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Research article

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European net-winged beetles of the *Pyropterus* clade, with the description of *Gomezzuritus* gen. nov. (Coleoptera: Lycidae)

Sergey V. KAZANTSEV¹ Michal MOTYKA² & Ladislav BOCAK^{3,*}

¹Insect Centre, Donetskaya 13–326, Moscow 109651, Russia.

¹A.N. Severtsov Institute of Ecology and Evolution RAS, 33 Leninsky Pr., Moscow 119071, Russia.

^{2,3}Biodiversity and Molecular Evolution, Czech Advanced Technology Research Institute, Centre of Region Hana, Slechtitelu 27, 779 00 Olomouc, Czech Republic.

* Corresponding author: ladislav.bocak@upol.cz

¹Email: kazantss@mail.ru

²Email: michal.motyka@upol.cz

¹[urn:lsid:zoobank.org:author:D78E9B05-04CB-4EFF-810E-68AD94FDD27C](https://zoobank.org/author/D78E9B05-04CB-4EFF-810E-68AD94FDD27C)

²[urn:lsid:zoobank.org:author:242DF8C7-1E68-45F7-AD24-C4BC0C5D0D94](https://zoobank.org/author/242DF8C7-1E68-45F7-AD24-C4BC0C5D0D94)

³[urn:lsid:zoobank.org:author:78383404-FF9F-46EA-A1AE-ACF3613E1D69](https://zoobank.org/author/78383404-FF9F-46EA-A1AE-ACF3613E1D69)

Abstract. We simultaneously considered morphology and molecular phylogeny to modify the generic classification of the ‘pyropterine clade’ (Lycidae, Erotinae, Dictyopterini). To place species previously included in *Benibotarus* Kôno, 1932 in reciprocally monophyletic genera, we propose *Gomezzuritus* gen. nov. with the type-species *Dictyopterus alternatus* Fairmaire, 1856. Further, we transfer *Gomezzuritus alternatus* (Fairmaire, 1856) comb. nov., *G. longicornis* (Reiche, 1878) comb. nov., and *G. rubripes* (Pic, 1897) comb. nov. from *Benibotarus* to *Gomezzuritus* gen. nov. The pyropterine clade contains five genera in the Palearctic region: *Pyropterus* Mulsant, 1838, *Gomezzuritus* gen. nov., *Helcophorus* Fairmaire, 1891, *Greenarus* Kazantsev, 1995, and *Benibotarus* Kôno, 1932. The arrangement of longitudinal elytral costae proved misleading for consideration of relationships. Two genera in distant positions share only four primary costae (*Pyropterus* and *Helcophorus*), and three similarly distant genera share the shortened primary costa 3, resulting in three primary and four secondary longitudinal costae (*Gomezzuritus*, *Greenarus*, and *Benibotarus*). The larva of *Gomezzuritus alternatus* is described in detail, and it is compared with the larvae of other Dictyopterini, including the presumed larva of *G. longicornis*.

Keywords. Lycidae, taxonomy, new genus, new combinations, immature stages.

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Introduction

The European beetle fauna is one of the least diverse, due to harsh Pleistocene climatic conditions (Hewitt 2000; Svenning 2003) but, simultaneously, is the most intensively studied (Löbl & Smetana 2007). Net-winged beetles (Elateroidea: Lycidae) are mainly tropical and represent a tiny fraction of European beetle diversity. Only thirteen species have been reported, two of them recently from Poland and Russia (Burakowski 1990; Kazantsev 1995, 2012a; Kazantsev *et al.* 2019). Further species occur in Northern Africa (6 spp.), the Caspian region (2 spp.), and southern Turkey (1 sp.; Motyka *et al.* 2023, 2023 in press). The Western Palaearctic fauna is almost completely isolated from East Asia when only three species occur from East Asia to Northeastern Europe, and one species is widespread in almost the entire Palaearctic region (Kazantsev 2012a; Motyka *et al.* 2022). No lycids occur in the dry area between the eastern Himalayas, Hindukush, and Elburz, and no genus is shared by the Palaearctic and Afrotropical regions (Masek *et al.* 2018). Despite such a limited diversity, the classification of Western Palaearctic fauna has only recently been modified in a series of morphology-based taxonomic studies that considered relationships of European, North American, and Eastern Palaearctic genera (Bocak & Bocakova 1987, 1991; Kazantsev 1995, 2004). Most European net-winged beetles are rare, and therefore, it is difficult to get tissue suitable for DNA isolation. Thanks to the effort of several colleagues, most Western Palaearctic species have recently been analyzed together with their relatives from Eastern Asia (Motyka *et al.* in press) (Fig. 1), and we can compare the morphology and DNA-based relationships and evaluate the diagnostic value of some traditionally used traits.

