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PRELIMINARY ANALYSIS OF PHYLOGENETIC RELATIONSHIPS AMONG PALAEARCTIC SIMULIINAE (DIPTERA, SIMULIIDAE) INFERRED FROM MORPHOLOGICAL CHARACTERS

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Preliminary Analysis of Phylogenetic Relationships Among Palaearctic Simuliinae (Diptera, Simuliidae) Inferred from Morphological Characters. Sukhomlin K. B. — Phylogenetic relationships among the Palaearctic genera of the subfamily Simuliinae are analyzed based on the matrix of 100 morphological characters and 37 taxa, including 6 outgroups. Parsimonic analysis was resulted in 3 consensus trees (weighting based on CI, RI and RC indices) of slightly different topology, which show monophyly of the subfamily Simuliinae, tribes Stegopternini, Nevermanniini, Wilhelmiini and Simuliini, and a possible sister-group relationships between the latter two tribes. Tribe Ectemniini is apparently a paraphyletic formation. The analysis also supports transferring of the Stegopternini and Nevermanniini from Prosimuliinae to Simuliinae.

Key words: Palaearctic Region, blackflies, Simuliidae, Simuliinae, phylogenetic relationships.

Предварительный анализ филогенетических отношений между палеарктическими Simuliinae (Diptera, Simuliidae) на основе морфологических признаков. Сухомлин Е. Б. — Филогенетические отношения между палеарктическими родами Simuliinae проанализированы на основе матрицы из 100 морфологических признаков и 37 таксонов, в том числе 6 внешних групп. В результате парсимонического анализа получены три кладограммы (взвешивание на основе индексов CI, RI и RC) с несколько отличной топологией, показывающие монофилию подсемейства Simuliinae, триб Stegopternini, Nevermanniini, Wilhelmiini и Simuliini и, возможно, сестринские отношения между последними двумя трибами. Триба Ectemniini, — по-видимому, парафилетическое образование. Проведенный анализ также подтверждает правильность перемещения триб Stegopternini и Nevermanniini из Prosimuliinae в Simuliinae.

Ключевые слова: мошки, Палеарктика, Simuliidae, Simuliinae, филогенетические взаимоотношения.

Introduction

Analysis of phylogenetic relationships within the family Simuliidae, including characters of the ground plan of the structure and evidences of monophyly of the family and its subfamilies, was provided by Rubtsov (1974). There are some differences between existing classifications in understanding relationships among subfamilies, their number, and number of the genus-group taxa in subfamilies.

Phylogeny of blackflies hardly was often discussed in the literature; in particular, position (or relationships among species) of the Nearctic genera *Twinnia* and *Gymnopais* (Wood, 1978), *Ectemnia* (Moulton, Adler, 1997), and *Parasimulium* (Wood, Borkent, 1982) have been discussed. More recently, basal divergences within Simuliidae were resolved based on molecular sequence data (Moulton, 2000; Borkent, Currie, 2001). All these phylogenetic reconstructions are based predominantly or exclusively on the Neartic taxa.

Adler et al. (2004) critically analyzed taxonomic characters and reconstructed phylogenetic relationships among the North American Simuliidae. Their higher classification of the blackflies is the least detailed and the

most lumped, with subdivision of the family into Parasimuliinae and Simuliinae, and the latter subfamily into Prosimuliini and Simuliini.

A. Yankovsky (2002) reconsidered position and status of certain family-group taxa and genera of the blackflies based mainly on Palaearctic material. Particularly, he used more detailed and split classification (including the subfamilies Prosimuliinae and Simuliinae, where Adler et al. (2004) would use the tribal rank), placed the tribes Stegopternini Enderlein, 1930 and Ectemnini Enderlein, 1930 in the subfamily Prosimuliinae and considered the tribe Wilhelmiini Baranov, 1926 in the basal position within the Simuliinae. In addition, several taxa, which are considered subgenera of the genus *Simulium* by Adler et al. (2004), he takes in the full generic rank.

Later, Sukhomlin (Sukhomlin et al., 2008; Sukhomlin, Zinchenko, 2009) critically analyzed vast number of morphological characters and proposed an intuitive scheme of phylogenetic relationships in the subfamily Simuliinae, in which Stegopternini and Ectemnini were transferred in this subfamily rather than left in the Prosimuliinae.

However, so far these propositions were not supported by any rigorous phylogenetic analyses, by means of computer phylogenetic techniques based on numerous taxa from a wider geographical region and a broad range of characters, both of adults and larvae.

This work aims the reconstruction of phylogenetic relationships among the genera of the subfamily Simuliinae (in the sense of Yankovsky, 2002), which is the largest and well represented in the Palaearctics. Monophyly of the tribes in the Simuliinae and their possible sister-group relationships are to be tested. We realize that such an analysis does not include and neglects certain genera (or subgenera and groups of species in the sense of Crosskey (1990)) occurring beyond the Palaearctic Region and is therefore only preliminary, but it covers a core of the Holarctic fauna and would be therefore of certain interest, giving an approximation towards understanding phylogenetic relationships in the whole subfamily.

In this study, the characters described by Rubtsov (1974), Wood (1982), Crosskey (1990), Yankovsky (2002), Adler et al. (2004) and others are combined in one matrix and supplemented by several characters proposed by the author; distribution of character states has been carefully revised based mostly on Palaearctic material.

We follow concepts of the genera as split by Rubtsov (1974), with additions by Yankovsky (2002), rather than as lumped by Crosskey (1990) for convenience of analysis.

Material and methods

To analyze the distribution of morphological characters among taxa of families group and family Simuliidae the matrix of 100 morphological characters in 37 taxa (table 1), including six outgroups was prepared in Nexus Data Editor program (Page, 2001).

The following representatives of the higher taxa were included in the matrix (only subfamily or genus names as given in the brackets appear in the matrix and plots): *Chaoborus crystallinus* De Geer (Chaoboridae), *Aedes cinereus* Meigen (Culicidae), *Chironomus plumosus* Linnaeus (Chironomidae), *Culicoides punctatus* Latreille (Ceratopogonidae), *Parasimulium stonei* Peterson (Parasimuliinae), *Prosimulium hirtipes* Fries (Prosimuliinae), *Stegopterna trigonia* Lundstroem, *Greniera fabri* Doby et David, *Cnephia pallipes* Fries, *Metacnephia saileri* Stone, *Sulcicnephia ovtshinnikovi* Rubtsov, *Hellihiella latipes* Meigen, *Byssodon maculatus* Meigen, *Psilocnetha lamachi* Doby et David, *Cnetha verna* Macquart, *Nevermannia latigonia* Rubtsov, *Eusimulium aureum* Fries, *Schoenbaueria pusilla* Fries, *Gomphostilbia shogakii* Rubtsov, *Morops yonakuniense* Takeushi, *Montisimulium montinum* Rubtsov, *Wilhelmia equina* Linnaeus, *Boophthora erythrocephala* De Geer, *Psilozia vittata* Zetterstedt, *Cleitosimulium argenteostriatum* Strobl, *Obuchovia auricoma* Meigen, *Paragnus bukovskii* Rubtsov, *Parabyssodon transiens* Rubtsov, *Archesimulium tuberosum* Lundstroem, *Striatosimulium multistriatum* Rubtsov, *Argentisimulium noelleri* Friedrichs, *Tetisimulium bezzii* Corti, *Phoretodagmia ephemeroptera* Rubtsov, *Odagmia ornata* Meigen, *Gnus corbis* Twinn, *Simulium morsitans* Edwards (all representing genera of the Simuliinae).

The most parsimonious trees were calculated by means of PAUP* 4.0b10 (Swofford, 2000). Most of the multistate characters were considered to be unordered (except 12, 18, 20, 22, 29, 32, 35, 36, 41, 43, 48, 58, 61, 71, 75, 89, 96, 97, which obviously form series in a range). To decrease impact of the characters, which are subject to homoplasy, the technique of successive weighting was applied. At the beginning of analysis all the states were tested as unweighted. A heuristic search was resulted in the numerous most parsimonious trees, and a strict consensus tree obtained from them was as on the fig. 7. It was followed by aposteriori weighting with the following algorithm: the weight of all characters in the consensus tree was calculated (based on CI, RI and RC meaning); these weights were assigned to characters, and the cycle was repeated until the same values in two consecutive cycles are returned (by default, in 4 repetitions). The last consensus tree of each cycle is considered to be the final result of the phylogenetic relationships analysis. The matrix and trees were then imported into WinClada (Nixon, 2002); resulted cladograms showing character numbers states (synapomorphies for each clade) were exported from this program, and bootstrap significance was also calculated with Nona (Goloboff, 1999) using default bootstrap parameters. Bootstrap meanings > 50 assigned to the clades on the tree ♂1 (the initial tree) were added to the cladograms manually.

Characters and character states

Head

1. **Antenna of imago:** (0) 9–10-segmented; (1) 11-segmented.
   State 1 occurs in (and is a possible synapomorphy of) Prosimuliinae and Simuliinae.
2. **Size of pedicel**: (0) as wide as scape; (1) reduced, not much wider than the first flagellomere, cylindrical and similar in both sexes.
   State 1 is a possible synapomorphy of Simuliidae.
3. **The structure of male eye**: (0) occurrence of discontinuity line between large upper facets and small lower facets; (1) no discontinuity line.
   State 1 occurs in the subfamily Parasimuliinae.
4. **Number of the upper corneal facets in the male eye**: (0) very numerous > 15; (1) 9–12 upper corneal facets.
   State 1 is a possible synapomorphy of the *Gomphostilbia–Morops* group.
5. **Female head**: (0) small, much narrower than the thorax; (1) large, slightly narrower than the thorax.
   State 1 is a possible synapomorphy of the subfamilies Prosimuliinae and Simuliinae.
6. **Frons of female**: (0) wide, wider (in posterior portion) than long; (1) narrow, narrower than long (fig.1).
   State 1 is a possible synapomorphy of the subfamilies Prosimuliinae and Simuliinae.
7. **Second segment of female maxillary palp**: (0) small, as wide as the third segment, with a small sensory vesicle; (1) large, 1.5 times as wide as the third segment, with a large sensory vesicle (fig 2).
   State 1 occurs in the genera *Cnetha*, *Nevermannia*, *Eusimulium*.

Thorax

8. **Coloration of imago thorax**: (0) black; (1) brownish or greyish red.
   State 1 occurs in representatives of Prosimuliinae, Stegopternini and Ectemniini.
9. **Coloration of imago thorax**: (0) uniformly matt (black or reddish); (1) notum, feet, sometimes abdomen with a pattern of silvery spots of various shape.
   State 1 is a possible synapomorphy of Nevermanniini, Wilhelmiini, and Simuliini.
10. **Silvery spots on scutum**: (0) scutum without silvery spots; (1) scutum with silvery spots or vittae.
    State 1 is a possible synapomorphy of tribes Nevermanniini, Wilhelmiini, and Simuliini. Silvery spots on the scutum are absent in some representatives of Nevermanniini (*Hellichiella*, *Byssodon*, *Psilocnetha*, and *Cnetha*), but in the other genera of this tribe silvery spots are clearly defined.
11. **Katepisternum**: (0) conspicuously reduced, almost pointed ventrally in profile; (1) convex ventrally, higher than long; (2) strongly outlined, convex ventrally, longer than high.
    State 1 occurs in Prosimuliinae. State 2 is a possible synapomorphy of Simuliinae.
12. **Katepisternal sulcus**: (0) absent; (1) not entirely developed, shallow and wide, along sides, open anteriorly; (2) fully developed, deep and narrow, closed anteriorly.
    State 1 occurs in Prosimuliinae. State 2 is a possible synapomorphy of Simuliinae.
13. **Katepisternal setae**: (0) absent; (1) present.
    Occurs in Parasimuliinae and the group *Morops–Gomphostilbia*.

