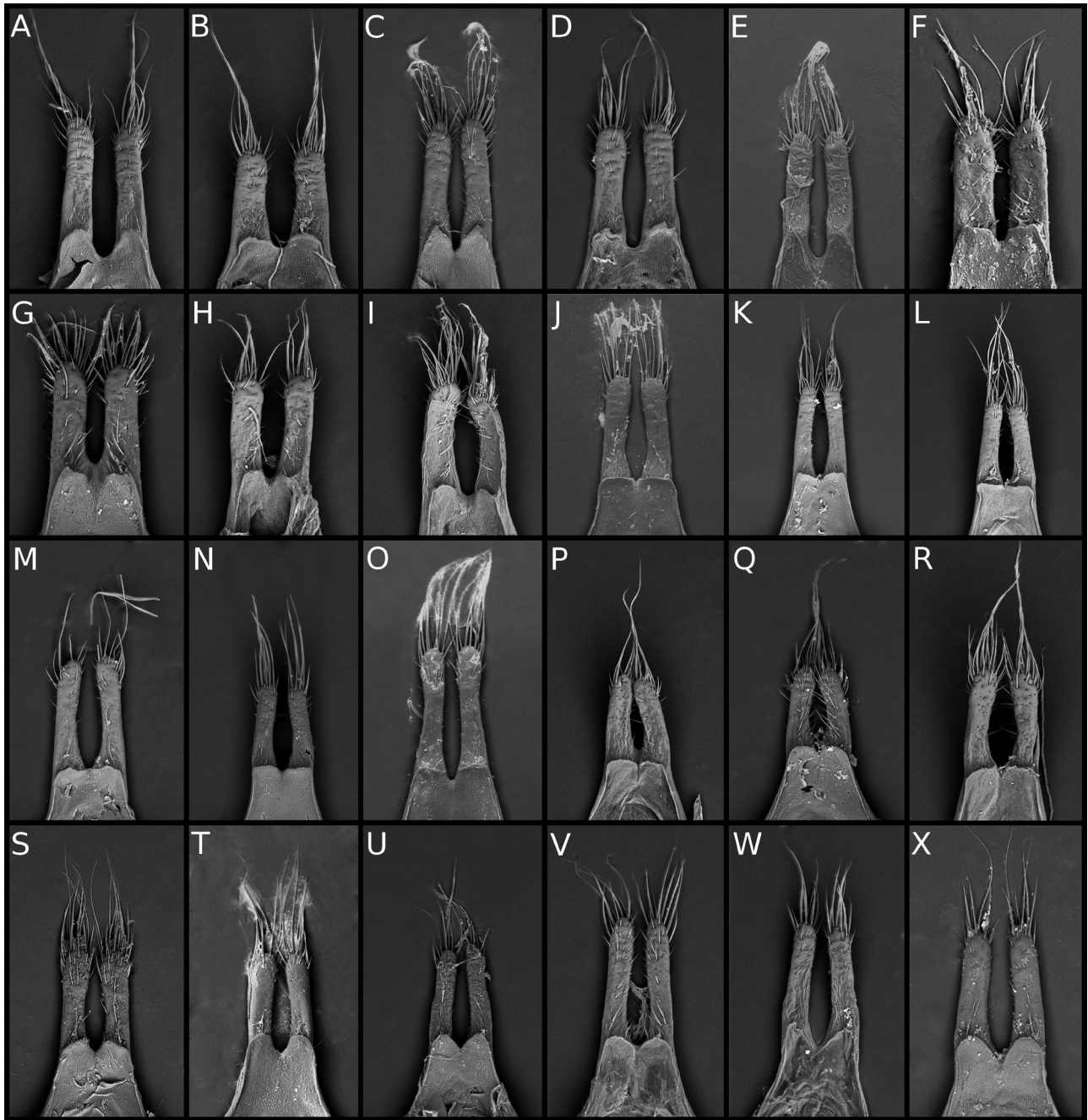


Figure 12. A–X, lateral lobes. A–E, *Ropalopus ungaricus ungaricus*, Slovakia, Slovakia, Poland, Austria and Montenegro, respectively. F–I, *Ropalopus ungaricus gallicus*, France. J–N, *Ropalopus ungaricus insubricus*, Italy, Croatia, Croatia, Croatia and Croatia, respectively. O, *Ropalopus ungaricus boreki*, Greece (Peloponnese). P–R, *Ropalopus ungaricus siculus*, Italy (Sicily). S, T, *Ropalopus ungaricus ossae*, Greece (Thessaly). U, V, *Ropalopus nataliyae*, Iran. W, X, *Ropalopus lederi*, Russia (north-west Caucasus).

stable character for distinguishing the specimens from Ukraine and the southern part of European Russia from those from the Balkans, the centre of the distribution of *R. insubricus insubricus sensu* Löbl & Smetana (2010).

The geographical distribution of all taxa is mapped and presented in Figure 20.

Species from the adopted group *Ropalopus ungaricus/insubricus* belong to the subgenus

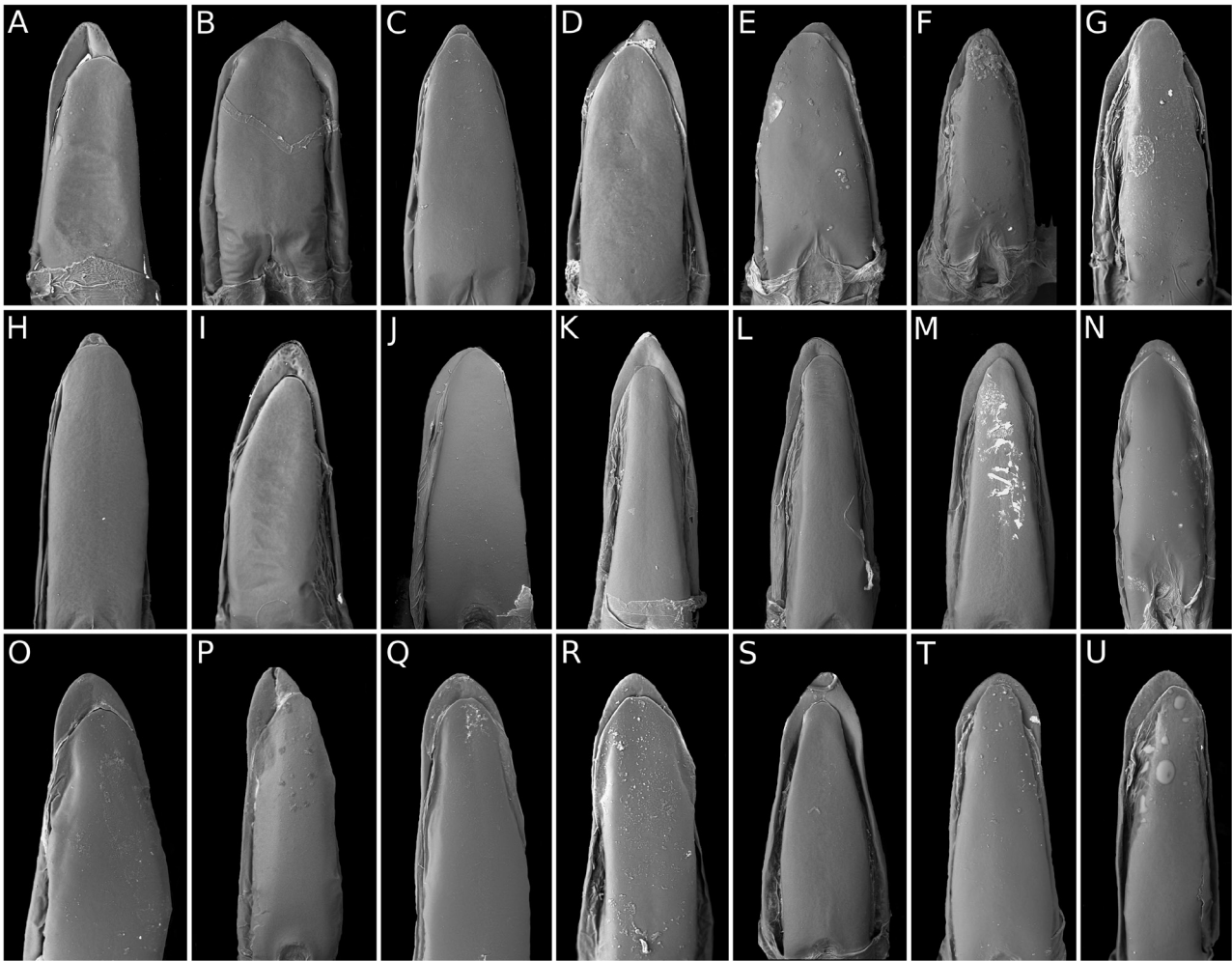


Figure 13. A–U, median lobes. A–E, *Ropalopus ungaricus ungaricus*, Slovakia, Slovakia, Poland, Austria and Montenegro, respectively. F–I, *Ropalopus ungaricus gallicus*, France. J–M, *Ropalopus ungaricus insubricus*, Italy, Croatia, Croatia and Croatia, respectively. N, *Ropalopus ungaricus boreki*, Greece (Peloponnese). O, *Ropalopus ungaricus siculus*, Italy (Sicily). P, Q, *Ropalopus ungaricus ossae*, Greece (Thessaly). R, S, *Ropalopus nataliyae*, Iran. T, U, *Ropalopus lederi*, Russia (north-west Caucasus).

Ropalopus Mulsant, 1839. As a result of this revision, a new taxonomic order in this group is proposed.

GENUS *ROPALOPUS* MULSANT, 1839

Ropalopus Mulsant, 1839, *Hist. Nat. Coléop. France, Longic.*: 39.

Type species: *Callidium insubricum* Germar, 1824; designated by Thomson (1864: 264).

SUBGENUS *ROPALOPUS* MULSANT, 1839

Type species: *Callidium insubricum* Germar, 1824; designated by Thomson (1864).

Synonyms

Calliopedia Binder, 1915: 186; type species: *Rhopalopus reitteri* Binder, 1915 (= *Callidium ungaricum* Herbst, 1784).

Euryoptera Horn, 1860: 571; type species: *Euryoptera sanguinicollis* Horn, 1860.

Rhopalopus L. Redtenbacher, 1845: 110 (unjustified emendation).

ROPALOPUS UNGARICUS (HERBST, 1784)

Distribution: Europe (including European Russia and westernmost Turkey) and North Africa (Algeria, probably also Morocco and Tunisia) (Fig. 20).

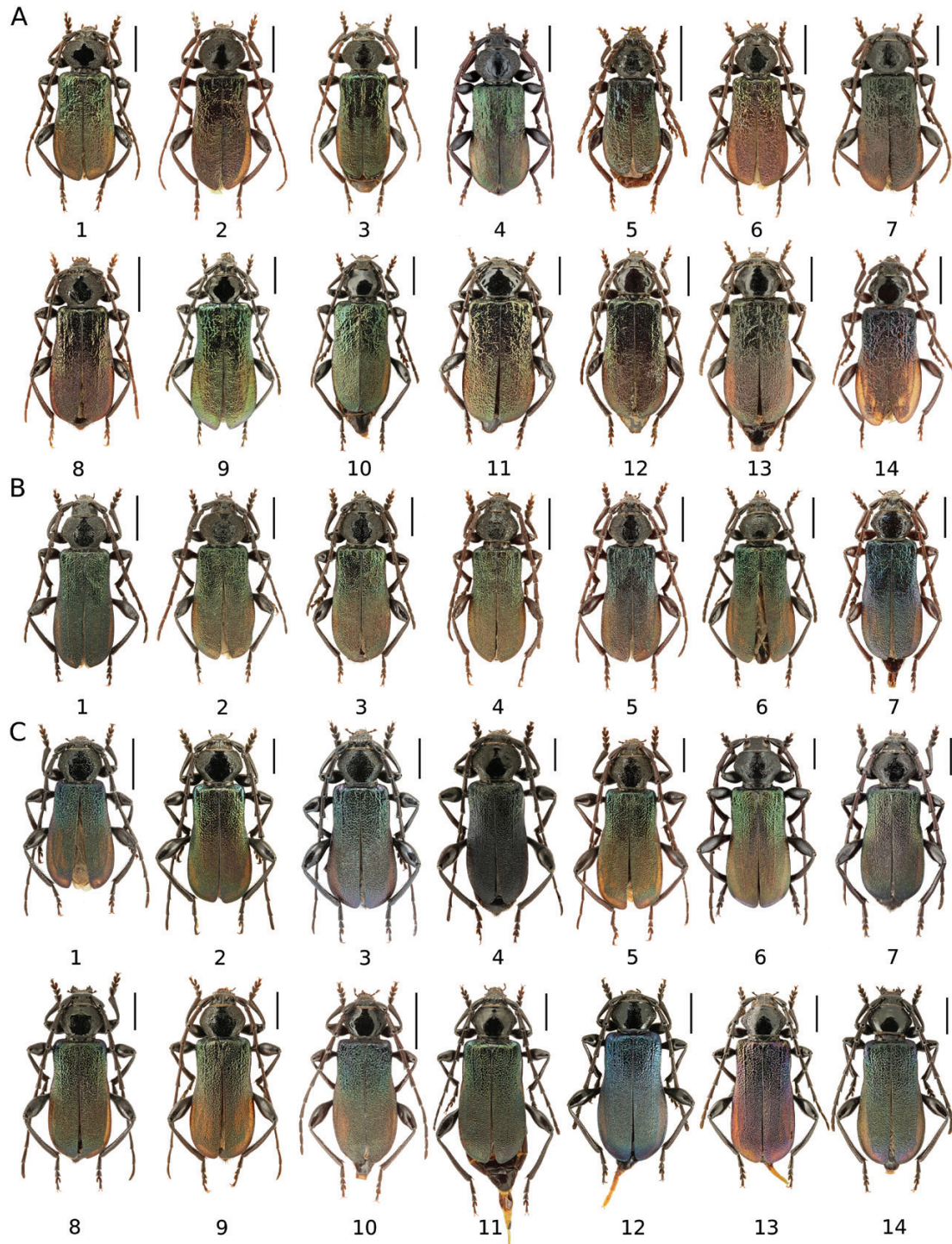


Figure 14. A1–C14, habitus (dorsal view). A, *Ropalopus ungaricus ungaricus*: 1–8, males, Poland, Czech Republic, Slovakia, Slovakia, Slovakia, Austria, France and Montenegro, respectively; 9–14, females, Poland, Czech Republic, Slovakia, Slovakia, France and Dalmatia, respectively. B, *Ropalopus ungaricus gallicus*: 1–5, males, France; 6–7, females, France. C, *Ropalopus ungaricus insubricus*: 1–9, males, Italy, Croatia, Croatia, Croatia, Croatia, Croatia, Bosnia and Herzegovina, Hungary and Ukraine, respectively; 10–14, females, Slovakia, Croatia, Croatia, Croatia and Hungary, respectively (photographs A4, C6, C7: www.hmyzfoto.cz). Scale bar: 5 mm.

