



The *Idioptera-Eloeophila* complex (Diptera: Limoniidae): a phylogenetic solution to an old taxonomic misunderstanding

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Abstract

Eloeophila Rondani, 1856 and *Idioptera* Macquart, 1834 are two genera of the family Limoniidae (Diptera) distinguished by the presence of a supernumerary cross-vein m-cu. Although these genera were previously combined, there has been a lack of phylogenetic tests to investigate the evolutionary relationship between them. In this study, we conducted a cladistic analysis that indicates that *Idioptera* form a clade within *Eloeophila*, and therefore the two genera should be synonymized under *Idioptera*. Consequently, 87 species of *Eloeophila* are transferred to *Idioptera*.

Keywords

Cranefly, Limnophilinae, morphology, syn. nov., Tipulomorpha

1. Introduction

Eloeophila Rondani, 1856 is a genus of the family Limoniidae (subfamily Limnophilinae) that currently comprises 84 extant and three fossil recognized species (Oosterbroek 2023). The distribution of this genus encompasses the Nearctic, Palearctic, Afrotropical and Oriental regions (Oosterbroek 2023). Although displaying considerable extant diversity, the fossil record of this genus is limited to the Eocene period, with only three fossil species described (Santos et al. 2022).

The taxonomic history of *Eloeophila* is complex. Initially, it was regarded as a subgenus of *Limnophila* Macquart until Savchenko and Krivolutskaya (1976) argued

for its removal from *Limnophila*. They advocated for its recognition as a distinct genus. Recently, there has been renewed interest in this genus, resulting in new species descriptions and revisions (Stary 2009; Podenas et al. 2020; Kato 2021; Santos et al. 2022).

Despite the abundance of species within the group, the structure of male terminalia remains relatively uniform (Stary 2009). Of course there are enough differences between species and in other structures in the genus, but there are a lot of resemblances in a wider scope. Some *Eloeophila* species exhibit distinguishable wing spots and markings that have been documented over time, but their

interspecific variability remains uncertain. Consequently, this has led to synonyms and a complex taxonomic history throughout the centuries. The only phylogenetic study that has addressed the placement of *Eloeophila* was conducted by Ribeiro (2008), which proposed a close relationship between *Eloeophila* and *Idioptera* Macquart, 1834.

Idioptera is a Holarctic genus that consists of only five extant species, which are characterized by banded wings. Macquart's (1834) description of *Idioptera* partially overlaps with that of *Eloeophila*, two genera of the family Limoniidae (Diptera) distinguished by the presence of a supernumerary cross-vein m-cu (Fig. 3). The challenge of distinguishing between these two genera has been evident since the early investigations. Edwards (1921) suggested merging the two genera into one. However, he did not explicitly address the priority of the name *Idioptera* over *Eloeophila*, and attributed several species classified under *Eloeophila* to *Idioptera* (e.g. *E. apicata* (Loew), *E. verralli* (Bergroth), *E. maculata* (Meigen) and *E. munda* (Loew)). Subsequently, Edwards (1938) once again separated both *Idioptera* and *Eloeophila* and treated them as subgenera of *Limnophila* sensu lato.

The aim of this study is to investigate the phylogenetic relationships between the species currently classified under *Eloeophila* and *Idioptera*. This research will contribute to a deeper understanding of the classification and taxonomy within this group. Our objective is not to provide a comprehensive redescription of every species within the genus but to present a phylogenetic hypothesis that encompasses a broader scope, indicating relationships among the main lineages of *Idioptera* and *Eloeophila*. Every analysis is inherently partial, and we made specific choices to facilitate a discussion of the primary divergences and their evolutionary history. This is not the "final solution" but rather the foundational step for future investigations. Our primary goal is to establish a broad contextual understanding of this complex of species.

2. Material and methods

2.1. Terminology and abbreviations

Descriptive terminology follows Cumming and Wood (2017). Wing vein nomenclature follows the interpretation of de Jong (2017), while the homology of male terminalia follows Ribeiro (2006). Abbreviations used in the figures are as follows: **A**, anal vein; **aed**, aedeagus; **b**, bulge of gonocoxite; **bM**, basal medial vein; **cg**, clasper of gonostylus; **CuA**, anterior cubital vein; **CuP**, posterior cubital vein; **cv**, supernumerary cross-vein; **d**, discal cell; **gx**, gonocoxite; **h**, humeral vein; **ib**, interbases of the aedeagal complex; **lg**, lobe of gonostylus; **M**, medial vein; **pm**, parameres; **R**, radial vein; **Rs**, radial sector veins; **Sc**, subcostal vein; **t9**, ninth abdominal tergite.

2.2. Sampling and taxonomy

Specimens examined for the comparative study are listed in Table S1. We thoroughly reviewed all taxonomic descriptions available in the literature regarding the *Idioptera-Eloeophila* complex. Many of the descriptions used are very informative, at least for the main morphological wing features. The taxonomic literature of the group includes some recent revisions and has a substantial collection of photos and recent illustrations, which provide a wealth of information on the morphology of the species, which could be successfully used in our comparative study.

We analyzed all available images, revisions and descriptions. While we directly observed only a few specimens, our examination encompassed every published information within these genera. We selected at least one species of each morphological unit taking in mind the diversity of places, number of available material, problematic and contested taxa, and revised species. Our sampling was a balanced expression of the morphological diversity avoiding redundancy (observed previous and posterior the phylogenetic analysis). Guided by this comprehensive review, we selected species that serve as representatives of the spectrum of variation.

As discussed posteriorly, most species, especially those related to or grouped around *E. maculata* (Meigen, 1804), exhibit a relatively homogeneous morphology. Including a large number of these similar species in our taxonomic sample would result only in redundant information. Therefore, we directed our focus towards more diverse and heterogeneous groups of species. We are confident that our data matrix provides a comprehensive representation of the morphological variation within our study group.

Outgroup taxa for this study consisted of species from the genera *Eupilaria* Alexander, 1932, *Phylidorea* Bigot, 1854 and *Euphylidorea* Alexander, 1972, with the root placed at *Eupilaria phoenosoma* (Alexander, 1931). The selection of outgroups was based on a previous study by Ribeiro (2008), which included a substantial sample of Limnophilinae lineages and genera with affinities with *Eloeophila*.

2.3. Phylogenetic analysis

The phylogenetic analysis was conducted based on the principle of parsimony. For character scoring, missing scoring of a character for a taxon was entered as '?' and inapplicability of a character to a taxon as '-'. The most parsimonious trees were obtained using both Equal Weights (EW) and Implied Weighting (IW) methods (Goloboff 1993). IW analysis involved combining various values of k (ranging from 2 to 6). Heuristic searches were conducted using tree-bisection reconnection (TBR) branch swapping, with 10,000 replicates and holding up to 100 trees for each replication. All characters were treated as unordered. The analyses were performed using

TNT (Goloboff et al. 2016), and the rooting was conducted following the outgroup method as revised by Nixon and Carpenter (1993). The characters used are defined and listed in the following (the number of steps for each character, for $k=3$, is shown within square brackets). The data matrix with 25 terminal taxa and 73 characters is presented in Table S2.

0. **Length of antenna:** 0 – shorter than combined length of head and thorax; 1 – longer than combined length of head and thorax. [4]
1. **Shape of wing:** 0 – middle of wing straight; 1 – middle of wing dilated (Fig. 6b). [1]
2. **Wing, spur at base of Rs:** 0 – absent; 1 – present (Fig. 5a). [5]
3. **Wing, Rs inclination:** 0 – straight or slightly inclined; 1 – inclined downwards (Fig. 4a). [1]
4. **Wing, tip of R_1 :** 0 – straight; 1 – curved (Fig. 4b). [1]
5. **Wing, length of distal section of R_1 (distal to point of contact with R_2):** 0 – shorter than twice length of R_2 ; 1 – longer than twice length of R_2 . [1]
6. **Wing, length of R_{2+3+4} :** 0 – longer than R_{2+3} ; 1 – shorter than or equal to R_{2+3} . [3]
7. **Wing, direction of tips of R_3 and R_4 :** 0 – parallel; 1 – divergent. [1]
8. **Wing, shape of R_4 :** 0 – straight; 1 – curved. [1]
9. **Wing, M_{1+2} :** 0 – unbranched; 1 – branched. [1]
10. **Wing, length of section of M_{1+2} distal to point of connection with m-m (distal M_{1+2}):** 0 – shorter than twice length of M_2 ; 1 – longer than twice length of M_2 . [1]
11. **Wing, tip of M_2 :** 0 – straight; 1 – curved downwards. [1]
12. **Wing, tip of M_4 :** 0 – curved downwards; 1 – straight. [2]
13. **Wing, length of discal cell:** 0 – at least 3 times longer than wide; 1 – shorter than 3 times longer than wide. [3]
14. **Wing, length of m-m:** 0 – shorter than half length of basal deflection of M_3 ; 1 – longer than half length of basal deflection of M_3 . [5]
15. **Wing, distance between tips of M_2 and M_3 :** (0) shorter than distance between tips of M_3 and M_4 ; (1) longer than distance between tips of M_3 and M_4 . [1]
16. **Wing, supernumerary m-cu:** 0 – absent; 1 – present. [1]
17. **Wing, insertion of supernumerary m-cu:** 0 – distal to level of origin of Rs; 1 – proximal to level of origin of Rs. [1]
18. **Wing, tip of anal vein:** 0 – straight or slightly arched; 1 – strongly arched (Fig. 5b). [1]
19. **Wing, spur in tip of A:** 0 – absent; 1 – present (Fig. 6b). [1]
20. **Wing, origin of C thinning:** 0 – between veins R_3 and R_4 ; 1 – between veins R_4 and R_5 . [1]
21. **Wing, marking on base of wing:** 0 – absent; 1 – present (Fig. 5a). [1]
22. **Wing, marking around sc-r:** 0 – absent; 1 – present (Fig. 3a). [1]
23. **Wing, marking on tip of Sc:** 0 – absent; 1 – present (Fig. 5b). [1]
24. **Wing, marking around humeral vein:** 0 – absent; 1 – present (Fig. 3a). [1]
25. **Wing, marking on distal margin of arculus:** 0 – absent; 1 – present (Fig. 4a). [1]
26. **Wing, marking between humeral vein and origin of Rs:** 0 – absent; 1 – present (Fig. 4a). [1]
27. **Wing, marking on base of Rs:** 0 – absent; 1 – present (Fig. 2b). [1]
28. **Wing, marking on tip of R_3 :** 0 – absent; 1 – present (Fig. 2b). [1]
29. **Wing, marking on tip of R_4 :** 0 – absent; 1 – present (Fig. 4a). [1]
30. **Wing, marking around basal deflection of R_5 :** 0 – absent; 1 – present (Fig. 2b). [1]
31. **Wing, size of marking around basal deflection of R_5 :** 0 – not surpassing r-m; 1 – reaching fork of bM (Fig. 5b). [1]
32. **Wing, marking on tip of R_5 :** 0 – absent; 1 – present (Fig. 6b). [1]
33. **Wing, marking on tips of medial and cubital veins:** 0 – absent; 1 – present (Fig. 5b). [1]
34. **Wing, marking on distal side of discal cell:** 0 – absent; 1 – present (Fig. 5b). [1]
35. **Wing, marking around m-cu:** 0 – absent; 1 – present (Fig. 2b). [1]
36. **Wing, connection of marking around m-cu with marking around medial fork and r-m:** 0 – not connected; 1 – connected (Fig. 6b). [1]
37. **Wing, marking on base of CuA:** 0 – absent; 1 – present (Fig. 5b). [1]
38. **Wing, double marking on anal vein:** 0 – absent; 1 – present (Fig. 5a). [1]
39. **Wing, distance between two anal vein markings:** 0 – close to each other, i.e. on same part of anal vein (Fig. 5a); 1 – far from each other, i.e. on different parts of anal vein such as one at base and one near end (Fig. 6a); 2 – fused (Fig. 5b). [1]
40. **Wing, marking on anal lobe:** 0 – absent; 1 – present (Fig. 6b). [2]
41. **Wing, patch connecting pterostigma with marking around basal deflection of R_5 :** 0 – absent; 1 – present (Fig. 6a). [1]
42. **Wing, patch connecting marking around sc-r with marking at basal deflection of R_5 :** 0 – absent; 1 – present (Fig. 6b). [1]
43. **Wing, patch connecting marking around m-cu with marking at tip of CuA:** 0 – absent; 1 – present (Fig. 6a). [2]
44. **Wing, patch connecting marking around m-cu with marking at tip of CuP:** 0 – absent; 1 – present (Fig. 6a). [1]
45. **Wing, patch connecting marking around humeral vein with marking at base of CuA:** 0 – absent; 1 – present (Fig. 6b). [1]
46. **Wing, color of patches:** 0 – uniformly dark; 1 – with a light core and a dark frame (Fig. 6a). [1]
47. **Wing, spots:** 0 – absent; 1 – present (Fig. 6b). [1]

