

Modern Classification and Distribution of the Family Issidae Spinola (Homoptera, Auchenorrhyncha: Fulgoroidea)

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Abstract—The modern classification of the family Issidae s. str. is presented according to which the family consists of 3 tribes: Issini, Hemisphaeriini, and Parahiraciini and comprises a total of 994 species and subspecies in 159 genera. The largest tribe, Issini, is distributed worldwide and comprises 129 genera with 755 species and subspecies. The tribes Hemisphaeriini and Parahiraciini are much smaller and mostly distributed in the Indo-Malayan Realm with some taxa also present in the Eastern Palaearctic and the Oceania. The tribe Hemisphaeriini consists of 15 genera with 187 species and subspecies while Parahiraciini includes 14 genera with 38 species. The Palaearctic and Indo-Malayan Realms have the richest faunas of Issidae. In contrast, Equatorial Africa has a very poor fauna of the family, whereas the Australian fauna is still almost undescribed. *Chimetopon camerunensis* Schmidt is recorded for the first time from Central African Republic and Gabon, and *Sarima erythrocyclus* Fennah, from Taveuni Island (Fiji).

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The goal of the present work is to summarize changes in classification of the family Issidae Spinola, 1839 which have appeared during the last 15 years, and to characterize the distribution of Issidae s. str.

Since publication of Fennah's work (1954), classification of the family Issidae has undergone considerable changes (Gnezdilov, 2008). Melichar's point of view (1906) on the independence of the family Caliscelidae Amyot et Serville, 1843 prevailed again (Emeljanov, 1999; Gnezdilov and Wilson, 2006; Gnezdilov, 2013d). Recently, I have suggested that the family Acanaloniidae Amyot et Serville, 1843 should be considered in a restricted sense, including only American genera (Gnezdilov, 2012b, 2012c, 2013b). The subfamily Trienopinae Fennah, 1954 was transferred to the family Tropiduchidae Stål, 1866 in the rank of a tribe (Gnezdilov, 2007, 2013b); the subfamily Tonginae Kirkaldy, 1907 and the tribe Colpopterini Gnezdilov, 2003 were transferred to the family Nogodiniidae Melichar, 1898 with their ranks changed to those of a tribe and a subfamily, respectively (Gnezdilov, 2007, 2012d), whereas the tribe Adenissini Dlabola, 1980 was placed into the family Caliscelidae (Gnezdilov, 2003, 2013d; Gnezdilov and Wilson, 2006). Some genera and species previously listed within Issidae (Metcalf, 1958) were transferred to the families Tropiduchidae, Nogodiniidae, and Ricaniidae (Gnezdilov, 2007, 2009a, 2009b, 2012a, 2013b; Stroiński et al., 2011). Thus, the scope of the family Issidae s. str. was reduced to three tribes: Issini Spinola, 1839; Hemisphaeriini Melichar, 1906; Parahiraciini Cheng et Yang, 1991, included into the nominotypical subfamily.

Taking into account all the taxonomic changes in the family Issidae published before July 2013 (Gnezdilov, 2002a, 2002b, 2003, 2004, 2005, 2009, 2010, 2012a, 2013a; Gnezdilov and Mazzoni, 2004; Gnezdilov et al., 2004, 2011; Gnezdilov and Wilson, 2005, 2007a, 2007b, 2008; Gnezdilov and O'Brien, 2006b; Gnezdilov and Malenovský, 2008; Gnezdilov and Fletcher, 2010; Gnezdilov and Hayashi, 2013), and also data in the work on the genus *Eusarima* Yang, 1994 prepared by me (Gnezdilov, in press), a total of 994 species and subspecies in 159 genera are known in the family Issidae Spinola s. str. The family is distributed in all the zoogeographic realms except the Antarctic. The real number of species in it must be considerably greater since the faunas of many regions, especially tropical ones, remain undescribed.

The family Issidae s. str., namely the tribe Issini, has been reliably known since the Early/Middle Miocene from Mexican and Dominican ambers in which the recent genera of the Neotropical fauna, in particular, the genus *Thionia* s. l., are represented (Grimaldi

and Engel, 2005, figs 2.25, 2.26; Stroiński and Szwed, 2008). The taxonomic position of other fossil species described in the family Issidae s. l. (Szwedo et al., 2004) needs to be elucidated.

The material studied is deposited in the following collections: MNHN (Muséum national d'Histoire naturelle, Paris, France), RBINS (Institut royal des Sciences naturelles de Belgique, Bruxelles, Belgique), ZSM (Zoologische Staatssammlung, München, Deutschland), and SAM (the South Australian Museum, Adelaide, Australia).

