

VILNIUS UNIVERSITY

Andrius Petrašiūnas

TAXONOMIC AND PHYLOGENETIC REVIEW OF THE
GENUS *TRICHOCERA* MEIGEN, 1803
(DIPTERA, TRICHOCERIDAE)

Summary of Doctoral Dissertation
Biomedical sciences, Zoology (05 B)

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VILNIAUS UNIVERSITETAS

Andrius Petrašiūnas

TAKSONOMINĖ IR FILOGENETINĖ GENTIES
TRICHOCERA MEIGEN, 1803
(DIPTERA, TRICHOCERIDAE) ANALIZĖ

Daktaro disertacijos santrauka
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INTRODUCTION

Genus *Trichocera* Meigen, 1803 currently comprises around 110 species, mostly from Holarctic region (Hågvar & Krzemińska, 2007), but several species were introduced into some South-Atlantic islands, Australian islands (Dahl & Krzemińska, 1997). Gnats of this genus are most often found in cool, humid mild climate during the autumn, winter and spring months around the Northern hemisphere. Adult insects are confined to biotopes rich in decomposing organic material (Dahl & Krzemińska, 1997).

During the early period of the studies, representatives of the genus *Trichocera* were most often considered belonging to different subfamilies of the Tipulidae (Meigen, 1804; Latreille, 1809; Rondani, 1856; Osten Sacken, 1869; Brunetti, 1911 and others). Later, based mostly on the similarities of the larval stages, they were considered a part of the Anisopodidae (Rhyphidae) family (Keilin, 1912; Bezzi, 1914; Alexander, 1921; 1924b) up until the 1924 when G. C. Crampton put them into separate family Trichoceridae.

The second part of the XX century saw different problems at the genus and subgenus levels scrutinized. In 1966 C. Dahl formed a new genus *Metatrachocera* with *T. lutea* Becher, 1886 being the type-species (Dahl, 1966a) and *T. hiemalis* (De Geer, 1776) became a nominotypical species of the genus *Trichocera*. Just after that, Alexander & Alexander (1967) considered *Metatrachocera* as one of the two subgenus-level taxa of the *Trichocera*, but this view was finally accepted only in 1976, when „A World catalogue of Trichoceridae“ appeared (Dahl & Alexander, 1976).

Some time had to pass until the subgenus *Metatrachocera* turned out to be paraphyletic, when E. Krzemińska found out that *T. (M.) garretti* Alexander, 1927 is closer to species of subgenus *Trichocera* by male eedeagal complex (Krzemińska, 1996). Following the view, Starý (1998) transferred the *hiemalis* group of species to subgenus *Trichocera* and rest of the species undependably of the peculiarities of gonocoxites and gonostyles were placed into subgenus *Metatrachocera*.

While describing new winter gnat species from Japan, Nakamura & Saigusa (1997) noted that definitions of *Metatrachocera* provided by C. Dahl and other authors are not precise and subgenus contains species of different origin. Later E. Krzemińska separated species with simple gonocoxites and gonostyles into new subgenus *Saltrichocera* (Krzemińska, 2002). Some of those species were attributed to subgenus on the basis of original descriptions, although those were lacking illustrations of the important structures. Not all of the world species ended up in one of the three subgenuses, therefore a more thorough analysis was needed with new descriptions of the species that lack illustrations.

Although mentioned (Krzemińska, 2002), phylogenetic analysis of the genus *Trichocera* was never published and relations of the species inside this genus left

unanalysed, contrary to those of genus *Nothotrichocera* (Krzemińska, 2001) or subfamily *Paracladurinae* (Krzemińska, 2005).

Winter gnats are rather complicated group in terms of identification and were more intensively studied at the end of the XX century (Valenta & Podėnas, 1985; Podėnas, 1989; 1991; 1993; 1995, etc.). Later research of the Trichoceridae intensified in other European countries, many new winter gnat species were described and so came the time to itemize the structure of the Lithuanian winter gnat fauna.

As many species of animals are going extinct around the world, lots of them disappear without us knowing about their existence. Therefore one of the main tasks for entomologists is the description of new species and inventory of the faunas of particular countries and regions.

Aims and tasks of the dissertation. The aim of this dissertation was to accomplish taxonomic and phylogenetic review of the genus *Trichocera* Meigen, 1803. The following tasks were formulated in order to achieve the aim:

1. To investigate the species composition of the genus *Trichocera* in Lithuania and determine their seasonal activity peaks;
2. To investigate as many as possible type specimens and specimens of different species, illustrating the structures important for the species identification that haven't yet been properly illustrated;
3. Compile a list of characters for the phylogenetic analysis and perform the analysis itself;
4. Perform the analysis of attributing the species to particular subgenus.
5. Compile a world catalogue of the recent species of the genus *Trichocera*.

