VILNIUS UNIVERSITY

Pavel Starkevič

TAXONOMIC AND PHYLOGENETIC REVIEW OF THE SUBGENUS *TIPULA (VESTIPLEX)* BEZZI, 1924 (DIPTERA, TIPULIDAE)

Summary of Doctoral Dissertation

Biomedical sciencies, Zoology (05 B)

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VILNIAUS UNIVERSITETAS

Pavel Starkevič

TAKSONOMINĖ IR FILOGENETINĖ POGENTĖS *TIPULA* (*VESTIPLEX)* BEZZI, 1924 (DIPTERA, TIPULIDAE) ANALIZĖ

Daktaro disertacijos santrauka

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INTRODUCTION

There are over five thousand crane fly species belonging to the family Tipulidae (Oosterbroek, 2011) currently described. This is one of the of the primitive groups of the suborder Nematocera with species distributed in all zoogeographic regions and found in various habitats.

Subgenus *Vestiplex* is phylogenetically young cranefly complex of the genus *Tipula* formed in neo-paleogene (Savchenko, 1960, 1964, 1983). Females of this subgenus have a specific ovipositor with strong and powerfully constructed, heavily sclerotized cerci and very small or rudimentary hypovalvae. This specialization is related to the transition of the females to living in xeromorphic conditions when ovipositor is used to lay eggs into dry and solid substrate. Male genital complex is very polymorphic.

There are 156 species of subgenus *Vestiplex* described so far (Oosterbroek, 2011). They are found in Holarctic and Oriental zoogeographic regions with no specimens known from other parts of the globe. The majority of the species are associated with the mountain systems (Pyrenees, Alps, Caucasus, and Himalayas), where they are found in altitudes up to 4500 m.

Adults of this group are commonly found in broad-leaved and coniferous forests, alpine meadows, tundra, steppe etc. Some species are of great importance, for example immature stages and adults of *T. semivittata* and *T. arctica* are basic food for birds in Caucasus and Greenland respectively (Brodo 1990; Hemmingsen & Jensen, 1957; Lantsov, 2003).

Bezzi (1924) was first to distinguish subgenus *Vestiplex*, based on features of *Tipula (Vestiplex) cisalpina* Riedel, 1913. Extent of subgenus was ascertained by Edwards (1931) and later corrected by Alexander (1933, 1935). Almost all species, that Riedel (1913) named *Nigromarginatae* were included into this group.

Mannheims (1953) dispersed Westpalaearctic species of subgenus *Vestiplex* into four groups. Later Savchenko performed morphological analysis and redistributed 64 *Vestiplex* species into those new species complexes. This distribution was based only on external features of body and genitalia, mainly on structure of male sternite IX. Eleven species groups are mentioned in different works (Alexander, 1918, 1920, 1928, 1934b, 1958, 1959, etc.; Savchenko, 1960, 1964, 1965) and it was stressed that as some relationships are clear, others are yet unknown because of the poor morphological knowledge of those species.

As the number of described species is even higher now, the question of position of separate species or subspecies and their relationships became more relevant. Some of the species are poorly morphologically known and require a correction of their placement inside subgenus *Vestiplex.* Some of the species don’t have their diagnostic features illustrated or are illustrated misleadingly and are not suitable for the identification of species. Precise and explicit illustration of diagnostic features is a key factor for identification of the species from poorly studied regions. Detail morphological analysis prepares a basis for construction of identification keys.

Aims and tasks of the dissertation. The aim of this dissertation was to accomplish taxonomic and phylogenetic review of the subgenus *Vestiplex* Bezzi, 1924. The following tasks were formulated in order to achieve the aim:

1. To investigate as many as possible type specimens and specimens of different species, illustrating the genital structures important for the species identification;
2. Compile a list of characters for the phylogenetic analysis and perform the analysis itself;
3. To divide the species of the subgenus *Vestiplex* in species groups.

Defensive statements:

1. New version of phylogeny and classification of the subgenus *Vestiplex* .
2. Detailed morphological analysis of the genital structures
3. Inner genital structures (adminiculum, genital bridge, IX sternite, vaginal apodeme, bursa copulatrix) enable separation of close species.

Novelty and significance of the study. One species new for science - *Tipula (Vestiplex) dhalma* Starkevich and Podenas, 2011 was described. The new synonym is proposed. One species should be restored from the synonymy. One subspecies would be restored to the species rank.

Three species were identified as new to the fauna of China. Two species were identified as new to the fauna of Myanmar. Female of *Tipula (Vestiplex) eurydice* Alexander, 1961 was described for the first time. Craneflies of subgenus *Vestiplex* are recorded in Thailand and S. Korea for the first time with two species identified as new to fauna of Thailand and one species new to the fauna of S. Korea.

Phylogenetic analysis of 103 species of the subgenus *Vestiplex* was performed for the first time. Classification of the subgenus based on the analysis of morphological features is presented.

This work contributes previous works on the phylogeny of different groups of Tipulidae (Brodo, 1987; Gelhaus, 2005; de Jong, 1993, 1994a, 1994b, 1995a, 1995b; Oosterbroek, 1980), adds to the knowledge on morphology of reproductive organs and could be used solving taxonomic questions of Tipulidae.

Volume and structure of the dissertation. The volume of dissertation is 128 pages (excluding appendix). The thesis is written in Lithuanian and consists of Introduction, Literature review, Material and methods, Results and discussion, Conclusions, List of refences (292 reference sources), Appendix (120 figures). The dissertation has 156 figures and 3 tables.

MATERIALS AND METHODS

The research material was acquired during the visits to foreign museums and by getting a loan or a gift from different institutions or scientists personally.

Part of used material were collected in Mongolia through ”*Selenge River Survey Expedition*“(2003-2006) and ”*Mongolian Aquatic Insect Survey*“ (2008-2010) projects by S. Podenas, J. Gelhaus and O. Yadamsuren. Some crane flies were given by T. Nakamura (Japan) and C. Yuong (USA).

Three visits to museums were made. These were as follows: Zoological institute Russian Academy of Sciences in St. Petersburg (11-27 October, 2009); Academy of Natural Sciences in Philadelphia, PA (February 17-March 9, 2011) and Smithsonian Institution in Washington, DC, USA (February 24-25, 2011).

Part of crane flies material acquired through the loans from: British Museum of Natural History, London, UK; Muséum d'histoire naturelle de Neuchâtel, Switzerland; Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany; California Academy of Sciences, San Francisco, Carnegie Museum of Natural History, Pittsburgh, Museum of Comparative Zoology, Harvard University, Cambridge, The University of Kansas Natural History Museum, University of Michigan Museum of Zoology, USA; Canadian National Collection of Insects, Ottawa, Canada; Vilnius University Zoological Museum, Lithuania.

Specimens were studied with Olympus SZ51, BX 40 and SZX10 microscopes. Genitalia for studies of inner structures were studied after boiling them in 10 percent NaOH solution for 10 minutes.

Terminology of morphological features generally follows that of McAlpine (1981).

The phylogenetic analysis was based on 55 characters. Winclada v.100 (Kevin C. Nixon) was used for assembling the character matrix, review and arrangement of cladograms. NONA v.2.0 (P. A. Goloboff 1993) and XPEE-WEE (P. A. Goloboff 1997) were used for the search of most parsimonious tree using equal weithing. Reductive coding was used (Strong and Lipscomb, 1999). Character polarities was found through outgroup comparison. Heuristic search option and tree bisection and reconnection algoritm was used. The settings were hold1000, mult*50, mult*max*. Strict consesnsus tree was given. *Tipula (Tipula) paludosa* Meigen, 1830 and *Tipula (Pterelachisus) irrorata* Macquart, 1826 was used as outgroup.

RESULTS AND DISCUSSION

Phylogenetic analysis

While analyzing the literature and crane fly specimens, 55 morphological characters were chosen for phylogenetic analysis. 103 crane fly species are included in the matrix.

The character states are:

1. **Antena**: *the shape of the flagellomere*: (0) without basal enlargement; (1) with basal enlargement; (2) with large basal enlargement.
2. **Male *nasus***: (0) present; (1) absent.
3. **Thorax**: *female wing*: (0) well developed; (1) semiatrophied; (2) atrophied.