Half of the Western Palaearctic net-winged beetles belong to Dictyopterini Houlbert, 1922 (Erotinae LeConte, 1881), representing two separate clades: *Dictyoptera* Latreille, 1829, which includes the widespread Palaearctic species *D. aurora* (Herbst, 1784) and several species known from East Asia and Northern America, and the clade that contains *Pyropterus* Mulsant, 1838, *Helcophorus* Fairmaire, 1891, and *Benibotarus* Kôno, 1932. When the relationships of Holarctic Dictyopterini are recovered from molecular data, the genus *Benibotarus* Kôno, 1932, is found to be polyphyletic (Fig. 1A; Motyka *et al.* in press).

Here we deal with the formal classification of the species of the pyropterine clade. The aim of the present study is to make all genera of the pyropterine clade reciprocally monophyletic. We compare relationships inferred based on different information sources, evaluate the diagnostic value of some traits, and propose a new genus. Further, we transfer some European species to the new genus and describe the previously unknown larva of the type species. Several larvae have recently been described for net-winged beetles (Pototskaya 1981; Bocak & Matsuda 2003; Levkanicova & Bocak 2009; Kazantsev & Nikitsky 2011; Kazantsev & Zaitsev 2021), and we can compare their morphological divergence and the contribution of larval morphology to the classification of the group.

Material and methods

The material was studied in major European museums housing the types of Lycidae. We dissected one individual of *Gomezzuritus alternatus* (Fairmaire, 1856) to present detailed morphology of the genus. Further, we dissected the male genitalia of all species of the clade to study the interspecific variability in the male genitalia. The voucher specimens were relaxed in 50% ethyl alcohol for several hours and then detached abdomens were treated with a hot 10% KOH solution to remove muscles and fat bodies. The larva was treated similarly, but for a shorter time. The external characters and genital morphology were observed under an Olympus SZX-16 microscope. Photographs were taken using an Olympus SZX16 stereo microscope equipped with a Canon M6 Mark II camera. We used Helicon Focus (www.heliconsoft.com) and Photoshop ver. 13.0 (Adobe Inc., San Jose, Ca, USA) to assemble photo stacks into figures showing the principal morphological traits.

The larvae used for morphological investigation and sequenced specimens bearing the UPOL voucher number are deposited in the collection of the Laboratory of Biodiversity and Molecular Evolution, CATRIN-CRH, Olomouc (LMBC).

Institutional abbreviations

ICM = Insect Centre Moscow, Russian Federation
LMBC = Biodiversity and Molecular Evolution, CATRIN, Olomouc, Czech Republic
MNHP = Muséum national d'histoire naturelle, Paris, France
NMPC = National Museum, Prague, Czech Republic
RCSL = R. Constantin Collection, Saint Lo, France
ZIMW = Zoological Institute and Museum, Polish Academy of Sciences, Warszawa, Poland
ZIN = Zoological Institute, Russian Academy of Sciences, St. Petersburg (Barovsky coll.).
ZMBC = Zoological Museum, Humboldt University, Berlin, Germany

Results

Taxonomy

Class Insecta Linnaeus, 1758
Order Coleoptera Linnaeus, 1758
Suborder Polyphaga Emery, 1886
Family Lycidae Laporte, 1838
Subfamily Erotinae LeConte, 1881
Tribe Dictyopterini Houlbert, 1922

The *Pyropterus* clade

Remarks

Dictyopterini was recently analyzed (Kazantsev 2004; Motyka *et al.* in press) and close relationships were recovered for a group of four genera: *Pyropterus*, *Helcophorus*, *Benibotarus*, and *Gomezzuritus* gen. nov., described here. Additionally, based on morphology, *Greenarus* Kazantsev, 1995 is added to this clade. The pyropterine genera are characterized by the wide pronotal areola that differs from the basally constricted areolae of other dictyopterine genera. Additionally, the antennomeres are subequal in length. None of these characters is clearly defined in all taxa and all specimens. The shape of the pronotal costae is particularly often variable, as net-winged beetles are soft-bodied. Therefore, we propose to use an informal designation, 'the *Pyropterus* clade'. We also avoid the description of a subtribe as Dictyopterini is a relatively small group and we are still unsure about the relationships of some dictyopterine taxa. An eventual reclassification would have to consider the entire global diversity.

Genera included in the pyropterine clade

Pyropterus, *Gomezzuritus* gen. nov., *Helcophorus*, *Greenarus*, and *Benibotarus*.

Distribution

The pyropterine clade is distributed in the Palaearctic, Nearctic, and Oriental (northern part only, i.e., northern Thailand and Laos) realms (Masek *et al.* 2018; Kazantsev, 2020). Fossil taxa of these groups have been recorded from Baltic and Rovno amber (Kazantsev & Perkovsky 2022).