48. **Bulge in base of gonocoxite:** 0 – absent; 1 – present (Fig. 7b). [1]
49. **Border of margin of bulge in base of gonocoxite:** 0 – smooth; 1 – serrated (Fig. 7b). [1]
50. **Distal bulge in gonocoxite:** 0 – absent; 1 – present (Fig. 7d). [2]
51. **Shape of clasper of gonostylus:** 0 – straight; 1 – curved (Fig. 9h). [1]
52. **Width of clasper of gonostylus:** 0 – flattened (Fig. 9d); 1 – rounded and thick (Fig. 9c). [1]
53. **Dorsal hump on base of clasper of gonostylus:** 0 – absent; 1 – present (Fig. 9e). [1]
54. **Ventral margin of clasper of gonostylus:** 0 – straight (Fig. 9b); 1 – pointed medially (Fig. 9j). [1]
55. **Distal end of clasper of gonostylus:** 0 – bifurcated in two teeth (Fig. 9c); 1 – non-bifurcated (Fig. 9h). [3]
56. **Distance between teeth of clasper of gonostylus:** 0 – close to each other (Fig. 9j); 1 – widely separated (Fig. 9c). [1]
57. **Length of ventral tooth of clasper of gonostylus:** 0 – shorter than or similar to dorsal tooth (Fig. 9j); 1 – much longer than dorsal tooth (Fig. 9c). [1]
58. **Margin between teeth of clasper of gonostylus:** 0 – smooth (Fig. 9g); 1 – serrated (Fig. 9c). [1]
59. **Anterior margin of clasper of gonostylus:** 0 – smooth (Fig. 9a); 1 – serrated (Fig. 9b). [4]
60. **Crest on anterior margin of clasper of gonostylus:** 0 – absent; 1 – present (Fig. 9h). [1]
61. **Pointed spur on crest of gonostylus:** 0 – absent; 1 – present (Fig. 9e). [1]
62. **Orientation of dorsal tooth of clasper of gonostylus:** 0 – straight (Fig. 9a); 1 – bent (Fig. 9i). [1]
63. **Connection of interbases of the aedeagal complex:** 0 – fused (Fig. 6a); 1 – non-fused (Fig. 7d). [2]
64. **Point of contact between interbases:** 0 – angulated (Fig. 7a); 1 – straight (Fig. 7d); 2 – curved (Fig. 8a). [2]
65. **Tip of distal branch of interbase:** 0 – straight (Fig. 7b); 1 – bent or curved (Fig. 8b). [3]
66. **Orientation of distal branch of interbases:** 0 – inclined (Fig. 7c); 1 – straight, i.e., parallel to aedeagus (Fig. 8c). [2]
67. **Ventral apodeme of parameres:** 0 – fused with sheath of aedeagus (Fig. 7a); 1 – detached from sheath of aedeagus (Fig. 7c). [1]
68. **Orientation of ventral apodeme of parameres:** 0 – pointing laterally (Fig. 7b); 1 – pointing medially (Fig. 8b); 2 – pointing anteriorly. [2]
69. **Long lateral branches of sheath of aedeagus:** 0 – absent; 1 – present. [1]
70. **Lower shelf (sheath of aedeagus):** 0 – not developed; 1 – developed (Fig. 8b). [1]
71. **Humps of lower shelf:** 0 – absent; 1 – present (Fig. 8d). [1]
72. **Median projection of lower shelf:** 0 – absent; 1 – present (Fig. 8d). [1]

3. Phylogenetic results

The parsimony analysis with implied weights resulted in a single most parsimonious tree, as shown in Fig. 1. This tree maintains the same topology across all the k values. The analysis with equal weights resulted in two most parsimonious trees of 106 steps, with a Consistency Index (CI) of 0.71 and Retention Index (RI) of 0.91. The consensus of both hypotheses only collapses outgroup structure. The synapomorphies of each clade, although not shown in Fig. 1, are listed within square brackets in the following discussion of each clade in a standardized format: [number of the character: plesiomorphic state – synapomorphic state]. Homoplastic characters are indicated by an asterisk (*). The figure with the primary tree indicating the homologies is shown in the Figure S1.

3.1. Outgroup taxa

In the phylogeny of Limnophilinae conducted by Ribeiro (2008), the clade *Eloeophila* + *Idioptera* was found to be related to *Eupilaria* and *Phylidorea*, primarily because of their blade-like interbases (Fig. 7). Other studies have shown that these genera are related (Edwards 1921; Podeniene 2004). Oosterbroek and Theowald (1991) found that *Euphylidorea* may be related to *Phylidorea* (Fig. 2b) and *Eloeophila*. However, the study of Ribeiro (2008) did not support this relationship. Despite this, these genera belong to a group of Limnophilinae that share some characteristics, such as a flattened gonostylus with constriction at the distal end and a rough and chitinized anterior margin of the gonostylus.

Ribeiro (2008) found that the genus *Eupilaria*, which is used here as an outgroup (Fig. 7a), is not monophyletic, similar to several other genera in Limnophilinae. However, a part of *Eupilaria*, along with *Idioptera*, forms a clade with *Eloeophila*. Our preliminary analysis reinforces that both *Euphylidorea* and *Phylidorea* may also be paraphyletic (Alexander 1942). For example, our analysis suggests that *Euphylidorea* (*Neophylidorea* Petersen) bears many similarities to *Phylidorea* (*Paraphylidorea* Savchenko) (Fig. 2a) as noted by Alexander (1972) and Petersen et al. (2012). According to Starý (2009), *Phylidorea*, *Idioptera* and *Eloeophila* have similar aedeagal complexes defined as “second order parameres”, but *Euphylidorea* may also be included (Fig. 7b).

3.2. Ingroup

Clade 1. Synapomorphies: [2*: 1-0]; [13: 0-1]; [16: 0-1]; [22: 0-1]; [23: 0-1]; [25: 0-1]; [64: 1-2]. — This clade comprises the species of the *Idioptera*-*Eloeophila* complex. Although the close relationship between the two genera has long been recognized, our analysis now reveals that *Idioptera* is nested within *Eloeophila*. From now on, all species previously classified as *Eloeophila* will be referred to in the text as assigned to *Idioptera*.

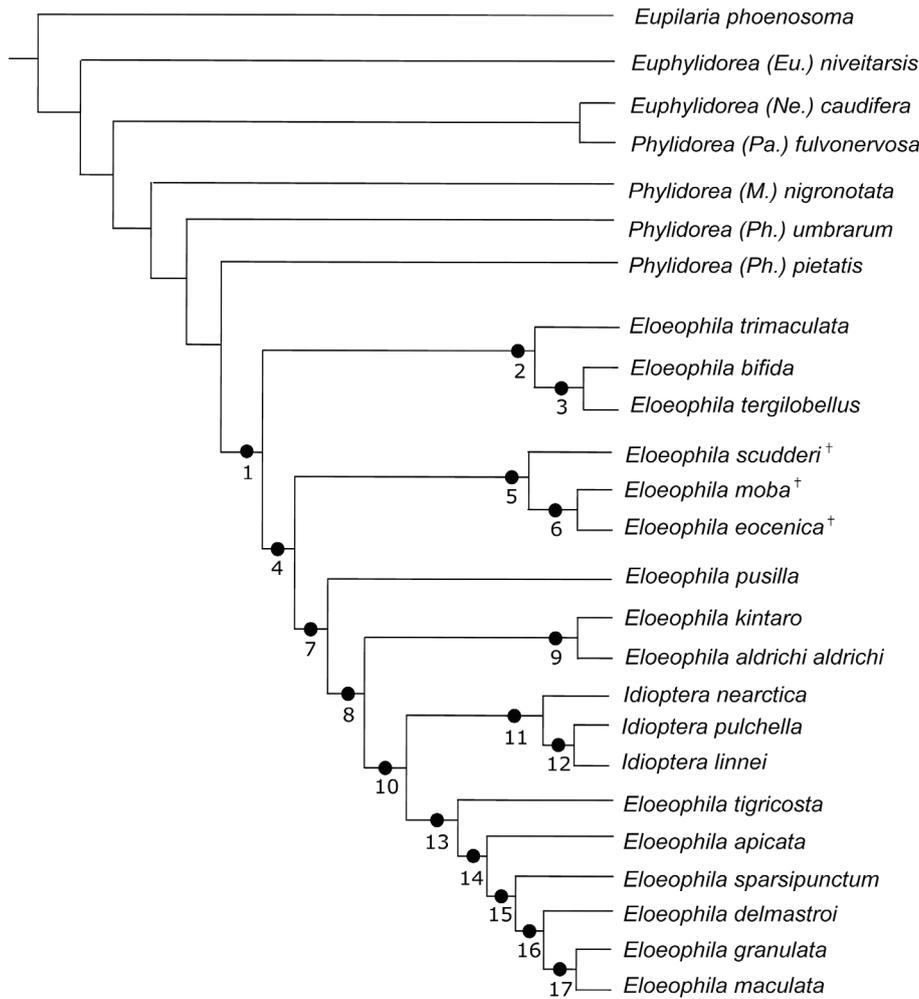


Figure 1. Phylogeny of the *Idioptera-Eloeophila* complex as yielded by all analyses. Names of species are as in their original genera. Extinct taxa are marked with a cross. The numbers indicated the clades.