Male terminalia

4. **IX tergite**: (0) simple; (1) weakly modified (Savchenko, 1960, 1964) (Fig. 1, A); (2) strongly modified, saucer type (Alexander, 1934a) (Fig. 1, B-G).
5. **IX tergite**: *sclerotisation*: (0) ordinarily sclerotized; (1) leathery (Savchenko 1960, 1964) (Fig. 1, B-D); (2) strongly sclerotized (Fig. 1, C).
6. **IX tergite**: *anterior part*: (0) simple; (1) narrow (Fig. 1, B-D); (2) round (Fig. 1, C); (3) broad (Fig. 1, G).
7. **IX tergite**: *median part*: (0) with desclerotized fusion (Fig. 1, A); (1) divided into two parts (Alexander, 1935) (Fig. 1, H-L).
8. **IX tergite**: *median posterior edge*: (0) simple; (1) with rounded lobes (Fig. 1, K); (2) with sclerotized long lobes (Fig. 1, L).
9. **IX tergite**: *posterior part*: (0) simple; (1) with one pair of appendages (Fig. 1, I-L).
10. **IX tergite**: *sclerotized, angle shaped appendages*: (0) absent; (1) present (Fig. 1, J).
11. **IX tergite**: *sclerotized, narrow appendages*: (0) absent; (1) present (Fig. 1, I).
12. **IX tergite**: *broad, rounded appendages*: (0) absent; (1) present (Fig. 1, K).
13. **IX tergite**: *toothed appendages*: (0) absent; (1) present. (Fig.1, L).
14. **IX tergite**: *raised sclerotized area in median part*: (0) absent; (1) present (Fig. 1, B).
15. **IX tergite**: *narrow staple in anterior part*: (0) absent; (1) present (Fig. 1, D)
16. **IX tergite**: *medial tooth*: (0) absent; (1) present (Fig. 1, C).
17. **IX tergite**: *lateral part*: (0) simple; (1) thorn shaped (Fig. 1, C); (2) splitted tooth shape (Fig. 1, G).
18. **IX tergite**: *small thorns on anterior part*: (0) absent; (1) present (Fig. 1, C).
19. **IX tergite**: *form*: (0) simple; (1) strongly narrow in dorsoventral aspect (Fig. 1, E).
20. **IX tergite**: *size*: (0) usual; (1) strongly reduced (Fig. 1, F).
21. **IX sternite**: (0) simple; (1) changed, with one pair of appendages.
22. **IX sternite**: short appendages with blunt hooked apex: (0) absent; (1) present.
23. **IX sternite**: finger shaped appendages: (0) absent; (1) present.
24. **IX sternite**: long, thin appendages with sharp or toothed apex: (0) absent; (1) present.
25. **IX sternite**: short appendages, with rounded apex: (0) absent; (1) present.
26. **Gonocoxite**: *apex*: (0) simple; (1) horn shaped; (2) needle shaped; (3) thorn shaped.
27. **Gonocoxite**: *posterior part*: (0) simple; (1) blunt thorn shaped; (2) sharp hook shaped.
28. **Outer gonostylus**: (0) simple; (1) strongly sclerotized.
29. **Inner gonostylus**: (0) simple; (1) incised on superior part; (2) extended.

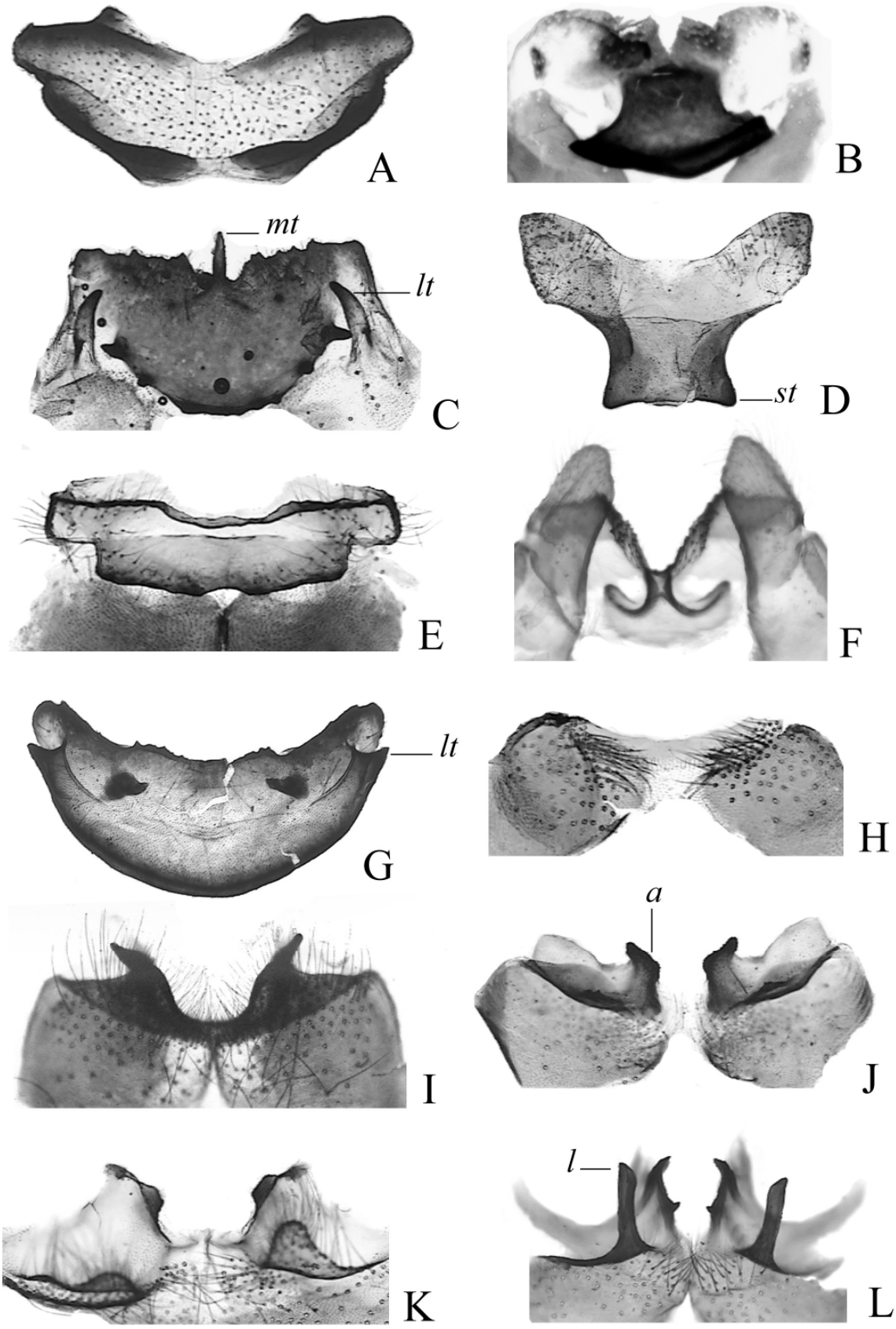

Figure 1. Morphological characters, IX tergite. A. *T. longitdinalis* B. T. *T. pauxilla* C. *T. excisa* D. *T. scripta* E. *T. arctica* F. *T. nubeculosa* G. *T. subcentralis* H. *T. himalayensis* I. *T. verecunda* J. *T. serricauda* K. *T. quasimarmoratipennis* L. *T. inaequidentata*. *mt* – medial tooth, *lt* – lateral tooth, *s* – staple, *a* – appendage, *l* – lobe.

30. **Inner gonostylus**: *anterior part*: (0) large extended; (1) rounded; (2) swollen; (3) small.
31. **Adminiculum**: *shape*: (0) furrow shaped (Fig. 2, A, C, D); (1) plate shaped (Fig. 2, B).
32. **Adminiculum**: *dorsal part*: (0) simple (Fig. 2, A-B); (1) with differentiated sclerite (Fig. 2, C); (2) the sclerite with widened lateral parts (Fig. 2, D).
33. **Adminiculum**: *short, broad furrow shaped sclerite*: (0) absent; (1) present.
34. **Adminiculum**: *short, papilla shaped appendages*: (0) absent; (1) present.

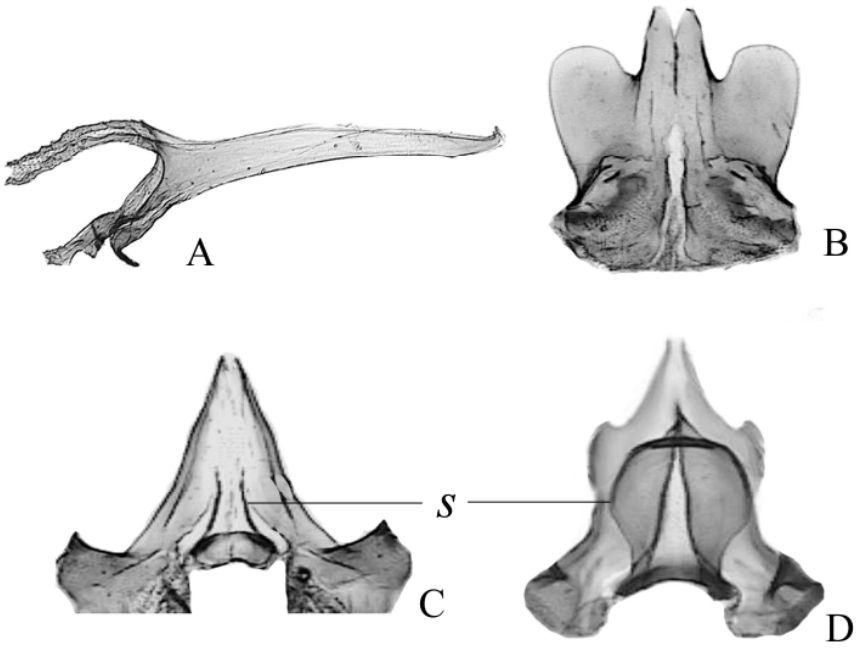

Figure 2. Morphological characters, adminiculum. A. *T. sintenisi* B. *T. montana* C. *T. himalayensis* D. *T. eurydice*, *s* – sclerite.

35. **Genital bridge**: (0) present; (1) reduced.
36. **Genital bridge**: (0) simple (Fig. 3, A); (1) complex (Fig. 3, B-C)
37. **Genital bridge**: *widened distal parts*: (0) absent; (1) present (Fig. 3, A)
38. **Genital bridge**: *oblong apodeme and splitted lateral parts*: (0) absent; (1) present (Fig. 3, B).
39. **Genital bridge**: *arched sclerite*: (0) absent; (1) present (Fig. 3, C).
40. **Semen pump**: (0) swollen; (1) medium sized; (2) small, flatten.
41. **Semen pump**: *anterior apodeme*: (0) small, narrow; (1) major, rounded.
42. **Semen pump**: *posterior apodeme*: (0) usual; (1) widened.
43. **Semen pump**: *compressor apodeme*: (0) continuous; (1) incised.
44. **Intromittent organ**: *distal part*: (0) without incisions; (1) with two incisions, trident shaped.
45. **Intromittent organ**: *broad distal part*: (0) absent; (1) present.
46. **Intromittent organ**: *desclerotized area*: (0) absent; (1) present.