Identification key to the genera of the *Pyropterus* clade

1. Each elytron with four longitudinal costae, no secondary costae present in the middle part of elytron, at most vestiges present in humeri 2
 - Each elytron with three longitudinal costae in the whole length, secondary costae present in the whole elytron (Fig. 1B, D–E) 3
2. Elytral cells strongly transverse *Pyropterus* Mulsant, 1838
 - Elytral cells quadrate or only slightly transverse *Helcophorus* Fairmaire, 1891
3. Male antennomeres 3–11 with decumbent pubescence, the apex of phallus simple 4
 - Male antennomeres 3–11 with erect pubescence, the apex of phallus preapically toothed (Fig. 2I–K) *Gomezzuritus* gen. nov.
4. Parameres of aedeagus complete *Benibotarus* Kôno, 1932
 - Parameres of aedeagus ventrally greatly incised *Greenarus* Kazantsev, 1995

Gomezzuritus gen. nov.

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Type species

Dictyopterus alternatus Fairmaire, 1856.

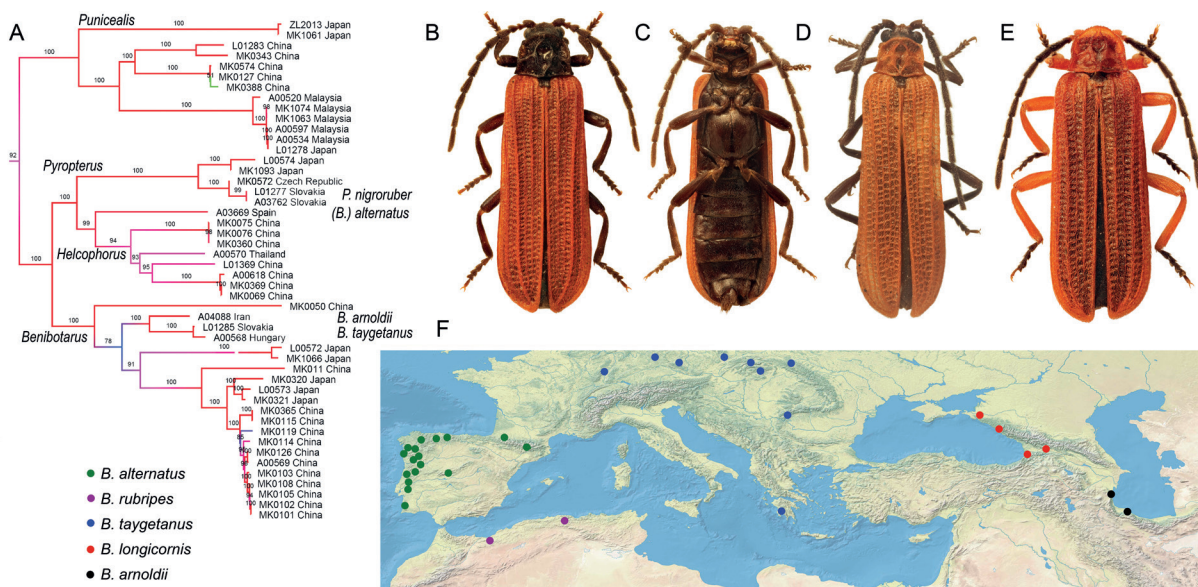


Fig. 1. Phylogenetic relationships of pyropterine genera and their closest relatives (modified from Motyka *et al.* in press). **B–E.** The general appearance of Western Palearctic Dictyopterini Houlbert, 1922. **B–C.** *Benibotarus alternatus* (Fairmaire, 1856), ♂. **D.** *B. longicornis* (Reiche, 1878), ♂. **E.** *B. rubripes* (Pic, 1897), ♂. **F.** Distribution of *Benibotarus* Kôno, 1932 in the Western Palearctic region. Nomenclature follows the placement of species before taxonomic changes discussed in the present study. The northern part of the range of *B. taygetanus* (Pic, 1905) is not shown (see Bocakova & Bocak 1987; Kazantsev 2012a).

Diagnosis

The adults of *Benibotarus*, *Greenarus*, and *Gomezzuritus* gen. nov. share three primary costae in each elytron and developed secondary costae. The new genus may be distinguished from *Benibotarus* and *Greenarus* by the general appearance (the elytra of *Gomezzuritus* are apparently more slender), erect pubescence on male antennomeres 3–11 (distinctly decumbent in *Benibotarus* and *Greenarus*), and noticeably more oval median pronotal areola (Figs 1B, 2G). More diamond-shaped/rhomboidal areolae are known in *Benibotarus* and *Greenarus*. *Pyropterus* has similarly wide roundish areola, but four primary costae in elytra. Additionally, *Gomezzuritus* differs from the other two genera in the preapically toothed median lobe of the aedeagus (Fig. 2I–K; Bocak & Bocakova 1987; Kazantsev 1995, 2004).

