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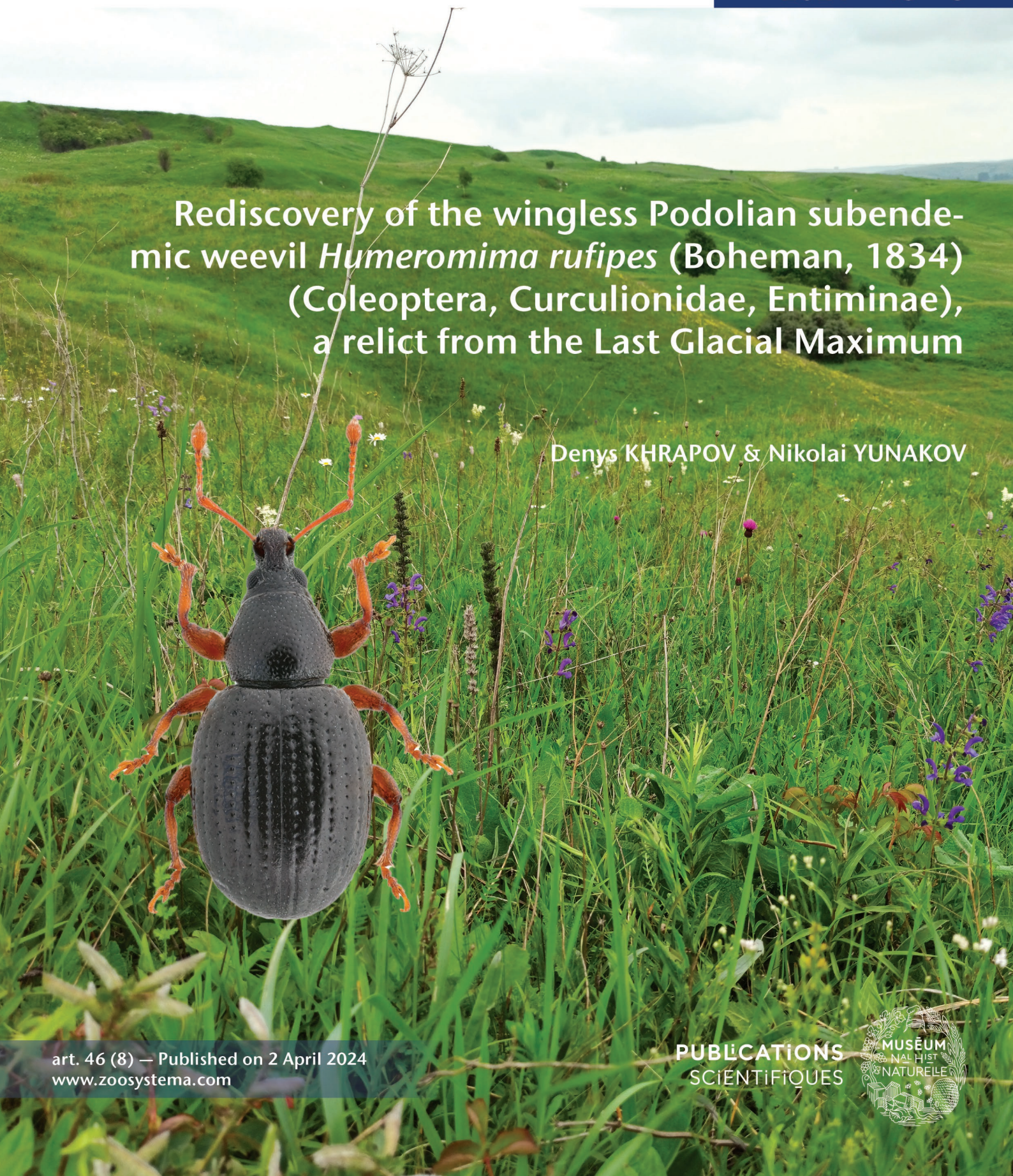
Rediscovery of the wingless Podolian subendemic weevil *Humeromima rufipes* (Boheman, 1834) (Coleoptera, Curculionidae, Entiminae), a relict from the Last Glacial Maximum

Denys KHRAPOV & Nikolai YUNAKOV



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Couverture / *Cover* :
Habitus of female of *Humeromima rufipes* (Boheman, 1834) and its habitats of meadow steppe, near Burshtyn, Kasova Hora, Ukraine.

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Rediscovery of the wingless Podolian subendemic weevil *Humeromima rufipes* (Boheman, 1834) (Coleoptera, Curculionidae, Entiminae), a relict from the Last Glacial Maximum

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ABSTRACT
A new systematic placement of *Humeromima rufipes* (Boheman, 1834) within the *Omias* generic complex is proposed as a result of a comprehensive morphological analysis. An improved redescription, including fine structures of male and female terminalia, is provided. Synapomorphies are revealed in the structures of female terminalia, male genitalia, mouthparts, and tarsi. The reduction of iridescent vestiture and the robustization of legs reflect a deep morpho-adaptive transformation of *H. rufipes* towards a geophilic lifestyle. The restricted range of *H. rufipes* suggests that it may be subendemic to Podolian Upland. Notably, the co-occurrence of obligate amphigonic species with hypothetical glacial forest microrefugia and a biodiversity hotspot of meadow steppes strongly suggests relict status of *H. rufipes* since the Last Glacial Maximum.

KEY WORD
Omiini,
glacial refugium,
new placement,
redescription.

RÉSUMÉ
Redécouverte du charançon aptère subendémique podolien Humeromima rufipes *(Boheman, 1834) (Coleoptera, Curculionidae, Entiminae), une espèce relicte de la dernière grande glaciation.*
Un nouveau placement systématique d'*Humeromima rufipes* (Boheman, 1834) au sein du complexe générique *Omias* est présenté comme résultat d'une analyse morphologique exhaustive. Une redescription améliorée prenant en compte les structures fines des terminalia mâles et femelles est proposée. Des synapomorphies dans les structures des terminalia femelles, des genitalia mâles, des pièces buccales et des tarses sont mises en évidence. La réduction de la vestiture irisée et le renforcement des pattes reflètent une profonde transformation morpho-adaptative de *H. rufipes* vers un mode de vie endogé. L'aire de répartition réduite de *H. rufipes* suggère qu'il s'agit d'une espèce subendémique du plateau Podolien. La concomitance d'espèces à amphigonie obligatoire avec d'hypothétiques microrefuges forestiers glaciaires et un « hotspot » de biodiversité de steppes herbeuses, suggère fortement que *H. rufipes* a un statut de relicte de la dernière grande glaciation.

MOTS CLÉS
Omiini,
refuge glaciaire,
nouvel emplacement,
redescription.

INTRODUCTION

Humeromima rufipes (Boheman, 1834) is a remarkable wingless weevil classified in the tribe Omiini Shuckard, 1840 (Alonso-Zarazaga & Lyal 1999). It remains relatively obscure to taxonomists in terms of detailed morphology, ecology, and distribution patterns. Most museums and private collections lack specimens on this taxon. Originally, it was placed into *Omias* (*sensu* Schoenherr) in the broader sense of the genus as defined by C. Boheman, encompassing species primarily from the following modern genera: *Baromiamima* Borovec, 2006, *Bryodaemon* Podlussány, 1998, *Humeromima* Podlussány, 1998, *Omiamima* Silfverberg, 1977, *Omias* Germar, 1817, *Rhinomias* Reitter, 1894, and *Urometopus* Formánek, 1904 (Alonso-Zarazaga *et al.* 2023).

Observations have revealed that five Central European species of *Omiamima* represent a conglomerate of taxa of distant morphological affinities, necessitating their reclassification into separate genera. Consequently, two genera were established: *Bryodaemon* for the Carpatho-Dinaric species-complex related to *Omias hanaki* Frivaldszky, 1865 and *Humeromima* for *O. rufipes* and its ambiguous congener, *O. nitidus* Boheman, 1842 (Podlussány 1998).

The original description of *Humeromima* is relatively brief and relies on a few features superficially distinguishing this genus from the rest of *Omiamima*. In particular, Podlussány (1998) described the presence of distinct humeral angles of the elytra. Closer examination reveals there are neither humeral angles nor calli on the elytra of *H. rufipes* ever and Podlussány misinterpreted the strong curvature of inflated elytra in this wingless weevil. Podlussány's study did not include an examination of the genitalia structure in either of the *Humeromima* species. Meanwhile, Formánek (1904) already provided a description and drawing of aedeagus outline of *H. rufipes*, and noticed its significant diagnostic specificity. Borovec (2006) revised the composition of Omiini and divided it into two groups: *Omias* generic complex and *Omiamima* generic complex; *Humeromima* was classified within the latter.

Since previous descriptions are missing many characters, it is important to provide a new comprehensive morphological analysis that serves as the foundation for taxonomic resolution regarding the phylogenetic relationships of *H. rufipes*.

The distribution of *H. rufipes* remains scarcely studied because of hidden behavior and difficulties with its distinction from other similar wingless species with small, glabrous, dark brown bodies. By 1980s distribution data included Austria (Redtenbacher 1874), Germany (Rapp 1934), Poland (Trella 1930), Romania (Liebmann 1920), Slovenia ['Carniolia'] (Marseul 1873), and Ukraine (Schoenherr 1834; Kuntze & Noskiewicz 1938). These data suggested a wide distribution of *H. rufipes*. Subsequently, Dieckmann (1980) critically reviewed all data available to him and noted that records from Germany, Austria, and "Siberia" are based on either mislabeling or misidentifications, and stated that *H. rufipes* occurs only in Poland (Przemyśl), Ukraine (Podolia, Volhynia), and Romania. We also reexamined specimens that had been mislabeled as 'Siberia' or uncertainly labeled as 'Austria'. However, we have not been able to allocate other vouchers referring to Germany.

MATERIAL AND METHODS

This study is based on 54 specimens of *Humeromima rufipes.* Material for this study originates mostly from the collections in the State Natural History Museum in Lviv, Ukraine, and private collection of Denys Khrapov, Lviv, Ukraine, with most specimens collected in Ukraine. Additional material from Romania comes from collections of the German Entomological Institute (Müncheberg, Germany), and the private collection Jiří Krátký (Hradec Králové, Czech Republic). The beetles were collected with pitfall traps by the first author in 10 locations of Ukraine in 2020 and 2021. Permanent plots were set in the western part of the Podolian Upland, in steppe and meadow-steppe biomes. A plot comprises a row of 20 pitfall traps at 5 m from each other. The area of each plot is *c.* 80 m². Preservative liquid for traps is 10% acetic acid + NaCl (75 g/L). Temporal resolution of sampling is *c.* 30 days. Co-occurrences come from original samples by the first author who collected *Humeromima rufipes*.