The system and boundaries of biogeographic realms follow those of Udvardy (1975), with the boundaries of the Western and Eastern Palaearctic and Nearctic emended by Emeljanov (1974). New Guinea is formally included in Oceania according to the scheme of Udvardy in spite of the fact that its fauna of Issidae is very similar to that of the Indo-Malayan Realm, since within the frame of this work it would be impossible to emend high-rank biogeographic boundaries based on the material on one family.

The genera are arranged alphabetically in the list below, with abbreviated names of the zoogeographic units in which the particular genus was recorded: WPL, Western Palaearctic Subrealm; EPL, Eastern Palaearctic Subrealm; AF, Afrotropical; IM, Indo-Malayan; OC, Pacific (Oceania); AUS, Australian; NA, Nearctic; NT, Neotropical Realm. The numbers of species and subspecies in the genus are also specified.

FAMILY ISSIDAE SPINOLA, 1839

Subfamily ISSINAE Spinola, 1839

Tribe Issini Spinola, 1839

Issoides Spinola, 1839 : 204. Type genus *Issus* Fabricius, 1803.

= Thioniinae Melichar, 1906. Type genus *Thionia* Stål, 1859.

I have suggested the system of subtribes of Issini (Gnezdilov, 2002c) which, however, was based solely on material of the Western Palaearctic fauna. Attribution of other genera needs further research.

1. **Abolloptera** Gnezdilov et O'Brien, 2006—1 (NA)
2. **Agalmatium** Emeljanov, 1971—6 (WPL)
3. **Alloscelis** Kusnezov, 1930—1 (WPL)
4. **Annisa** Stål, 1862—3 (NT)

5. **Amphiscepa** Germar, 1830—7 (NT)
6. **Anatolodus** Dlabola, 1982—5 (WPL)
= *Logvinenkoana* Gnezdilov, 2002
7. **Anatonga** Emeljanov, 2001—1 (WPL)
8. **Apsadaroptyx** Kirkaldy, 1907—1 (AUS)
9. **Argepara** Gnezdilov et Brien, 2008—2 (NT)
10. **Aztecus** Gnezdilov et O'Brien, 2008—6 (NT)
11. **Balduza** Gnezdilov et O'Brien, 2006—2 (NA)
12. **Balisticha** Jacobi, 1941—1 (IM)
13. **Bergevinium** Gnezdilov, 2003—8 (WPL)
14. **Bootheca** Emeljanov, 1964—1 (WPL)
15. **Brachyprosopa** Kusnezov, 1929—2 (WPL)
16. **Brahmaloka** Distant, 1906—1 (IM)
17. **Bubastia** Emeljanov, 1975—22 (WPL)
18. **Bumaya** Gnezdilov et O'Brien, 2008—1 (NT)
19. **Caepovultus** Gnezdilov et Wilson, 2007—2 (WPL)
20. **Cavatorium** Dlabola, 1980—4 (WPL)
21. **Celyphoma** Emeljanov, 1971—27: 24 (WPL) + 3 (EPL)
22. **Cheiloceps** Uhler, 1895—5 (NT)
23. **Chimetopon** Schmidt, 1910—1 (AF)
24. **Chlamydoptyx** Kirkaldy, 1907—6 (AUS)
= *Phaeopteryx* Kirkaldy, 1907
25. **Clybeccus** Gnezdilov, 2003—1 (WPL)
26. **Conosimus** Mulsant et Rey, 1855—6 (WPL)
27. **Coruncanus** Distant, 1916—1 (IM)
28. **Corymbius** Gnezdilov, 2002—1 (WPL)
29. **Darwallia** Gnezdilov, 2010—1 (IM)
30. **Diceroptera** Gnezdilov, 2011—1 (NT)
31. **Dracela** Signoret, 1861—3 (NT)
32. **DeLONGANA** Caldwell, 1945—1 (NT)
33. **Devagama** Distant, 1906—1 (IM)
34. **Duroides** Melichar, 1906—2 (NT)
35. **Eupilis** Walker, 1857—5 (IM)
36. **Euroxenus** Gnezdilov, 2009—1 (IM)
37. **Eusarima** Yang, 1994—34: 32 (IM) + 1 (WPL) + 1 (EPL)
(*Nepalium* Dlabola, 1997 : subgenus)
38. **Eusudasina** Yang, 1994—1 (IM)