The larva of *Gomezzuritus* gen. nov., being quite similar to *Pyropterus*, can be distinguished by the noticeably less transverse tergite 9 (only ca 1.3 × as wide as long), the location of abdominal spiracles at a distance from the dorsal edge of the epipleurite, and the larger size of the spiracle of abdominal segment 1 compared to the spiracles of segments 2–7. In contrast, *Pyropterus* has the tergite 9 conspicuously transverse (ca. twice wider than long), its abdominal spiracles are located at the dorsal edge of the epipleurite, and the spiracle of the abdominal segment 1 does not noticeably surpass in size those on segments 2–7 (Bocak & Matsuda 2003; Kazantsev & Nikitsky 2011). The larvae are known for two species of *Gomezzuritus* as *G. longicornis* comb. nov. whose larva was recently reported (Kazantsev & Zaitsev 2021) is transferred to this genus. As a result, the larva of *Benibotarus* remains unknown.

Larvae of several more distant Dictyopterini genera have been described. The larva of *Gomezzuritus* is easily distinguishable from that of *Dictyoptera* by the divided tergite 9 (Kazantsev & Nikitsky 2011; Motyka *et al.* 2022). The other known larva of Dictyopterini is *Punicealis medvedevi* Kazantsev, 1990. The larva was earlier reported as unidentified Dictyopterini by Levkanicova & Bocak (2009). Now, with a much denser sampling of Dictyopterini, the adult was associated with earlier sequenced larva (Fig. 1A; vouchers ZL2013 and MK1061). The larva of *P. medvedevi* differs from *Gomezzuritus* and *Pyropterus* in a relatively slender and simply rounded pygidium, entire tergites with an incomplete fracture in the middle of the longitudinal midline, and almost straight posterior margin of the ventral cranial plate (see Levkanicova & Bocak 2009).

Etymology

The new genus is named in honour of the Spanish entomologist Jesus Gomez-Zurita Frau (Barcelona, Spain), who is a well-known molecular ecologist and specialist in leaf beetles. Gender masculine.

Description of adult and larva

See Description of *Gomezzuritus alternatus*.

Included species

Gomezzuritus alternatus comb. nov., *G. longicornis* comb. nov., and *G. rubripennis* comb. nov.

Gomezzuritus alternatus (Fairmaire, 1856) comb. nov.

Figs 1A–B, 2–3, 4A–E

Dictyopterus alternatus – Fairmaire 1856: 531.

Dictyoptera alternata – Kleine 1942: 48.

Dictyopterus decipiens – Marseul 1875: 62.

Benibotarus alternatus – Bocak & Bocakova 1987: 114.

Diagnosis

The larva of *Gomezzuritus alternatus* is similar to that of *G. longicornis* reported by Kazantsev & Zaitsev (2021). It differs in the darker coloration, noticeably larger alveoles of the cuticle, and more distinct, light median membrane on abdominal tergite 9 (Fig. 3).

Material examined

SPAIN • 14 ♂♂, 8 ♀♀; Asturias, Las Agüeras, 35 km SW of Oviedo; 28 May 2022; D. Kusy, M. Motyka and L. Bocak leg.; LMBC • 4 ♂♂, 4 ♀♀, 6 larvae (various instars); Asturias, 25 km SW of Oviedo, Caranga de Abajo; 30 May 2022; D. Kusy, M. Motyka and L. Bocak leg.; LMBC • 3 ♂♂; Galicia, A Fonsagrada; 10 May 2019; A. Ocampo leg.; LMBC • 1 ♂; Cádiz, Grazalema; 10–17 May 1979; J. Jelinek leg.; NMPC • 1 spec.; Northern Spain, Curenco; Korb leg.; ZMBC (no exact data).

PORTUGAL • 2 specs; Coimbra, Serra do Buçaco; 1924; F. Hanus leg.; NMPC • 1 spec.; Algarve, Serra de Monchique; 24 Mar. 1967; R. Constantin leg.; RCSL.