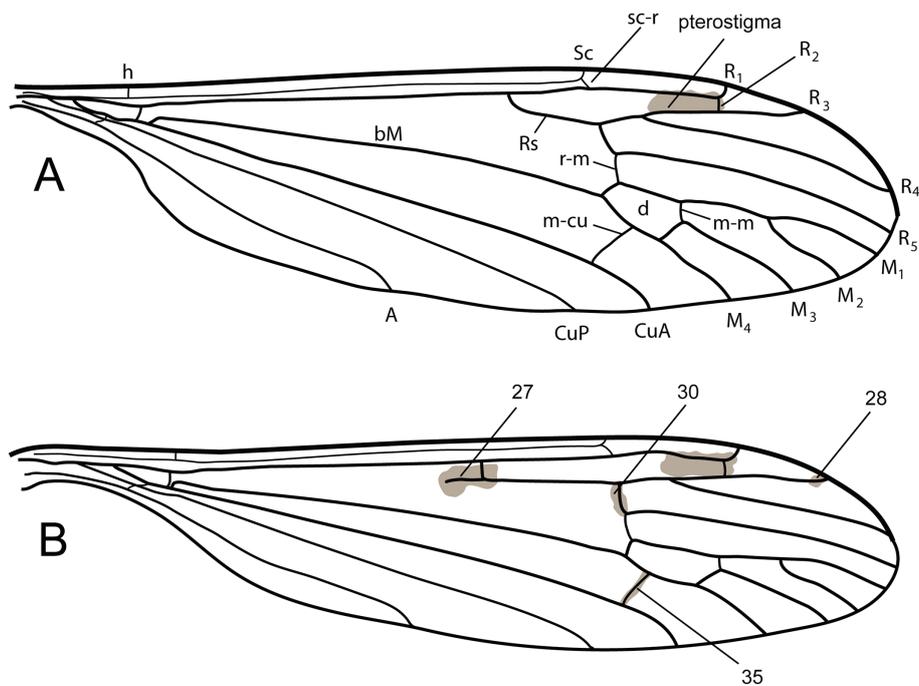


Figure 2. Wings of **a** *Phyllidorea (Paraphyllidorea) fulvonervosa* (Schummel), **b** *Phyllidorea (Phyllidorea) longicornis pietatis* (Alexander). Abbreviations: A = anal vein; bM = basal medial vein; CuA = anterior cubital vein; CuP = posterior cubital vein; d = discal cell; h = humeral vein; M = medial vein; R = radial vein; Rs = radial sector veins; Sc = subcostal vein.

This clade is distinguished mainly by a supernumerary m-cu [16: 0-1] (Fig. 3a). Edwards (1938) argued that the supernumerary cross-vein may be evanescent, disappearing in certain wings or even in both wings in some

Idioptera specimens. Alexander (1948) noted that one specimen of *I. angustior* (Alexander, 1919) **comb. nov.** lacks the supernumerary m-cu in both wings. Species of unrelated genera such as the pediicid *Nasiternella* Wahl-

gren show a similar cross-vein, which is obviously of independent origin. Despite these exceptions, this feature is remarkable in the clade.

Apart from this supernumerary m-cu, this clade is supported by additional synapomorphies, including the lack of a spur at the base of vein Rs [2: 1-0]. However, this feature is highly homoplastic in Limnophilinae (Ribeiro 2008). *Idioptera* wings have a short discal cell [13: 0-1], although this character is reversed in Clade 11. Also, there is a new set of markings for this clade, one each around sc-r [22: 0-1] (Fig. 3a), around the humeral vein [24: 0-1] (Fig. 3a), and on distal margin of the arculus [25: 0-1] (Fig. 4a). We have found one synapomorphy related to the male terminalia: a curved contact between interbases [64: 1-2] (Fig. 8a). Ribeiro (2008) supported the monophyly of the clade *Eloeophila* + *Idioptera* based primarily on the lack of well-developed lateral processes of the aedeagal sheath.

Clade 2. Synapomorphies: [15: 0-1]; [52: 0-1]; [56: 0-1]; [58: 0-1]; [59*: 0-1]; [65*: 0-1]. — Three species of our sample are grouped within this clade: *I. trimaculata* (Zetterstedt, 1838) **comb. nov.**, *I. bifida* (Alexander, 1921) **comb. nov.**, and *I. tergilobellus* (Kato, 2021) **comb. nov.** Contrary to other species of *Idioptera*, the species of this clade have a gonostylus not laterally flattened [52: 0-1] (Fig. 9b-c). Another notable feature of this clade is the longer distance between the teeth of the clasper of the gonostylus [56: 0-1]. When the gonostylus is forked, the teeth are often close to each other. However, in Clade 2 they are distant from each other, even if the teeth remain short, such as in *I. trimaculata* **comb. nov.**

Furthermore, members of this clade have the clasper with serrated margins, such as the anterior margin [59: 0-1] (Fig. 9b), which is homoplastic in Clade 13 and *P. (Paraphylidorea)*. Another serrated section is the margin between the teeth of the clasper of the gonostylus [58: 0-1] (Fig. 9c). The distal bulge of the gonocoxite is more centralized in species of this clade, although it is unclear in *I. bifida* **comb. nov.** This clade is also supported by an-

other homoplastic feature: bent dorsal branch of the interbase [65: 0-1] which is also present in Clade 9 and Clade 13. The base of the clasper of the gonostylus also has a distinctive membrane with a different texture. However, it is difficult to observe this in *I. bifida* **comb. nov.**, and it may be a potential target for new morphological studies. The wings of the species in this clade have very similar markings and another synapomorphy: the distance between the tips of M_2 and M_3 is longer than the distance between the tips of M_3 and M_4 [15: 0-1].

Idioptera trimaculata **comb. nov.** (Figs. 3b; 9b) was frequently referred to as distinct from other species of the genus. Edwards (1938) highlighted the long antennae, different venation, and reduced spots (Fig. 3b). Despite sharing features with the original *Idioptera* (Clade 11), Edwards (1938) placed this species in the genus *Eloeophila*. Starý (2009) also pointed out that *I. trimaculata* **comb. nov.** is an exceptional species of the genus, differing from the others. However, Ribeiro (2008) supported the monophyly of the genus *Eloeophila*, including *I. trimaculata* **comb. nov.**, but excluding other *Idioptera* species. *Idioptera trimaculata* **comb. nov.** differs from the other two species of this clade mainly by the short teeth of the clasper and with a more serrated margin between them, and by having non-fused interbases.

Clade 3. Synapomorphies: [57: 0-1]; [63*: 1-0]. — This clade, which includes *I. bifida* **comb. nov.** and *I. tergilobellus* **comb. nov.**, is sustained by a distinctive clasper of the gonostylus with a ventral tooth much longer than the dorsal tooth [57: 0-1] (Fig. 9c). A significant difference between the two species of the clade is the short lobe of the gonostylus of *I. tergilobellus* **comb. nov.** Although the wing of these species appear to be unmarked, there remains some markings (Fig. 3a). *Idioptera tergilobellus* **comb. nov.** has interbases fused [63: 1-0]. *Idioptera bifida* **comb. nov.** appears to have similar interbases. Both species have a dilated distal bulge on the gonocoxite, as well as a nearly subterminal gonostylus. The most noticeable feature shared between these species is the presence

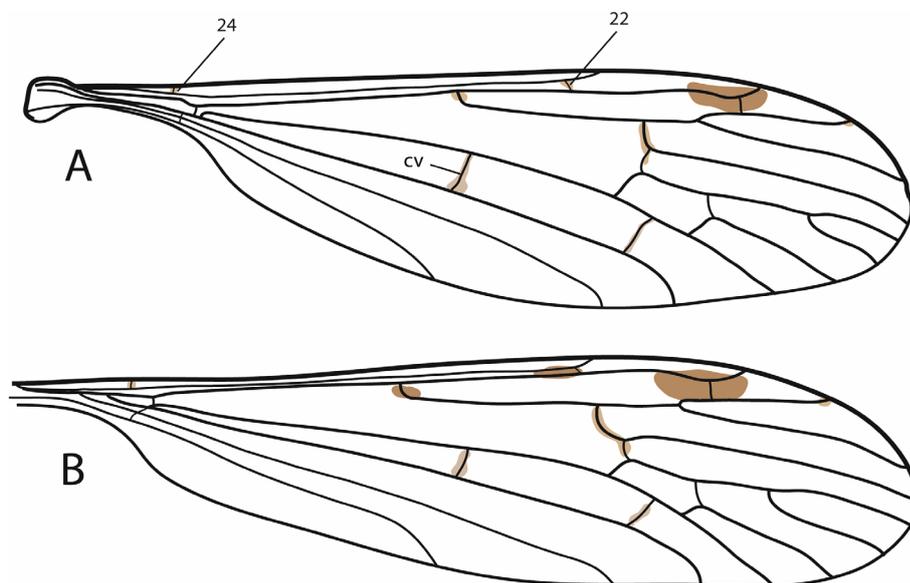


Figure 3. Wings of a *Idioptera tergilobellus* (Kato) **comb. nov.**, b *Idioptera trimaculata* (Zetterstedt) **comb. nov.** Abbreviation: cv = supernumerary cross-vein.

of dorsal extensions (paired lobes) on tergites, as evidenced in the description of *I. bifida* **comb. nov.** and in Kato (2021). The ninth tergite has a bifid central projection, with the more distal lobe being more evident in *I. bifida* **comb. nov.**

Clade 4. Synapomorphies: [0*: 1-0]; [18: 0-1]; [26: 0-1]; [29: 0-1]; [54: 0-1]. — This clade is supported by a set of seven markings on the wing. In an analysis of Palearctic *Eloeophila* species, Starý (2009) already highlighted the presence of “seven larger spots on the anterior margin of the wing”. This heptad pattern proposed by Edwards (1938) is composed of the following markings: around the humeral vein; between humeral vein and origin of Rs; on the base of Rs; around sc-r; pterostigma; on tip of R₃; on tip of R₄. Of the seven markings, six were already present. Only the marking between the humeral vein and origin of Rs [26: 0-1] (Fig. 4a) is a synapomorphy for this clade. These seven markings on the anterior margin of the wing are darker and larger, making them the most prominent. However, they may be weaker in certain extinct *Idioptera* such as *I. moba* (Podenas) **comb. nov.** and *I. eocenica* (Santos et al.) **comb. nov.**

The clade is also supported by the ventral margin of the clasper of the gonostylus pointed medially [54: 0-1] (Fig. 9j), and by two wing features: an arched tip of the anal vein [18: 0-1] and a marking at the tip of R₄ [29: 0-1] (Fig. 4a). This clade also has short antennae [0: 1-0], a reversal that also has changed in Clade 11. The size of the antennae is an important feature in identification keys and diagnoses. However, males have longer antennae compared to females in this genus. In species designated as having “long antenna”, as long as the length of the head and thorax combined, this feature is more evident in the males. The antennomeres of *Idioptera* have an almost rounded shape, but in some males, like in Clade 11, the oval flagellomeres are longer.

