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Thirty years of progress in research on jumping tree bugs and the World checklist of Isometopinae (Hemiptera: Heteroptera: Miridae)

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Abstract

A comprehensive synopsis of isometopine plant bugs, highlighting the thirty-year progress made with information on morphology, biology and zoogeography of extant and extinct taxa, is introduced. In addition, the feeding habit of isometopines is suggested to be at least partially spent as a lichen feeder. A total of 289 Isometopinae species are presented in the world checklist with the zoogeographical information. The direction of further studies on isometopine taxa is also suggested.

Key words: biodiversity, distribution, plant bugs, taxonomy, true bugs

Introduction

The plant bugs (Miridae) belonging to the infraorder Cimicomorpha and superfamily Miroidea are one of the most species-rich families of hemi-metabolous insects, with more than 11,300 described species (Schuh & Weirauch 2020). Mirids range in size from less than 2 mm to about 15 mm and are among the most delicate of all true bugs. Following the most recent literature (Wolski & Henry 2015, Schuh & Weirauch 2020), seven subfamilies are recognized within the Miridae: Bryocorinae, Cylapinae, Deraeocorinae, Isometopinae, Mirinae, Orthotylinae and Phylinae. The group with the least number of species and relatively poorly known biodiversity are the Isometopinae (jumping tree bugs).

In 1993, an extensive monographic study on jumping tree bugs by Herczek was published. On the occasion of the 30th anniversary of this work, as well as the 70th birthday of its author, we decided to present a short review that assesses the development of Isometopinae knowledge during the past 30 years. Herein we present the current World checklist and provide perspectives on where the field might develop.

Monophyly of Isometopinae and position within Miridae

The Isometopinae Fieber, 1860 are a highly autapomorphic group possessing paired ocelli, which are absent in all other members of the plant bug family Miridae (Herczek 1993, Cassis & Schuh 2012, Namyatova & Cassis

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2016, Yasunaga *et al.* 2017). This subfamily was considered to be the sister group to all other subfamilies based on morphology (Schuh 1974, 1976), but recent works using molecular data do not support this hypothesis (Schuh *et al.* 2009, Jung & Lee 2012).

Due to scarce information on habits, biology, and food preference, representatives are relatively rare in collections, with many species known from singletons or only a handful of specimens (Eyles 1971, Namyatova & Cassis 2016, Taszakowski *et al.* 2020). For this reason, only a few representatives of this subfamily are included in phylogenetic studies if at all, and in the case of molecular datasets they are almost absent (Schuh *et al.* 2009, Jung & Lee 2012, Kim & Jung 2019, Oh *et al.* 2023).

Morphology and character exploration

Isometopinae are a group of bugs with relatively small body size. Although the body length of *Gigantometopus rossi* Schwartz & Schuh, 1990 is 6.98 mm, most representatives are much smaller, and the body length ranges between 1.6 and 4 mm (Schwartz & Schuh 1990, Akingbohungbe 1996). The most characteristic feature of Isometopinae is the possession of ocelli, which distinguishes them from other Miridae. Moreover, they are characterized by their often holoptic eyes, often strongly antero-posteriorly flattened head, simple phallotheca, a membranous endosoma with an undifferentiated secondary gonopore, pretarsal claws often with a subapical tooth and saltatorial hind legs (Cassis & Schuh 2012, Henry 2017, Schuh & Weirauch 2020). An important feature of jumping tree bugs is the reduced number of femoral trichobothria, two and three on meso- and metafemora. The exceptions are Sophianini (three to four mesofemoral and four to five metafemoral trichobothria) and Gigantometopini (four to five mesofemoral and five to six metafemoral trichobothria) (Schuh 1975, Akingbohungbe 1996, Yasunaga 2017, Taszakowski *et al.* 2021a, b).

The most comprehensive information on Isometopine morphology can be found in the studies by Herczek (1993) and Akingbohungbe (1996). A detailed description of male genitalia structure was provided by Konstantinov (2003). Female genitalia have not been the subject of comparative studies; we only know them from particular species descriptions (Taszakowski *et al.* 2022).

Knowledge of the Isometopinae nymph's morphology is very poor and limited to a few descriptions or photos included in papers. Recent work indicates that nymphs may have unusual characteristics comparing to those of the other subfamilies and require extensive study (Yasunaga & Hayashi 2002, Yasunaga 2005, Yasunaga & Duwal 2006, Kim & Jung 2016, Çerçi & Dursun 2017, Yasunaga *et al.* 2017, Shishido *et al.* 2020, Kim *et al.* 2021, Yeshwanth *et al.* 2021).

Systematics and taxonomy of Isometopinae

Comprehensive information on the history of taxonomic and faunistic research on jumping tree bugs can be found in Herczek (1993). Since then, over 40 papers on jumping tree bugs have been published (Fig. 1). In the monographic study of the Isometopinae of Africa, Europe and the Middle East by Akingbohungbe (1996), the author described 37 new species. Following in the new century, in 2004 Lin described seven new species from Taiwan. Two years later, papers on jumping tree bugs from Yemen (Akingbohungbe 2006) and Nepal (Yasunaga & Duwal 2006) were published. Subsequently, in 2012, Henry & Carpintero reviewed the Isometopinae of Argentina and nearby areas of Brazil and Paraguay and described nine new species. In 2014, Herczek & Popov revised the genus *Metoisops* from late Eocene European amber, describing seven new species. Australian representatives of Isometopinae were the subject of research by Namyatova & Cassis (2016), who described seven new species and extensively discussed the distribution and host plant associations of the subfamily worldwide. In 2018, Krüger described ten new species from Liberia and three years later, Yeshwanth *et al.* (2021) revised the Isometopinae of India and Sri Lanka and described six new species. In summary, 152 species of Isometopinae have been described over the last 30 years, constituting over 50% of all known species.

Currently, six tribes, 53 genera and 289 species of Isometopinae are known, of which seven genera and 23 species are fossil taxa (see Checklist and Tab. 1).