Taxonomy

The classification of Entiminae Schoenherr, 1823 used in this study is based on Alonso-Zarazaga *et al.* (2023) and includes Sitonini Gistel, 1848. The phylogenetic determination of morphological characters is derived from a cladistic analysis of morphological data obtained from selected Entiminae taxa, including genera within Omiini, such as *Bryodaemon*, *Humeromima*, *Omiamima*, and *Rhinomias* (original results to be published soon).

Dissection

Specimens were soaked in warm water for 30 minutes to soften the tissues. Dirty specimens were cleaned in ultrasonic bath. Male and female terminalia were prepared by detaching the abdomen from the specimen and soaking it in hot 10% KOH solution for three minutes. Abdominal terga were cut along one side and placed in KOH solution for additional three minutes. The macerated parts were rinsed with distilled water and stained with Chlorazol-Black-E to highlight membranous structures. Terminalia were examined on a temporary slide with glycerol, and after examination, they were transferred to a microvial with glycerol and stored alongside their corresponding specimens.

Imaging

Photographs of the body were captured using a customized station comprising the following components: Krokus photographic enlarger, Nikon D3200 camera with Laowa 25mm Ultra Macro lens, Ring 48 LED illumination light, Manfrotto 454 stacking rails. Images of internal structures were obtained with another customized station equipped with Canon EOS 250D camera and microscope Plan objective lenses with

10×, 20×, 40× and 60× magnification, attached to LOMO BIOLAM P12 microscope. All serial images were processed using Zerene Stacker stacking software (https://zerenesystems.com/cms/stacker). Drawings were created in Inkscape 1.1.2 vector graphics editor (Inkscape 2022).

Terminology

Terminology of general morphological structures mostly follows Thompson (1992), Doyen (1966), and Lawrence *et al.* (2011). Terms related to the rostrum follow Oberprieler (1988), Morimoto *et al.* (2006), and Ting (1936), with terms for ventral structures from Lyal (1995); terms related to the male genitalia follow Wanat (2007) and Yunakov (2022); terms for the female terminalia follow Tanner (1927), Howden (1995), and Borovec (2009). Lacinial teeth are counted as those situated proximally of anterior horizontal line of palpiger.

Abbreviations

Institutions

MNHN	Muséum national d'Histoire naturelle, Paris;
NHRS	Naturhistoriska riksmuseet, Stockholm;
SDEI	Senckenberg Deutsches Entomologisches Institut, Müncheberg;
SMNHL	State Museum of Natural History, Lviv;
ZIN	Zoological Institute Russian Academy of Sciences, Saint Petersburg.

Private collections

Coll. KJC	Jiri Krátký, Hradec Králové;
Coll. KhDC	Denys Khrapov, Lviv.

Measurements

BL	length of body;
BW	width of body;
BH	height of body;
RL	length of rostrum;
RW	width of rostrum;
ELD	longitudinal diameter of eye;
EL	length of elytra;
EW	width of elytra;
PL	length of pronotum;
PW	width of pronotum;
VW	width of vertex (distance between medial margins of eyes).

Somatic morphology

as-am	anterior margin of antennal scrobes;
la-te	lacinial teeth;
li	ligula;
li-ca	cavity of ligula;
ocs	occipital sutures;
pp	prosternal process;
pr	prosternellum;
pta	posterior tentorial arms;
ptp	posterior tentorial pits;
tm3-lo	tarsomere 3 lobes.

Female genitalia

buc	bursa copulatrix;
co	collum;
co-mf	membranous formation in apical half of collum;
ds	ductus spermaticus;
fst8-ap	apodeme of female sternite 8;
fst8-lm	lamina of female sternite 8;
fst8-se	setae of female sternite 8;
no	nodulus (corpus);
ra	ramus;
sg	spermathecal gland;
ut	uterus;
va	vagina.

Male genitalia

ml-al	apical lobes of median lobe;
ml-amp	apical membranous plate of median lobe;
ml-ap	apodemes of median lobe;
mst8	male sternite 8;
mst9-ca	caput of apodeme of sternite 9.

Spatial analysis

Paleoenvironmental data

Locations of Last Glacial Maximum microrefugia of arboreal vegetation in Western and Eastern Carpathians are adopted from Mitka *et al.* (2014). Pleistocene vegetation data is compiled in GIS shape format by Ray & Adams (2001) (Fig. 1A). Vascular plant species richness raster layer indicating hypothetical refugia of meadow steppes in Podolian Upland is based on 75 × 75 km grid by Willner *et al.* (2021).

Assessment of endemism

All measurements were done in QGIS 3.22. Occurrence data of *H. rufipes* (points) were plotted to map (Fig. 1C). Nearest neighbor analysis was employed to detect spatial clustering, i.e., whether species occurrences were clustered, dispersed, or randomly distributed across a region, which is a significant additional factor in understanding endemism (Guerin *et al.* 2015). Extent of occurrence (EOO) refers to the region that encompasses all the currently known, inferred, or projected locations where a taxon is found, as enclosed by the shortest possible continuous imaginary boundary. Using vector research tools, a grid was added as an overlay to the EOO shape (features intersect). Then, occurrence data layer joined to grid (features contain). We excluded from spatial calculations the most remote old record from Iresti (Romania), since it is not confirmed by any additional collections since 1917. According to the IUCN (2012) recommendation to calculate Area of Occupancy (AOO), we used 2 × 2 km rectangle grid (Fig. 1B). Area is calculated in ellipsoid projection EPSG 7030. Protected areas vector shapes were downloaded from World Database on Protected Areas (WDPA; UNEP-WCMC and IUCN 2023). To analyze protection efficiency, we plotted AOO of *H. rufipes* on a WDPA shape.

Codes of provinces of Ukraine were adopted from Yunakov *et al.* (2018).

Community analysis

Alpha-diversity metrics, such as richness, relative abundance and evenness (Simpson and Shannon indices), were employed to analyze co-occurrence of *H. rufipes* with other Entiminae species (see Appendix 1). These calculations were carried out using the vegan R package (Oksanen *et al.* 2022).

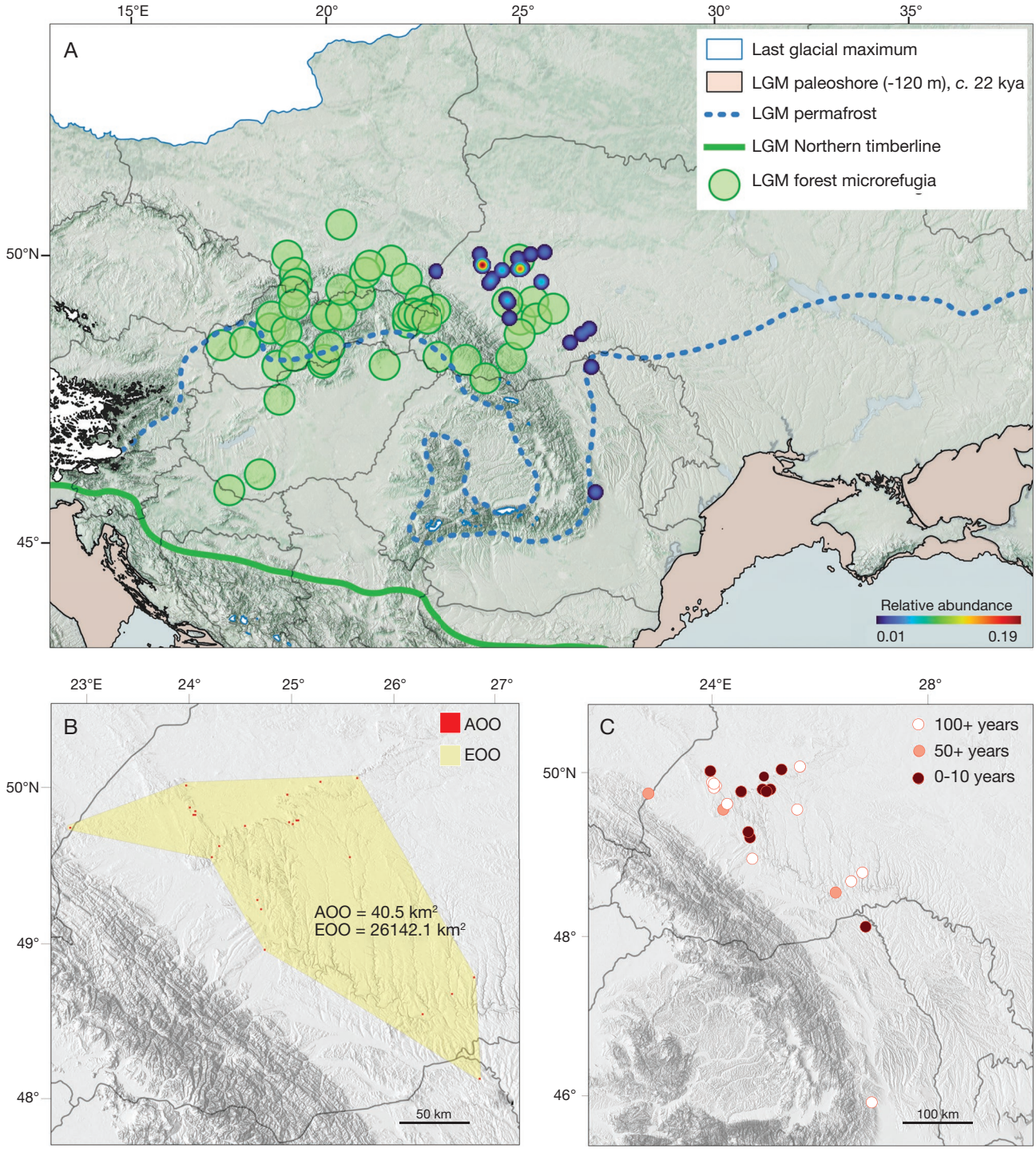

Fig. 1. — Distribution of *Humeromima rufipes* (Boheman, 1834): **A**, occurrences plotted as heat points, alongside paleoenvironmental data for central Europe; **B**, extent of occurrence (**EOO**) and Area of occupancy (**AOO**); **C**, temporal plot of occurrence data showing the number of years since the last collection of *H. rufipes* in each historic locality.

Selection of taxa for comparison

Considering the questionable systematic position of *Humeromima rufipes* we compared it with several genera of Omiini: *Omiamima mollina* (Boheman, 1834), *Omias puberulus* Boheman, 1834, *Omias murinus* (Boheman, 1842), *Bryodaemon hanakii* (Frivaldszky, 1865), and *Rhinomias forticornis* (Boheman, 1842). In addition, to improve differential diagnosis, we also compared it with unrelated taxa that are similar in general appearance, e.g. *Exomias* Bedel, 1883.

