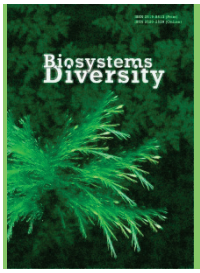

Biosystems Diversity

ISSN 2519-8513 (Print)
ISSN 2520-2529 (Online)
Biosyst. Divers.,
2022, 30(2), 119–136
doi: 10.15421/012212

Polyphyly of the genus *Stenurella* (Coleoptera, Cerambycidae): Consensus of morphological and molecular data

A. M. Zamoroka*, S. Trócoli**, V. Y. Shparyk*, D. V. Semaniuk*

*Vasyl Stefanyk Precarpathian National University, Ivano-Frankivsk, Ukraine
**Museum of Natural Sciences of Barcelona, Barcelona, Spain

Article info

Received 04.05.2022
Received in revised form 28.05.2022
Accepted 30.05.2022

Vasyl Stefanyk Precarpathian National University, Taras Shevchenko st., 54, Ivano-Frankivsk, 76018, Ukraine. Tel.: +38-050-250-97-09. E-mail: andrew.zamoroka@pnu.edu.ua

Museum of Natural Sciences of Barcelona, Passeig Picasso, s/n. E-08003, Barcelona, Spain. E-mail: sergitrocoli@gmail.com

Zamoroka, A. M., Trócoli, S., Shparyk, V. Y., & Semaniuk, D. V. (2022). Polyphyly of the genus Stenurella (Coleoptera, Cerambycidae): Consensus of morphological and molecular data. Biosystems Diversity, 30(2), 119–136. doi:10.15421/012212

Stenurella genus is represented by nine small-sized and widely distributed Palaearctic species. Representatives of the genus play a key role in the pollination of wild angiosperms, accelerate the detritus cycle and make a significant contribution to the forest food web. A number of species with heterogeneous morphological features found within the single *Stenurella* genus indicate the need for revision of the taxonomy this genus. The previous attempt to resolve the intrageneric composition of *Stenurella* was rather artificial because it did not take into an account evolutionary relationships. In this study we tested the existing model of *Stenurella* intrageneric subdivision using both morphological and molecular approaches. Our results showed that the genus *Stenurella* is polyphyletic and consists of two unrelated clades. The first clade comprises six species (*S. jaegeri*, *S. novercalis*, *S. bifasciata*, *S. melanura*, *S. hybridula* and *S. approximans*) and the second includes three species (*S. septempunctata*, *S. vaucheri* and *S. nigra*). Moreover, we found that the second clade is closely related to *Rutpela* due to both morphological and molecular phylogeny. Based on our findings, we revised the present structure of the genus *Stenurella* and transferred three species of the second clade to the genus *Rutpela*, sensu novo. The genus *Rutpela* was redescribed in the light of our results. Furthermore, we subdivided the genus *Stenurella*, sensu nov. into two subgenera, *Stenurella*, subgen. sensu nov. and *Priscostenurella*, subgen. sensu nov., respectively. Also, the genus *Rutpela*, sensu nov. was subdivided into four subgenera including *Nigrostenurella*, *Rutpela*, *Eduardvivesia*, subgen. nov. and *Nigromacularia*, subgen. nov. The assessment of the place of *Stenurella*, sensu novo and *Rutpela*, sensu novo within Lepturini based on molecular phylogeny, showed that *Stenurella*, sensu novo belongs to the *Anoplodera*-branch and *Rutpela*, sensu novo nested within the *Leptura*-branch. These together with morphological features confirmed our idea of the evolutionary distinctiveness of *Stenurella*, sensu novo and *Rutpela*, sensu novo. We assumed that the general external morphological similarity of *Stenurella*, sensu novo and *Rutpela*, sensu novo was the result of convergent evolution, driven by mimetic selection toward imitation of ants or wasps. Finally, our study establishes a natural phylogenetic taxonomy of *Stenurella*.

Keywords: longhorn beetles; morphometry; multigene analysis; phylogeny; new taxa; new combinations; new synonymy.

Introduction

The family of the longhorn beetles or Cerambycidae is one of the most diverse families in the order Coleoptera, and it has a species richness that surpasses that of many other families in the animal kingdom. The family, which has a worldwide distribution, consists of over 33 thousand described species (Slipinski & Escalona, 2013; Wang, 2017; Ruchin & Egorov, 2018a, 2018b). It is also plausible to suggest that the number of known species from this family will continue to grow in future. The striking diversity of the longhorn beetles complicates their taxonomy and presents a significant challenge to systematics. Currently, the taxonomy of the longhorn beetles is being critically revised in the light of the molecular phylogeny. This is caused by the fact that classical morphological taxonomy does not always adequately reflect the phylogenetic relationships between taxa due to numerous cases of parallel evolution, coevolution, homoplasia, etc. The rise of the new molecular system of the longhorn beetles occurs at different levels, starting with the species (Torres-Vila & Bonal, 2019; Zamoroka et al., 2019; Kajtoch et al., 2022) and genera (Kim et al., 2018; Karpiński et al., 2021), and ending with revision of higher taxa: tribes (Dascălu et al., 2021; Sutherland et al., 2021; Zamoroka, 2021), subfamilies (de Santana Souza et al., 2020; Lee & Lee, 2020) and the entire family (Nie et al., 2020). The solution to the problem of misinterpretations of phylogenetic relationships should be found by consensus of molecular methods and morphological data.

The small Palearctic genus *Stenurella* Villiers, 1974 comprises nine valid species (Danilevsky, 2020). However, Villiers (1974) distinguished the genus *Stenurella* (type species *Stenurella melanura* (Linnaeus, 1758)) for 11 species separating them from *Leptura* Linnaeus, 1758 (=*Stenura* Haldeman, 1847). Later, however, *Stenurella hecate* (Reitter, 1896) was separated into a monotypic genus *Xenoleptura* Danilevsky, Lobanov et Murzin, 1981 (Danilevsky et al., 1981). *Stenurella limbiventris* (Reitter, 1898) was synonymized with *Stenurella bifasciata* (Müller, 1776) (Danilevsky & Dzhavelidze, 1990). The remaining nine species constituted the current genus *Stenurella*: *S. approximans* (Rosenhauer, 1856), *S. bifasciata* (Müller, 1776), *S. hybridula* (Reitter, 1902), *S. jaegeri* (Hummel, 1825), *S. melanura* (Linnaeus, 1758), *S. nigra* (Linnaeus, 1758), *S. novercalis* (Reitter, 1901), *S. septempunctata* (Fabricius, 1793) and *S. vaucheri* (Bedel, 1900) (Danilevsky, 2020). It is of special interest that during the last 30 years at least ten potential new species of *Stenurella* have been described, and all these new species were synonymized and considered as colour forms or subspecies of the extant species (Löbl & Smetana, 2010; Özdikmen, 2013; Danilevsky, 2014, 2020; Vitali, 2018).

A number of species with heterogeneous morphological features found within the single *Stenurella* genus indicates the need for a taxonomic revision of this genus. Indeed, Özdikmen (2013) suggested a new approach to the intrageneric composition of *Stenurella* by subdividing it into six subgenera including *Stenurella* Villiers, 1974, *Priscostenurella* Özdikmen, 2013, *Stenurelloides* Özdikmen, 2013, *Nigrostenurella* Özdikmen, 2013, *Crassostenurella* Özdikmen, 2013 and *Iberostenurella* Özdikmen, 2013. Unfortunately, the proposed classification system was rather artificial and did not consider the evolutionary relationships within the *Stenurella* genus. Firstly, Özdikmen used the geographical principle when designating subgenera (e.g., *Crassostenurella*, *Iberostenurella*, *Stenurelloides*) and, at the same time, completely disregarded the phylo-

geny of the species groups. Secondly, the author placed species with very different morphological characteristics into the same subgenera (e.g. *Priscostenurella*). Furthermore, as indicated by our current study, these species had very different molecular phylogenetic patterns. Finally, Özdikmen did not provide the differential diagnoses for the proposed subgenera.

In the current study we tested Özdikmen's model of the intrageneric system for *Stenurella* using both morphological and molecular approaches. We revealed the polyphyly of *Stenurella* which splits into two unrelated lineages. Our study also confirmed *Rutpela* as a separate genus including one of two *Stenurella* lineages with three species: *S. nigra*, *S. septempunctata* and *S. vaucheri*.

Materials and methods

We examined 809 specimens of *Stenurella* sensu Villers (9 species): *S. melanura* (Linnaeus, 1758), *S. approximans* (Rosenhauer, 1856), *S. hybridula* (Reitter, 1902), *S. bifasciata* (Müller, 1776), *S. jaegeri* (Hummel, 1825), *S. novercalis* (Reitter, 1901), *S. nigra* (Linnaeus, 1758), *S. septempunctata* (Fabricius, 1793), *S. vaucheri* (Bedel, 1900); *Rutpela* (1 species): *R. maculata* (Poda, 1761); *Leptura* (4 species): *L. aethiops* Poda, 1761, *L. annularis* Fabricius, 1801, *L. aurulenta* Fabricius, 1793, *L. quadrifasciata* Linnaeus, 1758; and *Cerambyx* (2 species): *C. cerdo* Linnaeus, 1758, *C. scopolii* Füssli, 1775 as outgroup. The studied materials are deposited in multiple institutions which include: KUMN – The State Museum of Nature of Vasyl Karazin Kharkiv National University, Kharkiv, Ukraine; MCNB – Museum of Natural Sciences of Barcelona, Barcelona, Spain; MCNB(EV) – collection of Eduard Vives; MCNB(ST) – collection of Sergi Trócoli; MNHN – Muséum National d'Histoire Naturelle, Paris, France; 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. All 809 specimens were studied for colouration variability, and 140 specimens were selected for biometrical study (see below). The origin of the studied materials is presented in Table 1. Morphological study on *Stenurella*, *Leptura* and *Rutpela* was conducted by collecting both quantitative morphometric data and qualitative nonmetric data comprising 61 morphological characters (Table 2).

Table 1
The origin of the studied materials

Species	Collection	Country of origin
Leptura aethiops	KUMN, PNU, SMNH	Ukraine (n = 36)
L. annularis	KUMN, PNU, SMNH	Russia (European part) (n = 3), Ukraine (n = 117)
L. aurulenta	PNU	Slovenia (n = 1), Ukraine (n = 11)
L. quadrifasciata	KUMN, PNU, SMNH	Ukraine (n = 106)
Rutpela maculata	KUMN, PNU, SMNH, UZNU	Austria (n = 9), Croatia (n = 2), Liechtenstein (n = 4), Russia (European part) (n = 4), Slovenia (n = 2), Spain (n = 3), Switzerland (n = 3), Ukraine (n = 111)
R. nigra, comb. nov.	PNU, SMNH, UZNU	Moldova (n = 1), Poland (n = 1), Russia (European part) (n = 5), Ukraine (n = 63)
R. septempunctata, comb. nov.	KUMN, PNU	Bosnia and Herzegovina (n = 2), Georgia (n = 8), Ukraine (n = 3)
R. vaucheri, comb. nov.	MNHN, MCNB(EV)	Morocco (n = 2), Spain (n = 2)
Stenurella approximans	MCNB(ST)	Morocco (n = 4), Spain (n = 6)
S. bifasciata	KUMN, PNU, SMNH, UZNU	Georgia (n = 2), Russia (European part) (n = 9), Turkey (n = 2), Ukraine (n = 71)
S. hybridula	MCNB(ST)	Spain (n = 5)
S. jaegeri	PNU	Georgia (n = 7)
S. melanura	KUMN, PNU, SMNH, UZNU	Austria (n = 5), Georgia (n = 2), Italy (n = 3), Liechtenstein (n = 7), Poland (n = 2), Russia (European part and East Siberia) (n = 15), Spain (n = 11), Switzerland (n = 7), Ukraine (n = 128)
S. novercalis	PNU	Georgia (n = 4)
Cerambyx cerdo	PNU, SMNH	Ukraine (n = 10)
C. scopolii	KUMN, PNU, SMNH	Croatia (n = 2), Italy (n = 1), Ukraine (n = 7)

Table 2
Morphological data used for the study

Character code	*S. melanura*	*S. approximans*	*S. hybridula*	*S. bifasciata*	*S. jaegeri*	*S. novercalis*	*R. septempunctata*, comb. nov.	*R. vaucheri*, comb. nov.	*R. nigra*, comb. nov.	*R. inermis*	*R. maculata*	*L. annularis*	*L. aethiops*	*L. quadrifasciata*	*L. aurulenta*	*C. scopolii*	*C. cerdo*
H1 – Head colouration																	
– totally dark	+	+	+	+	+	+	–	–	(+)	–	–	+	+	+	+	+	+
– dark with light patterns	–	–	–	–	–	–	+	+	(+)	+	+	–	–	–	–	–	–
H2 – Mouth parts colouration																	
– totally dark	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+
– dark with light patterns	+	+	+	+	+	+	+	+	+	+	+	+	+	–	+	–	–
H3 – Head sculpture																	
– sparse and finely punctated	–	–	–	–	–	–	+	–	+	–	+	+	–	+	+	–	–
– dense and coarsely punctated	+	+	+	+	+	+	–	+	–	+	–	–	+	–	–	+	+
H4 – Head pubescence type																	
– recumbent	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–
– semirecumbent	+	+	+	+	+	+	+	–	+	+	+	–	–	+	+	–	–
– erect	–	–	–	–	–	–	–	+	–	–	–	–	+	–	–	–	–
– not applicable	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+
H5 – Head pubescence colouration																	
– totally dark	(+)	+	–	+	+	+	–	–	+	–	–	–	–	–	–	–	–
– totally light	(+)	–	+	–	–	–	+	+	–	+	+	+	+	+	+	–	–
– not applicable	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+
H6 – Head width to length ratio**																	
– 0.40–0.59	–	+	–	–	–	–	+	+	+	+	–	–	–	–	–	–	–
– 0.60–0.69	+	–	+	–	–	–	–	–	–	–	+	+	+	–	–	–	–
– 0.70–0.79	–	–	–	+	+	+	–	–	–	–	–	–	–	+	+	–	–
– 8.0–1.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+