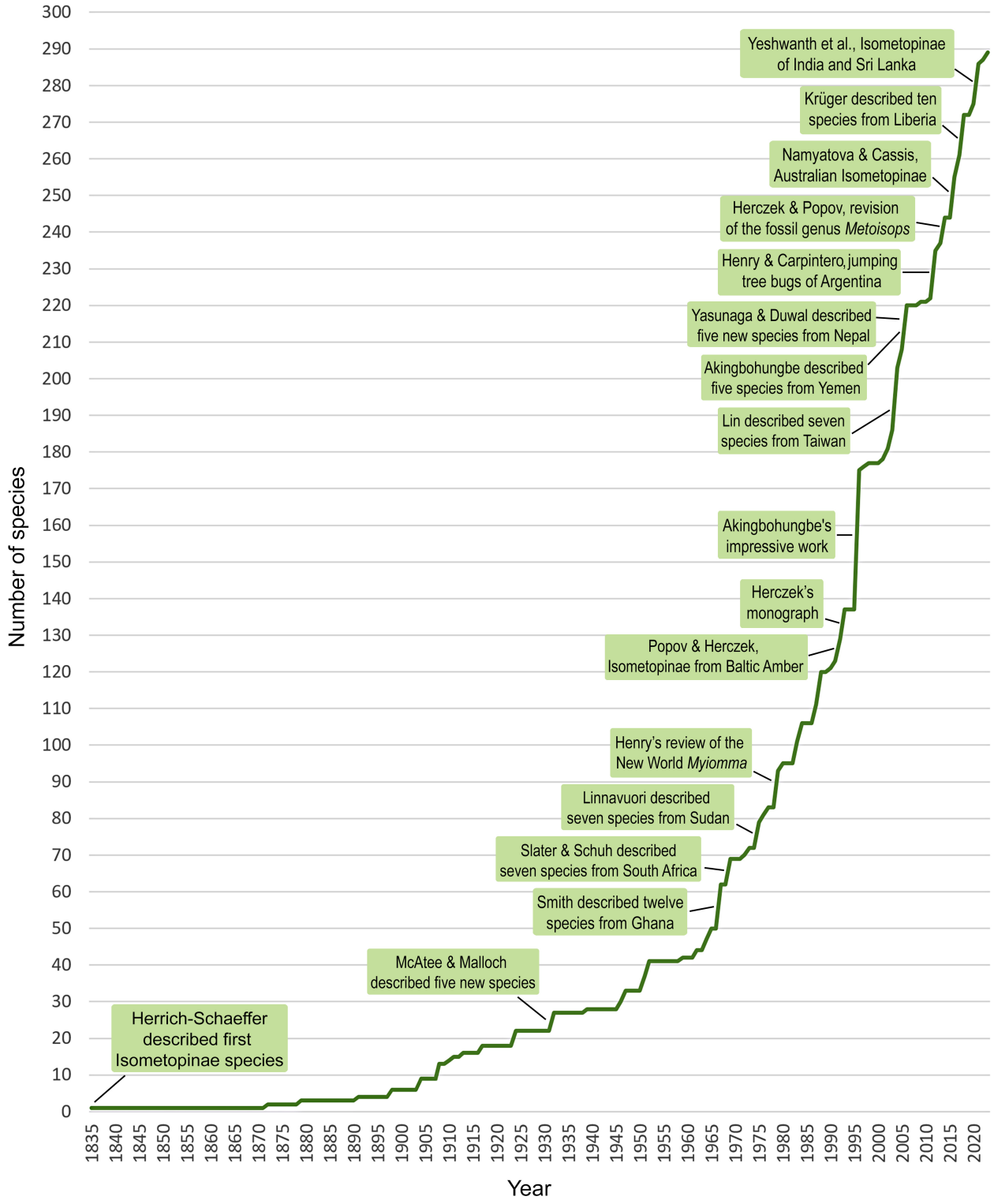

FIGURE 1. Progress of alpha taxonomic studies on Isometopinae.

The Diphlebini Bergroth, 1924 (Fig. 2A) includes only a single genus, *Diphleps* Bergroth, 1924 with five known species. Although the systematic position of Diphlebini is debatable (Herczek 1993, Akingbohungbe 1996, Konstantinov 2003, Cassis & Schuh 2012), we maintain this group in the Isometopinae, pending further study. Gigantometopini Herczek, 1993 (Figs 2B, 3A–C) is a small tribe containing nine genera and 27 species. The Isometopini Fieber, 1860 (Figs 2C, 3D–F) (14 genera, 127 species) and Myiommini Bergroth, 1924 (Fig. 2D) (15 genera, 108 species) are the most species-rich isometopine tribes. Most recently, in 2017, Yasunaga *et al.* (2017)

established the new tribe Sophianini Yasunaga, Yamada & Tsai, 2017 (Figs 2E, 3G, H) comprising two genera and ten species previously classified within Myiommini. The Electromyiommini Herczek, 1993 is an extinct tribe with four genera and eight species (Fig. 4).

The two genera, *Isometopus* Fieber, 1860 (Fig. 2C) and *Myiomma* Puton, 1872 (Fig. 2D), are distinguished by their high number of species, respectively 82 and 80. Representatives of these genera comprise 56% of all known jumping tree bugs. *Isometopus* and *Myiomma* probably are a 'convenience group' (Namyatova & Cassis 2016). Redescription and diagnosis of these genera across its distribution range is undoubtedly a challenge waiting to be undertaken. Twenty-three genera of jumping three bugs are monotypic.