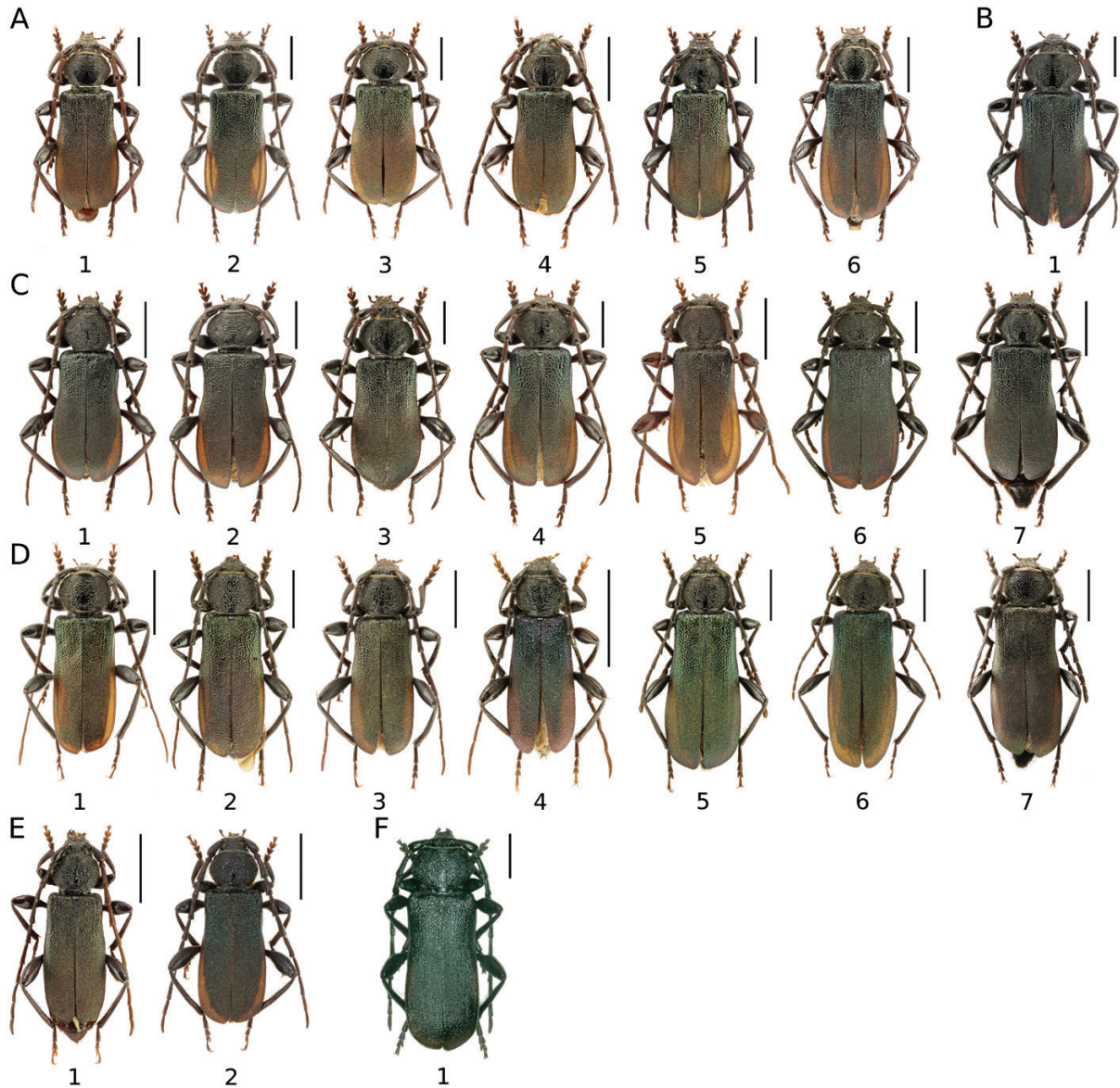


Figure 15. A1–F1, habitus (dorsal view). A, *Ropalopus ungaricus siculus*: 1–5, males, Italy (Sicily); 6, female, Italy (Sicily). B, *Ropalopus ungaricus boreki*: 1, male, Greece (Peloponnese). C, *Ropalopus ungaricus ossae*: 1 male holotype Greece (Thessaly); 2–5, male paratypes, Greece (Thessaly); 6–7, female paratypes, Greece (Thessaly). D, *Ropalopus nataliyae*: 1–4, males, Iran; 5–7, females, Iran. E, *Ropalopus lederi*: 1–2, males, Russia (north-west Caucasus). F, *Ropalopus hanae*: 1, male, Turkey (www.cerambyx.uochb.cz). Scale bar: 5 mm.

This is a highly variable taxon that to date has been considered a separate species apart from *R. insubricus* (with its three subspecies), *R. siculus* and the newly described *R. boreki sensu e.g. Danilevsky (2019a)*. Consequently, there was a difficult taxonomic situation, and many issues with both problematic specimens that show intermediate characters (and also probably some hybrids) and with determining the distribution of particular species in

Europe, especially in countries such as Italy, France, Hungary and Greece. Other issues concern some described varieties, e.g. *annulus* and *vogti*, that were transferred between the taxa *R. ungaricus* and *R. insubricus* (Sama, 2002).

Therefore, all European populations are reduced to subspecific level under this species. The following subspecies are proposed herein, with the specified distribution.

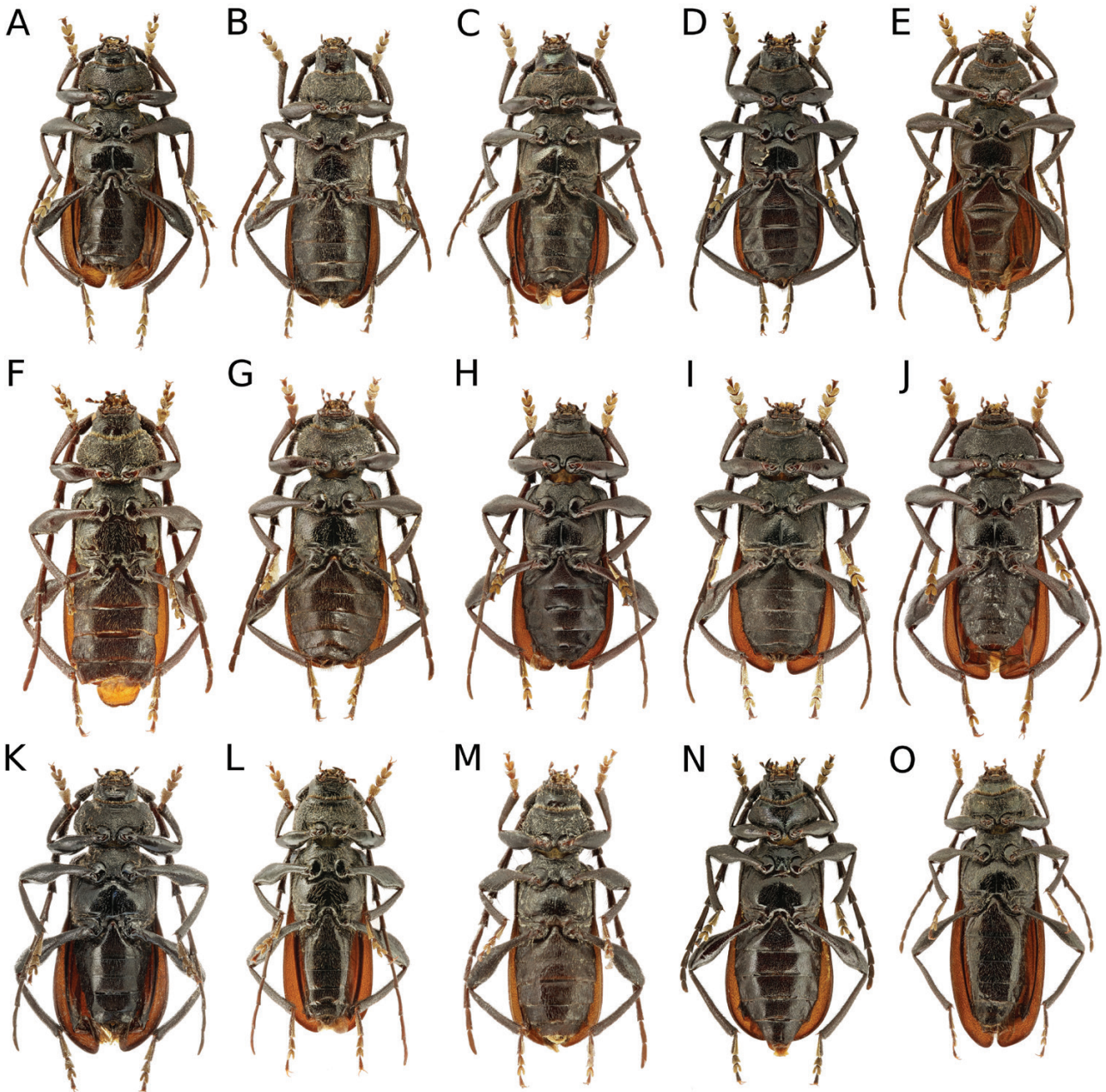


Figure 16. A–O, habitus (ventral view): A–M, males; N, O, females. A, *Ropalopus ungaricus ungaricus*, Poland. B, C, *Ropalopus ungaricus gallicus*, France. D, E, *Ropalopus ungaricus insubricus*, Hungary and Ukraine, respectively. F, G, *Ropalopus ungaricus siculus*, Italy (Sicily). H–J, *Ropalopus ungaricus ossae*, Greece (Thessaly) (H, holotype). K, *Ropalopus ungaricus boreki*, Greece (Peloponnese). L, *Ropalopus nataliyae*, Iran. M, *Ropalopus lederi*, Russia (north-west Caucasus). N, *Ropalopus ungaricus insubricus*, Hungary. O, *Ropalopus nataliyae*, Iran.

ROPALOPUS UNGARICUS UNGARICUS (HERBST, 1784)

(FIGS 1A, J, 2A–D, 3F, G, 4A–D, 5E–G, 6A, B, P, Q, 7A, O, P, 8A, N, O, 9A, B, 10A, B, K, L, 11A–E, 12A–E, 13A–E, 14A, 16A, 17A–F; SUPPORTING INFORMATION, FIGS S1A, B, P, Q, S2A, B, P, Q, S3A, J, S4A, 5A–C, P, Q, S6A–C)

Callidium ungaricum Herbst in Fuesslins, 1784, *Arch. Insectengesch.* 5: 96.

Type material examined: Lectotype (herein designated) male with four labels: (1)? SYNTYPE, *Callidium ungaricum* Herbst, 1784 labelled by

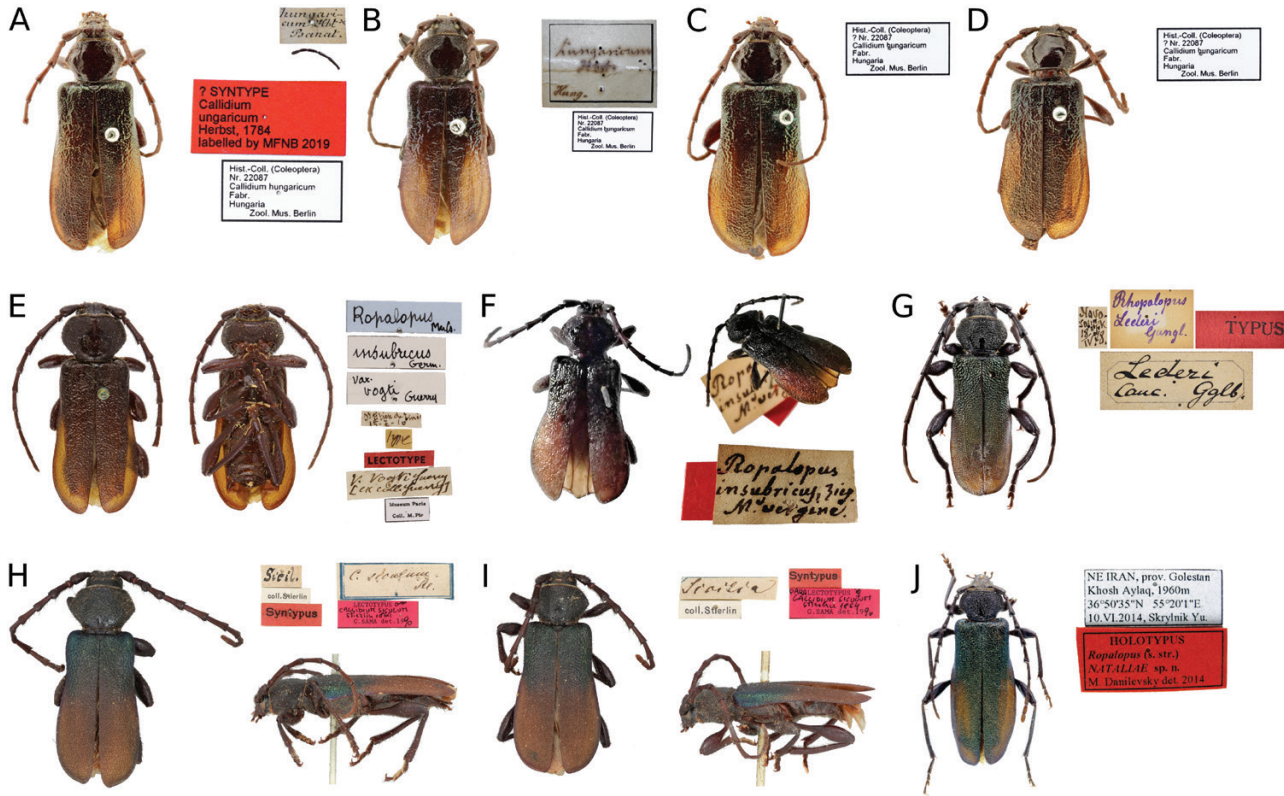


Figure 17. A–J, habitus (ventral/lateral view) of type material with labels. A, *Ropalopus ungaricus ungaricus*, lectotype. B–D, *Ropalopus ungaricus ungaricus*, specimens from Herbst’s collection. E, *Ropalopus insubricus* var. *vogti* sensu e.g. Sama (2002), lectotype (image: Azadeh Taghavian-Azari, MNHN). F, *Ropalopus insubricus* var. *annulus* sensu e.g. Sama (2002), lectotype (image: Roberta Improta, MZCM). G, *Ropalopus lederi*, lectotype (herein designated) (image: Schillhammer Harald, NHMW). H, *Ropalopus ungaricus siculus*, male, lectotype (image: Mandy Schröter, SDEI). I, *Ropalopus ungaricus siculus*, female, paralectotype (image: Mandy Schröter, SDEI). J, *Ropalopus nataliyae*, holotype (image: A. Slutsky).

Museum für Naturkunde Berlin 2019 (red); (2) *hungaricum* Hbt × Banat.; (3) Hist.-Coll. (Coleoptera), Nr. 22087, *Callidium hungaricum* Fabr. Hungaria, Zool. Mus. Berlin; and (4) L E C T O T Y P E, *Callidium ungaricum* Herbst in Fuesslins, 1784, des., 2019 (red).

Synonyms

- Callidium cognatum* Laicharting, 1784: 58.
- Cerambyx pannonicus* Gmelin, 1790: 1856.
- Ropalopus insubricus* var. *annulus* Costa, 1855: 30.
- Ropalopus insubricus* var. *vogti* Guerry, 1911: 99.