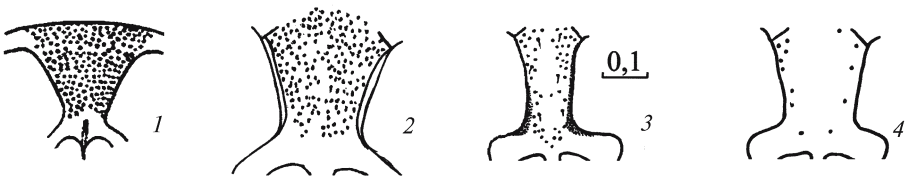

Fig. 1. Frons of female: *1 — Parasimulium* sp. (after Rubtsov, 1956 with changes), *2 — Pr. rufipes, 3 — Cn. verna, 4 — Sim. bergi* (after Kaplich et al., 2012).

Рис. 1. Форма лба самок*: 1 — Parasimulium sp.* (по Рубцову, 1956 с изменениями), *2 — Pr. rufipes, 3 — Cn. verna, 4 — Sim. bergi* (по Капличу и др., 2012).

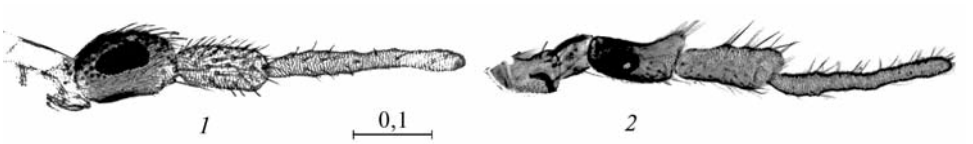

Fig. 2. Second segment of female maxillary palp: *1 — Cn. verna, 2 — Arg. noellery* (after Kahlich et al., 2012).

Рис. 2. Второй членик максиллярного щупика самки*: 1 — Cn. verna, 2 — Arg. noellery* (по Капличу и др., 2012).

Table 1. Character state matrix for cladistic parsimony analysis of the subfamily Simuliinae (character numbers and species as listed above)

Таблица 1. Матрица состояний признаков для кладистического парсимонического анализа подсемейства Simuliinae (номера признаков и виды перечислены выше)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chaoboridae	?	0	0	0	0	?	0	0	0	0	?	?	0	?	0	0	0	0	?	0	0	0	-	-	?	?	?	0	0	0	0	?	0	0	?	?	0	-	-	-	-	-	0	-	-	0	?	?	?	-
Chironomidae	?	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0	2	0	0	?	0	0	-	-	-	-	-	0	-	0	0	?	?	?	-
Culicidae	?	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	?	0	0	-	-	-	-	-	0	0	1	0	0	0	0	-
Ceratopogonidae	?	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	-	-	1	0	0	0	0	0	0	2	0	0	0	2	0	-	-	-	-	-	0	-	0	0	0	0	0	-
Parasimulinae	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Prosimulinae	1	1	0	0	1	1	0	1	0	0	1	1	0	0	0	1	0	1	1	0	1	1	1	1	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	1	0
Stegopterna	1	1	0	0	1	1	0	1	0	0	2	2	0	0	0	1	1	2	1	0	1	2	1	1	0	1	0	1	2	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	2	1	1	1
Greniera	1	1	0	0	1	1	0	1	0	0	2	2	0	0	0	1	1	2	1	0	1	2	1	1	0	1	0	1	2	0	1	0	1	0	0	1	0	0	0	0	0	0	1	0	1	0	2	1	1	1
Cnephia	1	1	0	0	0	1	0	1	0	0	2	2	0	0	0	1	1	2	1	0	1	2	1	1	0	0	0	0	1	0	1	0	1	0	1	1	0	0	0	0	0	0	2	0	1	3	2	1	1	0
Metacnephia	1	1	0	0	0	1	0	1	0	0	2	2	0	1	0	1	1	2	1	0	1	2	1	1	0	0	0	0	1	0	1	0	1	0	1	1	0	0	0	0	0	0	2	0	1	0	1	2	1	1
Sulcicnephia	1	1	0	0	0	1	0	1	0	0	2	2	0	0	0	1	1	2	1	0	0	2	1	1	1	0	0	0	0	1	1	0	1	0	1	1	0	0	0	0	0	0	2	0	4	0	1	2	1	1
Hellichiella	1	1	0	0	1	1	0	0	1	0	2	2	0	0	0	1	1	2	1	0	0	2	1	1	0	0	0	1	2	0	1	0	1	0	1	1	0	0	0	0	1	0	1	2	1	0	?	?	?	1
Byssodon	1	1	0	0	1	1	0	0	1	0	2	2	0	0	1	1	1	2	1	1	0	2	1	1	0	0	1	1	2	1	1	0	1	0	1	1	0	0	0	0	0	0	3	2	0	0	1	2	1	1
Psilocnetha	1	1	0	0	1	1	0	0	1	0	2	2	0	0	1	1	1	2	1	1	0	2	1	1	0	0	1	1	2	1	1	0	1	0	1	1	0	0	0	0	1	0	0	0	2	?	1	0	1	2	1	1
Cnetha	1	1	0	0	1	1	1	0	1	0	2	2	0	0	0	1	1	2	1	0	0	2	1	1	0	0	0	1	2	1	1	0	1	0	1	1	0	0	0	0	0	0	5	0	2	0	2	1	1	1
Nevermannia	1	1	0	0	1	1	1	0	1	1	2	2	0	0	0	1	1	2	1	0	0	2	1	1	1	0	0	1	2	1	1	0	1	0	1	1	0	1	-	0	1	0	5	4	3	3	2	1	1	1
Eusimulium	1	1	0	0	1	1	1	0	1	1	2	2	0	0	0	1	1	2	1	0	0	2	1	1	1	0	0	1	2	1	1	0	1	0	0	1	0	4	-	0	2	0	5	4	1	3	1	3	1	1
Schoenbaueria	1	1	0	0	1	1	0	0	1	1	2	2	0	0	0	1	1	2	1	0	0	2	1	1	0	0	1	1	2	1	1	2	1	0	1	1	0	0	0	0	0	0	4	1	4	0	1	3	1	1
Gomphostilbia	1	1	0	1	1	1	0	0	1	0	2	2	1	0	0	1	1	2	1	0	0	2	1	1	1	0	1	1	2	1	1	0	1	0	1	1	0	0	0	0	2	0	2	5	1	0	1	2	1	1
Morops	1	1	0	1	1	1	0	0	1	0	2	2	1	1	0	1	1	2	1	0	0	2	1	1	1	0	1	1	2	1	1	0	1	0	1	1	0	0	0	0	0	0	1	5	1	0	1	2	1	1
Montisimulium	1	1	0	0	1	1	0	0	1	0	2	2	0	0	0	1	1	2	1	0	0	2	1	1	0	0	0	1	2	1	1	0	1	0	1	1	0	2	-	1	0	0	3	0	2	0	?	?	?	?
Wilhelmia	1	1	0	0	1	1	0	0	1	0	2	2	0	1	1	1	1	2	1	1	0	2	1	1	0	0	0	1	2	1	1	2	1	1	3	1	0	3	-	0	1	0	2	0	1	5	2	1	1	1
Boophthora	1	1	0	0	1	1	0	0	1	1	2	2	0	0	0	1	1	2	1	4	0	2	1	1	1	0	1	1	2	1	1	2	1	1	4	0	0	0	0	0	1	0	2	6	2	0	1	1	1	1
Psilosia	1	1	0	0	1	1	0	0	1	1	2	2	0	0	0	1	1	2	1	4	0	2	1	1	1	0	1	1	1	1	1	2	1	1	0	0	0	0	0	0	1	0	1	3	1	3	2	1	1	1
Cleitosimulium	1	1	0	0	0	1	0	0	1	1	2	2	0	0	0	1	1	2	1	3	0	2	1	1	1	0	1	1	2	1	1	2	1	1	2	0	0	0	0	2	1	0	2	6	3	3	1	2	1	1
Obuchovia	1	1	0	0	1	1	0	0	1	1	2	2	0	0	0	1	1	2	1	3	0	2	1	1	1	0	0	1	2	1	1	2	1	1	2	1	0	1	-	0	1	0	2	4	1	3	2	1	1	0
Paragnus	1	1	0	0	1	1	0	0	1	1	2	2	0	0	0	1	1	2	1	4	0	2	1	1	1	0	1	1	2	1	1	2	1	1	2	1	1	0	0	0	2	0	2	5	0	0	1	2	1	1
Parabyssodon	1	1	0	0	1	1	0	0	1	1	2	2	0	0	0	1	1	2	1	3	0	2	1	1	1	0	1	1	2	1	1	0	1	1	2	1	2	0	0	0	2	0	2	6	0	0	1	3	1	0
Archesimulium	1	1	0	0	1	1	0	0	1	1	2	2	0	0	0	1	1	2	1	3	0	2	1	1	0	0	1	1	2	1	1	2	1	1	2	1	2	0	0	1	1	0	2	6	0	0	1	3	1	0
Striatosimulium	1	1	0	0	1	1	0	0	1	1	2	2	0	0	1	1	1	2	1	3	0	2	1	1	1	0	1	1	2	1	1	2	1	1	2	1	2	-	1	0	2	0	2	6	0	1	1	3	1	1
Argentisimulium	1	1	0	0	1	1	0	0	1	1	2	2	0	0	0	1	1	2	1	3	0	2	1	1	1	0	1	1	2	1	1	2	1	1	2	1	1	-	2	0	2	1	2	6	1	0	1	1	2	1
Tetisimulium	1	1	0	0	1	1	0	0	1	1	2	2	0	1	1	1	1	2	1	2	0	2	1	1	1	0	0	1	2	1	1	1	1	1	2	1	1	-	2	0	1	1	2	6	0	4	1	3	1	1
Phoretodagmia	1	1	0	0	1	1	0	0	1	1	2	2	0	1	0	1	1	2	1	3	0	2	1	1	1	0	1	1	2	1	1	1	1	1	2	1	1	-	2	0	2	1	2	6	0	4	1	3	1	1
Odagmia	1	1	0	0	1	1	0	0	1	1	2	2	0	1	0	1	1	2	1	3	0	2	1	1	1	0	1	1	2	1	1	1	1	1	2	1	1	-	2	0	2	1	2	6	0	4	1	4	1	1
Gnus	1	1	0	0	1	1	0	0	1	1	2	2	0	0	0	1	1	2	1	4	0	2	1	1	1	0	1	1	2	1	1	1	1	1	2	1	1	-	2	0	2	1	2	6	0	2	1	1	2	1
Simulium	1	1	0	0	1	1	0	0	1	1	2	2	0	0	0	1	1	2	1	3	0	2	1	1	1	0	1	1	2	1	1	2	1	1	2	1	1	-	2	0	2	1	2	6	0	0	1	3	1	1

Table 1. Character state matrix for cladistic parsimony analysis of the subfamily Simuliinae (character numbers and species as listed above)
Таблица 1. Матрица состояний признаков для кладистического парсимонического анализа подсемейства Simuliinae (номера признаков и виды перечислены выше)