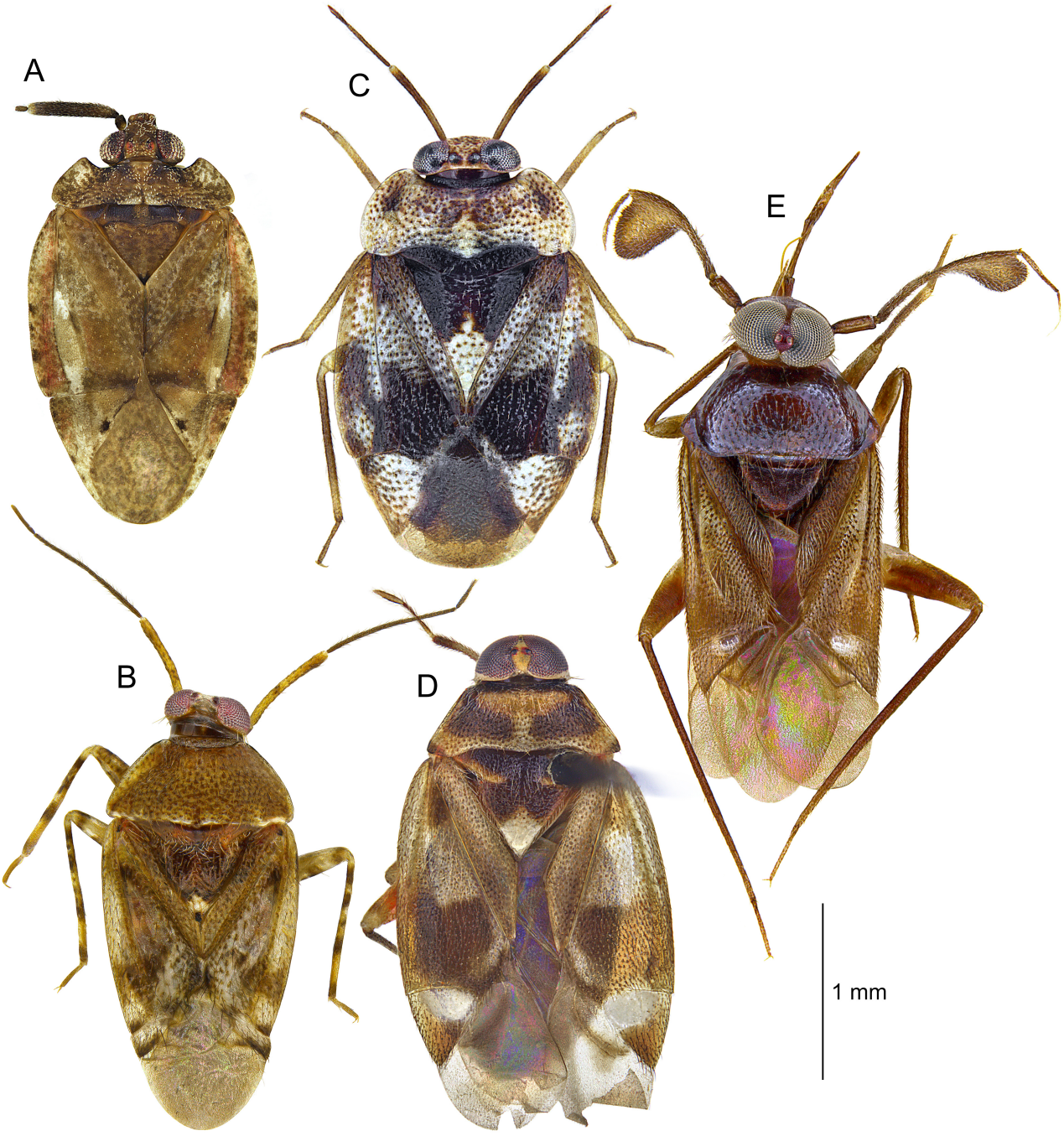

FIGURE 2. Habitus of representatives of five extant Isometopinae tribes. **A**. *Diphleps unica* Bergroth, 1924 (Diphlebini); **B**. *Bruneimetopus simulans* Taszakowski, Kim & Herczek, 2020 (Gigantometopini); **C**. *Isometopus mirificus* Mulsant & Rey, 1879 (Isometopini); **D**. *Myiomma milleri* (Hoberlandt, 1959) (Myiommini); **E**. *Sophianus palawanensis* Taszakowski, Kim & Herczek, 2021 (Sophianini).

FIGURE 3. Living specimens of Isometopinae in their natural habitat (Singapore). **A** & **B**. *Gigantometopus* spp.; **C**. Unknown Gigantometopini; **D** & **E**. Unknown Isometopini; **F**. *Isometopus* sp., nymph; **G**. *Alcecoris* sp.; **H**. *Alcecoris* sp., nymph. Photo credits: David Ball (**A**, **D**); Melvyn Yeo (**B**, **C**, **G**, **H**); KS Tan (**E**, **F**).

Checklist and zoogeography

The following checklist is based on the online catalog by Schuh (2002–2013). It also includes omitted species mentioned in the works of Linnavuori *et al.* (1998) and Akingbohungbe (2006) and the latest papers: Herczek & Popov (2011, 2012), Akingbohungbe (2012), Herczek *et al.* (2013, 2018, 2020), Kim & Jung (2016, 2021), Namyatova & Cassis (2016), Yasunaga *et al.* (2016, 2017), Çerçi & Dursun (2017), Hosseini (2017), Krüger (2018), Taszakowski *et al.* (2020, 2021a, b, 2022), Kim *et al.* (2021, 2023) and Yeshwanth *et al.* (2021).

Isometopus mahal Distant, 1911 was synonymized with *I. mirificus* Mulsant & Rey, 1879 by Carvalho (1951) but was treated as a valid species by Akingbohungbe (1996) and Yasunaga & Hayashi (2002). Fossil species were marked with a dagger (†). We have tried to review the available literature thoroughly, but there may be some omissions in the checklist. If you notice them, please kindly inform us.

The Wallace Line was adopted as the boundary between the Indomalayan and Australasian regions (Rueda *et al.* 2013). The boundary of the Palearctic region was adopted according to Aukema & Rieger (1995). It is worth noting here that the Ryukyu Islands and Taiwan are placed in the Palearctic region; however, the fauna of these islands refers clearly to the Indomalayan fauna.

Explanation of color markings of zoogeographical regions: ●—Afrotropical, ●—Australasian, ●—Indomalayan, ●—Nearctic, ●—Neotropical, ●—Palearctic.

subfamily: Isometopinae Fieber, 1860

tribe: Diphlebini Bergroth, 1924

genus: *Diphleps* Bergroth, 1924

1. *Diphleps henryi* Hernandez, 1998 ●
2. *Diphleps maldonadoi* Henry, 1977 ●
3. *Diphleps similaris* Henry, 1977 ●
4. *Diphleps unica* Bergroth, 1924 ●
5. *Diphleps yenli*† Santiago-Blay & Poinar, 1993

tribe: Electromyiommini† Herczek, 1993

genus: *Archemyiomma*† Herczek, 1993

6. *Archemyiomma carvalhoi*† Herczek, 1993
7. *Archemyiomma schaeferi*† Herczek & Popov, 2013

genus: *Clavimyiomma*† Popov & Herczek, 1992

8. *Clavimyiomma henryi*† Popov & Herczek, 1992

genus: *Electroisops*† Herczek & Popov, 1997

9. *Electroisops ritzkowskii*† Herczek & Popov, 1997

genus: *Electromyiomma*† Popov & Herczek, 1992

10. *Electromyiomma herczeki*† Kim & Jung, 2021
11. *Electromyiomma polonicum*† Popov & Herczek, 1992
12. *Electromyiomma schultzi*† Popov & Herczek, 1992
13. *Electromyiomma weitschati*† Popov & Herczek, 1992

tribe: Gigantometopini Herczek, 1993

genus: *Astroscopometopus* Yasunaga & Hayashi, 2002

14. *Astroscopometopus formosanus* (Lin, 2004) ●
15. *Astroscopometopus gryllocephalus* (Miyamoto, Yasunaga & Hayashi, 1996) ●
16. *Astroscopometopus hesaraghattaensis* Yeshwanth, Chérot & Henry, 2021 ●

