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INTEGRATIVE APPROACHES FOR PRECISE IDENTIFICATION AND RANGE DELIMITATION OF THE THREE MOST COMMON EUROPEAN *LEIOPUS* SPECIES (COLEOPTERA, CERAMBYCIDAE)

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Integrative Approaches for Precise Identification and Range Delimitation of the Three Most Common European *Leiopus* species (Coleoptera, Cerambycidae). Zamoroka, A. M. — *Leiopus nebulosus* (Linnaeus, 1758), *L. linnei* Wallin, Nylander & Kvamme, 2009 and *L. femoratus* Fairmaire, 1859 are the three most common European species of the long-horn beetle genus *Leiopus* Audinet-Serville, 1835. These species have often been misidentified due to their general morphological similarities. This study addresses the need for a simple and reliable method to differentiate *L. nebulosus, L. linnei*, and *L. femoratus.* Through the examination of a long series of specimens, specific morphological traits were identified, such as the shape of the femora on all legs and the width of the prosternal process, which allow for rapid and accurate differentiation between the three species. The findings led to the refinement of the diagnostic criteria for these species and the development of a straightforward identification key. Ecological niche modelling was employed to construct accurate global distribution maps for all three species. Additionally, the proposal to conserve the name *Leiopus linne*i under Article 23.9 of the Code was made.

Key words: longhorn beetles, morphology, integrative taxonomy, molecular phylogeny, niche modelling.

Introduction

By the end of the 20th century, *Leiopus nebulosus* Linnaeus, 1758, was considered the only widely distributed species in Europe (Brustel et al., 2002; Sama, 2002; Wallin et al., 2009; Löbl & Smetana, 2010). However, in the first decade of the 21st century, the rapid northward expansion of *Leiopus femoratus* Fairmaire, 1859, was noted. This expansion was observed almost simultaneously in Eastern Europe (Zamoroka & Kapelyukh, 2012; Zamoroka, 2022 b), Central Europe (Hedyessy & Kutasi, 2010; Klausnitzer et al., 2016), and Western Europe (Brustel et al., 2002; Troukens et al., 2017; Vitali, 2018; Touroult et al., 2019). At the present time, *L. femoratus* has reached the shores of the Baltic Sea and continues to spread northwards (Alekseev, 2020). Consequently, *L. femoratus* has become the second species of the genus with pan-European distribution. The third species known to have a Europe-wide distribution is *Leiopus linnei* Wallin, Nylander & Kvamme, 2009, which was described from Scandinavia, though its true range remained largely unknown for a decade (Wallin et al., 2009). Throughout the second decade of the 21st century, a series of publications reported the presence of *L. linnei* across Europe, with the exception of Southern Europe (Gutowski et al., 2010; Bukejs & Balalaikins, 2011; Zamoroka & Kapelyukh, 2012; Klausnitzer et al., 2016; Vitali, 2018).

All three species of *Leiopus* exhibit general morphological similarities, which has frequently led to confusion in their identification. Additionally, all three species display significant intraspecific variability in coloration, complicating rapid identification and often resulting in gross misidentifications. Wallin et al. (2009) proposed three approaches to distinguish *L. linnei* from its sibling species, *L. nebulosus*. These include 1) external morphological characteristics, 2) morphology of the male terminalia and spermatheca, and 3) DNA barcoding based on the first subunit of cytochrome c oxidase (COI or Cox1). While barcoding and terminalia dissection are labor-intensive and time-consuming, the morphological traits they suggested are unreliable and non-universal. Proper identification of *L. linnei* based on morphology, according to the keys provided in Wallin et al. (2009), requires extensive experience and the examination of a large number of specimens.

Rossa et al. (2017), in their brilliant paper, proposed a highly effective method for distinguishing *L. linnei* and *L. nebulosus* using wing morphometry. However, this method has several drawbacks. First, it is statistical in nature and requires a representative sample size, making the identification of single specimens impractical. Second, it remains a labor-intensive process, requiring a considerable amount of time. Third, it demands technical expertise and significant experience.

Leiopus femoratus is morphologically more distinct from *L. linnei* and *L. nebulosus*. However, this has not entirely prevented widespread misidentifications of this species by entomologists. For instance, *L. femoratus* was long confused with *L. nebulosus* and *L. linnei* in France (Brustel et al., 2002; Touroult et al., 2019), Italy (Biscaccianti & Petruzziello, 2007), and Lithuania (Tamutis et al., 2011). These numerous misidentifications led to an underestimation of the distribution of *L. femoratus* and challenges in understanding the species' contemporary range expansion.

In general, given the aforementioned challenges, there is a clear need for a simple and reliable method to differentiate *L. femoratus*, *L. nebulosus*, and *L. linnei*.

In the present study, I propose a simple and rapid approach for the identification of *L. nebulosus*, *L. linnei*, and *L. femoratus* based on the external morphology of imago. The selected morphological traits are reliable and consistently correspond with the structure of male terminalia with absolute certainty. Additionally, I have developed a straightforward and user-friendly key for identifying the three *Leiopus* species, accompanied by photographs of key diagnostic features to aid in species identification.

Material and Methods

Material examined. I have studied 733 specimens of *Leiopus* from Central and Eastern Europe, including 129 specimens of *L. nebulosus*, 130 specimens of *L. linnei* and 474 specimens of *L. femoratus* as follows.

Leiopus nebulosus: **Austria**: Nenzing (47.17100, 9.73238), 105 specimens, 2018 (R. Angeleri) (UZNU); **Liechtenstein**: Planken (47.17942, 9.54160), 1 specimen 2018 (R. Angeleri) (UZNU); **Switzerland**: Rüthi (47.29811, 9.52453), 1 specimen 2018 (R. Angeleri) 2018; Sennwald (47.27794, 9.50480), 3 specimens 2018 (R. Angeleri) (PUIF); **Ukraine**: Birky (51.836247, 25.168413), 1 specimen 10.VI.2022 (A. Zamoroka) (PUIF); Puhachivka (50.862099, 28.372758), 1 specimen 17. VI.2021 (O. Martsun) (PUIF); Rybne (48.943561, 24.589708), 1 specimen 13.III.2020 ex larva (A. Zamoroka) (PUIF); Tsuman' (50.877794, 25.916080), 1 specimen 08.VI.2019 (V. Chumak) (UZHNU); Uzhhorod (48.619884, 22.305281), 1 specimen 04.V.1960 (I. Zahajkevych) (SMNH); Crimea, "Verkhovyna" (probably Babugan Yaila) (44.627638, 34.284484), 4 specimens 26.V.1958 (I. Zahajkevych) (SMNH); Ala-Bach (44.617003, 34.227958), 2 specimens 25.V.1958 (I. Zahajkevych) (SMNH); Khyr-Alan (44.733589, 34.185227), 1 specimen 23.VI.1956 (I. Zahajkevych) (SMNH); Alushta (44.676655, 34.414552), 2 specimens 16.VI.1955 (I. Zahajkevych) (SMNH); Yamna (48.430654, 24.580668), 1 specimen 15.VII.1951 (I. Zahajkevych) (SMNH); Truscavets' (49.273606, 23.499561), 1 specimen 18.VIII.1931(SMNH); ibid. 1 specimen 08.VII.1932 (Sagan) (SMNH); Derman' (50.378488, 26.239034), 1 specimen 20.V.1907, collector unknown(SMNH); loc. unknown, 1 specimen 25.V (Lm) (SMNH).