Distribution: Europe; from eastern France through the Alps and Carpathians to westernmost Ukraine and central Romania, and from south-western Poland (the Sudetes) to central Italy (here through the Apennines) and to Montenegro in the Balkans (Fig. 20). According

to Horák et al. (2010b), it is extinct in Switzerland. All records from the southern part of European Russia certainly belong to *R. u. insubricus* or other related taxa. The records from Spain (Andalusia) and North Africa (Algeria, Atlas Mountains) must refer to different taxa, and the specimens require further study.

Diagnosis: The nominative subspecies is characterized by the basal half of its elytra having variably intense but always pronounced irregular wrinkles and its evenly tapered pronotum with stains at the sides almost merged at the upper and lower margins in males (Fig. 2B). Males can also be distinguished from the two other subspecies with a lustrous pronotum (*R. u. gallicus* and *R. u. insubricus*) by the intermediate length of the antennae, which are about as long as the elytra. Additionally, there are differences in the lateral lobes of the tegmen (Fig. 12A), which, on the one hand, are generally thinner and longer than those of *R. u. gallicus* (Fig. 12G) and, on the other hand, are clearly more robust and usually shorter compared

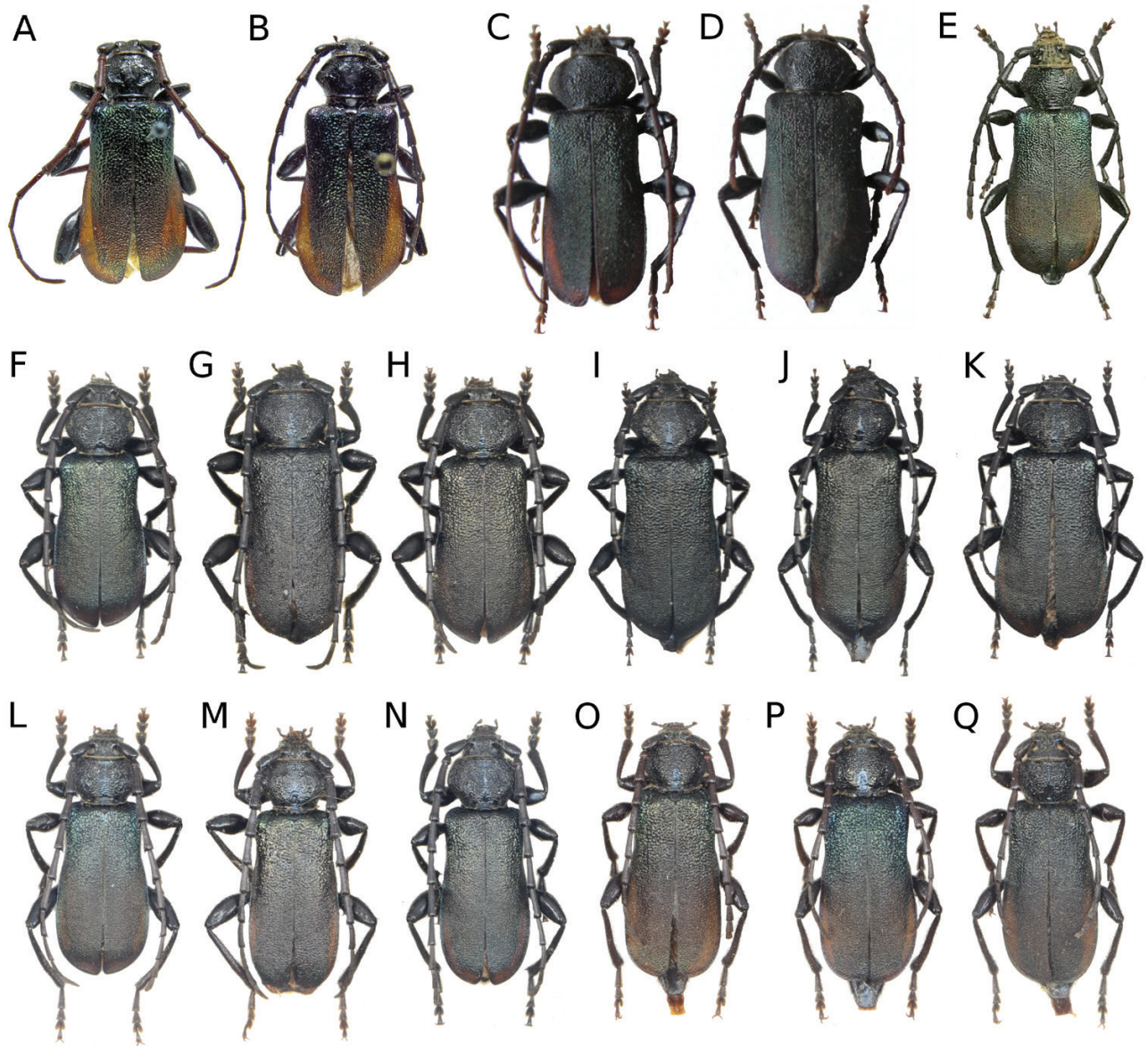


Figure 18. A–Q, habitus (ventral view) of peculiar specimens. A, B, *Ropalopus ungaricus insubricus*, Ukraine, male and female, respectively, specimens from the area near (~70 km south-east) the *locus typicus* of *Ropalopus insubricus fischeri sensu e.g. Löbl & Smetana (2010)* (image: M. L. Danilevsky). C, D, *Ropalopus hanae*, north Turkey (Kastamonu environs), male and female, respectively (image: N. and C. Auvray). E, *Ropalopus ungaricus ossae*, Greece (Kalabaka) (image: David Šanc). F–K, *Ropalopus ungaricus ossae*, Greece (www.cerambycidae-slama.cz). L–Q, *Ropalopus ungaricus* subsp., southern Italy (www.cerambycidae-slama.cz).

with *R. u. insubricus* (Fig. 12K). Moreover, the margin of the phallobase roof differs entirely from that of the last mentioned subspecies, and it always has a pronounced depression in the middle. The prosternal process (Fig. 9B) is relatively wide and rounded at the apex, and thus it is closest to *R. u. gallicus* (Fig. 9C), but it sometimes clearly expands at apex (Fig. 9A) or even bifurcates (Fig. 10K). Body length: 10.4–24.5 mm.

Remarks: *Ropalopus u. ungaricus* is definitely monophagous on maples (*Acer* spp.) or it is perhaps even solely associated ecologically with *Acer pseudoplatanus* L. There are no reliable data on the associations with other deciduous trees, such as *Ficus*, *Fraxinus*, *Alnus*, *Fagus* or *Salix*, and reports on development in conifers are obvious mistakes. The one on *Picea* after Binder (1915), which is also related to *Rhopalopus reitteri* Binder, 1915, clearly refers to *Callidium aeneum* (DeGeer, 1775).

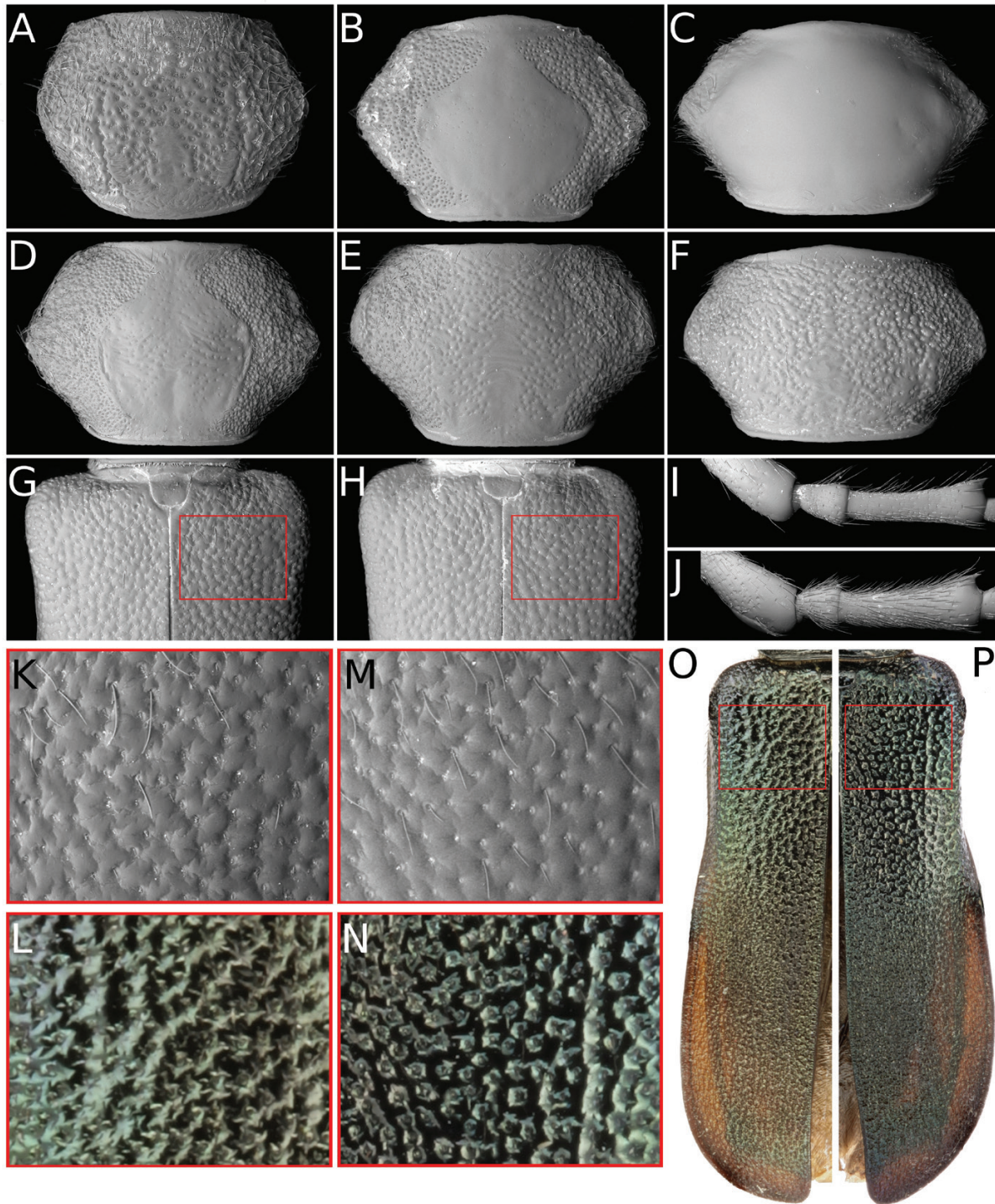


Figure 19. A–P, key characters of *Ropalopus*. A, *Ropalopus lederi*, male pronotum. B, *Ropalopus ungaricus ungaricus*, male pronotum. C, *Ropalopus ungaricus ungaricus*, female pronotum. D, *Ropalopus ungaricus gallicus*, male pronotum. E, *Ropalopus ungaricus siculus*, male pronotum. F, *Ropalopus ungaricus ossae*, female pronotum. G, *Ropalopus ungaricus ossae*, male elytra. H, *Ropalopus ungaricus boreki*, male elytra. I, *Ropalopus nataliyae*, second antennal joint. J, *Ropalopus ungaricus insubricus*, second antennal joint. K, L, *Ropalopus ungaricus ossae*, elytral sculpture. M, N, *Ropalopus ungaricus boreki*, elytral sculpture. O, *Ropalopus ungaricus ossae*, left elytron. P, *Ropalopus ungaricus boreki*, right elytron.

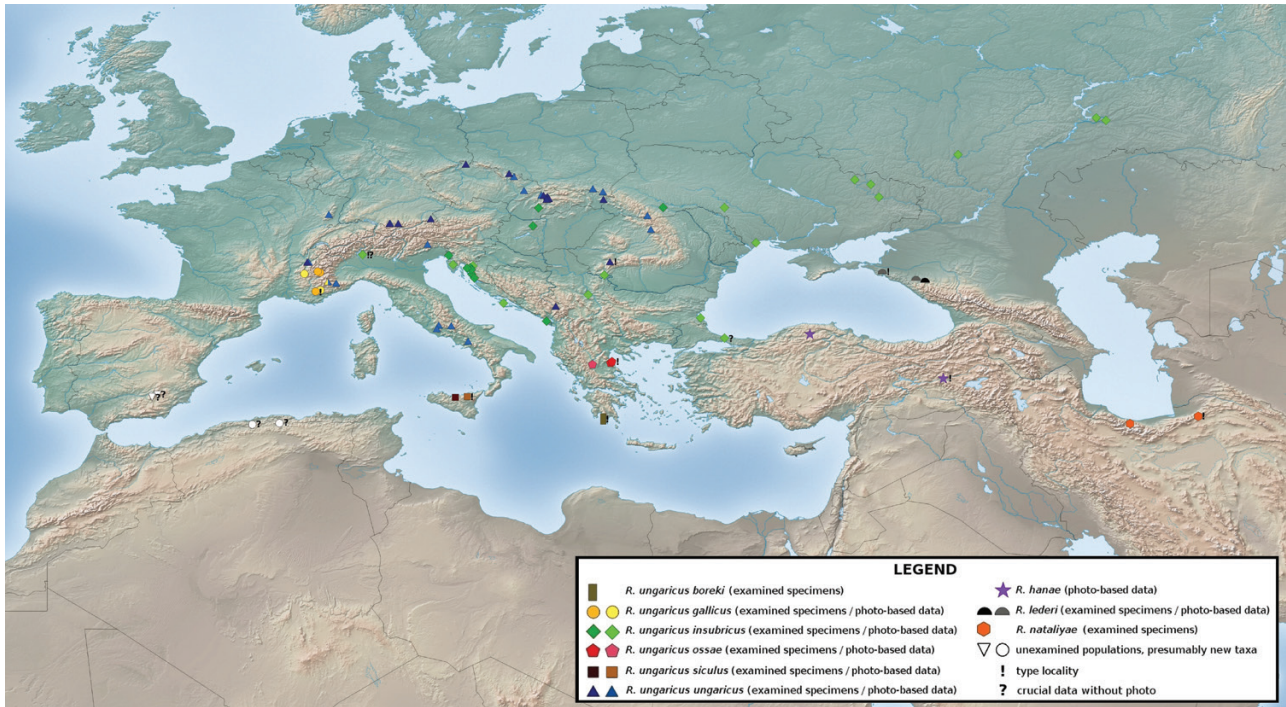


Figure 20. Distribution of *Ropalopus ungaricus/insubricus* taxa.

Hence, a corrected synonymy is proposed: *Cerambyx aeneum* DeGeer, 1775 = *Rhopalopus reitteri* Binder, 1915, and *Callidostola* Reitter, 1913 = *Calliopedia* Binder, 1915. Imagines of *R. u. ungaricus* occur in nature from June to August.

A lectotype from the former collection of Herbst housed in ZMB is herein designated (Fig. 17A) to fix the name on a single specimen.

