

Development of a Phylogenetic Model for the Tribe Micrarctiini (Lepidoptera, Arctiidae) by the SYNAP Method

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Abstract—A phylogenetic model for all the 18 genera of Micrarctiini (Lepidoptera, Arctiidae) of the World fauna is discussed. The SYNAP method was used for development of the model. For these purposes, 47 characters of the general appearance, male and female genitalia, and wing pattern were used. Based on these characteristics, an evolutionary trend from the plesiomorphic to apomorphic states was revealed. The genera *Apantesis* and *Amurrhyparia*, as well as *Notarctia*, differ from the other genera to the greatest extent. The other genera have formed two the main clades: *Grammia* + (*Diacrisia* + (*Rhyparia* + *Rhyparioides*)). *Neoarctia* + (*Palaearctia* + *Holarctia* + *Chelis*) and all the other genera have occupied separate positions. The latter group was divided into two clades: *Ebertarctia* + *Tancrea* + *Divarctia* with brachypterous females and *Centrarctia* + (*Sibirarctia* + (*Micrarctia* + *Hyperborea*)).

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The present paper belongs to a series of publications developing phylogenetic models for the tribes of the subfamily Arctiinae. Earlier, phylogenetic models were created for all the genera belonging to the more primitive tribe Callimorphini (Dubatolov, 2006), for all the genera of the tribe Arctiini (Dubatolov, 2008), and for the Palaearctic and Oriental genera of the tribe Spilosomini (Dubatolov, 2007).

MATERIALS AND METHODS

The composition of the tribe Micrarctiini coincides with that in the earlier classification of the subfamily elaborated on the basis of the fauna of the former USSR (Dubatolov, 1990) but with a supplement of North American species from the generic group *Neoarctia*–*Grammia* established by Ferguson (1985). In this capacity, the tribe comprises 18 genera confined to the Holarctic Region. Only a few of their representatives reach the Neotropics southwards as well as occur in the high mountains along the border between the Palaearctic and Oriental faunas. In the course of analysis of this tribe, all the 18 known taxa of the generic rank were studied not only on the basis of type species, but with assessment of almost all the species. The only exception is the genus *Grammia*, in which only 19 species were examined (more than 60% of the species composition), but they represented all the subgenera (*Grammia*, *Micrarctia*, and *Holarctia*).

A list of the species examined is given below:

Ebertarctia Dubatolov, 2004: *E. nordstroemi* (Brandt, 1947) (Iran, Khorosan). Two other species, *E. afghanicola* (Ebert, 1974) and *E. solitaria* (Ebert, 1974) (Afghanistan) were analyzed based on the detailed original descriptions.

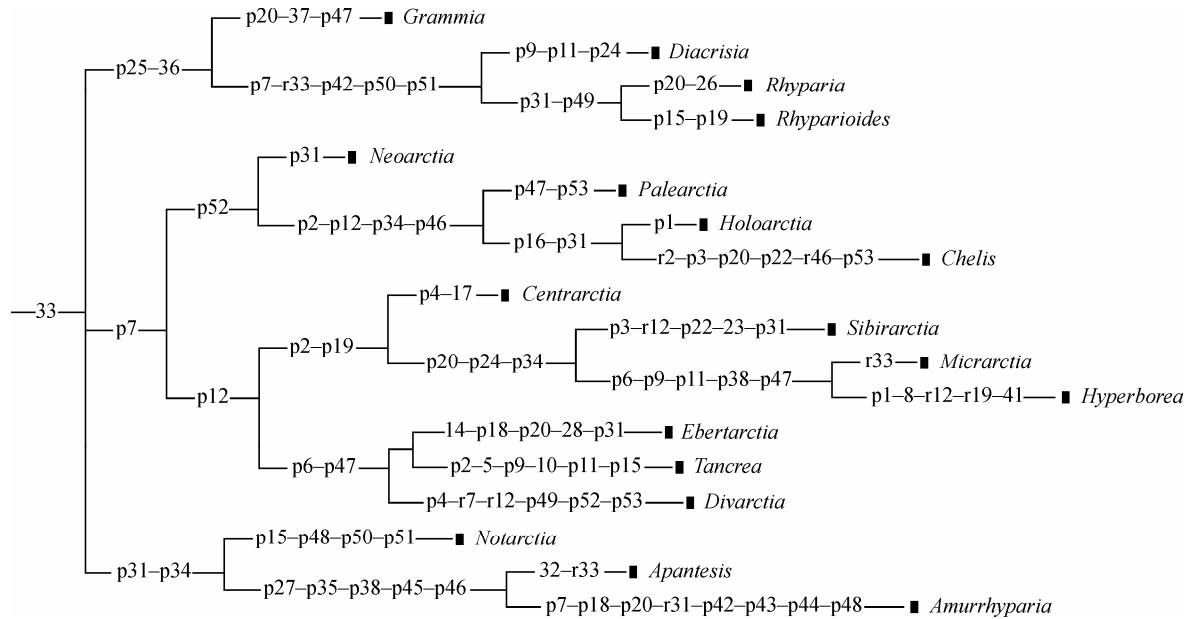
Divarctia Dubatolov, 1990: *D. diva* (Staudinger, 1887) (mountains in the eastern part of Middle Asia).