RESULTS

Subfamily Entiminae Schoenherr, 1823
Tribe Omiini Shuckard, 1840
Genus *Humeromima* Podlussány, 1998

Humeromima rufipes (Boheman, 1834)
(Figs 1-6)

Omias rufipes Boheman *in* Schoenherr, 1834: 500. — Rybiński 1901: 141. — Trella 1930: 7 (distribution). — Kuntze & Noskiewicz 1938: 345 (distribution). — Smreczyński 1966: 49 (key, distribution). — Formánek 1904b: 176 (key, redescription, figure of aedeagus shape). — Kubisz *et al.* 1998: 267 (distribution).

Omias rufulipes Marseul, 1873: 562 (unjustified emendation by virtue of Article 33.2.3).

Omiamima rufipes – Silfverberg 1977: 227. — Dieckmann 1980: 197 (key, distribution). — Mazur 2002: 230.

Humeromima rufipes – Podlussány 1998: 81. — Borovec 2013: 298. — Yunakov *et al.* 2018: 273 (distribution). — Khrapov & Yunakov 2020: 144 (distribution, figure)

Omias hanaki –[misidentification] Hildt 1893: 231 (distribution).

Material examined. — **Lectotype** (designation: Borovec 2015: 9) (Fig. 2A). **Ukraine** • ♂: "Omias / c.[irca] Volhyn.[ia], Bess.[er]" [manuscript by W. Besser's hand], "Typus [red, printed]"; "LECTOTYPUS *Omias rufipes* Boh. R. Borovec des. 2013 [red, printed]"; *Humeromima rufipes* (Boh.) R. Borovec det. 2013"; NHRS-JLKB 000020796.

Other material. — **Romania** • 2 specimens; Botosani County, near Cotusca; 2.VI.2018; J. Krátký leg.; coll. KJC • 5 specimens; Vrancea County, Iresti, 26.XI.1917; [45.91°N, 26.95°E]; bottom of eroded ravine, W. Liebmann leg.; SDEI (Liebmann 1920) (Fig. 2B). **Ukraine** • 1 ♀; Ivano-Frankivsk Province, "6/7 Wl" [= Vovchynets, 6.VII]; SMNHL • 1 ♂, 2 ♀; Ivano-Frankivsk Province, 5.5 km ESE Burshtyn, Kasova Hora, 15.VI.-28.VII.2020; 49°13'21"N, 24°42'15"E; 295 m a.s.l.; D. Khrapov & R. Panin leg.; steppe; pitfall trap; coll. KhDC, 26278• 1 ♀; Ivano-Frankivsk Province, 1.6 km E Kuropatnyky; 22.V-19.VI.2021; 49°17'2"N, 24°40'8"E; steppe; pitfall trap; D. Khrapov leg.; coll. KhDC, 27736 • 2 ♀; Lviv Province, "IV. Bóbrka" [= Bibrka, Apr.]; SMNHL • 3 ♀; "9/3 Zn" [= Lviv, Znesinnia, 9.III], "1."; SMNHL • 1 ♀; Lviv Province, "3/5 Zn" [= Lviv, Znesinnia, 3 May]; SMNHL • 2 ♀; Lviv Province, "3/5 Zn" [= Lviv, Znesinnia, 3 May], "Leopolis; leg. J. Mazurek"; SMNHL • 4 ♀; Lviv Province, "14/5 Zn" [= Lviv, Znesinnia, 14.V] • 1 ♀; Lviv Province, "9/11 Zn" [= Lviv, Znesinnia, 9 Sep.]; SMNHL • 1 ♀; Lviv Province, "18/5 Ph" [= Lviv, Pohulianka, 18 May]; SMNHL • 1 ♀; Lviv Province, Zolochiv, 1.4 km NW Buchyna, Mts. Drancha, 2.VI.-2.VIII.2019; 50°1'51"N, 25°16'58"E; 328 m a.s.l.; steppe; pitfall trap; leg. D. Khrapov & R. Panin; coll. KhDC, 27363 • 6 ♀; Lviv Province, 2.2 km NNW Yaktoriv; Mt. Chekhova; 16.VII.-01.VIII.2019; 49°45'44"N, 24°32'43"E; 260 m a.s.l.; steppe; pitfall trap; leg. D. Khrapov & R. Panin; coll. KhDC, 27364 • 1 specimen; *ibidem*, 22.V-27.VI.2020; coll. KhDC, 27365 • 1 ♂; Lviv Province, Zolochiv, 2 km NW Pidhirtsi, Mt. Mynych; 20.V-4.VII.2020; 49°57'12"N, 24°57'41"E; 330 m a.s.l.; steppe; pitfall trap; D. Khrapov & R. Panin leg.; coll. KhDC, 27366 • 1 ♂, 5 ♀; Lviv Province, Zolochiv, 0.5 km E Kyikiv, right bank of Zolochivka Riv.; 6.V-11.VI.2021; 49°46'58"N, 24°58'10"E; steppe; pitfall trap; leg. D. Khrapov & R. Panin; coll. KhDC, 27732 • 3 ♀; *ibidem*; MNHN-EC-EC30587, MNHN-EC-EC30588, MNHN-EC-EC30589 • 3 ♀; *ibidem*; 11.VI.-10.VII.2021; coll. KhDC, 27908 • 2 ♀; Lviv Province, Zolochiv, 1.5 km SE Trostianets; 7.V-11.VI.2021; 49°47'40"N, 25°3'25"E; steppe; pitfall trap; leg. D. Khrapov & R. Panin; coll. KhDC, 27735 • 3 ♀; Lviv Province, Zolochiv, 1.2 km W Osovytsia; 7.V-11.VI.2021; 49°47'16"N, 25°3'40"E; 350 m a.s.l.; steppe; pitfall trap; D. Khrapov & R. Panin leg.; coll. KhDC, 27738 • 1 ♀; Zolochiv, 1 km SSE Luka; 6.V-12.VI.2021; 49°46'24"N, 25°1'14"E; 318 m a.s.l.; steppe; pitfall trap; D. Khrapov & R. Panin leg.; coll. KhDC; 27761 • 1 ♀; idem, 12.VI-10.VII.2021; coll. KhDC, 26028 • 1 ♀; Lviv, Mokrotyn, Mt. Harai; 28.IV-31.V.2021; 50°0'53"N, 23°57'45"E; meadow; pitfall trap; D. Khrapov & A. Zatushevsky leg.; coll. KhDC; 27719 • 3 ♀; Ternopil Province, "Каменецъ-Подольскъ, В. и И. Якубовския 1907" [= Kamianets-Podilskyi; V. Jakubowski & I. Jakubowski leg.; 1907]; ZIN • 1 ♀; Ternopil Province, "Volhyn.", "coll. Kraatz", "rufipes / det. Formánek", "*Omias rufipes* Boh.", "SDEI Coleoptera # 303533"; SDEI.
Uncertainly labeled specimen. 1 ♂; "*rufipes* / Austria / Schröder", "*rufipes* / det. Formánek", "*Hyperomias rufipes* Boh.", "SDEI Coleoptera # 303535"; SDEI • 1 ♀;
Mislabeled specimen. "Sibiria", "rufipes / det. Formánek", "coll. Stierlin", "SDEI Coleoptera # 303532"; SDEI.

Redescription

Measurements

BL = 2.13-2.70 mm, BW = 1.08-1.43 mm, BH = 0.88-1.18 mm. (detailed measurements of each individuals are available in Appendix 3)

Vestiture (Figs 2; 3)

Body glabrous, with barely visible, sparse, short (15-20 µm), recumbent, piliform setae. Legs and antennae with sparse, recumbent, piliform setae; club tomentose. Tarsal hairy soles well developed.

Colour

Body shiny, dark brown to black, antennae and legs brown to dark brown.

Head (Fig. 4A-C)

Rostrum almost parallel-sided, distinctly abruptly separated from head capsule, not forming a common cone, RL/RW = 0.91-1.17. Pterygia slightly projecting from lateral contour of rostrum. Antennal scrobes dorsal, posteriorly open; dorsal margin of antennal scrobes reaching ⅔ length of rostrum. Epifrons distinctly edged, weakly convergent, at the level of antennal insertion two times wider than at base and 1.5 times narrower than vertex; flat, separated from vertex by weak transversal depression; finely sparsely punctate, interspaces between punctures twice wider than diameter of punctures; median carina and sulcus absent. Frons not separated from epistome by epistomal carina. Vertex flat longitudinally and weakly convex in transversal direction, VW/ELD = 1.13-1.29; median fovea small but distinct. Eyes subdorsal, oval, distinctly convex, contains about 10 ommatidia in ELD. Posterior tentorial pits merged into a single pit (Fig. 4C, I). Hypostomal-labial suture convergent medially. Occipital suture transverse.

Antennae (Fig. 4H)

Scape evenly curved and widened distally. 1st funicular antennomere distinctly larger than other antennomeres, L/W = 2.36; 2nd funicular antennomere L/W = 1.79; 3rd = 1.08; 4th = 0.95; 5th = 0.88; 6-7th antennomeres L/W = 1; club broadly spindle-shaped, 2.1 times longer than wide, weakly separated from funicle.

Fig. 2. — *Humeromima rufipes* (Boheman, 1834): **A**, lectotype, male, habitus dorsal, lateral, ventral view and labels. Photo credit: by Anna Jerve (NHRS); **B**, habitus of historical specimen (male) from most remote location in Romania. Photo credit: by Kevin Weissing (SDEI). Scale bars: 1 mm.