genus: *Gigantometopus* Schwartz & Schuh, 1990

17. *Gigantometopus coronobtectus* Kim, Taszakowski & Jung, 2021 ●
18. *Gigantometopus rossi* Schwartz & Schuh, 1990 ●
19. *Gigantometopus schuhi* Akingbohungbe, 2012 ●

genus: *Isometopidea* Poppius, 1913

20. *Isometopidea lieweni* Poppius, 1913 ●
21. *Isometopidea viraktamathi* Yeshwanth, Chérot & Henry, 2021 ●

genus: *Kohnometopus* Yasunaga, 2005

22. *Kohnometopus fraxini* Yasunaga, 2005 🔴
23. *Kohnometopus yangi* (Lin, 2005) 🔴
24. *Kohnometopus yasunagai* Taszakowski, Kim & Masłowski, 2022 🟤

genus: *Megalofaciatus* Taszakowski, Kim & Herczek, 2021

25. *Megalofaciatus foliotibialis* Taszakowski, Kim & Herczek, 2021 🟤
26. *Megalofaciatus gibbosus* Taszakowski, Kim & Herczek, 2021 🟤

genus: *Metoisops*† Popov & Herczek, 1992

27. *Metoisops akingbohungbei*† Herczek & Popov, 2014
28. *Metoisops consimilis*† Herczek & Popov, 2014
29. *Metoisops grabenhorsti*† Herczek & Popov, 2014
30. *Metoisops groehni*† Herczek & Popov, 2014
31. *Metoisops intergerivus*† Herczek & Popov, 2014
32. *Metoisops kerzhneri*† Popov & Herczek, 1992
33. *Metoisops michalskii*† Kim, Taszakowski & Herczek, 2023
34. *Metoisops popovi*† Kim, Taszakowski & Jung, 2023
35. *Metoisops punctatodiffusus*† Herczek & Popov, 2014
36. *Metoisops punctatus*† Popov & Herczek, 1993
37. *Metoisops variabilis*† Herczek & Popov, 2014

genus: *Sulawesimetopus* Herczek, Gorczyca & Taszakowski, 2018

38. *Sulawesimetopus henryi* Herczek, Gorczyca & Taszakowski, 2018 🟡

genus: *Planicapitus* Taszakowski, Kim & Herczek, 2020

39. *Planicapitus luteus* Taszakowski, Kim & Herczek, 2020 🟤

genus: *Bruneimetopus* Taszakowski, Kim & Herczek, 2020

40. *Bruneimetopus simulans* Taszakowski, Kim & Herczek, 2020 🟤

tribe: Isometopini Fieber, 1860

subtribe: Isometopina Fieber, 1860

genus: *Carayonischa* Akingbohungbe, 1996

41. *Carayonischa singularis* Akingbohungbe, 1996 🔵

genus: *Eurocrypha* Kirkaldy, 1908

42. *Eurocrypha thanatochlamys* Kirkaldy, 1908 🟡

genus: *Isometopiellus* Akingbohungbe, 1996

43. *Isometopiellus cylpoides* Akingbohungbe, 1996 🔵
44. *Isometopiellus heterocephalus* (Puton, 1898) 🔴
45. *Isometopiellus palliceps* (Wagner, 1973) 🔴
46. *Isometopiellus ugandanus* Akingbohungbe, 1996 🔵

genus: *Isometopus* Fieber, 1860

47. *Isometopus africanus* Herczek, 2004 🔵
48. *Isometopus albifrons* (Slater & Schuh, 1969) 🔵
49. *Isometopus amurensis* Kerzhner, 1988 🔴
50. *Isometopus angolensis* Hoberlandt, 1952 🔵
51. *Isometopus anlasi* Çerçi & Dursun, 2017 🔴
52. *Isometopus aureus* Akingbohungbe, 1996 🔴
53. *Isometopus beijingensis* Ren & Yang, 1988 🔴
54. *Isometopus bongensis* Krüger, 2018 🔵
55. *Isometopus bipunctatus* Lin, 2004 🔴
56. *Isometopus brevirostris* Akingbohungbe, 1996 🔵
57. *Isometopus chaiyaphum* Yasunaga, Duanthisan & Yamada, 2016 🟤
58. *Isometopus carnifrons* Akingbohungbe, 2006 🔴
59. *Isometopus citri* Ren, 1987 🔴
60. *Isometopus confusus* (Akingbohungbe, 1983) 🔵
61. *Isometopus cuneatus* (Distant, 1904) 🟤

62. *Isometopus deemingi* (Akingbohungbe, 1983)
63. *Isometopus discrepans* Akingbohungbe, 1996
64. *Isometopus diversiceps* Linnavuori, 1962
65. *Isometopus fallax* Akingbohungbe, 1996
66. *Isometopus fasciatus* Hsiao, 1964
67. *Isometopus frontalis* Akingbohungbe, 1996
68. *Isometopus fulvus* (Akingbohungbe, 1983)
69. *Isometopus gharaati* Akingbohungbe, 2012
70. *Isometopus hainanus* Hsiao, 1964
71. *Isometopus hananoi* Hasegawa, 1946
72. *Isometopus hasegawai* Miyamoto, 1965
73. *Isometopus insperatus* Akingbohungbe, 1996
74. *Isometopus intermedius* Akingbohungbe, 1996
75. *Isometopus intrusus* (Herrich-Schaeffer, 1835)
76. *Isometopus ishigaki* Yasunaga, 2005
77. *Isometopus japonicus* Hasegawa, 1946
78. *Isometopus jejuensis* Kim & Jung, 2016
79. *Isometopus kanako* Yasunaga & Duwal, 2006
80. *Isometopus kaznakovi* Kiritshenko, 1939
81. *Isometopus lineatifrons* Akingbohungbe, 1996
82. *Isometopus lini* Lin, 2004
83. *Isometopus linnavuorii* Hosseini, 2017
84. *Isometopus longirostris* Akingbohungbe, 1996
85. *Isometopus longisetosus* (Herczek, 1993)
86. *Isometopus lunaris* Linnavuori, 1975
87. *Isometopus maculipennis* Akingbohungbe, 2004
88. *Isometopus maculosus* Akingbohungbe, 1996
89. *Isometopus madagascariensis* (Polhemus, 1988)
90. *Isometopus mahal* (Distant, 1911)
91. *Isometopus marginatus* Ren & Yang, 1988
92. *Isometopus mirificus* Mulsant & Rey, 1879
93. *Isometopus mirus* Akingbohungbe, 2004
94. *Isometopus nagarjun* Yasunaga & Duwal, 2006
95. *Isometopus nigrans* Akingbohungbe, 1996
96. *Isometopus nigritulus* Akingbohungbe, 1996
97. *Isometopus nigrosignatus* Ren, 1987
98. *Isometopus nitidus* (Smith, 1967)
99. *Isometopus obesulus* Akingbohungbe, 1996
100. *Isometopus peltatus* McAtee & Malloch, 1932
101. *Isometopus peregrinus* Akingbohungbe, 1996
102. *Isometopus pictus* Linnavuori, 1975
103. *Isometopus praetermissum* Akingbohungbe, 2012
104. *Isometopus puberus* Ren, 1991
105. *Isometopus puncticollis* Akingbohungbe, 1996
106. *Isometopus quadrifasciatus* Wagner, 1973
107. *Isometopus quadrivittatus* Akingbohungbe, 2003
108. *Isometopus renae* Lin, 2004
109. *Isometopus rugiceps* Kerzhner, 1988
110. *Isometopus sepehrii* Linnavuori, Sarafrazi & Hosyni, 1998
111. *Isometopus shaowuensis* Ren, 1987
112. *Isometopus siamensis* Yasunaga & Yamada 2013
113. *Isometopus slateri* (Akingbohungbe, 1983)