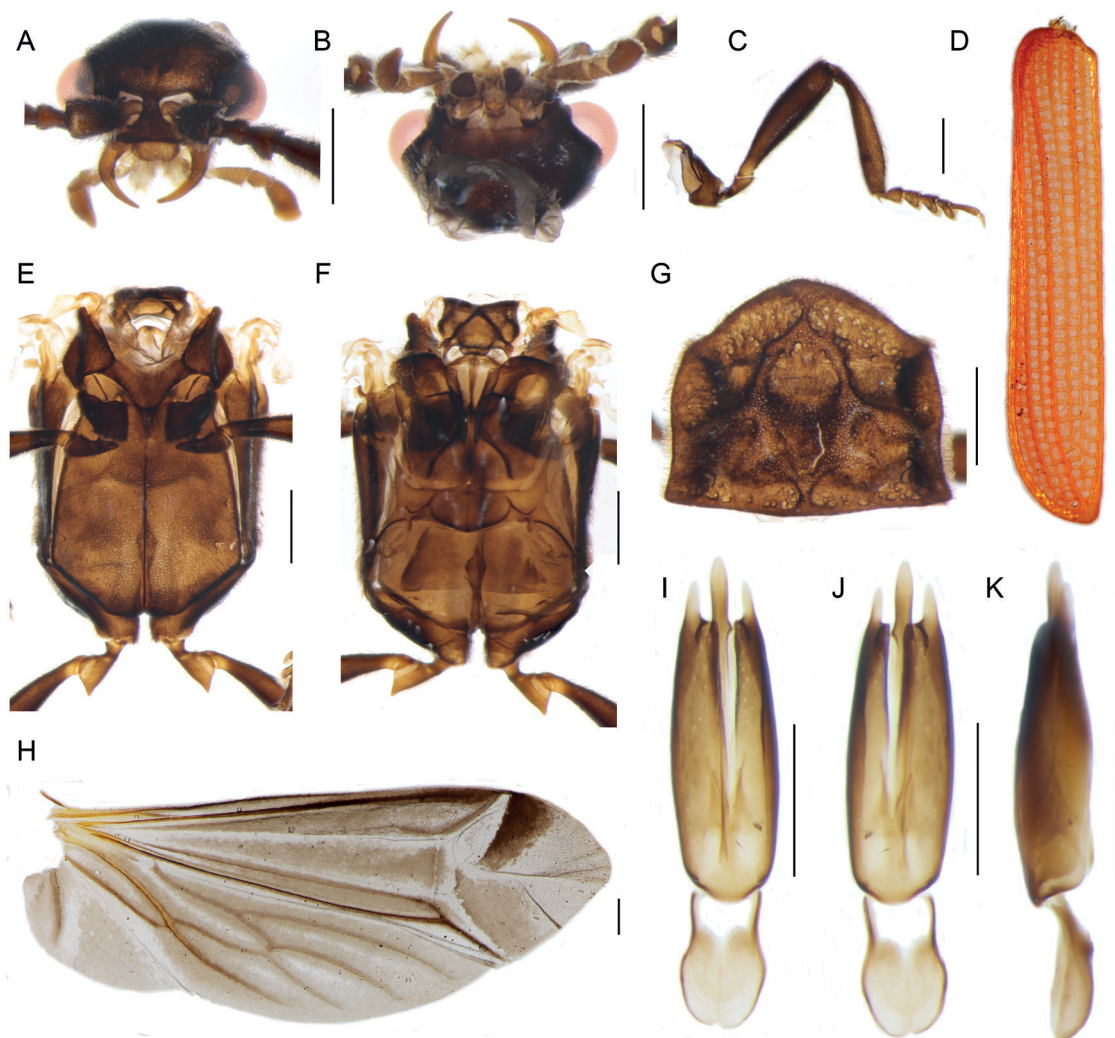


Fig. 2. *Gomezzuritus alternatus* (Fairmaire, 1856) comb. nov., ♂, dissected (LMBC), from Asturias, Las Agüeras, 35 km SW of Oviedo. **A.** Head, frontal view. **B.** Head, ventral view. **C.** Metathoracic leg. **D.** Elytron. **E.** Meso- and metathorax, ventral view. **F.** Ditto, dorsal view. **G.** Pronotum. **H.** Hind wing. **I–K.** Male genitalia. Scale bars = 0.5 mm.

Redescription

Adult (male)

BODY. Elongated, dorso-ventrally flattened (Fig 1B–C).

HEAD. Transverse, slightly exposed from pronotum. Eyes moderately large, spherical. Labial palps short, their ultimate palpomere widened; maxillary palps slender, their ultimate palpomere elongate, almost parallel-sided, flattened distally.

ANTENNA. 11-segmented, relatively long, slender, antennomeres only slightly flattened; pedicel (antennomere 2) subequal in length to antennomere 3 and noticeably shorter than antennomere 4 subequal and subsequent antennomeres; pubescence on antennomeres 3–11 short and erect (Figs 1B–C; 2G).

PRONOTUM. Transverse, triangularly produced anteriorly, almost straight at sides, with complete oval median areole and solid transverse lateral carinae; posterior angles small, acute (Figs 1B–C; 2A–B).

SCUTELLUM. Elongate, almost parallel-sided, triangularly emarginate at apex (Fig. 1B).

WINGS. Elytra elongate, flattened, with three distinct costae on the dorsal surface, with double rows of cells in their interstices; elytral pubescence relatively short and decumbent (Figs 1B; 2D). Metathoracic wings fully developed.

LEGS. Slender; hind trochanters relatively short, acute at posterior angles, femora and tibiae straight, subequal in length, slightly widening distally; tarsomeres 1–4 slightly widened; claws simple (Fig. 2C).