	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chaoboridae	-	-	0	0	0	0	0	0	?	0	0	0	0	?	0	-	0	0	0	0	0	?	?	?	-	-	-	0	0	0	0	0	0	0	-	0	-	0	0	-	0	0	0	0	0	?	?	-	-	-
Chironomidae	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	-	0	0	0	1	0	0	0	0	0	-	0	1	0	0	0	0	0	0	0	0	-	-	-
Culicidae	-	-	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	?	0	0	0	0	-	0	0	0	0	0	0	0	-	0	-	0	0	-	0	0	0	0	0	0	0	-	-	-
Ceratopogonidae	-	-	0	0	0	0	0	0	?	0	0	1	0	?	0	-	0	0	0	0	0	?	0	?	-	-	-	0	0	0	1	0	0	0	-	0	-	0	0	-	0	0	0	0	0	0	0	-	-	-
Parasimulinae	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1	1	-	2	1	0	?	?	0	0	1	0	1	1	1	1	1	0	1	0	0	1	0	1	0	0	1	1	0	0	0	0	0
Prosimulinae	0	0	1	0	1	1	0	0	0	0	0	1	0	0	1	0	1	1	1	-	2	1	3	2	0	1	1	1	0	0	1	1	1	1	0	1	0	0	1	0	1	1	1	1	1	0	0	0	0	0
Stegopterna	0	1	1	0	1	1	0	0	1	1	0	1	0	1	0	0	1	1	0	1	2	1	2	3	1	0	2	1	0	0	1	1	1	1	0	1	1	1	2	0	1	1	1	1	1	1	0	0	0	0
Greniera	0	1	1	0	1	1	0	0	2	1	0	1	1	1	0	1	1	1	0	1	2	1	2	3	1	2	2	1	0	0	1	1	1	1	0	1	1	1	2	0	1	1	1	1	1	0	0	0	0	0
Cnephia	0	1	1	0	1	1	0	0	2	1	0	1	0	2	0	0	1	1	0	0	0	0	2	1	2	1	2	1	0	0	1	1	1	1	0	1	1	2	1	0	1	1	1	1	1	0	0	0	0	0
Metacnephia	0	1	1	0	1	1	0	0	0	1	2	1	0	2	1	0	1	1	0	0	0	0	3	3	2	1	2	1	0	0	1	1	1	1	0	1	4	0	1	0	1	1	1	1	1	?	0	0	0	0
Sulcicnephia	0	1	1	0	1	1	0	0	0	1	2	1	0	2	0	0	1	1	0	0	0	3	3	1	1	1	2	1	0	0	1	1	1	1	0	1	4	0	2	0	1	1	1	1	1	3	1	0	0	0
Hellichiella	0	1	1	0	1	1	0	0	1	1	0	1	1	1	0	1	1	1	0	0	0	1	2	2	0	0	2	1	0	1	1	1	1	1	0	1	3	1	2	0	1	1	1	1	1	3	1	0	0	0
Byssodon	0	1	1	0	1	1	0	1	1	4	2	1	0	2	0	0	1	1	0	0	0	2	2	2	0	1	2	1	1	0	1	1	1	1	0	1	4	0	1	0	1	1	1	1	1	0	1	0	0	0
Psilocnetha	0	1	1	0	1	1	0	2	1	1	2	1	0	0	0	0	1	1	0	0	0	2	2	?	0	1	2	1	0	0	1	1	1	1	0	1	3	0	5	0	1	1	1	1	1	?	1	0	0	0
Cnetha	0	1	1	0	1	1	0	0	1	1	0	1	0	1	0	0	1	1	0	0	0	2	2	2	0	0	2	1	0	1	1	1	1	1	0	1	3	0	4	1	1	1	1	1	1	0	1	0	0	0
Nevermannia	0	1	1	0	1	1	0	0	1	2	0	1	0	1	0	0	1	1	0	0	1	2	2	2	1	1	2	1	0	1	1	1	1	1	0	1	3	0	4	1	1	1	1	1	1	0	1	0	0	0
Eusimulium	0	1	1	0	1	1	0	0	1	2	0	1	0	1	0	0	1	1	0	0	2	2	2	2	0	1	2	1	0	1	1	1	1	1	0	1	2	0	4	1	1	1	1	1	1	1	1	0	0	0
Schoenbaueria	0	1	1	0	1	1	0	0	1	1	1	1	0	2	0	0	1	1	0	0	0	3	2	2	1	2	2	1	0	1	1	1	1	1	0	1	2	1	3	0	1	1	1	1	1	0	1	0	0	0
Gomphostilbia	0	0	1	1	1	1	0	0	?	0	2	1	0	1	0	0	1	1	0	0	?	?	?	0	2	1	2	1	0	1	1	1	1	1	1	0	1	2	1	3	1	1	1	1	1	1	1	1	0	0	0
Morops	0	1	1	1	1	1	0	0	1	2	2	1	0	1	0	0	1	1	0	0	0	2	2	0	2	0	2	1	0	0	1	1	1	1	1	0	1	2	0	4	0	1	1	1	1	1	1	0	0	0
Montisimulium	0	0	1	0	1	1	0	0	?	?	0	1	0	1	0	0	1	1	0	0	2	1	2	3	2	1	2	1	0	1	1	1	1	1	1	0	1	2	1	3	0	1	1	1	1	1	0	1	0	0	0
Wilhelmia	1	1	1	0	1	1	0	0	1	2	1	1	0	0	0	0	1	1	0	0	1	0	2	1	1	2	2	1	0	0	1	1	1	1	1	1	4	0	5	0	1	1	1	1	1	4	2	0	0	0
Boophthora	1	1	1	0	1	1	0	0	1	1	2	1	0	2	0	0	1	1	0	0	1	0	2	0	0	2	2	1	0	1	1	1	1	1	0	1	2	1	3	0	1	1	1	1	1	2	1	0	0	0
Psilosia	1	1	1	0	1	1	0	0	1	2	2	1	0	2	0	0	1	1	0	0	1	0	2	0	0	3	2	1	0	0	1	1	1	1	0	1	2	0	2	0	1	1	1	1	1	1	1	0	0	0
Cleitosimulium	1	1	1	0	1	1	1	0	1	2	2	1	0	0	1	0	1	1	0	0	1	0	2	1	1	1	2	1	0	0	1	1	1	1	1	1	4	1	3	0	1	1	1	1	1	2	1	0	0	0
Obuchovia	0	1	1	0	1	1	1	0	2	2	2	1	0	2	0	0	1	1	0	0	1	3	2	1	2	1	2	1	0	0	1	1	1	1	1	1	4	1	3	1	1	1	1	1	1	?	1	0	0	0
Paragnus	0	1	1	0	1	1	0	0	2	2	2	1	0	0	0	0	1	1	0	0	0	0	2	0	2	1	2	1	0	0	1	1	1	1	1	0	1	4	0	1	0	1	1	1	1	1	?	1	0	0	0
Parabyssodon	1	1	1	0	1	1	0	1	1	2	2	1	0	1	0	0	1	1	0	0	0	0	2	0	2	1	2	1	1	0	1	1	1	1	1	0	1	2	0	4	1	1	1	1	1	1	1	1	0	0	0
Archesimulium	1	1	1	0	1	1	0	0	1	0	2	1	0	2	0	0	1	1	0	0	0	2	2	0	2	1	2	1	0	0	1	1	1	1	1	0	1	2	1	3	1	1	1	1	1	1	2	1	0	0	0
Striatosimulium	1	1	1	0	1	1	0	0	1	0	2	1	0	2	0	0	1	1	0	0	0	2	2	2	2	1	2	1	0	0	1	1	1	1	1	0	1	2	1	3	1	1	1	1	1	1	2	1	0	0	0
Argentisimulium	1	1	1	0	1	1	0	0	2	4	2	1	0	2	0	0	1	1	0	0	0	2	2	0	2	1	2	1	0	0	1	1	1	1	1	0	1	1	1	3	0	1	1	1	1	1	2	1	1	0	0
Tetisimulium	1	1	1	0	1	1	0	0	1	0	2	1	0	1	0	0	1	1	0	0	1	2	2	0	2	1	2	1	0	0	1	1	1	1	1	0	1	1	1	3	1	1	1	1	1	1	3	1	1	0	0
Phoretodagmia	1	1	1	0	1	1	0	1	0	0	0	1	0	0	0	0	1	1	0	0	1	2	1	1	2	1	2	1	0	0	1	1	1	1	1	1	1	2	1	3	1	1	1	1	1	1	1	1	1	0	0
Odagmia	1	1	1	0	1	1	0	0	2	2	2	0	1	0	2	0	0	1	1	0	0	0	2	2	0	2	1	2	1	0	0	1	1	1	1	0	1	1	2	1	3	1	1	1	1	1	1	1	1	0	0
Gnus	1	1	1	0	1	1	0	0	2	3	2	1	0	2	0	0	1	1	0	0	0	0	2	2	0	2	2	2	1	0	0	1	1	1	1	0	1	1	2	1	3	1	1	1	1	1	2	1	0	1	1
Simulium	1	1	1	0	1	1	0	0	1	4	2	1	0	2	0	0	1	1	0	0	0	0	2	0	2	2	2	1	0	0	1	1	1	1	1	0	1	2	1	3	1	1	1	1	1	1	2	1	0	1	1

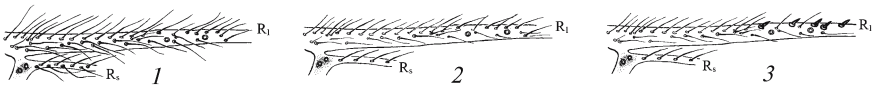

Fig. 3. Setulosity of the radius sector vein: *1 — Parasimulium sp., 2 — Pr. hirtipes, 3 — W. equina* (after Kahlich et al., 2012).

Рис. 3. Опушение радиальных жилок крыла: *1 — Parasimulium sp., 2 — Pr. hirtipes, 3 — W. equina* (по Капличу и др., 2012).

Fig. 4. Basal radial cell of wings: *1 — Cnephia pallipes, 2 — Simulium morsitans* (after Kaplich et al., 2012).

Рис. 4. Базально-радиальная ячейка крыла: *1 — Cnephia pallipes, 2 — Simulium morsitans* (по Капличу и др., 2012).

14. **Anepisternal membrane**: (0) bare; (1) setulose.
State 1 is a possible synapomorphy of *Tetisimulium*, *Odagmia*, and *Phoretodagmia*, and also in *Morops*, *Wilhelmia*, and *Metacnephia*, but possibly independently, due to homplasy.
15. **Dark pattern on the female scutum**: (0) absent; (1) lyrate.
State 1 occurs in the tribe Wilhelmiini and the genera *Byssodon*, *Psilocnetha*, *Striatosimulium*, and *Tetisimulium*, possibly due to homplasy.

Wing

16. **Shape**: (0) not broadened at base; (1) strongly broadened at base.
State 1 is a possible synapomorphy of Simuliidae.
17. **Setulosity of costal vein**: (0) irregularly piliform; (1) with hairs and spines.
State 1 is a possible synapomorphy of the subfamily Simuliinae.
18. **Setulosity of the radius sector (R_S) vein**: (0) long hairs; (1) short hairs; (2) short hairs and spines (fig. 3).
State 1 occurs in the Prosimuliinae. State 2 is hypothesized to be a synapomorphy of the Simuliinae.
19. **Radius sector (R_S)**: (0) widely branched into R_{2+3} and R_{4+5}; (1) not branched.
State 1 occurs in the subfamilies Prosimuliinae and Simuliinae and is believed to be their synapomorphy.
20. **Setulosity of vein R_1**: (0) only hairs along whole length; (1) base bare, the rest haired; (2) one half is haired, another half is haired and spinose; (3) one half is bare, another half is haired and spinose; (4) basal one-third is bare, medial one-third is haired, apical one-third is haired and spinose.
State 1 is found in the *Byssodon-Psilocnetha* group. State 2 is believed to be a synapomorphy of the tribe Wilhelmiini, and occurs also in the genus *Tetisimulium*, possibly due to homoplasy. State 3 is found in all members of the tribe Simuliini. State 4 is represented in the group *Boophthora-Psilozia*, genera *Paragnus* and *Gnus*, possibly due to homplasy.
21. **Basal radial cell of wings**: (0) shorter, at most ⅓ × as long as R_S; (1) longer, half as long as R_S (fig. 4).
State 1 occurs in the Prosimuliinae, members of Stegopternini and genera *Cnephia* and *Metacnephia* of the tribe Ectemniini.
22. **Basal medial cell**: (0) large; (1) small, but distinct; (2) entirely reduced.
State 1 is common in the subfamilies Parasimuliinae and Prosimuliinae. State 2 is a possible synapomorphy of the subfamily Simuliinae.
23. **False vein**: (0) feebly visible; (1) distinctive.
State 1 is present the subfamilies Prosimuliinae and Simuliinae.
24. **False vein**: (0) neither bifurcated at the tip, nor reaching the apical edge of the wing; (1) bifurcated at the tip, reaching the apical edge of the wing.
State 1 is a possible synapomorphy of the subfamilies Prosimuliinae and Simuliinae.