ROPALOPUS UNGARICUS INSUBRICUS (GERMAR, 1824) **stat. nov.**

(FIGS 1D, L, 2H–K, 3I–K, 4H–J, 5I–K, 6F, G, S, T, 7E, F, R–T, 8D, E, Q, 9D, 10D, E, M, N, 11J–N, 12J–N, 13J–M, 14C, 16D, E, N, 18A, B; SUPPORTING INFORMATION, FIGS S1F, G, S, T, S2F, G, S, T, S3C, L, S4C, S5F, G, S, T, S6G, H)

Callidium insubricum Germar, 1824, *Ins. spec. nov.* 1: 514.

Synonyms

Callidium fischeri Krynicki, 1829: 197, syn. nov.

Rhopalopus viridipennis Pic, 1926: 6.

Distribution: Europe; from northern Italy through Slovenia to Hungary, Slovakia and the Balkans and to westernmost Turkey, and through Romania and Ukraine to the southern part of European Russia (Fig.

20). It probably also occurs in Moldova, but with the centre of occurrence along the Adriatic Sea coast in Croatia and Montenegro. It is possibly already extinct in southern Austria. All the localities from France relate to another subspecies: *R. u. gallicus*, and partly to *R. u. ungaricus* (Table 1). Furthermore, the records from North Africa (Atlas Mountains) must refer to different taxa. *Ropalopus u. insubricus* was described from ‘Italia’; however, there are some issues in establishing the *locus typicus* (see Discussion for more details).

Diagnosis: This subspecies differs in its densely reticulated elytra without any wrinkles in its basal half, in combination with the unevenly tapered pronotum with large rhomboid area that is at most slightly punctate. Males can be distinguished from the two other subspecies with a lustrous pronotum (*R. u. gallicus* and *R. u. ungaricus*) by the length of antennae, which are clearly longer than the elytra, and the shape of stains with deeper punctation on each sides of pronotum that are narrow and irregular, never about to merge into each other (Fig. 2K). Additionally, there are differences in the lateral lobes (Fig. 12L), which are definitely finer and narrower in *R. u. insubricus*, and the margin of the phallobase roof is almost straight, with at most a small depression in the middle (Fig. 12N). They are much more similar to those of *R. u. boreki* (Fig. 12O). The prosternal process (Fig. 10D) is rather stable in shape (but it sometimes bifurcates in females, as in Fig. 10N),

and it is also closest to *R. u. boreki* (Fig. 10F). Females are more difficult to distinguish, and mainly the elytral macrosculpture in the basal part and slight wrinkles on the pronotum need to be taken into account. Body length: 14.0–31.0 mm.

Remarks: *Ropalopus u. insubricus* is a lowland–upland subspecies that only occurs at lower elevations, not higher than 600 m a.s.l. This makes it ecologically related to *R. u. boreki* from the Peloponnese. Taking the significant similarities in morphology of these two taxa into account, they are herein considered vicariant subspecies. Like all taxa of this group, it is ecologically associated with *Acer* spp., and although it was reported by many authors at least occasionally from other species of deciduous trees, such as *Alnus*, *Fagus*, *Ficus*, *Fraxinus* and *Salix* (e.g. by Bense, 1995; Sama, 2002), no such cases, that are fully confirmed, are known to the authors of this work. Adults appear in June and survive until August.

***ROPALOPUS UNGARICUS SICULUS* (STIERLIN,
1864) stat. nov.**

(FIGS 1F, M, 2M, N, 3L, 4L, M, 5L, 6I, J, U, 7H, I, U, 8G, H, R, 9E, 10G, 11P, R, 12P, R, 13O, 15A, 16F, G, 17H, I; SUPPORTING INFORMATION, FIGS S1I, J, U, S2I, J, U, S3E, M, S4E, S5I, J, U, S6I, J)

Callidium siculum Stierlin, 1864, *Berl. Entomol. Zeitschr.*, 8: 152.

Distribution: Italy (Sicily); apparently not in Algeria (Fig. 20). This taxon was described from Sicily where, according to Verdugo *et al.* (2016), it is known from five localities. Sama & Schurmann (1980) claimed that it seems to be located in the deciduous forests of the Madonie Mountains, but its presence was not ascertained in other Sicilian mountains despite detailed investigation. New records from Greece refer to the new subspecies *R. u. ossae*, and the old ones from the European part of Turkey, after Winkler (1929), are evidently mistakes and probably relate to *R. hanae* or even *R. u. insubricus*. Considering the biogeography of western Palaearctic Cerambycidae (Vitali & Schmitt, 2017), the records from North Africa (Algeria) must refer to another, as yet undescribed, taxon.

Diagnosis: The subspecies is characterized by the combination of its evenly tapered and relatively narrow pronotum with almost entirely punctate or wrinkled disc, rather light-coloured elytra of green or copper sheen and, in particular, by its pronounced and dense yellowish pubescence on the ventral side of the body, especially on the prosternum and mesosternum (Fig. 16F, G). Apart from the different character of the

ventral pubescence and lighter elytral coloration, it can be distinguished from *R. u. boreki*, inter alia, by different elytral sculpture and shape of the pronotum, and from *R. u. ossae* by the shorter antennae, which are usually only slightly longer than the elytra in males. There are also differences in the lateral lobes of the tegmen and the margin of the phallobase roof (Fig. 12P–R), especially compared with *R. u. boreki* (Fig. 12O). Body length: 14.0–20.2 mm according to Bense (1995) or up to 24.0–25.0 mm according to Hoskovec *et al.* (2019).

Remarks: *Ropalopus u. siculum* is known only from areas located at relatively high elevations, between 1100 and 1500 m a.s.l., in Sicily. In this regard, it seems to be more related to high-elevation taxa (*R. u. ungaricus* and *R. u. ossae*) rather than to lowland–upland subspecies (*R. u. insubricus* and *R. u. boreki*). Adults occur in June and July. This subspecies is indisputably associated ecologically with maples (*Acer* spp.), probably solely with *Acer campestre* L., which is remarkably distributed in the northern part of Sicily and in a relatively small area in north-eastern Algeria, close to the Tunisian border (Nagy & Ducci, 2004). However, as stated above, the records of *R. u. siculum* from North Africa are most probably related to another taxon that develops in *Acer obtusatum* Waldst. & Kit. ex Willd. (Peyerimhoff, 1919; Villiers, 1946).

***ROPALOPUS UNGARICUS BOREKI* RAPUZZI,
2017) stat. nov.**

(FIGS 1E, 2L, 4K, 6H, 7G, 8F, 10F, 11O, 12O, 13N, 15B, 16K; SUPPORTING INFORMATION, FIGS S1H, S2H, S3D, S4D, S5H)

Distribution: Greece (Peloponnese) (Fig. 20). This taxon was described from the vicinity of Neo Itilo (Lakonia), and no further locations are known to date.

Diagnosis: The subspecies is mainly characterized by its elytral sculpture, which is clearly separated around the middle and consists of deeper and larger points on the basal (metallic) half and much thinner and denser points on the second (matt) half (Fig. 19P), also by its pronotum, which is unevenly tapered towards the anterior and posterior margins and is uniformly densely punctate. Besides the elytral sculpture and shape of the pronotum, it can be distinguished from *R. u. siculum* by the completely different pubescence on the ventral side of the body (Fig. 16K and 16F, respectively) and from *R. u. ossae* by shorter antennae, which are as long as the elytra in males. Moreover, there are clear differences in the median lobe (Fig. 13N) and

tegmen (Fig. 11O), which in turn is the most similar to *R. u. insubricus* (Fig. 11J). Also, the prosternal process (Fig. 10F) is closest to *R. u. insubricus* (Fig. 10D). Generally, the specimens of *R. u. boreki* have dark, blackish green body colour, which seems to be constant in this taxon. According to the original description, all paratypes are similar to the holotype, and they do not show any significant variability. Body length of a male holotype: 22.0 mm.

Remarks: *Ropalopus u. boreki* is known only from the area located on the Greek Mediterranean Sea coast at low elevation of ~200–400 m a.s.l. The taxon probably does not exceed 500–600 m a.s.l., making it ecologically similar to *R. u. insubricus*, which is mainly distributed along the Adriatic Sea coast, in Italy, Croatia and Montenegro. Taking also into consideration the significant similarities in the morphology of these two taxa (e.g. pronotum, tegmen and prosternal process), they are considered herein vicariant subspecies. It is worth noting that *R. u. boreki* can be attracted to fermenting bait traps, unlike *R. u. siculus*. A series of type specimens was collected between 15 and 25 June (Rapuzzi, 2017). The only material that is known to date is rather poor and largely unavailable owing to the collectors' activity and the high prices that specimens of this taxon fetch at Internet auctions and entomological fairs.

ROPALOPUS UNGARICUS GALLICUS VARTANIS, 2018

(FIGS 1B, C, K, 2E–G, 3H, 4E–G, 5H, 6C–E, R, 7B–D, Q, 8B, C, P, 9C, 10C, 11F–I, 12F–I, 13F–I, 14B, 16B, C; SUPPORTING INFORMATION, FIGS S1C–E, R, S2C–E, R, S3B, K, S4B, S5D, E, R, S6D–F)

Distribution: South-eastern France (Fig. 20). This taxon was described from Aiguines, and several new localities in south-eastern France are herein added (Table 1). Most of these were incorrectly assigned to *R. u. insubricus*.

Diagnosis: *Ropalopus u. gallicus* is characterized by its relatively short elytra, the pronotum with its lustrous area predominantly slightly punctate and wrinkled (Fig. 2E), and the antennae, which are usually much shorter than the body in males. Moreover, the pubescence of the ventral side of the body is characteristic owing to the abundant long, whitish hairs (Fig. 16B), which is the best trait for distinguishing it from both of the closest taxa, *R. u. ungaricus* and *R. u. insubricus* (Fig. 16A and D, respectively). There are also clear differences in the shape of the lateral lobes (Fig. 12G), which are by far the shortest and widest in the discussed group. In contrast, the prosternal process (Fig. 9C) does not

seem to differ from *R. u. ungaricus* (Fig. 9B). Body length: 17.0–20.0 mm.

Remarks: Despite its original classification as a subspecies of *R. insubricus sensu* e.g. Sama (2002) and Vartanis (2018), this taxon is evidently more closely related to *R. u. ungaricus*, but the elytra at the base are less frequently and less markedly wrinkled. The type locality of this taxon lies at medium elevation of ~1000 m a.s.l.; thus, although it overlaps, in part, with the range of elevations inhabited by *R. u. ungaricus*, it can be regarded as a transitional elevation between the latter and *R. u. insubricus*. The imagines were collected in the first days of July. This subspecies is indisputably associated ecologically with maple (*Acer* sp.) (Vartanis, 2018).

ROPALOPUS UNGARICUS OSSAE subsp. nov.

(FIGS 1G, N, 2O, 3A, M, N, 4N, O, 5M, N, 6K, L, V, W, 7J, K, V, W, 8I, J, S, T, 9F, 10H, O, 11S, T, 12S, T, 13P, Q, 15C, 16H–J, 18E–K, SUPPORTING INFORMATION, FIGS S1K, L, V, W, S2K, L, V, W, S3F, N, S4F, S5K, L, V, W, S6K, L)

LSID:urn:lsid:zoobank.org:act:FDF45041-7065-4AEC-AA24-94D207C1599C

Type material examined: Fourteen ♂♂ and four ♀♀.

Holotype: Male (Figs 15C1, 16H), Greece, Thessaly, Stomio (Larissa), Mount Ossa, 1 July 2003, ~600 m a.s.l., on *Acer* sp., C. Cocquempot leg. (from CCC, deposited in ZMB).

Paratypes: Greece, Thessaly, Stomio (Larissa), Mount Ossa: nine ♂♂ and two ♀♀, 1 July 2003, ~600 m a.s.l., on *Acer* sp., C. Cocquempot leg.; two ♂♂, 25 June–14 July 2011, no collector data; two ♀♀, 15 June–1 July 2013, F. Fiedler leg.; one ♂, 11 July 2014, J. Steinhofner leg.; Spilia environs (Larissa), Mount Ossa: one ♂ and one ♀, 5 March 2016 and 30 April 2016 ex larva (12–16 May 2014, *Acer* sp.), J. Steinhofner leg.; one ♂, 17 April 2016 ex larva (9 July 2014, *Acer* sp.), J. Steinhofner leg. (deposited in CAW, CCC, CJS and CLKR).

Additional material studied, based on photographs: Central Greece, Thessaly: four ♂♂ and three ♀♀, Mount Ossa; one ♀, Kalabaka.

Description: Body length: males 14.1–23.0 mm (HT 22 mm), females 17.3–24.3 mm. Body width at elytral base: males 4.4–7.0 mm, females 5.3–7.7 mm. Body width behind middle: males 5.3–7.9 mm,

females 6.6–8.9 mm. Integument of whole body from dark brown to black; legs and antennae usually lighter; head and prothorax dark brown; elytra constantly dark with greenish brown metallic lustre. Pubescence of whole body made by sparse, short, brown and black hairs, more pronounced on basal part of elytra and sides of pronotum but completely lacking in its central part; on ventral side (Fig. 16H–J) rather constant, fine, dense and barely noticeable on abdomen and thorax, with slightly denser whitish hairs around mesosternal process and on prothorax. Head relatively small, strongly punctured; forehead strongly marked with longitudinal furrow of variable depth between antennal tubercles (Supporting Information, Fig. S1K, L); clypeus and labrum relatively wide and well pronounced; mandibles strong, wide and obtusely toothed (Fig. 1G); eyes large, surrounding antennal tubercles (Supporting Information, Fig. S2K). Antennae thick and robust, long, clearly exceeding elytral length by almost two last joints in males, and reaching two-thirds of elytral length in females; with denser and more pronounced erect setae on inner side. Antennomere 1 densely pubescent with thick recumbent setae; antennomere 2 triangular, about as long as wide at the widest point, with thicker longer and more erect setae (Supporting Information, Fig. S3F); antennomere 3 slightly longer than antennomeres 5–7; antennomere 4 about as long as antennomeres 8 and 9; apical joint ~5.0 times longer than wide in males and ~2.5 times in females; antennomeres 3–8 (sometimes to 9) with pronounced long tooth on inner side. Pronotum evenly tapered towards anterior and posterior margin, in males usually clearly transverse, ~1.6 times (HT 1.55) wider than long, elliptical in shape (Fig. 15C2), sometimes narrower and more rounded on sides (Fig. 15C5); in females smaller, narrower than elytra, ~1.6 times wider than long; in both sexes usually entirely punctate, but sometimes with glabrous smooth area near base; punctation variable, punctured or rugose, usually uniformly dense, sometimes more sparse in central part; always dense and fine at sides, forming there more-or-less visible, usually asymmetrical and narrow strips with sparse but clearly visible relatively long hairs (Fig. 3A); pubescence in remaining part of pronotum scant and short, barely perceptible, mainly along upper and lower edges. Prosternum finely and densely punctate, with sparse, short whitish pubescence and row of short, thick, dense erect hairs along upper edge. Prosternal process (Figs 9F, 10H) relatively narrow and rounded at apex. Elytra long, in males ~2.2 times (HT 2.23) longer than wide at base and ~1.9 times (HT 1.88) behind middle; in females ~2.3 and 1.9, respectively; almost parallel sided in anterior

third, then clearly expanding towards end; elytral sculpture mainly made by indistinct points with creased and convex surface between them (Fig. 19G, K, L), with gradual change in the depth and density of points towards the end (Fig. 19O); scutellum of variable shape, usually irregularly dotted. Mid and hind femora wide in males, narrower in females; posterior tibiae nearly straight, with distinct erect setae at inner margin.