39. **Euxaldar** Fennah, 1978—1 (IM)
 40. **Exortus** Gnezdilov, 2004—2 (NT)
 41. **Falcidius** Stål, 1866—10 (WPL)
 42. **Fieberium** Dlabola, 1980—13 (WPL)
 = *Lyrofrontium* Dlabola, 1982
 43. **Gabaloecca** Walker, 1870—1 (OC)
 44. **Givaka** Distant, 1906—1 (IM)
 45. **Granum** Gnezdilov, 2003—1 (WPL)
 46. **Hemisobium** Schmidt, 1911—3 (AF)
 47. **Heremon** Kirkaldy, 1903—5 (NT)
 48. **Hysteropterum** Amyot et Serville, 1843—6 (WPL)
 49. **Jagannata** Distant, 1906—2 (IM)
 50. **Iberanum** Gnezdilov, 2003—2 (WPL)
 51. **Ikonza** Hesse, 1925—1 (AF)
 52. **Inflatodus** Dlabola, 1982—6 (WPL)
 53. **Incasa** Gnezdilov et O'Brien, 2008—2 (NT)
 54. **Iranodus** Dlabola, 1980—6 (WPL)
 55. **Issus** Fabricius, 1803—32 (WPL)
 = *Archissus* Sergel, 1986
 56. **Kathleenum** Gnezdilov, 2004—2 (NA)
 57. **Katonella** Schmidt, 1911—4 (AF)
 58. **Kervillea** Bergevin, 1918—20 (WPL)
 = *Falcidiopsis* Kusnezov, 1930
 = *Hysterella* Logvinenko, 1977
 = *Quadrastylum* Dlabola, 1979
 59. **Kivupterum** Dlabola, 1985—5 (AF)
 60. **Kodaiana** Distant, 1916—1 (IM)
 61. **Kodaianella** Fennah, 1956—4: 3 (IM) + 1 (EPL/IM)
 62. **Kovacsiana** Synave, 1956—5: 4 (AF) + 1 (AF/WPL)
 63. **Latematium** Dlabola, 1979—3 (WPL)
 64. **Latilica** Emeljanov, 1971—10 (WPL)
 = *Dalmatium* Dlabola, 1980
 65. **Latissus** Dlabola, 1974—1 (WPL)
 66. **Lethierium** Dlabola, 1980—3 (WPL)
 67. **Libanissum** Dlabola, 1980—5 (WPL)
 = *Irakopterum* Dlabola, 1985
 68. **Lindbergatium** Dlabola, 1984—9 (WPL)
 69. **Lusanda** Stål, 1859—1 (IM)
 70. **Macrodarumoides** Che, Zhang et Wang, 2012—1 (IM)
 71. **Mulsantereum** Gnezdilov, 2002—4 (WPL)
 72. **Mycterodus** Spinola, 1839—79 (WPL)
 73. **Narayana** Distant, 1906—10 (IM)
 = *Sudasina* Distant, 1906
 74. **Neokodaiana** Yang, 1994—1 (IM)
 75. **Neosarima** Yang, 1994—2 (IM)
 76. **Nikomiklukha** Gnezdilov, 2010—3 (IM)
 77. **Numidius** Gnezdilov, Guglielmino et D'Urso, 2003—1 (WPL)
 78. **Orinda** Kirkaldy, 1907—2 (AUS)
 79. **Oronoqua** Fennah, 1947—2 (NT)
 80. **Palaeolithium** Gnezdilov, 2003—1 (WPL)
 81. **Palmallorcus** Gnezdilov, 2003—5 (WPL)
 = *Barbarissus* Gnezdilov, 2003
 82. **Pamphylium** Gnezdilov et Wilson, 2007—2 (WPL)
 83. **Paralixes** Caldwell, 1945—5: 3 (NA) + 1 (NT) + 1 (NA/NT)
 84. **Paranipeus** Melichar, 1906—1 (NT)
 85. **Parasarima** Yang, 1994—1 (IM)
 86. **Pentissus** Dlabola, 1980—1 (WPL)
 87. **Phasmena** Melichar, 1902—13: 8 (WPL) + 5 (EPL)
 88. **Picumna** Stål, 1864—10: 8 (NT) + 2 (NA)
 89. **Proteinissus** Fowler, 1904—8 (NT)
 = *Prothona* Caldwell, 1945
 = *Plummerana* Caldwell, 1945
 90. **Pseudochoutagus** Che, Zhang et Wang, 2011—2 (IM)
 91. **Pseudohemisphaerius** Melichar, 1906—1 (WPL)
 92. **Quadriva** Ghauri, 1965—12 (WPL)
 = *Hysterodus* Dlabola, 1980
 93. **Radha** Melichar, 1903—1 (IM)
 94. **Redarator** Distant, 1916—2 (IM)
 95. **Rhissolepus** Emeljanov, 1971—4 (WPL)
 96. **Samantiga** Distant, 1906—2 (IM)
 97. **Sarima** Melichar, 1903—23: 19 (IM) + 3 (OC) + 1 (AUS)