Legs

25. **Coloration**: (0) black; (1) spotted, often with silvery spots.
State 1 occurs in the tribes Nevermanniini, Simuliini and is their possible synapomorphy; however, it is present in species of the genus *Sulcicnephia*, possibly, due to homoplasy.
26. **Hind tibia spur**: (0) shorter than tibia width; (1) longer than tibia width.
State 1 is a possible synapomorphy of tribe Stegopternini.

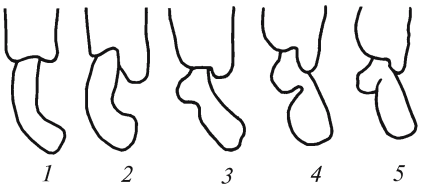

Fig. 5. Calcipala: *1 — C. pallipes, 2 — St. trigonia, 3 — Sch. pusilla, 4 — Arg. noellery, 5 — Sim. morsitans* (after Kaplich et al., 2012).

Рис. 5. Кальципала*: 1 — C. pallipes, 2 — St. trigonia, 3 — Sch. pusilla, 4 — Arg. noellery, 5 — Sim. morsitans* (по Капличу и др., 2012).

27. **Fore basitarsus**: (0) thin, cylindrical; (1) widened at its distal end.
Condition 1 is a possible synapomorphy of the tribe Simuliini and occurs in some Nevermanniini (*Byssodon*, *Psilocnetha*, *Schoenbaueria*, *Gomphostilbia*, *Morops*), apparently due to homoplasy.
28. **Shape of the distal edge of hind basitarsus**: (0) hind basitarsus laterally flattened and ventrally keeled; (1) basitarsus with projection.
State 1 occurs in the subfamily Parasimuliinae, and tribes Stegopternini, Nevermanniini, Wilhelmiini, Simuliini.
29. **Calcipala**: (0) not developed; (1) weakly developed; (2) well expressed (fig. 5).
State 1 occurs throughout of the subfamily Prosimuliinae, genera *Cnephia*, *Metacnephia* and is their possible synapomorphy. State 2 characterizes of the tribes Stegopternini, Nevermanniini, Wilhelmiini, Simuliini.
30. **Pedisulcus**: (0) not expressed; (1) well expressed.
State 1 is a possible synapomorphy of the tribes Nevermanniini, Wilhelmiini, Simuliini and also occurs in species of genera *Sulcicnephia*, probably due to homoplasy.
31. **Male claws**: (0) simple; (1) with grooved lobes of cuticle on dorsal side at base.
State 1 is found the family Simuliidae.
32. **Female claw**: (0) with a large basal tooth; (1) with a small basal tooth; (2) simple, without tooth.
State 1 is common in the subfamily Prosimuliinae and occurs also in the groups of the genera *Tetisimulium–Phoretodagmia–Odagmia–Gnus*. Condition 2 is a possible synapomorphy of the tribes Wilhelmiini and Simuliini.

Abdomen

33. **First abdominal segment of adults**: (0) without basal fringe; (1) with long hairs (basal fringe) at the edge on each side.
Condition 1 is a possible synapomorphy of the Simuliidae.
34. **Lateral silvery spots on male abdomen**: (0) absent; (1) present.
State 1 is a possible synapomorphy of the tribes Wilhelmiini and Simuliini.

Male genitalia

35. **Gonostylus**: (0) small cone-shaped; (1) nearly as long as gonocoxite; (2) longer than gonocoxite; (3) short and thin; (4) short and wide.
State 1 is a possible synapomorphy of the tribes Ectemniini and Nevermanniini. State 2 is attributing of the tribe Simuliini (excluding genera *Boophthora*, *Psilozia*). Condition 3 is a possible synapomorphy of the tribe Wilhelmiini. Condition 4 characterizes the genus *Boophthora*.
36. **Gonostylus apical spinules**: (0) two or more; (1) one apical; (2) no apical spinule.
State 1 is a possible synapomorphy of the tribes Ectemniini and Nevermanniini. State 2 is present in the tribe Simuliini (excluding genera *Boophthora*, *Psilozia*). Condition 3 is a possible synapomorphy of the genera of the tribe Wilhelmiini. Condition 4 characterizes the genus *Boophthora*.
37. **Tubercle at the gonostylus base**: (0) absent; (1) setulose; (2) spinose.
Condition 1 is a possible synapomorphy of the genera group *Argentisimulium*, *Tetisimulium*, *Phoretodagmia*, *Odagmia*, *Gnus* and *Simulium*. and occurs in the genus *Paragnus*, probably due to homoplasy. State 2 is attributing of the genera *Parabyssodon*, *Archesimulium*, *Striatosimulium*.
38. **Ventral plate of the aedeagus**: (0) lamellate; (1) lamellate with a medial keel; (2) lamellate with a posterior notch; (3) thin curved strip shaped; (4) V-shaped, without heel.
State 1 occurs in the genera *Nevermannia* and *Obuchovia*. State 2 is found in the genus *Montisimulium*. State 3 is a possible synapomorphy of the tribe Wilhelmiini. State 4 characterizes the genus *Eusimulium*.
39. **Ventral plate of the aedeagus**: (0) lamellate; (1) laterally compressed, with prominent lip and heel; (2) narrow wedge-shaped, with lip and heel.
State 1 is a possible synapomorphy of *Striatosimulium*, *Tetisimulium*, *Phoretodagmia*, *Odagmia*, *Gnus* and *Simulium* group. State 2 characterizes the genus *Argentisimulium*.

40. **Body of the ventral plate**: (0) without bending; (1) ventrally curved; (2) of complex shape.
State 1 is present in the genera *Psilocnetha*, *Montisimulium*, *Archesimulium*, in some cases, probably due to homoplasy. State 2 is a possible synapomorphy of *Cleitosimulium*.
41. **Apical lip of the ventral plate**: (0) poorly expressed, normally haired; (1) small, elevated, slightly haired; (2) large, haired.
State 1 is found in the tribe Wilhelmiini and also occurs in the genera *Boophthora–Psilozia–Cleitosimulium–Obuchovia*, possibly due to homoplasy. State 2 is represented in the species of tribe Simuliini.
42. **Denticles on the heel of ventral plate**: (0) lacking; (1) present.
Condition 1 is a possible synapomorphy of the group *Argentisimulium–Tetisimulium–Phoretodagmia–Odagmia–Gnus–Simulium* of the tribe Simuliini.
43. **Parameral spines**: (0) paramere without spines; (1) small undifferentiated spines; (2) small differentiated spines; (3) 3–5 big spines; (4) 2–3 big spines; (5) 1 big spike.
State 1 is a possible synapomorphy of the tribe Stegopternini. It is present in the genera *Hellichiella*, *Morops* and *Psilozia*, possibly due to homplasy. State 2 is a possible synapomorphy of the tribes Ectemniini, Wilhelmiini and Simuliini. State 3 characterizes species of the genus *Montisimulium*. State 4 is represented the species of the genus *Schoenbaueria*. Condition 5 is a possible synapomorphy of the *Cnetha–Nevermannia–Eusimulium* group.
44. **Aedeagus median sclerite**: (0) Y-shaped, incised; (1) T-shaped, incised; (2) wide, rounded, spatulate in apical portion; (3) widely rounded; (4) long thin plate; (5) elongate, unfolded; (6) elongate, transversally folded.
State 1 is typical for the genus *Schoenbaueria*. State 2 is a possible synapomorphy of the genera *Hellichiella* and *Byssodon*. Condition 3 characterizes the genus *Psilozia*. State 4 is an attribute of the *Nevermannia–Eusimulium* group and occurs in the *Obuchovia*, apparently, due to homoplasy. Condition 5 is a possible synapomorphy of the genera group *Gomphostilbia–Morops*. State 6 is common in the group *Parabyssodon–Archesimulium–Striatosimulium–Argentisimulium–Tetisimulium–Phoretodagmia– Odagmia–Gnus–Simulium*.
45. **Male X abdominal sternite**: (0) absent; (1) rectangular; (2) trapeziform; (3) lyrate; (4) triangular.
State 1 occurs in the tribes Stegopternini, Ectemniini, Wilhelmiini, and is a possible their synapomorphy. Condition 2 occurs in the genera *Cnetha*, *Montisimulium*, *Boophthora*, apparently, due to homoplasy. State 3 is typical for the genera *Nevermannia* and *Cleitosimulium*. Condition 4 is common in the genera *Sulcicnephia* and *Schoenbaueria*, probably due to homoplasy.

Female genitalia

46. **Hypogynial valve**: (0) simple, rectangular, approximated; (1) simple, rectangular, widely separated; (2) simple, with broadly rounded or truncated posteriorly; (3) markedly elongate; (4) with S-shaped curved medial edge; (5) elongated into narrow annular curved strips.
State 1 occurs only in the genus *Striatosimulium*. State 2 is found in the genus *Gnus*. State 3 is represented in the genera *Cnephia*, *Nevermannia*, *Eusimulium*, *Psilozia*, *Cleitosimulium*, *Obuchovia*, either as a synapomorphy or as a homplasy. State 4 is a possible synapomorphy of the *Tetisimulium–Phoretodagmia–Odagmia* group. State 5 is a possible synapomorphy of the tribe Wilhelmiini.
47. **Anal lobes**: (0) incomplete separation of X sternite; (1) anal lobes expressed, separated; (2) anal lobes narrow, elongated.
State 1 encodes all the states of the character in the Simuliidae except for the subfamily Parasimuliinae. State 2 is a possible synapomorphy of the subfamilies Prosimuliinae and the tribes Stegopternini and Wilhelmiini and occurs in the genera *Cnephia*, *Cnetha*, *Nevermannia*, *Psilozia*, *Obuchovia*, possibly due to homoplasy.
48. **Anal lobes**: (0) incomplete separation of the X sternite; (1) anal lobes expressed, separated; (2) medium-sized, rectangular; (3) medium-sized, triangular, undivided; (4) medium-sized, triangular, divided.
State 1 encodes all the states of the character in the Simuliidae except for the subfamily Parasimuliinae. State 2 is found in all members of the subfamily Simuliinae, except Stegopternini and Wilhelmiini. State 3 is represented in the genera *Eusimulium*, *Schoenbaueria*, *Parabyssodon*, *Archesimulium*, *Striatosimulium*, *Tetisimulium*, *Phoretodagmia* and *Simulium*, possibly as a homplasy. State 4 is a possible synapomorphy in the genus *Odagmia*.
49. **Anal lobes**: (0) incomplete separation of X sternite; (1) anal lobes expressed, separated; (2) large, wide.
State 1 encodes all the states of the character in the Simuliidae except for the subfamily Parasimuliinae. State 2 occurs in the genera *Boophthora*, *Argentisimulium* and *Gnus*.
50. **Stem of the genital fork:** (0) short, 1.5–2× as long as the height of the branches; (1) long, 2.5–4× as long as the height of the branches.
State 1 is a possible synapomorphy of subfamily Simuliinae.
51. **Divergence angle of the genital fork branches**: (0) < 90°; (1) > 90°.
State 1 is a possible synapomorphy of the tribes Wilhelmiini and Simuliini.
52. **Apodemes of the genital fork branches**: (0) absent; (1) present.
State 1 is a possible synapomorphy of the subfamily Simuliinae.

53. **Number of spermathecae**: (0) three; (1) one large, central.
State 1 is a possible synapomorphy of the family Simuliidae.
54. **Structure of the spermatheca surface**: (0) smooth; (1) shagreened surface with a hexagonal pattern.
State 1 is a possible synapomorphy of the *Gomphostilbia-Morops* group.
55. **Behavior of females in the process of blood sucking**: (0) females bite rapidly upon settling; (1) females spend a relatively long period of time crawling and probing before biting a host.
State 1 occurs in the family Simuliidae.