Sexual dimorphism is also present in the wing markings. Male wings may have stronger markings than female wings. This characteristic may lead to errors such as false new species based on “markless” wings. There is also variation in the color and intensity of the markings (Starý 2009), which requires a careful examination of designated synonyms. Many regional variations have been designated as subspecies or forms, and numerous species have been synonymized without thorough revision. Although not every variation is a distinct species, some defined species may consist of different lineages blended and amalgamated. While a comprehensive revision of the material is beyond the scope of this study, we acknowledge the necessity for such detailed examinations.

Clade 5. Synapomorphies: [3: 0-1]; [12: 0-1]; [14*: 1-0]. — This clade includes the extinct species of *Idioptera* (all from the Eocene). One species (*I. scudderi* (Santos et al.) **comb. nov.**) is from the Florissant Formation in Colorado, USA (Scudder 1894), and two species (*I. moba* and *I. trimaculata*) are from Baltic Amber. The clade is supported by the downward inclination of vein Rs [3: 0-1] (Fig. 4). The clade has two wing synapomorphies: a non-inclined tip of the vein M₄ [12: 0-1] and m-m shorter than half of the basal deflection of M₃ [14: 1-0]. The straight M₄ is a feature shared with an outgroup species, *Phylidorea* (*Macrolabina*) *nigronotata* (Siebke, 1870). The length of m-m is a more homoplastic character, with reversions outside the ingroup, such as in the outgroup species *Phylidorea* (*Phylidorea*) *pietatis* (Alexander, 1950), Clade 5, Clade 9, and *I. sparsipunctum* (Starý, 2009) **comb. nov.** Podenas (2003) highlighted that *I. moba* **comb. nov.** (Fig. 4b) is smaller than other *Idioptera*, measuring 6–7 mm. This species is similar in size to *I. eocenica* **comb. nov.** and *I. scudderi* (Santos et al.) **comb. nov.** (Fig. 4a). Podenas (2003) also stated that *I. moba* **comb. nov.** (Fig. 9a)

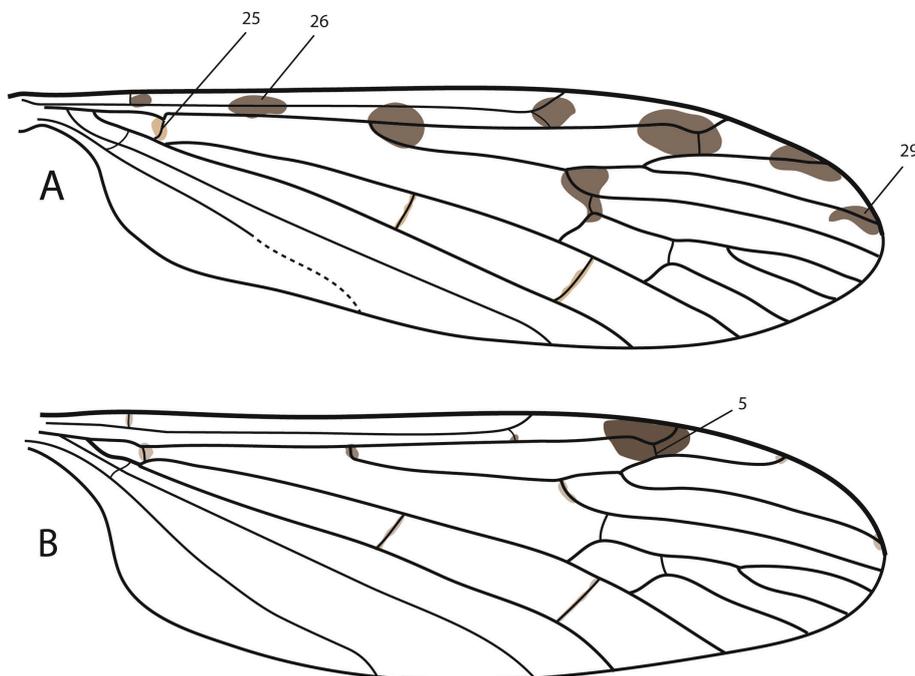


Figure 4. Wings of a *Idioptera scudderi* Santos et al. **comb. nov.**, b *Idioptera moba* Podenas **comb. nov.**

shares more terminalia features with *I. trimaculata* **comb. nov.** than with other *Idioptera*. However, these resemblances may be due to symplesiomorphies.

Finding synapomorphies related to the morphology of the male terminalia is complicated: only females of *I. eocenica* **comb. nov.** were found; the male terminalia of *I. scudderi* **comb. nov.** is unclear; and the aedeagal complex of *I. moba* **comb. nov.** is not completely shown. These three species were revised by Santos et al. (2022).

Clade 6. Synapomorphy: [5: 0-1]. — This clade groups *I. eocenica* **comb. nov.** with *I. moba* **comb. nov.**, both from Baltic Amber. Species in this clade are singletons, meaning they are only known from a single specimen each. The wings of these species have a tiny vein R_2 [5: 0-1]. The male terminalia of *I. moba* **comb. nov.** has an apomorphic ninth tergite with a convex middle tergite instead of the typical concavity. Starý (2009), however, stated that the shape of the ninth tergite is not precise and reliable for identifying subgroups in this genus. Unfortunately, there are no visible aedeagal structures such as parameres or interbases. Another problem in understanding the relationship between these species is that in *I. eocenica* **comb. nov.**, only the female was found, while for *I. moba* **comb. nov.**, only the male is known.

Podenas (2003) stated that wing of *I. moba* **comb. nov.** (Fig. 4b) resembles *I. trimaculata* **comb. nov.** but it is more due to plesiomorphies shared between them. Santos et al. (2022) highlighted the similarities among these Baltic Amber fossil species. Both species of Clade 6 have faint markings. Podenas (2003) only described the pterostigma for *I. moba* **comb. nov.**, although a thorough analysis may reveal the homologous markings (Fig. 4b). Other species of *Idioptera* have already been described as markless, such as *I. johnsoni* (Alexander, 1914) **comb. nov.** This highlights the importance of conducting a com-

prehensive analysis of the specimens to identify the subtle yet significant structures.

Clade 7. Synapomorphies: [2*: 0-1]; [21: 0-1]; [33: 0-1]; [34: 0-1]; [38: 0-1]; [60: 0-1]; [62*: 0-1]. — This clade is supported by a series of markings on the wing (Fig. 5a b). There is a marking on the distal portion of the discal cell [34: 0-1] (Fig. 5a) and a marking at the base of the wing [21: 0-1] (Fig. 5a). The marking at the base of the wing is most noticeable in certain *Idioptera* (Clade 11) because of the dark color of the wing markings in this clade. Furthermore, there are some small markings near the tips of the medial and cubital veins [33: 0-1]. These distal rounded markings are more easily distinguished in certain species, but they are consistently present in the clade. Sometimes the markings on the tips of M_1 and M_2 are so large that they may fuse with the markings on the tips of R_4 and R_5 . Another apomorphy in the wing is the presence of a double marking on the anal vein [38: 0-1] (Fig. 5a). The clade is also supported by the presence of a spur at the base of R_s [2: 0-1] (Fig. 5b) with a reversion in Clade 15.

The clade is also defined by features in the male terminalia. The most remarkable feature is the presence of a crest on the anterior margin of the clasper of the gonostylus [60: 0-1] (Fig. 9h). This crest may be highly developed (see Clade 9) or less visible due to a dorsal bend (Starý, 2009). The clasper of the gonostylus in this group is described as rectangular-shaped, flattened and blackened (Edwards 1938). Podenas et al. (2020) defined this as a “blade-shaped” clasper of gonostylus. The flattened shape is a plesiomorphy, but species of Clade 7 have a distinctively darkened rectangular clasper. The dorsal tooth of the clasper of gonostylus is bent downwards [62: 0-1] (Fig. 9d–j), which reinforces the rectangular shape of the clasper. At least, this clade lacks the distal bulge in the gonocoxite [50: 1-0], present in the outgroups.

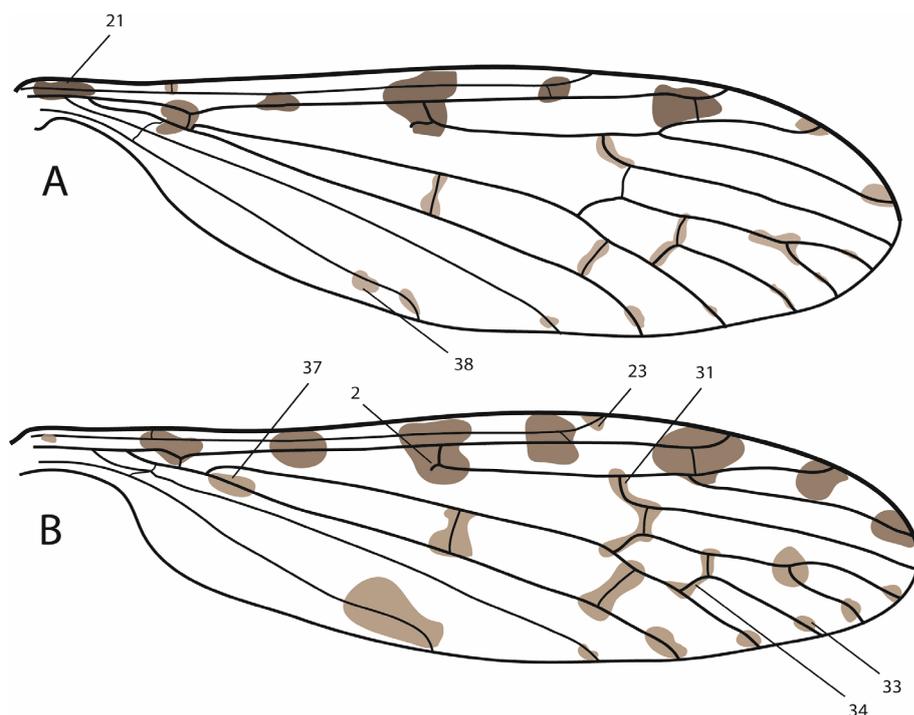


Figure 5. Wings of a *Idioptera pusilla* (Kuntze) **comb. nov.**, **b** *Idioptera aldrichi aldrichi* (Alexander) **comb. nov.**

A feature common in this clade is a great concentration of setulae on the tip of the wing. Alexander (1938) pointed out that species, such as *E. seticellula* (Alexander, 1938), may be different from other *Eloeophila*. This species lacks patches and a marking on R_5 but has a great concentration of wing setulae. He created a genus, *Trichephelia* Alexander, to cover this setose species. The presence of these setulae is sometimes hard to observe and delimit. Alexander (1957) stated that this feature is weak for diagnosis and posteriorly synonymized *Trichephelia* with *Eloeophila*. The presence of species with many setae in the wing was reinforced, for example, in the description and naming of *E. apicisetula* (Kato, 2021). Further analysis is needed to understand if the trichiation is a stable feature and if the group of species around *I. pusilla* **comb. nov.** in Clade 7 is equivalent to Alexander's *Trichephelia* genus. For now, we reinforce the synonym of *Trichephelia* under *Eloeophila*.