Defensive statements:

1. New version of phylogeny and classification of the genus *Trichocera*.
2. Peculiarities of the *Trichocera* male edeagal complex are the basis for attributing species to particular subgenus.
3. Elaborate formations of male gonostyli in species of *Trichocera* developed independently several times and the currently used definition of the subgenus *Metatrichocera* Dahl, 1966 is not accurate.

Novelty and significance of the study. One new for the science species of winter gnats was described. Taxonomic position of 96 examined species was checked and as a result 15 of those species were transferred from one subgenus to another. First phylogenetic analysis of the genus *Trichocera* was performed, new version of phylogeny and classification of the genus presented. A renewed catalogue of the world fauna of the genus *Trichocera* is prepared with structured data on 110 recent species of the genus, their biology, distribution, type specimen storage institutions etc. Type material of fifteen species is illustrated for the first time together with identification structures of the

females of four species and male of one species. A key for the identification of the 54 species of the world is compiled. Nine new for Lithuanian fauna species of winter gnats are identified.

The newly illustrated type material and structures of females and male of several species forms a basis for carrying out more thorough analysis of the winter gnat fauna in less accessed regions of the world (e. g. India, Mongolia, etc.) also aiding in more precise identification of the specimens of particular species. Data on periods of activity of particular species might be practically used in forensic entomology when preimaginal stages of winter gnats are one of only several groups of insects active during the cold season. The data collected during the investigations supplemented our knowledge about Lithuanian entomofauna and will be used renewing the “Catalogue of Lithuanian Diptera”. A fair collection of winter gnats (with some paratypes) from all over the world is accumulated and adds to the scientific value of the Museum of Zoology of Vilnius university (MZVU) where it is stored.

Volume and structure of the dissertation. The volume of dissertation is 152 pages (excluding appendix). The thesis is written in Lithuanian and consists of Introduction, Literature review, Materials and methods, Results and discussion, Conclusions, List of references (342 reference sources), Appendix (106 figures). The dissertation has 134 figures and 3 tables.

MATERIALS AND METHODS

The research material was acquired in three main ways – by the means of standard entomological techniques in different parts of Lithuania, during the short time visits to foreign museums and by getting a loan or a gift from different institutions or scientists personally.

Winter gnat specimens used in the study were collected by different scientists in Lithuania during the period of 2001 – 2009 by Jalas-model light trap (P. Ivinskis, V. Lopeta, A. Vilkas), Malaise traps (V. Buivydaitė, D. Činčiukas, S. Podėnas, P. Visarčuk, V. Ūselis), pitfall traps (D. Mikelaitis) and during the short-time trips by entomological net (G. Grašytė, R. Giedraitis, A. Kleišmantas, M. Margienė, J. Plechavičiūtė, S. Podėnas and author of dissertation) (Fig. 1).

Five short-time visits to museums and collections were made. These were as follows: Natural History Museum Vienna, Austria (17–22 March, 2008); Natural History Museum London, Great Britain, using the funds of EU SYNTHESYS program for the project „Evaluation of morphological features of genus *Trichocera* (Diptera: Trichoceridae) for later use in phylogenetic analysis“ (GB-TAF-4047) (2–30 June, 2008); Zoological institute Russian Academy of Sciences in St. Petersburg, Russia (17–24 November, 2008); personal collection of J. Starý, Olomouc, The Czech Republic (24

January – 4 February, 2009); Institute of Systematics and Evolution of Animals Polish Academy of Sciences in Krakow, Poland (4–8 April, 2009)

Some winter gnat material was acquired through the loans from: Department of Entomology of Smithsonian Institution, Washington, USA (type specimens of 15 species); Department of Entomology, California Academy of Sciences, San Francisco, USA (holotypes of *T. arnaudi* and *T. banffi*); Muséum d'histoire naturelle, Neuchâtel, Switzerland (holotype of *T. kotejai*). Some paratypes along with general specimens were received as a present from J. Starý, Olomouc, The Czech Republic and from T. Nakamura, Utsunomiya, Japan. Winter gnat specimens, collected on the island of Sardinia by M. Bardiani, D. Birtele, P. Cerretti, G. Chessa, E. Minari, G. Nardi, M. Tisato, D. Whitmore and M. Zapparoli during the Project „Arthropod diversity in South-west Sardinia” were acquired from Centro Nazionale per lo Studio e la Conservazione della Biodiversità Forestale, Verona, Italy. All the specimens collected in Lithuania or received as a present are deposited at the Museum of Zoology of Vilnius university (MZVU).

An annotated checklist of the recent world species of genus *Trichocera* was compiled. For each species the information is given in the following order: scientific name, synonyms, location of the type specimens, material examined during the current study, references of illustrations and distribution, some data on biology with references and other notes. New and already published illustrations of the structures used for the identification of the species are given in appendix.