Larva

56. **Number of larval instars**: (0) 3–4; (1) 4–11.
State 1 is a possible synapomorphy of the family Simuliidae.
57. **Larval body coloration**: (0) variously colored; (1) typically blackish dorsally and whitish ventrally.
State 1 is a possible synapomorphy of the *Cleitosimulium–Obuchovia* groups (Adler et al., 2004).
58. **Cuticle**: (0) without setae; (1) covered by spatulate setae; (2) covered by flabelliform setae.
State 1 is believed to be independently evolved in the genera *Byssodon*, *Parabyssodon*, and *Phoretodagmia*.
State 2 is a possible synapomorphy of the genus *Psilocnetha*.
59. **Frontoclypeal apotoma**: (0) V-shaped posteriorly; (1) U-shaped posteriorly; (2) expanded posteriorly.
State 1 is typical for representatives of the tribes Nevermanniini, Wilhelmiini and some genera of the tribe Simuliini. Condition 2 is found in all the members of *Greniera*, *Cnephia*, *Obuchovia*, *Paragnus*, *Argentisimulium*, *Odagmia*, and *Gnus*, possibly as a homplasy.
60. **Pattern of the frontoclypeal apotoma**: (0) positive (dark on light background), fuzzy; (1) positive cruciform, has 2 pairs of lateral spots; (2) positive cruciform, has a pair of lateral spots; (3) positive pyramidal; (4) negative (light on a dark background) H-shaped.
State 1 is a possible synapomorphy of the tribes Stegopternini, Ectemniini and some representatives of Nevermanniini (*Hellichiella*, *Psilocnetha*, *Cnetha*). Condition 2 is common in the tribe Wilhelmiini and majority species of the tribe Simuliini. State 3 a typical for the genus *Gnus*. State 4 occurs in *Byssodon*, *Argentisimulium*, and *Simulium*, possibly as a homplasy.
61. **Postgenal cleft**: (0) small, < 0.5× as high as length of the postgena, weakly developed; (1) medium-sized, 0.5× as high as length of the postgena; (2) large, > 0.5× as high as length of the postgena, well developed.
State 1 is a possible synapomorphy of the tribe Wilhelmiini. Condition 2 is a possible synapomorphy of the tribes Ectemniini and Simuliini (except genera *Phoretodagmia*, *Odagmia*), also occurs in the genera groups *Metacnephia–Sulcicnephia, Gomphostilbia–Morops,* and the genus *Byssodon*.
62. **Number of antennal joints**: (0) one; (1) three.
State 1 is a possible synapomorphy the subfamilies Prosimuliinae and Simuliinae.
63. **Basal joint of antenna**: (0) without notches; (1) with 5–7 additional notches.
State 1 occurs in the genera *Greniera* and *Hellichiella*, probably due to homoplasy.
64. **Length of antenna**: (0) almost as long as the labral-fan stalk; (1) markedly elongate, much longer than the labral-fan stalk; (2) shorter than labral-fan stalk.
State 1 is a possible synapomorphy of the tribes Stegopternini and Nevermanniini. State 2 is a common feature for the tribes Ectemniini and Simuliini, apparently due to homoplasy.
65. **Coloration of antenna**: (0) unicolour; (1) contrast.
State 1 is a possible synapomorphy of Prosimuliinae, also occurs in the genera *Metacnephia* and *Cleitosimulium*, probably due to homoplasy.
66. **Labral fan**: (0) smaller than larval head capsule; (1) more than larval head capsule.
State 1 is common for representatives the genera *Greniera* and *Hellichiella*.
67. **Number of ray rows in the labral fan**: (0) a large number of the rows rays; (1) reduced to three rows of rays.
State 1 is a possible synapomorphy of the family Simuliidae.
68. **Epipharyngeal stipe**: (0) absent; (1) stipe directed anteroventraly.
State 1 is a possible synapomorphy of the family Simuliidae.
69. **Hypostomal teeth**: (0) simple, unseparation; (1) with large difficult arranged teeth.
State 1 is a possible synapomorphy of the subfamilies Parasimuliinae and Prosimuliinae.
70. **Simple hypostomal teeth**: (0) uncollected in groups; (1) collected in three distinct groups.
State 1 is a possible synapomorphy of the tribe Stegopternini.
71. **Hypostomal teeth**: (0) small; (1) medium-sized; (2) large.
State 1 is represented in the tribe Wilhelmiini, genus *Nevermannia* and the groups *Boophthora–Psilozia*; *Cleitosimulium–Obuchovia*; *Tetisimulium–Phoretodagmia*, possibly as a homplasy. Condition 2 is a possible synapomorphy of the subfamilies Parasimuliinae, Prosimuliinae and the tribe Stegopternini, also occurs in the genera *Eusimulium* and *Montisimulium*, apparently, due to homoplasy.
72. **Anterior margin of the hypostoma**: (0) flat; (1) rough, median and lateral teeth are much larger than the sublateral teeth; (2) rough, median and lateral teeth slightly larger than the sublateral; (3) rounded as median tooth higher than others.
State 1 characterizes the subfamilies Parasimuliinae, Prosimuliinae, tribe Stegopternini, genera *Hellichiella* and *Montisimulium*. Condition 2 is common in the groups *Byssodon–Psilocnetha–Cnetha–*

Nevermannia–*Eusimulium* and *Archesimulium*–*Striatosimulium*–*Argentisimulium*–*Tetisimulium*–*Phoretodagmia*–*Odagmia*–*Gnus*–*Simulium*, apparently, due to homoplasy. Condition 3 is believed to be independently evolved in the three genera: *Sulcicnephia, Schoenbaueria,* and *Obuchovia*.

73. **Paralateral teeth of the hypostoma**: (0) small and not numerous; (1) numerous and large; (2) not numerous; (3) absent.
Condition 1 a typical for the genus *Phoretodagmia*. State 2 is a possible synapomorphy of the subfamily Simuliinae. Condition 3 is a possible synapomorphy of Prosimuliinae.
74. **Outer teeth of the larval mandible**: (0) reduced from anterior to posterior; (1) equal; (2) posterior and anterior teeth larger than the intermediate; (3) posterior tooth larger than others.
State 1 characterizes the tribes Ectemniini and Wilhelmiini, and *Cleitosimulium*–*Obuchovia* groups. Condition 2 is a possible synapomorphy of the tribe Nevermanniini, also occurs in the genus *Striatosimulium*, probably due to homoplasy. State 3 is a possible synapomorphy of representatives the subfamily Prosimuliinae and the tribe Stegopternini.
75. **Inner teeth of the mandible**: (0) shorter than outer teeth; (1) as long as outer teeth; (2) longer than outer teeth.
State 1 occurs in the genera *Greniera*, *Sulcicnephia*, *Nevermannia*, *Schoenbaueria*, *Wilhelmia,* and *Cleitosimulium*, probably due to homoplasy. Condition 2 is represented in the groups *Cnephia*–*Metacnephia*; *Gomphostilbia*–*Morops*–*Montisimulium*; *Obuchovia*–*Paragnus*–*Parabyssodon*–*Archesimulium*– *Striatosimulium*–*Argentisimulium*–*Tetisimulium*–*Phoretodagmia*–*Odagmia*–*Gnus*–*Simulium*, possibly due to homplasy.
76. **Teeth on the marginal plate of the mandible**: (0) very numerous and small; (1) one large and 1–4 small; (2) two small; (3) two large.
State 1 occurs in the subfamilies Prosimuliinae and Simuliinae. Condition 2 is a possible synapomorphy of the tribe Wilhelmiini. State 3 is typical for the genus *Psilozia*.
77. **Lateral sclerite of the prothoracic proleg**: (0) absent; (1) narrow, not vertically produced; (2) broad, with vertical portion well developed.
State 1 is typical for representatives of the subfamily Prosimuliinae. State 2 is a possible synapomorphy of the subfamily Simuliinae.
78. **Silk glands**: (0) small, unfolded; (1) large, folded.
State 1 is a possible synapomorphy of the family Simuliidae.
79. **Papilles of abdomen**: (0) absent; (1) present.
State 1 is represented in the genera *Byssodon* and *Parabyssodon*.
80. **Ventral bulge of the IX abdominal segment**: (0) absent; (1) one pair of large conical ventral bulges.
State 1 is found in all members of the tribes Nevermanniini and Simuliini (*Gomphostilbia*, *Montisimulium*, *Cnetha*, *Nevermannia*, *Eusimulium*, *Schoenbaueria*, *Obuchovia*, *Boophthora*).
81. **Anus**: (0) terminal (apical); (1) dorsal.
State 1 is a possible synapomorphy of the family Simuliidae and Chironomidae.
82. **Rectal papilles**: (0) paired; (1) three.
State 1 is a possible synapomorphy of the family Simuliidae.
83. **Anal sclerite**: (0) absent; (1) X-, Y-shaped structure on the dorsum of abdominal segment IX.
State 1 is a possible synapomorphy of the family Simuliidae.
84. **Location of the hooks on prothoracic prolegs and posterior circlet**: (0) irregularly arranged, but not in the linear fashion; (1) arranged in longitudinal rows.
State 1 characterizes the family Simuliidae.
85. **Posterior circlet**: (0) with a narrow ring of hooks; (1) with a wide ring of hooks.
State 1 is a possible synapomorphy of the tribe Wilhelmiini and independently happens also in the genera *Obuchovia*, *Cleitosimulium* and *Phoretodagmia*.
86. **Behavior of the pharate pupa**: (0) neither feeds, nor moves; (1) feeds and spins its cocoon.
State 1 is a possible synapomorphy of the family Simuliidae.

Pupa

87. **Cocoon**: (0) shapeless, loose; (1) triangular, delicate; (2) triangular, with thickened rim anteriorly; (3) triangular, with hornlike process grow anteriorly; (4) boot shaped (fig. 6).
State 1 is believed to be a synapomorphy of the tribe Stegopternini, and occurs in the genera *Cnephia*, *Argentisimulium*, *Tetisimulium*, possibly due to homoplasy. State 2 occurs in some representatives of the tribes Nevermanniini and Simuliini, possibly as a homplasy. Condition 3 is represented in the group *Hellichiella*, *Psilocnetha*, *Cnetha*, *Nevermannia*. State 4 is a possible synapomorphy of the tribe Wilhelmiini, and independently happens also in the generic groups *Metacnephia-Sulcicnephia*; *Cleitosimulium-Obuchovia-Paragnus*, and the genus *Byssodon*.
88. **Initial branching of the gill respiratory organ**: (0) a common gill base gives rise; (1) three main branches; (2) with filaments arising singly from knob.
State 1 is a possible synapomorphy of the family Simuliidae. State 2 occurs in the genus *Cnephia*.

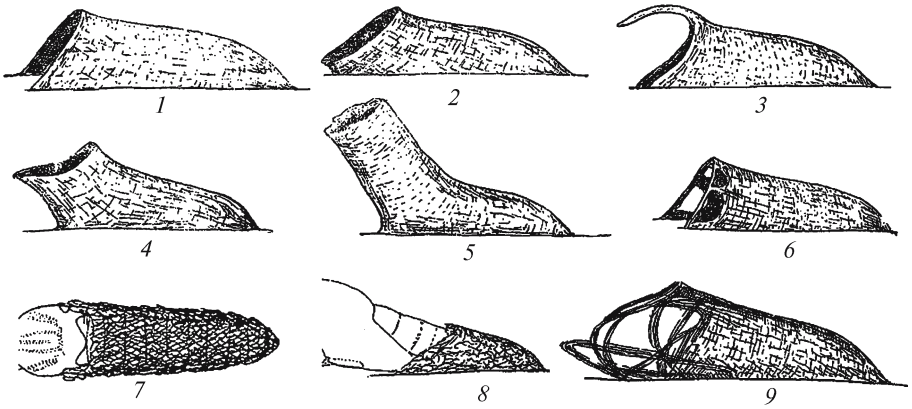

Fig. 6. Cocoon: *1* — triangular, with thickened rim anteriorly (*Boophthora*), *2* — triangular, with a collar (*Striatosimulium*), *3* — triangular, with horn-like process grow anteriorly (*Nevermannia*), *4* — boot shaped (*Byssodon*), *5* — boot shaped (*Sulcicnephia*), *6* — triangular, with the holes on the sides (*Simulium reptans*), *7* — triangular, delicate (*Stegopterna*), *8* — triangular, delicate (*Cnephia), 9* — with woven collar (*Gnus*) (after Rubtsov, 1956, with changes).