Male terminalia: Median lobe (Fig. 13P, Q) relatively slender, lanceolate, slightly narrowed before apex. Lateral lobes of tegmen short and robust, adjoining at ends, with external margin convex and relatively short hairs on top (Fig. 12S, T); margin of phallobase roof clearly concave at middle (Fig. 11S, T).

Differential diagnosis: *Ropalopus u. ossae* can be distinguished from *R. u. boreki* by its different elytral sculpture, which is additionally more uniform on its whole surface, by its pronotum, which is evenly tapered towards the anterior and posterior margins, and, in males, by constantly longer antennae and clearly different parameres, which are definitely shorter and more robust. The new subspecies is evidently more related to *R. u. siculus*, from which it is separated by longer antennae, the overall stronger structure of the body and its bigger size, and by the clearly shorter, sparser and less pronounced pubescence on the ventral side of the body (Fig. 16H and 16F, respectively). Moreover, there are differences in the margin of the phallobase roof, which is clearly concave in the middle, and in the lateral lobes with relatively short hairs that are additionally always remarkably twisted together on the top in the newly described subspecies (Fig. 12S–T and P–R, respectively). The prosternal process (Fig. 9F) is closest to *R. u. siculus* (Fig. 9E). Generally, specimens of *R. u. ossae* have a darker elytra colour, which is constant in this taxon; therefore, they seem to be blackish even in daylight, whereas specimens of *R. u. siculus* are normally green to brownish.

Remarks: The specimens of *R. u. ossae* were found at elevations between 500 and 1100 m a.s.l. They were collected on Mount Ossa (mostly on the eastern slopes) from the second half of June to mid-July. There is no doubt that the larvae of this taxon develop in the wood of maples (*Acer* spp.). Some unpublished records relating to other tree species, such as *Platanus* sp., have not been confirmed and are not supported herein. It is worth noting that there are independent ecological observations indicating a difference in behaviour between *R. u. ossae* and *R. u. siculus*; the taxon from Greece is frequently attracted to wine/sugar traps, unlike the Sicilian subspecies. There is also a series of peculiar specimens from the southern

part of continental Italy (Fig. 18L–Q; Sláma, 2018) that exhibit intermediate characters between these two taxa (see Discussion for more details).

Etymology: The specific epithet is a toponym referring to Mount Ossa (Greek: Όσσα) in the Larissa regional unit, Thessaly, Greece, which is the type locality of this new subspecies.

ROPALOPUS LEDERI (GANGLBAUER, 1882)

(FIGS 1I, 3D, E, 5C, D, 6N, O, 7M, N, 8M, 9H, 10J, 11W, X, 12W, X, 13T, U, 15E, 16M, 17G; SUPPORTING INFORMATION, FIGS S1N, O, S2N, O, S3H, I, S4H, S5N, O, S6O)

Rhopalopus lederi Ganglbauer, 1882, *Verh. zool.-bot. Ges.* 31[1881]: 747.

Type material examined: Lectotype (herein designated) male, with five labels: (1) TYPUS (red); (2) Novorossiysk 18 IV 78; (3) *Rhopalopus Lederi* Gangl.; (4) *Lederi* Cauc. Gglb.; and (5) L E C T O T Y P E, *Rhopalopus Lederi* Ganglbauer, 1882, des., 2019.

Synonyms

Rhopalopus nigripes Pic, 1926.

Distribution: The Caucasus and Crimea. It is present in southern Russia (Krasnodar Krai, Adygea), Georgia, Azerbaijan, Armenia and southern Crimea (Fig. 20). Although it has been reported from Turkey by Löbl & Smetana (2010), which was repeated by Danilevsky (2019a), its occurrence there was revised by Sama (1996). The record from Merzifon (south-western Samsun) after Adlbauer (1992) refers to *Ropalopus sculpturatus* (Pic, 1931). Therefore, *R. lederi* is to date not known to occur in Turkey. The reference from Palestine by Plavilstshikov (1940) is certainly a mistake and must refer either also to *R. sculpturatus* or is an incorrect citing of a record of *Ropalopus ledereri* (Fairmaire, 1866). A mention by Plavilstshikov (1940) from northern Iran is particularly interesting, because it might refer to *R. nataliyae* and, if so, this or those specimen(s) should have been taken into consideration when describing the species.

Diagnosis: *Ropalopus lederi* is generally distinctive owing to its long and pronounced body pubescence (especially, hairs on the pronotum and basal part of the elytra; Figs 3D, E, 5C, D), relatively slender antennae and tarsi (Fig. 8M), pronotum that is rounded in males, and elytra with only slight metallic lustre. It can be distinguished easily from its closest

relative, *R. nataliyae*, by the second antennal joint, which is almost spherical in *R. lederi* (Supporting Information, Fig. S3H) and clearly longer than wide in *R. nataliyae* (Supporting Information, Fig. S3G). The ventral side of the body (Fig. 16M) has a clearly visible yellowish pubescence, especially on the prothorax and mesothorax. According to Plavilstshikov (1940), the elytra are usually brown or dark brown, metallic, with a green, brown or purple lustre, and the legs are black or black–brown (*f. typica*), or red–brown to rusty (*ab. separatus* Pic). Body length: 9.0–23.0 mm.

Remarks: According to Plavilstshikov (1940), *R. lederi* inhabits deciduous and mixed forests, groves and orchards. Imagines are active from June to August. Although this author stated that the host plant remains unknown, a single pupa of this species was found in a maple trunk lying on the ground, most probably Trautvetter's maple *Acer heldreichii* Boiss. & Heldr. subsp. *trautvetteri* (Medw.) E. Murray, in June by Miroshnikov (Lobanov, 2003). Moreover, Miroshnikov (2010) noted the low elevation above sea level of his newly discovered locations (Gelendzhik environs, Pshadsky Pass, 150 m a.s.l.; Seversky District, Ubinskaya village, ~200 m a.s.l.), contrasting with the findings of this species in the western Caucasus, where it is mainly known from highland regions. Owing to the significant discrepancy in the elevations of inhabited habitats and the certain incompatibility concerning morphology between the specimens that were studied and some of them illustrated and available on the Internet (such as antenna thickness and shape of pronotum), the existence in this region of two forms isolated by elevation (analogous to *R. u. ungaricus* and *R. u. insubricus*) cannot be excluded.

A lectotype from the former collection of L. Ganglbauer housed in NHMW is herein designated (Fig. 17G) to fix the name to a single specimen.

ROPALOPUS HANAE SAMA & REJZEK, 2002

(FIGS 15F1, 18C, D)

Distribution: Turkey (Fig. 20). The species was described from the Buğlan Geçidi Pass located ~40 km north-west of Muş (eastern Turkey), but later it was also recorded several times from Mount Yarıligöz in the environs of Kastamonu (northern Turkey) (N. and C. Auvray, 2019, personal communication). Given that the second locality is located > 700 km to the north-west, the species is probably more widely distributed in most of north-eastern Turkey.

Diagnosis: *Ropalopus hanae* is mainly characterized by its elongate body and parallel-sided elytra with only

a slight green metallic lustre, a nearly flat head, lacking a longitudinal furrow between the eyes, entirely and densely microgranulate punctured, strongly transverse pronotum and slender antennae of the same length as the body (Sama & Rejzek, 2002). According to the original description, *R. hanae* differs from the closest related taxa, *R. lederi* and *R. u. siculus*, by its head lacking a longitudinal furrow between the antennal elevations and by the extremely fine punctures in the apical half of the elytra. Additionally, it can be distinguished easily from *R. u. siculus* by evidently more slender antennae and the entirely punctured pronotum. Body length of the male holotype (Fig. 15F1): 24.0 mm.

Remarks: The area of the type locality of *R. hanae* is situated at an elevation of 1640 m a.s.l. The specimen was collected between 22 and 23 June and captured on a branch of a living shrubby *Quercus* species. However, it is considered by the authors to develop in *Acer* spp., like the rest of the species in this group. Some maple trees were observed in the type locality (Sama & Rejzek, 2002). There are also records of a further 15 specimens (Fig. 18C, D) belonging to this species that were collected over several years in an *Acer–Quercus* forest on the slopes of Mount Yaraligozin (Kastamonu environs) in the second half of July (N. and C. Auvray, 2019, personal communication). This plot is located at an elevation of ~1400 m a.s.l. According to the collectors, all specimens were attracted to traps that were hung solely on oaks, and this tree species was dominant in the habitat. Although this might suggest a possible association with *Quercus*, larval development of *R. hanae* in *Acer* cannot be excluded on this basis.

ROPALOPUS NATALIYAE DANILEVSKY & SKRYLNIK,
2014

(Figs 1H, O, 3B, C, O, 5A, B, O, 6M, X, 7L, X, 8K, L, U, 9G, 10I, 11U, V, 12U, V, 13R, S, 15D, 16L, O, 17J; SUPPORTING INFORMATION, FIGS S1M, X, S2M, X, S3G, O, S4G, S5M, X, S6M, N)

Distribution: Northern Iran (Fig. 20). The species was described from the environs of Khoshyeylāq in Golestan Province (north-east Iran), but it is now also known from the environs of Marzanabad in Mazandaran Province (northern Iran).

The original description of *R. nataliyae* was based on a single female. Additional abundant material has since been collected, including several males hitherto unknown to science; therefore, the species can be redescribed herein in more detail.

Material examined: Sixteen ♂♂ and eleven ♀♀, north-east Iran, Golestan Province, 3 km south-west

of Khoshyeylāq, 24 May 2018, Lech Kruszelnicki leg.; one male: N Iran, Mazandaran Province, 28 km east of Marzanabad, 18 May 2018, Lech Kruszelnicki leg.

Redescription: Body length: 9.6–21.0 mm. Body width at elytral base: 3.1–6.0 mm. Body width behind middle: 3.3–7.5 mm. Body black; legs and antennae usually brown–black, sometimes slightly reddish. Pubescence of whole body yellowish, most pronounced on basal part of elytra and sides of pronotum but completely lacking in its central part, rather sparse on elytra, denser and erected on head, especially in the front part. Ventral side of body (Fig. 16L, O) with clearly visible, sparse, thin and long pubescence, denser on prosternum and mesosternum. Head between antennal tubercles with visible furrow, sometimes nearly flat; apical palpal joints elongated, triangular. Antennae relatively slender (slightly thinner in females) and short; in males usually slightly exceeding elytra, in females reaching to about apical elytral quarter. Antennomere 1 about equal in length to antennomere 4; antennomere 2 clearly longer than wide (ratio > 1:1.3; Supporting Information, Fig. S3G); antennomere 5 a little longer than antennomere 4; antennomeres 5–11 in males almost equal in length; antennomeres 3–9 in males with distinct apical internal spines (antennomeres 3–10 in females); outer angles of joints distinct but not protruding in spines; apical antennal joint about five times longer than wide in males and about two times in females. Prothorax variable in shape, in males usually more rounded (Fig. 3B, C) sometimes a little transverse, ~1.3 times wider than long; in females usually more transverse (Fig. 3O) ~1.5 times wider. Pronotum almost flat, usually entirely punctate but sometimes with glabrous smooth area near base; punctation variable, usually uniformly dense, sometimes sparser, rarely changing into transverse wrinkles, always dense and small at sides. Elytra black, with only slight brown–green metallic lustre, long, ~2.3 times longer than basal width in males and ~2.6 times in females; shape of elytra rather variable, generally almost parallel sided in males and parallel sided in anterior third, then clearly expanding towards end in females; elytral punctation regular and dense, in anterior part with sculpture more pronounced, much finer in posterior part; scutellum transverse, glabrous and semicircular, usually irregularly dotted. Mid and hind legs clearly longer in males; femora relatively wide in males, much narrower in females; posterior tibiae nearly straight, with distinct erect setae at inner margin. Prosternal process (Figs 9G, 10I) sharp at apex, relatively short, variable in width.

Male genitalia: Median lobe (Fig. 13R, S) rather variable in shape, relatively slender, lanceolate, slightly narrowed before apex. Lateral lobes of tegmen

of variable length, ~2–3 times shorter than length measured from tegmental ring to base of lateral lobes (Fig. 11U, V), slender, almost parallel sided; apex rounded, with long hairs concentrated on top and shorter ones on sides; margin of phallobase roof clearly concave at middle (Fig. 12U, V). The male habitus is shown in Fig. 15D1–4.

Differential diagnosis: *Ropalopus nataliyae* differs from all other species in this group by its second antennal joint, which is clearly longer than wide. Antennae are distinctly more slender in comparison to *R. ungaricus* subsp. and *R. hanae*. Imagines are relatively small, with only slight metallic lustre of elytra.

Remarks: The area of the type locality of *R. nataliyae* is situated at an elevation of ~2000 m a.s.l. Imagines were collected there along a canyon with scattered maples in the second half of May and at the beginning of June. There is no doubt that this species develops in the wood of maples, because numerous larval galleries and larvae themselves have been found on trunks and branches under the bark, and several imagines were later reared from this material. A few different *Acer* species are distributed in this region of Iran, and *R. nataliyae* is ecologically associated, at least, with *Acer monspessulanum* L.

PHYLOGENY

Morphological phylogenetic analysis: The genera of Callidiini exhibit a wide range of intraspecific morphological variation, thus it is difficult to distinguish good and constant characters for particular taxa. For the morphology-based phylogenetic analysis, we are able to score a total

of 34 ordered or unordered characters (Table 2; Supporting Information, Table S1). The maximum parsimony analysis based on morphological characters results in five equally long most parsimonious trees of a length of 105 steps. The strict consensus tree (Fig. 21) reveals the monophyly of the *Ropalopus ungaricus/insubricus* group, with *R. nataliyae*, *R. lederi* and *R. hanae* in an early-branching position. It also indicates *R. clavipes* in the position of a sister group to the clade of all remaining *Ropalopus* taxa considered. Strong monophyly of the clade comprising subspecies of *R. ungaricus* is underlined. In this group, the early-branching position of *R. u. siculus* and *R. u. ossae* is emphasized. However, these clades, in addition to clades comprising *R. u. boreki* and *R. u. insubricus*, receive only weak support. *Ropalopus u. insubricus* is sister to *R. u. ungaricus* and *R. u. gallicus*. The resemblance of the two last-mentioned taxa is strongly supported morphologically, which might indicate close sister relationships between them.

The majority consensus tree (Fig. 22) confirms the above-mentioned results, but *R. nataliyae* is revealed as a sister taxon to the clade consisting of the remaining species of the *Ropalopus ungaricus/insubricus* group.