ABDOMEN. With triangularly incised penultimate ventrite.

Female

Similar to male, but pubescence on antennomeres 3–11 decumbent.

Larva (3rd instar)

MEASUREMENTS. Length: 12.5 mm; width (at dorsum): 2.2 mm.

BODY. Elongate, sub-cylindrical, slightly tapering anteriorly and posteriorly. Sclerites light to dark brown, membranes yellowish white. Cuticle alveolate, with relatively large uniform alveoles (Fig. 3A–K).

HEAD. Strongly transverse, dorsally with semi-circular anterior margin; head capsule open ventrally; lateral sclerites not fused to cranium, but approximate anteriorly, with two anterior setae; dorsal cranial plate with pair of broadly separated setae at anterior margin, pair of large setae at disk and pair of setae at fronto-lateral corners; ventral plate broad, heart-shaped, with two anterior setae near lateral margin. Stemmata absent.

ANTENNA. Located fronto-laterally, relatively small, retractable, antennomere 1 (alternatively can be designated as an antennifer) short, circular sclerite; terminal antennomere elongate, ca 1.5 × as long as wide, with relatively large apical membranous bilobed slit and two short distal setae (Fig. 3D–F). Mandibles short, with approximate bases, relatively robust (Fig. 3B, D–F). Galea elongate, almost attaining apex of palpomere 2, basally fused with palpiger, located, with respect to palps, intero-dorsally, with several setae. Maxillary palps three-segmented; palpiger well developed, transverse, ca 1.5 × as wide as long, subequal in length to palpomeres 1 and 2 taken together, with numerous small apical and lateral setae; palpomeres 1 and 2 of approximately equal length, but palpomere 1 noticeably wider than palpomere 2; palpomere 3 conspicuously narrower than palpomere 2 and subequal in length to



Fig. 3. *Gomezzuritus alternatus* (Fairmaire, 1856), larva 3rd instar (LMBC), Asturias, 25 km SW of Oviedo, Caranga de Abajo. **A.** General appearance, lateral view. **B.** Head, pro- and mesothorax, ventral view. **C.** General appearance, lateral view after the treatment by KOH. **D–F.** Head, ventral, lateral, and dorsal view. **G, H.** Terminal abdominal segments, dorsal and ventral view. **I, J.** Head, thorax, and abdominal segment 1, dorsal, ventral view. **K.** Abdominal spiracle in segment 1. Scale bars: A–J = 0.5 mm.

palpomeres 1 and 2. Labial palps minute; prementum narrow, not divided by median suture; palps two-segmented; ligula absent (Fig. 3B, D–F).

THORAX. Thoracic terga similar to abdominal ones, with transverse sclerites divided medially into two parts by narrow membrane (Fig. 3I). Thoracic pleura consisting of two roundish sclerites, anterior epipleurite and posterior hypopleurite; in prothorax epipleurite absent, hypopleurite semi-fused to tergum. Mesothoracic epipleurite with relatively large, annular-biforous functional spiracle; metathoracic epipleurite with minute non-functional spiracle (Fig. 3A, C). Sternal sclerites small, heart-shaped, with two relatively short discal setae (Fig. 3A, C). Coxa about as long as wide; trochanter prominent, about as long and half as wide as femur. Coxa, trochanter, and femur with two relatively long setae each; tibia with numerous short setae. Claws elongate, shorter than tibiae (Fig. 3A, J).

ABDOMEN. Abdominal terga 1–8 transverse, sub-rectangular, with rounded corners, divided medially into two parts by membrane. Tergite 9 moderately transverse, ca $1.3 \times$ as wide as long, narrowed and rounded posteriorly, with median notch, divided medially by conspicuous light membrane, with six setae at posterior edge, two dorsally and four ventrally. Abdominal pleura consisting of two elongate sub-rectangular sclerites, larger epipleurite (more dorsal) and smaller sternopleurite (more ventral). Abdominal spiracles, present in segments 1–8, functional, annular-biforous, located in middle of dorsal half, far from dorsal edge of epipleurite; abdominal spiracle of segment 1 relatively large, like mesothoracic spiracle (Fig. 3A, C). Sternites transverse, sub-rectangular, with slightly rounded corners and pair of setae at posterior margin (Fig. 3H). Abdominal segment 10 tubular, located at ca 35° to axis of segment 9 (Fig. 3A, C, H).

Distribution

Portugal, NW Spain, and the Pyrenees (France and Spain).