Clade 8. Synapomorphies: [20: 0-1]; [37: 0-1]; [53: 0-1]; [65*: 0-1]. — This clade is supported by two wing features: the thinning of vein C between veins R_4 and R_5 [20: 0-1], and a marking at the base of vein CuA [37: 0-1 (Fig. 5b)]. There are also two male terminalia features: a dorsal spur at the base of the clasper of the gonostylus [53: 0-1] (Fig. 9e), and the distal branches of the interbases parallel to the aedeagus [65: 0-1] (Fig. 8c). The straight branch of the interbase is also shared with *Eupilaria phoenosoma* (Fig. 7a) (outgroup). Despite being enlarged in some species, such as *I. nearctica* (Alexander, 1966), the dorsal branch retains a straight side, which may be notable for species in Clade 8.

Clade 9. Synapomorphies: [14*: 1-0]; [23: 0-1]; [54: 0-1]; [61: 0-1]; [65*: 0-1]. — This clade is defined by a

pointed spur in the crest of the clasper of the gonostylus [61: 0-1] (Fig. 9e). In the species of this clade, the crest is tall and extends into a spur. The size of this spur is variable, and it may only be visible by an elevation in the crest, as seen in *I. aldrichi* (Alexander, 1927) **comb. nov.**, or even as tall as the remainder of the clasper such as in *I. kintaro* (Alexander, 1957) **comb. nov.** (Fig. 9e). Also, the clade is supported by a bent tip of the dorsal branch of the interbase [65: 0-1], clasper non-bifurcated [54: 0-1], and a short m-m [14: 1-0]. An additional synapomorphy for this group is a marking at the tip of Sc, separate from the large marking around sc-r [23: 0-1] (Fig. 5b). Species in this clade also have a narrow wing stalk.

Clade 10. Synapomorphies: [32: 0-1]; [41: 0-1]. — This clade is supported by two wing markings: a marking near the tip of R_5 [32: 0-1] and a patch that connects the pterostigma with the marking around the basal deflection of R_5 [41: 0-1] (Fig. 6a-b). These connecting patches are not exclusive to this clade. Other craneflies, such as *Dicranophragma* (*Dicranophragma*) *perlutum* (Alexander, 1955), may exhibit a similar pattern. However, it is an apomorphy in the phylogenetic context of the genus.

Clade 11. Synapomorphies: [0*: 0-1]; [6*: 0-1]; [10*: 0-1]; [13: 1-0]; [17: 0-1]; [39*: 0-1]; [43*: 0-1]; [46: 0-1]; [51: 0-1]. — This clade includes the species that were originally included in *Idioptera*. The inclusion of *Idioptera* within *Eloeophila* makes the latter paraphyletic. The definition of the genus *Idioptera* has always been controversial. Macquart (1834) established this genus based on the simultaneous presence of long antennae and supernumerary m-cu. Further diagnosis for this genus includes features present in other groups: supernumerary m-cu (as in *Eloeophila*), gonostylus without a serrated

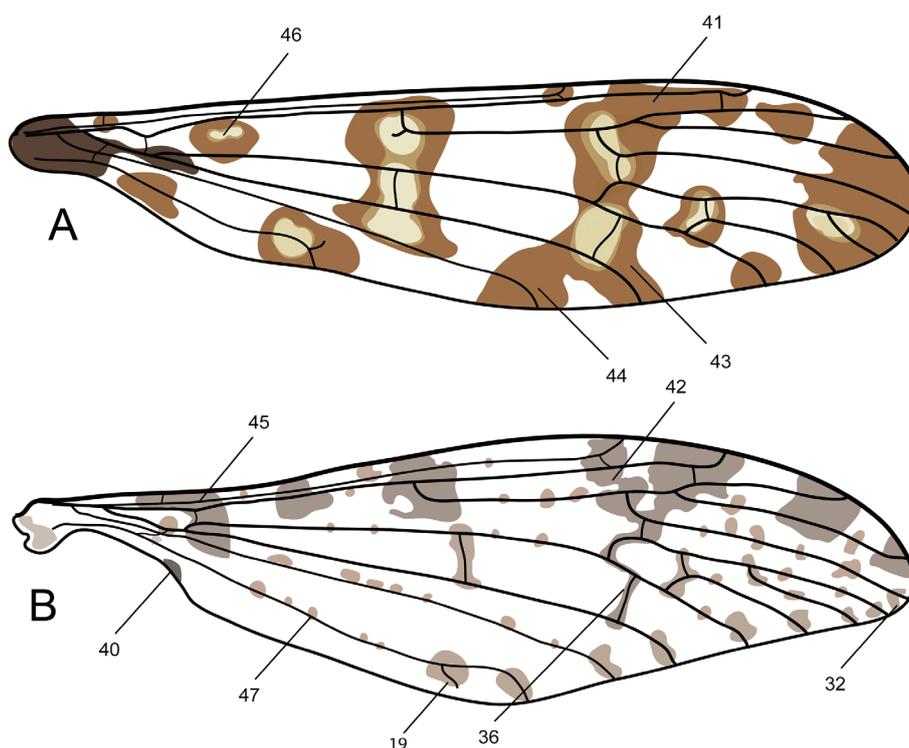


Figure 6. Wings of a *Idioptera pulchella* (Meigen), **b** *Idioptera maculata* (Meigen) **comb. nov.**

margin (as in *Phylidorea*), tip of R_1 up-curved (as in *Euphylidorea*), antenna slender (as in *I. trimaculata* **comb. nov.**), long discal cell (as in *Phylidorea*), and banded wings (as in *I. apicata* **comb. nov.**).

Edwards (1921) merged *Idioptera* with *Eloeophila*, but later (Edwards 1938) he redefined them as separated entities. The lack of a phylogenetic background for this group has obscured the true synapomorphies of this clade. Edwards (1938) argued that certain *Idioptera* species resemble *Phylidorea* in some aspects of the terminalia, the long discal cell and the long antenna. However, the supernumerary m-cu and wing markings are evidence of a concise *Idioptera*. The similarities between certain *Phyllidorea* species with the *Eloeophila* + *Idioptera* complex are also discussed by Alexander (1921).

Despite this, Clade 11 is strongly supported in our analysis, reinforcing the monophyly of the group that was originally named *Idioptera*. A recurring diagnostic feature

is the banded wings (Fig. 6a). This banded appearance is caused by the presence of large patches between the large markings. This group has an additional patch: one connecting the marking around m-cu with the marking at the tip of vein CuA [43: 0-1]. The banded appearance is reinforced by a distinctive feature. The wing patches of members of Clade 11 are enlarged and have a light core with a dark frame [46: 0-1]. The markings in this species of this clade are frequently larger than those in other groups, which supports the idea of a banded shape. These large transverse bicolor patches are very diagnostic for this group.

Two characters frequently observed as diagnostic features of this group are a long discal cell [13: 1-0] and a long antenna [0: 0-1]. They are considered as synapomorphies of this clade, although they may exhibit plasticity in *Idioptera*. Furthermore, this group is characterized in the wing by a supernumerary m-cu inserted proximal to the

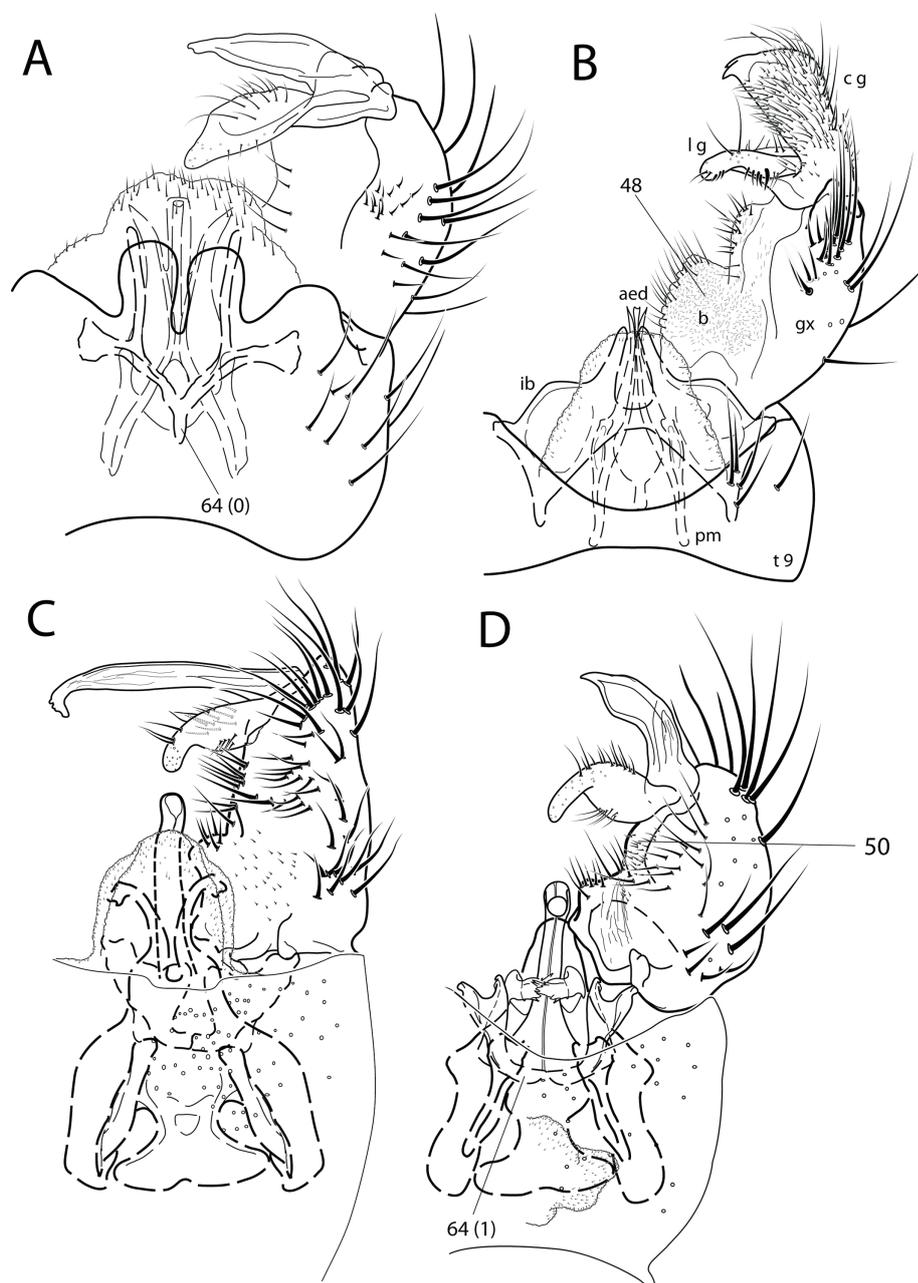


Figure 7. Male terminalia of the outgroup taxa, modified from Ribeiro (2008). **a** *Eupilaria phoenosoma* (Alexander); **b** *Euphylidorea niveitarsis* (Osten Sacken); **c** *Phylidorea (Phylidorea) umbrarum* (Krogerus); **d** *Phylidorea (Phylidorea) longicornis pietatis* (Alexander). Abbreviations: aed = aedeagus; b = bulge of gonocoxite; cg = clasper of gonostylus; gx = gonocoxite; ib = interbases; lg = lobe of gonostylus; pm = paremeres; t 9 = ninth tergite. — Orientation: dorsal view.

level of the origin of Rs [17: 0-1], the two anal vein markings far apart [39: 0-1], short R_{2+3+4} [6: 0-1], and distal M_{1+2} is longer than twice the length of M_2 [10: 0-1]. The male terminalia are distinguished from the other groups by the presence of a curved gonostylus [51: 0-1] (Fig. 9h). Despite its curved shape, the clasper of the gonostylus retains a flattened aspect.