Tancrea Püngeler, 1908: *T. pardalina* Püngeler, 1908 (deserts of Middle Asia).

Holarctia Ferguson, 1984: *H. cervini* (Fallou, 1864) (Alps), *H. puengeleri* (O. Bang-Haas, 1927) (mountains in Northern Eurasia, Southern Siberia, and Alaska), *H. marinae* Dubatolov, 1985 and *H. dubatolovi* Saldaitis et Ivinskis 2005 (Altai), *H. sordida* (McDunnough, 1921) (Northern Cordilleras).

Neoarctia Neumoegen et Dyar, 1893: *N. brucei* (Edwards, 1888) and *N. beanii* (Neumoegen, 1891) (Cordilleras). *N. lafontainei* Ferguson, 1995 was analyzed based on the detailed original description.

Palaearctia Ferguson, 1995: *P. mira* Dubatolov et Tshistjakov, 1989 (Altai), *P. glaphyra* (Eversmann, 1843), *P. wagneri* (Püngeler, 1918), *P. golbecki* Dubatolov, 1996, *P. gratiosa* (Grum-Grshimailo, 1890), *P. erschoffii* (Alpheraky, 1882), *P. ferghana* (Staudinger, 1887), *P. turkestanica* Dubatolov, 1996, and



Phylogenetic model for the genera of the tribe Micrarctiini obtained by the SYNAP method. Numerals correspond to the character numerals given in text; *p*, homoplasy, *r*, reversion.

P. gracilis Dubatolov, 1996 (mountains in the eastern part of Middle Asia), *P. marxi* (O. Bang-Haas, 1927), and *P. ammosovi* Dubatolov et Gurko, 2002 (Himalayas). *P. rasa* Saldaitis, Ivinskis et Churkin, 2000 (Karlyk Mts., Dzhungaria, Xinjiang, China), *P. variabilis* (Daniel, 1966) (Gindukush), and *P. hauensteini* Kautt, 1996 (Himalayas) were analyzed based on the detailed original descriptions.

Centrarctia Dubatolov, 1990: *C. mongolica* (Apheraky, 1888) (deserts and semideserts of Central Asia).

Sibirarctia Dubatolov, 1987: *S. kindermannii* (Staudinger, 1867) and *S. buraetica* (O. Bang-Haas, 1927) (Siberia, southern part of Russian Far East, Mongolia, and Northern China).

Chelis Rambur, 1866: *Ch. maculosa* (Gerning, 1780) (Southern Europe, southern part of West Siberia), *Ch. simplonica* (Anderregg, in Boisduval, 1840) (Alps), *Ch. caecilia* (Kindermann, in Lederer, 1853) (Southern Urals, mountains of Southern Siberia), *Ch. reticulata* (Christoph, 1887) (mountains of Western Asia and Caucasus), *Ch. ferghana* Dubatolov, 1988 and *Ch. strigulosa* (Böttcher, 1905) (Tien Shan), *Ch. dahurica* (Boisduval, 1834) (Southern Siberia and Mongolia).

Grammia Rambur, 1866: *G. quenseli* (Paykull, 1793) (northern part of Holarctic), *G. kodara* Dubatolov et Schmidt, 2005 (Northern Transbaikalia),

G. philipiana Ferguson, 1985 (Wrangel Island and Alaska), *G. virguncula* (W.F. Kirby, 1837), *G. anna* (Grote, 1864), *G. parthenice* (W.F. Kirby, 1837), *G. virgo* (Linnaeus, 1758), *G. ornata* (Packard, 1864), *G. blakei* (Grote, 1865), *G. williamsii* (Dogde, 1871), *G. nevadensis* (Grote et Robinson, 1866), *G. phyllira* (Drury, 1773), *G. oithona* (Strecker, 1878), *G. figurata* (Drury, 1773), *G. f-pallida* (Strecker, 1878), *G. (Mimarctia) arge* (Drury, 1773), *G. (M.) doris* (Boisduval, 1869), *G. (Holarctia) obliterated* (Stretch, 1885) (Siberia and North America). The North American species *G. allectans* Ferguson, 1995 was analyzed based on the detailed original description.