98. **Sarimodes** Matsumura, 1916—1 (IM)
= *Paravindilis* Yang, 1994
99. **Sarnus** Stål, 1866—4 (NT)
100. **Scorlupaster** Emeljanov, 1971—5 (WPL)
101. **Scorlupella** Emeljanov, 1971—10 (WPL)
102. **Semissus** Melichar, 1906—5 (WPL)
= *Theryana* Bergevin, 1922
103. **Sfaxis** Bergevin, 1917—4 (WPL)
= *Planocostium* Dlabola, 1982
104. **Sinesarima** Yang, 1994—3 (IM)
105. **Sivaloka** Distant, 1906—1 (IM)
106. **Stilbometopius** Gnezdilov et O'Brien, 2006—
1 (NA)
107. **Sundorrhinus** Gnezdilov, 2010—1 (IM)
108. **Syrgis** Stål, 1870—6 (IM)
109. **Tatva** Distant, 1906—1 (IM)
110. **Tautoprosopa** Emeljanov, 1978—1 (WPL)
= *Verticisium* Dlabola, 1979
111. **Tempsa** Stål, 1866—5 (IM)
112. **Tetrica** Stål, 1866—17: 11 (IM) + 3 (OC) +
2 (AUS) + 1 (EPL)
113. **Thabena** Stål, 1866—14 (IM)
= *Cibyra* Stål, 1861 (nom. praeocc.)
= *Gelastyra* Kirkaldy, 1904
= *Gelastyrella* Yang, 1994
= *Borbonissus* Bonfils, Attié et Reynaud, 2001
114. **Thabenoides** Distant, 1916—2 (IM)
= *Paratetrica* Distant, 1916
115. **Thabenula** Gnezdilov, Soulier-Perkins
et Bourgoïn, 2011—1 (IM)
116. **Thionia** Stål, 1859—72: 64 (NT) + 8 (NA)
117. **Thioniamorpha** Metcalf, 1938—1 (NT)
118. **Thioniella** Metcalf, 1938—1 (NT)
119. **Tingissus** Gnezdilov, 2003—2 (WPL)
120. **Traxanellus** Caldwell, 1945—1 (NT)
121. **Traxus** Metcalf, 1923—2 (NA)
122. **Tshurtshurnella** Kusnezov, 1927—40 (WPL)
123. **Tylanira** Ball, 1936—2 (NA)
124. **Ulixes** Stål, 1861—3 (NT)
125. **Ulixoides** Haupt, 1918—1 (NT)
126. **Vindilis** Stål, 1870—1 (IM)
127. **Vishnuloka** Distant, 1906—2 (IM)
= *Ardelia* Melichar, 1907

128. **Webbisanus** Dlabola, 1983—1 (WPL)
129. **Zopherisca** Emeljanov, 2001—3 (WPL)

Tribe **Parahiraciini** Cheng et Yang, 1991

Parahiraciinae Cheng et Yang, 1991 : 338. Type ge-
nus *Parahiracia* Ôuchi, 1940.

1. **Bardunia** Stål, 1863—8: 6 (IM) + 2 (OC)
= *Prosonoma* Melichar, 1906
2. **Duriopsilla** Fennah, 1956—1 (EPL)
3. **Flavina** Stål, 1861—9 (IM)
= *Dolia* Kirkaldy, 1907
= *Nilalohita* Distant, 1906
4. **Fortunia** Distant, 1909—4: 3 (EPL) + 1 (IM)
= *Clipeopsilus* Jacobi, 1944
= *Parahiracia* Ôuchi, 1940
5. **Fusiissus** Zhang et Chen, 2010—1 (EPL)
6. **Mincopius** Distant, 1909—1 (IM)
7. **Narinosus** Gnezdilov et Wilson, 2005—1 (EPL)
8. **Neodurium** Fennah, 1956—4: 2 (IM) +
1 (IM/EPL) + 1 (EPL)
9. **Neotetricodes** Zhang et Chen, 2012—2 (IM)
10. **Paratetricodes** Zhang et Chen, 2010—1 (EPL)
11. **Pinocchias** Gnezdilov et Wilson, 2005—1 (IM)
12. **Scantinius** Stål, 1866—2 (IM)
= *Dindinga* Distant, 1909
13. **Tetricodes** Fennah, 1956—2: 1 (EPL) +
1 (EPL/IM)
14. **Folifemurum** Che, Zhang et Wang, 2013—
1 (IM)

Tribe **Hemisphaeriini** Melichar, 1906

Hemisphaeriidae Melichar, 1906 : 3. Type genus
Hemisphaerius Schaum, 1850.