Female terminalia

47. **Cerci**: (0) simple; (1) strongly constructed (Alexander and Byers, 1981).
48. **Hypovalva**: (0) simple; (1) reduced.
49. **Hypovalva**: *seta shaped sclerite*: (0) absent; (1) present.

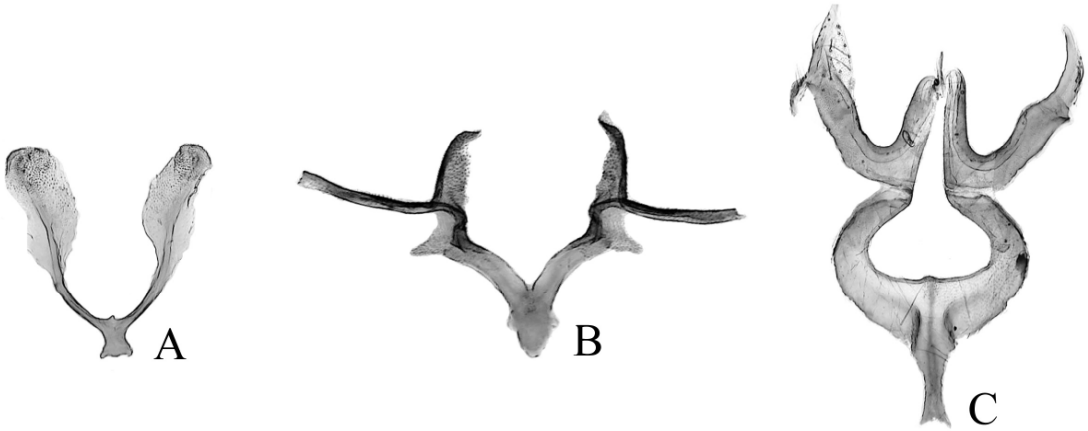

Figure 3. Morphological characters, genital bridge. A. *T. pallidicosta* B. *T. coquillettiana* C. *T. sintenisi*.

50. **Hypovalva**: *tooth shaped sclerite*: (0) absent; (1) present.
51. **IX sternite**: *shape*: (0) arch-shaped; (1) simple.
52. **IX sternite**: *apical part*: (0) extended, tongue shaped; (1) simple.
53. **IX sternite**: *surface*: (0) simple; (1) coated with filaments.
54. **Vaginal apodeme**: (0) with slightly sclerotized medial part; (1) strongly sclerotized; (2) membranous.
55. ***Bursa copulatrix***: (0) membranous; (1) slightly sclerotized; (2) strongly sclerotized.

Phylogenetic relationships

One cumulative cladogram was found from one thousand parsimonuous trees by strict consensus (L=137, Ci=53, Ri=93) (Figs. 4-9).

As can be seen from the figures 4-9, there are two clear large clades and 13 species groups in phylogenetic tree. The subgenus *Vestiplex* is characterized by two apomorphies: 47.1 – strongly constructed cerci and 48.1 – reduced hypovalva (Fig. 4).

The first clade is supported by 4.1 apomorphic character - weakly modified IX tergite. There is group of six species in this clade supported by three apomorphies: 34.1 – aedeagal guide with short papilla-shaped appendages, 44.1 – with two incisions, trident-shaped intromittent organ and 50.1 – tooth-shaped hypovalva. According to Savchenko (1960, 1964) these species are united into *virgatula* species group (Fig. 4).

Other species of first clade are supported by sclerotized (5.2) saucer type IX tergite (4.2) and seta-shaped hypovalva (49.1) (Fig. 5).

As can be seen from the figure 5, a group of three species separated in top of this clade. They are supported by three apomorphies: 20.1 - strongly reduced IX tergite, 33.1 - short, broad furrow-shaped aedeagal guide and 45.1 - short, widened in distal part intromittent organ. According to Savchenko (1964) these species are united into *nubeculosa* species group.

Next two species group are supported by leathery IX tergite (5.1) with narrow anterior part (6.1). First species group are separated by IX tergite with raised sclerotized area in median part (14.1). These species are united into *erectiloba* group (Savchenko, 1960, 1964). Second eight species are supported by two apomorphies: 15.1 - IX tergite with narrow staple in anterior part and 37.1 - genital bridge with widened distal parts. These species are united in *scripta* group (Savchenko, 1960, 1964).

As can be seen from the figure 5, a group of five species are separated by: 16.1 - IX tergite with medial tooth, 17.1 – thorn-shaped lateral part of the IX tergite and 18.1 - small thorns on anterior margin of IX tergite. These species are united into *excisa* species group (Mannheims, 1953; Savchenko, 1960, 1964; Theowald, 1968; Theowald and Mannheims, 1962).

The remainder of species is supported by broad anterior part of the IX tergite (6.3) (Fig. 6). These species are separated into two species groups, supported by: 36.1 – complex genital bridge, 42.1 - widened posterior apodeme of the semen pump, 46.1 – intromittent organ with desclerotized area and 46.1 – strongly sclerotized *bursa copulatrix*. Five species are supported by two apomorphies: 19.1 - strongly narrow in dorsoventral aspect IX tergite and 38.1 - genital bridge with oblong apodeme and splitted lateral parts. According to Savchenko (1960, 1964) these species are united into *coquillettiana* species group. Second group of 17 species is supported by IX tergite, which have splitted tooth-shaped lateral parts (17.2) and arched genital bridge (39.1) and united in *leucoprocta* species group (Savchenko 1960, 1964).

As can be seen from the figure 7 the second clade is supported by four apomorphies: 7.1 – IX tergite divided into two parts, 30.1 – rounded anterior part of inner gonostylus, 35.1 – reduced genital bridge, 51.1 – simple IX sternite which surface is coated by filaments (53.1). All species have aedeagal guide with differentiated sclerite except *T. nigrocostata*.

Two species group are supported by 27.1 apomorphic character - blunt thorn-shaped posterior part of the gonocoxite (Fig. 7). The first group is supported by: 22.1 - short appendages of IX sternite with blunt hooked apex and 30.2 – swollen anterior part of inner gonostylus. These species are united into *avicularia* species group (Savchenko, 1964). The second group is supported by sclerotized, angle-shaped appendages of IX tergite (10.1) and needle-shaped apex of the gonocoxite (26.2). These species united into *deserrata* species group by the author.

As can be seen from the figure 8 three species have specific strongly sclerotized outer gonostylus (28.1) and united into *himalayensis* species group (Alexander, 1963). A group of eight species are supported by two apomorphies: 11.1 – sclerotized, narrow appendages of IX tergite and 23.1 – finger-shaped appendages of IX sternite. Two species from this group - *T. divisotergata*, *T. verecunda* are united into *divisotergata* species group (Savchenko, 1964).

The remainder of species is supported by three apomorphies: 8.1 – inner posterior edge of IX tergite with rounded lobes, 26.3 – thorn-shaped apex of the gonocoxite and 30.3 - small anterior part of inner gonostylus (Fig. 9).

First species group is supported by: 8.2 - median poterior edge of IX tergite with sclerotized long lobes, 13.1 – toothed appendages of IX tergite, 25.1 – short appendages of IX sternite with rounded apex and 32.2 – the sclerite of aedeagal guide with widened lateral parts. These species are united into *eurydice* species group by the author.

Second species group is supported by: 12.1 – broad rounded appendages of IX tergite, 24.1 – long, thin appendages of IX sternite with sharp or toothed apex, 27.2 - sharp hook shaped posterior part of the gonocoxite. Three species from this group - *T. subtincta*, *T. distifurca* and *T. optanda* are united in *subtincta* species group (Savchenko, 1964).