Leiopus linnei: **Austria**: Düns (47.23077, 9.70340), 2 specimens 2018 (R. Angeleri) (UZNU); Nenzing (47.17100, 9.73238), 4 specimens 2018 (R. Angeleri) (PUIF); Thüringen (47.21214, 9.79930), 3 specimens (R. Angeleri) (UZNU); Morsch (47.29011, 9.69610), 3 specimens 2018 (R. Angeleri) (PUIF); **Liechtenstein**: Planken (47.17942, 9.54160), 1 specimen 2018 (R. Angeleri) (PUIF); **Poland**: Karwia (54.829379, 18.216271), 1 specimen 26.VIII.1922 (N. Morzem) (SMNH); Zarzecze (49.985208, 22.539908), 1 specimen 1918 (J. Kinel) (SMNH); Lubien (49.714184, 19.971947), 1 specimen 26.V.1913(SMNH); **Russia**: Zheleznovodsk (44.121894, 43.033049), 2 specimens 17.VI.2007 (S. Svetlov) (PUIF); **Switzerland**: Landquart (46.94714, 9.60849), 1 specimen 2018 (R. Angeleri) (UZNU); Luzein (46.95279, 9.73491), 2 specimens 2018 (R. Angeleri) (UZNU); Sennwald (47.27794, 9.50480), 5 specimens 2018 (R. Angeleri) (UZNU); **Ukraine**: Bykhiv (51.740581, 25.293560), 1 specimen 09.VI.2022 (A. Zamoroka) (PUIF); Opishnya (49.957195, 34.628167), 1 specimen 26.VI.2021 (Ye. Rybal'chenko) (PUIF); Kyiv (50.373903, 30.483525), 1 specimen 16.VI.2021(PUIF); Rybne (48.943561, 24.589708), 1 specimen 13. III.2020 ex larva (A. Zamoroka) (PUIF); Tsuman' (50.877794, 25.916080), 1 specimen 08.VI.2019 (V. Chumak) (UZNU); Kostryna (48.923895, 22.556065), 1 specimen 21.VI.2018 (N. Koval) (PUIF); Bohorodchazny (48.832830, 24.586739), 2 specimens 09.V.2018 (O. Varga) (PUIF); Vynohradiv (48.145197, 23.068058), 1 specimen 07.VI.2018, 1 specimen 23.VI.2016, 2 specimens 05.VI.2016 (O. Varga) (PUIF); Kremenets (50.095884, 25.698596), 2 specimens 05.VI.2018, 1 specimen 04.VI.2018 (A. Zamoroka) (PUIF); Sarny (51.319966, 26.675126), 1 specimen 17.VI.2017 (R. Zhuravchak) (PUIF); Ustechko (48.780632, 25.582993), 1 specimen 04.VI.2016 (A. Zamoroka) (PUIF); Kvasy (48.145477, 24.266293), 6 specimens 08.VII.2015, 1 specimen 18.VII.2015 (O. Varga) (PUIF); Haydary (49.646280, 36.333975), 1 specimen 13.VI.2015 (Yu. Skrylnyk) (PUIF); Vakalivschyna (51.036213, 34.926083), 1 specimen 03.VI.2015 (O. Hovorun) (PUIF); Hrymayliv (49.333747, 26.018337), 8 specimens 05.VI.2014 (A. Zamoroka) (PUIF); Mala Uholka (48.266397, 23.622580), 5 specimens 25.VI.2011 (V. Chumak) (PUIF); Hutys'ko (49.397280, 24.820511), 1 specimen 28.V.2011 (A. Zamoroka) (PUIF); Vyshniv (49.252378, 24.384337), 6 specimens 11.VI.2004 (A. Zamoroka) (PUIF); Kryvyi Rih (47.897596, 33.388656), 2 specimens 06.V.2003 (A. Holovatiuk) (PUIF); Ukrayinka (50.149147, 30.737058), 1 specimen 10.VI.1981 (I. Zahajkevych) (SMNH); Bortnychi (50.371209, 30.723327), 1 specimen 30.VI.1965 (I. Zahajkevych) (SMNH); Busheve (49.638584, 30.585019), 1 specimen 08.VII.1965, 1 specimen 20. VII.1965 (Giritz) (SMNH); Uzhhorod (48.619884, 22.305281), 1 specimen 16.V.1964, 1 specimen 04.V.1958, 2 specimens 04.VI.1958, 2 specimens 28.V.1958, 1 specimen 22.V.1952 (I. Zahajkevych, Giritz) (SMNH); Humnyska (49.971302, 24.725463), 1 specimen VI.1959 (I. Zahajkevych) (SMNH); Lviv (49.825097, 24.060820), 1 specimen 25.VI.1956 (I. Zahajkevych) (SMNH); Struha (48.798225, 27.295536), 3 specimens 16.V.1956 (I. Zahajkevych) (SMNH); Makiv (48.784084, 26.658180), 1 specimen 02VI.1955 (I. Zahajkevych) (SMNH); Kivertsi (50.841021, 25.438036), 3 specimens 26.VI.1954 (I. Zahajkevych) (SMNH); Briukhovychi (49.908609, 23.948353), 1 specimen 17.VI.1952, 2 specimens 27.V.1947 (I. Zahajkevych) (SMNH); Klishkivtsi (48.463128, 26.293189), 1 specimen 1951 (I. Zahajkevych) (SMNH); Kaniv (49.736286, 31.496484), 1 specimen 22.VIII.1946 (I. Zahajkevych) (SMNH); Klishkivtsi (48.463128, 26.293189), 1 specimen 02.VII.1951 (I. Zahajkevych) (SMNH); Lviv (49.825097, 24.060820), 1 specimen 29.V.1932, 1 ex VIII.1898 (J. Kinel) (SMNH); Truskavest' (49.273606, 23.499561), 1 specimen 18.VIII.1931 (Sagan) (SMNH); Vynnyky (49.806214, 24.103032), 1 specimen 06.VII.1925 (V. Lazorko) (SMNH); Zhytomyr (50.254615, 28.651639), 1 specimen 14.VI.1922 (Proschiga) (SMNH); Dora (48.483560, 24.588587), 1 specimen 06.VI.1918 (J. Kinel) (SMNH); Tulyn (48.843556, 26.052577), 1 specimen 1918 (J. Kinel) (SMNH); Horokhiv (50.497843, 24.759575), 1 specimen VII.1916 (SMNH); Tukhlia (48.917093, 23.466781), 1 specimen 24.VII.1911 (J. Kinel) (SMNH); Lviv (49.825097, 24.060820), 1 specimen 18.VI.1909 (J. Kinel) (SMNH); Skala-Podilska (48.844839, 26.193531), 1 specimen 22.VI.1906 (Hankevych) (SMNH); Chornushovychi (49.821269, 24.328728), 1 specimen 1896 (SMNH); Ivano-Frankove [Yaniv] (49.915140, 23.723955), 3 specimens n.d. (A. Stöckl) (SMNH); Kyrsanivka (48.564712, 28.987943), 1 specimen 09.VI n.d. (I. Zahajkevych) (SMNH); Kryvchytsi (49.843181, 24.072281), 1 specimen 1918 (J. Kinel) (SMNH); Lysynychi (49.829338, 24.117385), 1 specimen n.d. (A. Stöckl) (SMNH); Novosilky (49.773428, 24.653517), 1 specimen n.d. (Swiatkewicz) (SMNH); Syn'kiv (48.610309, 25.948516), 1 specimen n.d. (J. Kinel) (SMNH); Trostianets (50.472522, 34.989923), 1 specimen n.d. (Padiy) (SMNH); Zhuravlivka (50.016428, 36.276246), 2 specimens n.d. (I. Zahajkevych) (SMNH); 1 specimen 9.IX, L (no additional data) (SMNH); 1 specimen 02.VI, K (no additional data) (SMNH); 1 specimen 06.VI, K (no additional data) (SMNH); 1 specimen №1183, Osterloff, det J. Kinel [as *L. nebulosus*] (no additional data) (SMNH); 2 specimen A. Stöckl (no additional data) (SMNH); 3 specimen juli (no additional data) (SMNH); 1 specimen 19.VII, Spki (no additional data) (SMNH); 2 specimens from [former] Drohobych Museum (no additional data) (SMNH); 1 specimen 10.VI, K (no additional data) (SMNH); 1 specimen 22.VI, Lm (no additional data) (SMNH).

Leiopus femoratus: **Austria**: Nenzing (47.17100, 9.73238), 1 specimen 2018 (R. Angeleri) (PUIF); **Russia:** Zheleznovodsk (44.135931, 43.012799), 1 specimen 17.06.2007 (S. Svetlov) (PUIF); Maykop (44.587405, 40.101431), 3 specimens VI.1927 (Bogachev) (SMNH); Taganrog (7.207397, 38.900536), 1 specimen 1916 (SMNH); **Switzerland:** Luzein (46.95279, 9.73491), 1 specimen 2018 (R. Angeleri) (PUIF); **Ukraine:** Lviv (49.836049, 24.032107), 1 specimen 23.06.2023 (A. Zamoroka) (PUIF); Kyiv (50.459988, 30.338635), 1 specimen 29.06.2022 (I. Balashov) (PUIF); Uzhhorod (48.606049, 22.233151), 1 specimen 28.06.2022 (R. Mishustin) (PUIF); Kerch (45.355701, 36.46618), 1 specimen 27.06.2022(PUIF); Shkarivka (49.747543, 30.159587), 1 specimen 26.06.2022 (S. Oksenenko) (PUIF); Kyiv (50.457168, 30.524568), 1 specimen 15.06.2021 (H. Ladonko) (PUIF); Kyiv (50.370746, 30.481247), 1 specimen 13.06.2022 (D. Kogan) (PUIF); Kyiv (50.457222, 30.453812), 1 specimen 11.06.2022 (D. Davydov) (PUIF); Poltava (49.58308, 34.550607), 1 specimen 11.06.2022, 1 specimen 08.06.2022, 1 specimen 31.05.2022 (Ye. Rybal'chenko) (PUIF); Dzenzelivka (48.970883, 30.24663), 1 specimen 10.06.2022, 1 specimen 29.05.2022, 1 specimen 24.05.2022, 1 specimen 09.06.2021, 1 specimen 11.IV.2020, 1 specimen 15.05.2019, 1 specimen 17.06.2018, 1 specimen 31.05.2018, 1 specimen 11.05.2018 (L. Ilminska) (PUIF); Dubliany (49.904344, 24.120326), 1 specimen 29.05.2022(PUIF); Bila Tserkva (49.802810, 30.134760), 1 specimen 24.05.2022 (S. Bud'ko) (PUIF); Dnipro (48.466342, 35.005790), 1 specimen 23.05.2022 (V. Voropayev) (PUIF); Odesa (46.454167, 30.755833), 1 specimen 21.05.2022 (M. Kormyzhenko) (PUIF); Koroleve (48.151831, 23.128075), 1 specimen 18.05.2022, 1 specimen 30.06.2021, 1 specimen 03.06.2020, 1 specimen 12.05.2019, 1 specimen 29.05.2015 (V. Hleba) (PUIF); Dibrova (49.187195, 24.449378), 1 specimen 15.05.2022 (A. Zamoroka) (PUIF); Voronenka (48.289959, 24.48422), 1 specimen 11.05.2022(PUIF); Antonivka (47.520568, 32.116276), 1 specimen 11.05.2022 (R. Stepovyi) (PUIF); Kolomya (48.530492, 25.041205), 1 specimen 10.05.2022(PUIF); Voron'ky (50.229844, 33.021077), 1 specimen 26.07.2021 (Ya. Kukhar) (PUIF); Velyka Berezyna (50.036532, 27.443024), 1 specimen 19.06.2021 (O. Hryb) (PUIF); Kluziv (48.950415, 24.729336), 1 specimen 03.06.2021 (A. Zamoroka) (PUIF); Ostroh (50.329074, 26.515150), 1 specimen 02.06.2021 (R. Stanyslava) (PUIF); Kherson (46.674046, 32.774581), 1 specimen 27.05.2021 (R. Mishustin) (PUIF); Novobobrivs'ke (44.505956, 33.9069), 1 specimen 07.06.2020(PUIF); Yakovenkove (45.069138, 36.266647), 1 specimen VI.2020 (N. Matushkina) (PUIF); Huliaipole (47.691059, 36.235859), 1 specimen 28.05.2020 (V. Voropayev) (PUIF); Khomiakivka (48.865693, 24.813170), 1 specimen 09.06.2018 (V. Shparyk) (PUIF); Kharkiv (50.042794, 36.277928), 1 specimen 22.05.2018 (Boris Loboda) (PUIF); Tarashcha (49.568798, 30.526366), 1 specimen 18.05.2018 (PUIF); Krylos (49.094611, 24.715435), 2 specimens 06.07.2017 (A. Zamoroka) (PUIF); Sokil (49.097814, 24.625454), 13.10.2013, 100 specimens, ex larva (A. Zamoroka & V. Shparyk) (PUIF); Maydan (49.003915, 24.581331), 28.02.2014, 29 specimens, ex larva (A. Zamoroka & V. Shparyk) (PUIF); Ivano-Frankivsk (48.919498, 24.695032), 16.02.2014, 262 specimens, ex larva(A. Zamoroka & V. Shparyk) (PUIF); Tsenzhiv (48.996120, 24.597246), 28.02.2014, 14 specimens, ex larva, (A. Zamoroka & V. Shparyk) (PUIF); Husyna Polyana (49.825022,36.269025), 1 specimen 27.06.2012 (B. Loboda) (PUIF); Sarny (51.319095, 26.676664), 1 specimen 26.06.2011 (R. Zhuravchak) (PUIF); Yaremche (48.445419, 24.548383), 1 specimen 15.05.2011 (V. Tymochko) (PUIF); Medynya (49.082380, 24.566411), 1 specimen 22.07.2010 (A. Zamoroka) (PUIF); Bezlyudivka (49.860822, 36.248003), 1 specimen 01.05.2010, 2 specimens 19.06.2010 (O. Sluts'kyi) (PUIF); Vynohradiv (48.136045, 23.073577), 1 specimen 08.07.2009 (R. Panin) (PUIF); Kharkiv (50.018579, 36.304545), 1 specimen 03.06.2009 (O. Sluts'kyi) (PUIF); Bezlyudivka (49.860822, 36.248003), 1 specimen 02.06.2009 (B. Loboda) (PUIF); Kukilnyky (49.189377, 24.805619), 1 specimen 14.05.2009 (A. Zamoroka) (PUIF); Kryvyi Rih (47.897536, 33.390658), 1 specimen 05.05.2003 (A. Holovatiuk) (PUIF); Crimea (45.359028, 34.397000 — centroid), 1 specimen 1955 (Zahajkevych) (SMNH); Perevalne (44.819524, 34.335159), 1 specimen 08.06.1958(SMNH); Simferopol (44.943492, 34.130105), 1 specimen 02.06.1953 (Maltsev) (SMNH); Sudak (44.841726, 34.958015), 1 specimen 16.06.1904 (D. Glazunov) (SMNH).