114. *Isometopus sudanicus* Akingbohungbe, 2006 ●
115. *Isometopus taeniaticeps* Puton, 1898 ●
116. *Isometopus takaii* Yasunaga, 2005 ●
117. *Isometopus tianjinus* Hsiao, 1964 ●
118. *Isometopus tibialis* (Akingbohungbe, 1983) ●
119. *Isometopus transvaalensis* (Slater & Schuh, 1969) ●
120. *Isometopus turneri* (Slater & Schuh, 1969) ●
121. *Isometopus typicus* (Distant, 1910) ●
122. *Isometopus vanharteni* Akingbohungbe, 2006 ●
123. *Isometopus variabilis* Akingbohungbe, 1996 ●
124. *Isometopus wacriensis* (Smith, 1967) ●
125. *Isometopus webbi* Yeshwanth, Chérot & Henry, 2021 ●
126. *Isometopus wolskii* Yeshwanth, Chérot & Henry, 2021 ●
127. *Isometopus yemenensis* Akingbohungbe, 2003 ●
128. *Isometopus yoshizawai* Yasunaga & Duwal, 2006 ●

genus: *Lindbergiola* Carvalho, 1951

129. *Lindbergiola aureopilosa* Carvalho, 1951 ●
130. *Lindbergiola bicolor* (McAtee & Malloch, 1932) ●
131. *Lindbergiola jarmilae* Hoberlandt, 1952 ●

genus: *Paloniella* Poppius, 1915

132. *Paloniella annulata* (Ren & Huang, 1987) ●
133. *Paloniella bedfordi* (Hesse, 1947) ●
134. *Paloniella cuneata* (Slater & Schuh, 1969) ●
135. *Paloniella erinacea* Krüger, 2018 ●
136. *Paloniella feana* (Distant, 1904) ●
137. *Paloniella flavicolor* Akingbohungbe, 2004 ●
138. *Paloniella garmsi* Krüger, 2018 ●
139. *Paloniella latifrons* Akingbohungbe, 1996 ●
140. *Paloniella microchelys* Yasunaga, Duanthisan & Yamada, 2016 ●
141. *Paloniella montana* (Ren & Yang, 1988) ●
142. *Paloniella mutabilis* Akingbohungbe, 1996 ●
143. *Paloniella niger* (Linnavuori, 1975) ●
144. *Paloniella nodifrons* Akingbohungbe, 2003 ●
145. *Paloniella ovata* Akingbohungbe, 2006 ●
146. *Paloniella parallela* Yasunaga & Hayashi, 2002 ● ●
147. *Paloniella pellucida* Akingbohungbe, 1996 ●
148. *Paloniella pseudotyloides* Akingbohungbe, 1996 ●
149. *Paloniella senegalensis* Akingbohungbe, 1996 ●
150. *Paloniella suffuscipennis* Akingbohungbe, 1996 ●
151. *Paloniella tafoensis* Akingbohungbe, 1996 ●
152. *Paloniella umbrosa* (Slater & Schuh, 1969) ●
153. *Paloniella xizangana* (Ren, 1988) ●

genus: *Ptisca* McAtee & Malloch, 1932

154. *Ptisca blattiformis* McAtee & Malloch, 1932 ●
155. *Ptisca liberiense* Krüger, 2018 ●

genus: *Smithopus* Akingbohungbe, 1996

156. *Smithopus ghanaiensis* (Smith, 1967) ●
157. *Smithopus scutellaris* (Linnavuori, 1975) ●