Character code	*S. melanura*	*S. approximans*	*S. hybridula*	*S. bifasciata*	*S. jaegeri*	*S. novercalis*	*R. septempunctata*, comb. nov.	*R. vaucheri*, comb. nov.	*R. nigra*, comb. nov.	*R. inermis*	*R. maculata*	*L. annularis*	*L. aethiops*	*L. quadrifasciata*	*L. aurulenta*	*C. scopolii*	*C. cerdo*
H7 – Frons width to length ratio**																	
– less 1.0	–	–	–	–	–	–	+	+	+	+	+	–	–	–	–	–	–
– 1.0–1.5	–	+	+	+	+	+	–	–	–	–	–	+	+	–	–	–	–
– over 1.5	+	–	–	–	–	–	–	–	–	–	–	–	–	+	+	+	+
H8 – Transverse depression on frons																	
– present	–	–	–	–	–	–	+	+	+	+	+	+	+	+	+	+	+
– absent	+	+	+	+	+	+	–	–	–	–	–	–	–	–	–	–	–
H9 – Clypeus width to length ratio**																	
less 2.0	–	+	+	+	–	–	+	+	+	+	+	–	+	+	+	–	–
2.0–4.0	+	–	–	–	+	+	–	–	–	–	–	+	–	–	–	–	–
over 4.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+
H10 – Tempora shape																	
– smoothed	–	–	–	–	–	–	+	–	+	+	+	–	–	–	–	+	+
– tuberous	+	+	+	+	+	+	–	+	–	–	–	–	–	–	–	–	–
– protruding	–	–	–	–	–	–	–	–	–	–	–	+	+	+	+	–	–
A1 – Antennae colouration in males																	
– totally dark	+	+	–	+	+	+	–	–	+	–	–	–	+	+	+	+	+
– totally light	–	–	–	–	–	–	+	+	–	–	–	–	–	–	–	–	–
– antennomeres 3–11 annulated	–	–	–	–	–	–	–	–	–	+	+	–	–	–	–	–	–
– antennomeres 7–11 light	–	–	+	–	–	–	–	–	–	–	–	+	–	–	–	–	–
A2 – Antennae colouration in females																	
– totally dark	+	–	+	+	+	+	–	–	+	–	–	–	+	–	+	+	+
– totally light	–	–	–	–	–	–	+	+	–	–	–	+	–	–	–	–	–
– antennomeres 3–11 annulated	–	–	–	–	–	–	–	–	–	+	+	–	–	–	–	–	–
– antennomeres 7–11 light	–	+	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–
A3 – Antennomeres 4th to 5th length ratio**																	
– less 0.6	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–
– 0.7–0.8	–	–	–	–	–	–	+	–	+	+	+	–	–	–	–	–	–
– over 0.8	+	+	+	+	+	+	–	–	–	–	–	+	+	+	+	+	+
A4 – 1st antennomere length to width ratio**																	
– 2.00–2.49	–	–	–	–	–	–	–	–	–	–	–	–	+	+	+	+	+
– 2.50–2.99	–	–	–	+	+	+	–	–	–	–	–	+	–	–	–	–	–
– 3.00–3.49	+	+	+	–	–	–	–	+	+	+	+	–	–	–	–	–	–
– 3.50–3.99	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–
A5 – Length ratio of 1st antennomere to occiput**																	
– less 1.09	–	–	–	–	–	–	–	–	–	–	–	+	+	+	+	+	–
– 1.10–1.19	+	–	–	–	+	–	–	–	–	+	+	–	–	–	–	–	–
– 1.20–1.30	–	+	+	+		+	+	–	+	–	–	–	–	–	–	–	–
– over 1.31	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	+
A6 – Shape of 5–10th antennomeres																	
– cylindrical	+	+	+	+	+	+	+	+	+	+	+	–	–	–	–	–	–
– flattened	–	–	–	–	–	–	–	–	–	–	–	+	+	+	+	–	–
– nodulated	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+
P1– Pronotum colouration																	
– totally dark	+	+	+	+	+	+	–	+	+	+	–	+	+	+	+	+	+
– totally light	–	–	–	–	–	–	(+)	–	–	–	–	–	–	–	–	–	–
– dark with light patterns	–	–	–	–	–	–	(+)	–	–	–	+	–	–	–	–	–	–
P2 – Pronotal front transverse sulcus																	
– present	–	–	–	–	–	–	–	–	–	+	–	+	+	+	+	+	+
– absent	+	+	+	+	+	+	+	+	+	–	+	–	–	–	–	–	–
P3 – Pronotal basal transverse sulcus																	
– deep	–	–	–	–	–	–	–	–	–	+	–	+	+	+	+	+	+
– shallow	+	+	+	+	+	+	+	+	+	–	+	–	–	–	–	–	–
P4 – Interruption of pronotal basal depression																	
– present	+	+	+	+	+	+	+	+	+	+	+	–	–	–	–	–	–
– absent	–	–	–	–	–	–	–	–	–	–	–	+	+	+	+	+	+
P5 – Lateral shape of pronotum in females																	
– completely smooth	+	+	+	+	+	+	+	+	+	–	–	+	+	+	+	–	–
– with distinct tubercle	–	–	–	–	–	–	–	–	–	+	+	–	–	–	–	–	–
– with acuminate tubercle	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+
P6 – Lateral shape of pronotum in males																	
– completely smooth	+	+	+	+	+	+	+	+	+	–	–	+	+	+	–	–	–
– with blunted tubercle	–	–	–	–	–	–	–	–	–	+	+	–	–	–	+	–	–
– with acuminate tubercle	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+
P7 – Shape of pronotal median glabrous area																	
– rotund	+	–	–	+	+	+	–	–	–	–	–	–	–	–	–	–	–
– short line	–	+	+	–	–	–	–	–	–	+	+	–	+	+	+	–	–
– long line	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–
– absent	–	–	–	–	–	–	+	+	+	–	–	–	–	–	–	+	+
P8 – Pronotal width to length ratio**																	
– less 0.80	–	–	–	–	–	–	+	+	+	+	+	–	–	–	–	–	–
– 0.81–0.90	–	+	–	+	+	–	–	–	–	–	–	+	+	–	–	–	–
– 0.91–1.00	+	–	+	–	–	+	–	–	–	–	–	–	–	+	–	–	–
– over 1.00	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	+

Character code	*S. melanura*	*S. approximans*	*S. hybridula*	*S. bifasciata*	*S. jaegeri*	*S. novercalis*	*R. septempunctata*, comb. nov.	*R. vaucheri*, comb. nov.	*R. nigra*, comb. nov.	*R. inermis*	*R. maculata*	*L. annularis*	*L. aethiops*	*L. quadrifasciata*	*L. aurulenta*	*C. scopolii*	*C. cerdo*
P9– Pronotal sculpture																	
– sparse and finely punctated	–	–	–	+	–	–	+	–	+	–	–	–	–	–	–	–	–
– dense and finely punctated	–	–	–	–	–	–	–	+	–	+	+	–	–	–	–	–	–
– dense and coarsely punctated	+	+	+	–	+	+	–	–	–	–	–	+	+	+	+	–	–
– wrinkled without punctation	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+
P10 – Pronotal pubescens type																	
– recumbent	–	–	–	–	–	–	–	–	–	+	+	–	–	+	+	–	–
– semirecumbent	+	+	–	+	+	+	+	+	+	–	–	–	–	–	–	–	–
– erect	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–
–both recumbent and erect	–	–	–	–	–	–	–	–	–	–	–	+	+	–	–	–	–
– not applicable	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+
P11 – Pronotal pubescence colouration																	
– totally dark	(+)	–	–	+	+	+	–	–	+	–	–	–	–	–	–	–	–
– totally light	(+)	+	+	–	–	–	+	+	–	+	+	+	+	+	+	–	–
– not applicable	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+
P12 – Length ratio of pronotal base to elytral shoulders**																	
– 0.60–0.69	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+
– 0.70–0.79	+	+	+	–	+	+	–	–	–	+	+	+	–	–	–	–	–
– 0.80–0.89	–	–	–	+	–	–	+	+	+	–	–	–	+	+	+	–	–
P13 – Type of pronotal hind angles																	
– simple	–	–	–	–	–	–	+	+	+	+	+	+	+	+	+	–	–
– double	+	+	+	+	+	+	–	–	–	–	–	–	–	–	–	–	–
– not appear	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+
P14 – Depth of pronotum base truncation																	
– weakly	–	–	–	–	–	–	–	–	–	–	–	+	+	+	+	–	–
– moderate	+	+	+	+	+	+	–	+	–	–	+	–	–	–	–	–	–
– deep	–	–	–	–	–	–	+	–	+	+	–	–	–	–	–	–	–
– not appear	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+
P15 – Type of pronotal base margination																	
– simple	–	–	–	–	–	–	+	+	+	+	+	+	+	+	+	–	–
– double	+	+	+	+	+	+	–	–	–	–	–	–	–	–	–	–	–
– not appear	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+
S1 – Scutellum apex shape																	
– narrowly rounded	+	+	+	+	+	+	–	–	–	–	–	–	–	–	–	–	–
– narrowly sharpened	–	–	–	–	–	–	+	+	+	+	+	–	–	–	–	–	–
– widely rounded	–	–	–	–	–	–	–	–	–	–	–	+	+	+	+	–	–
– semicircle	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+
T1 – Mesosternal protrusion shape																	
– conical	+	+	+	+	+	+	–	–	–	–	–	–	–	–	–	–	–
– parallel	–	–	–	–	–	–	+	+	+	+	+	+	+	+	+	+	–
– apically expanded	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+
T2 – Modification of metaventrite in males																	
– smooth	+	+	+	+	+	+	–	–	–	–	–	+	+	+	+	+	+
– with two small tubercles	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–
– with two dents	–	–	–	–	–	–	–	+	+	–	–	–	–	–	–	–	–
– with two carinae	–	–	–	–	–	–	–	–	–	+	+	–	–	–	–	–	–
T3 – Depth of metaventrite protrusion emargination in males																	
– weak	–	–	–	–	–	–	+	+	+	+	+	+	+	+	+	+	+
– deep	+	+	+	+	+	+	–	–	–	–	–	–	–	–	–	–	–
E1 – Elytra colouration in males																	
– fulvous	+	–	+	+	+	+	–	–	–	–	–	–	–	–	–	–	–
– black	–	–	–	–	–	–	–	–	+	–	–	–	+	–	–	+	–
– red	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
– orange	–	–	–	–	–	–	+	+	–	+	+	+	–	+	+	–	–
– black-brown	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+
E2 – Elytra colouration in females																	
– fulvous	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–
– black	–	–	–	–	–	–	–	–	+	–	–	–	+	–	–	+	–
– red	+	+	–	+	+	+	–	–	–	–	–	–	–	–	–	–	–
– orange	–	–	–	–	–	–	+	+	–	+	+	+	–	+	+	–	–
– black-brown	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+
E3 – Type of black pattern on elytra in males																	
– transverse bands	–	–	–	–	–	–	+	+	–	+	+	+	–	+	+	–	–
– not appear	+	+	+	+	+	+	–	–	+	–	–	–	+	–	–	+	+
E4 – Type of black pattern on elytra in females																	
– transverse bands	–	–	–	–	–	–	+	+	–	+	+	+	–	+	+	–	–
– longitudinal band	+	+	–	–	+	+	–	–	–	–	–	–	–	–	–	–	–
– both longitudinal and transverse bands	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–
– not appear	–	–	+	–	–	–	–	–	+	–	–	–	+	–	–	+	+
E5 – Elytral width to length ratio**																	
– less 0.43	–	–	–	–	–	–	+	+	+	+	+	–	–	–	–	+	+
– 0.44–0.47	+	+	+	+	+	+	–	–	–	–	–	+	+	–	–	–	–
– over 0.47	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–	–

Character code	*S. melanura*	*S. approximans*	*S. hybridula*	*S. bifasciata*	*S. jaegeri*	*S. novercalis*	*R. septempunctata*, comb. nov.	*R. vaucheri*, comb. nov.	*R. nigra*, comb. nov.	*R. inermis*	*R. maculata*	*L. annularis*	*L. aethiops*	*L. quadrifasciata*	*L. aurulenta*	*C. scopolii*	*C. cerdo*
E6 – Elytral sculpture																	
– sparse and fine punctated	–	–	–	–	–	–	+	–	+	+	+	–	–	–	–	–	–
– dense and fine punctated	–	–	–	–	–	–	–	–	–	–	–	+	–	+	+	–	–
– sparse and coarsely punctated	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–
– dense and coarsely punctated	+	+	+	+	+	+	–	+	–	–	–	–	–	–	–	–	–
– wrinkled	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+
E7 – Elytral pubescence colouration																	
– totally dark	(+)	–	–	(+)	–	–	–	–	+	–	–	–	+	–	–	–	–
– totally light	(+)	+	+	(+)	–	–	+	+	–	+	+	–	–	–	–	+	+
– with patches of light and dark pubescence	–	–	–	–	+	+	–	–	–	–	–	+	–	+	+	–	–
Ab1 – Pygidium colouration																	
– totally dark	+	+	+	–	–	+	–	–	–	–	–	+	+	+	+	+	+
– totally light	–	–	–	+	+	–	–	–	–	–	–	–	–	–	–	–	–
– patched light and dark	–	–	–	–	–	–	+	+	+	+	+	–	–	–	–	–	–
Ab2 – Abdomen colouration in females																	
– totally dark	+	+	–	–	–	–	–	–	–	–	–	+	+	+	+	+	+
– patched light and dark	–	–	+	+	+	+	+	+	+	+	+	–	–	–	–	–	–
Ab3 – Abdomen colouration in males																	
– totally dark	+	+	+	–	–	+	–	–	–	–	–	+	+	+	+	+	+
– patched light and dark	–	–	–	+	+	–	+	+	+	+	+	–	–	–	–	–	–
Ab4 – Abdominal punctation density																	
– sparse	–	–	–	–	–	–	+	+	+	–	–	–	–	–	–	+	+
– dense	+	+	+	+	+	+	–	–	–	+	+	+	+	+	+	–	–
Ab5 – Abdominal pubescence colouration																	
– totally light	(+)	+	+	+	+	+	+	+	+	+	+	+	+	+	(+)	+	+
– totally dark	(+)	–	–	–	–	–	–	–	–	–	–	–	–	–	(+)	–	–
Ab6 – Abdominal pubescens density																	
– sparse	+	+	+	+	+	+	+	+	+	+	+	–	–	–	–	+	+
– dense	–	–	–	–	–	–	–	–	–	–	–	+	+	+	+	–	–
Ab7 – Shape of pygidium apex																	
– rounded	+	+	+	+	+	+	+	+	+	+	+	–	–	–	–	+	+
– truncated	–	–	–	–	–	–	–	–	–	–	–	+	+	+	+	–	–
L1 – I pair of legs colouration in males																	
– totally dark	+	+	+	(+)	–	–	–	–	+	–	–	+	+	+	–	+	+
– totally light	–	–	–	(+)	–	–	–	–	–	+	–	–	–	–	+	–	–
– both dark and light parts present	–	–	–	–	+	+	+	+	–	–	+	–	–	–	–	–	–
L2 – I pair of legs colouration in females																	
– totally dark	+	+	+	(+)	–	–	–	–	+	–	–	–	+	+	–	+	+
– totally light	–	–	–	(+)	+	+	–	–	–	+	+	+	–	–	+	–	–
– both dark and light parts present	–	–	–	–	–	–	+	+	–	–	–	–	–	–	–	–	–
L3 – II pair of legs colouration in males																	
– totally dark	+	+	+	(+)	–	–	–	–	+	–	–	–	+	+	–	+	+
– totally light	–	–	–	(+)	–	–	–	–	–	+	–	–	–	–	–	–	–
– both dark and light parts present	–	–	–	–	+	+	+	+	–	–	+	+	–	–	+	–	–
L4 – II pair of legs colouration in females																	
– totally dark	+	+	+	(+)	–	–	–	–	+	–	–	–	+	+	–	+	+
– totally light	–	–	–	(+)	–	–	–	–	–	+	–	–	–	–	–	–	–
– both dark and light parts present	–	–	–	–	+	+	+	+	–	–	+	+	–	–	+	–	–
L5 – III pair of legs colouration in males																	
– totally dark	+	+	+	(+)	–	–	–	–	+	–	–	–	+	+	–	+	+
– totally light	–	–	–	(+)	–	–	–	–	–	–	–	–	–	–	–	–	–
– both dark and light parts present	–	–	–	–	+	+	+	+	–	+	+	+	–	–	+	–	–
L6 – III pair of legs colouration in females																	
– totally dark	+	+	+	(+)	–	–	–	–	+	–	–	–	+	+	–	+	+
– totally light	–	–	–	(+)	–	–	–	–	–	–	–	–	–	–	–	–	–
– both dark and light parts present	–	–	–	–	+	+	+	+	–	+	+	+	–	–	+	–	–
L7 – Shape of metatibia in males																	
– normal	+	+	+	+	+	+	+	+	+	–	–	–	–	+	+	+	+
– curved	–	–	–	–	–	–	–	–	–	–	–	+	+	–	–	–	–
– dentate	–	–	–	–	–	–	–	–	–	+	+	–	–	–	–	–	–
L8 – Depth of III metatarsomere bisection																	
– 1/4 of its length	–	–	–	–	–	–	+	+	+	–	–	–	–	–	–	–	–
– 1/3 of its length	–	–	–	+	+	+	–	–	–	–	–	+	+	–	–	–	–
– 1/2 of its length	+	+	+	–	–	–	–	–	–	+	+	–	–	–	–	–	–
– 3/4 of its length	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	+	+
L9 – Length ratio of metatibia to I metatarsomere**																	
– 1.00–1.39	–	–	–	–	–	–	+	–	+	–	–	+	–	–	–	–	–
– 1.40–1.69	+	–	+	+	–	+	–	+	–	+	+	–	+	+	–	–	–
– 1.70–1.99	–	+	–	–	+	–	–	–	–	–	–	–	–	–	+	–	–
– 2.00–3.99	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–
– over 4.00	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+
L10 – Length ratio of metatibia to metatarsus**																	
– 0.50–0.69	–	–	–	–	–	–	+	–	–	–	–	+	+	–	–	–	–