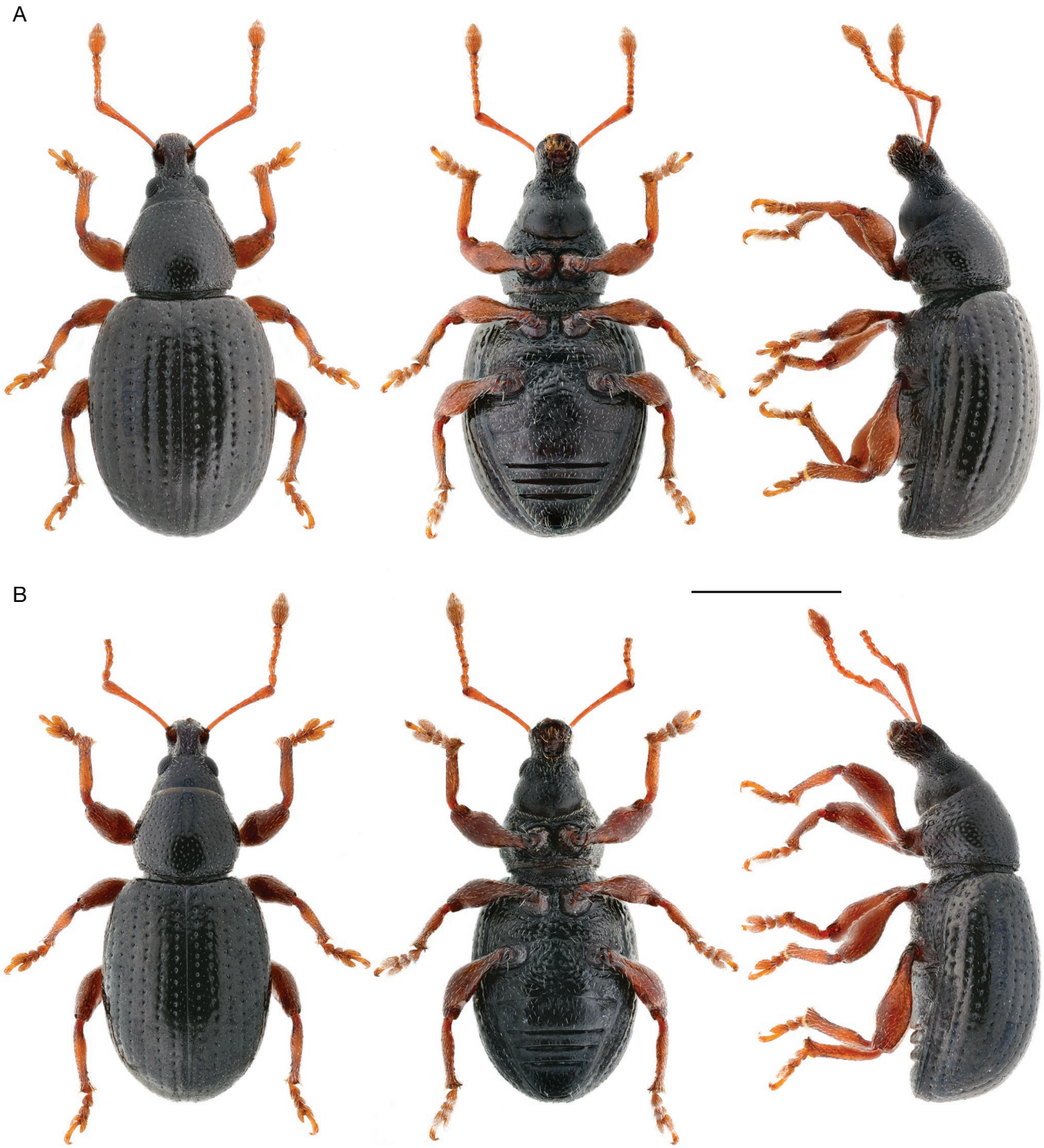

FIG. 3. — *Humeromima rufipes* (Boheman, 1834): **A**, dorsal, ventral, lateral habitus of female (27761, Luka); **B**, dorsal, ventral, lateral habitus of male (27732, 0.5 km E Kyikiv). Scale bar: 1 mm.

Maxilla (Fig. 4E)

Lacinia with four long, straight, clustered teeth. Palpiger with two setae. Palpomere 1 quadrate, palpomere 3 L/W = 0.95, with convex sensillar field. Stipes oblong; stipes-palpiger articulation fused.

Labium (Fig. 4F, G)

Prementum cordate, with two premental setae; ligula extended beyond anterior margin of prementum, ligula in lateral aspect with cavity, anterior process well sclerotized, rounded, with straight dorsal margin; palpomeres L/W: 1st = 0.68; 2nd = 1.15; 3rd = 1.9.

Thorax
Pronotum convex at sides, maximum width posteriad the middle; PL/PW = 0.81-0.9; pronotal disc convex; anterior constriction absent; pronotum at base narrower than base of elytra; punctures piliferous, shallow, narrower than punctures in elytral striae; spaces between punctures equal 1-2 diameter of a puncture. Prosternal process without projection. Prosternellum in ventral aspect forms long process, fused with hypomera, in lateral aspect forms well developed blunt projection (Fig. 4O, P). Mesoventrite and metaventrite with coarse sculpture. Anterior margin of mesonotum concave, prephragmal arms protruded, longitudinal mesothoracic suture well defined (Fig. 4N). Scutellar shield completely reduced.

Elytra
Ovate, weakly convex at sides; EL/EW = 1.21-1.33; disc weakly convex; striae thin, with distinctly edged deep punctures, bearing short, barely visible seta (Fig. 4D); intervals 1.5-2 times as long as puncture diameter; interstriae weakly convex, sparsely punctate with very small punctures bearing short seta, 2.5 times wider than striae. Anterior margin of elytra weakly emarginate.

Legs (Fig. 4J-L)
Femora swollen in middle part, unarmed. Protibia weakly widened at apex, lateral margin almost straight; medial margin entire, sharp, and sinuate in apical half, sparsely pilose; mucro well developed, spur absent. Metatibia widened at apex; medial margin entire, sharp, sinuate in apical half, slightly more densely pilose than mesotibia; mucro well developed, spur absent. Tarsus (Fig. 4M): L/W of 1st tarsomere = 0.75, 2nd = 0.6, 3rd = 1.05, onychium = 4.5; lobes of tarsomere 3 elongate; claws equal, connate at base.

Abdomen (Fig. 4Q)
Ventrite 1 with coarse sculpture, intercoxal process obtuse; posterior margin of male ventrite 1 weakly emarginate, in female straight; female ventrite 5 with glabrous field and long piliform setae near apex.

Male terminalia (Fig. 5A-E)
Sternite 8 weakly sclerotized, composed of lanceolate hemisternites. Sternite 9 with lamina weakly sclerotized and divergently forked arms; apodeme thick, straight, with well developed caput. Median lobe parallel-sided, with ventral wall weakly sclerotized; apical preostial process distinct, apical membranous plate and apical lobes well developed; apodemes 2.5 times longer than median lobe. Endophallus semifolded inside median lobe, with lateral ostial valves distinct, weakly sclerotized; armature comprises large unpaired ostial sclerite and large needle-shaped spicules; endophallic sclerite well developed, asymmetrically twisted, flagellar sheath absent, dorsal plate massive. Tegmen with tegminal ring closed; parameres free medially on base, nearly as long as apodeme, apodeme straight.

Female terminalia (Fig. 5F-I)
Ovipositor telescopic, with long sparse setae; styli vestigial. Spermatheca Y-shaped, with thin wall and reticulate sculpture; ramus as long as collum; collum with membranous formation in apical half; velum absent; cornu well developed; nodulus weakly swollen; spermathecal gland narrow, 4.5 times longer than spermatheca; spermathecal duct inserted at uterus. Bursa copulatrix oval, with distal extension without armature. Sternite 8 with apodeme 2.84 times longer than lamina, bifurcate in basal part, margo basalis distinct, caput small; lamina well sclerotized; anterior margin deeply sinuate; setae long, bilaterally aggregated.

Differential diagnosis
In general appearance *Humeromima rufipes* resembles *Omias* with defoliated vestiture, and having vestiture most similar to *Omias oertzeni* Stierlin, 1887. From most of *Omias*, it differs in the following characters: body glabrous, with very small (length: 15-20 μm) sparse setae, visible only at highest magnifications; bases of elytra broadly rounded, resembling pseudo humeral calli; rostrum separated from head capsule by transverse depression; epifrons distinctly edged; maxilla with four long, straight, clustered lacinial teeth; tibiae mucronate; endophallus not exceeding length of aedeagal apodemes, with well-developed, needle-shaped spicules of various sizes; spermatheca Y-shaped, ramus as long as collum; apodeme of female 8th sternite strongly forked in basal part, apical margin of lamina deeply emarginate. From *Humeromima nitida* (Boheman, 1842) it differs by the transverse depression on the rostrum, epifrons distinctly edged, 1st funicular antennomere almost as wide as 2nd; antennal scape less curved and widened distally. From the glabrous species of the genera *Bryodaemon* and *Exomias*, *H. rufipes* differs by the transverse depression of the epifrons, and peculiar structure of aedeagus bearing membranous lobes and preostial process. From *Bryodaemon* it also differs by having two equal tarsal claws, narrower epifrons and broadly rounded anterior margin of elytra. From *Exomias* it also differs by having longer rostrum, narrower epifrons, dorsal position of the antennal scrobes, well defined and slightly projecting pterygia.

Distribution
Poland (Trella 1930), Ukraine: IFR LWI TER (Schoenherr 1834; Kuntze & Noskiewicz 1938; Yunakov *et al.* 2018; Khrapov & Yunakov 2020), Romania (Liebmann 1920).

Habitat
H. rufipes occurs mostly in meadow steppes and rock steppes at the hilltops, but maximal abundance is registered in grass steppes.

Co-occurrence
In terms of alpha-diversity the community of Entiminae in the study area is moderately even (Simpson mean= 0.23, Shannon mean = 1.42) and represented by 24 species (Fig. 7A). 87.84% of the community is represented by 10 species arranged by