Institution abbreviations. The studied materials are deposited in scientific institutions which include:

PUIF — Zoological Museum of Vasyl Stefanyk Precarpathian National University, Ivano-Frankivsk, Ukraine;

SMNH — State Museum of Natural History, Lviv, Ukraine;

UZNU — Entomological collection of Uhzhhorod National University, Uzhhorod, Ukraine.

Anatomy, microscopy and photography. Sixty specimens were dissected for study of the male terminalia, including 20 specimens of *L. nebulosus*, 20 specimens of *L. linnei*, 20 specimens of *L. femoratus*. The photographs of the beetles were made using 10 MP USB camera Series C-mount USB3.0 attached to a Nikon SMZ-1 stereomicroscope at 20× and 40× magnification. Images were then aligned and stacked in the ToupTek ToupViev v.×64, 4.7.14643.20190511 software package and additionally, enhanced in Adobe Photoshop CS3 v. 10.0 for publishing purposes.

Morphometry. To statistically justify the feasibility of using new diagnostic features, I conducted a morphometric analysis employing the integrated tools of the ToupTek ToupView v.×64, version 4.7.14643.20190511 software package. The measurement scheme for the features and the calculation of body part indices is presented in figure 1. Specifically, six indices were calculated for 11 morphological features (Fig. 1). These indices were chosen to account for proportional relationships between various body parts, ensuring that variations in absolute size do not obscure underlying patterns. This approach enhances the robustness of the analysis by reducing the influence of individual or population-level size differences, thereby improving the reliability of the diagnostic features under investigation.

1) Frons Index (FI) (Fig. 1, *a*) — this index represents the ratio of the shortest width of the frons between the eyes (X1) to the length of the frons from the vertex

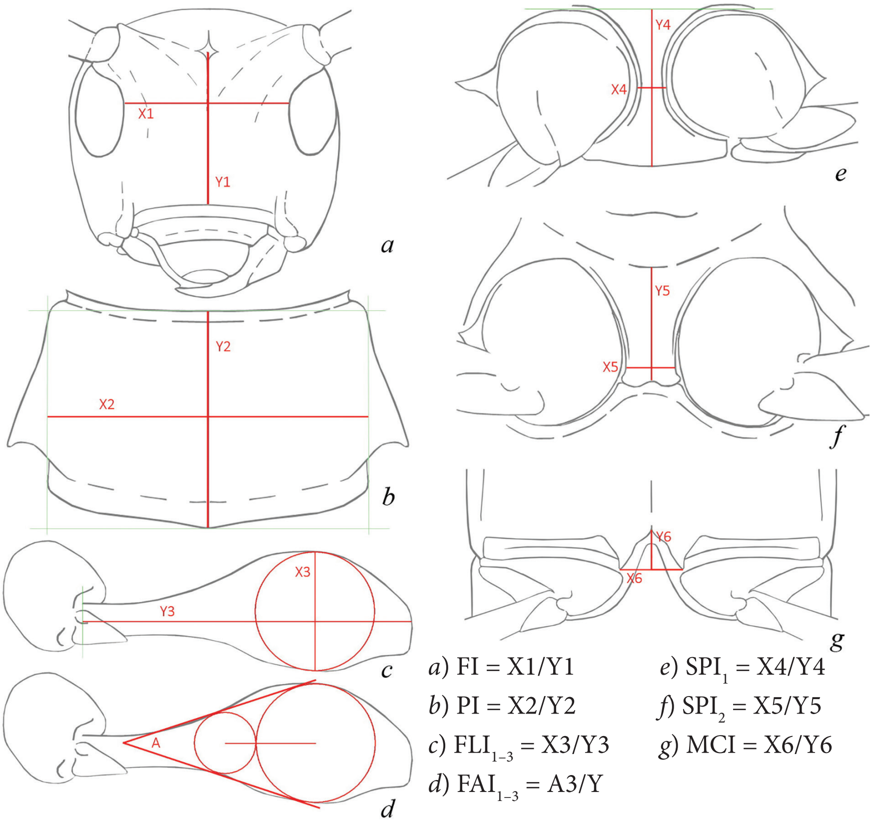

Fig. 1. Measurement schemes for morphometric parameters and calculation of body part indices: *a* — head; *b* — зronotum; *c–d* — femur; *e* — prosternum; *f* — mesosternum, *g* — metasternum. X, Y, and A represent measurement parameters. For index abbreviations, refer to the text

to the clypeus (Y1). 2) Pronotum Index (PI) (Fig. 1, *b*) — this index is calculated as the ratio of the shortest width of the pronotum across the center of its disc, excluding lateral projections (X2), to its shortest length measured from the anterior to the posterior edge through the center of the disc (Y2). 3) Pro-, Meso-, and Metafemur Linear Index (FLI1-3) (Fig. 1, *c*) — this index is the ratio of the maximum diameter of the circle inscribed in the club-shaped expansion of the femur (X3) to the linear length of the femur, measured from its base at the connection with the trochanter to its apex (Y3). 4) Pro-, Meso-, and Metafemur Angular Index (FAI$_{1-3}$) (Fig. 1, *d*) — This index is the angle (A) formed by the intersection of two lines tangent to the circles of maximum diamter inscribed in the central and proximal parts of the club-shaped expansion of the femur. 5) Pro- and Mesosternum Process Index (SPI$_{1-2}$) (Fig. 1, *e, f*) — this index represents the ratio of the minimum width of the sternal process (X4; X5) to the central line connecting the distal end of the sternal process to an imaginary line joining the proximal edges of the coxal cavities (Y4; Y5). 6) Metasternum Concavity Depth Index (MCI) (Fig. 1, *g*) — this index is calculated as the ratio of the maximum distance between the tips of the posterior thoracic projections (X6) to the maximum depth of the concavity between them (Y6).

The t-test statistical technique was employed to assess significant differences between morphometric features. Specifically, a two-sample t-test was used to compare the means of different groups. A p-value of less than 0.05 was considered indicative of statistically significant differences between the groups.

Bioinformatic analysis. To verify the accuracy of morphological identification of *Leiopus* species in GenBank, 38 barcodes were analyzed (Table 1; Fig. 5). These barcodes represent partial sequences of the mitochondrial cytochrome c oxidase subunit I (COI) gene. *Acanthocinus aedilis* Linnaeus, 1758 and *Acanthocinus griseus* (Fabricius, 1793) were used as outgroups to root the tree.

The analysis was conducted using Seaview 5.0, a multi-platform software for multiple sequence alignment, molecular phylogenetic analysis, and tree reconciliation (Gouy et al., 2021). Multiple alignments were generated with the MUSCLE (Multiple Sequence Comparison by Log-Expectation) algorithm integrated into Seaview 5.0. Alignments were manually revised and edited to correct regions with missing data and exclude unalignable positions.

Phylogenetic trees were constructed using maximum-likelihood methods with the PhyML algorithm (Guindon et al., 2010). The analyses employed a general time-reversible (GTR) model of sequence evolution, with branch support evaluated by approximate likelihood-ratio tests (aLRT) based on the log ratio between the likelihood of the current tree and the best alternative (Anisimova & Gascuel, 2006; Guindon et al., 2010). The optimal tree topology was inferred using a combination of nearest-neighbor interchange (NNI) and subtree pruning and regrafting (SPR) algorithms. The neighbor-joining (BioNJ) algorithm was used to optimize tree topology for branch distance estimation (Gascuel, 1997).

Niche and environment suitability modelling. The GIS software DIVA-GIS v. 7.5.0.0 was used for range mapping, ecological niche modelling, and assessing environmental suitability of *Leiopus* species. Bioclimatic data were sourced from WorldClim v. 1.3 at a resolution of 2.5 arc minutes, offering information on average climatic conditions for the period between 1950 and 2000. The model incorporated 19 bioclimatic variables, which are as follows: BIO1: Annual mean temperature; BIO2: Mean monthlytemperature range (mean of monthly maximum temperature minus minimum temperature); BIO3: Isothermality (BIO2/BIO7 multiplied by 100); BIO4: Temperature seasonality (standard deviation multiplied by 100); BIO5: Maximum temperature of the warmest month; BIO6: Minimum temperature of the coldest month; BIO7: Temperature annual range (BIO5 minus BIO6); BIO8: Mean temperature of the wettest quarter; BIO9: Mean temperature of the driest quarter; BIO10: Mean temperature of the warmest quarter; BIO11: Mean temperature of the coldest quarter; BIO12: Annual precipitation; BIO13: Precipitation of the wettest month; BIO14: Precipitation of the driest month; BIO15: Precipitation seasonality (coefficient of variation); BIO16: Precipitation of the wettest quarter; BIO17: Precipitation of the driest quarter; BIO18: Precipitation of the warmest quarter; BIO19: Precipitation of the coldest quarter.