Hyperborea Grum-Grshimailo, [1900]: *H. czekanowskii* Grum-Grshimailo, [1900] (mountain parts of Sichuan and Quinhai, China).

Micrarctia Seitz, 1910: *M. trigona* (Leech, 1899) (mountains of Sichuan and Tzinkhai, China).

Notarctia M.E. Smith, 1938: *N. proxima* (Guerin-Meneville, [1844]) (North and Central America). The closely related species *N. mormonica* (Stretch, 1873) (southern part of North America) was not examined.

Apantesis Walker, 1855: *A. phalerata* (Harris, 1841), *A. vittata* (Fabricius, 1787), *A. nais* (Drury, 1773) (North America). *A. carlotta* Ferguson, 1985 was analyzed based on the detailed original description.

Diacrisia Hübner, [1819]: *D. sannio* (Linnaeus, 1758) (subtranspalaeartic species), *D. irene* Butler, 1881 (southern part of the Far East).

Rhyparioides, Butler, 1877: *Rh. nebulosa* Butler, 1877, *Rh. amurensis* (Bremer, 1861) (southern part of Far East), *Rh. metelkana* (Lederer, 1861) (Europe, southern parts of Siberia and the Far East), *Rh. subvaria* (Walker, 1855) (China).

Rhyparia Hübner, [1820]: *Rh. purpurata* (Linnaeus, 1758) (transpalaeartic species)

Amurrhyparia Dubatolov, 1990: *A. leopardinula* (Strand, 1919) (Amur basin and Northern China).

Altogether, 47 characters of the general appearance, genital structures (of both sexes), and also a type of the wing pattern were used; vectors of the evolution from the plesiomorphic to apomorphic states were hypothesized for all the characters. On the whole, the plesiomorphic states of the characters were determined by their comparison with those of the representatives of the more primitive tribe Callimorphini (Dubatolov, 2006) or with the representatives of the subfamily Lithosiinae regarded as a sibling-group.

The list of the characters used is given below. The numerals of characters correspond to those in the cladogram obtained, which is caused by the fact that several characters selected for the analysis were later excluded from the final analysis as inconsistent or ambiguous with regard to vectors of their evolution; the former numeration being, however, preserved.

(1) Antennal comb: long (plesiomorphic state); short (apomorphic state). Long antennal comb is characteristic of several Callimorphini, being regarded, therefore, as a plesiomorphy.

(2) Shape and size of eyes: large and ovate (plesiomorphic state); small (apomorphic state). Large hemispheroid eyes are a plesiomorphic state of Callimorphini (Dubatolov, 2006).

(3) Pubescence of eyes: absent (plesiomorphic state); present (apomorphic state). The absence of eye pubescence is a plesiomorphic state of all Noctuoidea, including Lithosiinae and Callimorphini (Dubatolov, 2006).

(4) Fore tibia: without apical spurs (plesiomorphic state); with apical spurs (apomorphic state). The absence of apical spurs on fore tibia is a plesiomorphy of Callimorphini (Dubatolov, 2006).

(5) Hind tibia: with two pairs of spurs (plesiomorphic state); with a single pair of spurs (apomorphic state). The presence of two pairs of spurs on hind tibia is a plesiomorphy of Callimorphini (Dubatolov, 2006).

(6) Female wings: well developed (plesiomorphic state); shortened (apomorphic state). Well developed female wings are a plesiomorphic state of all Lepidoptera, including Lithosiinae and Callimorphini.

(7) Venation of wings: R2 vein starts from central cell (plesiomorphic state); R2 on a common stalk with R3+5. Starting of R2 from the central cell is shared with the representatives of Lithosiinae.

(8) Translucence of wings: absent (plesiomorphic state); present (apomorphic state). Non-transparent wings are a plesiomorphic state of all Noctuoidea, including Lithosiinae and Callimorphini.

(9) Male wings: moderately broad (plesiomorphic state); very broad, geometrid-like (apomorphic state). Moderately broaden wings is a plesiomorphy of all Noctuoidea, including Callimorphini.