Clade 12. Synapomorphy: [44: 0-1]. — This clade represents the Palearctic species of the original genus *Idioptera*. The clade is defined by the presence of a patch connecting the marking around m-cu with the marking at the tip of vein CuP [44: 0-1] (Fig. 6a). This additional patch reinforced the banded appearance of *Idioptera*

wings. These “banded wings” (Fig. 6a) were identified as a diagnostic feature of the original genus *Idioptera*.

Clade 13. Synapomorphies: [59*: 0-1]; [64: 0-1]; [71: 0-1]. — This clade contains the bulk of the diversity of the entire *Idioptera-Eloeophila* complex. The group is supported by the serrated margin of the bulge in the base of the gonocoxite [59: 0-1] (Fig. 8d). The ventral tooth of the clasper of the gonostylus is more rounded in this clade. The clade also has a bent tip of the dorsal branch of the interbase [64: 0-1] and humps on the lower shelf [71: 0-1]. These membranous projected humps were evidenced by Starý (2009). He referred to them as a lateral projection of the lower shelf (“lpsH”). To avoid confusion

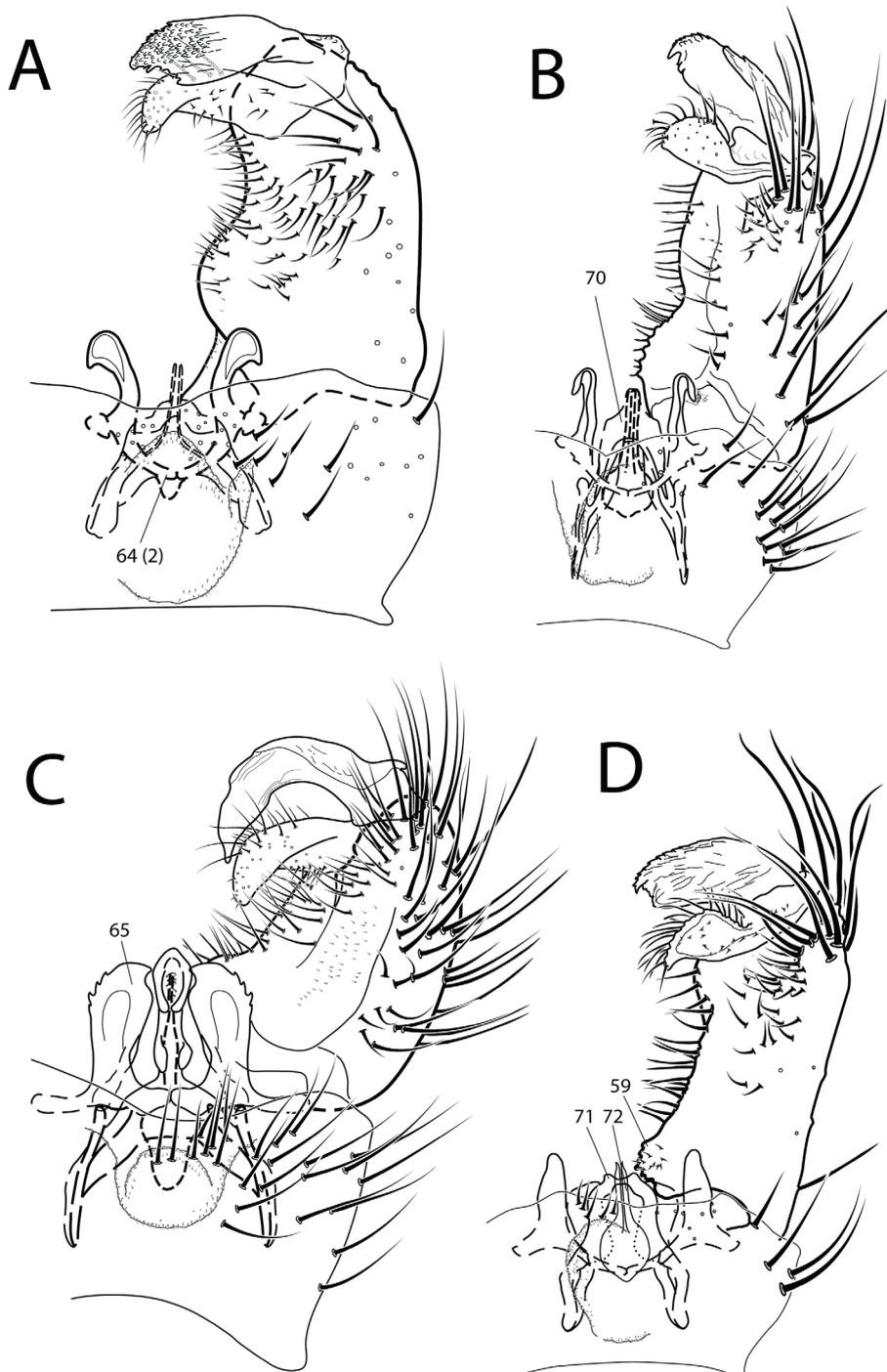


Figure 8. Male terminalia of the *Idioptera* modified from Ribeiro (2008). **a** *Idioptera trimaculata* (Zetterstedt) **comb. nov.**; **b** *Idioptera aldrichi* (Alexander) **comb. nov.**; **c** *Idioptera nearctica* (Alexander); **d** *Idioptera maculata* (Meigen) **comb. nov.** — Orientation: dorsal view.

with the lateral projection of the sheath of the aedeagus, we will refer to it as the humps of the lower shelf.

Clade 14. Synapomorphies: [40*: 0-1]; [42: 0-1]; [45: 0-1]; [72: 0-1]. — This clade groups the banded wing *I. apicata* **comb. nov.** with the spotted wing *Eloeophila*. This clade is supported by a patch connecting the marking around sc-r with the marking around the basal deflection of R₅ [42: 0-1] (Fig. 6b). This results in a characteristic Y-shaped pattern in the distal part of the wing. Another patch of this group is located between the marking around the humeral vein and the marking at the base of CuA vein [45: 0-1]. Although the original genus *Idioptera* (Clade 11) was referenced as having banded wings, the species in Clade 14 have more patches and “bands” on their wings.

Additionally, this clade is supported by a marking on the anal lobe near the margin [40: 0-1] (Fig. 6b). The clade is also defined by the presence of a median projection of the lower shelf [72: 0-1] (Fig. 8b). As defined by Starý (2009), this pointed projection (“mplsh”) emerged from the lower shelf in the direction of the aedeagus. It may be an extension of the anterior margin of the vesica. In some species, such as *I. maculata* **comb. nov.**, the mplsh are shorter and more rounded.

Clade 15. Synapomorphies: [2*: 1-0]; [36: 0-1]; [47: 0-1]. — This clade groups the *Idioptera* with spotted wings. The main feature of this group is the presence of

spots. The spots are a set of numerous small dark rounded markings [47: 0-1] (Fig. 6b). Mainly, the spots are located along the longitudinal veins, but they may also be found on the anal lobe and in the costal cell, such as in *I. granulata* (Edwards, 1926) **comb. nov.** Schiner (1863) utilized the German term “buntgefleckt” (translated as “spot” or “freckle”) to describe these small rounded marks. He described the genus *Ephelia*, to group species of spotted wings. The term “spots” is also employed in subsequent studies such as Starý (2009).

Schiner’s (1863) *Ephelia* was synonymized under *Eloeophila* and is now synonymized under *Idioptera*. Besides the spots, Clade 15 species have a long marking around m-cu [36: 0-1] and lack a spur at the origin of Rs [2: 1-0] (Fig. 6b). Edwards (1938) redefined *Eloeophila* as a combination of a supernumerary m-cu vein and wings with spots while still classifying it as a subgenus of *Limnophila* Macquart. This definition was adopted by Dieneske (1987) and other publications. This traditional genus definition is closely linked to the group of species with spotted wings. The number and intensity of wing spots may vary.

Clade 16. Synapomorphy: [19: 0-1]. — Members of this clade share a spur at the tip of the anal vein [19: 0-1] (Fig. 6b). Some species, like *I. linnei* (Oosterbroek, 1992), have a spur distally on the anal vein. However, the spur of the wings of this clade is characterized by a distinctive orientation, directed towards the anal lobe. This spur is present in the base of the arched tip of the anal vein but