Results

The examination of a long series of *L. nebulosus*, *L. linnei*, and *L. femoratus* specimens revealed morphological traits that enable rapid and accurate differentiation of the three species. These traits are supported by morphometric analysis (Table 1), which was conducted primarily to identify the most prominent morphological features for the development of a simple and practical key for distinguishing between *L. nebulosus*, *L. linnei*, and *L. femoratus*. The analysis revealed that not all initially selected traits are equally useful for this purpose. Specifically, certain morphometric traits overlap significantly among the three species (e. g., PI, $FLI_{1\text{-}3}$, $SPI_{1\text{-}2}$, MCI), whereas others show statistically significant differences between them (Table 2). Overall, the most important traits for distinguishing these three species are the shape and size of the frons, pronotum, prosternum process, and femoral club. The combination of these four traits creates unique patterns for each species. However, very rapid and accurate identification of the species can be achieved using only two traits: the shape and size of the prosternum process and the femoral club.

Table 1. **Morphometric indexes (average ± standard deviation) showing**

Morphological features	*Leiopus nebulosus*			*Leiopus linnei*			*Leiopus femoratus*		
	male n = 15	female n = 15	species n = 30	male n = 15	female n = 15	species n = 30	male n = 15	female n = 15	species n = 30
Frons index, FI, rel. un.	0.92 ± 0.01	0.98 ± 0.04	0.95 ± 0.04	1.06 ± 0.03	1.06 ± 0.02	1.06 ± 0.02	1.11 ± 0.07	1.10 ± 0.08	1.10 ± 0.07
Pronotum index, PI, rel. un.	0.72 ± 0.01	0.72 ± 0.01	0.72 ± 0.01	0.79 ± 0.01	0.73 ± 0.01	0.76 ± 0.03	0.80 ± 0.01	0.81 ± 0.04	0.81 ± 0.02
Profemur linear index, FLI_1, rel. un.	0.42 ± 0.01	0.42 ± 0.01	0.42 ± 0.01	0.33 ± 0.02	0.34 ± 0.01	0.33 ± 0.01	0.42 ± 0.01	0.40 ± 0.01	0.40 ± 0.02
Mesofemur linear index, FLI_2, rel. un.	0.35 ± 0.01	0.31 ± 0.01	0.32 ± 0.02	0.31 ± 0.02	0.31 ± 0.02	0.31 ± 0.01	0.37 ± 0.01	0.35 ± 0.01	0.36 ± 0.02
Metafemur linear index, r FLI_3, el. un.	0.32 ± 0.01	0.30 ± 0.01	0.31 ± 0.01	0.28 ± 0.02	0.27 ± 0.01	0.27 ± 0.01	0.33 ± 0.01	0.29 ± 0.01	0.31 ± 0.02
Profemur angular index, FAI_1, deg.	31.09 ± 0.47	26.32 ± 0.03	28.71 ± 2.44	17.41 ± 0.21	21.10 ± 0.03	19.23 ± 1.88	39.99 ± 0.03	32.43 ± 0.04	36.21 ± 3.85
Mesofemur angular index, FAI_2, deg.	38.23 ± 0.27	32.57 ± 0.02	35.39 ± 2.88	23.41 ± 0.12	27.45 ± 0.03	25.43 ± 2.06	37.89 ± 0.26	34.75 ± 0.02	36.32 ± 1.61
Metafemur angular index, FAI_3, deg.	23.21 ± 0.10	27.84 ± 0.02	25.53 ± 2.36	18.48 ± 0.19	18.02 ± 0.04	18.25 ± 0.27	33.49 ± 0.02	27.77 ± 0.05	30.63 ± 2.91
Prosternum process index, SPI_1, rel. un.	0.19 ± 0.02	0.18 ± 0.02	0.18 ± 0.02	0.15 ± 0.02	0.12 ± 0.01	0.14 ± 0.03	0.08 ± 0.01	0.09 ± 0.01	0.09 ± 0.01
Mesosternum process index, SPI_2, rel. un.	0.39 ± 0.03	0.44 ± 0.01	0.41 ± 0.03	0.51 ± 0.01	0.44 ± 0.02	0.47 ± 0.04	0.18 ± 0.01	0.37 ± 0.02	0.27 ± 0.09
Metasternum concavity depth index, MCI, rel. un.	0.36 ± 0.03	0.41 ± 0.02	0.38 ± 0.03	0.50 ± 0.00	0.40 ± 0.00	0.45 ± 0.05	0.49 ± 0.01	0.57 ± 0.02	0.53 ± 0.04

Note. rel. un. — relative units; deg. — angular degree.

To validate the reliability of the new diagnostic traits, they were compared against the identification of *L. nebulosus*, *L. linnei*, and *L. femoratus* based on male terminalia. The findings were subsequently extrapolated to females to facilitate their identification. Specifically, the aedeagus of *L. nebulosus* is distinguished by the indistinct apical tooth (Fig. 2, *a, b*), which clearly differentiates it from *L. linnei* (Fig. 2, *e, f*), where the apical tooth is sharply pronounced. In *L. femoratus*, the aedeagus is significantly narrowed with a blunt apex, lacking any sign of an apical tooth. Additionally, the morphology of the parameres differs among the three species. The parameres of *L. femoratus* (Fig. 2, *k, l*) are the most distinctive, shaped like a pair of curved, club-like projections. The parameres of *L. nebulosus* and *L. linnei* are more similar, but with a key difference: in *L. linnei*, they are greatly elongated (Fig. 2, *g, h*), while in *L. nebulosus*, they are shorter (Fig. 2, *c, d*). Thus, all three species are easily distinguishable by the morphology of their terminalia, eliminating the possibility of misidentification when correlated with external mor-

Table 2. **Pairwise comparison of morphological features in *L. nebulosus*, *L. linnei*, and *L. femoratus* using Student's t-test (significant differences at p ≤ 0.05 highlighted)**

Morphological features	Intraspecies variation (ν = 28)			Interspecies variation (ν = 58)		
	Leiopus nebulosus male / female t_1	*Leiopus linnei* male / female t_2	*Leiopus femoratus* male / female t_3	*Leiopus nebulosus*/ *Leiopus linnei* t_4	*Leiopus nebulosus*/ *Leiopus femoratus* t_5	*Leiopus linnei*/ *Leiopus femoratus* t_6
Frons index, FI, rel. un.	1.73	0.09	0.18	**3.688**	**2.525**	0,678
Pronotum index, PI, rel. un.	1.22	**7.76**	0.34	1.216	**5.256**	1.723
Profemur linear index, FLI_1, rel. un.	0.27	1.31	1.70	**8.595**	1.117	**12.160**
Mesofemur linear index, FLI_2, rel. un.	**6.31**	1.09	**4.79**	0.938	1.724	**25.159**
Metafemur linear index, r FLI_3, el. un.	**3.37**	**0.37**	**3.72**	**4.020**	0.057	**2.399**
Profemur angular index, FAI_1, deg.	10.14	18.06	297.87	6.054	2.525	5.051
Mesofemur angular index, FAI_2, deg.	**21.07**	**35.05**	**12.30**	**4.940**	0.385	**8.473**
Metafemur angular index, FAI_3, deg.	47.42	2.44	109.88	3.104	3.010	4.279
Prosternum process index, SPI_1, rel. un.	0.56	1.83	0.319	**2.575**	**6.704**	**2.053**
Mesosternum process index, SPI_2, rel. un.	**2.51**	**4.97**	**8.01**	1.595	**3.099**	**2.317**
Metasternum concavity depth index, MCI, rel. un.	**3.31**	**79.64**	**4.03**	1.763	**5.127**	**3.134**

Note. rel. un. — relative units; deg. — angular degree.

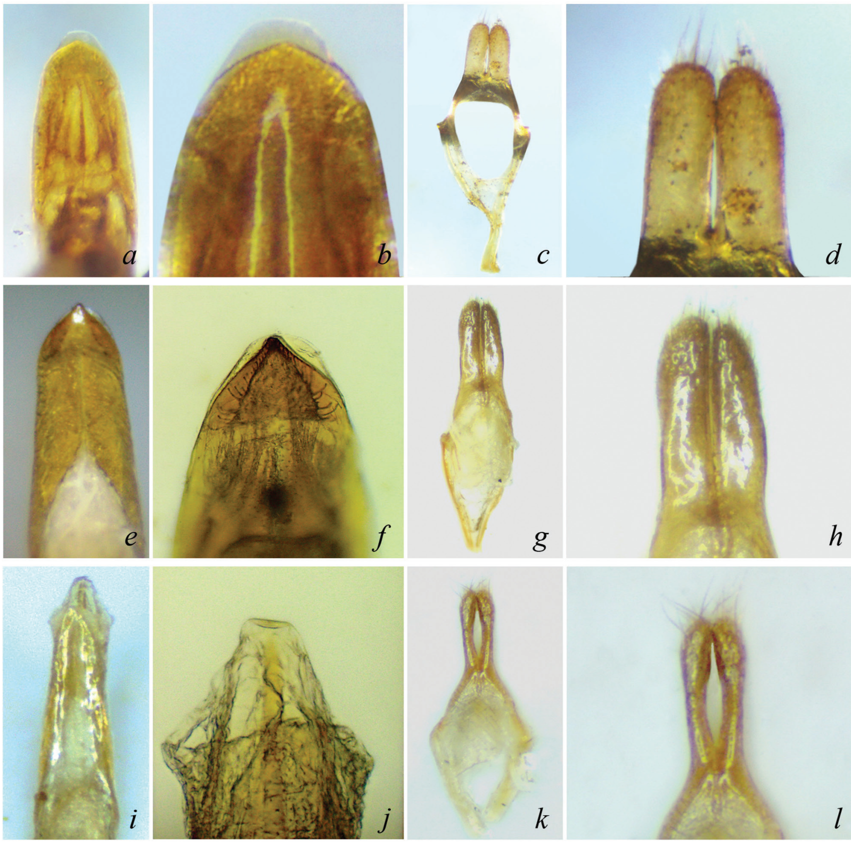

Fig. 2. Male terminalia of *L. nebulosus (a–d), L. linnei* (*e–h*) and *L. femoratus* (*i–l*): *a*, *e*, *i* —aedeagus: *b*, *f, j* — tip of aedeagus; *c, g, k* — tegmen; *d, h, l* — parameres

phological features, particularly the new diagnostic traits such as femur thickness (Fig. 3) and the width of the prosternal process (Fig. 4).