Character code	*S. melanura*	*S. approximans*	*S. hybridula*	*S. bifasciata*	*S. jaegeri*	*S. novercalis*	*R. septempunctata*, comb. nov.	*R. vaucheri*, comb. nov.	*R. nigra*, comb. nov.	*R. inermis*	*R. maculata*	*L. annularis*	*L. aethiops*	*L. quadrifasciata*	*L. aurulenta*	*C. scopolii*	*C. cerdo*
– 0.70–0.89	+	–	+	+	+	+	–	+	+	+	+	–	–	+	–	–	–
– 0.90–0.99	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–
– 1.00–1.19	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–
– over 1.20	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+
L11 – Length ratio of 1st to 2–5th metatarsomeres**																	
– less 0.90	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+
– 0.90–0.99	–	–	–	–	–	–	–	–	–	+	+	+	+	+	+	–	–
– 1.00–1.09	+	–	–	+	+	+	+	–	–	–	–	–	–	–	–	–	–
– 1.10–1.19	–	+	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–
– 1.20–1.29	–	–	+	–	–	–	–	+	–	–	–	–	–	–	–	–	–
L12 – I–III protarsomeres width in males																	
– narrowed	+	+	+	+	+	+	–	–	–	–	–	–	–	–	–	–	–
– expanded	–	–	–	–	–	–	+	+	+	+	+	+	+	+	+	+	+

Notes: ** – generalized morphometric data, for details see Table 3; (+) – character varies within populations or species range.

Morphometric data (Fig. 1) of the insects' bodies were instrumentally measured by the approaches of DLTCamViewer x86, 3.7.7892 software package, using USB camera DLT-Cam PRO 5 MP attached to a Nikon SMZ-1 stereomicroscope at 20× and 40× magnifications.

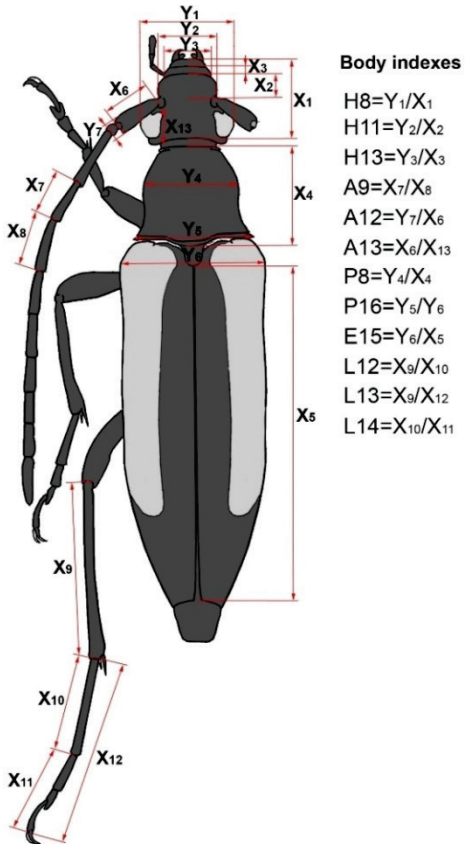

Fig. 1. The scheme of biometrical measurements and the formulas of body index calculations used in the study (for abbreviations, e.g., H8, H11 etc., see Table 2) on the example of *Stenurella melanura*

Further we calculated the body indexes (Fig. 1) for each morphometrical parameter (Table 3) because of the wide variation of intraspecies and interspecies body size. We measured proportions in head, antennae, pronotum, elytra and hind leg. For biometric study, we used the sample of 10 randomly selected specimens of 10 species (5 females and 5 males; n = 100) from different parts of their geographical range. Measurements for specimens (n = 20) of additional four species were taken in the limited samples because of their rarity. These include *S. hybridula* (3 females and 2 males, n = 5), *S. jaegeri* (4 females and 3 males, n = 7), *S. novercalis* (2 females and 2 males, n = 4) and *Rutpela vaucheri*, comb. nov. (2 females and 2 males, n = 4). *Rutpela vaucheri*, comb. nov. is an extremely rare species known only from 5 specimens (we studied 4 of 5 available specimens) including type material deposited in MNHN. Additionally, we included to the study *R. inermis*. Since no specimens of *R. inermis* were available to our study, we reconstructed its body proportions using the available photos and published data (Daniel & Daniel, 1898; Danilevsky, 2014) with additional personal comments of M. Danilevsky. Therefore, we believe that the measurements of *R. inermis* are approximate and could not to be considered as statistically significant. Additionally, we measured 10 specimens of *C. cerdo* Linnaeus, 1758 and 10 specimens of *C. scopolii* Füssli, 1775 which we used as an outgroup for morphological phylogenetic analysis.

The collection of qualitative nonmetric data was conducted to determine the patterns and scope of morphological variations and their suitability for taxa differentiation. We used all studied specimens (n = 809), which were collected within the entire Palearctic including North Africa, Europe, Asia Minor, Caucasus and Siberia. We studied colouration and sculpture of integument (including head, antennae, pronotum, elytra, legs and abdomen), type and colouration of pubescence, shape and proportions of external body parts (including shape of head tempora, pronotum, thorax, legs and pygidium).

Photographs of the body structures were taken by USB camera DLT-Cam PRO 5 MP. The habitus photographs of the entire beetles were taken using Nikon D90 camera. Images were then aligned and stacked in the DLTCamViewer x86, 3.7.7892 software package and additionally, enhanced in Adobe Photoshop CS3 v. 10.0 for publishing purposes.

Morphological data analysis consisted of evaluation and selection of characters' groups to distinguish genera-level taxa. This is because different characters have different weights for distinguishing taxa. Therefore, we identified those groups of morphological features that make the greatest contribution to the differentiation of genera-level taxa. For this purpose, we assembled a logical matrix of characters and consecutively performed Discriminant Analysis (DA) and Canonical Analysis (CA), using the Statistica 8 software package (Hill & Lewicki, 2006). DA was used for determination of both individual variables and their groups which discriminated between studied species and genera. DA was performed under Stepwise Regression model-building technique (Jennrich, 1977). The F value was used for statistical significance in the discrimination between groups (e.g., genera). Following DA, we performed CA for computing the classification statistics and visualization of the results (Hill & Lewicki, 2006).

Next, on the basis of characters with the largest contribution to the distinguishing of genera, identified by DA and CA, we conducted morphological phylogenetic analysis. *Cerambyx cerdo* and *C. scopolii* were used to root the tree. The data was processed using Mesquite v. 3.61 (Maddison, W. P., & Maddison, D. R. (2019). Mesquite: A modular system for evolutionary analysis. www.mesquiteproject.org) heuristic search under the criterion of maximize MrBayes Score. The rearranging of trees was estimated using Subtree Pruning Regrafting (SPR) algorithm with retention 1000 of equally good trees to store during the search (MAXTREES). The tree of greatest likelihood was selected automatically using nearest-neighbour interchange (NNI) algorithm with minimize objection function.

Table 3
The body indexes calculated from biometrical measurements of *Stenurella*, sensu nov., *Rutpela*, sensu nov. and *Leptura* s. str.; data presented in format of average value ± standard deviation; for character codes see Table 2; for formulas see Figure 1

Species	Character code												n
	H6	H7	H10	A3	A4	A5	P8	P12	E5	L9	L10	L11	
S. melanura	0.69 ± 0.11	1.86 ± 0.44	2.40 ± 0.31	0.87 ± 0.07	3.07 ± 0.4	1.10 ± 0.12	0.91 ± 0.06	0.74 ± 0.03	0.45 ± 0.02	1.56 ± 0.19	0.80 ± 0.08	1.04 ± 0.05	10
S. approximans	0.57 ± 0.03	1.14 ± 0.06	1.87 ± 0.19	0.89 ± 0.05	3.11 ± 0.24	1.29 ± 0.14	0.89 ± 0.06	0.76 ± 0.02	0.44 ± 0.01	1.99 ± 0.09	1.06 ± 0.06	1.13 ± 0.04	10
S. hybridula	0.61 ± 0.04	1.05 ± 0.12	1.85 ± 0.16	0.86 ± 0.04	3.31 ± 0.42	1.26 ± 0.23	0.92 ± 0.08	0.76 ± 0.03	0.44 ± 0.02	1.43 ± 0.14	0.84 ± 0.11	1.24 ± 0.05	5
S. bifasciata	0.70 ± 0.11	1.35 ± 0.19	1.82 ± 0.26	0.88 ± 0.05	2.89 ± 0.32	1.26 ± 0.18	0.83 ± 0.08	0.82 ± 0.06	0.47 ± 0.03	1.61 ± 0.12	0.79 ± 0.07	1.00 ± 0.12	10
S. jaegeri	0.70 ± 0.07	1.50 ± 0.18	2.29 ± 0.38	0.84 ± 0.04	2.72 ± 0.3	1.13 ± 0.11	0.89 ± 0.05	0.78 ± 0.04	0.45 ± 0.06	1.76 ± 0.17	0.89 ± 0.07	1.03 ± 0.07	7
S. novercalis	0.70 ± 0.03	1.49 ± 0.07	2.21 ± 0.18	0.91 ± 0.04	2.68 ± 0.23	1.17 ± 0.06	0.93 ± 0.06	0.76 ± 0.01	0.46 ± 0.02	1.67 ± 0.25	0.83 ± 0.15	1.01 ± 0.03	4
R. septempunctata, comb. nov.	0.43 ± 0.02	0.56 ± 0.05	1.61 ± 0.13	0.79 ± 0.05	3.87 ± 0.43	1.31 ± 0.13	0.74 ± 0.03	0.86 ± 0.03	0.42 ± 0.02	1.17 ± 0.07	0.59 ± 0.06	1.06 ± 0.09	10
R. vaucheri, comb. nov.	0.52 ± 0.03	0.98 ± 0.06	2.00 ± 0.05	0.54 ± 0.04	3.50 ± 0.18	1.47 ± 0.08	0.79 ± 0.07	0.86 ± 0.03	0.41 ± 0.03	1.52 ± 0.09	0.85 ± 0.04	1.25 ± 0.04	4
R. nigra, comb. nov.	0.47 ± 0.04	0.69 ± 0.07	2.00 ± 0.04	0.73 ± 0.06	3.48 ± 0.17	1.28 ± 0.03	0.74 ± 0.03	0.89 ± 0.03	0.41 ± 0.02	1.34 ± 0.2	0.72 ± 0.11	1.17 ± 0.11	10
*R. inermis**	0.56	0.98	2.00	0.69	3.01	0.94	0.74	0.79	0.39	1.79	0.90	1.01	*
R. maculata	0.47 ± 0.07	0.65 ± 0.06	2.58 ± 0.15	0.75 ± 0.04	3.28 ± 0.23	1.10 ± 0.07	0.73 ± 0.05	0.76 ± 0.03	0.43 ± 0.02	1.55 ± 0.18	0.76 ± 0.08	0.99 ± 0.05	10
L. annularis	0.60 ± 0.08	1.40 ± 0.18	2.08 ± 0.37	0.80 ± 0.05	2.63 ± 0.38	0.85 ± 0.08	0.75 ± 0.05	0.78 ± 0.03	0.44 ± 0.01	1.38 ± 0.19	0.67 ± 0.10	1.00 ± 0.11	10
L. aethiops	0.60 ± 0.07	1.41 ± 0.19	1.96 ± 0.17	0.89 ± 0.07	2.48 ± 0.11	0.91 ± 0.09	0.86 ± 0.05	0.82 ± 0.05	0.44 ± 0.01	1.43 ± 0.20	0.69 ± 0.09	0.96 ± 0.05	10
L. quadrifasciata	0.71 ± 0.06	1.71 ± 0.22	2.15 ± 0.11	0.74 ± 0.04	2.26 ± 0.36	0.89 ± 0.12	0.94 ± 0.07	0.80 ± 0.03	0.49 ± 0.04	1.54 ± 0.17	0.74 ± 0.08	0.92 ± 0.07	10
L. aurulenta	0.83 ± 0.07	1.92 ± 0.07	2.35 ± 0.18	0.84 ± 0.06	2.37 ± 0.23	1.04 ± 0.09	1.03 ± 0.09	0.80 ± 0.03	0.53 ± 0.02	1.86 ± 0.11	0.91 ± 0.06	0.97 ± 0.04	10
C. cerdo	0.98 ± 0.06	1.36 ± 0.18	5.60 ± 0.10	0.87 ± 0.06	2.08 ± 0.25	1.54 ± 0.24	1.12 ± 0.08	0.65 ± 0.03	0.43 ± 0.03	4.25 ± 0.36	1.41 ± 0.16	0.49 ± 0.06	10
C. scopolii	0.98 ± 0.06	2.30 ± 0.20	5.36 ± 0.23	0.75 ± 0.05	2.10 ± 0.38	1.24 ± 0.10	1.04 ± 0.01	0.65 ± 0.02	0.41 ± 0.01	3.26 ± 0.42	1.18 ± 0.16	0.54 ± 0.02	10

Note: * – for *Rutpela inermis* morphological data was compiled from several sources (see methods).

We used publicly available DNA partial sequences of three genes (Table 4) including the mitochondrial genes 16S ribosomal RNA (16S rRNA) and cytochrome c oxidase I (COI) and nuclear gene 28S ribosomal RNA (28S rRNA) generated from GenBank as a FASTA file. We produced consolidated sequences for COI and 28S rRNA from the sets of separate specimens of the same species. This allowed us to avoid the statistical noises caused by multiple point mutations which spread within the different populations of certain species.