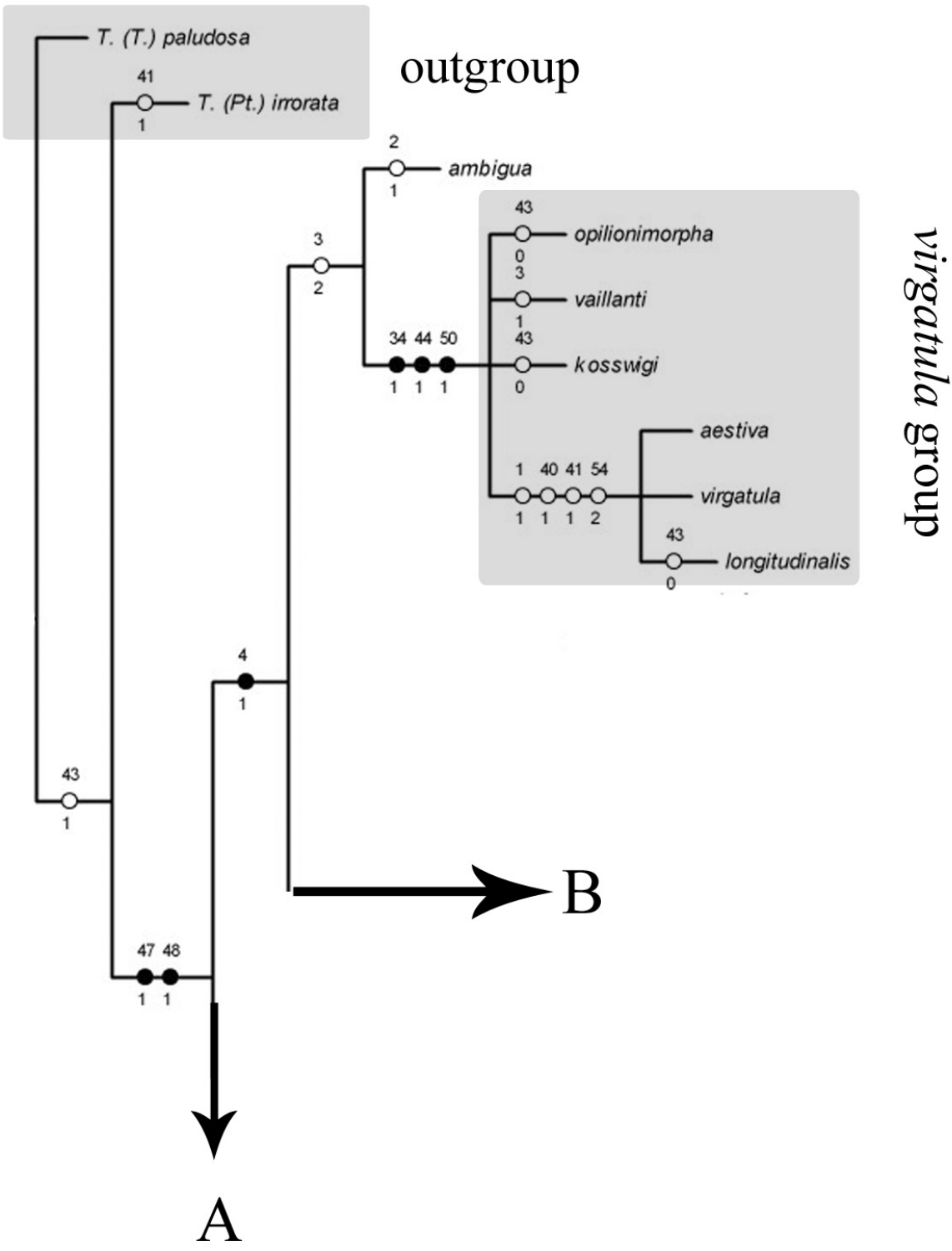

Figure 4. The strict consensus cladogram of 1000 most parsimonious cladograms acquired by EW. Black circles – apomorphies, open circle – homoplastic synapomorphy. Digits above circles – numbers of the characters, below – state of the character.

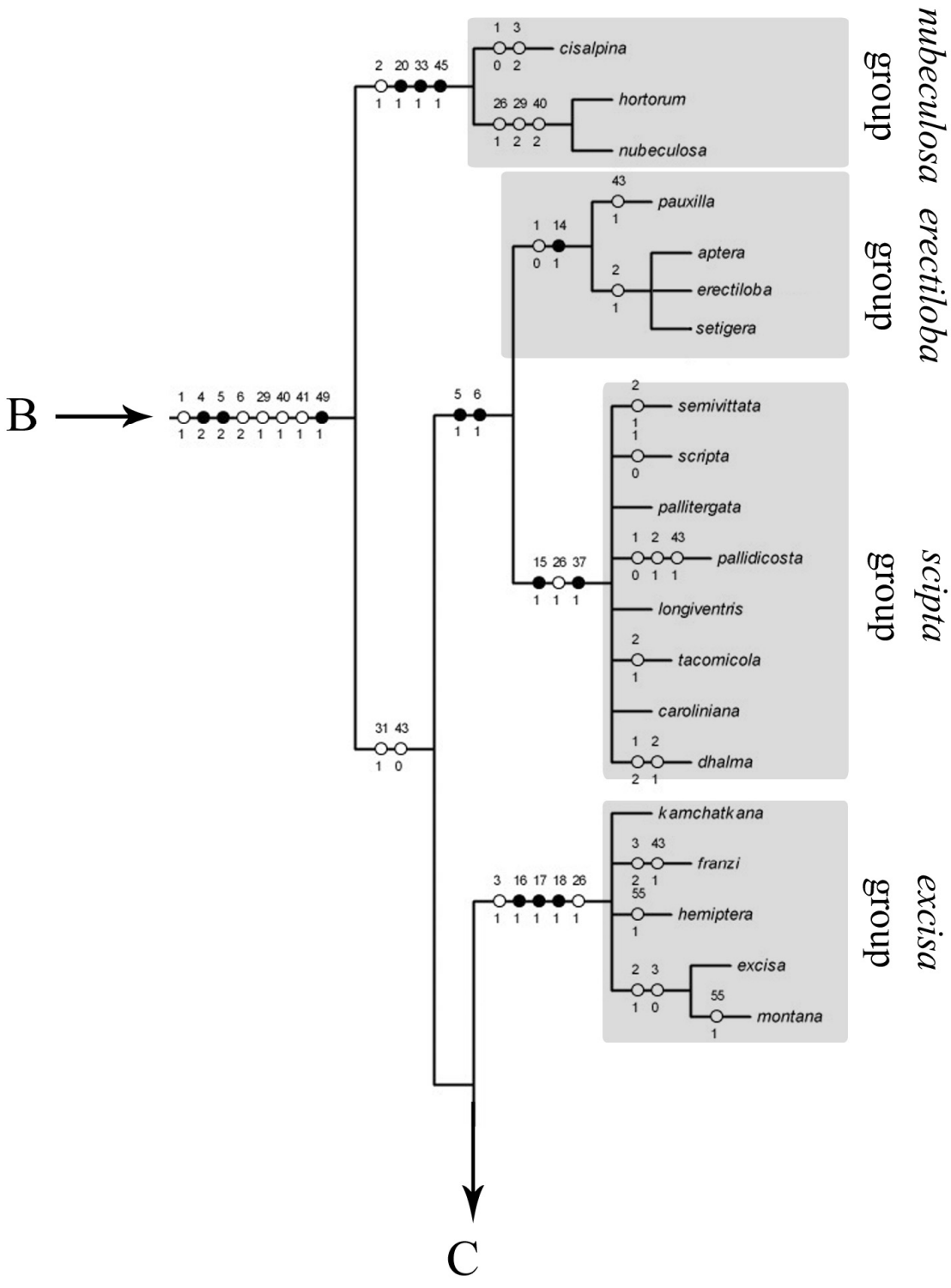

Figure 5. (Beginning in Fig. 4). The strict consensus cladogram of 1000 most parsimonious cladograms acquired by EW. Black circles – apomorphies, open circle – homoplastic synapomorphy. Digits above circles – numbers of the characters, below – state of the character.

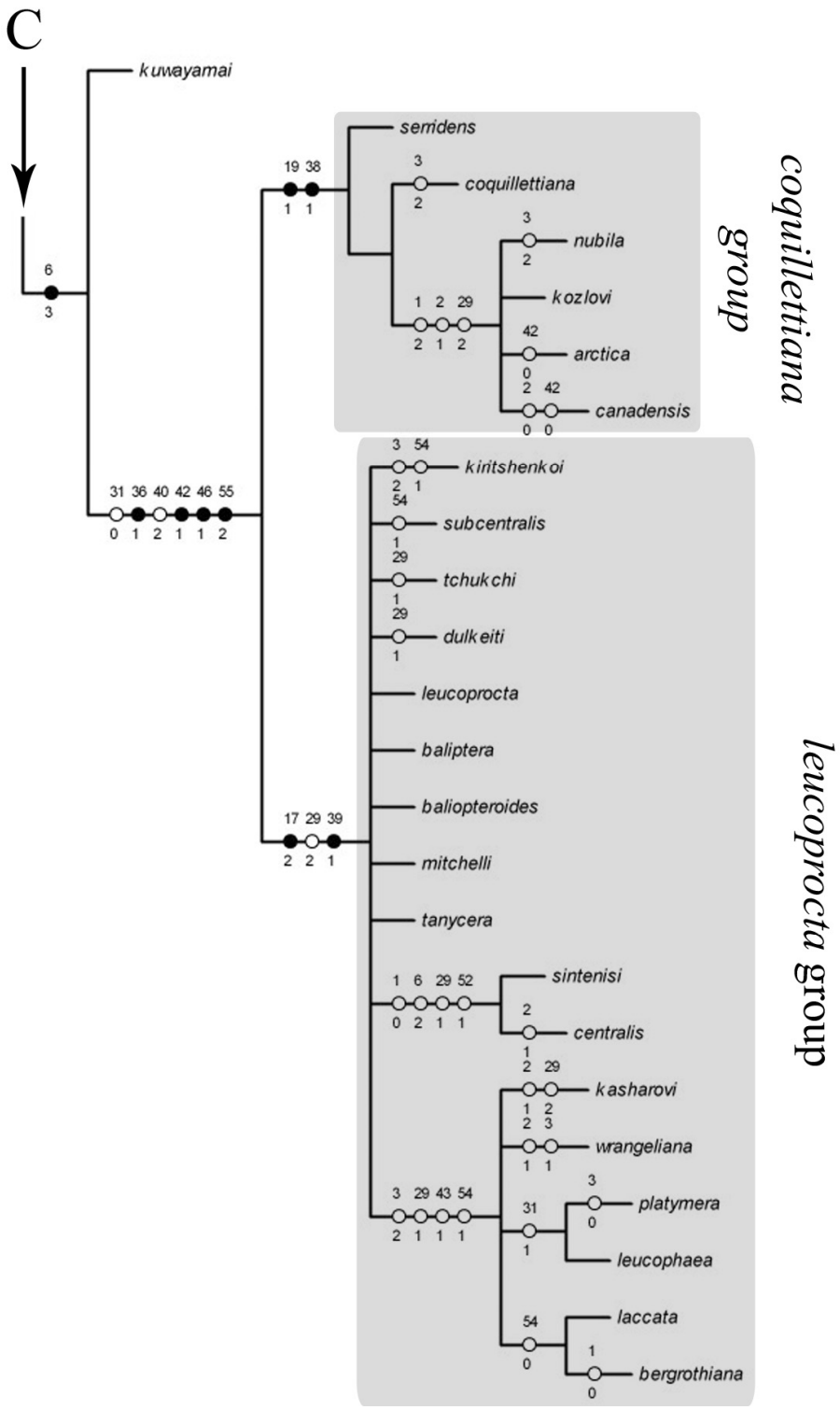

Figure 6. (Beginning in Fig. 5). The strict consensus cladogram of 1000 most parsimonious cladograms acquired by EW. Black circles – apomorphies, open circle – homoplastic synapomorphy. Digits above circles – numbers of the characters, below – state of the character.