The femora of *L. nebulosus* (FAI_1 = 28.71, FAI_2 = 35.39, FAI_3 = 25.53; Fig. 3, *a–f*) and *L. femoratus* (FAI_1 = 36.21, FAI_2 = 36.32, FAI_3 = 30.63; Fig. 3, *m–r*) are distinctly thickened in their posterior third, forming a pronounced club-like shape. In contrast, the femora of *L. linnei* (FAI_1 = 19.23, FAI_2 = 25.43, FAI_3 = 18.25; Fig. 3, *g–l*) are weakly and uniformly thickened (t_4 = 6.054 (FAI_1), t_4 = 4.940 (FAI_2), t_4 = 3,104 (FAI_3), t_6 = 5.051 (FAI_1), t_6 = 8.473 (FAI_2), t_6 = 4.279 (FAI_3), ν = 58), without a sharply defined club in the posterior third. Sexual dimorphism in femur thickness is weakly expressed (Table 1). However, it can be noted that in males of all three species (Table 1; Fig. 3, *a–c*, *g–i*, *m–o*), the femora are thicker than in females (Table 1; Fig. 3, *d–f*, *j–l*, *p–r*) with significant statistical differences (Table 2).

The prosternal process in *L. femoratus* is very narrow (SPI_1 = 0.09; Fig. 4, *n, q*), with its width equal to twice the margin width of the procoxal cavities. In contrast, the prosternal process in *L. nebulosus* (SPI_1 = 0.18; Fig. 4, *b*, *e*) and *L. linnei* (SPI_1 = 0.14; Fig. 4, *h*, *k*) is broader, with a width at least twice that of the combined width of the procoxal cavity margins. Sexual dimorphism in the morphology of the prosternal process is weakly expressed (Table 1). In females (Table 1; Fig. 4, *e, k, q*), the

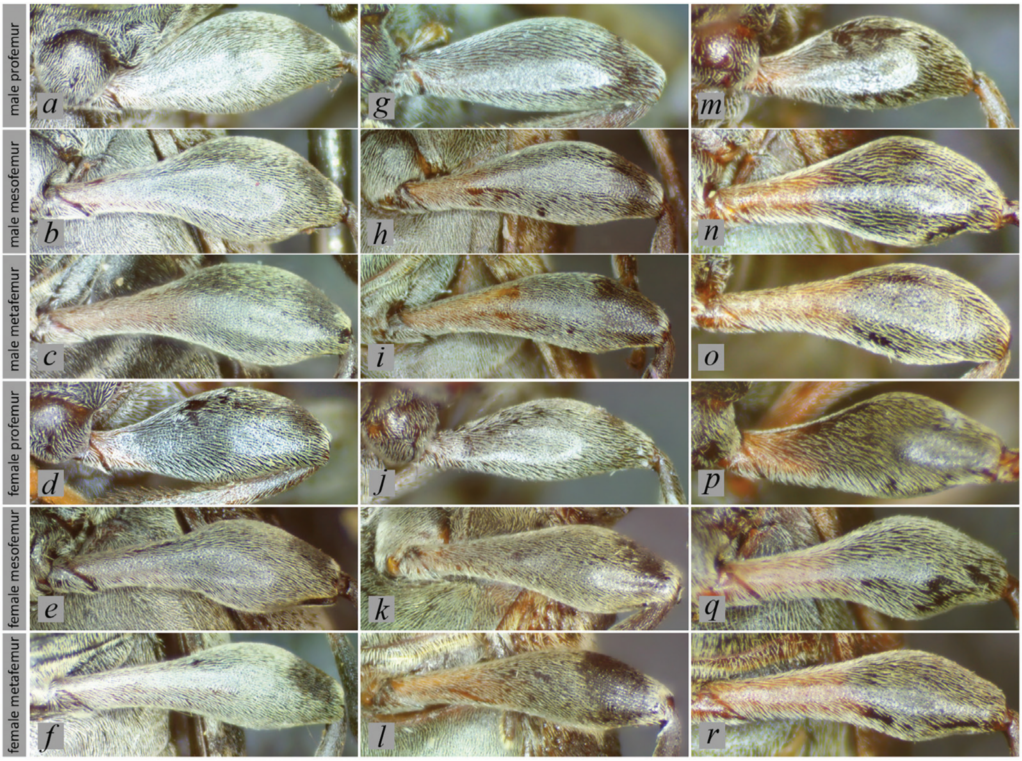

Fig. 3. The femora shape of *L. nebulosus*: *a–c* — male; *d–f* — female; *L. linnei*: *g–i* — male; *j–l* — female; and *L. femoratus: m–o* — male; *p–r* — female

process is slightly wider than in males (Table 1; Fig. 4, b, h, n), and statistically are insignificant (Table 2). The width of the mesosternal process can also be used to differentiate the three species. However, this trait varies between males and females (Table 1). In *L. nebulosus* (Fig. 4, *c*, *f*) and *L. linnei* (Fig. 4, *i*, *l*), the mesosternal process is broad and its difference is statistically insignificant ($t_4 = 1.595$ (SPI_2), $\nu = 58$), whereas in *L. femoratus* it is significantly narrower ($t_5 = 3.099$ (SPI_2), $t_6 = 2.317$ (SPI_2), $\nu = 58$; Fig. 4, *o*, *r*).

The results obtained in this study allowed for the refinement of diagnoses for *L. nebulosus*, *L. linnei*, and *L. femoratus*, as outlined below.

Revised diagnosis for *L. nebulosus*: The frons is moderately narrowed and elongated (FI = 0.95 ± 0.04) and flat, slightly protruding between the eyes. The pronotum is transverse (PI = 0.72 ± 0.01). The elytra are not convex in the scutellar region. The prosternal process is broad (SPI_1 = 0.18 ± 0.02), twice the width of the combined procoxal cavity margins. The femora are sharply expanded in the posterior third (FAI_1 = 28.71 ± 2.44, FAI_2 = 35.39 ± 2.88, FAI_3 = 25.53 ± 2.36), forming a club-like shape. The apex of the aedeagus is rounded with indistinct apical tooth. The parameres are short.

Revised diagnosis for *L. linnei*: The frons is wide, subquadrate (FI = 1.06 ± 0.02) and convex, prominently protruding between the eyes. The pronotum is transverse (PI = 0.76 ± 0.03). The elytra are not convex in the scutellar region. The pros-

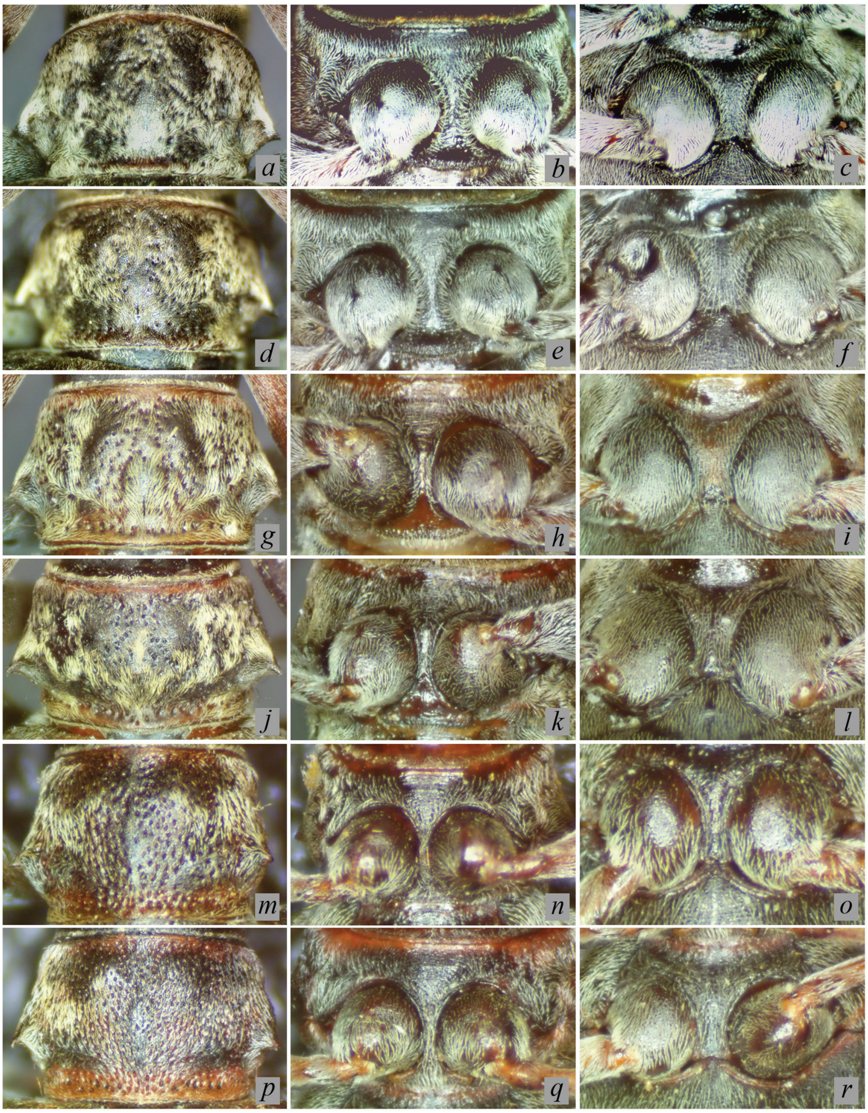

Fig. 4. The shape of pronotum (*a, d, g, j, m, p*), prosternum (*b, e, h, k, n, q*) and mesosternum (*c, f, i, l, o, r*) in *L. nebulosus: a–c* — male; *d–f* — female; *L. linnei: g–i* — male*; j–*l — female and *L. femoratus*: *m–o* — male; *p–r* — female

ternal process is broad (SPI_1 = 0.14 ± 0.03), twice the width of the combined procoxal cavity margins. The femora are weakly and uniformly thickened along their entire length (FAI_1 = 19.23 ± 1.88, FAI_2 = 25.43 ± 2.06, FAI_3 = 18.25 ± 0.27), not club-like. The apex of the aedeagus is pointed, with a distinct tooth. The parameres are narrow and greatly elongated.