Biology

The species is poorly represented in major European museum collections, but it is quite common in the mountain forests of Portugal (the whole country) and western and northern Spain (Galicia, Cantabria, Asturias, Basque Country, and the Pyrenees; only a few reports are known from Castile and Leon and from Madrid province; Fig. 1F; www.inaturalist.org [accessed 25 Jun. 2022]). Adults occur from late March to mid-June, commonly sitting on herb and fern leaves, flying in late afternoon or early evening hours or when disturbed (Fig. 4D). We collected most specimens in old pine forests in lower mountain elevations in the Asturias province (Fig. 4F). The larvae were collected from moist red-rotten pine wood in the place where adults were common (Fig. 4C–D). Red-rotten wood (Fig. 4C, E) was repeatedly found to be a preferred substrate, as for the larvae of the closely related *Pyropterus nigroruber*. Larvae of different ages aggregating in a group were found as has been observed in other lycids (Bocak & Matsuda 2003).

Gomezzuritus longicornis (Reiche, 1878) comb. nov.

Fig. 1D

Eros longicornis – Reiche 1878: XXVII.

Dictyopterus longicornis – Bourgeois 1882: 73.

Dictyoptera longicornis – Kleine 1942: 49.

Pyropterus schelkovnikovi – Barovskij 1930: 615.

Benibotarus schelkovnikovi – Bocak & Bocakova 1987: 115.

Benibotarus longicornis – Bocak & Bocakova 1987: 115. — Kazantsev 1995: 38. — Kazantsev 2012a: 389.

Material examined

GEORGIA • ♂ (holotype of *E. longicornis*); Adjaria, Batumi (no further data); MNHP • 1 ♂ (*Pyropterus schelkovnikovi* typ. un.' [Barovskij's manuscript label: "Holotype of *P. schelkovnikovi*"]); Caucasus, Distr. Gori, Bakuriani; alt. 2000 m; 20 Jul. 1912; M. Kozlovskij leg.; ZIN • 1 ♂; Abkhasia, Sukhumi, Mt. Bograt, park Vira; 3 Dec. 1931; B. Rohdendorf leg.; ICM.

RUSSIA • 3 larvae; NW Caucasus, Adygeya, Guzeripl, env. Mt Filimonova; alt. 1200 m; 43.9981° N, 40.1695° E; 15 Jun. 2007; A. Zaitsev leg.; under the bark of a dead tree; ICM.

Remarks

The species is closely related to *G. alternatus* and transferred to *Gomezzuritus*. The earlier described larva of this species (Kazantsev & Zaitsev 2021) was collected in Northwestern Caucasus, where no other dictyopterine taxa occur. Its similarity with *G. alternatus* confirms the relationships of these species.



Fig. 4. *Gomezzuritus alternatus* (Fairmaire, 1856). **A, D.** Adults in nature, Spain, Asturias, Las Agüeras, 35 km SW of Oviedo. **B.** Adults in nature, Spain, Las Agüeras. **C, E.** Larva 3rd instar in nature, Caranga de Abajo. **F.** Spain, Caranga de Abajo, habitat with common occurrence of *G. alternatus* (Fairmaire, 1856) comb. nov. Photographs: M. Motyke (A, D); L. Bocak (B–C, E–F).

Gomezzuritus rubripes (Pic, 1897) comb. nov.

Fig. 1E

Eros (Pyropterus) rubripes – Pic 1897: 220.

Pyropterus rubripes Pic – Kleine 1933: 38.

Remark

Pyropterus rubripes is transferred from *Pyropterus* to *Gomezzuritus* based on morphological similarity.

Material examined

ALGERIA • 1 ♀ (lectotype of *E. rubripes*); Forêt des Beni Ghorbi; Jun. 1897; MNHP.

MOROCCO • 1 ♂; Rif Mts, Bab-Berret–Ketama road; alt. 1600 m; 34.933° N, 04.6001° W; 1 May 2002; J. Kalab leg.; *Cedrus* forest; first record from Morocco; ICM.

Discussion

The classification of net-winged beetles has recently been intensively studied and substantially modified based on morphology, ribosomal, mitochondrial, and genomic data (Kazantsev 2004, 2005, 2012b; Bocak & Bocakova 2008; Kusy *et al.* 2019; Motyka *et al.* 2021). Dictyopterini is now a part of Erotinae that contains ~120 described species in the Holarctic region. Therefore, the western Palaearctic fauna must be studied in the context of the whole Northern Hemisphere. The recent molecular phylogeny included ~30 of 68 described species of Dictyopterini and suggested a deep rooting of the branch containing the here described *Gomezzuritus* gen. nov. (Fig. 1A; Motyka *et al.* in press). The genus is one of the early splits inferred for European species. Other deeply rooted western Palaearctic species are *Platycis minuta* (Thomson, 1764), *Dictyoptera aurora* (Herbst, 1784), and *Pyropterus nigroruber* (De Geer, 1774). The deep splits in the tree were well-supported, and most genera and species in the analysis were placed in full agreement with their morphological traits and earlier recovered relationships (Fig. 1A; Kazantsev 2004; Motyka *et al.* in press). As such, also the pyropterine clade is proposed in agreement with previous studies that suggested the relationships of *Pyropterus*, *Helcophorus*, and *Benibotarus* (Kazantsev 2004). However, the robustness of the molecular tree stands in contrast with affinities suggested by the arrangement of elytral costae in respective genera.