1. **Bolbosphaerius** Gnezdilov, 2013—1 (IM)
2. **Choutagus** Zhang, Wang et Che, 2006—1 (IM)
3. **Epyhemisphaerius** Chan et Yang, 1994—1 (IM)
4. **Euhemisphaerius** Chan et Yang, 1994—4 (IM)
5. **Gergithoides** Schumacher, 1915—6: 4 (IM) + 1
(EPL/IM) + 1 (EPL)
= *Daruma* Matsumura, 1916 (nom. praeocc.)
= *Darumara* Metcalf, 1952
6. **Gergithus** Stål, 1870—65: 55 (IM) + 6 (EPL/IM)
+ 3 (EPL) + 1 (distribution unknown)
= *Ishiharanus* Hori, 1969

7. **Hemiphile** Metcalf, 1952—1 (OC)
8. **Hemisphaerius** Schaum, 1850—95: 62 (IM) + 24 (OC) + 3 (IM/EPL) + 1 (EPL) + 1 (IM/OC) + 4 (distribution unknown)
9. **Hemisphaeroides** Melichar, 1903—2 (IM)
10. **Hysteropterissus** Melichar, 1906—1 (OC)
11. **Hysterosphaerius** Melichar, 1906—1 (IM)
12. **Macrodaruma** Fennah, 1978—1 (IM)
13. **Mongoliana** Distant, 1909—6: 5 (IM) + 1 (IM/EPL)
14. **Neogergithoides** Sun, Meng et Wang, 2012—1 (IM)
15. **Rotundiforma** Meng, Wang et Qin, 2013—1 (IM)

*Species of Uncertain Taxonomic Position
in the Family Issidae*

1. *Gilda vittiventris* Walker, 1870 (OC)
2. *Hysteroodus bloetei* Dlabola, 1982 (WPL)
3. *Hysteropterum pallidum* Melichar, 1906 (WPL)
4. *Hysteropterum subangulare* Rey, 1891 (WPL)
5. *Hysteropterum boreale* Melichar, 1902 (IM). The species does not belong to the genus *Hysteropterum* Amyot et Serville (unpublished data of V.M. Gnezdilov).
6. *Hysteropterum sodale* Walker, 1870 (IM)
7. *Issus algiricus* Lucas, 1849 (WPL)
8. *Issus concolor* Walker, 1851 (type locality unknown)
9. *Issus harimensis* Matsumura, 1913 (EPL). The species does not belong to the genus *Issus* Fabricius (unpublished data of V.M. Gnezdilov).
10. *Issus servillei* Spinola, 1839 (NT)
11. *Issus walkeri* Metcalf, 1958 (IM)
12. *Libanissum malickyi* Dlabola, 1989 (WPL)
13. *Paratetrica distanti* Baker, 1927 (IM)
14. *Thabenoides smedleyi* Baker, 1927 (IM)

Genera not Belonging to the Family Issidae

Buca Walker, 1858, a monotypic genus from Brazil, probably belonging to the family Tropiciduchidae Stål.

Ziartissus Qadri et Mirza, 1966, a monotypic genus from Pakistan. Judging by the description (Qadri

and Mirza, 1966), it does not belong to the family Issidae, yet elucidation of its taxonomic position requires the study of the type material whose location is unknown.

New Faunistic Records

Sarima erythrocyclus Fennah, 1950.

Material. Fiji. 1 ♀, Fiji, Taveuni, May, A.M. Lea, "S. Austr. Museum specimen" (SAM).

Chimetopon camerunensis Schmidt, 1910.

Material. Cameroon. 1 ♀, Nkolbisson, 2.IV.1968, test de Meguémé, B. de Miré leg. (MNHN); 1 ♀, Nkolbisson, 4.X.1968, B. de Miré leg. (MNHN); 1 ♂, Caméroun-Bi, Nkolbisson -r. Mgob-Doum, 26.VII.1963, L. Segers leg. (ZSM); 1 ♂, Ebedda, II.1959, J. Mouchet leg. (MNHN); 1 ♂, Ebom, 3.XII.1969, "Test Cacao" (RBINS); 1 ♂, Nyemeyong, Juillet 1969, "Test Cacao" (MNHN); 1 ♀, Nyemeyong, 24.VI.1969, "Test Cacao" (MNHN); 1 ♀, Etoa, 4.XI.1969, "Test Cacao" (MNHN); 1 ♂, Evin-dissi, Août 1967, "Test Cacao" (MNHN); 1 ♀, Oban, 13.III.1973, "Test Cacao" (MNHN); 1 ♀, Anala II, 28.IX.1967, "Test cacaoyer" (MNHN); 1 ♂, N Kong-Bilanda, 13.I.1970, "Test Cacao" (MNHN); 1 ♀, Ebakoua, 5.I.1970, "Test Cacao" (MNHN); 1 ♀, Metoui, 5.XI.1970, "Test Cacao" (MNHN). **Central African Republic.** 1 ♂, Boukoko, 15.V.1968, M. Boulard leg. (MNHN). **Gabon.** 1 ♂, Ipassa station, 30.IV–16.V.1974, piège de Malaise, Mission M. Donskoff et J. Le Breton (RBINS).