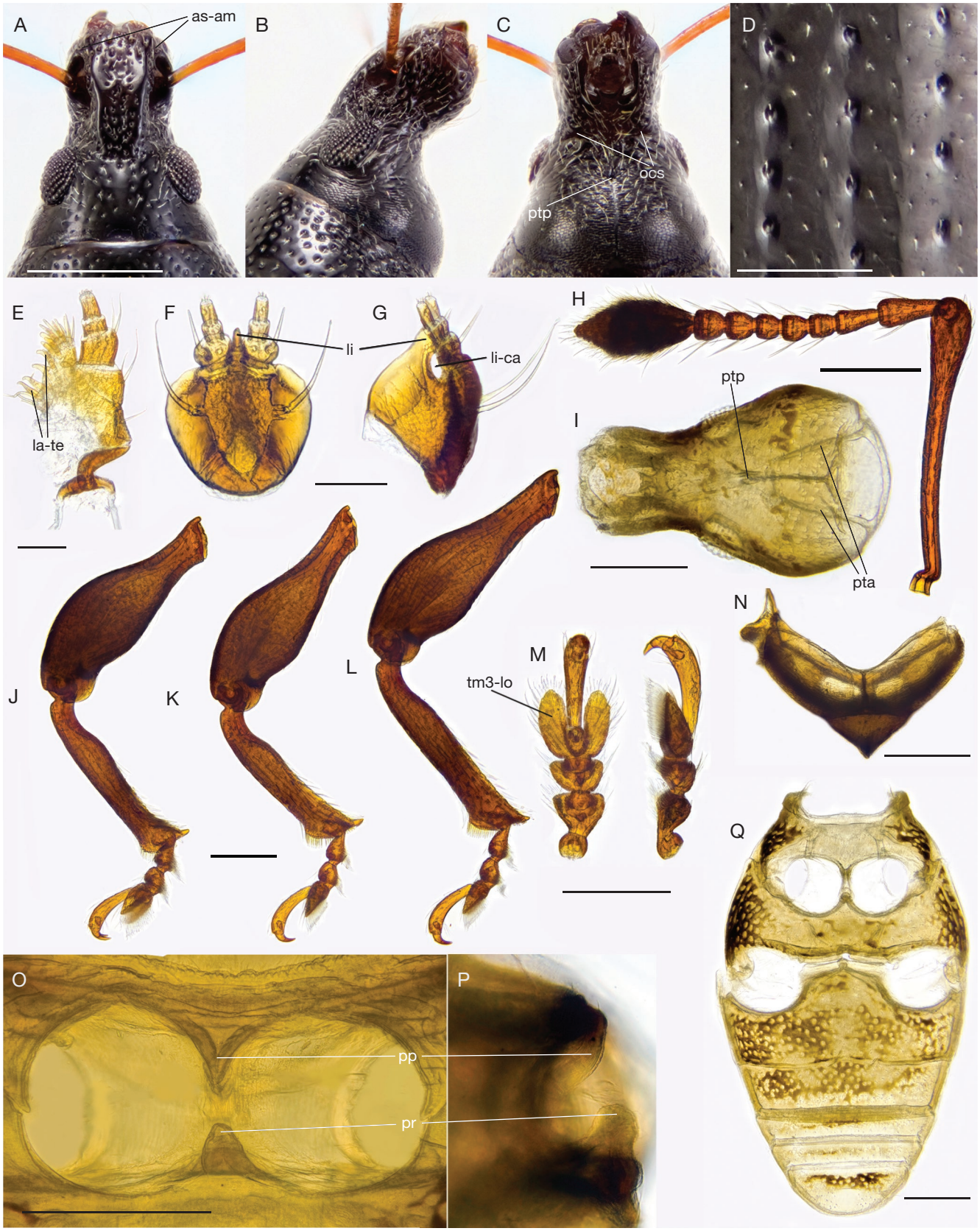

FIG. 4. — *Humeromima rufipes* (Boheman, 1834), morphology, female (27365, Mt. Chekhova): **A**, head, dorsal view; **B**, head, lateral view; **C**, head, ventral view; **D**, scales of elytra; **E**, maxilla; **F**, labium, ventral view; **G**, labium, lateral view; **H**, antenna; **I**, head, (cleared specimen); **J**, fore leg; **K**, middle leg; **L**, hind leg; **M**, tarsus, dorsal and lateral; **N**, mesonotum; **O**, coxal cavities, ventral view; **P**, coxal cavities, lateral view; **Q**, sterna of pterothorax and ventrites (cleared specimen). Abbreviations: **as-am**, anterior margin of antennal scrobes; **la-te**, lacinial teeth; **li**, ligula; **li-ca**, cavity of ligula; **ocs**, occipital sutures; **pp**, prosternal process; **pr**, prosternellum; **pta**, posterior tentorial arms; **ptp**, posterior tentorial pits; **tm3-lo**, tarsomere 3 lobes. Scale bars: A-C, H, J-O, 200 µm; D, µm; E-G, 50 µm; I, Q, 300 µm.

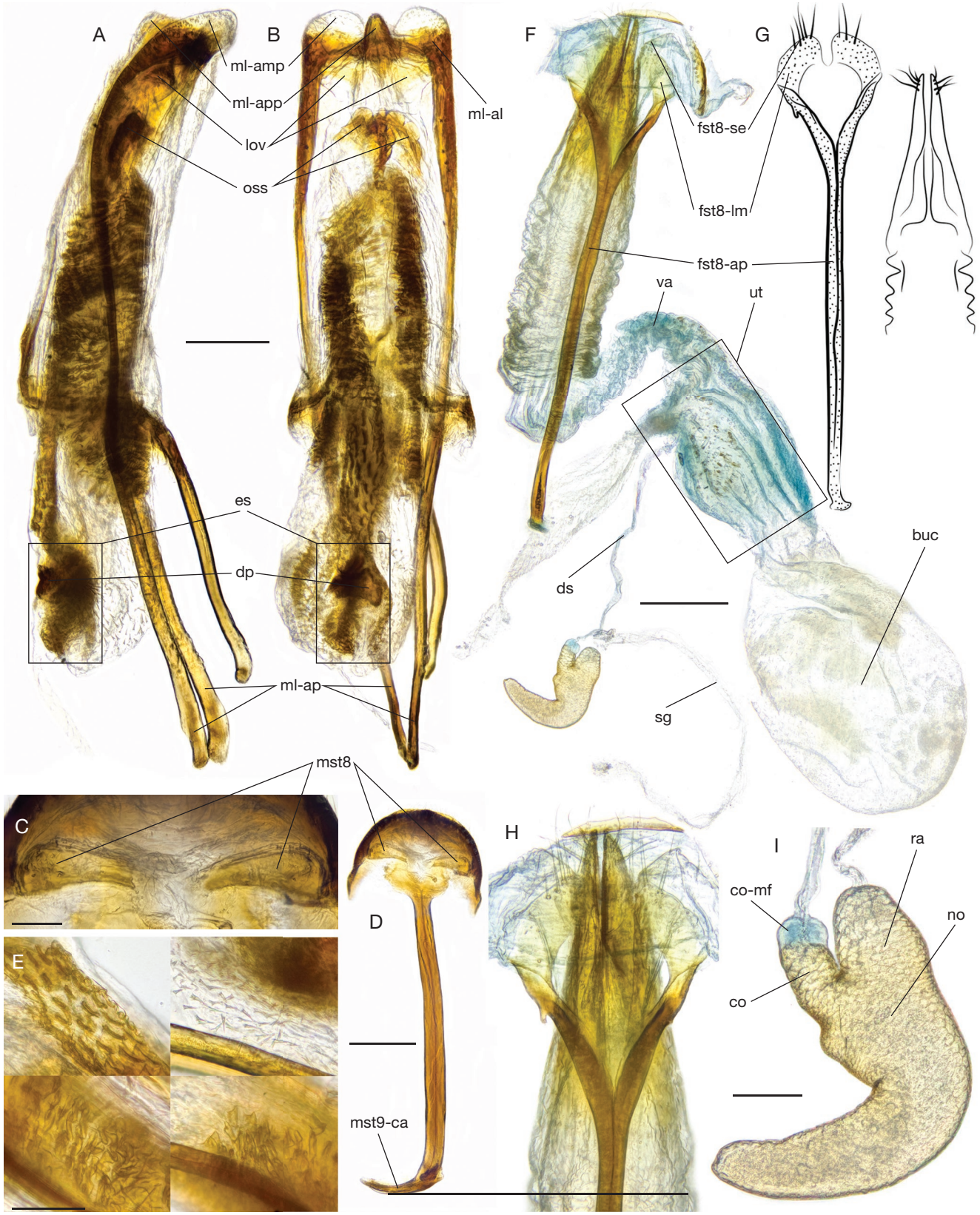

Fig. 5. — *Humeromima rufipes* (Boheman, 1834), morphology: **A**, aedeagus, lateral view; **B**, aedeagus, dorsal view; **C**, male sternite 8; **D**, male sternite 8 and 9; **E**, endophallus armatute; **F**, female terminalia; **G**, female sternite 8 and ovipositor; **H**, apical part of female terminalia (magnified); **I**, spermatheca. Abbreviations: **buc**, bursa copulatrix; **co**, collum; **co-mf**, membranous formation in apical half of collum; **dp**, dorsal plate; **ds**, ductus spermaticus; **es**, endophallic sclerite; **fst8-ap**, apodeme of female sternite 8; **fst8-lm**, lamina of female sternite 8; **fst8-se**, setae of female sternite 8; **lov**, lateral ostial valves; **ml-al**, apical lobes of median lobe; **ml-amp**, apical membranous plate of median lobe; **ml-ap**, apodemes of median lobe; **ml-app**, apical preostial process; **mst8**, male sternite 8; **mst9-ca**, caput of apodeme of sternite 9; **no**, nodulus (= corpus); **oss**, ostial sclerite; **ra**, ramus; **sg**, spermathecal gland; **ut**, uterus; **va**, vagina. Scale bars: A, B, 100 µm; C, E, I, 50 µm; D, F-H, 200 µm; I, Q, 300 µm.

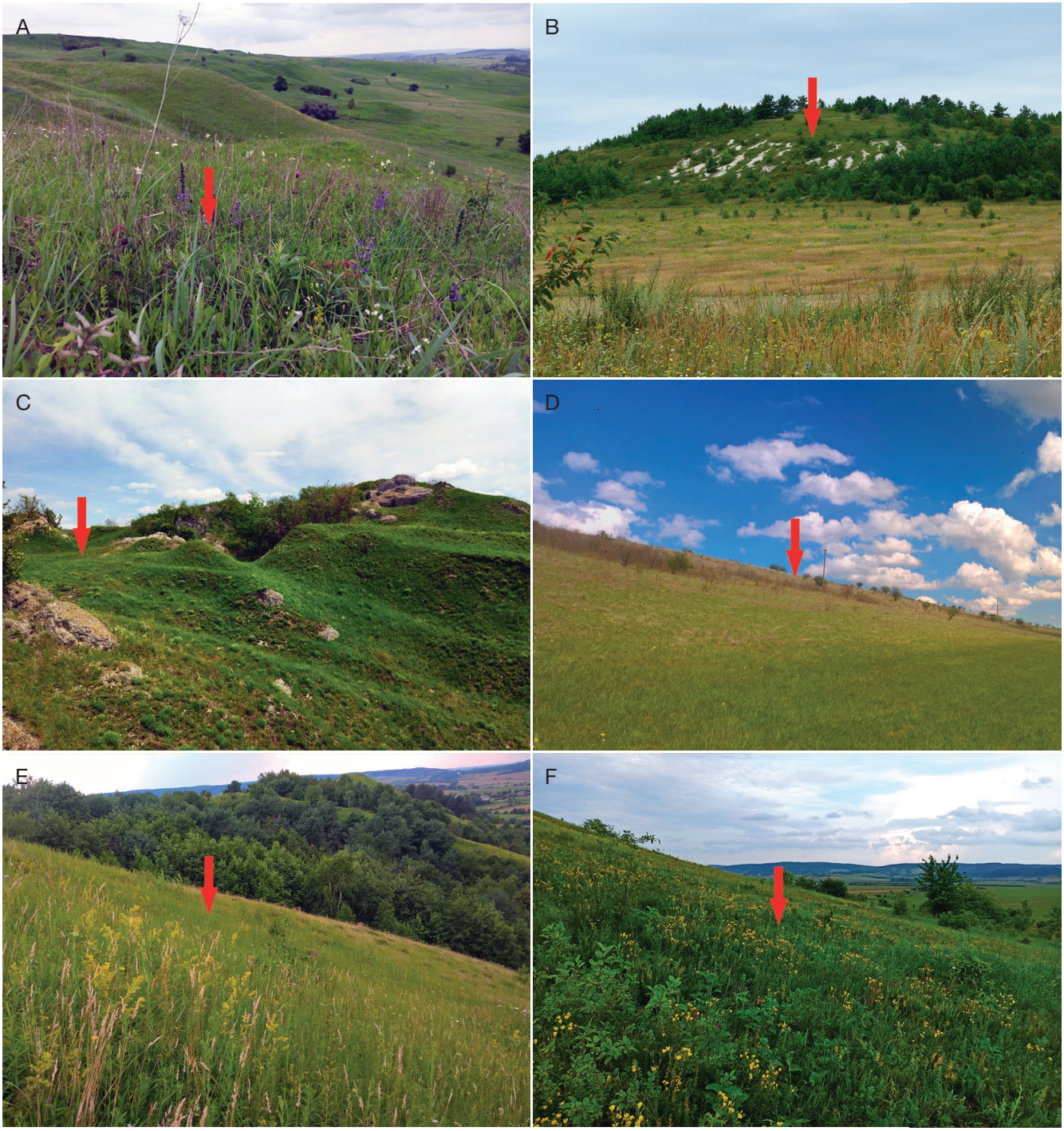

Fig. 6. — Habitats of *Humeromima rufipes* (Boheman, 1834): **A**, meadow steppe, near Burshtyn, Kasova Hora, IFR; **B**, rock steppe, near Buchyna, Mts. Drancha, LWI; **C**, rock steppe, near Kuropatnyky, IFR; **D**, grass steppe, near Kyikiv, LWI; **E**, meadow steppe, near Mokrotyn, Mt. Harai, LWI; **F**, meadow steppe, Yaktoriv, Mt. Chekhova, LWI.