The common name ‘net-winged beetles’ refers to the presence of costae in the elytra and they are so characteristic that they misled some paleoentomologists into describing a Burmese amber tenebrionoid in the Lycidae (Molino-Olmedo *et al.* 2020; Bocak *et al.* 2022). The elytral cells are formed by longitudinal and transverse costae (Fig. 2D; Bocak & Bocakova 1987; Kazantsev 2004, 2005). Although some groups may have only longitudinal costae (e.g., Macrolycini, Lyropaeini, and Lycini; Kazantsev, 2005; Kusy *et al.* 2021), all dictyopterines have both. The longitudinal costae are regularly differentiated into four robust ones, called primary costae, and five weaker ones called secondary costae. All costae can be shortened, sometimes the secondary costae are absent, or their negligible vestiges are restricted to the humeri, eventually, the strength of all costae can be subequal. There are two different costal patterns present in the pyropterine clade: four full-length costae (*Pyropterus*, *Helcophorus*) and three primary costae, and four secondary costae in the middle of the elytron (i.e., the shortened costa 3; *Benibotarus*, *Greenarus*, *Gomezzuritus*). The most parsimonious explanation for the observed pattern is a common ancestor of *Helcophorus* and *Pyropterus* and a common ancestor of the remaining genera. However, molecular analyses point to an independent origin of three costae in *Gomezzuritus* and *Benibotarus* (Fig. 1A). Therefore, we looked for morphological traits that would support such non-parsimonious evolution. We found out that *Helcophorus* and *Gomezzuritus* are noticeably slenderer than *Benibotarus* and differ from it also in the erect antennal pubescence of males (these characters had never been

considered of any importance and used for taxonomic purposes before). Otherwise, in terms of external morphology, the two clades are almost identical.

We can speculate about the reasons for the observed incongruence between morphology and molecular relationships. First, it is known that the modern western Palaearctic fauna is a small remnant of the thriving fauna of warm and humid Europe in the Paleocene and Eocene (Greenwood & Wing 1995; Zachos *et al.* 2001; Bocek *et al.* 2018; Motyka *et al.* in press). The number of net-winged beetles reported from Baltic and Rovno amber deposits is continually growing, and it has been shown that the elytral costae were variably arranged already in the Eocene net-winged beetles (Kleine 1940; Winkler 1987; Kazantsev 2013, 2019; Kazantsev & Perkovsky, 2022; Kazantsev & Bocak 2022). Now, the number of known fossils from Eocene amber surpasses the species richness of modern fauna in the region. High diversity and a long time increase the probability of the independent origin of similar structures as seen in the repeated origin of the shortened primary costa 1 in the hyperdiverse Metriorrhynchini (*Leptotrichalus* Kleine versus the genera of the trichaline clade; Sklenarova *et al.* 2014; Bocek & Bocak 2017; Motyka *et al.* 2021). Analogically, costa 3 can be shortened in some stenopterous lycids (Kazantsev 2020; Kusy *et al.* 2022). The costae of net-winged beetles are more apparent than in related elateroid families and very probably evolved as a strengthening structure in a soft-bodied group from rows of cells in well-sclerotized relatives, such as Artematopodidae, some Eucnemidae, and Elateridae (McKenna *et al.* 2019). A similar structure of the elytra was found also in some extinct groups of Cantharidae and other soft-bodied elateroids (Hsiao *et al.* 2021; Fanti & Pankowski 2020). Therefore, we may suggest that as some species become slender-bodied, the changes in the shape of the body might have led to the loss of some costae. A similar loss of costae is known for example in very slender *Leptotrichalus* Kleine, 1925, and in slender *Dilophotes* Waterhouse, 1879 (Motyka *et al.* 2018). Yet, other lineages although having the shortened costae retain a robust body, e.g., *Diatrichalus* Kleine, 1926 (Bocek & Bocak 2017).

We can conclude that phylogenetic research greatly benefits from the availability of molecular data that can indicate parallel evolution in cases when morphology alone cannot provide strong evidence as different traits can indicate contradicting relationships (Ranasinghe *et al.* 2022). We mostly study the modern species representing terminal branches that are a result of long evolution under different conditions. Especially in such groups as dictyopterine net-winged beetles that were severely impoverished due to aridification and cooling of the Western Palaearctic region (Hewitt 2000, Svenning 2003, Bocek *et al.* 2018), what remains is only a fraction of lost diversity. We cannot expect that even intensive paleontological research will provide complete information on the extinct Cenozoic European fauna, but the integration of comparative morphology, molecular phylogenetics, and paleoentomology improves our understanding of morphological evolution.

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