Traits of Distribution of the Family Issidae

The universally distributed tribe Issini is the largest in the family; it comprises 129 genera with 755 species and subspecies. The tribes Hemisphaeriini Melichar (15 genera with 187 species and subspecies) and Parahiraciini Cheng et Yang (14 genera with 38 species), which considerably cede to Issini in species richness, are mainly distributed in the Indo-Malayan Realm, only marginally advancing into the Eastern Palearctic and the Oceania.

Representatives of the family are absent in South Africa (with the exception of one species in North Namibia), on Madagascar and the Seychelles, in New Zealand (Larivière et al., 2010), and on Tasmania (M.J. Fletcher, personal communication). In Oceania, Issidae are known only from New Guinea, some small Indonesian islands, the Solomon Islands, and Fiji.

The regional faunas are studied very unevenly. For example, the known fauna of Issidae on one of the largest islands, New Guinea, counts only 14 species described by Walker (1870) and Melichar, (1906) more than 100 years ago, whereas the well-studied fauna of Taiwan includes 80 species (Chan and Yang, 1994; Chan et al., 2013). Even by comparing the areas of these two islands, with no account of landscape differences, one can conclude that the fauna of New Guinea is known by only 0.7%.

The known Palaearctic fauna includes 64 genera with 445 species and subspecies. The best studied is the fauna of the Western Palaearctic counting 51 genera with 407 species (here and below, species and genera with ranges positioned in two realms or subrealms are taken into account in each of these units); all of them belong to the tribe Issini, 47 genera being endemic to the subrealm. The fauna of the Eastern Palaearctic is much poorer, comprising 15 genera with 38 species and subspecies; yet, besides Issini (4 genera, 11 species), it includes representatives of the tribes Parahiraciini (7 genera, 11 species) and Hemisphaeriini (4 genera, 16 species and subspecies), 4 monotypic genera of Parahiraciini being endemic to this subrealm. Regular description of the rich fauna of China has only started, and the number of genera and species known from the Eastern Palaearctic will certainly increase in the future.

The second in the degree of exploration and the number of the species described is the Indo-Malayan fauna: 62 genera with 330 species and subspecies, including 39 genera and 152 species of the tribe Issini (33 endemic genera), 10 genera and 27 species of Parahiraciini (6 endemic genera), and 13 genera and 151 species and subspecies of Hemisphaeriini (9 endemic genera).

The fauna of the Neotropical Realm counts 25 genera with 137 species and subspecies of the tribe Issini, 22 genera being endemic. The apparent scarcity of the Neotropical fauna as compared with those of the Western Palaearctic and the Indo-Malayan Realm can be explained by insufficient knowledge of Central and South America. Revision of the New World genera of Issidae has started only recently (Gnezdilov and O'Brien, 2006b, 2008), whereas the largest genus of the tribe Issini, *Thionia*, is now regarded as composite; therefore, further study is required to resolve the structure of the complex *Thionia* s.l. (Stroiński and Szwedlo, 2008).

In the Nearctic, Issidae are present only in the south of the US, where the northern distribution boundary of the Neotropical genera passes. Issidae must have disappeared from the greater part of North America and Europe, because the tropical (subtropical) climate ceased to exist in those territories since the Miocene (Davis et al., 2002). The Nearctic fauna consists of 9 genera with 24 species of the tribe Issini, 6 genera being endemic to it.

The fauna of the Afrotropical Realm is formed only by 6 genera of the tribe Issini with 19 species, most of the genera (5) being endemic. The South African species previously included in the family Issidae (Fennah, 1967a) belong to the families Caliscelidae (Caliscelini), Tropicuchidae (Gaetuliini = Elicini), and Nogodinidae (Mithymnini) (Gnezdilov, 2007; Gnezdilov and Bourgoin, 2009). *Isobium gibbosum* Melichar, 1906, originally described from Madagascar in the family Issidae (Melichar, 1906), in fact belongs to the family Ricaniidae (Stroiński et al., 2011). The only reliably known representative of the family in South Africa is *Ikonza lawrencei* Hesse, 1925 from North Namibia (Hesse, 1925).