relative abundance as follows: *Cathormiocerus aristatus* (Gyllenhal, 1827) [27.06], *Humeromima rufipes* [12.94], *Trachyphloeus parallelus* Seidlitz, 1868 [8.68], *Otiorhynchus raucus* (Fabricius, 1777) [8.24], *O. ovatus* (Linnaeus, 1758) [7.06], *O. velutinus* Germar, 1823 [5.88], *Trachyphloeus alternans* Gyllenhal, 1834 [5.49], *T. spinimanus* Germar, 1823 [5.49], *Centricnemus leucogrammus* (Germar, 1823) [4.71], *Sitona languidus* Gyllenhal, 1834 [2.75]. The remainder 17 species share 1.96-0.39% each. Remarkably, the top 10 species co-occurring with subendemic *H. rufipes* have wide-ranging West Palaearctic or Transpalaearctic distributions (Fig. 7B; Appendices 1; 2).

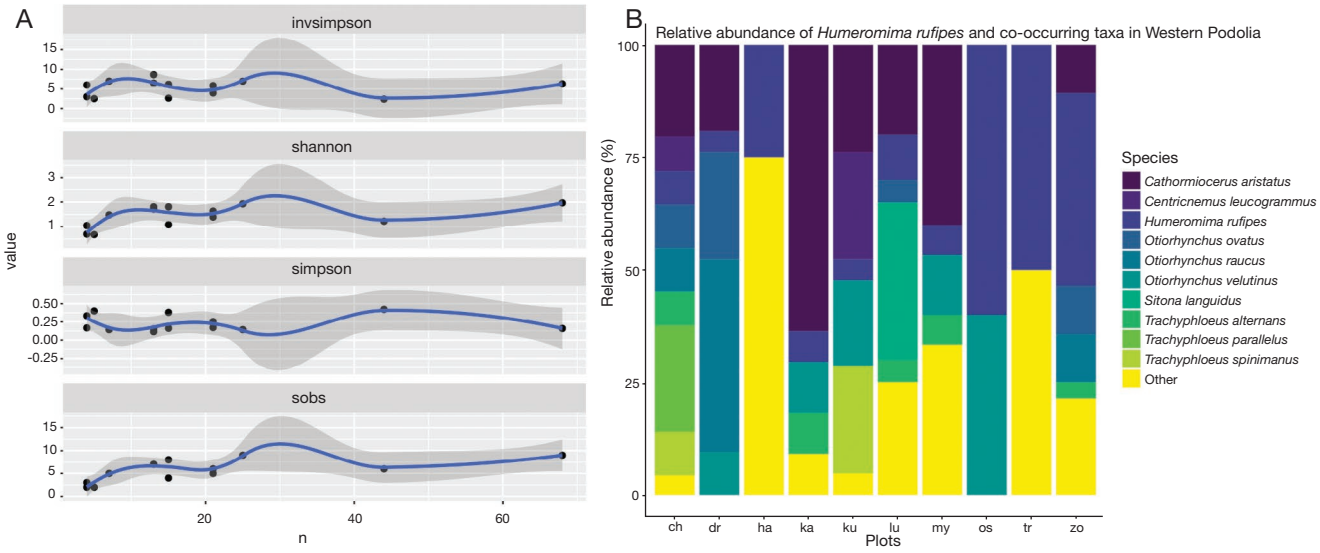

Fig. 7. — Alpha-diversity characteristics of the grass litter Entiminae community (*Humeromima rufipes* (Boheman, 1834) and co-occurring species) in Western Podolia: **A**, evenness of the community evaluated using Shannon and Simpson indices; **B**, top 10 grass litter Entiminae species in Western Podolia. Abbreviations: **Invsimpson**, 1/Simpson (inverted Simpson); **n**, the total number of specimens per sample; **Sobs**, the number of observed species.

DISCUSSION

Taxonomic relationships

Our analysis of morphological characters places *Humeromima rufipes* in *Omias* generic complex, in contrast with placement of *Humeromima* within *Omiamima* generic complex proposed by Borovec (2006). Among Omiini, *H. rufipes* shares with *Omias* two non-homoplastic synapomorphies in the structure of the female terminalia: apical margin of lamina of female sternite 8 emarginate; setae of female sternite 8 bilaterally aggregated; and the following homoplastic synapomorphies in the structure of mouthparts: lacinial teeth clustered, stipes-palpiger articulation fused, prementum cordate, prementum with defined cavity of ligula; in the structure of the head capsule: lateral portion of antennal scrobes absent, anterior margin of antennal scrobes broad; in the structure of the legs: lobes of tarsomere 3 elongate; in the structure of the male genitalia: sternite 8 narrow, lanceolate (probably reversed from membranous), apical preostial process of median lobe present, apical membranous plate on median lobe, apical lobes present.

Humeromima is based on five homoplastic apomorphies: basal part of apodeme of female sternite 8 forked, apodeme connected to apical margin of lamina, caput of apodeme present; vestiture of ventrites setose; endophallus semifolded inside median lobe.

It is important to remark that despite the close relationship between *Humeromima* and *Omias*, the latter demonstrates broad morphological variation. For instance, comparing *Omias borysthenicus* Korotyaev, 1991 with *O. oertzeni*, we can see significant differences in the structure of head capsule, body size and vestiture (Germann *et al.* 2023). Similar morphological variability could be observed among many other species across *Omias*. This makes it impossible to unite *Humeromima* with *Omias* until a comprehensive phylogenetic reconstruction of *Omias* is done. To resolve this, analysis should include as many lineages as possible covering the broadest morphological space, if not all species of *Omias*.

Morphological adaptation

A trend to robustization in the structure of the legs and completely reduced vestiture, differentiates *Humeromima rufipes*, characterizing it as a significantly derived species in adaptation to soil habitat (Osella 1979), compared to *Omias*. Among *Omias*, a similar transformation can be observed in *Omias oertzeni*, a peculiar species that demonstrates a complete reduction of iridescent scales.

Distribution

Type locality

Dieckmann (1980) determined that the type locality is 'Volhynia' based on the original description. However, it is important to note that *H. rufipes* is not found in Volhynia, a large lowland wooded region situated to the north of the Podolian Upland. Consequently, we propose a more precise geographic location for the type locality, which is likely in the vicinity of Kremenets, despite the original label indicating 'Volhynia'. This determination is based on a logical analysis of the species distribution and an examination of the professional activities of Wilibald Besser, who collected plants and insects in the area surrounding Kremenets from 1809 to 1831 (Zaverukha 1984). Besser's activities closely coincide with areas where *H. rufipes* is known to be found.

Previous records from Chernivtsi, Khmelnytsky, and Vinnytsia Provinces of Ukraine are based on aggregated data from 'Podolia' (Yunakov *et al.* 2018) and are not confirmed by any material.

There is a doubtful record from Maramures Mountains, Romania [Tocarnia, forest, skirt 11.VI.2007, under Certina, 47°51'43"N, 24°22'4"E, 1075 m; *ibidem*, 13.VI.2007] (Nițu

2008). This record is based on two specimens that have been lost from the collection of Institutul de Speologie Emil Racoviță (Eugene Nițu personal comm.). As a recent survey suggested (Yunakov *et al.* 2018), a record of *Bryodaemon hanakii* from Ternopil Province by Hildt (1893) is apparently based on misidentification of *H. rufipes*.

The Polish Biodiversity Information Database (Biodiversity Map 2023) has no occurrence data based on specimens from Poland, while a single point on the map is based on a literature source (Trella 1930). The database interprets *H. rufipes* as critically endangered in Poland according to the Polish Red List classification.

Endemism assessment shows an extremely small area of occupancy for *H. rufipes* compared to the extent of its occurrence (AOO = 40.5 km² and EOO = 26142.1 km², frequency = 31 occurrences). Occurrences are clustered in NW Podolian Upland (Nearest neighbour index = 0.55) where the species shows maximal abundance (Fig. 1). 27.1 km² of AOO is under protection in following protected areas of Ukraine: Znesennia Regional Landscape Park, Zagrebellia Regional Landscape Park, Podilski Tovtry National Park, Pivnichne Podillia National Park, Kremenetski Hory National Park, Kozakova dolina State Zakaznik (Sanctuary), Kasova gora State Nature Monument, Dnistrovskyi Canyon National Park, and Bystrytsia Nadvirnianska River valley Emerald Network.

Habitat

According to Smreczyński (1966), *H. rufipes* inhabits forested slopes. Our data reveal it rather lives in mosaic patches of grasslands and forests where its preferences vary from meadow steppes at foothills to rock steppes at the hilltops. (Fig. 6A-F). No records from forest biotopes are known.

95.5% of the species range (AOO) lays within the western part of the Podolian Upland, where *H. rufipes* is constrained to meadow steppes and rock steppes. The persistence of obligate amphigonic populations within glacial forest microrefugia which was reconstructed from palynological analysis (Mitka *et al.* 2014), as well as co-occurrence with the hotspot of biodiversity of meadow steppes detected in Podolian Upland (Roleček *et al.* 2019, Willner *et al.* 2021) overall supports its relict subendemic status since the Last Glacial Maximum.