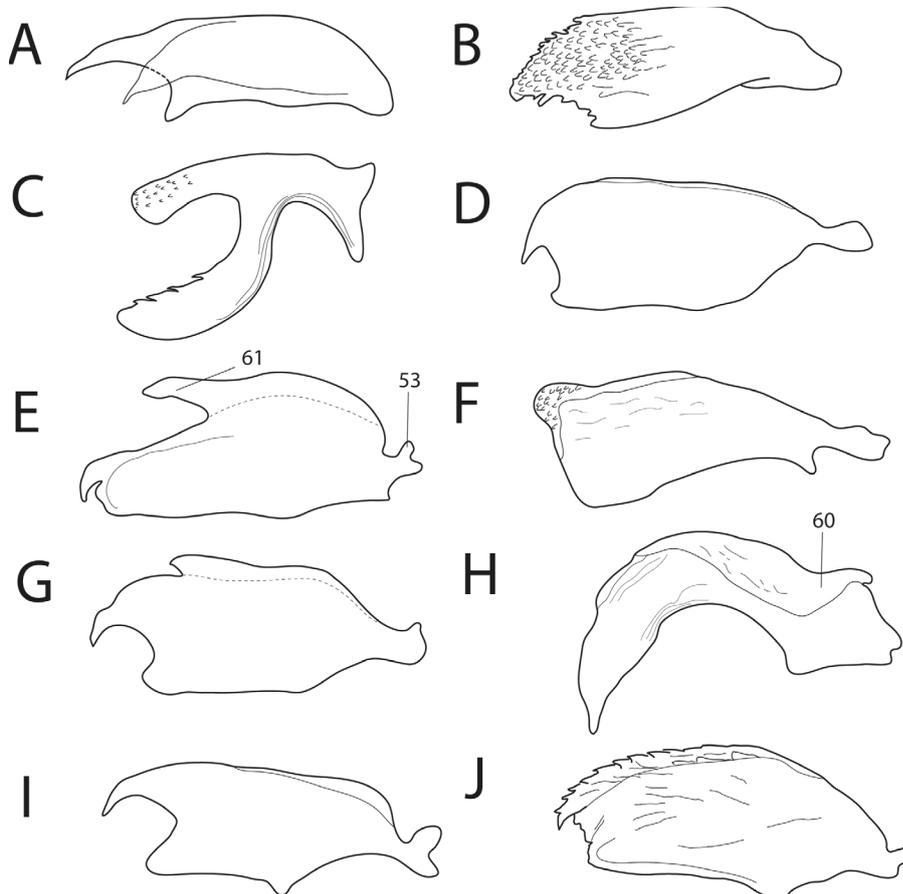


Figure 9. Clasper of gonostylus of different species of *Idioptera*, representing the main morphological variations found within the genus.— **a** *Idioptera moba* Podenas **comb. nov.** modified from Podenas (2003); **b** *Idioptera trimaculata* (Zetterstedt) **comb. nov.** modified from Ribeiro (2008); **c** *Idioptera tergilobellus* (Kato) **comb. nov.** modified from Kato, 2021; **d** *Idioptera pusilla* (Kuntze) **comb. nov.** modified from Starý (2009); **e** *Eloeophila kintaro* (Alexander) **comb. nov.** modified from Kato (2021); **f** *Eloeophila shannoni* (Alexander) **comb. nov.** modified from Alexander (1945); **g** *Eloeophila apicata* (Loew) **comb. nov.** modified from Starý (2009); **h** *Idioptera nearctica* (Alexander); **i** *Eloeophila miliaria* (Egger) **comb. nov.** modified from Kolcsar et al. (2023); **j** *Idioptera maculata* (Meigen) **comb. nov.** — Orientation: lateral view, with the base of clasper in the right (compare cg in Fig. 7b)

does not reach the posterior margin of the wing and it is more evident in males.

Clade 17. Synapomorphy: [1: 0-1]. — Members of this clade have large wings. This enlarged shape (Fig. 6b) is due to an extended posterior margin in the middle of the wing [1: 0-1], as seen in *I. maculata* **comb. nov.** (Fig. 6b). This feature is more evident in the males.

3.3. Phylogenetic overview of the genus *Idioptera*

A phylogenetic analysis of the *Idioptera-Eloeophila* complex was conducted using a data matrix consisting of 25 terminal taxa and 73 characters. The selection of terminal taxa was not arbitrary, but rather based on a meticulous review of available morphological information in the taxonomic literature, as well as direct observation of specimens from both the ingroup and outgroup. The resulting data matrix effectively captures the full range of morphological variation observed within the study group. Based on our findings, we reexamined the diversity of morphologies and we placed each species in the evolutionary background.

The paraphyly of *Eloeophila* generates a taxonomic problem. There are two solutions for this scenario. A solution for this would be to elevate six clades to genus level: Clade 2 (species related to *I. trimaculata* **comb. nov.**), Clade 5 (fossil species related to *I. moba* **comb. nov.**), the old genus *Trichephelia* (species related to *I. pusilla* **comb. nov.**), Clade 9 (species related to *I. aldrichi* **comb. nov.**), Clade 11 (original concept of *Idioptera*), and Clade 13 (old genus *Ephelia*). The other solution is to synonymize both valid genera under the same genus. We chose the last option to retain the conspicuous synapomorphy for this genus: the distinctive supernumerary m-cu and the better supported analysis. Further studies with better internal representation may support or not the independence of the six lineages included in *Idioptera*.

Although *Eloeophila* is much more diverse, the oldest name is *Idioptera*. *Eloeophila* was described by Rondani in 1856, while *Idioptera* was described by Macquart in 1834. From a taxonomic perspective, the older name *Idioptera* must be used to comply with the Principle of Priority of the Code. So, the entire lineage must be *Idioptera*. This act requires 89 taxonomic changes, which we have summarized below.

Based on this analysis and the acceptance of *Eloeophila* as a junior synonym of *Idioptera*, we can establish a phylogenetic framework that predicts the most probable classification of all described species (over 80 species) into the clades illustrated in Figure 1. Such a scheme is informed by the distribution of the derived character states, as revealed by a thorough examination of the descriptions of all the species and reinforced the stability of main clades present in the now expanded concept of the genus *Idioptera*. However, it is important to note that this framework should be considered provisional and subject to further validation through additional testing.

3.3.1. Genus *Idioptera* (for clades, compare Fig. 1)

Clade 2

I. trimaculata (Zetterstedt) **comb. nov.**

Clade 3

I. bifida (Alexander) **comb. nov.**

I. tergilobellus (Kato) **comb. nov.**

Clade 4

Clade 5

I. eocenica (Santos et al.) **comb. nov.**

I. moba (Podenas) **comb. nov.**

I. scudderi (Santos et al.) **comb. nov.**

Clade 7

I. apicisetula (Kato) **comb. nov.**

I. apiculata (Alexander) **comb. nov.**

I. laciniata (Edwards) **comb. nov.**

I. maroccana (Starý) **comb. nov.**

I. martinovskyi (Starý) **comb. nov.**

I. minor (Starý) **comb. nov.**

I. mundata (Loew) **comb. nov.**

I. persalsa (Alexander) **comb. nov.**

I. pusilla (Kuntze) **comb. nov.**

I. seticellula (Alexander) **comb. nov.**

I. ussuriiana iwatensis (Alexander) **comb. nov.**

I. ussuriiana ussuriiana (Alexander) **comb. nov.**

I. verralli (Bergroth) **comb. nov.**

Clade 8

Clade 9

I. abrupta (Alexander) **comb. nov.**

I. aldrichi aldrichi (Alexander) **comb. nov.**

I. aldrichi alticrista (Alexander) **comb. nov.**

I. aldrichi collata (Alexander) **comb. nov.**

I. amamiana (Alexander) **comb. nov.**

I. angustior (Alexander) **comb. nov.**

I. aprilina (Osten Sacken) **comb. nov.**

I. igorota (Alexander) **comb. nov.**

I. irene (Alexander) **comb. nov.**

I. johnsoni (Alexander) **comb. nov.**

I. kintaro (Alexander) **comb. nov.**

I. miliaria (Egger) **comb. nov.**

I. modoc (Alexander) **comb. nov.**

I. nupta (Alexander) **comb. nov.**

I. sabrina (Alexander) **comb. nov.**

I. serenensis (Alexander) **comb. nov.**

I. serotinella (Alexander) **comb. nov.**

I. solstitialis (Alexander) **comb. nov.**

I. subaprilina (Alexander) **comb. nov.**

I. superlineata (Doane) **comb. nov.**

I. verrucosa (Savchenko) **comb. nov.**

Clade 10

Clade 11

I. fasciolata (Osten Sacken)

I. linnei (Oosterbroek)

I. mcclureana (Alexander)
I. nearctica (Alexander)
I. pulchella (Meigen)

Clade 13

I. aleator (Alexander) **comb. nov.**
I. angolensis (Alexander) **comb. nov.**
I. apicata (Loew) **comb. nov.**
I. bicolorata (Alexander) **comb. nov.**
I. bipartita (Starý) **comb. nov.**
I. canidorsalis (Kato) **comb. nov.**
I. concreta (Edwards) **comb. nov.**
I. czernyi (Strobl) **comb. nov.**
I. delicola (Alexander) **comb. nov.**
I. delmastroi (Starý) **comb. nov.**
I. diacis (Alexander) **comb. nov.**
I. dietziana (Alexander) **comb. nov.**
I. dravidiana (Alexander) **comb. nov.**
I. dubiosa (Alexander) **comb. nov.**
I. dulitensis (Edwards) **comb. nov.**
I. edentata (Alexander) **comb. nov.**
I. enischnophallus (Kato) **comb. nov.**
I. fascipennis (Brunetti) **comb. nov.**
I. fumigata (Alexander) **comb. nov.**
I. fuscoanalis (Alexander) **comb. nov.**
I. granulata (Edwards) **comb. nov.**
I. hadrophallus (Kato) **comb. nov.**
I. latinigra (Alexander) **comb. nov.**
I. lilliputina (Alexander) **comb. nov.**
I. lucasi (Starý) **comb. nov.**
I. maculata (Meigen) **comb. nov.**
I. marmorataeformis (Riedel) **comb. nov.**
I. marmorea (Alexander) **comb. nov.**
I. ornata (Brunetti) **comb. nov.**
I. oxyacantha (Alexander) **comb. nov.**
I. paraprilinea (Alexander) **comb. nov.**
I. pectinistylus (Starý) **comb. nov.**
I. perdilata (Alexander) **comb. nov.**
I. pluriguttula (Alexander) **comb. nov.**
I. prolongata (Alexander) **comb. nov.**
I. punctulata (Starý) **comb. nov.**
I. serrulata (Alexander) **comb. nov.**
I. shannoni (Alexander) **comb. nov.**
I. similissima (Alexander) **comb. nov.**
I. smithersi (Alexander) **comb. nov.**
I. sparsipunctum (Starý) **comb. nov.**
I. subannulata (Alexander) **comb. nov.**
I. subdilata (Alexander) **comb. nov.**
I. submarmorata (Verrall) **comb. nov.**
I. suenisoni (Alexander) **comb. nov.**
I. tigricosta (Starý) **comb. nov.**
I. urania (Speiser) **comb. nov.**
I. venaguttula (Alexander) **comb. nov.**
I. vernata (Alexander) **comb. nov.**
I. villiersi (Alexander) **comb. nov.**
I. woodgatei (Alexander) **comb. nov.**

4. Zoogeography

The geographical distribution of the genus *Idioptera* is extensive, with a concentration of diversity observed in the United States, Europe and Japan. However, this distribution pattern may be influenced by a bias in research efforts. In the Nearctic Region, the genus is found across Canada to New Mexico in the United States. Several Palearctic species exhibit a wide range of distribution (Oosterbroek 2023), for example *I. maculata* **comb. nov.** is present in 37 countries and *I. pulchella* in 27 countries. The genus is present in the Oriental Region, from Iran to Borneo. Notably, members of some clades, such as clades 5 and 11, have species present on both sides of the Pacific. This Nearctic-Palearctic distribution pattern is ancient, as evidenced by a clade that includes Eocene fossils from Baltic Amber and Colorado in the United States.

In the Afrotropical Region, there are nine species of *Idioptera*. The relatively low number of species found in this region is likely attributed to a bias in sampling, similar to other regions such as China (with 5 species) and Malaysia (with 3 species).