Table 4
The GenBank accession numbers of genes sequences used in the study

Species	16S rRNA	COI*	28S rRNA*
Alosterna tabacicolor	–	HQ948280.1; KJ961935.1; KM440194.1; KM440979.1; KM441377.1;	–
Anastrangalia dubia dubia	–	KM444190.1; KM285974.1; KM286142.1;	–
Anastrangalia dubia sequensi	HM034772.1;	KY683642.1; AF332923.1; MN609573.1;	HM046524.1;
Anastrangalia sanguinolenta	–	HQ954049.1; KJ962498.1; KM286319.1; KM443756.1; KM444617.1;	–
Anoplodera sexguttata	–	KJ966542.1; KM439643.1; KM447872.1; KM450584.1; KU909582.1;	–
Anoploderomorpha izumii	–	FJ559044.1;	–
Brachyleptura champlaini	–	HM411938.1; HQ551592.1;	–
Brachyleptura rubrica	AJ841409.1;	–	–
Cerambyx cerdo	–	KM285966.1; KJ159152.1; KF247263.1;	–
Cerambyx scopolii	–	KU917190.1; JF889538.1; KM286114.1; KM451191.1;	–
Cortodera femorata	–	KJ966406.1; KU910483.1; KU914327.1; KU914836.1;	–
Cortodera humeralis	KX087264.1;	HQ954073.1; KM285870.1; KM286194.1; KU914520.1; KU919048.1;	–
Cortodera militaris	–	KM842145.1; KM841473.1; KM850678.1; KM850702.1; MF638834.1;	–
Dinoptera collaris	–	KM450437.1; KM449303.1; KM286140.1; KM446985.1; JF889454.1	–
Gaurotes tuberculicollis	KF737721.1;	KF737784.1;	KF142135.1;
Gaurotes virginea	HQ832599.1;	HQ954589.1; KJ961983.1; KM445527.1; KM439292.1; KM445387.1;	–
Gibbocerambyx aurovirgatus	KF737736.1;	KF737799.1;	KF142115.1;
Grammoptera ruficornis	DQ202613.1;	HQ954598.1; KM445734.1; KM286150.1; KM443767.1; KM447320.1;	–
Hemadius oenochrous	AB703463.1;	AB703463.1;	–
Judolia bangi	HM034785.1;	–	HM046536.1;
Judolia cerambyciformis	–	HQ954555.1; KU906517.1; KU916384.1; KM286357.1; KM445175.1;	–
Judolia sexmaculata	HM034788.1;	KM443765.1; KM445106.1; HQ559267.1; KJ963030.1;	HM046539.1;
Lamia textor	–	KJ961885.1; KM445206.1; MH613743.1; KJ965883.1; KJ966718.1;	–
Lamiomimus gottschei	KF737764.1;	KY683678.1;	HM046546.1; MN851203.1;
Leptura aethiops	AF332921.1;	KM451953.1; KY683603.1; KY683629.1;	HM046547.1;
Leptura annularis	HM034792.1;	KY683714.1; KY683632.1; KU914996.1; KM443478.1; KM451359.1;	HM046542.1;
Leptura aurosericans	KF737720.1;	KF737783.1;	KF142136.1;
Leptura aurulenta	–	KM286090.1; KM443336.1;	–

Species	16S rRNA	COI*	28S rRNA*
Leptura dudodeciguttata	HQ832604.1;	KY683662.1;	HQ832607.1;
Leptura quadrifasciata	–	KU919023.1; KU908893.1; KJ963368.1; KM446982.1; KM441356.1;	–
Lepturalia nigripes	–	KJ966853.1;	–
Lepturobosca chrysocoma	–	JF888490.1; JF888491.1; KM845232.1; KM845483.1; MF634891.1;	–
Lepturobosca virens	–	KJ966357.1; KJ966717.1; KJ967231.1; KM286296.1; KM441311.1;	–
Monochamus sutor	AB533603.1;	AY260843.1; AY264403.1; EU556670.1; EU556676.1; EU556682.1;	KC692745.1;
Morimus asper	–	JX969629.1; KM286055.1; MH613717.1; MH613719.1; MH613718.1;	–
Rutpela maculata	–	MH020343.1; KU914676.1; KU910296.1; KU907795.1; KM446337.1;	KP419628.1; MN851205.1;
Rutpela nigra comb. nov.	KX087348.1;	MH020344.1; KU915828.1; KU908354.1; KM449359.1; KM442043.1;	–
Rutpela septempunctata comb. nov.	–	KM452170.1;	–
Oedecnema gebleri	HM034778.1;	KY683625.1; MN905230.1;	HM046530.1; MN851222.1;
Pachyta bicuneata	HM034794.1;	DQ223727.1; GU003931.1; KF247291.1; HM062973.1;	HM046544.1;
Pachyta quadrimaculata	–	KM440118.1; KM441670.1; KM450998.1; KU906393.1; KU914386.1;	–
Paracorymbia fulva	–	KM286048.1; KM448870.1; KM447220.1; KM451616.1; KM448408.1;	–
Paracorymbia maculicornis	–	HM909037.1; HQ954583.1; KJ963072.1; JF889535.1; KM286178.1;	–
Paracorymbia variicornis	HM034793.1;	–	HM046543.1;
Pidonia alticollis	–	KY683696.1;	–
Pidonia gibbicollis	HM034777;	–	HM046529.1;
Pidonia lurida	–	HQ954590.1; KU906557.1; KU914297.1; KM286007.1; KM440086.1;	–
Pidonia scripta	–	JF887394.1; JF887395.1; JF887397.1; JF887399.1; JF887401.1;	–
Pidonia similis	HM034771.1;	HM062968.1;	HM046523.1;
Prionus asiaticus	HM034784.1;	–	HM046535.1;
Prionus coriarius	–	JF889828.1; KJ964237.1; KM286000.1; KM441011.1; KU908107.1;	–
Prionus gahani	GU130422.1;	–	–
Prionus laticollis	–	KU255661.1; MH110202.1;	KP419600.1; MN851234.1;
Pygoleptura nigrella	–	JF887362.1; KM847187.1; KM850512.1; KM850767.1;	–
Rhagium inquisitor	–	HM433492.1; HQ954550.1; KJ962550.1; KM285814.1; KM440357.1;	–
Rhagium mordax	–	HQ948267.1; HQ954457.1; KJ962620.1; KM285811.1; KM441365.1;	–
Stenurella bifasciata	–	KU919187.1; KU912935.1; KM440660.1; KM285769.1; KM447494.1;	–
Stenurella melanura	–	MH020459.1; KM448663.1; KU910533.1; KM286273.1; KU918065.1;	–
Stictoleptura canadensis	–	KM843803.1; KM843727.1; HM411725.1; HM411726.1; HM411727.1;	–
Stictoleptura rubra	HM034773.1;	JF889870.1; KJ963544.1; KM285821.1; KM286101.1; KJ967273.1;	–
Stictoleptura scutellata	–	HQ954584.1; KM443028.1; KM285952.1; KM440943.1; KU907814.1;	–
Stictoleptura succedanea	KY796052.1;	KY796052.1;	–
Strangalia attenuata	HM034780.1;	KM449502.1; MH020329.1; KM449936.1; MH020328.1;	HM046532.1;
Strangalia luteicornis	–	KJ164383.1; KM850262.1;	HM156701.1;
Typocerus lugubris	–	HM433510.1;	–
Typocerus sparsus	–	HQ984293.1;	–
Typocerus velutinus	AJ841410.1;	AY165677.1; HM411732.1; HM411733.1; HM411734.1;	–
Xestoleptura behrensii	–	KU876487.1; KU876488.1;	–
Xestoleptura crassipes	–	JF888515.1; JF887771.1; JF888525.1; JF888523.1; JF888522.1;	–
Total sequenced species:	28	64	21

Note: * – distinct sequences used for construction of consolidate sequences (see methods).

The genes were assembled in the matrix as follows: 16S rRNA – COI – 28S rRNA with the total length 1,535 kilobase (kb). While the species set with 16S rRNA+COI+28S rRNA sequences (n = 21) was limited, we filled the gaps of missing species with COI sequences, which overlap at least 40% of their length. The resulting matrix constitutes of the species set (n = 39) which contained 77% of three genes (16S rRNA+ COI+28S rRNA) sequences and 23% of one gene (COI) sequences.

Multiple alignments were generated using the Muscle software in the environment of SeaView 4 (Gouy et al., 2010). Alignments were provided with unlimited iterations and were edited manually to correct regions containing missing data and to exclude unalignable positions.

Phylogenetic trees were constructed using maximum-likelihood (ML) and Bayesian methods with PhyML (Guindon & Gascuel, 2003). Analyses were performed following a general time-reversible (GTR) model of sequence evolution. We performed an approximate likelihood-ratio test (aLRT) for branch support based on the Log Ratio between the likelihood value of the current tree and that of the best alternative (Anisimova & Gascuel, 2006; Guindon et al., 2010). The optimal tree's structure was estimated using the best combination of nearest-neighbour interchange (NNI) and Subtree Pruning Regrafting (SPR) algorithms. We also used the neighbour-joining algorithm (BioNJ) optimizing trees' topology for estimation of branch distances (Gascuel, 1997).

Results

Morphological phylogeny. The results of statistical processing of morphological characters and phylogenetic analysis revealed the polyphyly of *Stenurella* sensu Villiers. We identified the groups of morphological characters that make the greatest contribution to taxon discrimination. This allowed us to remove little-informative characters for further phylogenetic analysis. According to the results of DA (Table 5), morphological characters of pronotum ($F_{apr.}$ = 46953.0, P < 0.0001), abdomen ($F_{apr.}$ = 256.95, P < 0.0001) and thorax ($F_{apr.}$ = 50.45, P < 0.0001) make the largest contribution to discrimination of genera-level taxa. The Wilks' Lambda coefficients come to zero for all groups of morphological characters indicating that genera-level taxa are statistically significantly discriminated.

Table 5

Contribution of morphological characters' groups in discrimination of genera-level taxa extracted from Discriminant Analysis

Group of characters	Wilks' Lambda	The approximate F	P
Head	1.0×10^{-6}	14.33	6.0×10^{-4}
Antennae	2.1×10^{-4}	18.50	0.0
Pronotum	1.0×10^{-8}	46953.00	0.0
Thorax	5.7×10^{-4}	50.45	0.0
Elytra	3.0×10^{-5}	18.96	0.0
Abdomen	0.0	256.95	0.0
Legs	0.0	14.81	8.7×10^{-4}
Morphometric data only	0.0	35.33	0.0
All (morphometric and nonmetric) data	0.0	5242×10^{4}	0.0

The morphological characters that represent the most variable patterns (i.e., colouration of elytra and legs) make a minor contribution to discrimination of the studied taxa. Therefore, we can conclude that colour patterns are unreliable characters for distinction of genera. It should be noted, however, that contribution of morphometric data only in discrimination of genera-level taxa was moderate ($F_{apr.}$ = 35.33, P < 0.0001). Im-

portantly, the DA coefficients alone cannot tell us between which of the genera-level taxa the respective groups of morphological characters discriminate. Therefore, we performed canonical analysis for estimation and visualization (Fig. 2) of how groups of morphological characters discriminate between genera-level taxa by plotting the individual scores for the groups of morphological characters.

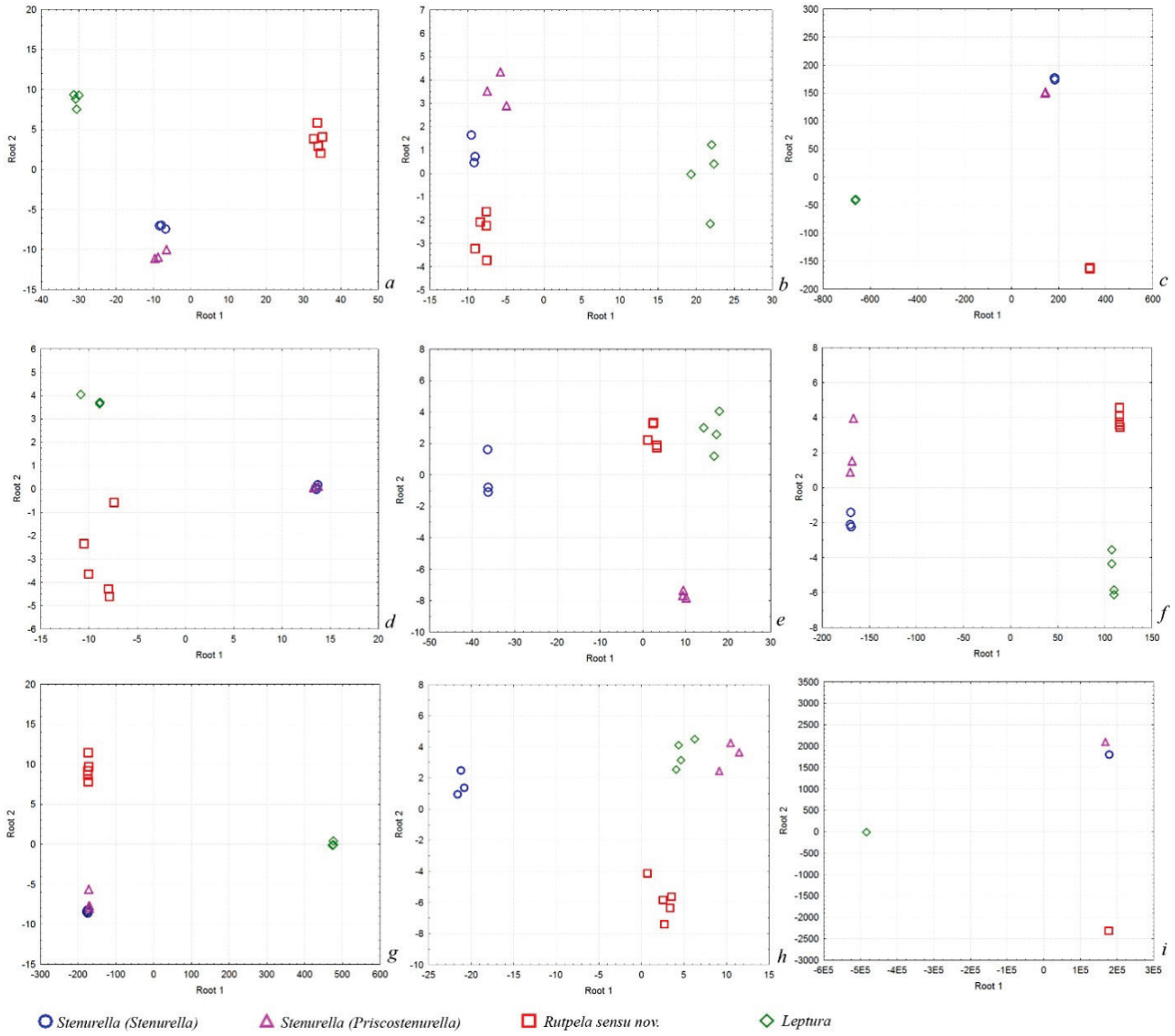

Fig. 2. The discrimination of genera-level taxa of *Stenurella* sensu novo, *Rutpela* sensu novo and *Leptura* s. str. by groups of morphological characters: head (*a*), antennae (*b*), pronotum (*c*), thorax (*d*), elytra (*e*), abdomen (*f*), legs (*g*), morphometric data only (*h*), all data (*j*)

We found that some groups of morphological characters are useful for distinction of genera and others for distinction of subgenera and species. The genera-level taxa were completely separated using groups of morphological characters of head (Fig. 2a), pronotum (Fig. 2c), thorax (Fig. 2d) and legs (Fig. 2g). These clearly demonstrated the polyphyly of *Stenurella* and distinctiveness of *Stenurella*, sensu novo and *Rutpela*, sensu novo. Finally, morphological characters of thorax (Fig. 2d) well discriminate the subgenera-level taxa within *Rutpela*, sensu novo, but not in other genera. The group characters that represent the antennae morphology (Fig. 2b) well discriminate separate species but not higher taxa. The elytra colouration patterns (Fig. 2e) are largely uninformative for genera distinction because of high intraspecies and interspecies variability. Surprisingly, we found that using only morphometric data was not informative enough (Fig. 2h) for discrimination of genera-level taxa. Our findings show that using the separate morphometric groups of characters is not sufficient to entirely differentiate genera-level taxa. In fact, only a complete set of morphometric and nonmetric morphological characters (Fig. 2i) allows qualitative discrimination of genera-level taxa.