(10) Tympanic apparatus: normal, non-hypertrophied (plesiomorphic state); hypertrophied (apomorphic state). Non-hypertrophied tympanic apparatus is a plesiomorphy of all Noctuoidea, including Callimorphini (Dubatolov, 2006).

(11) Body: body broad (plesiomorphic state); body narrow (apomorphic state). Broad body is a plesiomorphy of Noctuoidea, including Lithosiinae and Callimorphini (Dubatolov, 2006).

(12) Uncus: long, comparable with the width of tegumen (plesiomorphic state); shortened, pronouncedly shorter than tegumen (apomorphic state). Long uncus is a plesiomorphy of all Noctuoidea, including Lithosiinae and Callimorphini.

(14) Uncus shape: apically pointed (plesiomorphic state); widened (apomorphic state). Apically pointed uncus is a plesiomorphy of all Noctuoidea, including Lithosiinae and Callimorphini.

(15) Medial dilation of uncus: absent (plesiomorphic state); present (apomorphic state). Simple uncus is a plesiomorphy of all Noctuoidea, including Lithosiinae and Callimorphini.

(16) Curvature of uncus: inconspicuous (plesiomorphic state); pronounced (apomorphic state). Inconspicuously curved uncus is a plesiomorphy of all Noctuoidea, including Lithosiinae and Callimorphini.

(17) Tegumen: ordinary (plesiomorphic state); widened, with prominences (apomorphic state).

(18) Subuncal processes: absent (plesiomorphic state); present (apomorphic state). The absence of subuncal processes is a plesiomorphic state of all Noctuoidea, including Lithosiinae and Callimorphini.

(19) Apical process of valva in width: wide (plesiomorphic state); narrow (apomorphic state). Widened apical process of valva is a plesiomorphic state of Callimorphini (Dubatolov, 2006).

(20) Apical process of valva in length: short (plesiomorphic state); long (apomorphic state). In spite of the long cucullus is a plesiomorphy of many Noctuoidea, including Callimorphini, the elongation of the apical process of valva is regarded here as a reversion; this is indirectly ascertained by the shortened apical process of valva to be a plesiomorphy of the tribe Arctiini, from which the tribe Micrarctiini, presumably, diverged.

(22) Two additional apical processes of valva (besides long cucullus): absent (plesiomorphic state); present (apomorphic state). The apomorphic state of this character is observed only in two genera of Micrarctiini.

(23) Two additional apical processes of valva (besides long cucullus) in length: short (plesiomorphic state); long (apomorphic state). Elongated processes are regarded to be an apomorphic state as compared to short ones, since this character is a novelty.

(24) Extension of ventral angle of valva: absent (plesiomorphic state); present (apomorphic state).

(25) Harpe-like fold of valva: absent (plesiomorphic state); present (apomorphic state).

(26) Harpe-like fold of valva in length and shape: short, not exceeding its width (plesiomorphic state); long, exceeding its width (apomorphic state). Lower expression of a character is more ancestral in comparison with its high expression.

(27) Fold of ventral margin of valva: absent or very short (plesiomorphic state); present and well developed (apomorphic state, novelty).

(28) Junction of valval costa with juxta: absent (plesiomorphic state); present (apomorphic state, novelty).

(31) Juxta length: short (plesiomorphic state); long (apomorphic state). Short juxta is a plesiomorphy of Callimorphini (Dubatolov, 2006).

(32) Median prominence of juxta: absent (plesiomorphic state); present (apomorphic state). The simple shape of a structure is generally considered a plesiomorphy.

(33) Saccus length: short (plesiomorphic state); long (apomorphic state). Short saccus is a plesiomorphy of Noctuoidea, including Callimorphini.

(34) Apical dentation of aedeagus: absent (plesiomorphic state); present (apomorphic state). The absence of apical dents is characteristic of Callimorphini.

(35) Hypertrophy of apical sclerotization of aedeagus: absent (plesiomorphic state); present (apomorphic state). The absence of sclerotizations at aedeagus apex is characteristic of Callimorphini.

(36) Curvature of aedeagus: weakly expressed (plesiomorphic state); strongly expressed (apomorphic state). Straight aedeagus is characteristic of the more primitive Callimorphini.

(37) Vesica: short, markedly shorter than aedeagus (plesiomorphic state); of equal length with aedeagus or longer (apomorphic state). Very long vesica is a novelty.