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6. References

- Alexander CP (1914) New or little-known craneflies from the United States and Canada. Tipulidae, Diptera. Proceedings of the Academy of Natural Sciences of Philadelphia 66: 579–606.
- Alexander CP (1919) New Nearctic crane-flies (Rhyphidae and Tipulidae, Diptera). Part VII. Canadian Entomologist 51: 162–172. <https://doi.org/10.4039/Ent51162-6>
- Alexander CP (1921) New Nearctic crane-flies (Tipulidae, Diptera). Part XI. Canadian Entomologist 53: 132–137. <https://doi.org/10.4039/Ent53132-6>
- Alexander CP (1927) Undescribed crane-flies from the Holarctic region in the United States national museum. Proceedings of the United States National Museum 72(2): 1–17.
- Alexander CP (1931) New or little-known Tipulidae from the Philippines (Diptera). X. Philippine Journal of Science 46: 9–38.
- Alexander CP (1932) New or little-known Tipulidae from the Philippines (Diptera). XIV. Philippine Journal of Science 48: 21–49.
- Alexander CP (1933) New or little-known Tipulidae from eastern Asia (Diptera). XV. Philippine Journal of Science 52: 131–166.
- Alexander CP (1938) New or insufficiently-known crane-flies from the Nearctic region (Tipulidae, Diptera). Part IV. Bulletin of the Brooklyn Entomological Society 33: 71–78.

- Alexander CP (1942) Family Tipulidae. In: Crampton GC, Curran CH, Alexander CP (Eds) Guide to the Insects of Connecticut. Part VI. The Diptera or True Flies of Connecticut. Connecticut State Geological and Natural History Survey, Connecticut, pp. 196–486.
- Alexander CP (1945) Records and descriptions of North American crane-flies (Diptera). Part V. Tipuloidea of the Grand Teton National Park and Teton National Forest, Wyoming. *American Midland Naturalist* 33: 391–439.
- Alexander CP (1948) Records and descriptions of North American crane-flies (Diptera). Part VII. The Tipuloidea of Utah. I. *American Midland Naturalist* 39: 1–82. <https://doi.org/10.2307/2421428>
- Alexander CP (1950) Undescribed species of Japanese crane-flies (Diptera: Tipulidae). Part VII. *Annals of the Entomological Society of America* 43: 418–436.
- Alexander CP (1955) Records and descriptions of Japanese Tipulidae (Diptera). Part IV. The crane-flies of Shikoku. IV. *Philippine Journal of Science* 83: 263–306.
- Alexander CP (1957) Records and descriptions of Japanese Tipulidae (Diptera). Part V. The crane-flies of Honshu. I. *Philippine Journal of Science* 85: 349–388.
- Alexander CP (1966) Undescribed species of Nearctic Tipulidae (Diptera). VII. *Great Basin Naturalist* 26: 1–8. <https://doi.org/10.5962/bhl.part.14259>
- Alexander CP (1972) New subgenera of North American crane flies (Tipulidae: Diptera). *Entomological News* 83: 29–37.
- Bigot JMF (1854) Essai d'une classification générale et synoptique de l'ordre des insectes diptères (3e mémoire). *Tribu de Tipulidii (mihi)*. *Annales de la Société Entomologique de France* (3)2: 447–482.
- Cumming J, Wood DM (2017) Adult morphology and terminology. In: Kirk-Spriggs AH, Sinclair BJ (Eds) *Manual of Afrotropical Diptera*. Volume 1. Introductory chapters and keys to Diptera families. *Suricata* 4, South African National Biodiversity Institute, Pretoria, pp. 89–133.
- de Jong H (2017) Limoniidae and Tipulidae (crane flies). In: Kirk-Spriggs AH, Sinclair BJ (Eds) *Manual of Afrotropical Diptera*. Volume 2. Nematoceros Diptera and lower Brachycera. *Suricata* 5, South African National Biodiversity Institute, Pretoria, pp. 427–477.
- Dienske JW (1987) An illustrated key to the genera and subgenera of the western palaeartic Limoniidae (Insecta, Diptera) including a description of the external morphology. *Stuttgarter Beiträge zur Naturkunde (A)* 409: 1–52.
- Edwards FW (1921) British Limnobiidae: some records and corrections. *Transactions of the Royal Entomological Society of London* 1921: 196–230. <https://doi.org/10.1111/j.1365-2311.1921.tb02806.x>
- Edwards FW (1926) Diptera Nematocera from the mountains of Borneo. *Sarawak Museum Journal* 3: 243–278.
- Edwards FW (1938) British short-palped craneflies. Taxonomy of adults. *Transactions of the Society for British Entomology* 5: 1–168.
- Egger J (1863) Dipterologische Beiträge. *Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien* 13: 1101–1110.
- Goloboff PA (1993) Estimating character weights during tree search. *Cladistics* 9(1): 83–91. <https://doi.org/10.1111/j.1096-0031.1993.tb00209.x>
- Goloboff PA, Catalano SA (2016) TNT version 1.5, including a full implementation of phylogenetic morphometrics. *Cladistics* 32(3): 221–238. <https://doi.org/10.1111/cla.12160>
- Kato D (2021) Taxonomic study of the genus *Eloeophila* Rondani, 1856 of Japan (Limoniidae, Diptera). *Zootaxa* 4995: 425–451. <https://doi.org/10.11646/zootaxa.4995.3.2>
- Kolcsar LP, Oosterbroek P, Olsen KM, Paramonov NM, Gavryushin DI, Piliipenko VE, Polevoi A, Eiroa E, Andersson M, Dufour C, Syrratt M, Kurina O, Lindstrom M, Starý J, Lantsov VI, Wiedenska J, Pape T, Friman M, Peeters K, Gritsch W, Salmela J, Viitanen E, Aristophanous M, Janevic D, Watanabe K (2023) Contribution to the knowledge of Cylindrotomidae, Pediciidae and Tipulidae (Diptera: Tipuloidea): first records of 86 species from various European countries. *Diversity* 15(336): 1–31. <https://doi.org/10.3390/d15030336>
- Loew H (1871) Beschreibungen europäischer Dipteren. Systematische Beschreibung der bekannten europäischen zweiflügeligen Insecten. Von Johann Wilhelm Meigen. Neunter Theil oder dritter Supplementband. Beschreibung europäischer Dipteren. Zweiter Band. H.W. Schmidt, Halle 2(i–vii) 1–320.
- Macquart J (1834) *Histoire naturelle des Insectes. Dipteres. Ouvrage accompagnée de planches*. Tome premier. N.E. Roret Paris, pp. 1–578. <https://doi.org/10.5962/bhl.title.14274>
- Meigen JW (1804) Klassifikation und Beschreibung der europäischen zweiflügeligen Insekten (Diptera Linn.). Erster Band. Abt. I & II. Reichard, Braunschweig [= Brunswick], pp. i–xxviii, 1–314.
- Nixon KC, Carpenter JM (1993) On outgroups. *Cladistics* 9: 413–426. <https://doi.org/10.1111/j.1096-0031.1993.tb00234.x>
- Oosterbroek P (1992) A new name for *Tipula fasciata* Linnaeus, 1767. In: Savchenko EN, Oosterbroek P, Starý J (Eds) *Family Limoniidae. Catalogue of Palaearctic Diptera* 1: 183–369.
- Oosterbroek P (2023) *Catalogue of the Craneflies of the World (Insecta, Diptera, Nematocera, Tipuloidea)*. Available from: <http://ccw.naturalis.nl> (accessed 10 March 2022).
- Oosterbroek P, Theowald B (1991) Phylogeny of the Tipuloidea based on characters of larvae and pupae (Diptera, Nematocera) with an index to the literature except Tipulidae. *Tijdschrift voor Entomologie* 134: 211–267.
- Petersen JD, Petersen MJ, Courtney GW (2012) Description of a new subgenus *Neophylidorea* (Diptera: Tipulidae) and a new species. *Zootaxa* 3555: 40–54. <https://doi.org/10.11646/zootaxa.3555.1.2>
- Podenas S (2003) First fossil *Eloeophila* Rondani, 1856 (Diptera: Limoniidae) from Baltic amber (Eocene). *Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg* 87: 125–130.
- Podenas S, Park SJ, Byun HW, Kim AY, Klein TA, Kim HC, Auktikalniene R (2020) New data on Limoniinae and Limnophilinae crane flies (Diptera: Limoniidae) of Korea. *Journal of Species Research* 9: 492–531.
- Podeniene V (2004) Records on little-known larvae of *Idioptera pulchella* (Meigen, 1830) (Diptera, Limoniidae, Limnophilinae). *Acta Zoologica Lituonica* 14: 37–41. <https://doi.org/10.1080/13921657.2004.10512589>
- Ribeiro GC (2006) Homology of the gonostylus parts in crane flies, with emphasis on the families Tipulidae and Limoniidae (Diptera, Tipulomorpha). *Zootaxa* 1110: 47–57. <https://doi.org/10.11646/zootaxa.1110.1.5>
- Ribeiro GC (2008) Phylogeny of the Limnophilinae (Limoniidae) and early evolution of the Tipulomorpha (Diptera). *Invertebrate Systematics* 22: 627–694. <https://doi.org/10.1071/IS08017>
- Rondani C (1856) *Dipterologiae Italicae Prodrum*. *Genera Italica ordinis dipterorum ordinatim disposita et distincta et in familias et stirpes aggregata*. A. Stocchih [sic], Parmae [= Parma] 1: 1–228. <https://doi.org/10.5962/bhl.title.8160>
- Santos D, Klein BMT, Ribeiro GC (2022) The fossil record of *Eloeophila* (Diptera: Tipuloidea: Limoniidae). *Historical Biology*: 1–6. <https://doi.org/10.1080/08912963.2022.2147429>

- Savchenko EN, Krivolutskaia GO (1976) Limoniidae of the South Kuril Islands and South Sakhalin. Akademiy Nauk Ukrainskoy SSR, "Naukova Dumka", Kiev, 160 pp.
- Schiner JR (1863) Vorläufiger Commentar zum dipterologischen Theile der Fauna austriaca. V [concl.]. Wiener Entomologische Monatschrift 7: 217–226.
- Scudder SH (1894) Tertiary Tipulidae, with special reference to those of Florissant, Colorado. Proceedings of the American Philosophical Society 163–245.
- Siebke H (1870) Beretning om en i Sommeren 1869 foretagen entomologisk Reise gjennem Ringerike, Hallingdal og Valdres. Nyt Magazin for Naturvidenskapene 17: 246–314.
- Starý J (2009) West Palaearctic species of the genus *Eloeophila* (Diptera: Limoniidae). European Journal of Entomology 106: 425–440. <https://doi.org/10.14411/eje.2009.054>
- Zetterstedt JW (1838) Sectio tertia. Diptera. Dipterologis Scandinaviae amicis et popularibus carissimus. In: Insecta Lapponica. Voss, Lipsiae [= Leipzig]: 477–868.

Supplementary Material 1

Tables S1, S2

Authors: Santos D, Ribeiro GC (2024)

Data type: .docx

Explanation notes: **Table S1.** List of species and specimens examined. — **Table S2.** Character matrix used for phylogenetic analyses.

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Supplementary Material 2

Figure S1

Authors: Santos D, Ribeiro GC (2024)

Data type: .jpg

Explanation note: Primary tree indicating the distribution of characters.

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