CONCLUSIONS

Humeromima rufipes is revealed to be affined to the *Omias* rather than to the *Omiamima* generic complex. This suggestion is supported by synapomorphies in the structure of female terminalia, male genitalia, mouthparts, and tarsi. Despite its close affinity with *Omias*, *H. rufipes* has a number of autapomorphies: basal part of apodeme of female sternite 8 forked, forming margo basalis, caput of apodeme present; vestiture of ventrites setose; endophallus semifolded inside median lobe. Since we failed to find specimens for dissection, and *H. nitida* was not included in the analysis, the monophyly of the genus *Humeromima* remains unresolved. By the complete reduction of the iridescent vestiture and pilosity, *H. rufipes* demonstrates deep morpho-adaptive transformation to geophilic life, similar to the trend observed in other *Omias*, e.g. *O. oertzeni* (original observation).

This amphigonic species and habitat specialist is constrained to meadow steppes and rock steppes and hence is suggested to be subendemic of Podolian Upland. Its co-occurrence with hypothetical glacial forest microrefugia, as well as with hotspot of biodiversity of meadow steppes, strongly suggests relict status of *H. rufipes* since the Last Glacial Maximum.

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APPENDICES

APPENDIX 1. — Co-occurrence of *Humeromima rufipes* (Boheman, 1834) with other grass litter Entiminae species. Abbreviations: **GS**, grass steppe; **MS**, meadow steppe; **RS**, rocky steppe; **n**, number of specimens per sample; **lat**, decimal latitude; **long**, decimal longitude; **elev.**, elevation in meters; Plots: **lu**, Luka; **os**, Osovytsia; **dr**, Drancha Mts.; **tr**, Trostianets; **ku**, Kuropatnyky; **my**, Mt. Mynych; **ch**, Mt. Chekhova; **ka**, Kasova Hora; **ha**, Mt. Harai; **zo**, 0.5 km E Kyikiv.

Obs	taxon	plot	locality	sample	date	dateTo	habitat	lat.	long.	elev.	n
27028	*Otiorhynchus ligustici*	zo	0.5 km E Kyikiv	zo44352	5/6/2021	6/11/2021	GS	49.783	24.970	288	1
27031	*Cathormiocerus aristatus*	zo	0.5 km E Kyikiv	zo44352	5/6/2021	6/11/2021	GS	49.783	24.970	288	3
27731	*Stomodes gyrosicollis*	zo	0.5 km E Kyikiv	zo44352	5/6/2021	6/11/2021	GS	49.783	24.970	288	2
27732	*Humeromima rufipes*	zo	0.5 km E Kyikiv	zo44352	5/6/2021	6/11/2021	GS	49.783	24.970	288	9
27013	*Otiorhynchus ovatus*	zo	0.5 km E Kyikiv	zo44506	6/11/2021	7/10/2021	GS	49.783	24.970	288	3
27014	*Otiorhynchus raucus*	zo	0.5 km E Kyikiv	zo44506	6/11/2021	7/10/2021	GS	49.783	24.970	288	3
27015	*Polydrusus inustus*	zo	0.5 km E Kyikiv	zo44506	6/11/2021	7/10/2021	GS	49.783	24.970	288	1
27017	*Foucartia squamulata*	zo	0.5 km E Kyikiv	zo44506	6/11/2021	7/10/2021	GS	49.783	24.970	288	1
27019	*Barynotus obscurus*	zo	0.5 km E Kyikiv	zo44506	6/11/2021	7/10/2021	GS	49.783	24.970	288	1
27024	*Trachyphloeus alternans*	zo	0.5 km E Kyikiv	zo44506	6/11/2021	7/10/2021	GS	49.783	24.970	288	1
27908	*Humeromima rufipes*	zo	0.5 km E Kyikiv	zo44506	6/11/2021	7/10/2021	GS	49.783	24.970	288	3
26012	*Cathormiocerus aristatus*	lu	Luka	lu44352	5/6/2021	6/12/2021	RS	49.773	25.021	318	4
26013	*Trachyphloeus alternans*	lu	Luka	lu44352	5/6/2021	6/12/2021	RS	49.773	25.021	318	1
26014	*Sitona languidus*	lu	Luka	lu44352	5/6/2021	6/12/2021	RS	49.773	25.021	318	4
26016	*Sitona lineatus*	lu	Luka	lu44352	5/6/2021	6/12/2021	RS	49.773	25.021	318	1
26017	*Sitona inops*	lu	Luka	lu44352	5/6/2021	6/12/2021	RS	49.773	25.021	318	1
26020	*Phyllobius maculicornis*	lu	Luka	lu44352	5/6/2021	6/12/2021	RS	49.773	25.021	318	1
27761	*Humeromima rufipes*	lu	Luka	lu44352	5/6/2021	6/12/2021	RS	49.773	25.021	318	1
26025	*Otiorhynchus ligustici*	lu	Luka	lu44536	6/12/2021	7/10/2021	RS	49.773	25.021	318	1
26026	*Otiorhynchus ovatus*	lu	Luka	lu44536	6/12/2021	7/10/2021	RS	49.773	25.021	318	1
26029	*Sitona languidus*	lu	Luka	lu44536	6/12/2021	7/10/2021	RS	49.773	25.021	318	3
26033	*Sitona lineatus*	lu	Luka	lu44536	6/12/2021	7/10/2021	RS	49.773	25.021	318	1
26028	*Humeromima rufipes*	lu	Luka	lu44536	6/12/2021	7/10/2021	RS	49.773	25.021	318	1
26068	*Otiorhynchus velutinus*	os	Osovytsia	os44382	5/7/2021	6/11/2021	MS	49.788	25.061	350	2
27738	*Humeromima rufipes*	os	Osovytsia	os44382	5/7/2021	6/11/2021	MS	49.788	25.061	350	3
26829	*Otiorhynchus ovatus*	dr	Drancha Mts.	dr210619	6/21/2019	8/2/2019	RS	50.031	25.283	328	5
26830	*Otiorhynchus raucus*	dr	Drancha Mts.	dr210619	6/21/2019	8/2/2019	RS	50.031	25.283	328	9
26834	*Cathormiocerus aristatus*	dr	Drancha Mts.	dr210619	6/21/2019	8/2/2019	RS	50.031	25.283	328	4
27231	*Otiorhynchus velutinus*	dr	Drancha Mts.	dr210619	6/21/2019	8/2/2019	RS	50.031	25.283	328	2
27363	*Humeromima rufipes*	dr	Drancha Mts.	dr210619	6/21/2019	8/2/2019	RS	50.031	25.283	328	1
27734	*Otiorhynchus chrysostictus*	tr	Trostianets	tr44382	5/7/2021	6/11/2021	MS	49.794	25.057	385	2
27735	*Humeromima rufipes*	tr	Trostianets	tr44382	5/7/2021	6/11/2021	MS	49.794	25.057	385	2
27006	*Otiorhynchus velutinus*	ku	Kuropatnyky	ku220521	5/22/2021	6/19/2021	RS	49.284	24.669	265	4
27007	*Foucartia squamulata*	ku	Kuropatnyky	ku220521	5/22/2021	6/19/2021	RS	49.284	24.669	265	1
27008	*Cathormiocerus aristatus*	ku	Kuropatnyky	ku220521	5/22/2021	6/19/2021	RS	49.284	24.669	265	5
27009	*Centricnemus leucogrammus*	ku	Kuropatnyky	ku220521	5/22/2021	6/19/2021	RS	49.284	24.669	265	5
27011	*Trachyphloeus spinimanus*	ku	Kuropatnyky	ku220521	5/22/2021	6/19/2021	RS	49.284	24.669	265	5
27736	*Humeromima rufipes*	ku	Kuropatnyky	ku220521	5/22/2021	6/19/2021	RS	49.284	24.669	265	1
26776	*Foucartia squamulata*	my	Mt. Mynych	my200520	5/20/2020	7/4/2020	MS	49.953	24.961	330	1
26777	*Cathormiocerus aristatus*	my	Mt. Mynych	my200520	5/20/2020	7/4/2020	MS	49.953	24.961	330	6
26778	*Otiorhynchus velutinus*	my	Mt. Mynych	my200520	5/20/2020	7/4/2020	MS	49.953	24.961	330	2
26782	*Trachyphloeus alternans*	my	Mt. Mynych	my200520	5/20/2020	7/4/2020	MS	49.953	24.961	330	1
27195	*Otiorhynchus chrysostictus*	my	Mt. Mynych	my200520	5/20/2020	7/4/2020	MS	49.953	24.961	330	2
27305	*Stomodes gyrosicollis*	my	Mt. Mynych	my200520	5/20/2020	7/4/2020	MS	49.953	24.961	330	1
27410	*Exomias chevrolati*	my	Mt. Mynych	my200520	5/20/2020	7/4/2020	MS	49.953	24.961	330	1
27366	*Humeromima rufipes*	my	Mt. Mynych	my200520	5/20/2020	7/4/2020	MS	49.953	24.961	330	1
26314	*Otiorhynchus raucus*	ch	Mt. Chekhova	ch160719	7/16/2019	8/1/2019	MS	49.762	24.545	260	9
26315	*Otiorhynchus ovatus*	ch	Mt. Chekhova	ch160719	7/16/2019	8/1/2019	MS	49.762	24.545	260	6
26316	*Centricnemus leucogrammus*	ch	Mt. Chekhova	ch160719	7/16/2019	8/1/2019	MS	49.762	24.545	260	4
26320	*Cathormiocerus aristatus*	ch	Mt. Chekhova	ch160719	7/16/2019	8/1/2019	MS	49.762	24.545	260	12
26321	*Trachyphloeus alternans*	ch	Mt. Chekhova	ch160719	7/16/2019	8/1/2019	MS	49.762	24.545	260	5
26322	*Trachyphloeus spinimanus*	ch	Mt. Chekhova	ch160719	7/16/2019	8/1/2019	MS	49.762	24.545	260	3
26323	*Trachyphloeus parallelus*	ch	Mt. Chekhova	ch160719	7/16/2019	8/1/2019	MS	49.762	24.545	260	21
26327	*Cycloderes pilosulus*	ch	Mt. Chekhova	ch160719	7/16/2019	8/1/2019	MS	49.762	24.545	260	2
27364	*Humeromima rufipes*	ch	Mt. Chekhova	ch160719	7/16/2019	8/1/2019	MS	49.762	24.545	260	6
26343	*Otiorhynchus ovatus*	ch	Mt. Chekhova	ch220520	5/22/2020	6/27/2020	MS	49.762	24.545	260	3
26344	*Otiorhynchus ligustici*	ch	Mt. Chekhova	ch220520	5/22/2020	6/27/2020	MS	49.762	24.545	260	1
26348	*Centricnemus leucogrammus*	ch	Mt. Chekhova	ch220520	5/22/2020	6/27/2020	MS	49.762	24.545	260	3
26349	*Cycloderes pilosulus*	ch	Mt. Chekhova	ch220520	5/22/2020	6/27/2020	MS	49.762	24.545	260	1
26351	*Trachyphloeus parallelus*	ch	Mt. Chekhova	ch220520	5/22/2020	6/27/2020	MS	49.762	24.545	260	1
26352	*Cathormiocerus aristatus*	ch	Mt. Chekhova	ch220520	5/22/2020	6/27/2020	MS	49.762	24.545	260	7
26353	*Trachyphloeus alternans*	ch	Mt. Chekhova	ch220520	5/22/2020	6/27/2020	MS	49.762	24.545	260	2
26358	*Trachyphloeus spinimanus*	ch	Mt. Chekhova	ch220520	5/22/2020	6/27/2020	MS	49.762	24.545	260	6

Appendix 1. — Continuation.