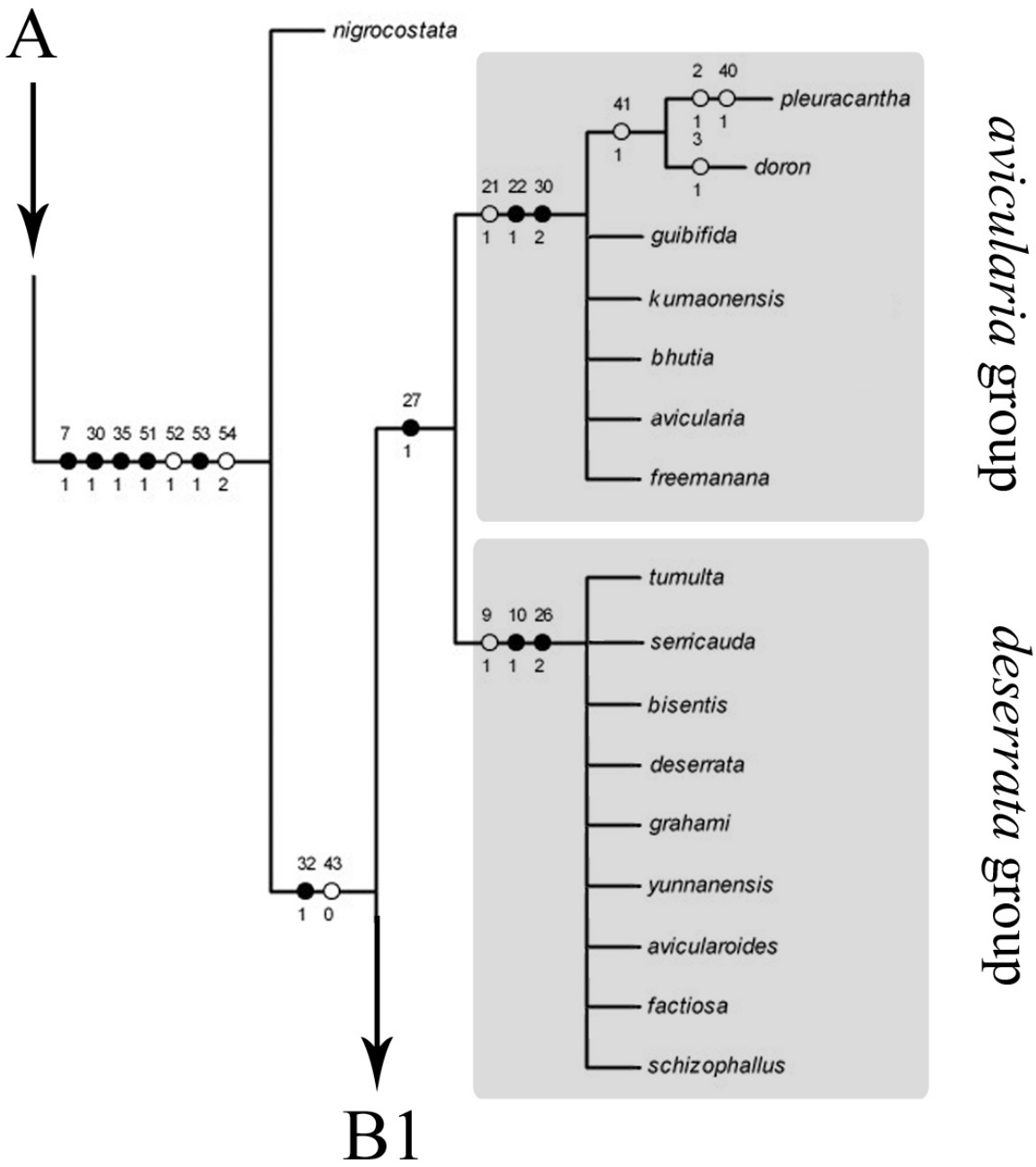

Figure 7. (Beginning in Fig. 6). The strict consensus cladogram of 1000 most parsimonious cladograms acquired by EW. Black circles – apomorphies, open circle – homoplastic synapomorphy. Digits above circles – numbers of the characters, below – state of the character.

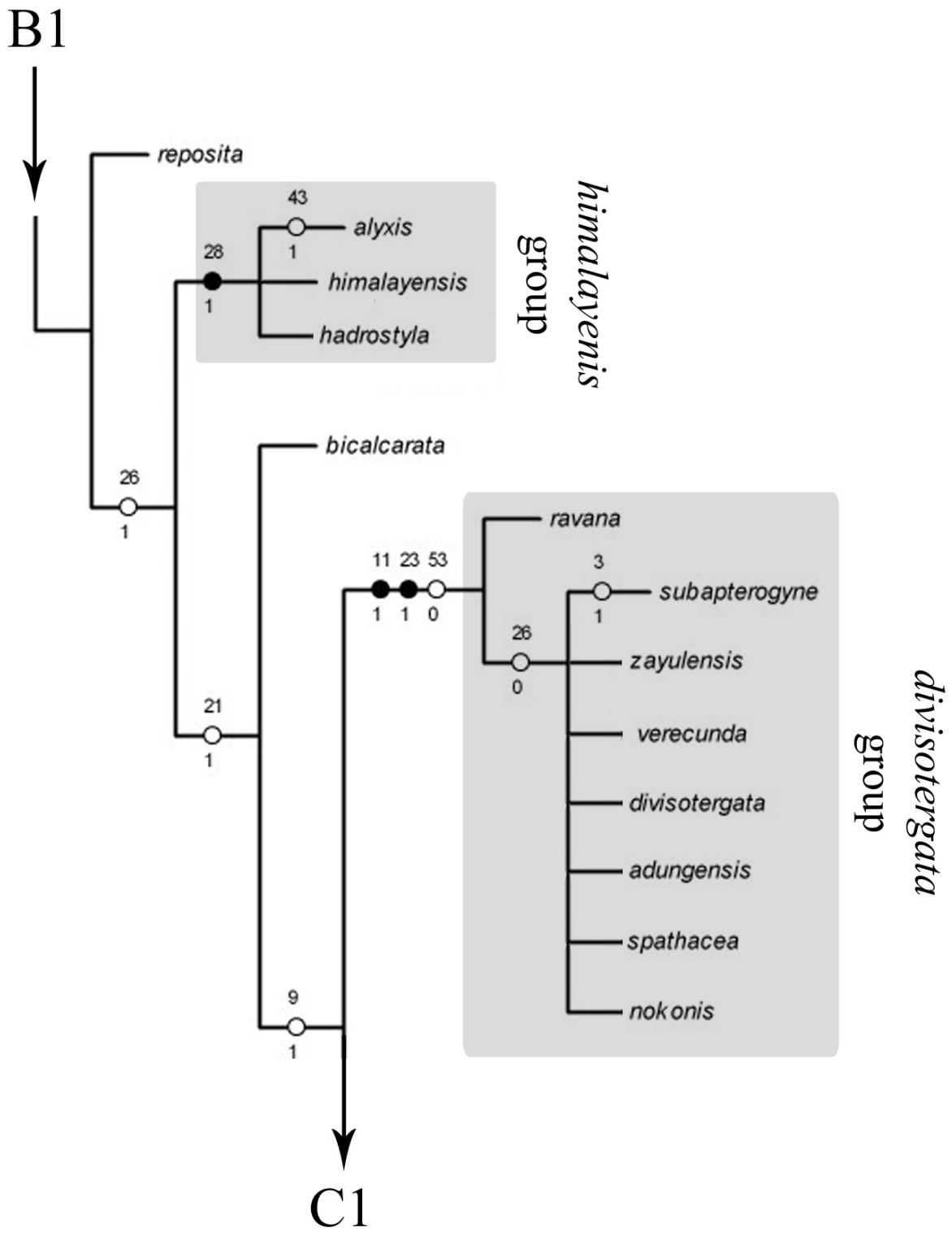

Figure 8. (Beginning in Fig. 7). The strict consensus cladogram of 1000 most parsimonious cladograms acquired by EW. Black circles – apomorphies, open circle – homoplastic synapomorphy. Digits above circles – numbers of the characters, below – state of the character.