subtribe: Nesocryphina Herczek, 1993

genus: *Australotopus* Namyatova & Cassis, 2016

158. *Australotopus cooperensis* Namyatova & Cassis, 2016 ●

genus: *Fronsonia* Herczek, 1993

159. *Fronsonia ochracea* Herczek, 1993 🟡

genus: *Jozefus* Herczek, 1993

160. *Jozefus brunetus* Namyatova & Cassis, 2016 🟡

161. *Jozefus guineiensis* Herczek, 1993 🟡

162. *Jozefus monteithi* Namyatova & Cassis, 2016 🟡

genus: *Nesocrypha* Kirkaldy, 1908

163. *Nesocrypha corticicola* Kirkaldy, 1908 🟡

genus: *Paratopus* Herczek, 1993

164. *Paratopus brunocapitus* Namyatova & Cassis, 2016 🟡

165. *Paratopus flavocapitus* Namyatova & Cassis, 2016 🟡

166. *Paratopus ovatus* (Herczek, 1991) 🟡

genus: *Popoviana* Herczek & Popov, 1997

167. *Popoviana fijiensis* (Herczek, 1993) 🟡

tribe: Myiommini Bergroth, 1924

genus: *Namaquaropus* Akingbohungbe, 2004

168. *Namaquaropus niger* Akingbohungbe, 2004 🔵

subtribe: Myiommina Bergroth, 1924

genus: *Bongiella* Krüger, 2018

169. *Bongiella nodistylis* Krüger, 2018 🔵

genus: *Brailovskiocoris* Henry, 1980

170. *Brailovskiocoris nocturnus* (Brailovsky, 1976) 🟢🟣

genus: *Corticoris* McAtee & Malloch, 1922

171. *Corticoris infuscatus* Henry & Herring, 1979 🟢🟣

172. *Corticoris libertus* (Gibson, 1917) 🟢

173. *Corticoris mexicanus* Henry & Herring, 1979 🟣

174. *Corticoris pallidus* Henry, 1984 🟢

175. *Corticoris pintoi* Henry, 1984 🟢

176. *Corticoris pubescens* Henry, 1984 🟢

177. *Corticoris pulchellus* (Heidemann, 1908) 🟢

178. *Corticoris signatus* (Heidemann, 1908) 🟢

179. *Corticoris unicolor* (Heidemann, 1908) 🟢

genus: *Lidopiella* Henry, 1980

180. *Lidopiella slateri* Henry, 1980 🟣

genus: *Lidopus* Gibson, 1917

181. *Lidopus heidemanni* Gibson, 1917 🟢

182. *Lidopus schwarzi* (McAtee & Malloch, 1924) 🟣

genus: *Myiomma* Puton, 1872

183. *Myiomma adusta* Herczek, 2004 🔵

184. *Myiomma affinis* (Hoberlandt, 1952) 🔵

185. *Myiomma albalata* Namyatova & Cassis, 2016 🟡

186. *Myiomma albicoxa* Smith, 1967 🔵

187. *Myiomma albiscutellata* Smith, 1967 🔵

188. *Myiomma albostiolata* Krüger, 2018 🔵

189. *Myiomma altica* Ren, 1987 🔴

190. *Myiomma amaranion* Herczek & Popov, 2006 🟡

191. *Myiomma apicalis* Henry & Carpintero, 2012 🟣

192. *Myiomma argentinensis* Henry & Carpintero, 2012 🟣

193. *Myiomma austroccidens* Yasunaga, Yamada & Tsai, 2017 🔴

194. *Myiomma basseti* Namyatova & Cassis, 2016 🟡

195. *Myiomma belavadii* Yeshwanth, Chérot & Henry, 2021 🟤

196. *Myiomma bionotata* Henry & Carpintero, 2012 🟣

197. *Myiomma brasilianum* Henry, 1979 🟣

198. *Myiomma bredoi* Akingbohungbe, 1996
199. *Myiomma brunnea* Krüger, 2018
200. *Myiomma capeneri* Slater & Schuh, 1969
201. *Myiomma capitatum* Henry, 1979
202. *Myiomma choui* Lin & Yang, 2004
203. *Myiomma cixiiforme* (Uhler, 1891)
204. *Myiomma cobbeni* Akingbohungbe, 2003
205. *Myiomma confusa* Akingbohungbe, 1996
206. *Myiomma dundoensis* (Hoberlandt, 1952)
207. *Myiomma fasciata* Smith, 1967
208. *Myiomma ferruginea* Akingbohungbe, 1996
209. *Myiomma fieberi* Puton, 1872
210. *Myiomma fulva* Smith, 1967
211. *Myiomma fuscipes* Krüger, 2018
212. *Myiomma fusiforme* Henry, 1979
213. *Myiomma goellneri* Krüger, 2018
214. *Myiomma hemialba* (Carvalho, 1951)
215. *Myiomma impunctata* Smith, 1967
216. *Myiomma jankotejai* Herczek & Popov, 2006
217. *Myiomma juniperina* Linnavuori, 1975
218. *Myiomma keltoni* Henry, 1984
219. *Myiomma kentingense* Yasunaga, Yamada & Tsai, 2017
220. *Myiomma kukai* Yasunaga & Hayashi, 2002
221. *Myiomma lansburyi* (Carvalho, 1951)
222. *Myiomma latifrons* Herczek, 2004
223. *Myiomma linearis* Akingbohungbe, 1996
224. *Myiomma lutea* McAtee & Malloch, 1932
225. *Myiomma maculata* Akingbohungbe, 2003
226. *Myiomma mexicanum* Henry, 1979
227. *Myiomma milleri* (Hoberlandt, 1959)
228. *Myiomma minor* Akingbohungbe, 1996
229. *Myiomma minutum* Miyamoto, 1965
230. *Myiomma montana* Linnavuori, 1975
231. *Myiomma nigricole* Akingbohungbe, 2006
232. *Myiomma nigra* Smith, 1967
233. *Myiomma obscura* Akingbohungbe, 1996
234. *Myiomma ornatum* Henry, 1979
235. *Myiomma ostentans* Akingbohungbe, 1996
236. *Myiomma pallidopleura* Henry & Carpintero, 2012
237. *Myiomma pallipes* Henry & Carpintero, 2012
238. *Myiomma phuvasae* Yasunaga, Duanthisan & Yamada, 2016
239. *Myiomma piceicola* Akingbohungbe, 1996
240. *Myiomma qinlingensis* Qi, 2005
241. *Myiomma ramamurthyi* Yeshwanth, Chérot & Henry, 2021
242. *Myiomma rubida* Akingbohungbe, 1996
243. *Myiomma rubra* Smith, 1967
244. *Myiomma rubrooculatum* Henry, 1979
245. *Myiomma rubrovenata* Smith, 1967
246. *Myiomma samuelsoni* Miyamoto, 1965
247. *Myiomma schmitzi* Slater, 1976
248. *Myiomma schuhi* Henry, 1979
249. *Myiomma scotti* Herczek, 2004

250. *Myiomma scutellata* Henry & Carpintero, 2012
251. *Myiomma semipallidum* Henry, 1979
252. *Myiomma surinamensis* (Carvalho & Rosas, 1962)
253. *Myiomma takahashii* Yasunaga & Hayashi, 2002
254. *Myiomma uniformis* Henry & Carpintero, 2012
255. *Myiomma ussuriensis* Ostapenko, 2001
256. *Myiomma variabilis* Krüger, 2018
257. *Myiomma verticata* Smith, 1967
258. *Myiomma vittata* McAtee & Malloch, 1932
259. *Myiomma vittaticornis* Akingbohungbe, 1996
260. *Myiomma voigti*† (Popov & Herczek, 1992)
261. *Myiomma zandeana* Linnavuori, 1975
262. *Myiomma zhengi* Lin & Yang, 2004

genus: *Myiopus* Henry, 1980

263. *Myiopus woldai* Henry, 1980

genus: *Slateropus* Akingbohungbe, 1996

264. *Slateropus miriformis* (Slater & Schuh, 1969)
265. *Slateropus perplexus* Akingbohungbe, 1996

genus: *Wetmorea* McAtee & Malloch, 1924

266. *Wetmorea notabilis* McAtee & Malloch, 1924

subtribe: Plaumannocorina Herczek, 1993

genus: *Aristotelesia* Carvalho, 1947

267. *Aristotelesia carioca* Carvalho, 1947
268. *Aristotelesia fuscata* Henry & Carpintero, 2012
269. *Aristotelesia medialis* Henry & Carpintero, 2012