The maximum likelihood tree (Fig. 3) from morphological phylogeny clearly showed the polyphyly of the genus *Stenurella* sensu Villiers which consists of two independent clades. The first clade represents six species of the genus *Stenurella* sensu Villiers (i.e. *S. jaegeri*, *S. novercalis*, *S. bifasciata*, *S. melanura*, *S. hybridula* and *S. approximans*). The second clade combines the remainder three species of *Stenurella* sensu Villiers (*S. septempunctata*, *S. vaucheri* and *S. nigra*) and two species of *Rutpela* sensu Nakane & Ohbayashi (i.e. *R. inermis* and *R. maculata*). Both clades of *Stenurella* sensu Villiers are non-related to each other and likely represent separate genera contrary to the extant classification. Hereinafter we use the name *Stenurella*, sensu novo to circumscribe the species of the first clade and *Rutpela*, sensu novo for the species of the second clade. Furthermore, *Rutpela*, sensu novo is related to *Leptura* s. str. which includes the following species: *L. quadrifasciata*, *L. aurulenta*, *L. annularis* and *L. aethiops*.

Topologically, the clade of *Stenurella*, sensu novo splits into two lineages: melanura-lineage and bifasciata-lineage. The first lineage includes the following species: *S. melanura*, *S. hybridula* and *S. approximans*. We found that *S. melanura* and *S. hybridula* are the closest relatives, and both related to *S. approximans*. *Bifasciata*-lineage includes another three species: *S. jaegeri*, *S. novercalis* and *S. bifasciata*. We found that *S. jaegeri* and *S. novercalis* are more closely related to each other than to *S. bifasciata*.

The clade of *Rutpela*, sensu novo is deeply branched and is represented by a number of the successive sister lineages (*nigra*-lineage, *maculata*-

lineage, *septempunctata*-lineage and *vaucheri*-lineage). The *nigra*-lineage is basal within the clade of *Rutpela* including the sole species *Rutpela nigra*, comb. nov. The remaining four species constitute the crown of the tree. *Rutpela inermis* and *R. maculata* belong to the maculata-lineage. Both are closely related each other and traditionally classified together (Danilevsky, 2014, 2020). It should be noted that data on *R. inermis*, included to the current analysis, is not statistically significant (see methods) and some stochasticity is allowed. *Rutpela vaucheri*, comb. nov. and *R. septempunctata*, comb. nov. represent another crown clade which splits into two separate lineages, including *vaucheri*-lineage and *septempunctata*-lineage. According to CA (Fig. 2d), all four lineages are well separated and represent distinct subgenera. Clade of *Leptura* s.str. represents a dense cluster of successive sister branches of *L. aethiops*, *L. annularis*, *L. quadrifasciata* and *L. aurulenta*.

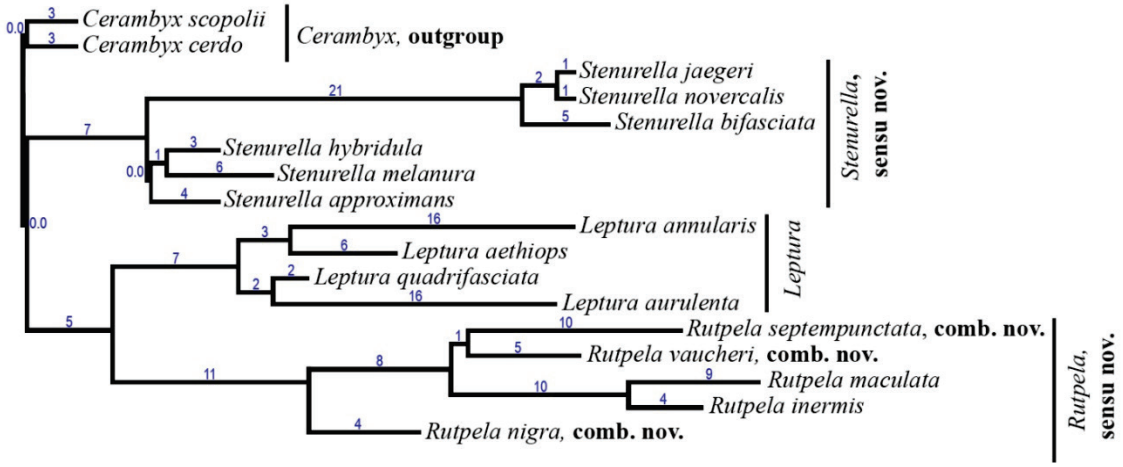

Fig. 3. The polyphyly hypothesis of *Stenurella* sensu Villiers based on morphological phylogeny: the values represent the branches length; *Cerambyx cerdo* and *C. scopolii* were used to root the tree

Molecular phylogeny. Our molecular phylogenetic analysis confirmed the results of morphological phylogeny lending support to the hypothesis that *Stenurella* is polyphylous. The phylogenetic tree (Fig. 4) constructed based on the consensus COI sequences showed several patterns similar to our morphological analysis. Firstly, it showed merging of *R. nigra*, comb. nov., *R. septempunctata*, comb. nov. and *R. maculata* into the one group (SH-like = 0.82), which we identified as a genus *Rutpela*, sensu novo. Secondly, *S. melanura* and *S. bifasciata* appear as separate group which represent genus *Stenurella*, sensu novo (SH-like = 0.89). Thirdly, we found high molecular affinity of *Rutpela*, sensu novo and *Leptura* s. str. (SH-like = 0.82) and placed *Stenurella*, sensu novo as a sister group to both of them. The topology of the molecular phylogenetic tree of *Rutpela*, sensu novo was identical to the morphological tree, and consisted of deep separated branches of the certain species. *Rutpela nigra*, comb. nov. represented the basal branch of *Rutpela*, sensu novo, *R. septempunctata*, comb. nov. and *R. maculata* successively branched off forming the crown of *Rutpela*, sensu novo.

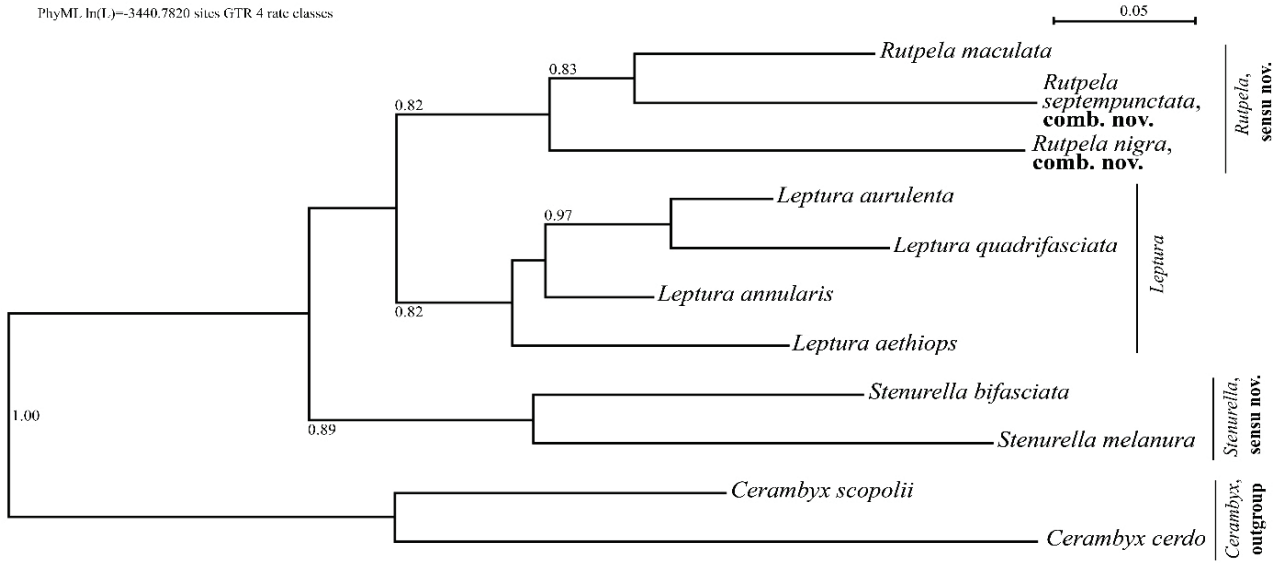

Fig. 4. The polyphyly hypothesis of *Stenurella* sensu Villiers based on COI sequences phylogeny: the branch support SH-like values are shown with the threshold rule SH > 0.70; *Cerambyx cerdo* and *C. scopolii* were used to root the tree

Next, we conducted phylogenetic analysis for assessment of the place of *Stenurella*, sensu novo, *Rutpela*, sensu novo and *Leptura* s.str. within Lepturini using sequences of three genes: 16S rRNA + COI + 28S rRNA. We obtained a well-resolved phylogenetic maximum likelihood tree (Fig. 5) with strong support of nearly all branches based on aLRT. Our findings showed that Lepturini splits into two main clades: *Anoplodera*-branch and *Leptura*-branch. The first of them includes *Anoplodera* Mulsant, 1839, *Judolia* Mulsant, 1863, *Oedecnema* Dejean, 1835, and *Stenurella*, sensu novo. The second consists of *Grammoptera* Dejean, 1835, *Leptura* Linnaeus, 1758, *Rutpela*, sensu novo, *Stictoleptura* Casey, 1924, *Strangalia* Audinet-Serville, 1835, *Typocerus* LeConte, 1850, and *Xestoleptura* Casey, 1913. Thus, *Stenurella*, sensu novo nested within *Anoplodera*-branch and *Rutpela*, sensu novo – within *Leptura*-branch. Moreover, nesting of *Rutpela*, sensu novo within the *Leptura*-branch showed that it is well separated and distantly related to other genera. We hypothesized that either 1) *Rutpela*, sensu novo is an ancient taxonomically isolated relict group or 2) genomes of the possible relatives of *Rutpela*, sensu novo are not sequenced yet.

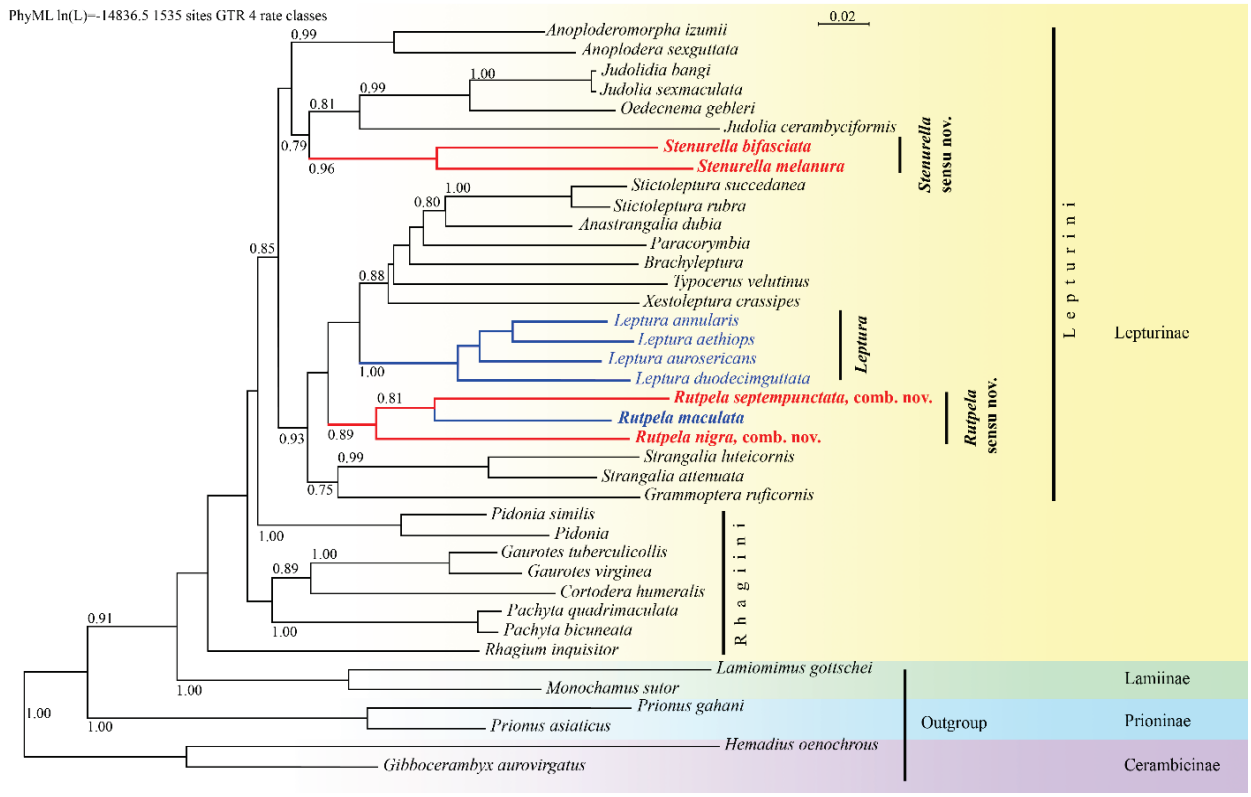

Fig. 5. The three genes (16S rRNA+COI+28S rRNA) tree illustrating the phylogenetic hypothesis of relationships of *Stenurella* sensu novo, *Rutpela* sensu novo and *Leptura* s. str. within Lepturini; the branch support SH-like values are shown with the threshold rule SH > 0.70

Discussion

Our study yielded consistent results from both morphological and molecular data analysis, and it demonstrated the polyphyly of *Stenurella* sensu Villiers. Specifically, we have established that *Stenurella* sensu Villiers consists of two independent clades, namely *Stenurella*, sensu novo and *Rutpela*, sensu novo. Moreover, both these genera belong to different evolutionary lineages. While *Stenurella*, sensu novo belongs to the *Anoplodera*-branch, *Rutpela*, sensu novo belongs to the *Leptura*-branch (Fig. 5). We assumed that the external morphological similarity of *Stenurella*, sensu novo and *Rutpela*, sensu novo was the result of convergent evolution. Since adults of both genera spend most of the time on flowers feeding pollen and nectar, their evolution was, probably, driven by mimetic selection toward imitation of ants or wasps.