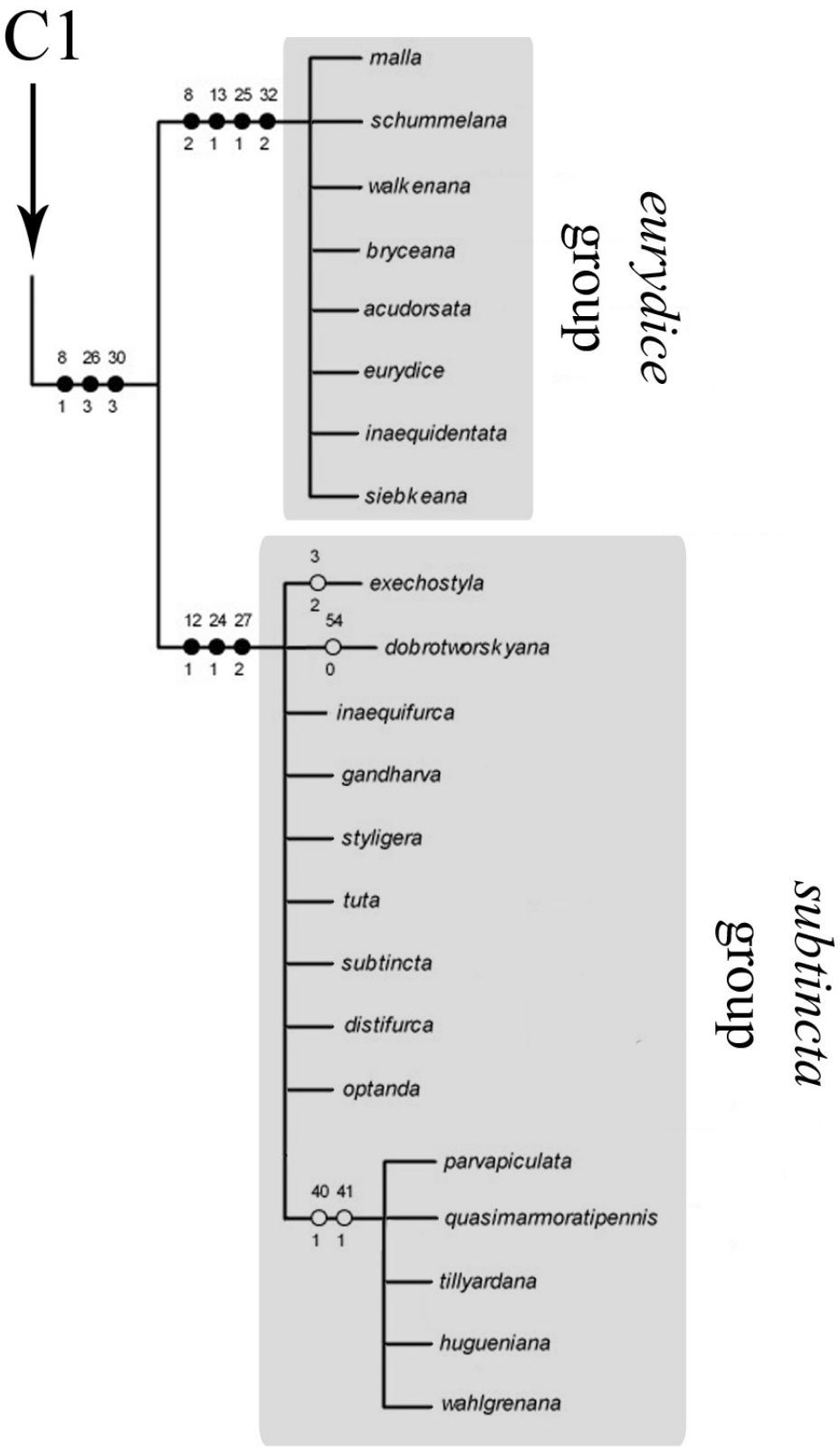

Figure 9. (Beginning in Fig. 8). The strict consensus cladogram of 1000 most parsimonious cladograms acquired by EW. Black circles – apomorphies, open circle – homoplastic synapomorphy. Digits above circles – numbers of the characters, below – state of the character.

Approach of species groups

According to phylogenetic analysis and literature data, the subgenus *Vestiplex* is divided into 13 species groups. Eleven species groups are mentioned in different works (Alexander, 1918, 1920, 1928, 1934b, 1958, 1959, 1963, etc.; Edwards, 1928; Hemmingsen, 1956; Mannheims, 1953; Savchenko 1960, 1964, 1965; Theowald and Mannheims, 1962; Theowald, 1968), two species groups – *deserrata* and *eurydice* are described by the author.

virgatula species group

Tipula (Vestiplex) aestiva Savchenko, 1960
Tipula (Vestiplex) fernandezi Theowald, 1972
Tipula (Vestiplex) fragilicornis Riedel, 1913
Tipula (Vestiplex) longitudinalis Nielsen, 1929
Tipula (Vestiplex) opilionimorpha aligera Savchenko, 1956
Tipula (Vestiplex) opilionimorpha opilionimorpha Savchenko, 1955
Tipula (Vestiplex) relicta Dia and Theowald, 1982
Tipula (Vestiplex) vaillanti andalucia Dufour and Oosterbroek, 1990
Tipula (Vestiplex) vaillanti vaillanti Theowald, 1977
Tipula (Vestiplex) virgatula montivaga Savchenko, 1960
Tipula (Vestiplex) virgatula virgatula Riedel, 1913

nubeculosa species group

Tipula (Vestiplex) cisalpina Riedel, 1913
Tipula (Vestiplex) hemapterandra Bezzi, 1924
Tipula (Vestiplex) hortorum Linnaeus, 1758
Tipula (Vestiplex) nubeculosa Meigen, 1804
Tipula (Vestiplex) saccai Mannheims, 1950

scripta species group

Tipula (Vestiplex) caroliniana Alexander, 1916
Tipula (Vestiplex) dhalma Starkevich and Podenas, 2011
Tipula (Vestiplex) longiventris Loew, 1863
Tipula (Vestiplex) pallidicosta pallidicosta Pierre, 1924
Tipula (Vestiplex) pallidicosta pullata Savchenko, 1960
Tipula (Vestiplex) pallitergata Alexander, 1934
Tipula (Vestiplex) scripta hartigi Mannheims, 1950
Tipula (Vestiplex) scripta immunda Alexander, 1934
Tipula (Vestiplex) scripta intermixta Riedel, 1913
Tipula (Vestiplex) scripta scripta Meigen, 1830
Tipula (Vestiplex) semivittata dissimilis Savchenko, 1964
Tipula (Vestiplex) semivittata semivittata Savchenko, 1960
Tipula (Vestiplex) subscripta Edwards, 1928
Tipula (Vestiplex) tacomicola Alexander, 1949

Tipula (Vestiplex) tumididens Savchenko, 1988

erectiloba species group

Tipula (Vestiplex) aptera Savchenko, 1955
Tipula (Vestiplex) erectiloba Alexander, 1940
Tipula (Vestiplex) pauxilla Savchenko, 1960
Tipula (Vestiplex) setigera Savchenko, 1960

excisa species group

Tipula (Vestiplex) crolina Dufour, 1992
Tipula (Vestiplex) excisa carpatica Erhan and Theowald, 1961
Tipula (Vestiplex) excisa excisa Schummel, 1833
Tipula (Vestiplex) franzi Mannheims, 1950
Tipula (Vestiplex) hemiptera hemiptera Mannheims, 1953
Tipula (Vestiplex) hemiptera strobliana Mannheims, 1966
Tipula (Vestiplex) kamchatkana Alexander, 1934
Tipula (Vestiplex) montana excisoides Alexander, 1934
Tipula (Vestiplex) montana montana Curtis, 1834
Tipula (Vestiplex) montana verberneae Mannheims and Theowald, 1959
Tipula (Vestiplex) riedeliana Mannheims, 1953
Tipula (Vestiplex) sexspinosa Strobl, 1898

coquillettiana species group

Tipula (Vestiplex) arctica Curtis, 1835
Tipula (Vestiplex) coquillettiana Alexander, 1924
Tipula (Vestiplex) hirticeps Savchenko, 1960
Tipula (Vestiplex) kozlovi Savchenko, 1960
Tipula (Vestiplex) nubila Savchenko, 1960
Tipula (Vestiplex) serridens Alexander, 1920
Tipula (Vestiplex) canadensis Loew, 1864

leucoprocta species group

Tipula (Vestiplex) balioptera Loew, 1863
Tipula (Vestiplex) baliopteroides Alexander, 1945
Tipula (Vestiplex) bergrothiana Alexander, 1918
Tipula (Vestiplex) centralis Loew, 1864
Tipula (Vestiplex) coronifera Savchenko, 1960
Tipula (Vestiplex) kashkarovi Stackelberg, 1944
Tipula (Vestiplex) kiritshenkoi Savchenko, 1960
Tipula (Vestiplex) laccata Lundstrom and Frey, 1916
Tipula (Vestiplex) leucophaea Doane, 1901
Tipula (Vestiplex) leucoprocta Mik, 1889
Tipula (Vestiplex) mitchelli Edwards, 1927

Tipula (Vestiplex) platymera Walker, 1856
Tipula (Vestiplex) sintenisi Lackschewitz, 1933
Tipula (Vestiplex) subcentralis Alexander, 1918
Tipula (Vestiplex) tchukchi obtusidens Savchenko, 1964
Tipula (Vestiplex) tchukchi tchukchi Alexander, 1934
Tipula (Vestiplex) wrangeliana Stackelberg, 1944
Tipula (Vestiplex) tanycera Alexander, 1961
Tipula (Vestiplex) aldrichiana Alexander, 1929
Tipula (Vestiplex) perretti Alexander, 1928

himalayensis species group

Tipula (Vestiplex) himalayensis Brunetti, 1911
Tipula (Vestiplex) alyxis Alexander, 1963
Tipula (Vestiplex) hadrostyla Alexander, 1970
Tipula (Vestiplex) nigroapicalis Brunetti, 1911

deserrata species group

Tipula (Vestiplex) chiswellana Alexander, 1964
Tipula (Vestiplex) deserrata Alexander, 1934
Tipula (Vestiplex) factiosa Alexander, 1940
Tipula (Vestiplex) serricauda Alexander, 1914
Tipula (Vestiplex) tumulta Alexander, 1934
Tipula (Vestiplex) grahami Alexander, 1933
Tipula (Vestiplex) avicularoides Alexander, 1936
Tipula (Vestiplex) bisentis Alexander, 1951
Tipula (Vestiplex) schizophallus Alexander, 1973
Tipula (Vestiplex) yunnanensis Alexander, 1942
Tipula (Vestiplex) jiangi Yang and Yang, 1991
Tipula (Vestiplex) medioflava Yang and Yang, 1999
Tipula (Vestiplex) xanthocephala Yang and Yang, 1991