Revised diagnosis for *L. femoratus*: The frons is wide, transversely subrectangular (FI = 1.10 ± 0.07) highly convex, and strongly protruding between the eyes. The pronotum is subquadrate (PI = 0.81 ± 0.02), slightly transverse. The elytra are convex in the scutellar region. The prosternal process is very narrow (SPI_1 = 0.09 ± 0.01), not wider than the combined procoxal cavity margins. The

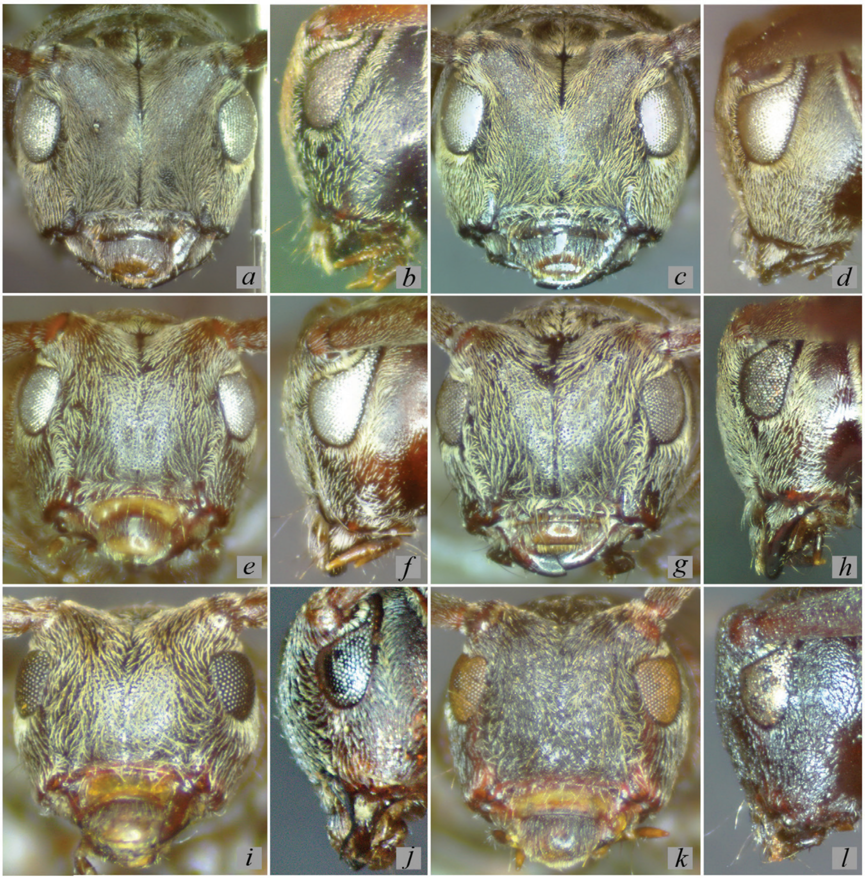

Fig. 5. The frontal and lateral shape of head in *L. nebulosus: a–b* — male; *c — d* — female; *L. linnei*: *e–f* — male; *g–h* — female and *L. femoratus: i–j* — male; *k–l* — female

femora are sharply expanded in the posterior third (FAI_1 = 36.21 ± 3.85, FAI_2 = 36.32 ± 1.61, FAI_3 = 30.63 ± 2.91), forming a club-like shape. The apex of the aedeagus is narrow and blunt. The parameres are narrow, club-shaped, and curved in an arc.

Identification Key to *Leiopus* Species:

1. Pronotum distinctly transverse (Fig. 4, *a*, *d*, *g*, *j)*; prosternal process broad (Fig. 4, *b*, *e*, *h*, *k*). 2

— Pronotum roughly square (Fig. 4, *m*, *p*); prosternal process very narrow (Fig. 4, *n*, *q*); femora sharply thickened into a club shape in the posterior third (Fig. 3, *m–r*). .... *L. femoratus*

2 Frons subquadrate (width-to-length ratio is ≥1.00). Femora smoothly thickened posteriorly, without a pronounced club (Fig. 3, *g–l*). .... *L. linnei*

— Frons vertically elongated (width-to-length ratio is ≤ 0.95). Femora sharply thickened into a club shape in the posterior third (Fig. 3, *a–f*). ...... *L. nebulosus*

Proposal for Conserving the Name *Leiopus linnei* nomen protectum.

Danilevsky & Tavakilian (2022) have proposed reviving the name *Cerambyx taeniatus* Gmelin, 1790 = *Leiopus taeniatus* (Gmelin, 1790), which was often considered a junior synonym of *Leiopus nebulosus*, to replace the name *Leiopus linnei*, for which they considered *Leiopus taeniatus* to be a senior synonym. I propose the name *Leiopus linnei* to be conserved under Article 23.9 of the Code. Specifically, *Leiopus taeniatus* is considered a *nomen oblitum* as it has not been used as a valid name in zoological publications since 1899 (Article 23.9.1.1 of the Code). In contrast, *Leiopus linnei* has been used as a valid name in over 25 publications by more than 10 authors since 2009 (Article 23.9.1.2 of the Code). Key publications where *Leiopus linnei* is used include: Wallin et al. (2009); Drumont & Wallin (2009); Gutowski et al. (2010); Löbl & Smetana (2010); Bukejs & Balalaikins (2011); Zamoroka & Kapelyukh (2012, 2016); Zamoroka et al. (2012); Kvamme & Wallin (2013); Lacoste (2013); Hendrich et al. (2014); Górski & Tatur-Dytkowski (2015); Plewa et al. (2014, 2015); Monnerat et al. (2015); Siering & Shumka (2015); Klausnitzer et al. (2016); Rossa et al. (2017); Doychev et al. (2018); Dunskis & Barševskis (2018); Olbrycht & Trzeciak (2018); Vitali (2018); Zamoroka (2018, 2022 b); Gradinarov & Petrova (2019); Danilevsky (2020); Micas & Van Meer (2020); Miłkowski & Mokrzycki (2021); Ruchin et al. (2021); Babytskiy et al. (2023); Comelade (2023); Roques et al. (2023); Zamoroka et al. (2023); Zamoroka & Mykhailiuk-Zamoroka (2023).

Discussion

The method I propose for distinguishing *L. nebulosus*, *L. linnei*, and *L. femoratus* is simple and reliable, allowing for rapid species identification of individual specimens and significantly reducing the time required to process large volumes of material. This method utilizes four primary morphological traits: 1) the shape of the pronotum; 2) the shape of the prosternal process; 3) the shape of the frons; and 4) the shape of the femora. Each species exhibits a distinct combination of these traits, ensuring accurate identification. Specifically, *L. nebulosus* is characterized by a narrowed frons (Fig. 5, *a*, *c*), transverse pronotum (Fig. 4, *a*, *d*), a broad prosternal process (Fig. 4, *b*, *e*), and clearly club-shaped femora (Fig. 3, *a*–*f*). In contrast, *L. linnei* has a subquadrate frons (Fig. 5, *e*, *g*), transverse pronotum (Fig. 4, *g*, *j*), a broad prosternal process (Fig. 4, *h*, *k*), but femora that are uniformly thickened and not club-shaped (Fig. 3, *g*–*l*). Conversely, *L. femoratus* is distinguished by a transversely subrectangular frons (Fig. 5, *i*, *k*), square pronotum (Fig. 4, *m*, *p*), a very narrow prosternal process (Fig. 4, *n*, *q*), and distinctly club-shaped femora (Fig. 3, *m*–r).

Previously, the identification of *Leiopus* species relied on a significantly more complex combination of traits (Wallin et al., 2009; Zamoroka & Kapeliukh, 2012; Rossa et al., 2017), which often led to identification errors when terminalia dissection was not performed. Wallin et al. (2009) emphasized the shape and size of the frons in *L. nebulosus* and *L. linnei* as key morphological differences between these species. Specifically, *L. linnei* has a broader and more convex frons compared to *L. nebulosus*. However, as demonstrated in Fig. 5, the width and convexity of the frons in *L. femoratus* are even more pronounced than in *L. linnei*, which could lead to misinterpretation when distinguishing between these two species.

Other external morphological features indicated by Wallin et al. (2009) (e. g., microsculpture of the pronotum, coloration of setae) are highly variable not only within the species as a whole but also frequently within single populations of both *L. nebulosus* and *L. linnei*. Thus, distinguishing *L. nebulosus* from *L. linnei* without dissection of the terminalia has a considerable potential for error. A more accurate, though more sophisticated, method for distinguishing these two species was proposed by Rossa et al. (2017). Their approach has a very low probability of error, which is a significant advantage. However, this method requires dissection of the hind wings and the use of specialized software, which is often impractical under certain circumstances.

The differentiation of *L. femoratus* from *L. nebulosus* and *L. linnei* has been minimally addressed in the existing literature. Bense (1995) proposed using the size and shape of the lateral spines on the pronotum as a key distinguishing feature. However, this characteristic proved to be highly variable, leading to numerous misidentifications of *L. femoratus*, particularly in Southern and Western Europe (Brustel et al., 2003; Biscaccianti & Petruzziello, 2007; Touroult et al., 2019). This confusion may also extend to the species described from Italy as *Leiopus settei* Sama, 1985. This species shares many morphological traits with *L. femoratus*, and it is likely that they should be considered a single species. A definitive resolution to this issue may require a thorough examination of the type material for *L. settei*. In our previous work (Zamoroka & Kapelyukh, 2012), we proposed a more precise method for identifying *L. femoratus* based on the shape of the pronotum, as well as the sculpture and coloration of the elytra. Nonetheless, even these refined characteristics, particularly the coloration of the elytral cuticle, still allowed for a potential margin of error.