Рис. 6. Форма кокона: *1* — простой *(Boophthora)*, *2* — с воротничком *(Striatosimulium), 3* — простой, с роговидным выростом *(Nevermannia), 4* — башмаковидный *(Byssodon), 5* — сапожковидный *(Sulcicnephia), 6* — простой, с отверстиями по бокам *(Simulium reptans), 7* — треугольный, ажурный *(Stegopterna), 8* — бесформенный *(Cnephia), 9* — с плетеным воротничком *(Gnus)* (по Рубцову, 1956 с изменениями).

89. **Number of filaments in the gill**: (0) unbranched respiratory organ; (1) gill with numerous slender filaments, the number of 20–30; (2) slender filaments, the number of 10–16; (3) slender filaments, the number of 6–8; (4) slender filaments, the number of 4; (5) short, swollen.
State 1 is a possible synapomorphy of the Parasimuliinae, Prosimuliinae, the tribe Ectemniini; however, it rises in species of the genera *Byssodon* and *Paragnus*, apparently, due to homoplasy. Condition 2 is typical for the tribe Stegopternini, it occurs in the genera *Sulcicnephia, Hellichiella, Gnus*, possibly as a homplasy. State 3 is represented in the genera *Schoenbaueria, Gomphostilbia, Cleitosimulium–Obuchovia,* in the group *Archesimulium–Striatosimulium–Argentisimulium–Tetisimulium–Phoretodagmia–Odagmia–Simulium*, apparently, due to homoplasy. Condition 4 occurs in the genera *Cnephia–Nevermannia–Eusimulium, Morops,* and *Parabyssodon.*
90. **Arrangement of the gill filaments**: (0) in different planes; (1) in the same plane.
State 1 is believed to be a synapomorphy of several groups *Cnetha–Nevermannia–Eusimulium*; *Parabyssodon–Archesimulium–Striatosimulium*; *Tetisimulium–Phoretodagmia–Odagmia–Gnus–Simulium.*
91. **The regulatory apparatus of spiracle**: (0) absent; (1) present.
State 1 is typical for the family Simuliidae.
92. **Mesothoracic spiracle by pharate adult**: (0) communicates directly with the base of the pupal gill; (1) spiracle is situated somewhat more dorsally.
State 1 is a possible synapomorphy of the subfamilies Prosimuliinae and Simuliinae.
93. **Plastron network**: (0) does not covering entire pupal gill; (1) covering entire pupal gill.
State 1 is a possible synapomorphy of the subfamilies Prosimuliinae and Simuliinae.
94. **Felt chamber of the gill**: (0) present; (1) lost.
State 1 is common in the subfamilies Prosimuliinae and Simuliinae.
95. **Structure of the abdominal segments**: (0) abdominal segments III-VIII with tergites and sternites apparently undivided; (1) abdominal segments III-VIII with tergites and sternites widely separated by pleural membrane.
State 1 is common for the family Simuliidae.
96. **Chaetotaxy of abdominal tergites**: (0) tergites V–IX each with an anterior row of spine combs; (1) tergites VI–IX each with an anterior row of spine combs; (2) tergites VII–IX each with an anterior row of spine combs; (3) tergites VII or VIII each with an anterior row of spine combs; (4) spine combs absent.
State 1 is believed to be independently evolved in some genera the subfamily Simuliinae: *Stegopterna*, *Eusimulium*, *Psilozia*, *Parabyssodon* and the groups *Gomphostilbia–Morops*; *Phoretodagmia–Odagmia*. Condition 2 occurs in the genera *Boophthora*, *Cleitosimulium*, *Archesimulium*, *Argentisimulium*, *Striatosimulium*, *Gnus* and *Simulium*. State 3 is represented in the genera *Sulcicnephia*, *Hellichiella* and *Tetisimulium*, possibly as a homplasy. Condition 4 is a possible synapomorphy of the tribe Wilhelmiini.
97. **Terminal spines of abdomen**: (0) long, situated orthogonally to the pupal body; (1) small; (2) absent.
State 1 is a possible synapomorphy of the tribes Nevermanniini and Simuliini. State 2 is typical for the tribe Wilhelmiini.

Karyology

98. **Chromosomal inversion in middle of IIIL-1 arm**: (0) absent; (1) present.
State 1 is a possible synapomorphy of the *Argentisimulium*, *Tetisimulium*, *Phoretodagmia*, *Odagmia* group.
99. **Chromosomal inversion in base of IIIL arm**: (0) absent; (1) present.
State 1 is represented in the group *Gnus-Simulium*.
100. **Chromosomal inversion in base of IIIS arm**: (0) absent; (1) present.
State 1 is typical for the group *Gnus-Simulium*.

Results and discussion

The initial consensus tree (length = 494, CI = 34, RI = 62) from the shortest parsimony trees that was found by heuristic search (*hs*) in the program PAUP* is shown in fig. 7; it shows multiple polytomies and looks to be poorly resolved. To access higher resolution with mainly dichotomic branching, the technique of successive reweighting was applied. Four successive reweighting of characters carried by the value of **CI** (*consistency index*) and **RC** (*rescaled consistency*) were resulted in the trees 8, 9 and 10, correspondingly (length = 417, CI = 41, RI = 71; length = 417, CI = 41, RI = 71; length = 418, CI = 40, RI = 71, correspondingly).

The bootstrap calculation for both **CI** and **RC** resulting trees showed the reliability of monophyly (bootstrap is higher than 50%) only for 7 branches (fig. 8–10), including: Simuliidae, Prosimuliinae + Simuliinae, Simuliinae, *Stegopterna* + *Greniera*, *Cnetha* + *Nevermannia* + *Eusimulium, Nevermannia* + *Eusimulium, Gomphostilbia* + *Morops, Byssodon* + *Psilocnetha,* Wilhelmiini + Simuliini, *Tetisimulium* + *Phoretodagmia* + *Odagmia, Phoretodagmia* + *Odagmia*.

Further analysis was based on the assumption that the multistate characters 12, 18, 20, 22, 29, 32, 35–36, 41, 43, 48, 58, 61, 71, 75, 89, and 96–97 are ordered.

This analysis clearly shows the subfamily Simuliinae (in the sense accepted in this paper) to be monophyletic. Its monophyly is supported by the numerous synapomorphies as shown on fig. 8–9 and 100 % bootstrap. Unique synapomorphies supporting monophyly of the subfamily Simuliinae are as follows: imago antenna 11-segmented; katepisternal sulcus fully developed, deep and narrow, locked anteriorly; costal wing haired and spiniose; radial wing veins short haired and spinose; basal medial cell of wing reduced; apodemes on branches of the genital fork present. Such a monophyletic subfamily includes the tribes Stegopternini, Ectemniini, Nevermanniini, Wilhelmiini, and Simuliini; the Stegopternini and Ectemnini clearly belong in this subfamily rather than Prosimuliinae, as Yankovsky (2002) suggested.

In the Simuliinae, monophyly of the tribe Stegopternini (*Stegopterna* + *Greniera*) is supported by the synapomorphies **26[1]**, **70[1]**, 74[1] and 76 % bootstrap. The unique synapomorphies supporting the monophyly of Stegopternini are the long hind tibial spurs and simple hypostomal teeth arranged in three distinct groups.

The tribe Ectemniini (defined to include the genera *Cnephia, Metacnephia, Sulcicnephia* in this analysis) is found to be a paraphyletic formation in two of the three analyses; however, in the RI reweighted tree, it appears monophyletic based on the hypotheses of 5° and 72° reversal, and independent development of 35[1], 43[2], 64[2], 74[1], all highly subject to homoplasies.

The tribe Nevermanniini (genera *Hellihiella, Byssodon, Psilocnetha, Cnetha, Nevermannia, Eusimulium, Schoenbaueria, Gomphostilbia, Morops, Montisimulium*) is monophyletic in the CI and RC reweighting analyses, and supported by the characters 64[1], 72[2], 87[2] (homoplastic). Bootstrap of this branch is 64–76 %, indicating moderately good support for its monophyly.

In the tribe Nevermanniini, several genera groups are recognized. The lineage *Gomphostilbia* + *Morops* is supported by the synapomorphies **4[1],** 13[1], 27[1], 44[5], **54[1]**, 75[2] and shows 70–76 % bootstrap. Unique synapomorphies are the presence of 9–12 upper

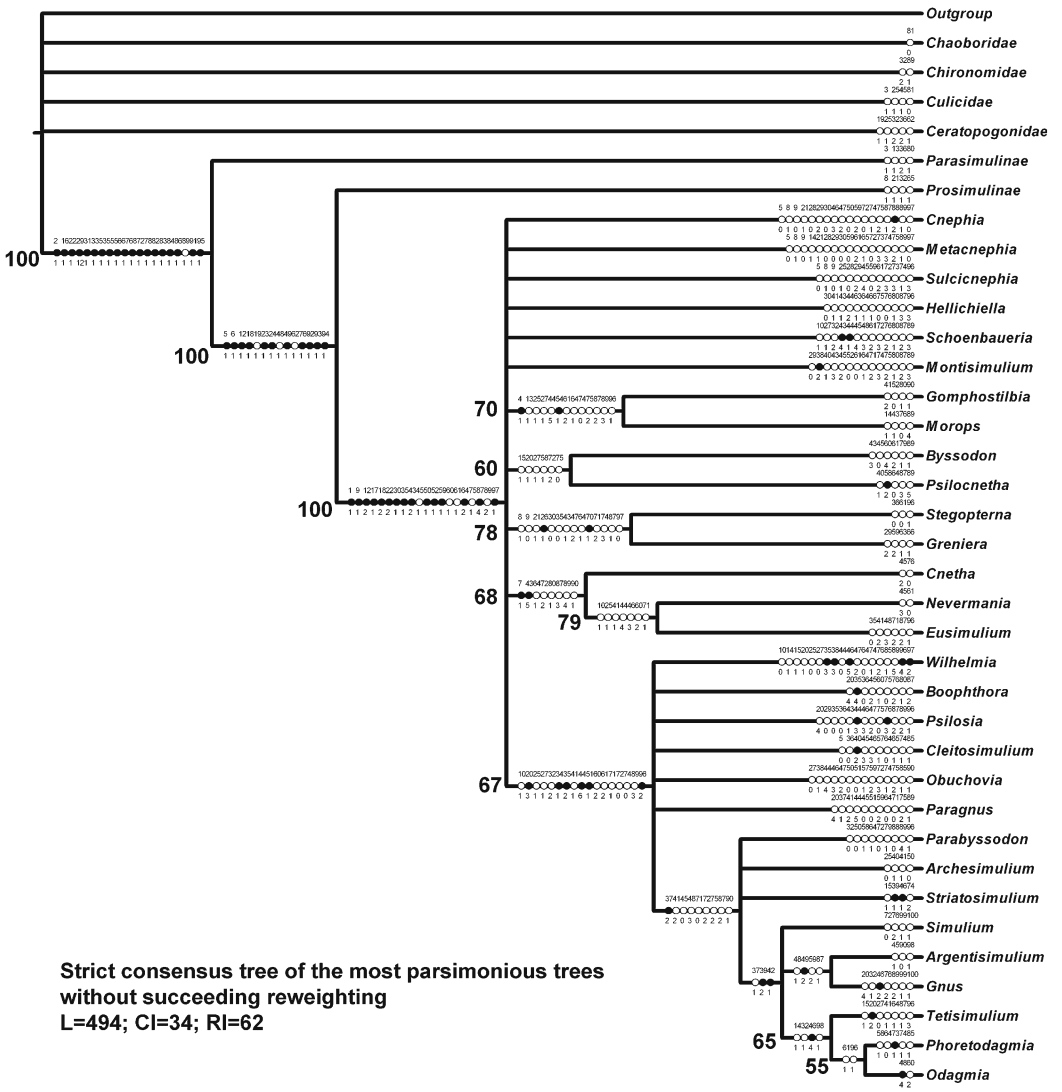

Fig. 7. Relationships of Palaearctic Simuliinae genera. The strict consensus tree of the most parsimonious trees**.** Bootstraps higher than 50 % are given in bold left and below of the clades.