genus: *Joceliana* Carvalho, 1984

270. *Joceliana graziae* Carvalho, 1984

genus: *Plaumannocoris* Carvalho, 1947

271. *Plaumannocoris rarus* Carvalho, 1947

subtribe: Tottina Herczek, 1993

genus: *Paratotta* Herczek, 1993

272. *Paratotta orientalis* Herczek, 1993

genus: *Totta* Ghauri & Ghauri, 1983

273. *Totta puspae* Yasunaga & Duwal, 2006
274. *Totta rufercorna* Lin & Yang, 2004
275. *Totta zaherii* Ghauri & Ghauri, 1983

tribe: Sophianini Yasunaga, Yamada & Tsai, 2017

genus: *Alcecoris* McAtee & Malloch, 1924

276. *Alcecoris fraxinusae* Lin, 2004
277. *Alcecoris formosanus* Lin, 2004
278. *Alcecoris globosus* Carvalho, 1951
279. *Alcecoris lamellatus* (Ren & Yang, 1988)
280. *Alcecoris linyangorum* Yasunaga, Yamada & Tsai, 2017
281. *Alcecoris cochlearatus* Yasunaga, Yamada & Tsai, 2017
282. *Alcecoris periscopus* McAtee & Malloch, 1924
283. *Alcecoris heissi* Herczek & Popov, 2011

genus: *Sophianus* Distant, 1904

284. *Sophianus alces* Distant, 1904
285. *Sophianus kerzhneri* Lin, 2009
286. *Sophianus palawanensis* Taszakowski, Kim & Herczek, 2021

Incertae sedis

genus: *Hoffheinsoria*† Herczek & Popov, 2012

287. *Hoffheinsoria robusta*† Herczek & Popov, 2012

genus: *Isomyiomma*† Herczek, Popov & Drohojowska, 2020

288. *Isomyiomma hirta*† Herczek, Popov & Drohojowska, 2020

genus: *Sagarmathametopus* Yasunaga & Duwal, 2006

289. *Sagarmathametopus fuscescens* Yasunaga & Duwal, 2006 ●

Isometopinae is a group inhabiting mainly the Old World, from which 222 out of 266 extant species are known (83%). The greatest species diversity occurs in the Afrotropical region—95 species. Seventy-four species are known from the Palearctic region, 40 from the Indomalayan region and 19 from the Australasian region. The New World is represented by only 44 species, 30 in the Neotropical region and 14 in the Nearctic region.

Over the last 30 years, significant progress has been achieved in studying the fauna of the Afrotropical, Palearctic, Australasian, and especially the Indomalayan region (67% of known species from the latter area have been described). Relatively little attention has been paid to the New World Isometopinae. Ten Neotropical species (Hernandez 1998, Henry & Carpintero 2012) and no Nearctic species were described.

The occurrence of higher taxa in particular zoogeographic regions is presented in Table 1. Diphlebini are a group limited in range to the New World. Gigantometopini and Sophianini occur in Australasian and Indomalayan regions, as well as warm areas of the Palearctic. Representatives of Isometopini are known from the Old World, while Myiommini are the most widely distributed tribe of jumping tree bugs and are characterized by a cosmopolitan range. There is no modern analysis of the distribution of Isometopinae. Discussion of distribution was presented by Herczek (1993) and Namyatova & Cassis (2016).

TABLE 1. Summary of abundance and zoogeography of higher taxa of extant Isometopinae. Explanation of color markings of zoogeographical regions: ●—Afrotropical, ●—Australasian, ●—Indomalayan, ●—Nearctic, ●—Neotropical, ●—Palearctic.

tribe	number of genera	number of species	subtribe	number of genera	number of species
Diphlebini ●●	1	4		-	
Gigantometopini ●●●	8	16		-	
Isometopini ●●●●	14	127	Isometopina ●●●●	8	117
			Nesocryphina ●	6	10
Myiommini ●●●●●●	15	107	Myiommina ●●●●●●	9	97
			Plaumannocorina ●	3	5
			Tottina ●●●	2	4
			incertae sedis ●	1	1
Sophianini ●●●	2	11		-	
incertae sedis ●	1	1		-	
Together	41	266			