Winclada v.1.00 (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 v.1.3 (© P. A. Goloboff 1997) were used for the search of most parsimonious trees using the equal weighting and implied weighting techniques (Nihei & De Carvalho, 2007). The settings each time were hold10000, mult*200, performing heuristic search „tree-bisection reconnection branch swapping“ with 200 repeats.



Figure 1. Map of material collection localities in Lithuania.

RESULTS AND DISCUSSION

Phylogenetic analysis

Character states

While analyzing the literature and winter gnat specimens, 37 characters were selected for phylogenetic analysis and the matrix of their states was compiled (fig. 2). 85 recent winter gnat species are included in the matrix, mostly those that were available for direct study by the author of dissertation or those with published comprehensive descriptions and illustrations.

The character states are:

Head, antennae, thorax

1. First antennal flagellomere (*f1*): (0), shorter or up to 1,5 times longer than the second flagellomere (*f2*); (1), up to twice longer than *f2*; (2), two and more times longer than *f2*.
2. First antennal flagellomere: (0), not thickened; (1), clearly enlarged.
3. Setosity of *f1*: (0) , has no clearly distinguishable long setae, flagellomeres covered in pubescence; (1), verticils rather short, at most 2 times longer than pubescence; (2), terminal verticals are clearly visible and 3-4 times longer than pubescence.
4. Length of *f1* compared to pedicellum: (0), 3-4 times longer; (1), *f1* less than 3 times longer than pedicellum.
5. Setosity of pleurons: (0), pleura bare; (1), setae visible on mesothoracic epimeron; (2), setae on mesothoracic epimeron and metepisternum; (3), setae only on metepisternum.

Wing

6. Subcostal vein enters wing margin: (0), proximad of *rr* cross-vein; (1), at the equal line with *rr*; (2), more distally than *rr*.
7. Lower edge of the R cell, relation of R2+3 and R2+3+4: (0), R2+3 at most twice as long as R2+3+4; (1), R2+3 equal to R2+3+4; (2), R2+3 shorter than R2+3+4.
8. Relation of the second (mM1+2) and the first (bM1+2) part of the M1+2 vein: (0), mM1+2 three or more times longer than bM1+2; (1), mM1+2 1,5-2,5 times longer than bM1+2; (2), mM1+2 up to 1,5 times longer than bM1+2; (3), mM1+2 equal to bM1+2.
9. Third part of the M1+2 vein: (0), shorter than M1 vein; (1), equal or longer than M1.
10. Veins M1 and M2 diverge towards the wing margin: (0), in widening manner; (1), parallel.
11. Vein *mcu* enters: (0), into branching of M3+4 or more distally into M4; (1), proximad the branching of M3+4.

12. A2 vein dorsally: (0), covered in setae up to the bend; (1), bare or with several setae at the very base.
13. Spotting pattern of the wing: (0), wing clear, without spots or sometimes with one on *rm*; (1), several clear spots on *rm*, *mcu* and elsewhere; (2), whole wing is spotted.

Legs

14. Proportion of the last tarsomere (*t5*) and length of the claw of the hind legs: (0), last tarsomere 3 or more times longer than the claw; (1), *t5* twice longer than the claw; (2), length of the claw exceeds half of the last tarsomere.
15. Form of the claw: (0), claw weakly bent, scythe-like; (1), claw distinctly bent, sickle-like.

Male terminalia

16. Medial part of the IX sternite: (0), with setae; (1), without setae.
17. Sternite IX: (0), with only shallow pit or without any; (1), desclerotised, with deep excision.
18. Bridge of the gonocoxites: (0), near the base of gonocoxites, straight and not merged, or merges widely; (1), bridge is clearly arched but not merged; (2), bridge is arched, sclerotized and merges in the middle; (3), merges differently.
19. Width of gonostyles and gonocoxites: (0), gonocoxites slender, slightly wider than gonostyles; (1), gonocoxites up to two times wider than gonostyles; (2), gonocoxites enlarged, balloon-like, more than two times wider than gonostyles.
20. Outgrowths of gonostyles: (0), there are no outgrowths or bulges, gonostyles simple; (1), little-distinct tubercle at the inner base of gonostyle; (2), clear but short outgrowth at the base; (3), one large outgrowth on gonostyle; (4), several outgrowths or other complex structures visible.
21. Membrane between the lateral apodemes and base of parameres: (0), no membrane visible or it has a central spine; (1), membrane without the central spine, tightly covers the edeagus and repeats its form; (2), forms a clear hood-like sheath.
22. Parameres: (0), very short, twice shorter than edeagus or longer, but directed vertically upwards; (1) as long as edeagus or longer than it, bent at the base, straight further; (2), long, 2-3 times longer than edeagus, more or less equally bent at entire length; (3), very long, more than three times longer than edeagus.
23. Parameres at the base (dorsal view): (0), narrow; (1), wide.
24. Lateral apodemes: (0), “twisted”; (1), “not twisted”.
25. Lateral apodemes: (0), distanced from the basal apodemes, but have dorsal apodemes; (1), directed towards basal apodemes and close to those, but rather narrow; (2), chunky and close to basal apodemes and parameres; (3), distanced from the basal apodemes and parameres; (4), very narrow and long (3 times longer than width), distanced from the basal apodemes, sometimes close to parameres.