Рис. 7. Кладограмма связей между родами подсемейства Simuliinae Палеарктики. Консенсусное дерево из парсимонических деревьев. Бутстреп больше 50 % выделен жирным шрифтом.

corneal facets in the male eyes, and hexagonally shagreened spermatheca surface. Among the characters assumed homoplastic, there are the haired katepisternum and elongate, nonfolded gonofurca (aedeagus median sclerite), which confirming the validity of group selection.

The *Hellichiella* + *Byssodon* + *Psilocnetha* lineage sharing synapomorphies **44**[2] (or also 75° and 87[3]) is very poorly supported on the CI and RC weighted trees with 2–3 % bootstrap (but not appear on the RI tree). Its unique synapomorphy is the broad, rounded, apically widened gonofurca. The triangular pupal cocoon, with hornlike process growing anteriorly is its other valuable character, though subject to homoplasy.

Byssodon + *Psilocnetha* is supported as a monophyletic lineage by the synapomorphies 15[1] (female scutal pattern distinctly lyrate), 20[1] (the setulose vein R_1 — except its base bare), 27[1] (foreleg basitarsus widened on the distal end), sometimes 58[1], 72[2], 75°, and 80° (reversals) and 55–60 % bootstrap.

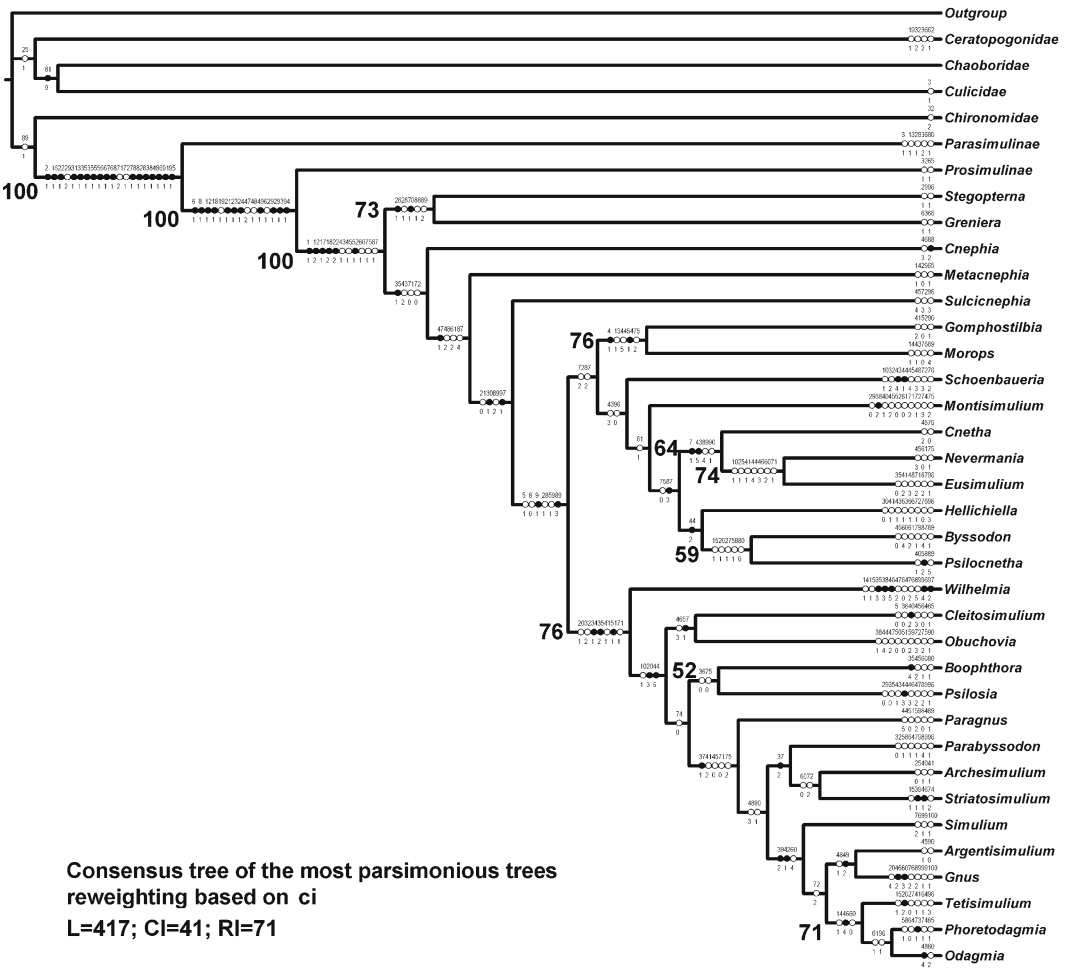

Fig. 8. Relationships of Simuliinae genera. A consensus tree of the most parsimonious trees obtained from the analysis with reweighting based on the ***CI.*** Bootstraps higher than 50 % are given in bold left and below of the clades.

Рис. 8. Кладограмма связей между родами подсемейства Simuliinae. Консенссное дерево из парсимонических деревьев, полученное при перевзвешивании по ***CI.*** Бутстреп больше 50 % выделен жирным шрифтом.

The lineage *Schoenbaueria* + *Cnetha* + *Nevermannia* + *Eusimulium* is a monophyletic formation with synapomorphy **43[4]** (presence of 2–3 large spikes in male paramere) only on the RC tree with 10 % bootstrap.

Monophyly of the group of genera *Cnetha* + *Nevermannia* + *Eusimulium* is supported by synapomorphies **7[1], 43[5],** 89[4], 90[1] and 65–76 % bootstrap. The unique synapomorphies are the presence of big 2nd segment of female maxillary palp with big sensory vesicle and 1 big spike on male paramere. The presence of four slender filaments in pupal gill and arrangement of pupal gill filaments in the same plane are the synapomorphies occurring elsewhere.

The lineage *Nevermannia* + *Eusimulium* is a very well supported by the synapomorphies 25[1], 41[1], 44[4], 46[3], 60[2], 71[1] and 74–83 % bootstrap. All these characters are subject to homoplasy (spotted legs colouration of imago, often with silvery spots; apical lip of ventral plate small, elevated, slightly covered by setae, long thin plate-shapes aedeagus median sclerite; female hypogynial valve markedly elongate; pattern of larval frontoclypeal apotoma positive cruciform with pair of lateral spots), but in combination clearly showing monophyly of this group.

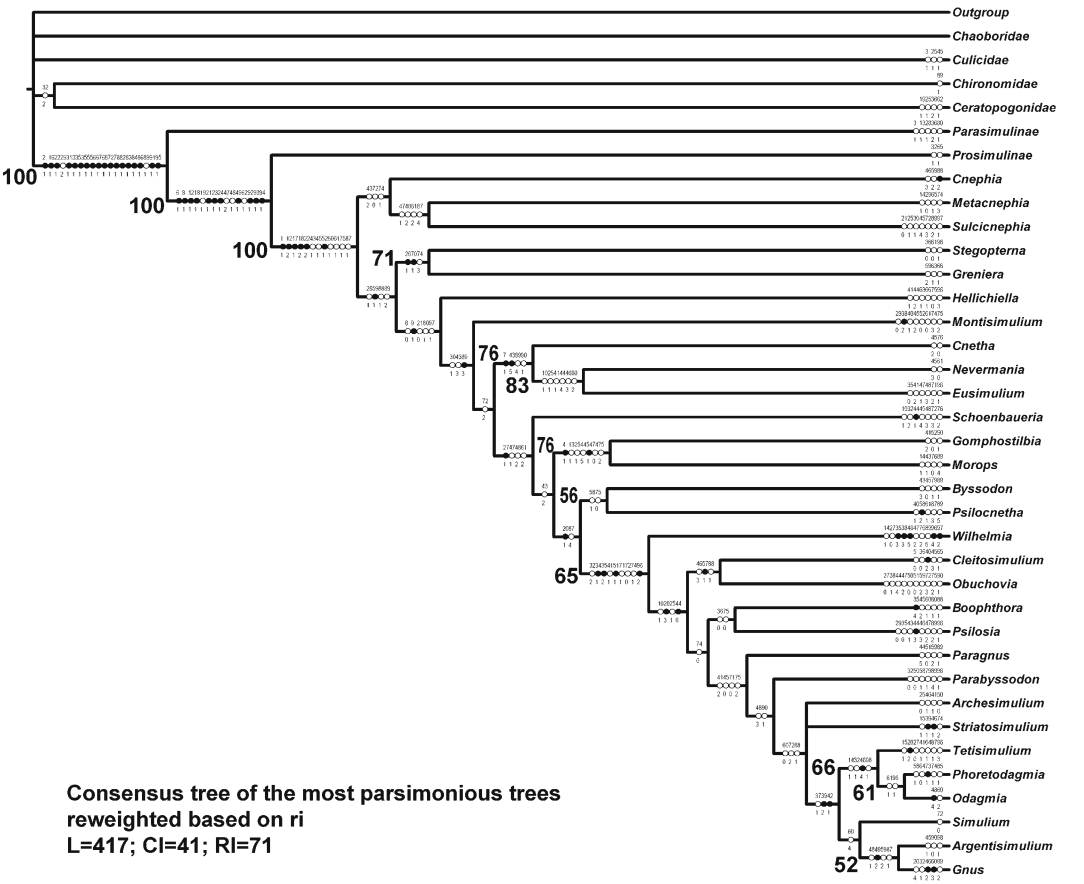

Fig. 9. Relationships of Simuliinae genera. A consensus tree of the most parsimonious trees obtained from the analysis with reweighting based on the ***RI.*** Bootstraps higher than 50% are given in bold left and below of the clades.

Рис. 9. Кладограмма связей между родами подсемейства Simuliinae. Консенссное дерево из парсимонических деревьев, полученное при перевзвешивании по ***RI***. Бутстреп больше 50 % выделен жирным шрифтом.

In the subfamily Simuliinae, the monophyly of the lineage Wilhelmiini + Simuliini is supported by the synapomorphies 20^1, 32^2, $\mathbf{34^1}$, $\mathbf{35^2}$, 41^1, $\mathbf{51^2}$, 71^1 and 67–76 % bootstrap. Unique synapomorphies are the presence of lateral silvery spots on male abdomen; gonostylus longer than gonocoxite; genital fork branches angle is more than 90°. Of the characters considered to be subject to homoplasy are the small cushion-like, poorly setulose apical lip of ventral plate (gonosternum) and the female claw simple, without a tooth at base.

Monophyly of the tribe Wilhelmiini, represented in the PalaearcticRegion by one genus *Wilhelmia* (and several closely related genera in other regions), in its turn, is supported by the synapomorphies 14^1, 15^1, $\mathbf{35^3}$, $\mathbf{38^3}$, $\mathbf{46^5}$, 47^2, 64°, 76^2, 89^5, $\mathbf{96^4}$, $\mathbf{97^2}$. Of them, the short and thin gonostylus; thin curved strip-shaped ventral plate of aedeagus; female hypogynial valve elongated in the narrow annular curved strips; absence of spine combs in pupal abdominal tergites; absence of terminal spines in pupal abdomen are unique. The setulose anepistemal membrane; scutal pattern clear lyre-shaped on the female scutum; short and swollen filaments in pupal gill; larval antenna almost as long as the labral-fan stalk; two small teeth on marginal plate of larval mandible are homoplastic synapomorphies of the tribe.