Issues with the accurate identification of *L. nebulosus*, *L. linnei*, and *L. femoratus* have broader implications, including the quality of molecular data based on such identifications. It is important to note that Wallin et al. (2009), in their original description of *L. linnei*, provided its barcode (COI) to differentiate it from *L. nebulosus*. The comparison of the consensus barcodes of *L. linnei* and *L. nebulosus* is shown in Fig. 7. Thus, both species can be easily distinguished by their barcodes. However, my verification of the barcode data in GenBank for the respective species of the genus *Leiopus* revealed a significant proportion of errors (Fig. 6) in the morphological identification of *L. nebulosus* and *L. linnei* using the available morphological keys. Specifically, only 38.5% of the barcodes for *L. linnei* were correctly identified morphologically. The remaining 61.5% were misidentified as *L. nebulosus* but actually belong to *L. linnei* based on their barcodes. Similarly, for the barcoded specimens of *L. nebulosus*, only 57.1% were correctly identified, with 42.9% erroneously classified as *L. linnei*. It should be noted that possible hybridization between these two species can be excluded given their clear genetic divergence, in contrast to the case studied earlier with *Anastrangalia dubia* Scopoli, 1763 (Zamoroka et al., 2019). Overall, the case of *L. nebulosus* and *L. linnei* represents an interesting evolutionary scenario where morphological convergence within a genus is observed alongside clearly defined genetic divergence. Similar cases of convergent evolution have been observed in other longhorn beetles, but only within a single tribe or subfamily (Zamoroka et al., 2022; Zamoroka, 2022 a). This phenomenon within a

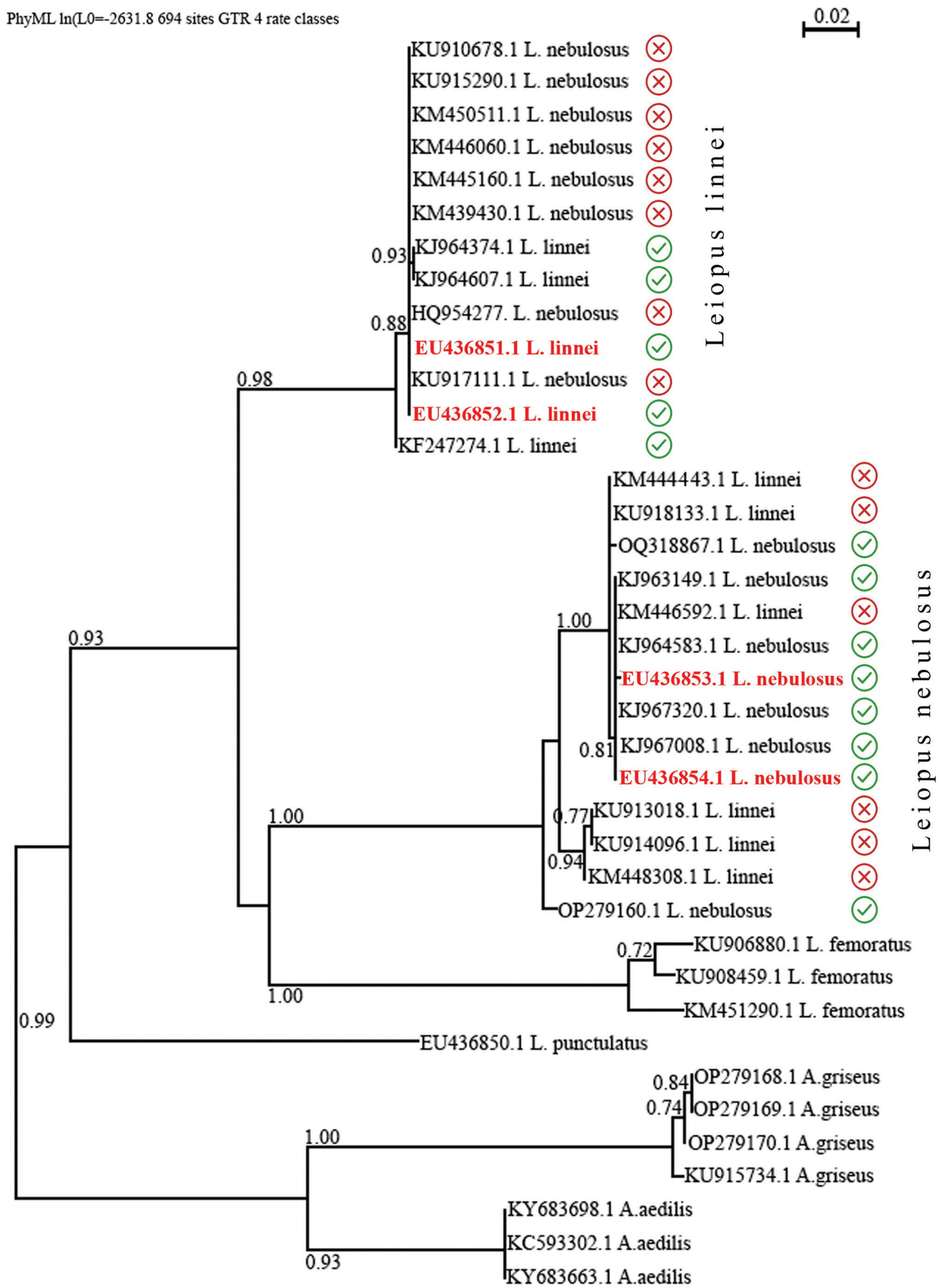

Fig. 6. Corresponding of the barcodes available in GenBank to different species of *Leiopus*; highlighted are the original barcode vouchers from the publication by Wallin et al. (2009)

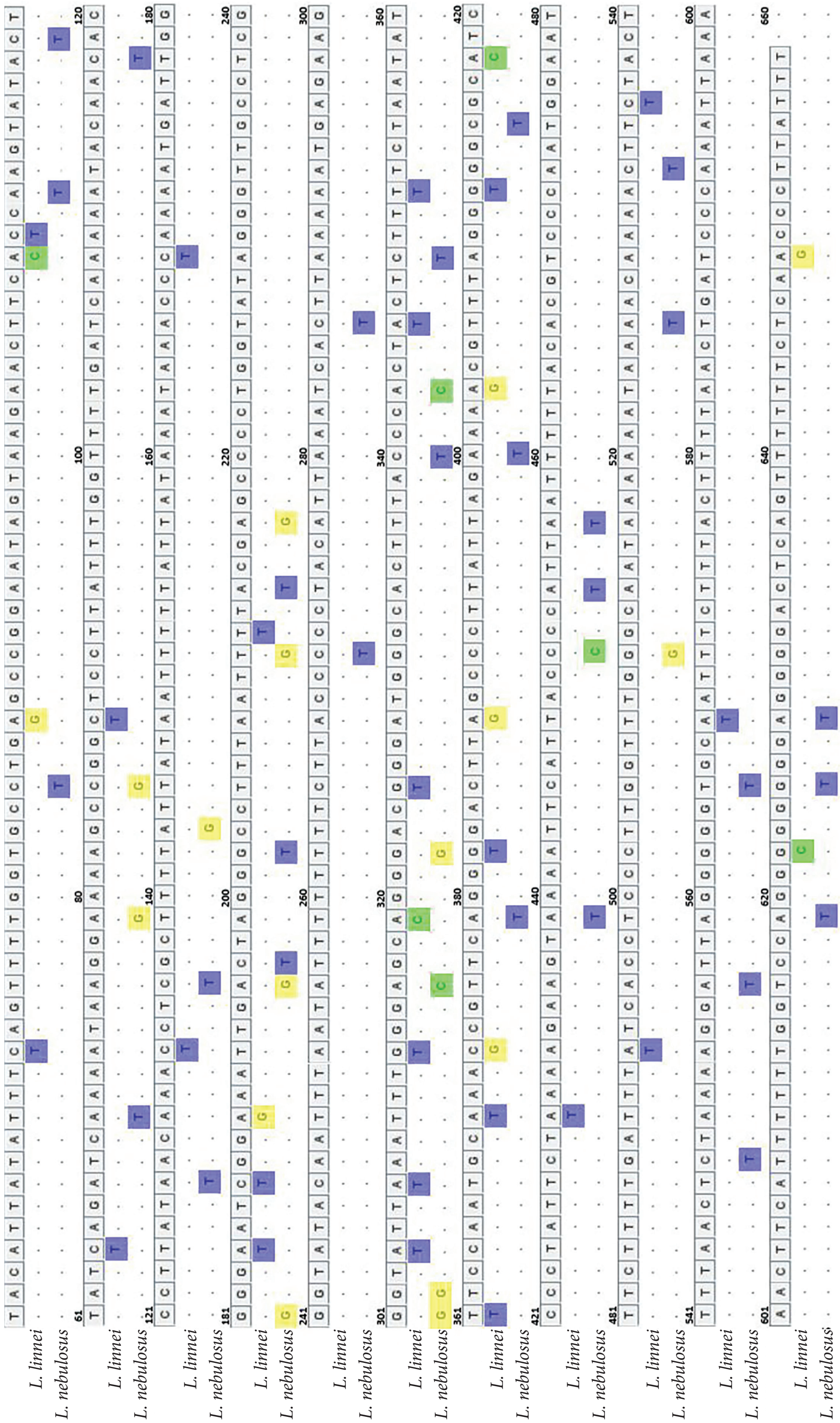

Fig. 7. Comparison of the 658-nucleotide consensus COI sequence of *L. linnei* and *L. nebulosus*

Table 3. **Corrected data on the differentiation of *L. nebulosus* and *L. linnei* based on barcodes in GenBank. Highlighted with bold are the original barcode vouchers from Wallin et al. (2009)**

GenBank voucher	Current identification	Corrected identification
KU910678.1	*L. nebulosus*	*L. linnei*
KU915290.1	*L. nebulosus*	*L. linnei*
KM450511.1	*L. nebulosus*	*L. linnei*
KM446060.1	*L. nebulosus*	*L. linnei*
KM445160.1	*L. nebulosus*	*L. linnei*
KM439430.1	*L. nebulosus*	*L. linnei*
KJ964374.1	*L. linnei*	*L. linnei*
KJ964607.1	*L. linnei*	*L. linnei*
HQ954277.1	*L. nebulosus*	*L. linnei*
EU436851.1	*L. linnei*	*L. linnei*
KU917111.1	*L. nebulosus*	*L. linnei*
EU436852.1	*L. linnei*	*L. linnei*
KF247274.1	*L. linnei*	*L. linnei*
KM444443	*L. linnei*	*L. nebulosus*
KU918133.1	*L. linnei*	*L. nebulosus*
OQ318867.1	*L. nebulosus*	*L. nebulosus*
KJ963149.1	*L. nebulosus*	*L. nebulosus*
KM446592.1	*L. linnei*	*L. nebulosus*
KJ964583.1	*L. nebulosus*	*L. nebulosus*
EU436853.1	*L. nebulosus*	*L. nebulosus*
KJ967320.1	*L. nebulosus*	*L. nebulosus*
KJ967008.1	*L. nebulosus*	*L. nebulosus*
EU436854.1	*L. nebulosus*	*L. nebulosus*
KU913018.1	*L. linnei*	*L. nebulosus*
KU914096.1	*L. linnei*	*L. nebulosus*
KM448308.1	*L. linnei*	*L. nebulosus*
OP279160.1	*L. nebulosus*	*L. nebulosus*

single genus of longhorn beetles is previously unreported. The corrected data for the differentiation of *L. nebulosus* and *L. linnei* based on barcodes in GenBank are presented in Table 3.