DISCUSSION

PHYLOGENY

The placement of *R. nataliyae*, *R. lederi* and *R. hanae* at the base of the tree shows that these particular species are unique among other *Ropalopus* taxa in this group, e.g. in the shape of the prosternal process, the microsculpture of the body or the shape of the second antennal joint. A large number of unique synapomorphic characters

KEY TO SPECIES OF THE *ROPALOPUS UNGARICUS/INSUBRICUS* GROUP

1. Head with longitudinal furrow between antennal elevation 2
 - Head without longitudinal furrow between antennal elevation; elytra parallel sided, not wider toward apex than at base, with extremely fine punctures in apical half. Distributed in Turkey *R. hanae*
2. Second antennal joint about as long as wide (Fig. 19J) 3
 - Second antennal joint clearly longer than wide (ratio $\geq 1:1.3$) (Fig. 19I); antennae slender; elytra with only slight metallic lustre; prosternal process relatively short and sharpened (Fig. 9G). Distributed in northern Iran *R. nataliyae*
3. Pubescence of body long and pronounced; pronotum in males rounded (Fig. 19A); antennae and tarsi more slender (Fig. 8M); second antennal joint almost spherical; elytra with only slight metallic lustre; prosternal process narrow and sharpened (Fig. 9H). Distributed in Caucasus and Crimea *R. lederi*
 - Pubescence of body short and sparse; pronotum hexagonal (Fig. 19D); antennae and tarsi more robust (Fig. 8D); second antennal joint more triangular; elytra with distinct metallic lustre; prosternal process relatively wide, never truly sharpened (Fig. 9C). Distributed in Europe and North Africa *R. ungaricus*

KEY TO SUBSPECIES OF *ROPALOPUS UNGARICUS*

1. Pronotum in males with distinct, shining large rhomboid unpunctured or at most finely punctate area (Fig. 19B); in females, almost completely unpunctured (Fig. 19C) 2
 - Pronotum in both sexes uniformly densely punctate or rugose, often with small unpunctured area near base at middle (Fig. 19E, F) 4
2. Basal half of elytra at least slightly irregularly wrinkled; pronotum evenly tapered towards anterior and posterior margin; stains with deeper punctation on each sides of pronotum in males almost merged at anterior and posterior margin, rather uniform (Fig. 2B); antennae in males shorter, as long as or at most slightly longer than elytra 3
 - Basal half of elytra without wrinkles, regularly punctured; pronotum unevenly tapered towards anterior and posterior margins, wide and raised at base then cordate; stains with deeper punctation on each sides of pronotum in males narrow and irregular, never about to merge into each other (Fig. 2K); antennae in males clearly longer than elytra. Distributed in Europe from northern Italy through the Balkans to westernmost Turkey, and through Ukraine to southern part of European Russia, not higher than 600 m a.s.l. *R. u. insubricus*
3. Ventral side of body with sparse and short pubescence (Fig. 16A); antennae in males as long as or slightly longer than elytra; lustrous area on pronotum at most with fine, barely noticeable punctation. Distributed in Europe from eastern France to westernmost Ukraine and eastern Romania, and from south-western Poland to central Italy and Montenegro, excluding southeastern France, not lower than 600 m a.s.l. *R. u. ungaricus*
 - Ventral side of body with abundant and long white pubescence (Fig. 16B); antennae in males usually much shorter than elytra; lustrous area on pronotum usually slightly punctate and wrinkled. Distributed in southeastern France *R. u. gallicus*
4. Elytral sculpture more uniform on whole surface, with gradual change in depth and density of points towards end (similarly shiny) (Fig. 19O), mainly made by indistinct points with creased and convex surface between them (Fig. 19G, K, L), greenish brown; pronotum evenly tapered towards anterior and posterior margins 5
 - Elytral sculpture clearly separated around middle, with deeper and larger points on basal half (metallic) and much thinner and denser on second half (matt) (Fig. 19P); sculpture on first half mainly composed of clearly separated points (vermiculate in some places) with wide, flat surface between them (Fig. 19H, M, N), blackish green; pronotum unevenly tapered towards anterior and posterior margins, wide and raised at base then cordate; antennae in males as long as elytra; lateral lobes of tegmen long and slender, parallel sided with external margin concave and relatively long hairs on top (Fig. 12O). Distributed in southern Greece (Peloponnese) *R. u. boreki*
5. Ventral side of body with dense, erect, yellowish pubescence especially on prosternum (Fig. 16F); antennae in males slightly longer than elytra; lateral lobes of tegmen short and robust, adjoining at ends, with external margin convex; margin of phallobase roof almost straight, with small depression at middle and relatively long hairs on top (Fig. 12P–R). Distributed in Sicily *R. u. siculus*
 - Ventral side of body with sparse and short pubescence (Fig. 16H); antennae in males clearly longer than elytra; lateral lobes of tegmen short and robust, adjoining at ends, with external margin convex; margin of phallobase roof clearly concave at middle, and relatively short hairs on top (Fig. 12S, T). Distributed in central Greece (Thessaly) *R. u. ossae*

in the second dichotomy of the phylogeny reflects that these three species differ in diagnostic features from the remainder of the genus. The strict consensus tree strongly indicates that the European populations, consisting of six subspecies of *R. ungaricus*, form a separate clade. The taxa that inhabit the Mediterranean

zone are similar to each other, with only a few good morphological differences. Based on the generated trees, they are probably evolutionarily older taxa than those that reach the central part of Europe. Moreover, it seems that *R. u. ungaricus* and *R. u. gallicus* are closely related and somewhat morphologically dissimilar from other

subspecies of *R. ungaricus*, because they have several unique characters, such as longitudinal wrinkles on the basal part of the elytra and sparse pubescence on their lower part.

Taking into consideration our analysis of the tree, the following scenario offers a fairly probable explanation of the distribution of these taxa. It seems that the most recent common ancestor of this group was probably present in the territory of the Near East and the Balkan Peninsula. In this region, four separate evolutionary lineages have emerged, from which the current species *R. hanae*, *R. lederi*, *R. nataliyae* and *R. ungaricus* originate. The ancestor of the last-mentioned species most probably inhabited the territory of the Balkan Peninsula, from where its migration process was initiated towards Europe. Probably, it was a thermophilic species that colonized the region of southern Europe (the Apennines and the Balkan Peninsula). Subsequently, during the Messinian salinity crisis (~5.96–5.33 Mya), when the level of the Mediterranean Sea had dropped by as much as 1500 m (Clauzon *et al.*, 1996) and a land bridge

existed between Europe and North Africa, it extended its range to what is now Algeria, and afterwards apparently to mountainous areas of southern Spain (in what is now Andalusia). Along with the colonization of northern areas of Europe, the form adapted to a more moderate climate began to emerge.

The differentiation of individual taxa possibly became more intensive during the Pleistocene. The temperature fluctuations (alternate glacials and interglacials) were most probably the main factors responsible for these processes, along with changes in the vegetation. As a consequence, the areas where these forms occurred started to shrink, which, in turn, could result in fragmentation of their ranges. Vitali & Schmitt (2017) indicated several refugial areas for longhorn beetles in the western Palaearctic region. The thermophilic forms could survive in southern Italy, including Sicily (the Apennine refugium), in the Illyria region (the Illyrian refugium) and in Greece (the Balkan refugium). However, the populations existing in Algeria (the Maghreb refugium) and Spain (the Iberian refugium) must have been isolated much earlier than the Last

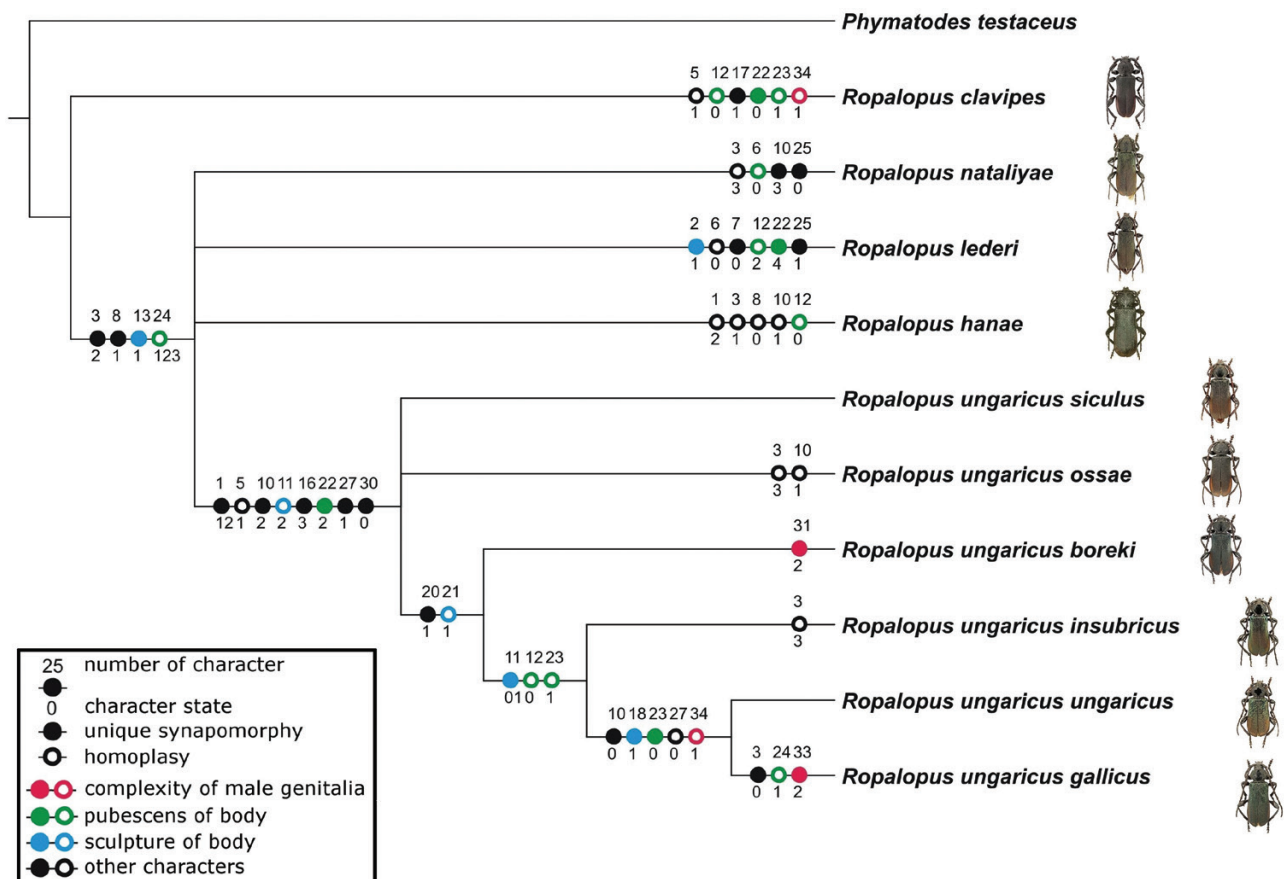


Figure 21. Results of the phylogenetic analyses based on strict consensus of most parsimonious trees resulting from the morphological analysis, with mapped characters.

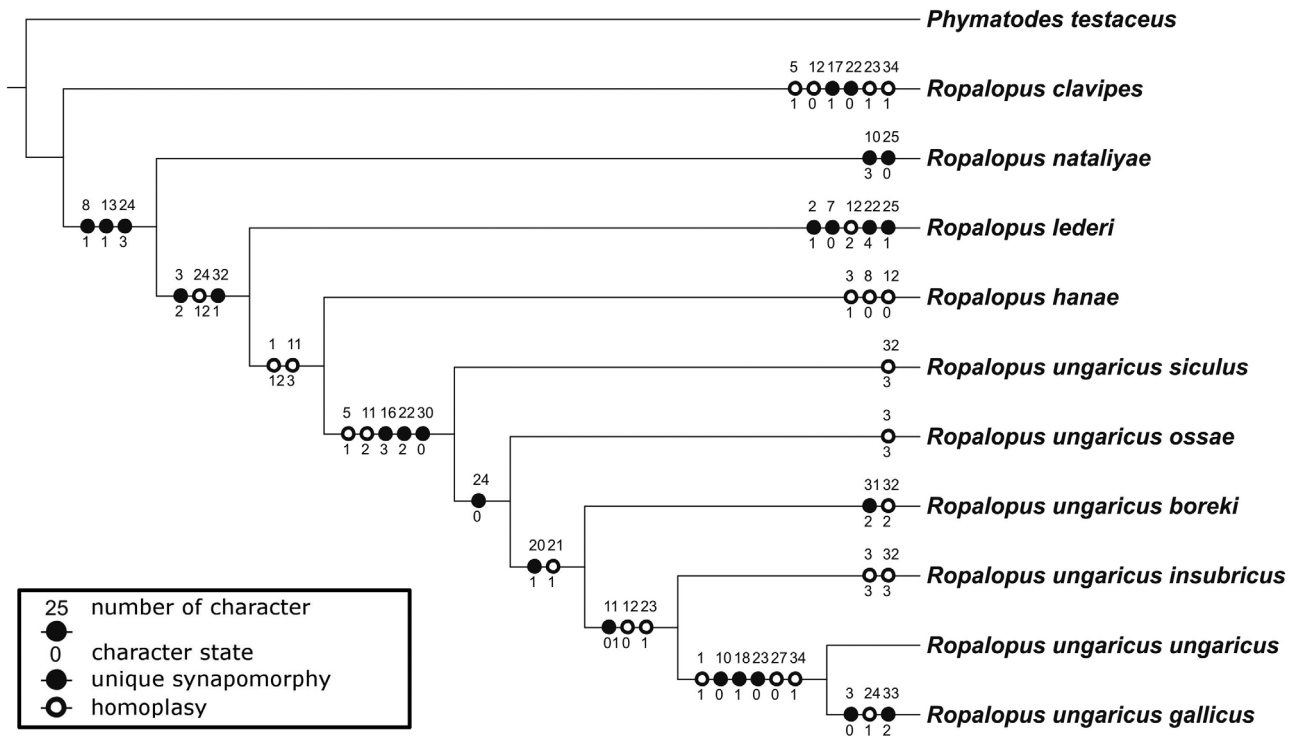


Figure 22. Results of the phylogenetic analyses based on majority rule consensus of most parsimonious trees resulting from the morphological analysis, with mapped characters.

Ice Age, which is supported by strong distinction of cerambycid assemblages of both of these regions (Vitali & Schmitt, 2017). Subsequently, as a result of geographical isolation, the processes of speciation have been initiated, resulting in the differentiation of currently existing taxa: *R. u. ossae* (central Greece and possibly southern Italy), *R. u. boreki* (Peloponnese) and *R. u. siculus* (Sicily).

Owing to the direct activity of the ice sheet, the range of the mesophilic form was also fragmented. The cooling of the climate resulted in the survival of this form in the west, probably only in the Provence refugium, which seems to have a important role in the postglacial recolonization processes (Vitali & Schmitt, 2017). Moreover, phylogenetic studies suggest that the sycamore maple *A. pseudoplatanus* L. (probably the only host plant of the mesophilic form) had a refugial site in this region, in or near the Alps (Neophytou *et al.*, 2019). As time passed, the population existing in this region changed owing to the reduced gene flow, which eventually gave rise to a new taxon: *R. u. gallicus*.

In the remaining eastern area, the previously mentioned ancestor survived only in the northern part of the Balkan Peninsula (or also in the Apennine Peninsula as a metapopulation). By selecting different environmental conditions (lowlands along river valleys and hilly uplands vs. mountain habitats), the populations began to differentiate. The speciation

mechanisms that started here have initiated the formation of two taxa in this region: *R. u. ungaricus* (dispersing over mountain areas) and *R. u. insubricus* (preferring higher temperatures at lower elevations).