Most of the species listed in the family Issidae from the Mascarenes (Williams, 1982) and Seychelles (Distant, 1909, 1917; Holzinger et al., 2008) actually belong to the families Nogodinidae (Tongini) and Tropicuchidae (Trienopini), respectively (Gnezdilov, 2007, 2009b). It is interesting to note that the fauna of Nogodinidae from the Seychelles and Mascarenes is formed only by the species of the tribe Tongini, which are distributed in the Indo-Malayan, Australian, and Pacific Realms but are absent in continental Africa. Two species really belonging to Issidae are known only from the Réunion Island (Bonfils et al., 2001; Gnezdilov, 2009b); they also represent the Indo-Malayan fauna but must have been introduced to the island already in the historical time (Gnezdilov, 2009b), since Réunion is a volcanic island only 2 million years old (Richardson et al., 2001), whereas no species of Issidae occur in South Africa and on Madagascar which could have been the most likely faunistic "donors." The species *Hysteropterum solidum* Melichar, 1911 and *H. ecarinatum* Synave, 1956, described from East and South Africa, respectively (Melichar, 1911; Synave, 1956), belong to the family Nogodinidae (Gnezdilov, 2012a).

The fauna of Oceania is comparatively poor, comprising only 8 genera with 37 species and subspecies: 3 genera and 7 species of Issini (1 endemic genus),

1 genus and 2 species of Parahiraciini, and 3 genera and 27 species and subspecies of Hemisphaeriini (2 endemic genera). The species previously described in the family Issidae from the small islands of Oceania (Distant, 1913; Fennah, 1958, 1967b), belong to the family Nogodinidae (Tongini), with the exception of *Sarima erythrocyclus* Fennah, 1950, recorded on three islands of the Fiji Archipelago: Viti Levu, Ovalau, and Taveuni (Fennah, 1950; Wilson, 2009; see above), and *Hemisphaerius penumbrosus* Fennah, 1955 from Santa Isabel Island (the Solomon Islands) (Fennah, 1955). Thus, Taveuni Island, which is crossed by the 180° meridian, may be considered the easternmost point of the family distribution.

The fauna of the Australian Realm is practically undescribed: 5 genera with 12 species of the tribe Issini (3 endemic genera) are known only from Queensland and New South Wales (Gnezdilov and Fletcher, 2010). The whole continent, with the exception of its eastern part has not been studied!

DISCUSSION

I share the opinion of Emeljanov (1972), Eskov (1984), Sergeev (2010), and other authors that it is the natural conditions which determine the pattern of distribution of recent species; therefore, the range of a species does not fully reflect the history of its dispersal. For instance, the global climate changed from glaciations to warmings not less than 20 times during the Pleistocene, every cycle lasting about 10 000 years (Gibbs, 2007). It is clear that such events were followed by changes both in the species composition of communities and in the ranges of some species which survived climatic fluctuations.

The reasons for the extreme paucity of the fauna of Issidae in Equatorial Africa are not clear. I have found several undescribed genera and species in collections but they do not change the state of things. The only Equatorial African species may be *Chimetopon camerunensis* Schmidt, 1910 known from Cameroon (Schmidt, 1910), the Central African Republic, and Gabon. There are no data on the ecology of this species in the literature; several specimens have been collected in cacao plantations (see the above material).

According to the data of Tallis (1991, cited after Cox and Moore, 1995), 26–10 thousand years ago, in the most arid period during the last glaciation, most part of the humid tropical forests in the Zaire basin may have been replaced by dry grass associations and

savannas. The study of the lake level dynamics has shown that the driest period in tropical Africa took place 20–15 thousand years ago. This explains the fact that practically all the Afrotropical representatives of Issidae inhabit steppe-like landscapes. Does this mean that Issidae penetrated into tropical Africa only in the period of glacial aridization? In any case, fragments of the rain forest were always preserved; some ecologists suggest that high taxonomic diversity in the rain forest associations is partly due to their glacial fragmentation which resulted in isolation of some populations (Cox and Moore, 1995).