(38) Orientation of fore-wing pattern: transverse (plesiomorphic state); longitudinal (apomorphic state). Transverse orientation of the forewing pattern is a plesiomorphy of all Lepidoptera, including Callimorphini.

(41) Fore-wing veins coloration: same as wing background (plesiomorphic state); paler than wing background (apomorphic state). The absence of paleness along veins is a plesiomorphy of all Lepidoptera, including Callimorphini.

(42) Pattern on forewing upper side and underside: identical (plesiomorphic state); different (apomorphic state).

(43) Dorsal groove of uncus: absent (plesiomorphic state); present (apomorphic state, novelty).

(44) Cucullus shape: simple, without processes (plesiomorphic state); intricate, with processes (apomorphic state). Simple cucullus is a plesiomorphy of all Noctuoidea, including Callimorphini.

(45) Hypertrophy of sclerotization and twisting of ductus bursae: absent (plesiomorphic state); present (apomorphic state, novelty).

(46) Anterior apophyses: present (plesiomorphic state); absent (apomorphic state, novelty).

(47) Reduction of anterior apophyses: indistinct (plesiomorphic state); apophyses very shortened (apomorphic state, novelty).

(48) Modification of anterior apophyses into sclerotized inflations: absent (plesiomorphic state); present but apophyses very short (apomorphic state, novelty).

(49) Asymmetry of sinus vaginalis (right side being more pronouncedly concaved): absent (plesiomorphic state); present (apomorphic state). A novelty of the group; sinus vaginalis is symmetrical in Callimorphini.

(50) Sinus vaginalis: non submerged (plesiomorphic state); submerged (apomorphic state, novelty).

(51) Lateral sclerotized plates of antevaginal plate (occasionally modified into folds of sinus vaginalis): absent (plesiomorphic state); present (apomorphic state, novelty).

(52) Number of signi: four (plesiomorphic state); two or absent (apomorphic state). The presence of four signi is a plesiomorphy of Callimorphini (Dubatolov, 2006).

(53) Bulla seminalis: large, turned aside (plesiomorphic state); small, not turned aside (apomorphic state). Small bulla is a plesiomorphy of all Noc-tuoidea, including Callimorphini.

The distribution of character states among the genera of the tribe Micrarctiini is shown in Tables 1 and 2.

The only assumption was made in the course of the study. It was caused by an insufficient knowledge of the genital structures in brachypterous females which remain unstudied in species belonging to the genera *Ebertarctia* and *Micrarctia*; meantime, the author failed to obtain permission to examine the genitalia in the only female specimen of *Tancrea* available. Since both studied genera with short-winged females (*Divarctia* and *Hyperborea*) are characterized by a reduction of the anterior apophyses, this state has been extrapolated to unstudied genera, because *Ebertarctia* is closely related to *Divarctia*, whereas *Micrarctia* is closely related to *Hyperborea*. The cladogram obtained is represented in the figure.

For the phylogenetic analysis, the SYNAP method elaborated by Baikov (1999) was used, with the help of SYNAP420 program. In this method and program, unlike other analogous methods, the assessment of trends of the character changes from plesiomorphic to

apomorphic state is specified personally by the researcher. This allows a more correct (in our opinion) approach to determination of plesiomorphies, based not only on a single outer group whose certain representatives can possess characters in the apomorphic state. This method also allows a more correct understanding of the reversions, equated with apomorphies. One more significant positive trait of the method used is a possibility of specification of "weight" to characters by the expert. This is very important in the situation when a unique character (novelty) appears for the first time and is absent in all the other groups, in this case its carriers are undoubtedly closely related. Such characters will be assigned the maximum weight to simplify construction of the cladogram. A considerable "weight" is also assigned to characters possessing, in the opinion of the expert, the especial importance for the taxonomy of the group. On the whole, the SYNAP method and classical cladistic PAUP method, despite the noticeable difference between them in the methodology, provide similar or almost identical dendrograms. This may be seen when comparing phylogenetic models developed with the use of both methods for five genera of the tribe Callimorphini (Da Costa and Weler, 2005; Dubatolov, 2006) as well as for six genera of the tribe Spilosomini (Bendib, 1998; Dubatolov, 2007).