Our findings of the polyphyly of *Stenurella* sensu Villiers and resultant intrageneric relations were significantly different from the intrageneric subdivision previously proposed by Özdikmen (2013) and later accepted by Danilevsky (2014, 2020). In fact, we found the crucial differences between our findings and Özdikmen's observations (Fig. 6). In contrast to Özdikmen's data, our findings showed the close affinity of *melanura*-lineage and *bifasciata*-lineage.

According to our results, *melanura*-lineage includes the type species *S. melanura*, and *S. hybridula*, and *S. approximans*, all of which are closely related (Fig. 3). Özdikmen, however, placed each of these species in the separate subgenera *Stenurella*, *Iberostenurella* and *Crassostenurella*, respectively. His proposal was based on the female abdomen colouration, type of pronotal pubescens and the length ratio of metatibia to the first metatarsomere. While Özdikmen defined the pronotal sculpture of *S. hybridula* (*Iberostenurella*) as finely and densely punctated, that characteristic, according to our findings, does not differ significantly from that of *S. melanura* and *S. approximans*. Similarly, a number of other morphological characters used by Özdikmen to draw his conclusions do not vary significantly among *Stenurella*, *Iberostenurella* and *Crassostenurella*.

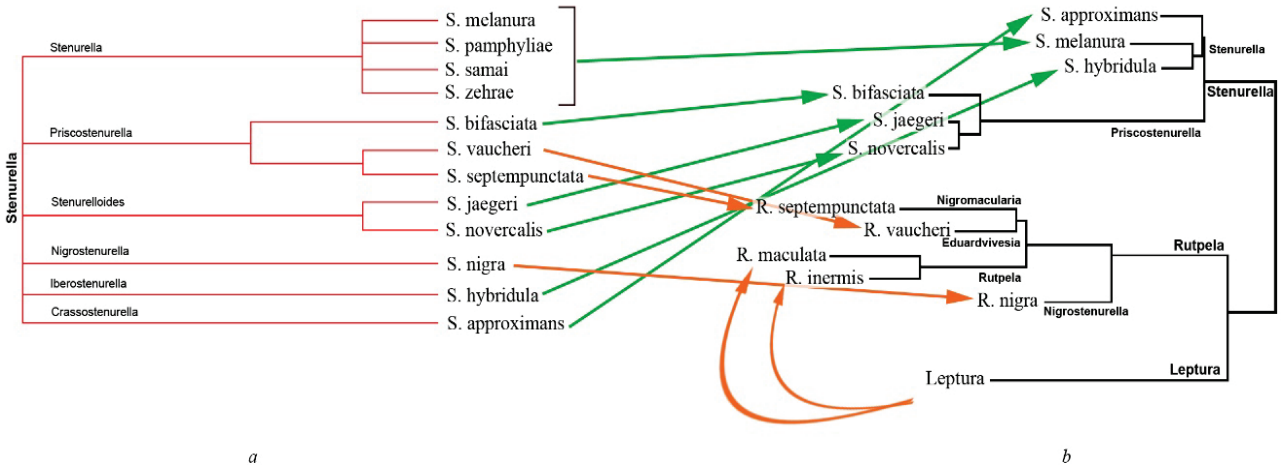

Fig. 6. The comparison of two models describing relationships within *Stenurella* sensu Villiers as proposed (reconstructed from the text) by Özdikmen (2013) (*a*) and our study (*b*); taxonomic transfers are shown by arrows

Our study found no substantial reason for designating *S. melanura*, *S. hybridula* and *S. approximans* into separate subgenera. We suggest that subgenera *Iberostenurella* and *Crassostenurella* are synonyms of subgenus *Stenurella*. Özdikmen also included three additional species in subgenus *Stenurella*. These are *S. samai* Rapuzzi, 1995, *S. pamphyliae* Rapuzzi & Sama, 2009 and *S. zehrae* Özdikmen et al., 2012. All of these species are currently synonymized with *S. melanura* (Danilevsky, 2014, 2020; Vitali, 2018). Similarly, Danilevsky (2014, 2020) considered all of these species as subspecies of *S. melanura* (i.e., *S. melanura samai*, *S. melanura pamphyliae*, *S. melanura zehrae*).

Our analysis revealed that the bifasciata-lineage consisted of three species *S. bifasciata*, *S. jaegeri* and *S. novercalis*, which were grouped in a dense cluster on our tree (Fig. 3). In contrast, Özdikmen nested *S. jaegeri* and *S. novercalis* into the separate subgenus *Stenurelloides* based on partly red coloured legs, deep and dense punctation of pronotum. Surprisingly, he claimed that the abdomen of *Stenurelloides* was coloured black. In fact, the black abdomen is typical for males of *S. novercalis* contrary to the red or partly red coloured abdominal sternites in females of *S. novercalis* and in both sexes of *S. jaegeri*. Our observations coincide with previously published data (Danilevsky & Dzhavelidze, 1990; Danilevsky, 2014). Furthermore, Özdikmen nested *S. bifasciata* within *R. septempunctata*, comb. nov. and *R. vaucheri*, comb. nov. into subgenus *Priscostenurella*. However, according to his own description (Özdikmen, 2013), *S. bifasciata* is closer to *S. melanura* than to *R. septempunctata*, comb. nov. and *R. vaucheri*, comb. nov. Our findings (Fig. 3, 5) demonstrated that *R. septempunctata*, comb. nov. and *R. vaucheri*, comb. nov. belong to *Rutpela*, sensu novo. *S. bifasciata*, *S. jaegeri* and *S. novercalis* were found combined in the dense cluster (Fig. 3) indicating close relation to each other. Therefore, we propose to synonymize *Stenurelloides* with *Priscostenurella* and transfer *S. jaegeri* and *S. novercalis* to *Priscostenurella* and exclude *R. septempunctata*, comb. nov. and *R. vaucheri*, comb. nov. from *Priscostenurella*.

We showed (Fig. 3, 5) that clade *Rutpela*, sensu novo is a sister to *Leptura* rather than a part of *Stenurella* sensu Villiers. The clade *Rutpela*, sensu novo includes *R. nigra*, comb. nov., *R. maculata*, *R. inermis*, *R. septempunctata*, comb. nov. and *R. vaucheri*, comb. nov. (Fig. 3, 5). Özdikmen (2013), however, placed *R. nigra*, comb. nov., *R. septempunctata*, comb. nov. and *R. vaucheri*, comb. nov. in two different subgenera, *Nigrostenurella* and *Priscostenurella*, within *Stenurella* sensu Villiers (Fig. 6a). A specific morphological feature of this clade is a pair of longitudinal carinae or their secondary modification on metaventrite in males (Fig. 7). This feature was suggested as unique for *R. maculata* and it was the reason for separating *R. maculata* into genus *Rutpela* (Nakane & Ohbayashi, 1957). *Rutpela*, however, was synonymized and moved as subgenus into *Leptura* by Villiers (1978). Next, Nakane & Ohbayashi (1957), who misinterpreted the taxonomical value of the male metaventral carinae, concluded the affinity of *Rutpela* and *Oedecnema* Dejean, 1835 bearing a very similar feature. This claim was repeated in multiple publications and, specifically, in the studies by Danilevsky's (2014, 2020). Based on the results of our phylogenetic analysis (Fig. 5), *Oedecnema* was grouped within *Judolia* Mulsant, 1863. Nevertheless, metaventral carinae are not a unique feature of *R. maculata*, and they are present in males of most of the species of *Rutpela*, sensu novo. Indeed, Danilevsky reported (personal communication, January 23, 2020) the presence of very small laminated carinae on the males' metaventrite in *R. inermis*.

We also found short carinae terminated by big claw-like thorns in males of *R. nigra*, comb. nov. (Fig. 7a, b). These carinae, however, were reduced and presented only by small thorns in *R. vaucheri*, comb. nov. (Fig. 7e). Similarly, in *R. septempunctata*, comb. nov. these carinae and thorns were highly reduced and presented by poorly distinguishable tubercles (Fig. 7f). We believe that the degree of metaventral carinae reduction is an apomorphy and well agree with phylogenetic nesting of these species within *Rutpela*, sensu novo in both morphological (Fig. 3) and molecular (Fig. 5) trees. *Rutpela nigra*, comb. nov. nested in the base of the clade of *Rutpela*, sensu novo. We assumed that *N. nigra* comb. nov. was an ancient lineage which branched off from the main stem very early during the evolution. Consistently, *R. nigra*, comb. nov. shows both morphological and molecular patterns which distinguish it from the other species of *Rutpela*, sensu novo. These findings allowed us to place *R. nigra*, comb. nov. in the separate subgenus *Nigrostenurella* Özdikmen, 2013. The crown of *Rutpela*, sensu novo constitute a cluster of four species distributed within *maculata*-lineage, *vaucheri*-lineage, and *septempunctata*-lineage. *Maculata*-lineage consists of two species, *R. maculata* and *R. inermis*, which share a number of prominent morphological characters, including tuberculated pronotum, carinated male's metaventrite, dentated male's metatibia, and annulated antennae. This allows us to recognise this lineage as a separate subgenus *Rutpela* Nakane & Ohbayashi, 1957.

Despite the fact that *R. vaucheri*, comb. nov. and *R. septempunctata*, comb. nov. nested within one clade, both of them are deeply separated with significant branch length (Fig. 3). We suggested that both lineages diverged early from common ancestor and evolved in different ways. This idea was confirmed by CA (Fig. 2d) and their distinct morphology (Fig. 7e, 7f, 8e, 8f). In particular, *R. vaucheri*, comb. nov. is characterised by a short head (Fig. 9h), 4-th antennomere twice shorter than 5-th one, short and rough punctated pronotom (Fig. 8f), male's metaventrite with the pair of prominent thorns (Fig. 7e). Contrary to these, morphology of *R. septempunctata*, comb. nov. is distinct with elongated body and legs (Fig. 10k), sparse pronotal punctation (Fig. 8e), 4th antennomere only a quarter shorter than 5th one, male's metaventrite without prominent thorns (Fig. 7f). We believe that the most morphological features in *R. vaucheri*, comb. nov. are more ancient and closer to ancestral form than in *R. septempunctata*, comb. nov. These features were conserved in *vaucheri*-lineage due to its very restricted range and stable environment of its existence. Thus, we propose to establish two subgenera for both species: *Eduardvivesia*, subgen. nov. for *R. vaucheri*, comb. nov., and *Nigromacularia*, subgen. nov. for *R. septempunctata*, comb. nov.

Genus *Rutpela* Nakane & Ohbayashi, 1957, sensu novo

Type species: *Leptura maculata* Poda, 1761: 74, Greece.

Diagnosis: body elongated and narrowed. Head (Fig. 9e-h) elongated (H6 = 0.49 ± 0.05; hereinafter, for abbreviation (e.g., H6) see Table 2; for biometric data see Table 3) with smoothed tempora (Fig. 9e-h). Length of the fourth antennomere is 1/2 (A3 = 0.54 ± 0.04) or 2/3 (A3 = 0.74 ± 0.04) of the fifth one. Pronotum elongated (P8 = 0.75 ± 0.02), with long and simple hind angles (Fig. 8i-k). Pronotal base deeply concave on both sides from the centre. Males' metaventrite bearing a pair of carinae or thorns (Fig. 7). Fourth metatarsomere narrow, shallowly (1/4) bilobed. The 1–4th protarsomeres are expanded in males.

Distribution: Palearctic.

Remarks: the colouration of integument varies from black to orange or yellow. Head, antennae, pronotum, elytra and legs are often light coloured (orange or yellow) with black patterns. Abdomen is always lightly coloured (red, orange or yellow).

Subgenus *Nigrostenurella* Özdikmen, 2013

Type species: *Leptura nigra* Linnaeus, 1758: 358, Europe.

Diagnosis: head tempora completely smoothed, not protruding (Fig. 9e). Pronotum with fine and sparse punctation. Males' metaventrite with a pair of small carinae terminated with big claw-like thorns (Fig. 8a-b).

Distribution: West Palearctic (except North Africa).

Species: *Rutpela* (*Nigrostenurella*) *nigra* (Linnaeus, 1758): 358, comb. nov. (Fig. 10g).

Remarks: integument is completely black (Fig. 10g) except abdominal sternites. In some cases, head and pronotum are red coloured (Danilevsky, 2014: 350; Vitali, 2018: 102, Fig. 185), and elytra can be fulvous (Jacek Kurzawa, personal communication, January 29, 2020) or red coloured (Danilevsky, 2014: 350).

Subgenus *Rutpela* Nakane & Ohbayashi, 1957

Type species: *Leptura maculata* Poda, 1761: 74, Greece.

Diagnosis: head tempora smoothed, weakly defined (Fig. 9f). Pronotum with distinct lateral tuberculum and deep anterior transverse sulcus, finely and densely punctated (Fig. 8c). Males' metaventrite with a pair of laminate carinae without thorns (Fig. 7c, d). Males' metatibia dentate on the inner surface.

Distribution: West Palearctic.

Species: *Rutpela* (*Rutpela*) *maculata* (Poda, 1761): 37 (Fig. 10h).

Species: *Rutpela* (*Rutpela*) *inermis* (K. Daniel & J. Daniel, 1898): 74 (Fig. 10i).

Remarks: integument is black with yellow. Elytra is with five mostly incomplete black transverse bands (Fig. 10h, i). Antennae are annulated, in exceptional cases are completely yellow or black. Antennomeres from 5th to 10th are cylindrically shaped unlike depressed and expanded ones in *Leptura*.

Subgenus *Eduardvivesia*, subgen. nov.

Type species: *Leptura* (*Stenura*) *vaucheri* Bedel, 1900: 336, Morocco.

Diagnosis: head moderately elongated (H6 = 0.52 ± 0.03, Fig. 9h). Tempora small, slightly protruding. The fourth antennomere twice shorter than the fifth one (A3 = 0.53 ± 0.04). Pronotum moderately deep and densely punctated (Fig. 8f). Males' metaventrite only with a pair of very small thorns (Fig. 7e).

Etymology: subgenus named in honour of Eduard Vives, Catalan entomologist, who has studied the longhorn beetles for many years.

Distribution: Circum-Gibraltar.

Species: *Rutpela* (*Eduardvivesia*) *vaucheri* Bedel, 1900: 336, comb. nov. (Fig. 10j).

Remarks: integument is black, except yellowish small spot on the occiput, with yellow or orange elytra, abdomen and legs. Elytra is with five black transverse bands which are incomplete in males (Fig. 10j). Antennae are predominantly light coloured.