This type of distribution, where ranges abut in such a way that only part of each population is in contact, is specific to assumptions of parapatric speciation, such as, for instance, as described by Bush & Butlin (2004). A similar case was also described in the *Rhagoletis suavis* (Loew, 1862) species group (Diptera: Tephritidae), where taxa are allopatric or, when parapatric, they are allochronically and elevationally isolated (Bush & Smith, 1998). In contrast, in the genus *Heliconius* Kluk, 1780 (Lepidoptera: Nymphalidae), the closely related taxa are often parapatric, but differ in aridity or elevational requirements (Jiggins *et al.*, 1997). Another example, this time regarding the discussed longhorn beetle family, was presented by Nakamine & Takeda (2008) in the flightless genus *Mesechthistatus* Breuning, 1950. All four endemic species [*Mesechthistatus binodosus* (Waterhouse, 1881), *Mesechthistatus fujisanus* Hayashi, 1957, *Mesechthistatus furciferus* (Bates, 1884) and *Mesechthistatus taniguchii* (Seki, 1944)] are distributed parapatrically in Honshu Island, Japan.

The mechanisms of parapatric speciation are usually combined with a host shift (e.g. Bush & Butlin, 2004), which is unlikely to occur in *Ropalopus u.*

insubricus and *R. u. ungaricus* (or might only concern possible monophagous associations of *R. u. ungaricus* with *A. pseudoplatanus*). Such cases without a host shift, where parapatric speciation cannot be excluded, are also known from other groups, e.g. *Heliconius* butterflies (Mallet *et al.*, 1998). According to Jiggins *et al.* (1997), the observations in the parapatric *Heliconius erato* group strongly suggested that speciation occurred after climatic adaptation, but before any change in host plant ecology. A different situation seems to appear in our group, where the infraspecific taxa of *R. ungaricus* are still at an early stage of speciation, and a shift in host plant has not yet occurred (or it has not been completed).

The current distribution of the particular subspecies of *R. ungaricus* results from the recolonization of the populations, which possibly occurred ~11 000 years ago, after the Last Glacial Period. *Ropalopus u. insubricus* began to spread out through the lowlands west to Italy and up to the southern areas of European Russia in the East, while *R. u. ungaricus* was extending along with the mountain ranges and, most probably, it spread from the territory of today's Romania through the Carpathians and the Alps to Italy, where it presently occurs at higher elevations in the Apennines. Most probably, *R. u. gallicus* expanded its range only slightly, together with climate warming, because its further expansion has been prevented either by the nominal subspecies or by the too high elevations. Currently, taxa that evolved from the mesophilic ancestor occurring in the cooler part of Europe (*R. u. ungaricus* and *R. u. gallicus*) inhabit the cooler climate zone of the mountain areas, while *R. u. insubricus* is only present in areas with lower elevation. Likewise, the descendants of the thermophilic ancestor (*R. u. ossae* and *R. u. siculus*) inhabit mountainous areas with higher annual temperatures, while *R. u. boreki* occurs at lower elevations in the Peloponnese. *Ropalopus u. insubricus* and *R. u. boreki* are therefore considered as vicariant taxa that inhabit analogous ecological zones, mainly along the Adriatic and the Ionian coast, that do not exceed the elevation of highlands.

Owing to the fact that we have not had the opportunity to examine any specimens originating from Spain (the Baetic System) (González *et al.*, 2007) or North Africa (Djurdjura Mountains, Mouzaïa Mountains) (Villiers, 1946), it is difficult to conclude their relationship to other taxa, but it is likely that these strongly isolated populations represent different, as yet undescribed taxa.

EUROPEAN POPULATIONS OF *ROPALOPUS UNGARICUS*

The convergence of numerous morphological features within the European populations of the discussed *R. ungaricus/insubricus* group reveals a close affinity of the taxa. Several key characters that are used in the

literature to differentiate the European taxa, such as the sculpture of the basal part of the elytra, presence of a tooth on the inner side of particular antennomeres, and shape of hind tibiae or the prosternal process (e.g. Bense, 1995; Sama, 2002), are shown to represent only individual variability or sexual dimorphism. The analysis of the collected material reveals variation along a gradient in some of these features (results discussed in detail in the Taxonomy section).

Although the shape of the lateral lobes of the tegmen may vary to a certain extent in particular taxa, it may serve as a good differential feature. Despite the usually significant differences in the parameres between *R. u. ungaricus* and *R. u. insubricus*, copulation and reproduction between them is still possible. Besides the findings of intermediate forms (hybrids) at the contact zone of particular taxa (e.g. *R. u. ungaricus* and *R. u. gallicus* in south-eastern France or *R. u. ungaricus* and *R. u. insubricus* in central Slovakia or Montenegro), which suggests that they still maintain some gene flow in these locations, the hybridization of these species was also shown by Sama (2002). He reported on experimental crossing of all the three known (at that time) European taxa (*R. ungaricus*, *R. insubricus* and *R. siculus*) that were represented by geographically well-separated populations. However, the experiments were performed in laboratory conditions, and the offspring that were obtained have not been presented anywhere. The existence of different parameres in individuals of closely related subspecies has already been shown in the longhorn beetle family, e.g. between *Saperda populnea balsamifera* (Motschulsky, 1860) and *Saperda populnea lapponica* Wallin, Kvamme & Bergsten, 2017 (Wallin *et al.*, 2017).

It should be noted that owing to the rarity of these beetles, the majority of the specimens come from private collections and, as a result, they usually represent only the centre of the occurrence of a particular taxon, because collectors are driven by the greatest chance to obtain material. Therefore, individuals from the edge of their range of distribution are usually represented inadequately. However, their dissimilarity can be noticed immediately when such specimens (e.g. Figs 14A8, B5, C6, C10, 17E) are studied.

Variability at the subspecific, rather than specific, level is also suggested by the fact that several of the characters, which usually allow the differentiation of European taxa, apply only to males. Females are morphologically much more uniform and difficult to diagnose. The characters such as length of the antennae, shape of the pronotum or its punctation are of even less importance in their case. Many difficulties can arise when identifying females between subspecies such as *R. u. gallicus* and *R. u. insubricus* (e.g. Fig. 14B7 vs. C12), or *R. u. siculus* and *R. u. boreki*. The subspecific relationship regarding the European

populations is also highlighted by the presence of some strong and stable morphological characters in taxa from the Caucasus and Middle East, such as the ratio of the second antennal joint in *R. nataliyae*, lack of a furrow on the head in *R. hanae* or the character of the body pubescence in *R. lederi*. Sláma (2018), based on the examination of long series of specimens from different populations, also shared this point of view by questioning the species status of the European taxa, also including here the already known *R. boreki sensu e.g. Danilevsky (2019a)*.

Doubts on species identity in the European taxa also arose from morphological comparisons of the immature stages (Švácha & Danilevsky, 1988). These authors could not find any distinguishing characters between the larvae of *R. insubricus* and *R. ungaricus*, and could find only one rather insignificant character of the mentum for *R. siculus sensu e.g. Sama, 2002*). Moreover, given that the examined material was scanty, it is possible that the difference resulted from individual variability. The lack of differences is even more interesting since the examined material came from the most distant edges of the range: the Voronezh region of Russia in the east, Castellane (France) in the west and from Tizi-n-Test (Algeria, as originally stated in the book, but the Tizi-n-Test is a small pass in the High Atlas Mountains in Morocco) in the south. In fact, there were obvious mistakes in assigning the larval material to individual taxa in this group when considering the current knowledge on their distribution and the elevation they inhabit. The material collected in the Voronezh region and assigned to *R. ungaricus sensu e.g. Sama (2002)* undoubtedly belongs to *R. u. insubricus*. In turn, the material identified as *R. insubricus sensu e.g. Sama (2002)* was collected in Castellane, thus it must represent *R. u. gallicus* (near its type locality), which is closely related to the nominative subspecies. Likewise, the material from North Africa also seems to be confused, because it evidently belongs to another new subspecies distributed in this region and certainly not to *R. u. insubricus*. Therefore, it appears that the true larva of *R. u. ungaricus* has probably not been studied at all (sic!). Nevertheless, the examined material still represented at least two different taxa (*R. u. insubricus* and *R. u. gallicus*) in addition to the properly identified *R. u. siculus* (the larvae were collected in Sicily). The results of this examination clearly support subspecific (rather than specific) status for these taxa.

Supporting a more modern definition of subspecies, proposed by Wallin *et al.* (2017) [... subspecies are defined as potentially incipient species in allopatry or parapatry that are diagnosable by at least one presumably heritable trait. Hence the only necessary properties of subspecies are that they are potentially incipient species under the USC (i.e. potentially on their way to become

separately evolving metapopulation lineages), they are currently diagnosable by at least one trait that is heritable and not environmentally determined, and that they are geographically defined. Reciprocal monophyly or not in neutral markers, quantitative thresholds like the 75% rule, reproductive compatibility or degree of gene flow should not be part of the definition.], we are inclining to the conclusion that all European populations from this group are currently at an insufficient level of differentiation to consider them as separate species, but rather as subspecies of one species, *R. ungaricus*. However, we agree that although every biological species must go through a subspecies stage, this condition does not mean that every subspecies will become a species, as is also possible in this case.

Elevation above the sea level appears to be the main factor of differentiation between two of the most problematic (with regard to geographical distribution) taxa: *R. u. ungaricus* and *R. u. insubricus*. The authors are not aware of any records of the nominative subspecies at elevations < 600 m a.s.l., as was confirmed by other scientists (e.g. Kašák & Foit, 2018; 760 m a.s.l.). According to the literature, the maximum elevation for this taxon is ~1200 m a.s.l. (Sláma, 1998; Kašák & Foit, 2018), but it probably reaches the maximum elevation of occurrence of its host plant, *A. pseudoplatanus*, which is ~1500 m a.s.l. (and 1300 m a.s.l. was confirmed for larvae). On the contrary, the highest locality for *R. u. insubricus* was found to be 550 m a.s.l., and this taxon is most common at elevations between 200 and 300 m a.s.l. *Ropalopus u. boreki* appears to be a vicariant taxon of *R. u. insubricus*, but additional data has to be gathered and analysed, because it is known from only a single location from the Ionian coast. *Ropalopus u. gallicus* is known to inhabit localities at ~800–1000 m a.s.l., thus it overlaps, in part, with the nominative subspecies yet still clearly occurs higher than *R. u. insubricus*, with which it has generally been confused. The situation is also clear in the case of *R. u. siculus*, which is known to occur only at high elevations between 1100 and 1800 m a.s.l. *Ropalopus u. ossae*, although closely related to *R. u. siculus*, appears to inhabit locations at a greater range of elevations (from ~500 to 1100 m a.s.l.). Hence, in this regard, it is closer to the nominative subspecies.

REMARKS ON TYPE MATERIAL AND DISTRIBUTION

According to Sama (2002), the type material of *R. ungaricus* and *R. insubricus* seems to be lost irretrievably, and neotypes should be selected. This is only partly the case, because a series from the original ex collection of Herbst (housed in ZMB) contains at least one specimen (female) that can certainly be considered as a syntype. Therefore, a neotype is not appropriate, and a lectotype needs to be designated for *R. ungaricus*, which was done above.

Definitely, a more complex situation applies to *R. insubricus sensu* e.g. Löbl & Smetana (2010) and its *locus typicus* in 'Italia', as stated in the original paper (Germar, 1824). According to the Titan database (2018), the type material ('holotype!') of this taxon is preserved in ZMB as a part of the ex collection of Germar. Although there are three specimens labelled as '*Callidium insubricum*', only one of them belongs to the nominative subspecies, and all three were collected in Istria, which cannot be accepted as the type locality because this region belonged to the Napoleonic Kingdom of Italy only between 1805 and 1814 (F. Vitali, 2019, personal communication). The *locus typicus* must be considered to be Insubria, which means the plain between the lakes of Lombardy. This historical region comprised the north-western part of Lombardy between the Alps and the lakes of Lombardy, as well as the Swiss Alps and a small part of the eastern Piedmont. Although mountainous areas that are optimal for *R. u. ungaricus* (> 600 m a.s.l.) occupy the greater part of this region, the lowlands suitable for *R. u. insubricus* extend here between the villages of Varese and Como in the north and Novara in the south, thus this area needs to be accepted as the type locality of this taxon. It also seems to be confirmed by the original description [*Callidium insubricum* Ziegleri: *punctatum, atrum, elytris coriaceis, aeneis. Habitat in Italia. Statura Call. violacei sed multo majus, C. clavipes adhuc superans. Caput canaliculatum, atrum. Antennae corporis longitudine nigrae, articulis primis apice subtus spinosis. Thorax transversim ovatus, planus, vage punctatus, ater. Coleoptera plana, apice magis deplanata latiora, coriacea, atro-coerulea, aeneo-nitidula, lineis utrinque duabus elevatis. Corpus subtus atrum. Pedes atri, femoribus subito et valde clavatis.*], which, although relatively scanty, still contains several formulations that, when combined, allow the description to be assigned to *R. u. insubricus*. Moreover, the characteristic elytral wrinkles and its green colour are evidently not mentioned. According to B. Jaeger from ZMB (2019, personal communication), Germar's collection was split among several institutions and private collections by his nephew. Although there is no type material of *Callidium insubricum* in the collection of the Martin Luther University (Zentralmagazin Naturwissenschaftlicher Sammlungen, Halle, Germany; K. Schneider, 2019, personal communication), the second institution regarding the amount of material received, we cannot exclude the possibility that these specimens survived and are still preserved in one of the private collections, which will be difficult to trace. Hence, we have decided not to designate a neotype in this case.

We also discuss two varieties described under *R. insubricus*, but transferred later to *R. ungaricus sensu* e.g. Sama (2002) by the same author, who also

designated lectotypes in both cases. The form *annulus* (Fig. 17F), which was collected in the mountainous area of Campania, represents a typical specimen of *R. u. ungaricus*, whereas the second form, *vogti* (Fig. 17E), required a more detailed examination. This variety was described from a locality situated ~70 km from the *locus typicus* of *R. insubricus gallicus sensu* Vartanis (2018). Therefore, there was a strong suspicion that this newly described subspecies, which represents a distinct taxon, is a synonym of *R. insubricus* var. *vogti sensu* Sama (2002). However, examinations of the photographs of this specimen do not allow us to state clearly whether it represents *R. u. ungaricus* or *R. u. gallicus*. The depicted specimen shows intermediate characters of both subspecies (such as pronounced pubescence on the prosternum but only on its edges, or intermediate length of the antennae), in addition to some unusual features (e.g. the shape of the pronotum). According to the original description by Guerry (1911), the few specimens that were collected at this plot have a blackish elytra, which cannot be observed in specimens of *R. u. gallicus*. Scanty research material and the fact that this form was found at the contact zone of the previously mentioned subspecies suggest a hybrid of these two taxa, rather than a separate taxon. Therefore, *R. insubricus gallicus sensu* Vartanis (2018) is not considered a synonym of *R. insubricus* var. *vogti sensu* Sama (2002).