RESULTS

Judging by the obtained cladogram (figure), the most isolated position within the tribe is occupied by the genera *Apantesis* and *Amurrhyparia*. These genera share several reliable apomorphies: hypertrophy of sclerotization and twisting of the ductus bursae; hypertrophy of apical sclerotization and strong apical dentation of the aedeagus; development of well-expressed fold of the ventral margin of valva. However, although the forewing pattern orientation is transformed from the transverse to longitudinal one in both genera, it is hardly a derivate of a single type. The genus *Notarctia* seems to be more or less closely related to these genera. It is characterized, similarly to *Apantesis* + *Amurrhyparia*, by a long juxta and apical dents of the aedeagus. *Notarctia* and the generic group of *Diacrisia*, *Rhyparioides*, and *Rhyparia* share the following character: the antevaginal plate possesses two lateral sclerotized plates, which are either bent inwardly (in two former genera) or merged with the sinus vaginalis and forming its sides.

On the other hand, *Diacrisia*, *Rhyparioides*, and *Rhyparia* show a synapomorphy with the genus

Table 1. Distribution of plesiomorphic (P) and apomorphic (A) states of characters (1–26) in tribe Micrarctiini

Genus	1	2	3	4	5	6	7	8	9	10	11	12	14	15	16	17	18	19	20	22	23	24	25	26
<i>Ebertarctia</i> Dubatolov, 2004	P	P	P	P	P	A	A	P	P	P	P	A	A	P	P	P	A	P	A	P	M	P	P	M
<i>Divarctia</i> Dubatolov, 1990	P	P	P	A	P	A	P	P	P	P	P	P	P	P	P	P	P	M	P	P	M	P	P	M
<i>Tancrea</i> Püngeler, 1898	P	A	P	P	A	A	A	P	A	A	A	A	P	A	P	P	P	M	P	P	M	P	P	M
<i>Holoarctia</i> Ferguson, 1984	A	A	P	P	P	P	A	P	P	P	P	A	P	P	A	P	P	M	P	P	M	P	P	M
<i>Neoarctia</i> Neumoegen et Dyar, 1983:1893	P	P	P	P	P	P	A	P	P	P	P	P	P	P	P	P	P	M	P	P	M	P	P	M
<i>Palaearctia</i> Ferguson, 1995	B	A	P	P	P	B	A	P	P	P	B	A	P	P	P	P	P	M	P	P	M	P	P	M
<i>Centrarctia</i> Dubatolov, 1990	P	A	P	A	P	P	A	P	P	P	P	A	P	P	P	A	P	A	P	P	M	P	P	M
<i>Sibirarctia</i> Dubatolov, 1987	P	A	A	P	P	P	A	P	P	P	P	P	P	P	P	P	P	A	A	A	A	A	P	M
<i>Chelis</i> Rambur, 1866	P	P	A	P	P	P	A	P	P	P	P	A	P	P	A	P	P	P	A	A	P	B	P	M
<i>Grammia</i> Rambur, 1866	P	B	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	A	P	M	P	A	P
<i>Hyperborea</i> Grum-Grshimailo, [1900]	A	A	P	P	P	A	A	A	A	P	A	P	P	P	P	P	P	P	A	P	M	A	P	M
<i>Micrartia</i> Seitz, 1910	P	A	P	P	P	A	A	P	A	P	A	A	P	P	P	P	P	A	A	P	M	A	P	M
<i>Notarctia</i> M.E. Smith, 1938	P	P	P	P	P	P	P	P	P	P	P	P	P	A	P	P	P	M	P	P	M	P	P	M
<i>Apantesis</i> Walker, 1855	P	P	P	P	P	P	A	P	P	P	P	P	P	P	P	P	P	M	P	P	M	P	P	M
<i>Diacrisia</i> Hübner, [1819]	P	P	P	P	P	P	A	P	A	P	A	P	P	P	P	P	P	B	P	P	M	A	A	P
<i>Rhyparioides</i> , Butler, 1877	B	P	P	P	P	P	A	P	P	P	P	P	P	A	P	P	P	A	P	P	M	P	A	P
<i>Rhyparia</i> Hübner, [1820]	P	P	P	P	P	P	A	P	P	P	P	P	P	P	P	P	P	P	A	P	M	P	A	A
<i>Amurrhyparia</i> Dubatolov, 1990	P	P	P	P	P	P	A	P	P	P	P	P	P	P	P	P	A	P	A	P	M	P	P	M
Weight of character	1	1	1	1	1	3	2	1	1	1	1	1	1	1	3	1	1	1	1	1	1	4	5	1

Notes: B, polymorphism; M, vector of character change absent.