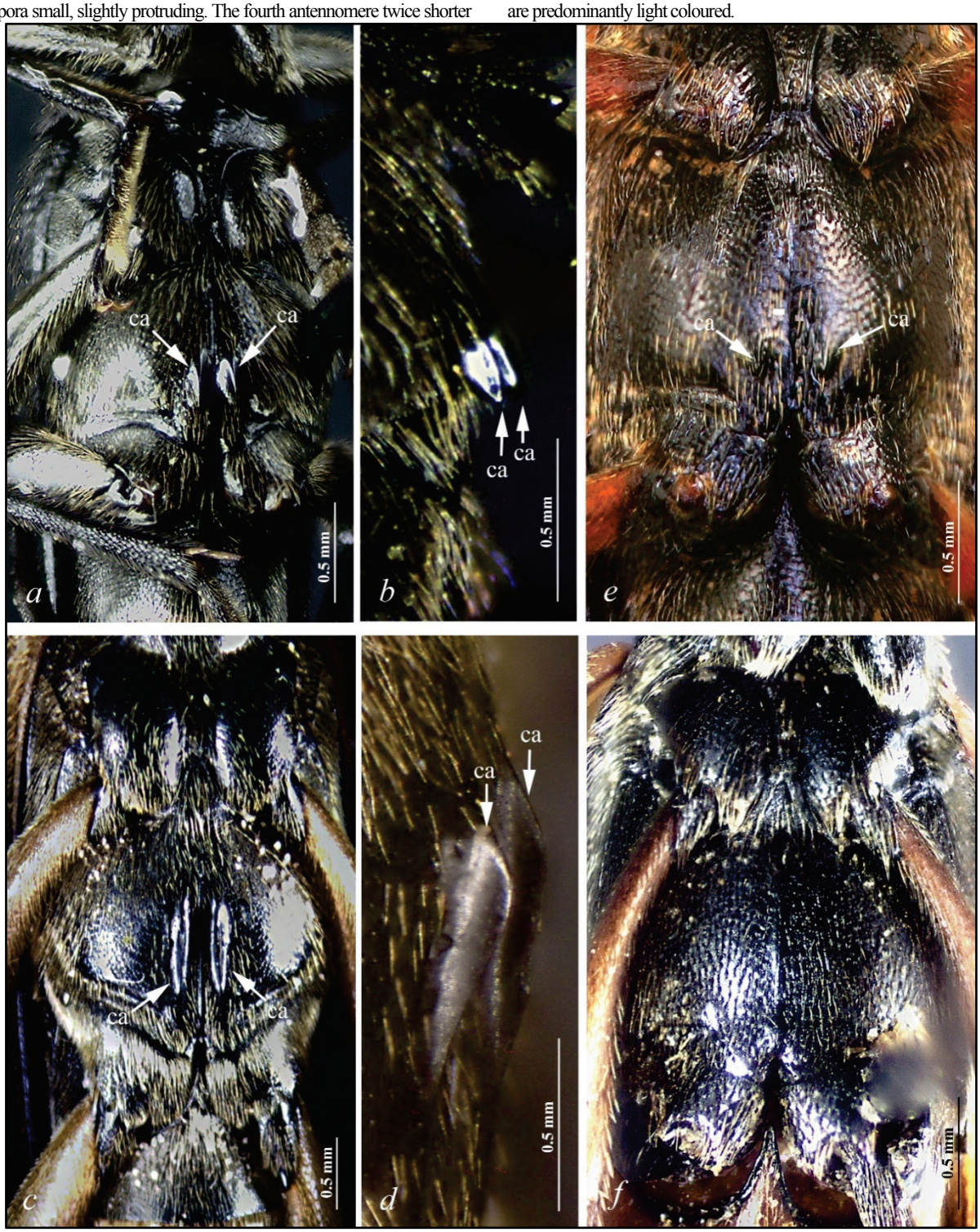

Fig. 7. Morphological features of males' thorax in *Rutpela* sensu novo: *R. nigra* comb. nov. frontal (*a*) and lateral (*b*) views, *R. maculata* frontal (c) and lateral (*d*) views, *R. vaucheri* comb. nov. frontal (*e*) view, *R. septempunctata* comb. nov. frontal (*f*) view; labels: *ca* – carina; *R. vaucheri* comb. nov., photo credit: Eduard Vives

Subgenus *Nigromacularia*, subgen. nov.

Type species: *Leptura septempunctata* Fabricius 1793: 346, Hungary.

Diagnosis: head tempora completely smoothed (Fig. 9g). Pronotum is with fine and sparse punctation (Fig. 8e). Males' metaventrite with a pair of poorly distinguishable tubercles (Fig. 7f). Hind legs very long (L10 = 0.59 ± 0.06). Etymology: Latin: *niger* – black and *macula* – spot.

Distribution: Pannono-Anatolian.

Species: *Rutpela* (*Nigromacularia*) *septempunctata* Fabricius 1793: 346, comb. nov. (Fig. 10k).

Remarks: integument colouration varies from completely black (*Rutpela* (*Nigromacularia*) *septempunctata latenigra* (Pic, 1915), comb. nov.) to completely orange (*Rutpela* (*Nigromacularia*) *septempunctata septempunctata* (Fabricius, 1793), comb. nov.). Elytra is orange or yellow coloured with five mostly incomplete black transverse bands, typically presented by distinct spots (Fig. 10k). Antennae are predominantly light coloured.

Genus *Stenurella* Villiers, 1974: 214, sensu novo

Type species: *Leptura melanura* Linnaeus, 1758: 397, Europe.

Diagnosis: body slightly elongated. Head moderately elongated with well-developed protruded tempora (Fig. 9a–d). Length of the fourth antennomere (A3 = 0.87 ± 0.02) about the same as the fifth one. Pronotum nearly spherical (Fig. 8a, b), slightly elongated (P8 = 0.9 ± 0.04), with short protruding binary hind angles (Fig. 8g, h). Pronotal base nearly narrow and weakly curved. Males' metaventrite simple (without carinae or thorns). Fourth metatarsomere narrow, deeply (from 1/3 to 1/2 of its length) bilobed. The width of 1–4th protarsomeres is similar in both sexes.

Distribution: Palearctic.

Remarks: integument is black coloured. Elytra is lightly coloured with a distinct sexual dimorphism. Legs are typically black, in some cases red. Abdomen is black or red.

Fig. 8. Details of pronotum morphology in *Stenurella* sensu novo and *Rutpela* sensu novo: a general view of pronotum of *S. melanura* (a), *S. bifasciata* (*b*), *Rutpela maculata* (*c*), *R. nigra* comb. nov. (*d*), *R. septempunctata* comb. nov. (*e*), *R. vaucheri* comb. nov. (*f*); details of the structure of pronotal posterior angle: double angle in *S. melanura* (*g*), *S. bifasciata* (*h*), and simple angle in *R. maculata* (*c*), *R. nigra* comb. nov. (*d*), *R. septempunctata* comb. nov. (*e*), *R. vaucheri* comb. nov. (*f*); lables: *oa* – outer angle, *ia* – inner angle, *sa* – simple angle, *su* – sulcus; *R. vaucheri* comb. nov. – photo credit: Eduard Vives

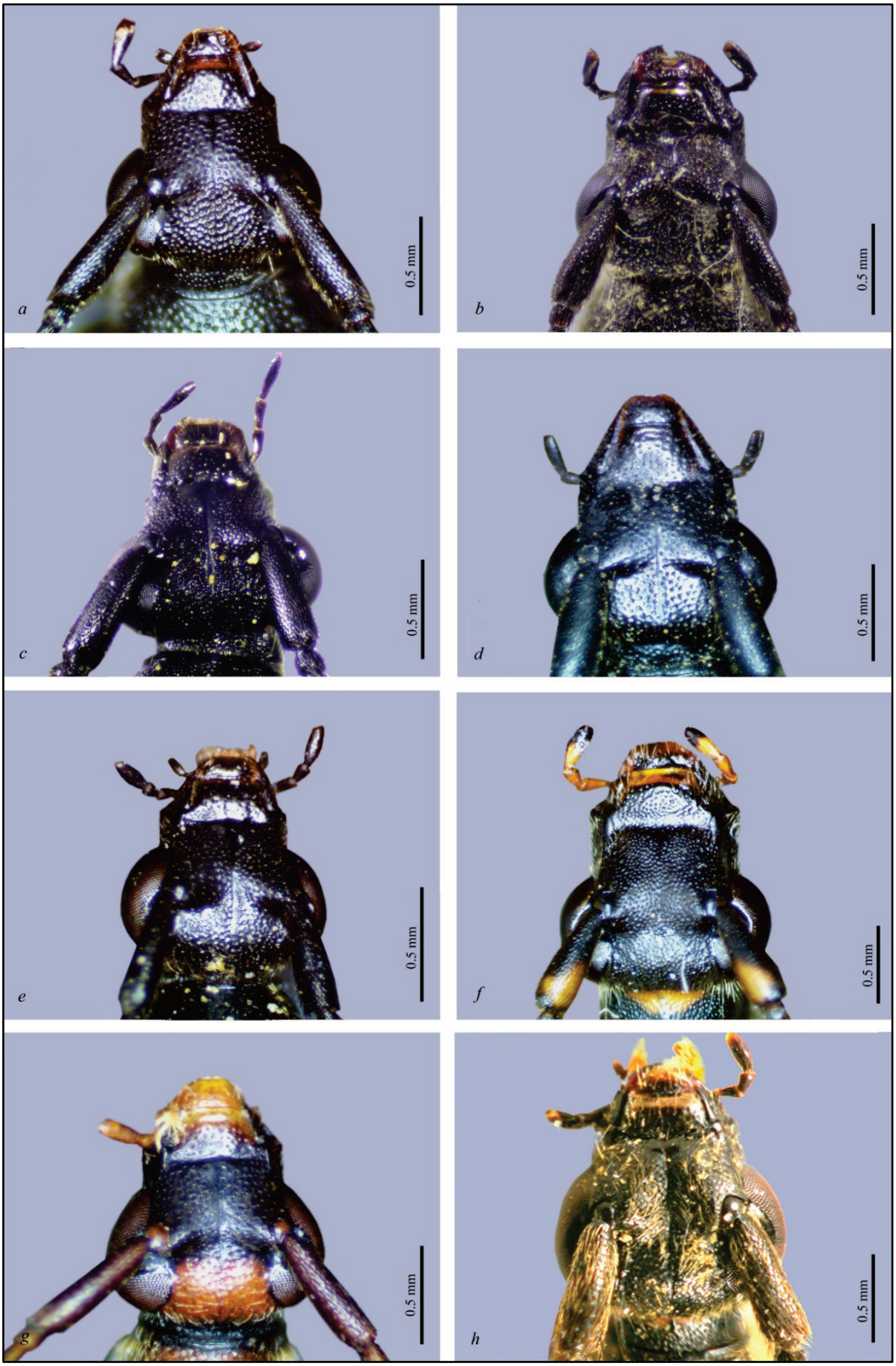

Fig. 9. Details of head morphology in *Stenurella*, sensu novo and *Rutpela*, sensu novo: *S. melanura* (*a*), *S. hybridula* (*b*), *S. approximans* (*c*), *S. bifasciata* (*d*), *R. nigra*, comb. nov. (*e*), *R. maculata* (*f*), *R. septempunctata*, comb. nov. (*g*), *R. vaucheri* comb. nov. (*h*); *R. vaucheri*, comb. nov. – photo credit: Eduard Vives

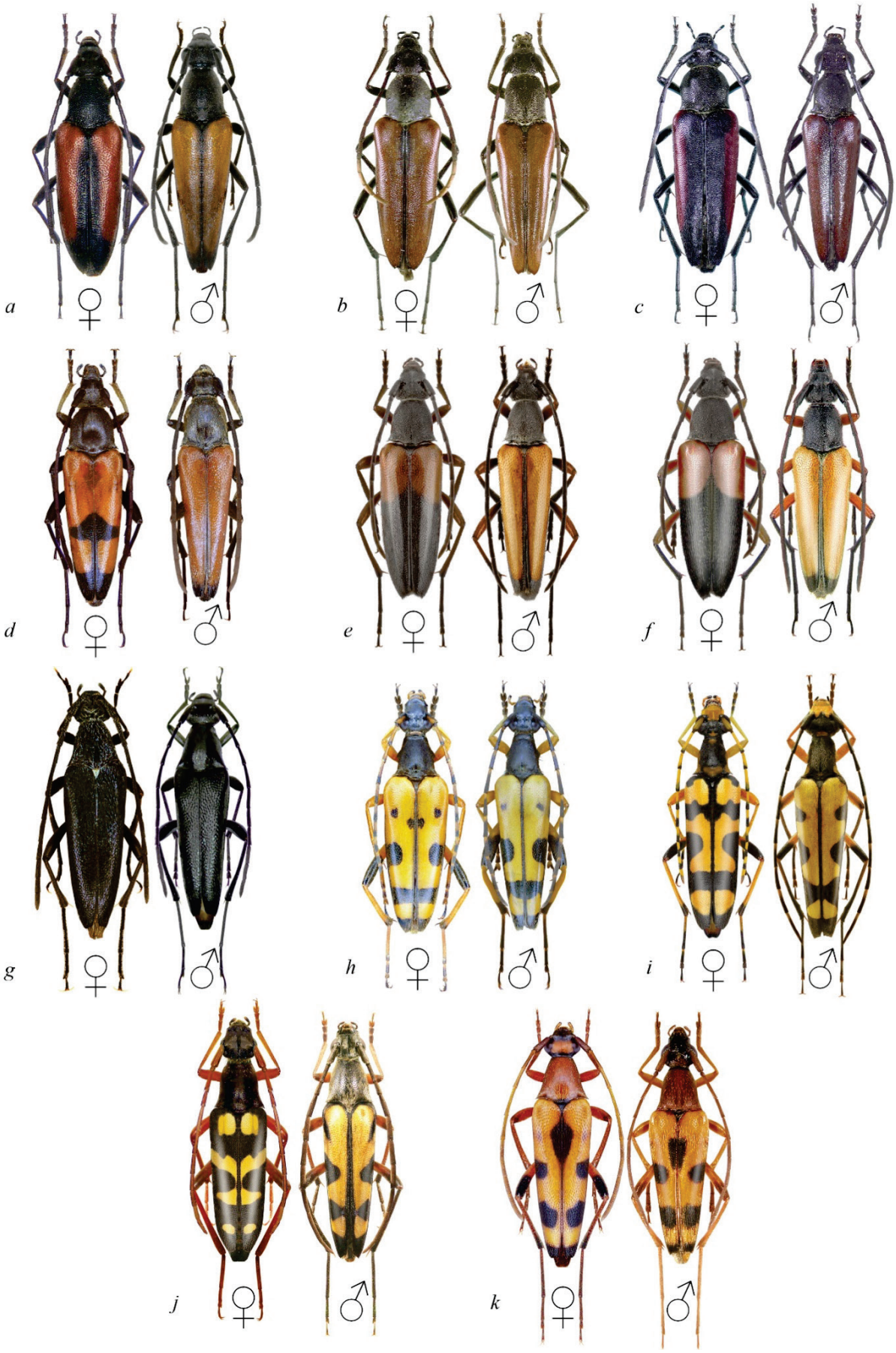

Fig. 10. Habitus of *Stenurella*, sensu novo and *Rutpela* sensu novo: *S.* (*Stenurella*) *melanura* (*a*), *S.* (*Stenurella*) *hybridula* (*b*), *S.* (*Stenurella*) *approximans* (*c*), *S.* (*Priscostenurella*) *bifasciata* (*d*), *S.* (*Priscostenurella*) *jaegeri* (*e*), *S.* (*Priscostenurella*) *novercalis* (*f*), *Rutpela* (*Nigrostenurella*) *nigra*, comb. nov. (*g*), *R.* (*Rutpela*) *maculata* (*h*), *R.* (*Rutpela*) *inermis* (*i*), *R.* (*Eduardvivesia*) *vaucheri* comb. nov. (*j*), *R.* (*Nigromacularia*) *septempunctata* comb. nov. (*k*); the scale is not preserved

Subgenus *Stenurella* Villiers, 1974: 214, subgen. sensu novo
Iberostenurella Özdikmen, 2013: 527, syn. nov.,
Crassostenurella Özdikmen, 2013: 526, syn. nov.
Type species: *Leptura melanura* Linnaeus, 1758: 397, Europe.