Obs	taxon	plot	locality	sample	date	dateTo	habitat	lat.	long.	elev.	n
27365	*Humeromima rufipes*	ch	Mt. Chekhova	ch220520	5/22/2020	6/27/2020	MS	49.762	24.545	260	1
26270	*Otiorhynchus velutinus*	ka	Kasova Hora	ka150620	6/15/2020	7/28/2020	MS	49.223	24.704	295	5
26273	*Trachyphloeus alternans*	ka	Kasova Hora	ka150620	6/15/2020	7/28/2020	MS	49.223	24.704	295	4
26274	*Cathormiocerus aristatus*	ka	Kasova Hora	ka150620	6/15/2020	7/28/2020	MS	49.223	24.704	295	28
27313	*Stomodes gyrosicollis*	ka	Kasova Hora	ka150620	6/15/2020	7/28/2020	MS	49.223	24.704	295	2
27447	*Brachysomus setiger*	ka	Kasova Hora	ka150620	6/15/2020	7/28/2020	MS	49.223	24.704	295	2
26278	*Humeromima rufipes*	ka	Kasova Hora	ka150620	6/15/2020	7/28/2020	MS	49.223	24.704	295	3
27718	*Otiorhynchus tristis*	ha	Mt. Harai	ha280421	4/28/2021	5/31/2021	MS	50.015	23.963	310	2
27780	*Exomias pellucidus*	ha	Mt. Harai	ha280421	4/28/2021	5/31/2021	MS	50.015	23.963	310	1
27719	*Humeromima rufipes*	ha	Mt. Harai	ha280421	4/28/2021	5/31/2021	MS	50.015	23.963	310	1

Appendix 2. — Abundance of grass litter Entiminae species in Western Podolia. Abbreviations: Reproduction type (**RT**): **P**, parthenogenetic, **A**, amphigonic. Plots: **lu**, Luka; **os**, Osovytsia; **dr**, Drancha Mts.; **tr**, Trostianets; **ku**, Kuropatnyky; **my**, Mt. Mynych; **ch**, Mt. Chekhova; **ka**, Kasova Hora; **ha**, Mt. Harai; **zo**, 0.5 km E Kyikiv; **n**, total number of specimens.

		Plots										
Taxon	**RT**	**ch**	**dr**	**ha**	**ka**	**ku**	**lu**	**my**	**os**	**tr**	**zo**	**n**
Cathormiocerus aristatus	P	19	4	–	28	5	4	6	–	–	3	69
Humeromima rufipes	A	7	1	1	3	1	2	1	3	2	12	33
Trachyphloeus parallelus	P	22	–	–	–	–	–	–	–	–	–	22
Otiorhynchus raucus	P	9	9	–	–	–	–	–	–	–	3	21
Otiorhynchus ovatus	P	9	5	–	–	–	1	–	–	–	3	18
Otiorhynchus velutinus	P	–	2	–	5	4	–	2	2	–	–	15
Trachyphloeus alternans	P	7	–	–	4	–	1	1	–	–	1	14
Trachyphloeus spinimanus	P	9	–	–	–	5	–	–	–	–	–	14
Centricnemus leucogrammus	A	7	–	–	–	5	–	–	–	–	–	12
Sitona languidus	A	–	–	–	–	–	7	–	–	–	–	7
Stomodes gyrosicollis	P	–	–	–	2	–	–	1	–	–	2	5
Otiorhynchus chrysostictus	A	–	–	–	–	–	–	2	–	2	–	4
Cycloderes pilosulus	P	3	–	–	–	–	–	–	–	–	–	3
Foucartia squamulata	P	–	–	–	–	1	–	1	–	–	1	3
Otiorhynchus ligustici	P	1	–	–	–	–	1	–	–	–	1	3
Brachysomus setiger	A	–	–	–	2	–	–	–	–	–	–	2
Otiorhynchus tristis	P	–	–	2	–	–	–	–	–	–	–	2
Sitona lineatus	A	–	–	–	–	–	2	–	–	–	–	2
Barynotus obscurus	P	–	–	–	–	–	–	–	–	–	1	1
Exomias chevrolati	A	–	–	–	–	–	–	1	–	–	–	1
Exomias pellucidus	A	–	–	1	–	–	–	–	–	–	–	1
Phyllobius maculicornis	A	–	–	–	–	–	1	–	–	–	–	1
Polydrusus inustus	P	–	–	–	–	–	–	–	–	–	1	1
Sitona inops	A	–	–	–	–	–	1	–	–	–	–	1

Appendix 3. — Measurements of *Humeromima rufipes* (Boheman, 1834). The specimen number refers to the number of observations detailed in Appendix 1. Abbreviations: **BH**, height of body; **BL**, length of body; **BW**, width of body; **RL**, length of rostrum; **RW**, width of rostrum; **VW**, width of vertex (distance between interior margins of eyes); **ELD**, longitudinal diameter of eye; **EL**, length of elytra; **EW**, width of elytra; **PL**, length of pronotum; **PW**, width of pronotum. Plots: **lu**, 1 km SSE Luka; **os**, 1.2 km W Osovytsia; **dr**, Drancha Mts.; **tr**, 1.5 km SE Trostianets; **ku**, Kuropatnyky; **my**, Mt. Mynych; **ch**, Mt. Chekhova; **ka**, Kasova Hora; **ha**, Mt. Harai; **zo**, 0.5 km E Kyikiv.

specimen	sex	Plot	BL	BW	BH	RL	RW	VW	ELD	EL	EW	PL	PW	RL/RW	VW/ELD	PL/PW	EL/EW	EL/BH
27366_1	m	my	2.13	1.08	0.88	0.25	0.28	0.18	0.15	1.35	1.08	0.58	0.68	0.91	1.17	0.85	1.26	1.54
27719_2	f	ha	2.50	1.30	0.98	0.35	0.30	0.23	0.20	1.65	1.30	0.68	0.83	1.17	1.13	0.82	1.27	1.69
27363_3	f	dr	2.65	1.38	1.13	0.35	0.33	0.23	0.18	1.75	1.38	0.65	0.80	1.08	1.29	0.81	1.27	1.56
26278_4	f	ka	2.55	1.35	1.08	0.33	0.33	0.23	0.20	1.70	1.35	0.68	0.80	1.00	1.13	0.84	1.26	1.58
26278_5	f	ka	2.63	1.43	1.15	0.35	0.33	0.23	0.18	1.78	1.43	0.73	0.88	1.08	1.29	0.83	1.25	1.54
27732_6	f	zo	2.38	1.25	0.98	0.30	0.30	0.20	0.18	1.58	1.25	0.65	0.78	1.00	1.14	0.84	1.26	1.62
27732_7	f	zo	2.50	1.25	1.03	0.33	0.33	0.23	0.18	1.63	1.25	0.70	0.80	1.00	1.29	0.88	1.30	1.59
27732_8	m	zo	2.30	1.13	0.90	0.30	0.30	0.23	0.20	1.50	1.13	0.63	0.73	1.00	1.13	0.86	1.33	1.67
27732_9	f	zo	2.70	1.43	1.18	0.35	0.33	0.23	0.20	1.83	1.43	0.73	0.88	1.08	1.13	0.83	1.28	1.55
27732_10	f	zo	2.58	1.40	1.10	0.33	0.33	0.23	0.18	1.70	1.40	0.73	0.88	1.00	1.29	0.83	1.21	1.55
27732_11	f	zo	2.30	1.20	0.95	0.30	0.30	0.23	0.18	1.55	1.20	0.63	0.75	1.00	1.29	0.83	1.29	1.63
27364_12	f	ch	2.55	1.33	1.05	0.33	0.33	0.23	0.18	1.73	1.33	0.70	0.80	1.00	1.29	0.88	1.30	1.64
27364_13	f	ch	2.63	1.40	1.15	0.35	0.33	0.25	0.20	1.70	1.40	0.75	0.85	1.08	1.25	0.88	1.21	1.48
27364_14	f	ch	2.63	1.38	1.18	0.33	0.33	0.25	0.20	1.78	1.38	0.73	0.85	1.00	1.25	0.85	1.29	1.51
27364_15	f	ch	2.75	1.45	1.15	0.35	0.35	0.25	0.20	1.80	1.45	0.80	0.88	1.00	1.25	0.91	1.24	1.57
27364_16	f	ch	2.65	1.40	1.18	0.35	0.35	0.25	0.20	1.78	1.40	0.73	0.88	1.00	1.25	0.83	1.27	1.51
27364_17	f	ch	2.40	1.28	1.03	0.33	0.33	0.23	0.18	1.63	1.28	0.65	0.78	1.00	1.29	0.84	1.27	1.59
27761_18	f	lu	2.70	1.43	1.18	0.35	0.33	0.23	0.18	1.85	1.43	0.70	0.85	1.08	1.29	0.82	1.30	1.57
26028_19	f	lu	2.43	1.28	1.00	0.33	0.33	0.20	0.18	1.63	1.28	0.65	0.75	1.00	1.14	0.87	1.27	1.63
27736_20	f	ku	2.63	1.35	1.15	0.35	0.33	0.23	0.20	1.73	1.35	0.70	0.85	1.08	1.13	0.82	1.28	1.50
27738_21	f	os	2.63	1.43	1.13	0.33	0.33	0.25	0.20	1.75	1.43	0.75	0.83	1.00	1.25	0.91	1.23	1.56
27738_22	f	os	2.55	1.33	1.08	0.33	0.30	0.23	0.20	1.73	1.33	0.68	0.80	1.08	1.13	0.84	1.30	1.60
27738_23	f	os	2.38	1.23	0.93	0.33	0.30	0.23	0.18	1.60	1.23	0.63	0.73	1.08	1.29	0.86	1.31	1.73
27735_24	f	tr	2.48	1.25	1.03	0.33	0.30	0.23	0.20	1.60	1.25	0.63	0.75	1.08	1.13	0.83	1.28	1.56
27735_25	f	tr	2.43	1.25	0.98	0.33	0.33	0.23	0.20	1.60	1.25	0.68	0.75	1.00	1.13	0.90	1.28	1.64