Table 2. Distribution of plesiomorphic (P) and apomorphic (A) states of characters (27–53) in tribe Micrarctiini

Genus	27	28	31	32	33	34	35	36	37	38	41	42	43	44	45	46	47	48	49	50	51	52	53
<i>Ebertarctia</i>	P	A	A	P	A	P	P	P	P	P	P	P	P	P	?	?	A	?	?	?	?	?	?
<i>Divarctia</i>	P	P	P	P	A	P	P	P	P	P	P	P	P	P	P	P	A	P	A	P	P	A	A
<i>Tancrea</i>	P	P	P	P	A	P	P	P	P	P	P	P	P	P	?	?	A	?	?	?	?	?	?
<i>Holoarctia</i>	P	P	A	P	A	A	P	P	P	B	P	P	P	P	P	A	M	P	P	P	P	A	P
<i>Neoarctia</i>	P	P	A	P	A	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	A	P
<i>Palaearctia</i>	P	P	B	P	A	A	P	P	P	B	B	P	P	P	P	A	A	P	P	P	P	A	A
<i>Centrarctia</i>	P	P	?	P	A	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P
<i>Sibirarctia</i>	P	P	A	P	A	A	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P
<i>Chelis</i>	P	P	A	P	A	A	P	P	P	B	B	P	P	P	P	P	P	P	P	P	P	A	A
<i>Grammia</i>	P	P	P	P	A	P	P	A	A	B	B	P	P	P	P	P	A	P	P	P	P	P	P
<i>Hyperborea</i>	P	P	P	P	A	A	P	P	P	A	A	P	P	P	P	P	A	P	P	P	P	P	P
<i>Micrartia</i>	P	P	P	P	P	A	P	P	P	A	P	P	P	P	?	?	A	?	?	?	?	?	?
<i>Notarctia</i>	P	P	A	P	A	A	P	P	P	P	P	P	P	P	P	P	P	A	P	A	A	P	P
<i>Apantesis</i>	A	P	A	A	P	A	A	P	P	A	P	P	P	P	A	A	M	B	P	P	P	P	P
<i>Diacrisia</i>	P	P	P	P	P	P	A	P	P	P	A	P	P	P	P	P	P	P	P	A	A	P	P
<i>Rhyparioides</i>	P	P	A	P	P	P	A	P	P	P	A	P	P	P	P	P	P	P	A	A	A	A	P
<i>Rhyparia</i>	P	P	A	P	P	P	A	P	P	P	A	P	P	P	P	P	P	P	A	A	A	A	P
<i>Amurrhyparia</i>	A	P	P	P	A	A	A	P	P	A	P	A	A	A	A	A	M	A	P	P	P	P	P
Weight of character	1	1	1	1	1	1	3	1	1	1	1	1	5	5	3	1	1	1	5	1	4	4	1

Notes: B, polymorphism; M, vector of character change absent; ?, state of character undetermined.

Grammia: development of a harpe on the inner side of the valva, which is formed by a fold of the lower margin of costa. This fold is rather small in species belonging to the genus *Grammia*, strikingly increasing in size in *Diacrisia* and *Rhyparioides*, and reaching its maximum size in *Rhyparia*. On the contrary, the fold is only slightly traced in *Notarctia*, being nearly undetectable. Despite the evidently monophyletic origin of these four genera, it is impossible to establish which of the two genera, *Grammia* or *Notarctia*, is more closely related to the complex of *Diacrisia* + *Rhyparioides* + *Rhyparia*. In the cladogram analyzed, the genus *Notarctia* forms a separate lineage only because of the fact that the fold on the inner valval side of its representatives is hardly traceable and its presence was not designated in the matrix. Within this generic group, *Rhyparioides* and *Rhyparia* appear to be most similar, sharing the apomorphic character: asymmetry of the sinus vaginalis whose right wall is more markedly invaginated than the left one, which is better pronounced in *Rhyparia*.

All the remaining genera are characterized by two synapomorphies: the absence of a fold of the ventral valval margin and a considerable enlargement of the saccus. These genera form four groups. The group of *Grammia* + *Diacrisia* + *Rhyparioides* + *Rhyparia* was discussed above. The other genera are characterized by the R2 vein branching from the radial stalk, instead of the central cell.