Diagnosis: pronotum near spherical (P8 = 0.91 ± 0.01), deeply and densely punctated (Fig. 8a). Fourth metatarsomere bilobed, divided into 1/2 of its length.

Distribution: Palearctic.

Species:

Stenurella (*Stenurella*) *melanura* (Linnaeus, 1758): 397 (Fig. 10a).
Stenurella (*Stenurella*) *hybridula* (Reitter, 1902): 188 (Fig. 10b).
Stenurella (*Stenurella*) *approximans* (Rosenhauer, 1856):305 (Fig.10c).

Remarks: integument is black, except elytra. In some cases, abdomen is light coloured (*S. hybridula*). Elytra is monochromic fulvous (males) or reddish (females) with black longitudinal sutural band, which varies in patterns size and colour intensity.

Subgenus *Priscostenurella* Özdikmen, 2013: 516, subgen. sensu novo
Stenurelloides Özdikmen, 2013: 523, syn. nov.
Type species: *Leptura bifasciata* O. F. Müller, 1776: 93, Denmark.

Diagnosis: pronotum slightly elongated (P8 = 0.88 ± 0.05), punctation varies in depth and density (Fig. 8b). The fourth metatarsomere is 1/3 bilobed.

Distribution: Palearctic.

Species: *Stenurella* (*Priscostenurella*) *bifasciata* (O. F. Müller, 1776): 93 (Fig. 10d).
Stenurella (*Priscostenurella*) *jaegeri* (Hummel, 1825): 68 (Fig. 10e).
Stenurella (*Priscostenurella*) *novercalis* (Reitter, 1901): 78 (Fig. 10f).

Remarks: integument is black, except light coloured elytra and abdomen. The elytra are monochromic fulvous (males) or reddish (female) with 1–2 black apical transverse bands. Sutural band is rare. The legs colouration varies from completely red to completely black.

Conclusion

In summary, our results clearly demonstrate the consensus of morphological and molecular approaches to solving the taxonomic puzzle of *Stenurella* genus. The combination of these research methods has revealed the natural phylogenetic taxonomy of the genus *Stenurella* and species that have been mistakenly included in it for decades. Moreover, with the help of multigene analysis, we were able to resolve evolutionary links between species and their phylogenetic position in the Lepturini tribe. We proposed a new evolutionary model of the taxonomy *Stenurella* sensu Villiers, which includes two independent branches. We excluded from the genus *Stenella* sensu Villiers three species that have been transferred to the genus *Rutpela*, sensu novo: *R.* (*Nigrostenurella*) *nigra*, comb. nov., *R.* (*Eduardvivesia*) *vauchery*, comb. nov. and *R.* (*Nigromacularia*) *septempunctata*, comb. nov. Thus, we redescribed genus *Rutpela*, sensu novo and subdivided it into four subgenera, namely *Nigrostenurella* Özdikmen, 2013, *Rutpela* Nakane & Ohbayashi, 1957, *Eduardvivesia*, subgen. nov. and *Nigromacularia*, subgen. nov. We also proposed a new classification for the genus *Stenurella*, sensu novo, which we subdivided into two subgenera: *Stenurella* Villiers, 1974 and *Priscostenurella* Özdikmen, 2013. Further phylogenetic studies of the longhorn beetles should be provided by the active use and combination of modern morphological and molecular methods and approaches. The ultimate goal of such research is to establish the natural evolutionary system of Cerambycidae.

We are grateful to Mr. Emili Armengol (Spain), Mr. Manuel Baena (Spain), Dr. Vasyl Chumak (Ukraine), Dr. Maxym Chumak (Ukraine), Mr. Pedro Coello (Spain), Dr. Mikhail Danilevsky (Russia), Dr. Olexander Drogvalenko (Ukraine), Mr. Yaroslav Kapelyukh (Ukraine), Mr. Oleksander Kravchenko (Ukraine), Mr. Jacek Kurzawa (Poland), Dr. Olexander Mateleshko (Ukraine), Mr. Ruslan Panin (Ukraine), Mr. Giampaolo Proscia (Italy), Dr. Volodymyr Rizun (Ukraine), Mr. Pablo Sanz (Spain), Dr. Yuri Skrylnyk (Ukraine), Mr. Miquel Tomàs (Spain), Mr. Jose Luis Torres (Spain), Mr. José María Urbano (Spain), Mr. Eduard Vives (Spain) for their support and providing additional materials and advice for our study. We are also grateful to Dr. Alexander Boyko (Canada) for manuscript proofreading.

References

Anisimova, M., & Gascuel, O. (2006). Approximate likelihood ratio test for branches: A fast, accurate and powerful alternative. Systematic Biology, 55(4), 539–552.

Bedel, L. E. M. (1900). Descriptions de deux Coléoptères nouveaux, du Nord de l'Afrique [Descriptions of two new beetles from North Africa]. Bulletin de la Société Entomologique de France, 5(17), 335–337 (in French).

Daniel, K., & Daniel, J. (1898). Zwanzig neue Arten aus dem paläarktischen Faunengebiet [Twenty new species for Palearctic fauna]. Coleopteren-Studien, 2(7), 61–82 (in German).

Danilevsky, M. L. (2014). Zhuki-usachi (Coleoptera, Cerambycoidea) Rossii i sosednikh stran [Longicorn beetles (Coleoptera, Cerambycoidea) of Russia and adjacent countries]. Part 1. HSC, Moscow (in Russian).

Danilevsky, M. L. (2020). Chrysomeloidea I (Vesperidae, Disteniidae, Cerambycidae). Updated and Revised Second Edition: 6/1 (Catalogue of Palaearctic Coleoptera). Koninklijke Brill N. V., Leiden.

Danilevsky, M. L., & Dzhavelidze, I. G. (1990). K voprosu o taksonomicheskom statuse nekotorykh vidov roda *Stenurella* Villiers, 1974 (Coleoptera, Cerambycidae) s novymi dannymi po faune zhukov-usachey Gruzii [On taxonomic status of some species of genus *Stenurella* Villiers, 1974 (Coleoptera, Cerambycidae) with new data on Georgian longicorn beetles]. Proceedings of the Academy of Science of Georgian SSR, Series Biology, 16(2), 125–130 (in Russian).

Dascălu, M. M., Caba, F. G., & Fusu, L. (2021). DNA barcoding in Dorcadionini (Coleoptera, Cerambycidae) uncovers mitochondrial-morphological discordance and the hybridogenic origin of several subspecies. Organisms Diversity and Evolution, 22, 205–229.

De Santana Souza, D., Marinoni, L., Laura Monné, M., & Gómez-Zurita, J. (2020). Molecular phylogenetic assessment of the tribal classification of Lamiinae (Coleoptera: Cerambycidae). Molecular Phylogenetics and Evolution, 145, 106736.

Fabricius, J. C. (1793). Entomologia systematica emendata et aucta. Secundum classes ordines, genera, species adjectis synonymis, locis, observationibus, descriptionibus [Entomological systematics based on classes, orders, genera and species with additions of synonyms, locations, observations, and descriptions]. Vol. 1(2). C. G. Proft, Hafniae (in Latin).

Gascuel, O. (1997). BIONJ: An improved version of the NJ algorithm based on a simple model of sequence data. Molecular Biology Evolution, 14(7), 685–695.

Gouy, M., Guindon, S., & Gascuel, O. (2010). SeaView version 4: A multiplatform graphical user interface for sequence alignment and phylogenetic tree building. Molecular Biology Evolution, 27(2), 221–224.

Guindon, S., & Gascuel, O. (2003). A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. Systematic Biology, 52, 696–704.

Guindon, S., Dufayard, J.-F., Lefort, V., Anisimova, M., Hordijk, W., & Gascuel, O. (2010). New algorithms and methods to estimate maximum-likelihood phylogenies: Assessing the performance of PhyML 3.0. Systematic Biology, 59(3), 307–321.

Hill, T., & Lewicki, P. (2006). Statistics: Methods and applications. A comprehensive reference for science, industry and data mining. StatSoft Inc., Tulsa.

Hummel, A. D. (1825). Essais Entomologiques N° IV. Insectes de 1825. V. Novae Species Variorum [Entomological essays N° IV. Insects of 1825. V. A new species]. Essais Entomologiques, 4, 1–72 (in French).

Jennrich, R. I. (1977). Stepwise regression. In: Enslein, K., Ralston, A., & Wilf, H. S. (Eds.). Mathematical methods for digital computers. Vol. 3(4). Wiley, New York. Pp. 58–75.

Kajtoch, Ł., Gronowska, M., Plewa, R., Kadej, M., Smolis, A., Jaworski, T., & Gutowski, J. M. (2022). A review of saproxylic beetle intra- and interspecific genetics: Current state of the knowledge and perspectives, The European Zoological Journal, 89(1), 481–501.

Karpiński, L., Szczepański, W. T., Plewa, R., Kruszelnicki, L., Koszela, K., & Hilszczański, J. (2021). The first molecular insight into the genus *Turanium* Baeckmann, 1922 (Coleoptera: Cerambycidae: Callidiini) with a description of a new species from Middle Asia. Arthropod Systematics and Phylogeny, 79, 465–484.

Kim, S., de Medeiros, B. A. S., Byun, B.-K., Lee, S., Kang, J.-H., Lee, B., & Farrell, B. D. (2018). West meets East: How do rainforest beetles become circum-Pacific? Evolutionary origin of *Callipogon relictus* and allied species (Cerambycidae: Prioninae) in the New and Old Worlds. Molecular Phylogenetics and Evolution, 125, 163–176.

Lee, S., & Lee, S. (2020). Multigene phylogeny uncovers oviposition-related evolutionary history of Cerambycinae (Coleoptera: Cerambycidae). Molecular Phylogenetics and Evolution, 145, 106707.

Linnaeus, C. (1758) Systema naturae per regna tria naturae secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis [The system of nature through the three kingdoms of nature subdivided into classes, orders, genera, species, with characteristics, differential diagnosis, synonyms, and locations]. Systema Naturae. Editio 10. Laur. Salvius, Holmiae (in Latin).

Lobanov, A. L., Danilevsky, M. L., & Murzin, S. V. (1981). Systematic list of longicorn beetles (Coleoptera, Cerambycidae) of the USSR. I. Entomologicheskoje Obozrenie, 60(4), 784–803.

Löbl, I., & Smetana, A. (2010). Catalogue of Palaearctic Coleoptera. Vol. 6: Chrysomeloidea. Apollo Books, Stenstrup.

Müller, O. F. (1776). Zoologiae Danicae prodromus, seu animalium Daniae et Norvegiae indigenarum characteres, nomina, et synonyma imprimis popularium [Zoological prodromus of Denmark, or the characteristics of the native animals of Denmark and Norway, the names and synonyms of the native animals]. Hafniae, Hallager (in Latin).

Nakane, T., & Ohbayashi, K. (1957). Notes on the genera and species of Lepturinae (Coleoptera, Cerambycidae) with special reference to their male genitalia. Scientific Reports of the Saikyo University, Natural Science & Living Science A series, 2(4), 47–52.

Nie, R., Vogler, A. P., Yang, X.-K., & Lin, M. (2021). Higher-level phylogeny of longhorn beetles (Coleoptera: Chrysomeloidea) inferred from mitochondrial genomes. Systematic Entomology, 46, 56–70.

Özdikmen, H. (2013). An attempt on subgeneric composition of the genus *Stenurella* Villiers, 1974 (Cerambycidae: Lepturinae: Lepturini). Munis Entomology and Zoology, 8(2), 509–531.

Poda von Neuhaus, N. (1761). Insecta Musei Graecensis, quae in ordines, genera et species Juxta Systema Naturae Caroli Linnaei digessit Nicolaus Poda Widmanstad [Insects of the Museums of Grecee, including orders, genera and species according to Systema Nature of Carolus Linnaeus processed by Nicolaus Poda Widmanstad]. Facsimilé Publié par W. Junk en 1915 (in Latin).

Reitter, E. (1901). Uebersicht der Arten der Coleopteren-Gattung *Strangalia* Serv., aus der Verwandtschaft der *St. melanura* L. und *bifasciata* Müll [Overview of the species of the Coleoptera genus *Strangalia* Serv., related to *St. melanura* and *bifasciata* Müll]. Wiener Entomologische Zeitung, 20(4), 77–80 (in German).

Reitter, E. (1902). Neue Coleopteren aus Europa und den Angrenzenden Ländern [A new Coleoptera from Europe and adjacent countries]. Deutsche Entomologische Zeitschrift, 2, 187–188 (in German).

Rosenhauer, W. G. (1856). Die Thiere Andalusiens nach dem Resultate einer Reise Zusammengestellt [The animals of Andalusia compiled according to the results of a journey]. Theodor Blaesing, Erlangen (in German).

Ruchin, A. B., & Egorov, L. V. (2018a). Fauna of longicorn beetles (Coleoptera: Cerambycidae) of Mordovia. Russian Entomological Journal, 27(2), 161–177.

Ruchin, A. B., & Egorov, L. V. (2018b). *Leptura aurulenta* (Coleoptera, Cerambycidae), a new record of a very rare species in Russia. Nature Conservation Research, 3(1), 88–91.

Slipinski, A., & Escalona, H., (2013). Australian longhorn beetles (Coleoptera: Cerambycidae). Volume 1: Introduction and subfamily Lamiinae. Csiro Publishing, Collingwood.

Sutherland, L. N., Schnepp, K. E., Powell, G. S., & Bybee, S. M. (2021). Phylogenetic Placement of the Plesioclytini (Coleoptera: Cerambycidae: Cerambycinae). Diversity, 13, 597.

Torres-Vila, L., & Bonal, R. (2019). DNA barcoding of large oak-living cerambycids: Diagnostic tool, phylogenetic insights and natural hybridization between *Cerambyx cerdo* and *Cerambyx welensii* (Coleoptera: Cerambycidae). Bulletin of Entomological Research, 109(5), 583–594.

Villiers, A. (1974). Une nouvelle nomenclature des Lepturines de France (Col. Cerambycidae) [A new systematics of Lepturinae of France]. L'Entomologiste, 30, 207–217 (in French).

Villiers, A. (1978). Faune des Coléoptères de France I. Cerambycidae. Encyclopédie Entomologique. Vol. 42 [The beetle fauna of France I. Cerambycidae. Encyclopaedia of Entomology. Vol. 42]. Paul Lechevalier, Paris (in French).

Vitali, F. (2018). Atlas of the insects of the grand-duchy of Luxembourg: Coleoptera, Cerambycidae. Ferrantia 79, Musée National D'histoire Naturelle, Luxembourg.

Zamoroka, A. M. (2021). Is Clytini monophyletic? The evidence from five-gene phylogenetic analysis. Proceedings of the State Natural History Museum, 37, 191–214.

Zamoroka, A. M., Semaniuk, D. V., Shparyk, V. Y., Mykytyn, T. V., & Skrypnyk, S. V. (2019). Taxonomic position of *Anastrangalia reyi* and *A. sequensi* (Coleoptera, Cerambycidae) based on molecular and morphological data. Vestnik Zoologii, 53(3), 209–226.