Monophyly of the tribe Simuliini (represented in this analysis by the genera *Boophthora, Psilozia, Cleitosimulium, Obuchovia, Paragnus, Parabyssodon, Archesimulium,*

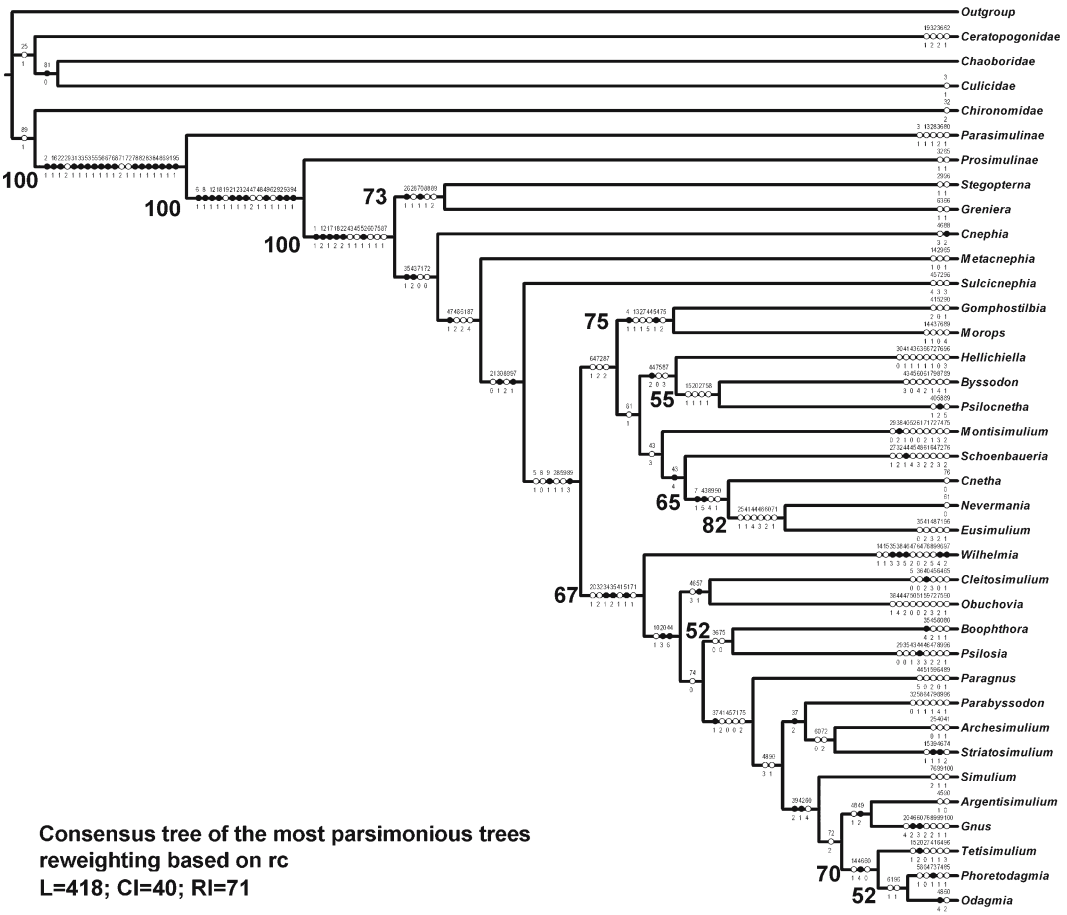

Fig. 10. Relationships of Simuliinae genera. A consensus tree of the most parsimonious trees obtained from the analysis with reweighting based on the ***RC.*** Bootstrap values are transferred from the 50 % majority consensus tree, where applicable).

Рис. 10. Кладограмма связей между родами подсемейства Simuliinae. Консенссное дерево из парсимонических деревьев, полученное при перевзвешивании по ***RC.*** Показаны значения бутстрепа больше 50 %.

Striatosimulium, Argentisimulium, Tetisimulium, Phoretodagmia, Odagmia, Gnus, Simulium) is based on three synapomorphies, 10^1 (scutum with silvery spots or strips), $\mathbf{20^3}$ (vein R_1 bare in basal half, haired and spinulose in apical half), $\mathbf{44^6}$ (elongated, transversely folded median sclerite of aedeagus)**,** but bootstrap is less than 50 % (33–35 %), indicating a low reliability of this result and certain possibility of paraphyly of the tribe.

In the tribe Simuliini, we recognize several lineages based on this analysis. The group *Cleitosimulium* + *Obuchovia* is supported by a unique synapomorphy $\mathbf{57^1}$ (larval body coloration: blackish dorsally and whitish ventrally) and homoplastic characters 46^3 (female hypogynial valve markedly elongate) and 88^1 (initial branching pupa gill respiratory organ of three main branches), with bootstrap 32–34 %.

The lineage *Boophthora* + *Psilozia* is based only on homoplastic (reversal) characters 36° (two or more gonostylus apical spines) and 75° (internal teeth of larval mandible shorter than outer teeth), with bootstrap 48–52 %.

The group of genera *Gnus* + *Simulium* + *Argentisimulium* + *Tetisimulium* + *Phoretodagmia* + *Odagmia* shares three synapomorphies, $\mathbf{37^1}$ (tubercle at the gonostylus base setulose), $\mathbf{39^1}$ (ventral plate of the aedeagus laterally compressed, with lip and heel) and $\mathbf{42^1}$ (denticles on the gonosternum (ventral plate) present), and sometimes 60^4 (pattern of the frontoclypeal apotoma negative H-shaped) with 36–52 % bootstrap.

The clade *Gnus* + *Argentisimulium* possesses synapomorphies 48^1 (anal lobes expressed, separated), 49^2 (anal lobes large and wide). 72^2 (two small teeth on marginal plate of larval mandible), **95^1** (chromosomal inversions in base of IIIL arm), **96^1** (chromosomal inversions in base of IIIS arm) and 80 % bootstrap.

The lineage *Tetisimulium* + *Phoretodagmia* + *Odagmia* is supported by the synapomorphies 14^1 (anepistemal membrane haired), 32^1 (female claw with small basal tooth), **46^4** (female hypogynial valve with S-shaped curved medial edge) 60°, 98^1 and 66–72 % bootstrap.

The genera *Phoretodagmia* + *Odagmia* also form a group, supported by the synapomorphies 61^1 (postgenetal cleft the medium-sized and slightly exceeds the height chitinous nodes) 96^1 (tergites VI–IX each with an anterior row of spine combs) and 52–61 % bootstrap. Both characters are subject to homoplasy. Branch bootstrap is not high, but reliable, indicate monophyly of these genera.

Conclusion

The results of the parsimony analysis clearly support our earlier hypothesis that Stegopternini and Ectemnini are closer related to other Simuliinae than to Prosimuliinae and proposition to remove these tribes from the latter subfamily and to transfer them into Simuliinae. In addition, the tribes Stegopternini, Nevermanniini, Wilhelmiini and Simuliini (at least in the Palaearctic Region) are found to be monophyletic. The tribe Ectemniini is apparently a paraphyletic formation, as it was based on diagnostic characters absent in other Simuliinae in plesiomorphic mode or possible reversals. In the subfamily Simuliinae, the monophyly of the lineage Wilhelmiini + Simuliini is well supported, and the basal position of the Wilhelmiini was not supported at all. The genus *Boophthora* is shown to belong in the tribe Simuliini.

These suggestions are preliminary to a certain degree, as the genera occurring in the Afrotropical, Oriental, Australasian and Neotropical Regions were neglected in this analysis. They are believed not be closely related to the Palaearctic genera and thus not affecting much on the position of the tribes discussed above. Forthcoming phylogenetic analyses, based both on morphological data and molecular sequences must clarify relationships of the genera in details.

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Adler P. H., Currie D. C., Wood D. M. The black flies (Simuliidae) of North America. — New York : Cornel University Press, 2004. — 942 p.

Borkent A., Currie D. C. Discovery of the female of Parasimulium (Astoneomyia) melanderi Stone (Diptera: Simuliidae) in a cave in British Columbia, with a discussion of its phylogenetic position // Proceedings of the Entomological Society of Washington. — 2001. — **103**. — P. 546–553.

Crosskey R. W. The natural history of blackflies. — Chichester : John Wiley & Sons Ltd., 1990. — 711 p.

Goloboff P. A. NONA (NO NAME) ver. 2. — Tucumán, Argentina: Published by the author, 1999. — Available from http://www.cladistics.com/aboutNona.htm

Kaplich V. M., Sukhomlin K. B., Zinchenko A. P. Keys to blackflies (Diptera: Simuliidae) of Poles'e. — Minsk : Novoe znanie, 2012. — 477 p. — Russian : *Каплич В. М., Сухомлин Е. Б., Зинченко А. П.* Определитель мошек (Diptera: Simuliidae) Полесья.

Moulton J. K. Molecular sequence data resolves basal divergences within Simuliidae (Diptera) // Systematic Entomology. — 2000. — **25.** — P. 95–113.

Moulton J. K., Adler P. H. The genus Ectemnia (Diptera: Simuliidae): taxonomy, polytene chromosomes, new species, and phylogeny // Can. J. Zool. —1997. — **75.** — P. 1896–1915.

Nixon K. C. WinClada ver. 1.00.08. —Ithaca, NY : Published by the author, 2002. — Available from http: // www. cladistics. com/aboutWinc. htm Accessed on May 26, 2011.

Page R. D. E. NEXUS Data Editor. Ver. 0.5. 0. A program to edit NEXUS format data files. — 2001. — Available from http://taxonomy.zoology.gla.ac.uk/rod/NDE/nde. html Accessed on May 26, 2011.

Rubtsov I. A. Evolution, phylogeny and classification of blackflies (Diptera, Simuliidae) // Proceedings of the Zoological Institute AS USSR. — 1974. — **53.** — P. 230–281. — Russian : *Рубцов И. А.* Об эволюции, филогении и классификации мошек (Diptera, Simuliidae).

Sukhomlin E. B., Zinchenko A. P. Phylogenetic relationships of the tribe of blackflies the Palaearctics Simuliini // Proceedings of the international scientific conference "Synthetic Theory of Evolution: status, problems and prospects", dedicated to the 200th anniversary of the birth of Charles Darwin and the 150th anniversary of the publication of the book "The Origin of Species by Means of Natural Selection... " (Ukraine, Lugansk, 15—19 June 2009) / Ed. I. Sokolov. — Lugansk : Elton—2, 2009. — P. 45–47. — Russian : *Сухомлин Е. Б., Зинченко А. П.* Филогенетические отношения мошек трибы Simuliini Палеарктики.

Sukhomlin E. , Ussova Z., Kaplich V., Zinchenko A. Phylogeny of Black Flies of [the] Subfamily Simuliinae in [the] Palearctic[s] // The 3rd Internetional Simuliidae Symposium, including the 29th meeting of the British Simuliid Group, the 7th European Simuliidae Simposium and EMCA Blackfly working group. — Vilnius, Sept. 9–12, 2008 : Abstract book. — Vilnius, 2008. — P. 51.

Swofford D. L. PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4. — Sunderland, Massachusetts : Sinauer Associates, 2000.

Wood D. M. Taxonomy of the Nearctic species of Twinnia and Gymnopais (Diptera: Simuliidae), and a discussion of the ancestry of the Simuliidae // Canad. Entomologist. — 1978. — **110,** N 12. — P. 1297–1337.

Wood D. M., Borkent A. Description of the female of Parasimulium crosskeyi Peterson (Diptera: Simuliidae) and the phylogenetic position of the genus // Memoirs of the Entomological Society of Washington. — 1982. — **10.** — P. 193–210.

Yankovsky A. B. Keys to the blackflies (Diptera: Simuliidae) of Russia and adjacent territories (former USSR). — Saint Petersburg : Publishing House of the Russian Academy of Sciences, 2002. — 570 p. — Russian : *Янковский А. В.* Определитель мошек (Diptera: Simuliidae) России и сопредельных территорий (бывшего СССР).