The refined diagnoses I propose for *L. nebulosus*, *L. linnei*, and *L. femoratus* not only allow for easy differentiation of these species but also help clarify and understand their global distributions. As correctly noted by Rossa et al. (2017), the range of *L. linnei* is significantly broader than that of *L. nebulosus*. Danilevsky & Tavakilian (2022) identify Western Siberia as the eastern boundary of *L. linnei*'s distribution, where *L. nebulosus* is entirely absent. The eastern limit of *L. nebulosus*'s range, however, remains unclear. The distribution of both species resembles that of *Tetrops praeustus* Linnaeus, 1758, and *Tetrops peterkai* Škorepa, 2020, within Europe (Zamoroka & Zinenko, 2024). This likely indicates distinct centers of origin in these two cases.

The analysis of georeferenced records for all three species enabled the extraction of their ecological characteristics (Table 4) using the BIOCLIM modeling tool. The

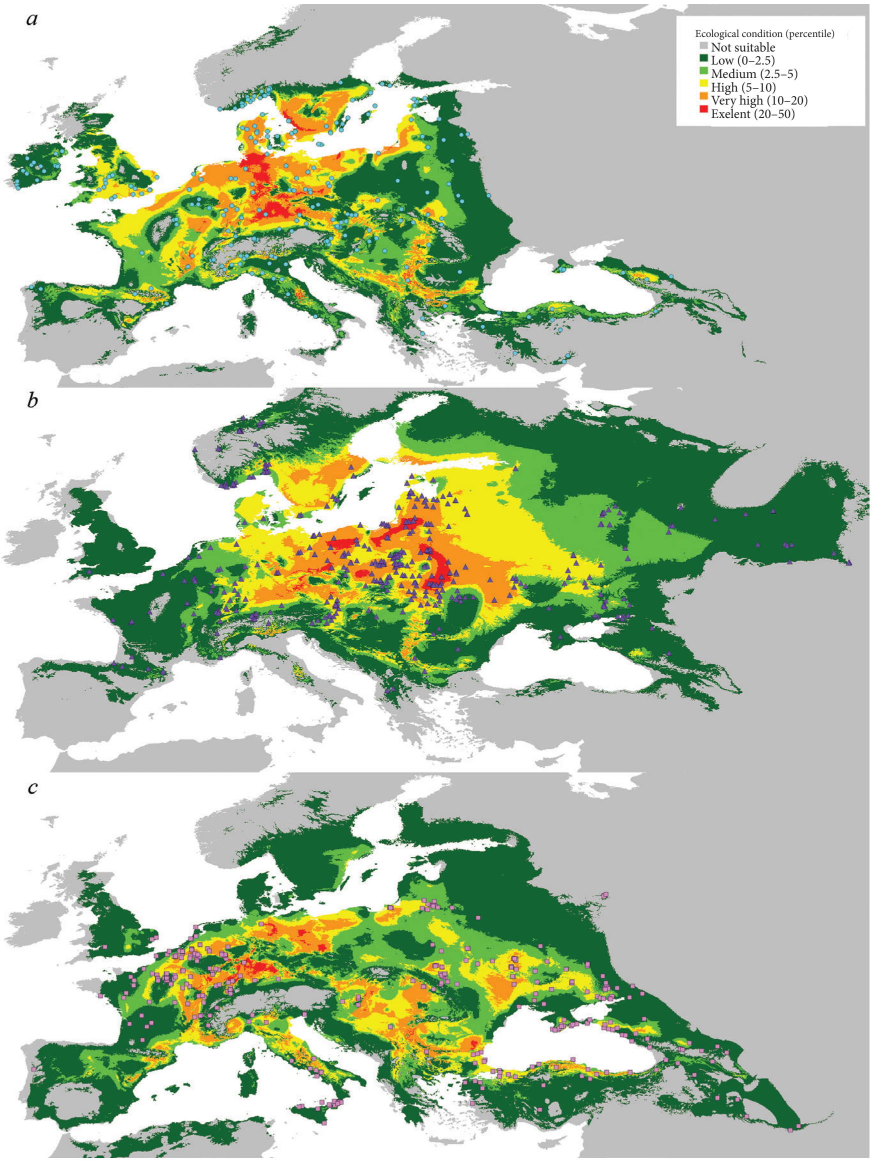

Fig. 8. Records and range models of *L. nebulosus* (*a*), *L. linnei* (*b*) and *L. femoratus* (*c*)

data indicate that *L. linnei* occupies regions with a more continental climate compared to *L. nebulosus*, including drier and colder conditions. In contrast, *L. femoratus* is a more xerothermophilous species than both *L. nebulosus* and *L. linnei*.

The analysis of available and verified data using ecological niche modeling has enabled me to construct the most accurate global distributions (Fig. 8) for all three studied species of the genus *Leiopus*. As a result of the modeling, it was established that the range of *L. nebulosus* covers most of Europe, Asia Minor, the Caucasus, and Crimea (Fig. 8, *a*). However, the species is absent from Eastern and Northern Europe. In the north, the range of *L. nebulosus* extends up to 60 degrees latitude in southern Fennoscandia. To the east, its range reaches 28 degrees longitude, exclud-

Table 4. **Bioclimatic features (mean ± standard deviation) of *Leiopus* species, extracted from BIOCLIM geospatial model**

Code	Bioclimatic indicator	*Leiopus nebulosus*	*Leiopus linnei*	*Leiopus femoratus*
BIO1	Annual mean temperature, °C	8.7 ± 2.0	7.4 ± 1.8	9.8 ± 2.4
BIO2	Mean monthly temperature range, °C	8.0 ± 1.5	8.1 ± 1.2	8.4 ± 1.1
BIO3	Isothermality, °C	30.8 ± 5.0	27.5 ± 3.9	30.3 ± 4.9
BIO4	Temperature seasonality, °C	678.4 ± 124.0	811.9 ± 158.6	751.8 ± 162.2
BIO5	Maximum temperature of the warmest month, °C	22.7 ± 2.9	23.0 ± 2.5	24.9 ± 2.4
BIO6	Minimum temperature of the coldest month, °C	-3.4 ± 3.1	-6.8 ± 3.6	–3.5 ± 4.4
BIO7	Temperature annual range, °C	26.1 ± 4.3	29.8 ± 4.8	28.3 ± 4.7
BIO8	Mean temperature of the wettest quarter, °C	12.7 ± 5.3	15.4 ± 4.4	13.6 ± 5.4
BIO9	Mean temperature of the driest quarter, °C	4.4 ± 6.1	0.0 ± 4.8	6.1 ± 8.4
BIO10	Mean temperature of the warmest quarter, °C	17.0 ± 2.1	17.1 ± 1.9	18.9 ± 2.2
BIO11	Mean temperature of the coldest quarter, °C	0.4 ± 2.9	-2.7 ± 3.2	0.5 ± 4.0
BIO12	Annual precipitation, mm	750.1 ± 205.3	701.3 ± 224.1	685.5 ± 151.4
BIO13	Precipitation of the wettest month, mm	89.3 ± 24.8	89.3 ± 26.7	83.2 ± 21.5
BIO14	Precipitation of the driest month, mm	40.4 ± 14.3	35.3 ± 12.9	37.0 ± 13.1
BIO15	Precipitation seasonality, mm	27.1 ± 9.9	31.9 ± 8.8	26.6 ± 13.4
BIO16	Precipitation of the wettest quarter, mm	250.3 ± 69.5	247.8 ± 76.4	227.8 ± 58.7
BIO17	Precipitation of the driest quarter, mm	132.9 ± 46.2	116.8 ± 42.2	124.0 ± 39.7
BIO18	Precipitation of the warmest quarter, mm	213.1 ± 64.1	231.5 ± 55.7	188.5 ± 60.0
BIO19	Precipitation of the coldest quarter, mm	168.2 ± 70.0	139.5 ± 68.7	166.5 ± 60.3

ing Crimea and the Caucasus. Further east of this boundary, isolated populations of *L. nebulosus* may exist, but they remain undiscovered. All previously known records of *L. nebulosus* east of this boundary have been attributed to *L. linnei* and *L. femoratus* (Zamoroka, 2022 b; 2023). Within this range, *L. nebulosus* is represented by two subspecies: *L. n. nebulosus* and *L. n. caucasicus*. The former inhabits Europe, while the latter is found in Asia Minor, the Caucasus region, and the Crimean Mountains (Löbl & Smetana, 2010).

Leiopus linnei has a significantly wider distribution than *L. nebulosus*. Its presence is recorded in Northern Europe at latitudes of at least 63 degrees, and its eastern range extends to 63 degrees longitude (Fig. 8, *b*). However, *L. linnei* is not found in Southern Europe or Asia Minor, and in the Caucasus, it is limited to the northern part of the region.

The complex situation surrounding the original range of *L. femoratus* is directly linked to identification errors and confusion with *L. linnei* and *L. nebulosus* (Brustel et al., 2003; Tamutis et al., 2011; Touroult et al., 2019). The species has long been well documented in Crimea, the Caucasus, and Asia Minor (Zahajkevych, 1991; Sama, 2003; Barteniev, 2009; Löbl & Smetana, 2010; Zamoroka & Kapelyukh, 2012; Özdikmen & Laz, 2022), yet remained unrecorded in the Balkans and the Apennines. It is highly likely that *L. femoratus* was present in both regions prior to its recent range expansion across Europe. Its historical distribution likely encompassed all of Southern Europe, with the possible exception of the Iberian Peninsula. Documented expansions of the range of *L. femoratus*, driven by contemporary climate change, are well established (Merkl, 2008; Löbl & Smetana, 2010; Zamoroka & Kapelyukh, 2012; Vitali, 2018). Currently, the species is known across most of Europe, excluding the northern regions. In Eastern Europe, its range extends as far as the Don River. Additionally, *L. femoratus* is found in the Caucasus, northern Iran, and Asia Minor (Fig. 8, *c*). As the climate continues to warm, further range expansion of *L. femoratus* is expected.

Conclusions

The new approaches to the morphological identification of *L. nebulosus*, *L. linnei*, and *L. femoratus* that I have proposed have enabled a comprehensive revision of available material from Central and Eastern Europe. They have also allowed refinement of the global distributions of all three species through ecological niche modelling and habitat suitability analysis.

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