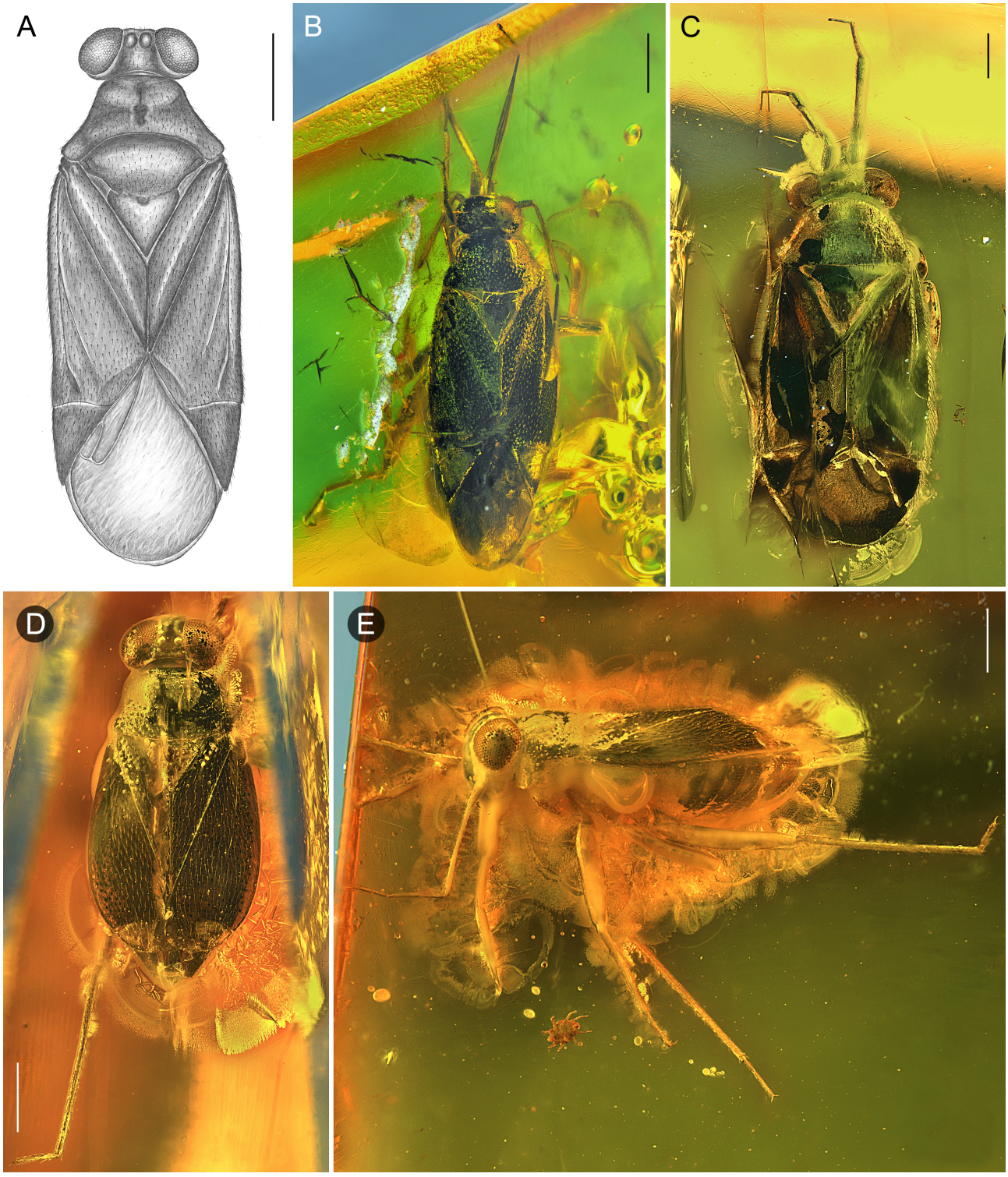

FIGURE 4. Fossil representatives of Isometopinae. **A**. *Electromyiomma polonicum*; **B**. *Archemyiomma schaeferi*; **C**. *Hoffheinsoria robusta*; **D**, **E**. *Clavimyiomma henryi*.

Fossils

Isometopinae live on the bark of trees (Namyatova & Cassis 2016, Yasunaga 2017), which predisposes them, like Cylapinae (Wolski 2021), to be more easily fossilized in resins than the other groups of Miridae, given that most of the described fossils are cylapines and isometopines (Schuh & Weirauch, 2020). Nevertheless, the first species

of fossil representative of jumping tree bugs was described just over 30 years ago (Popov & Herczek 1992). As we already mentioned, seven genera and 23 species of Isometopinae are of fossil taxa (Popov & Herczek 2008; Herczek & Popov 2012, 2014; Herczek *et al.* 2013, 2020; Kim & Jung 2021; Kim *et al.* 2023). Eight species classified into four genera belong to the entirely fossil tribe Electromyiommini (Fig. 4A, B, D, E). Until recently, the aforementioned tribe also included the genus *Metoisops*, which, with 11 species, is the most numerous of the fossil genera of Isometopinae. In 2023, Kim *et al.* transferred the *Metoisops* to the Gigantometopini. Two extant genera, *Diphleps* and *Myiomma*, have one fossil representative each. In addition, it is herein noticed that two species, *Hoffheinsoria robusta* (Fig. 4C) and *Isomyiomma hirta*, currently have *incertae sedis* status. Except *Diphleps yenli*, which is known from Miocene Dominican amber (Santiago-Blay & Poinar 1993), all other fossil representatives of jumping tree bugs come from Eocene Baltic amber (Popov & Herczek 2008; Herczek & Popov 2012, 2014; Herczek *et al.* 2013, 2020; Kim & Jung 2021; Kim *et al.* 2023).

The *incertae sedis* taxa and the genera included in Electromyiommini certainly require further research regarding their systematic position (Kim *et al.* 2023).

Biology

Jumping tree bugs have a cryptic habit, which results in rare observations in their natural environment. They are typically collected on tree bark or in low light and damp conditions (Akingbohungbe 1996, Yeshwanth *et al.* 2021). The few papers that mention the biology of Isometopinae indicate that they are zoophagous, feeding commonly on scales (Wheeler & Henry 1978, Ghauri & Ghauri 1983, Henry 1984, Akingbohungbe 1996, Wheeler 2001). However, this information only applies to a few species in the genera *Diphleps* (Diphlebini), *Isometopus* and *Paloniella* (Isometopini) and *Corticoris*, *Myiomma* & *Lidopus* (Myiommini). We still have no knowledge of the trophic relationships of representatives of Gigantometopini and Sophianini. Photos of representatives of these tribes (and other isometopines), included in various papers (e.g., Kim & Jung 2016; Yeshwanth *et al.* 2021) as well as images increasingly available on the Internet, show bugs that appear to feed on lichen growing on tree bark (Fig. 3). These observations confirm previous suggestions of several authors (McAtee & Malloch 1924, Schuh 1976). The high quality of the abovementioned photos enables us to see what the bugs feed; however, there are no visible arthropods. It may be conceivable that feeding on scales is opportunistic feeding due to the fact that scales are immobile, and phytophagous insects (including plant bugs) sometimes feed on the other arthropods (Cobben 1978, Eubanks *et al.* 2003). In addition, previous phylogenetic studies hypothesized the close relationship between Isometopinae and Cylapinae (Schuh *et al.* 2009, Oh *et al.* 2023). Given that relatively small groups within Miridae (e.g., Bryocorinae, Cylapinae, and Isometopinae) have more specific feeding habits, and the cylapines are well known as to a large extent fungivorous group (Gossner & Damken 2018, Kim *et al.* 2019, Wolski 2021), it is highly possible that the isometopines are lichen feeder and not strictly zoophagous.

Namyatova & Cassis (2016) presented a discussion of the distribution and host plant associations of the subfamily on a worldwide basis. Trees or large shrubs are most plant records for Isometopinae. Nevertheless, few species are known from small shrubs, vines or herbs. The greatest number of species was recorded from angiosperms.

Conclusions

Most of the work on Isometopinae is strictly taxonomic. Papers on micromorphology and anatomy, zoogeography and biology are very few. Upcoming challenges include describing nymphal stages; learning about biology, especially trophic relationships; establishing the systematic position of *Diphleps*; redescription and diagnosis of the dumping genera *Isometopus* and *Myiomma* as well as fossil tribe Electromyiommini. Finally, jumping tree bugs require a globally based systematic to integrate the largely Old and New World classifications.

It seems that these goals may be achieved, especially considering the possibility of observing Isometopinae in their natural environment, which is becoming increasingly frequent thanks to the developing citizen science trend. Hopefully these life habit observations can be linked to the published record to continue to build our holistic knowledge of these enigmatic insects over the next thirty years.

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