Ropalopus u. gallicus exhibits several good and stable characters that enable its easy distinction from the remaining taxa. However, it is still more closely related to the nominal subspecies than to *R. u. insubricus*. It is puzzling why it was described as a subspecies of the last-mentioned taxon instead of the nominative form, and why it is constantly confused with *R. u. insubricus*. This is probably attributable to the fact that there are no obvious wrinkles on the basal part of the elytra, which feature has been indicated as a main key character for *R. u. ungaricus* (e.g. by Bense, 1995; Sama, 2002). The situation in Spain is particularly interesting. We were not able to access any specimens or even photographs of any material from this country. Nonetheless, the literature data record the occurrence of only *R. insubricus sensu* Sama (2002) and from only three localities in two provinces (Jaén and Granada), both in eastern Andalusia (González et al., 2007). The plots are located at an elevation of ~1000 m a.s.l., thereby impossible for *R. u. insubricus*. Additionally, taking biogeography into account (Vitali & Schmitt, 2017), it is also doubtful that this area is occupied by *R. u. gallicus*, because the Pyrenees act here as a strong dispersal barrier, not only during glacial conditions. Thus, it is likely that another new taxon might be distributed in this region of Spain. Material from the Iberian Peninsula requires further study.

There is also a series of peculiar specimens from the southern part of continental Italy (Fig. 18L–Q) that exhibit intermediate characters between *R. u. siculus* and *R. u. ossae*. According to Sláma (2018, personal communication), they differ from Greek subspecies by several features, such as less robust body, longer and narrower elytra and thinner femora in males, and might represent a new subspecies. However, owing to both the unavailability of these specimens for study and a clearly visible gradient in some key characters (e.g. corpulence and colour of the body, length of the antennae), they are not considered herein as a new taxon but only as an intermediate form, which seems to be rather closer to *R. u. ossae*. Further examination of populations from this region, particularly the characters on the ventral side of the body and male terminalia, is still required.

Regarding the north-easternmost territory in Ukraine (except the Carpathians) and European Russia (except the Caucasus), only one taxon is distributed there, *R. u. insubricus*. To date, *R. insubricus fischeri sensu Löbl & Smetana (2010)* (described from near Kharkov) was known to occur in this region. However, specimens from this area do not differ from those from the Balkans; thereby, this taxon is synonymized here. Sama (2002) completely ignored this subspecies, although he still recorded *R. insubricus* for Ukraine following Bense (1995). It seems that Danilevsky (2019b), based on his study of a long series from the Kharkov and Samara environs, noticed this earlier, claiming that the elytral sculpture and size of all Russian and Ukrainian specimens is the same as in the nominal subspecies. He also mentioned that all determinations from this region in Plavistshikov's collection were marked by Plavistshikov with a question mark. However, none of those authors ultimately decided to synonymize the taxon. Danilevsky (2019b) considered all Russian and Ukrainian populations as one taxon, *R. insubricus* subsp. *fischeri*, including those from Crimea, Odessa and Podolia. Additionally, he shared his doubts on the constancy of the shape of the prosternal process and hind tibia among the specimens from the entire region of its occurrence.

IUCN RED LIST PROTECTION STATUS

Three taxa are included in the IUCN Red List of Threatened Species: *R. insubricus*, *R. siculus* and *R. ungaricus sensu Löbl & Smetana (2010)*. The following threat categories have been assigned: NT (Near Threatened), NT and EN (Endangered), respectively (IUCN, 2019). They were assessed inter alia based on an estimated area of occupancy, which results directly from taxonomic classification. The lack of *R. boreki sensu Danilevsky (2019a)* on the list

is attributable to the relatively short time that has elapsed since its description. The need for taxonomic revision has already been mentioned by the authors.

Regarding *R. u. insubricus*, the European regional assessment listed it as NT because it is suspected to be endemic to Europe with a scattered and rare distribution. It seems to be declining in some parts of its distribution area (e.g. Hungary and Romania), although it is a polyphagous species with suitable habitats available (Horák *et al.*, 2010a). The following countries are involved in its current range: Austria, Bosnia and Herzegovina, Bulgaria, Croatia, Czech Republic, France, Greece, Hungary, Italy, Montenegro, North Macedonia, Romania, Serbia, Slovenia, Spain, Turkey and Ukraine (Horák *et al.*, 2010a). On the one hand, the area of *R. u. gallicus* was included; on the other hand, it is not mentioned as being present in European Russia. The authors noticed that this taxon was also recorded from the Atlas Mountains, but they indicated that those records might be related to a different species. Taking the current knowledge on the distribution of this subspecies into account, with its maximal range in the east reaching European Russia and Turkey in Europe, it can be regarded as a European endemic; however, not when considering *R. ungaricus* as a whole, because it also reaches into North Africa. According to Horák *et al.* (2010a), it is an obligate saproxylic and mostly montane taxon, whose larvae develop in broad-leaved trees, especially in *Acer*, but also in *Alnus*, *Fagus*, *Ficus* and *Fraxinus*. The main threat is habitat loss (including removal of maples from the forests), but also forest fragmentation and replacement of native species with newly introduced species. However, based on our current knowledge, it is a lowland–highland taxon that requires higher temperatures, and the data referring to its development in host plants other than maples are not supported here (although this is the only taxon of the whole group in which polyphagy cannot be excluded). All these data should be taken into account when assessing a threat category, even if a decision is made to treat these subspecies separately.

Ropalopus u. ungaricus has been listed in the European regional assessment as Endangered because it is highly dependent on old maple trees that have to be in open stands. Moreover, its distribution in Europe is scattered and localized, and it is rare in its entire range of occurrence. It is assumed that the area of occupancy is < 500 km² (Horák *et al.*, 2010b). The authors listed the following countries as the area of occurrence of this taxon: Austria, Bosnia and Herzegovina, Bulgaria, Croatia, Czech Republic, France, Germany, Hungary, Italy, Montenegro, Poland, Romania, Russia, Serbia, Slovakia, Slovenia and Ukraine. Additionally, Switzerland is mentioned as a region where it is already extinct. These data are mostly correct, but this subspecies certainly

does not occur in the European part of Russia, and in Ukraine it reaches only the eastern Carpathians in the westernmost part of the country. According to Horák *et al.* (2010b), it is an obligate saproxylic taxon, the larvae of which develop in broad-leaved trees, especially in *Acer*, rarely also in *Alnus*, *Fagus*, *Ficus*, *Fraxinus* and *Salix*. In fact, this taxon is undoubtedly a monophage on *Acer*, possibly solely on *A. pseudoplatanus*. Habitat loss and its overshadowing together with the loss of traditional management systems are major threats in this case. In conclusion, *R. u. ungaricus* should be considered a relict of the European mountain forests.

Verdugo *et al.* (2016) assessed *R. u. siculus* as NT based on incorrect distributional data (Greece, Italy and Turkey). In fact, this subspecies is endemic to Sicily. In Greece, *R. u. ossae* (Thessaly) and *R. u. boreki* (Peloponnese) are distributed. Old records from the European part of Turkey, after Winkler (1929), undoubtedly relate to another species. Therefore, its extent of occurrence (estimated as ~97 600 km²) and its area of occupancy (estimated to be < 500 km²) are, in fact, even lower. According to Verdugo *et al.* (2016), owing to the fact that the population is severely fragmented and may go extinct, with a reduced probability of recolonization, this taxon is close to being qualified for a Threatened category under Criterion B. Severely fragmented forest habitats in northern Sicily, leading to the increased isolation of beetle subpopulations, are key factors in this case. This subspecies is indisputably associated with *Acer*, probably solely with *A. campestre*, which in Sicily is found only in the northern part.

A clear taxonomic system, proposed herein, is necessary to make possible a proper assessment of both the estimated area of occupancy and the extent of occurrence, in addition to its current populational trends, the evaluation of its threat category and, finally, the insurance of an adequate protection for these beetles. It is an option to treat *R. ungaricus* as one species during the Red List assessment. If subspecies are treated separately, *R. u. boreki*, *R. u. gallicus* and *R. u. ossae* should also be included.

ACKNOWLEDGEMENTS

We are deeply indebted to Christian Cocquemot (French National Institute for Agricultural Research Joint Research Units Centre de Biologie et de Gestion des Populations, France), Josef Steinhöfer (Germany) and Adam Woźniak (Poland) for providing the key specimens for analysis and for their valuable comments that have significantly improved this paper; also to numerous colleagues who contributed to this study by providing additional specimens [Bartłomiej Bujnik (Poland), Radosław Plewa (Forest Research Institute, Poland) and Tomasz Wróbel (Poland)] or

sharing photographs and important data [Mikhail Danilevsky (A. N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Russia), Milan Sláma (Czech Republic), Maxim Lazarev (State Budget Professional Educational Institution of the Moscow Region 'Chekhov technical college', Russia), Aleš Sedláček and Petr Boža (Czech Republic), Nicole and Claude Auvray (France), Karla Schneider (Martin Luther University, Germany) and David Šanc (Czech Republic)]. We would also like to show our gratitude to Magdalena Kowalewska-Groszkowska (MIZ) for conducting several SEM sessions. Additionally, for their valuable comments on the manuscript, we thank Roman and Maria Hołyński (MIZ), Pierpaolo Rapuzzi (Italy), Petr Švácha (Institute of Entomology, Czech Academy of Sciences, Czech Republic) and Francesco Vitali (Musée national d'histoire naturelle de Luxembourg, Luxembourg). We also want to thank the curators of the following institutions for the loan of specimens and photographs sent: Azadeh Taghavian (MNHN), Roberta Improta (MZCM), Harald Schillhammer (NHWM), Mandy Schröter and Stephan M. Blank (SDEI), Bernd Jaeger (ZMB) and Roland Dobosz (USMB). Furthermore, we are grateful to Tomasz Huflejt (MIZ) and Wiesław Szczepański (Poland) for their help with translation of original Latin and Russian publications, and to Maák István Elek (MIZ) for the linguistic correction. Finally, we are indebted to two anonymous reviewers and the Associate Editor Maxwell Barclay, whose detailed comments helped to improve this work significantly.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. A–X, heads (ventral view): A–O, males; P–X, females. A, B, *Ropalopus ungaricus ungaricus*, Austria and Montenegro, respectively. C–E, *Ropalopus ungaricus gallicus*, France. F, G, *Ropalopus ungaricus insubricus*, Croatia. H, *Ropalopus ungaricus boreki*, Greece (Peloponnese). I, J, *Ropalopus ungaricus siculus*, Italy (Sicily). K, L, *Ropalopus ungaricus ossae*, Greece (Thessaly). M, *Ropalopus nataliyae*, Iran. N, O, *Ropalopus lederi*, Russia (north-west Caucasus). P, Q, *Ropalopus ungaricus ungaricus*, Poland and Slovakia, respectively. R, *Ropalopus ungaricus gallicus*, France. S, T, *Ropalopus ungaricus insubricus*, Croatia. U, *Ropalopus ungaricus siculus*, Italy (Sicily). V, W, *Ropalopus ungaricus ossae*, Greece (Thessaly). X, *R. nataliyae*, Iran.

Figure S2. A–X, heads (lateral view): A–O, males; P–X, females. A, B, *Ropalopus ungaricus ungaricus*, Austria and Slovakia, respectively. C–E, *Ropalopus ungaricus gallicus*, France. F, G, *Ropalopus ungaricus insubricus*, Croatia. H, *Ropalopus ungaricus boreki*, Greece (Peloponnese). I, J, *Ropalopus ungaricus siculus*, Italy (Sicily). K, L, *Ropalopus ungaricus ossae*, Greece (Thessaly). M, *Ropalopus nataliyae*, Iran. N, O, *Ropalopus lederi*, Russia (north-west Caucasus). P, Q, *Ropalopus ungaricus ungaricus*, Poland and Slovakia, respectively. R, *Ropalopus ungaricus gallicus*, France. S, T, *Ropalopus ungaricus insubricus*, Croatia. U, *Ropalopus ungaricus siculus*, Italy (Sicily). V, W, *Ropalopus ungaricus ossae*, Greece (Thessaly). X, *Ropalopus nataliyae*, Iran.

Figure S3. A–O, first three antennal joints: A–I, males; J–O, females. A, *Ropalopus ungaricus ungaricus*, Austria. B, *Ropalopus ungaricus gallicus*, France. C, *Ropalopus ungaricus insubricus*, Croatia. D, *Ropalopus ungaricus boreki*, Greece (Peloponnese). E, *Ropalopus ungaricus siculus*, Italy (Sicily). F, *Ropalopus ungaricus ossae*, Greece (Thessaly). G, *Ropalopus nataliyae*, Iran. H, I, *Ropalopus lederi*, Russia (north-west Caucasus). J, *Ropalopus ungaricus ungaricus*, Poland. K, *Ropalopus ungaricus gallicus*, France. L, *Ropalopus ungaricus insubricus*, Croatia. M, *Ropalopus ungaricus siculus*, Italy (Sicily). N, *Ropalopus ungaricus ossae*, Greece (Thessaly). O, *Ropalopus nataliyae*, Iran.

Figure S4. A–H, antennal microsculpture, males. A, *Ropalopus ungaricus ungaricus*, Austria. B, *Ropalopus ungaricus gallicus*, France. C, *Ropalopus ungaricus insubricus*, Croatia. D, *Ropalopus ungaricus boreki*, Greece (Peloponnese). E, *Ropalopus ungaricus siculus*, Italy (Sicily). F, *Ropalopus ungaricus ossae*, Greece (Thessaly). G, *Ropalopus nataliyae*, Iran. H, *Ropalopus lederi*, Russia (north-west Caucasus).

Figure S5. A–X, pronotal sculpture: A–O, males; P–X, females. A–C, *Ropalopus ungaricus ungaricus*, Austria, Poland and Slovakia, respectively. D, E, *Ropalopus ungaricus gallicus*, France. F, G, *Ropalopus ungaricus insubricus*, Croatia. H, *Ropalopus ungaricus boreki*, Greece (Peloponnese). I, J, *Ropalopus ungaricus siculus*, Italy (Sicily). K, L, *Ropalopus ungaricus ossae*, Greece (Thessaly). M, *Ropalopus nataliyae*, Iran. N, O, *Ropalopus lederi*, Russia (north-west Caucasus); P, Q, *Ropalopus ungaricus ungaricus*, Poland and Slovakia, respectively. R, *Ropalopus ungaricus gallicus*, France. S, T, *Ropalopus ungaricus insubricus*, Croatia. U, *Ropalopus ungaricus siculus*, Italy (Sicily); V, W, *Ropalopus ungaricus ossae*, Greece (Thessaly). X, *Ropalopus nataliyae*, Iran.

Figure S6. A–O, pygidia, males. A–C, *Ropalopus ungaricus ungaricus*, Poland, Austria and Slovakia, respectively. D–F, *Ropalopus ungaricus gallicus*, France. G, H, *Ropalopus ungaricus insubricus*, Croatia. I, J, *Ropalopus ungaricus siculus*, Italy (Sicily). K, L, *Ropalopus ungaricus ossae*, Greece (Thessaly). M, N, *Ropalopus nataliyae*, Iran. O, *Ropalopus lederi*, Russia (north-west Caucasus).

Table S1. Data matrix of 34 morphological characters for 14 taxa. Symbols: ?, characters not observed; –, inapplicable characters.

Appendix S1. *Ropalopus.nex*: morphological data matrix in Nexus format.