Issidae which existed in forests before the glaciation may have become completely extinct. If this is true, then *Chimetopon camerunensis*, possessing well-developed 3-lobed hind wings (which are more typical of tropical forest species among Issidae), should be considered as relict species. Its range lies in the Guinea-Congolese Subregion of the Afrotropical Region according to Mekaev (1981), where the pre-Miocene African mammal fauna was preserved while in the other parts of the continent it was replaced by the Hipparion fauna. In the opinion of Mekaev (1981), the mammal fauna of East and South Africa originated from the Miocene-Pliocene Hipparion fauna of Eurasia. This is also true for East African Issidae, represented by four genera (*Hemisobium* Schmidt, 1911, *Katonella* Schmidt, 1911, *Kovacsiana* Synave, 1956, and *Kivupterum* Dlabola, 1985) closely related to the Western Palaearctic ones. So far, it has been impossible to explain why Issidae did not penetrate into South Africa, for instance, at the turn of the Miocene and Pliocene together with the Hipparion fauna, as it happened with Caliscelidae [the genus *Rhinogaster* Fennah, 1949, includes 3 species—2 of which are distributed in India and 1, in the RSA (Gnezdilov, 2011a)], whereas the “issid biomorph” is represented there by Trepiduchidae and Nogodinidae (Gnezdilov, 2013c). Replacement of the true Issidae by Trepiduchidae, Nogodinidae, Ricaniidae, and Flatidae in arid and subarid biocenoses is also characteristic of Madagascar (Gnezdilov, 2013c).

The fauna of Australia (Gnezdilov and Fletcher, 2010) is a derivative of the Indo-Malayan fauna. Issidae may have penetrated into Australia comparatively recently since contact between Southeast Asia and Australia was established only in the Pliocene-Pleistocene (Eskov, 1984); however, they either could not already reach New Zealand or, having reached it by other ways, disappeared during Pleistocene glaci-

ations. One more open question is why Issidae were not found on Tasmania while at least one macropterous species reached the Fiji Islands. In the latter case, however, *Sarima erythrocyclus* Fennah may have migrated to Fiji from the Indo-Malayan Realm via the Pacific islands, bypassing Australia. A similar variant of dispersal was described by Soulier-Perkins (2000) for the *Makota* group of genera in the family Lophopidae Stål (Fulgoroidea). However, aerial dispersal of the sub-brachypterous Issidae appears much less probable than that of macropterous species. In particular, the distribution pattern of the genus *Bardunia* Stål, in which closely related species inhabit Engano Island, Sumatra, and New Guinea (Gnezdilov, 2011b), can be most probably explained by changes in the ocean level during Pleistocene glaciation and, consequently, the possibility of terrestrial dispersal. It should be certainly borne in mind that species may get to the islands as macropterous forms and later become sub-brachypterous, although no macropterous forms have so far been recorded in the sub-brachypterous species of Issidae. The development of brachyptery is one of the principal evolutionary trends in Issidae (Gnezdilov, 2013c).

The fauna of each zoogeographic realm is highly endemic, with a small number of shared genera and species. At the same time, dispersal of some species with cargoes in the historical time can be considered as proved (Gnezdilov and O'Brien, 2006a; Gnezdilov, 2009b). The best examples of this phenomenon are given below.

Issus coleoptratus (Fabricius, 1781) is a Western Palaearctic species which was recorded outside its natural range on Saint Helena Island in the Atlantic (Synave, 1976) and also described as *Issus quadriguttatus* Walker, 1851 from Hong Kong (Gnezdilov et al., 2004). The Hong Kong record was not confirmed later; it may have resulted from a labeling error though the finding of an occasionally introduced specimen is also possible.

Agalmatium bilobum (Fieber, 1877) is a south European species which was inadvertently introduced into California in the 1940s and became a vine pest there (Schlinger, 1958; Gnezdilov and O'Brien, 2006a).

Thabena brunnifrons (Bonfils, Attie et Reynaud, 2001) is an Indo-Malayan species which can now be found on Réunion Island (Gnezdilov, 2009b). It was also recorded in Singapore and on Taiwan (Chan et al.,

2013). The genus *Thabena* Stål includes 14 species and is mainly distributed in the Indo-Malayan Realm. *Th. brunnifrons* may have been introduced to Réunion Island in the historical time, since Mauritius Island (a big island in the Mascarenes group, close to Réunion) was used as a transit port on the route from East Asia to Europe by the Dutch East India Company already at the beginning of the XVII century (Allen, 1999).

As a peculiar case, one can also mention the description of *Thabena fissala* (Fieber, 1876) from Portugal and of *Thabenula sulcata* (Fieber, 1876) from Sicily by Fieber (1876); both species are in fact typically Indo-Malayan (Gnezdilov et al., 2011). These descriptions either resulted from labeling errors or reflected actual cases of shipment of Indo-Malayan species to Europe by sea. Insects certainly had little chance of surviving the long sea journeys in the past centuries; yet at present the probability of introduction in this way is many times greater.

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