Within the next group (*Neoarctia*, *Palaearctia*, *Holarctia*, and *Chelis*), a number of signi in the bursa copulatrix decreases to 2, or signi are entirely lost. In addition, the bulla seminalis is also reduced, which is, however, observed in the genus *Centrarctia* belonging to the parallel clade. Among the rest of the genera (*Centrarctia*, *Sibirarctia*, *Hyperborea*, *Micrarctia*), the first genus seems to be the most peculiar, since its representatives possess (in addition to the above character) a naked sclerotized apical spur on the fore tibia, markedly shortened uncus, and dilated tegumen bearing a cone-shaped structure on the dorsal wall. Among the remaining genera of this group, *Hyperborea* and *Micrarctia* show the closest resemblance based on the broadened wings, narrow body, and apically divided valva. Moreover, the females of the genus *Micrarctia* are presumably brachypterous, which is reliably known for the closely related genus *Hyperborea*.

Two other generic groups are similar to each other in the shortened uncus. The first group comprises the

genera *Centrarctia*, *Sibirarctia*, *Micrarctia*, and *Hyperborea*. These genera are characterized by smaller eyes (presumably, an adaptation to the diurnal activity of adults) and narrow cucullus. In the other genera (*Divarctia*, *Ebertarctia*, and *Tancrea*), the females are brachypterous. The relationship between the two former genera is obvious: in contrast to the other genera of Micrarctiini, they possess symplesiomorphy (the ventral margin of the valva upwardly bents) as well as synapomorphy (brachypterous females). However, the presence of the later character in *Ebertarctia* is only hypothesized, since its females are not known though the males are rather common. All the remaining genera belonging to the tribe Micrarctiini do not possess the afore-described fold of the ventral margin of the valva. Moreover, the genus *Tancrea* is only provisionally attributed to this group, since the females, whose characters are very important for elucidation of relationships, have not been examined. Among these three genera, *Divarctia* is the most deviate owing to the presence of naked sclerotized apical spurs on the fore tibia of its representatives.

DISCUSSION

Taking into consideration the fact that none of the genera belonging to Micrarctiini is confined to the western part of Eurasia and that this tribe is nearly exclusively distributed in the Holarctic (only several species occur in the Neotropical Region), the Asian-American origin of this tribe can be assumed. The initial radiation of Micrarctiini is supposed to have happened in the time of isolation of Asia and North America from Europe, i.e., in the Palaeogene, none of the clades obtained belonging to a certain geographical region. As a result, the radiation of the genera belonging to Micrarctiini might occur in both the continents (Asia and North America), with several representatives migrating from the North America via Beringia to Asia (e.g., *Grammia*) (Dubatolov, 2004), whereas the others migrated in the opposite direction (e.g., *Holarctia* and *Hyperborea*).

When individual clades are considered, divergence of the warm-requiring *Grammia* and *Diacrisia* + *Rhyparioides* can be associated with separation of the North-American and East-Asian faunas in one of the periods of the Palaeogene, and divergence of the closely related genera *Diacrisia*, *Rhyparia*, and *Rhyparioides* must have happened in Eastern Asia. In contrast, separation of the North-American alpine genus *Neoarctia* from the predominantly Palaeartic clade

Palaearctia + *Holarctia* + *Chelis* might have taken place later, in the Neogene or Pleistocene. The phylogenetic hypothesis for *Palaearctia* + (*Holarctia* + *Chelis*) represented in the cladogram does not seem to be sufficiently proved because the characters uniting two of the latter genera (pronounced curvature of the uncus and long juxta) may also be convergent. On the other hand, the two the former genera are closely related to each other in the simple rhomb-shaped valvae and they comprise alpine species, while in *Chelis*, the valvae bear processes, and the species belonging to this genus are confined to the steppe localities. Therefore, another phylogenetic hypothesis seems to be consistent: (*Palaearctia* + *Holarctia*) + *Chelis*. This hypothesis more properly corresponds to the divergence of the steppe and alpine faunas, the genus *Palaearctia* having been formed in the mountains of Tien-Shan, Pamir-Alai, and the Himalayas, whereas *Holarctia* most probably originated in the northeastern part of Asia.

The next large clade *Centrarctia* + *Divarctia* is almost entirely confined to the Palaearctic (the only genus *Hyperborea* locally occurs in North America, in Alaska). It is more correct to date its radiation to the period of isolation of the non-arctic Asian fauna from the North-American one, i.e., to the second half of the Pliocene–Pleistocene. Then the two subclades were formed, one of which being restricted to the mountains and plains of Middle Asia (*Ebertarctia* + *Tancrea* + *Divarctia*), where it must have originated, while the second one (*Centrarctia* + *Sibirarctia* + *Micrarctia* + *Hyperborea*) was confined to Central and Eastern Asia.

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