divisotergata species group

Tipula (Vestiplex) verecunda Alexander, 1924
Tipula (Vestiplex) divisotergata Alexander, 1932
Tipula (Vestiplex) zayulensis Alexander, 1963
Tipula (Vestiplex) adungensis Alexander, 1963
Tipula (Vestiplex) rongtoensis Alexander, 1963
Tipula (Vestiplex) halteroptera Alexander, 1951
Tipula (Vestiplex) ravana Alexander, 1953
Tipula (Vestiplex) spathacea Alexander, 1963
Tipula (Vestiplex) siddartha Alexander, 1961
Tipula (Vestiplex) subapterogyne Alexander, 1920
Tipula (Vestiplex) nokonis Alexander, 1928
Tipula (Vestiplex) gedehana de Meijere, 1911

avicularia species group

Tipula (Vestiplex) avicularia Edwards, 1928
Tipula (Vestiplex) bhutia Alexander, 1959
Tipula (Vestiplex) doron Alexander, 1961
Tipula (Vestiplex) freemanana Alexander, 1963
Tipula (Vestiplex) guibifida Yang and Yang, 1992
Tipula (Vestiplex) kumaonensis Alexander, 1961
Tipula (Vestiplex) pleuracantha Edwards, 1928
Tipula (Vestiplex) subbifida Alexander, 1953

subtincta species group

Tipula (Vestiplex) distifurca Alexander, 1942
Tipula (Vestiplex) optanda Alexander, 1935
Tipula (Vestiplex) dobrotworskyana Alexander, 1968
Tipula (Vestiplex) exechostyla Alexander, 1964
Tipula (Vestiplex) gandharva Alexander, 1951
Tipula (Vestiplex) hugueniniana Alexander, 1971
Tipula (Vestiplex) inaequifurca Alexander, 1949
Tipula (Vestiplex) parvapiculata Alexander, 1934
Tipula (Vestiplex) quasimarmoratipennis Brunetti, 1912
Tipula (Vestiplex) styligera Alexander, 1927
Tipula (Vestiplex) subtincta Brunetti, 1912
Tipula (Vestiplex) tillyardana Alexander, 1970
Tipula (Vestiplex) tuta Alexander, 1936
Tipula (Vestiplex) wahlgrenana Alexander, 1968
Tipula (Vestiplex) apicifurcata Yang and Yang, 1992

eurydice species group

Tipula (Vestiplex) acudorsata Alexander, 1970
Tipula (Vestiplex) bryceana Alexander, 1964
Tipula (Vestiplex) eurydice Alexander, 1961
Tipula (Vestiplex) inaequidentata Alexander, 1927
Tipula (Vestiplex) malla malla Alexander, 1959
Tipula (Vestiplex) malla placibilis Alexander, 1968
Tipula (Vestiplex) schummelana Alexander, 1968
Tipula (Vestiplex) siebkeana Alexander, 1970
Tipula (Vestiplex) walkeriana Alexander, 1971

unplaced species

Tipula (Vestiplex) ambigua Savchenko, 1964
Tipula (Vestiplex) bicalcarata Savchenko, 1965
Tipula (Vestiplex) kuwayamai Alexander, 1921

Tipula (Vestiplex) nigrocostata Alexander, 1925
Tipula (Vestiplex) reposita Walker, 1848

Unexamined and unpreparated species in need of morphological analysis for correct classification

Tipula (Vestiplex) churchillensis Alexander, 1940
Tipula (Vestiplex) serrulata Loew, 1864
Tipula (Vestiplex) mediovittata Mik
Tipula (Vestiplex) scandens Edwards, 1928
Tipula (Vestiplex) teshionis Alexander, 1921
Tipula (Vestiplex) biserra Edwards, 1921
Tipula (Vestiplex) papandajanica Edwards, 1932
Tipula (Vestiplex) takahashiana Alexander, 1938
Tipula (Vestiplex) tardigrada Edwards, 1928
Tipula (Vestiplex) arisanensis Edwards, 1921
Tipula (Vestiplex) foliacea Alexander, 1924.
Tipula (Vestiplex) inquinata Alexander, 1938
Tipula (Vestiplex) rhimma Alexander, 1961
Tipula (Vestiplex) immsiana Alexander, 1970
Tipula (Vestiplex) theowaldana Alexander, 1964
Tipula (Vestiplex) rana Alexander, 1959
Tipula (Vestiplex) czizekiana Alexander, 1970
Tipula (Vestiplex) nestor Alexander, 1934
Tipula (Vestiplex) cremeri Alexander, 1941
Tipula (Vestiplex) immota Alexander, 1935
Tipula (Vestiplex) bicornuta Alexander, 1920
Tipula (Vestiplex) subtestata Alexander, 1938
Tipula (Vestiplex) testata Alexander, 1935
Tipula (Vestiplex) bicornigera Alexander, 1938
Tipula (Vestiplex) xingshana Yang and Yang, 1997
Tipula (Vestiplex) longarmata Yang and Yang, 1999
Tipula (Vestiplex) proboscelongata Yang and Yang, 1991
Tipula (Vestiplex) kwanhsienana Alexander, 1934

Description of the new species

Tipula (Vestiplex) dhalma new species was described and illustrated from adult specimens collected by Dr. T. Nakamura in July 1993 in the Primorsky Krai of the Far Eastern Federal District of Russia (Starkevich and Podenas, 2011). This new species is most similar to *Tipula (Vestiplex) scripta scripta* Meigen, 1830 and other species of *T. (V.) scripta* Meigen, 1830 complex.

The new species is characterised by this diagnosis: medium sized crane fly (14.9-23.7 mm) with gray thorax, brownish yellow base and darkened tip of abdomen and distinctly brownish wings spotted with translucent areas. Anennal flagellum elongate, each flagellomere sinuous. Male: ninth tergum leathery; the main body of the tergal saucer is pale with the caudal margin broadly emarginate, the cephalic border appearing as an

elevated darkened plate with emarginate margins; inner gonostylus swollen, with small posterior angle and rounded “rostrum“; gonocoxite with point-apexed narrow posterior horn-shaped lobe. Female: abdomen elongate, slightly exceeding wing length; hypogynial valves reduced, rod shaped, divided by single, median U-shaped incision, posterior margin of 8 sternite with two deep lateral incisions outside bases of hypovalvae, thus lateral margins of sclerite bearing elongate lobes.

T. (V.) dhalma is most similar to *T. (V.) scripta scripta*, which is widely spread and rather common throughout whole Palaearctic. Similarities are observed in wing pattern, body coloration and male genitalia. The clearest differences between *T. (V.) dhalma* and *T. (V.) scripta scripta* are in structure of flagellomeres and in details of male and female genitalia. Flagellomeres of *T. (V.) dhalma* are sinuous, with widened basal and subapical parts and deep ventral and dorsal notches, flagellomeres of *T. (V.) scripta scripta* are straight with slightly widened bases. Staple of ninth tergum of *T. (V.) dhalma* with extended and sharpened proximal angles, when these structures of *T. (V.) scripta* are smaller and rounded. Inner gonostylus of *T. (V.) dhalma* has wide darkened and blunt posterodorsal angle, when same structure in *T. (V.) scripta* is sharp and narrow. Posterior lobe of gonocoxite of *T. (V.) dhalma* is strongly narrowed and darkened at tip, same structure of *T. (V.) scripta* is smoothly narrowed towards tip. Biggest differences between species is seen in structure of ovipositor. Posterior margin of eighth sternite of *T. (V.) dhalma* with two deep lateral incisions outside bases of hypovalvae, thus lateral margins of sclerite bearing elongate lobes. Ovipositors of *T. (V.) scripta scripta*, *T. (V.) pallidicosta pallidicosta* Pierre, 1924 and *T. (V.) tumididens* Savchenko, 1988 have very shallow lateral incisions outside bases of hypovalvae, thus lateral lobes of eighth sternite missing. Such incisions are completely missing in *T. (V.) scripta intermixta*. Other species belonging to “*scripta*” group and known from Far East of Russia is *T. (V.) pallitergata* Alexander, 1934. It has similar structure of flagellomeres as *T. (V.) dhalma*. Staple of ninth tergum of *T. (V.) pallitergata* is very small, inner gonostylus has sharpened and somewhat hook-shaped posterodorsal angle

The male of *T. (V.) dhalma* will key in Savchenko (1964) to *T. (V.) scripta scripta* and *T. (V.) scripta immunda*, in Sidorenko (1999) to *T. (V.) scripta immunda*, female will key in Savchenko (1964) to *T. (V.) pallidicosta pallidicosta*.

First records of *Tipula (Vestiplex)* craneflies for China, Myanmar, Thailand and S. Korea

Three species - *Tipula (Vestiplex) adungensis* Alexander, 1963, *Tipula (Vestiplex) eurydice* Alexander, 1961 and *Tipula (Vestiplex) verecunda* Alexander, 1924 were identified as new to the fauna of China.

Two species - *Tipula (Vestiplex) distifurca* Alexander, 1942 and *Tipula (Vestiplex) himalayensis* Brunetti, 1911 were identified as new to the fauna of Myanmar.

Female of *Tipula (Vestiplex) eurydice* Alexander, 1961 is described for the first time.

Craneflies of subgenus *Vestiplex* are recorded in Thailand and S. Korea for the first time (**publication coauthored with C. W. Young under preparation**).

Two species - *Tipula (Vestiplex) reposita* Walker, 1848 and *Tipula (Vestiplex) tuta* Alexander, 1936 were identified as new to fauna of Thailand.

Tipula (Vestiplex) serricauda Alexander, 1914 was identified as new to fauna of S. Korea.

CONCLUSIONS

1. Subgenus *Tipula (Vestiplex)* is a monophyletic crane fly group which is characterized by such synapomorphies: powerfully constructed cerci and reduced hypovalva. Male IX tergite is of two main forms: concave sclerotized saucer type or longitudinally divided into two parts.

2. Based on the performed analysis thirteen species groups were found in subgenus *Vestiplex*. Two species groups are described for the first time.

3. Inner genital structures (adminiculum, genital bridge, IX sternite, vaginal apodeme, *bursa copulatrix*), that were not investigated and ilustrated earlier by other scientists, allow to identify the species complexes and enable separation of close species.

4. One Far East species of the crane flies - *Tipula (Vestiplex) dhalma* Starkevich & Podenas, 2011 – was described as new to science.

5. Three species were added to the fauna of China and now 52 species of subgenus *Tipula (Vestiplex)* are known from this country. Two species were added to the fauna of Myanmar (8 species known in total). Craneflies of subgenus *Tipula (Vestiplex)* were also recorded in Thailand and S. Korea for the first time, respectively two and one species were added to the list.

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ĮVADAS

Darbo aktualumas. Šiuo metu aprašyta virš 5 tūkstančių rūšių priklausančių šeimai Tipulidae (Oosterbroek, 2011). Tai viena iš seniausių ir primityviausių pobūrio Nematocera grupių, kurios rūšys paplitusios visose zoogeografinėse srityse ir aptinkamos įvairiuose biotopuose. Ilgakojų uodų lervos turi didelę reikšmę ekosistemose – skaidant paklotę jos praturtina dirvožiemį organinėmis medžiagomis. Kai kurios rūšys yra kultūrinių augalų kenkėjai. Suaugėliai yra maistas plėšriems vabzdžiams, voragyviams, paukščiams bei smulkiems žinduoliams (Savchenko, 1983).

Pogentė *Vestiplex* – tai geologiškai jauna, specializuota genties *Tipula* ilgakojų uodų grupė, susiformavusi paleogeno – neogeno periodų laikotarpyje (Savchenko, 1960, 1964a, 1983). Šios pogentės patelėms būdingas specifinis kiaušdėtis: stambūs, stipriai sklerotizuoti dantytu paviršiumi cerkai bei redukuotos VIII sternito valvos. Tai susiję su perėjimu prie kseromorfinio gyvenimo būdo, kuomet patelės kiaušdėtis pritaikytas dėti kiaušinius giliai į kietą sausą substratą. Patinų genitaliniam kompleksui būdingas didelis polimorfiškumas.

Šiuo metu aprašytos 156 pogentės *Vestiplex* rūšys ir 14 porūšių (Oosterbroek, 2011). Jos paplitusios Holarktinėje ir Orientalinėje zoogeografinėse srityse. Dauguma rūšių susijusios su kalnų sistemomis (Alpės, Pirėnai, Kaukazas ir Himalajai), kur sutinkamos iki 4500 m. aukštyje. Suaugėliai sutinkami plačialapių, mišriuose, rečiau spygliuočių miškuose, alpinėse pievose, stepėse, tundroje, kur su kitomis ilgakojų uodų gupėmis yra dominuojančios (Savchenko, 1960, 1964a). Kai kurios rūšys turi didelę reikšmę: pvz. Kaukaze dominuojančios *T. semivittata*, Grenlandijoje dominuojančios *T. arctica* lervos ir suaugėliai yra pagrindinis paukščių maisto komponentas (Brodo 1990; Curtis, 1835; Hemmingsen & Jensen, 1957; Lantsov, 2003).

Pirmas pogentę *Vestiplex* išskyrė Bezzi (1924), remdamasis *Tipula (Vestiplex) cisalpina* Riedel 1913 rūšies požymiais. Pogentės apimtį nustatė Edwards (1931), vėliau patikslino Alexander (1933c, 1935c). Šiai grupei buvo priskirtos beveik visos rūšys, kurias Riedel (1913) buvo sujungęs į *Nigromarginatae* grupę.

Mannheims (1953), tiriant Vakarų Palearktikos *Vestiplex*, suskirstė rūšis į 4 grupes. Vėliau, atliekant morfologinę analizę, Savčenko perskirstė rūšis dalį tuo metu žinomų rūšių į jau aprašytus bei naujai išskirtus rūšių kompleksus. Šis skirstymas rėmėsi tik išoriniais kūno ir genitalijų požymiais, daugiausiai, patino IX sandara. Viso įvairiuose darbuose minima 11 rūšių grupių (Alexander 1934d, 1958, 1959, 1963; Savchenko, 1960, 1964a, 1965). Savčenko pabrėžia, kad nors vienų rūšių giminystės ryšiai yra aiškūs, kitų rūšių dėl menko morfologinio ištirtumo jie lieka vis dar nežinomi.

Šiuo metu, rūšių skaičiui smarkiai padidėjus, giminystės ryšių, atskirų rūšių ir porūšių taksonominės pozicijos klausimas tapo aktualus. Dalis rūšių, būdamos morfologiškai mažai išnagrinėtos, reikalauja giminystės ryšių patikslinimo pogentės *Vestiplex* viduje. Dalies rūšių diagnostinės struktūros yra neiliustruotos arba iliustruotos netiksliai ir netinka rūšių identifikavimui. Tikslios ir detalios diagnostinių struktūrų iliustracijos yra labai svarbios identifikuojant rūšis iš mažai tyrinėtų vietovių. Detali morfologinė analizė pateikia medžiagą apibūdinimo lentelių ruošimui.

Tyrimų tikslas ir uždaviniai

Disertacinio darbo tikslas - taksonominė filogenetinė pogentės *Vestiplex* Bezzi, 1924 analizė.

Tikslui pasiekti buvo iškelti šie uždaviniai:

1. Ištirti kuo didesnio rūšių skaičiaus tipinę medžiagą, pateikti svarbias identifikacijai genitalinių struktūrų iliustracijas;
2. Aprašyti filogenetiškai svarbius požymius bei atlikti filogenetinę analizę;
3. Suskirstyti pogentės *Vestiplex* rūšis į kompleksus.

Ginamieji disertacijos teiginiai: 1. Nauja pogentės filogenija ir klasifikacija; 2. Detali genitalinių struktūrų morfologijos analizė; 2. Vidinės genitalinės struktūros (adminikulumas, genitalinis tiltas, IX sternitas, vaginalinė apodema, kopuliacinė kamera) leidžia identifikuoti artimas rūšis.

Darbo naujumas ir jo reikšmė

Atrasta ir aprašyta nauja mokslui ilgakojų uodų rūšis *Tipula (Vestiplex) dhalma* Starkevich and Podenas, 2011. Viena rūšis sinonimizuota, kita rūšis atstatyta iš sinonimo. Viena porūšiui siūloma grąžinti savarankiškos rūšies statusą.

Identifikuotos trys naujos Kinijos ir dvi naujos Mianmaro faunai ilgakojų uodų rūšys. Vienos iš jų pirmą kartą aprašoma patelė. Pirmą kartą pogentės *Vestiplex* atstovai registruojami Tailando ir P. Korėjos faunai – atitinkamai dvi ir viena rūšis.

Pirmą kartą, remiantis morfologiniais požymiais, atlikta pogentės *Vestiplex* filogenetinė analizė, kurios metu išnagrinėtos 103 rūšys. Remiantis gautais rezultatais aptariami visų pogentės *Vestilex* žinomų rūšių giminystės ryšiai.

Parengtas ištirtos medžiagos genitalinių struktūrų iliustracijų katalogas. Daugumai rūšių pirmą kartą pateiktos vidinių genitalinių struktūrų iliustracijos.

Genitalinių struktūrų katalogas yra labai naudingas identifikuojant rūšis iš įvairių mažai tyrinėtų vietų.

Atliktas darbas prisideda prie sąrašo darbu skirtų šeimos Tipulidae atskirų grupių filogenijos nagrinėjimui (Brodo, 1987; Gelhaus, 1995; de Jong, 1993, 1994a, 1994b, 1995a, 1995b; Oosterbroek, 1980), papildo žinias apie reproduktivinių organų morfologiją bei gali būti panauduotas sprendžiant šeimos Tipulidae taksonominius klausimus.

IŠVADOS

1. Pogentė *Vestiplex* tai monofiletinė ilgakojų uodų grupė, kurią charakterizuoja tokios sinapomorfijos kaip stipriai pakitę, stambūs, su dantytu apatiniu paviršiumi cerkai bei redukuotos valvos. Patino IX tergitui būdingos dvi pagrindinės formos: padalintas į dvi atskiras skiltis bei semtuvo tipo.

2. Remiantis atlikta filogenetine analize nustatyta, kad pogentės *Vestiplex* rūšys grupuojasi į 13 kompleksų. 2 rūšių kompleksai išskiriami pirmą kartą.

3. Vidinės genitalinės struktūros (adminikulumas, genitalinis tiltas, IX sternitas, vaginalinė apodema, kopuliacinė kamera), kurios anksčiau nebuvo tirtos ir iliustruotos, leidžia identifikuoti rūšių kompleksus, ir gali būti panaudojamos artimų rūšių identifikavimui.

4. Iš Rusijos Tolimųjų Rytų aprašyta nauja mokslui ilgakojų uodų rūšis – *Tipula (Vestiplex) dhalma* Starkevich & Podenas, 2011, priklausanti *scripta* rūšių grupei.

5. Papildžius Kinijos fauna 3 naujomis rūšimis, dabar jos faunoje žinomos 52 pogentės *Vestiplex* rūšys. Papildžius Mianmaro fauna 2 naujomis rūšimis, dabar čia žinomos 8 *Vestiplex* rūšys. Atradus 2 naujas rūšis Tailandui ir 1 naują rūšį P. Korėjai, pogentės *Vestiplex* atstovai šiose šalyse minimi pirmą kartą.

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