26. Membrane between the lateral apodemes (*la*): (0), *la* not connected by membrane; (1), connected by hardly visible membrane; (2), clear membrane is visible at the base of *la*; (3), *la* apodemes connected by membrane almost throughout all their length.
27. Basal apodemes (dorsal view): (0), parallel; (1), approaching each other.
28. Edeagal apodeme: (0), finger-like, equally wide through all the length, reaches up to 1/3 of the length of edeagus; (1), fingerlike, but of various width; (2), short, pointed, triangular; (3), wide, fin-like.

Female terminalia

29. Ovipositor: (0), short and wide, length slightly exceeds the width near the base; (1), narrow, at least twice as long as wide.
30. Ovipositor compared to VIII sternite: (0), ovipositor shorter than sternite; (1), ovipositor subequal or slightly longer than sternite; (2), ovipositor twice as long as sternite.
31. Form of the vaginal apodeme: (0), very short, wide and triangular; (1), wide at the proximal part, narrowing towards the end, but wider part extends further than the middle of the fork; (2), wide at the proximal part and triangularly narrows towards the center, further narrow; (3), equally narrow along all the length.
32. Proximal parts of the vaginal apodeme: (0), proximal part wide, not fork-like; (1), proximal part fork-like, lateral parts of the fork narrow and widely set apart, with deep oval excision; (2), lateral parts of the fork narrow, forming full or almost full ellipse; (3), lateral parts of the fork narrow, shorter, parallel; (4), lateral parts of the fork very short.
33. Genital plate: (0), without depression; (1), apex with depression, forming obtuse angle; (2), apex with depression, forming acute or straight angle.
34. Form of the apex of supragenital plate: (0), apex rounded or flat; (1), apex triangular.
35. Number of setae on supragenital plate: (0), two setae (or three); (1), four setae (or five); (2), six or more setae; (3), supragenital plate bare.
36. Sclerotised parts of the spermathecal ducts: (0), shorter or subequal to the diameter of the spermatheca; (1), longer than diameter of spermatheca.
37. Setose area of the ovipositor: (0), reaches up to 1/3 of the ovipositor; (1), covers 1/3 to 1/2 of the ovipositor length; (2), reaches the middle of the ovipositor; (3), covers almost all the length of the ovipositor; (4), not clearly delimited.

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Figure 2. Data matrix.

Differential weighting of the characters

Using the data matrix, most parsimonious trees were searched applying several weighting techniques – equal weighting (EW) and implied weighting (IW) and results are given in table 1.

In the XPEE-WEE software (applies implied weighting) fit value of every character i is calculated using the equation $fi = k/(k + esi)$ where k is a constant of concavity and esi is the number of extra steps for character i (Goloboff, 1993). The lower the value of k , the bigger the difference between the characters with extra-steps and characters without and the weighting itself becomes more drastic. When the k value increases, fit value of the character decreases and the character weighting becomes closer to that used in equal weighting (EW) technique. Although the effects of different k values were properly analyzed (Goloboff, 1993) and checked experimentally (Turner & Zandee, 1995), authors haven't provided clear answers which of the values of the constant of concavity is best.

Implied weighting was used also because: 1) it calculates the trees in one action and the result is not influenced by the primary weights applied to characters (Kaila, 1999); 2) consistency of the final cladograms is determined using not all of the available topologies (Harbach & Kitching, 1998); 3) lower margin of the fit function is not zero, therefore the possibility of discarding some of the characters decreases (Nihei & De Carvalho, 2007); 4) this method is not reducing the impact of multistate characters (Goloboff, 1993).

All the values (1 to 6) of the constant of concavity were used by us while searching for the most parsimonious tree and the parameters of all the searches are given in table 1.

Table 1. Parameters of the cladograms found by different weighting techniques

Weighting technique used							
	EW	IW (k=1)	IW (k=2)	IW (k=3)	IW (k=4)	IW (k=5)	IW (k=6)
Number of trees	80	1	4	4	5	4	5
Length	428	476	469	470	463	462	460
Fitness	-	898	1211	1406	1566	1697	1811
CI index	17	15	15	15	16	16	16
RI index	57	51	52	52	53	53	53
Parameters of the cladograms found by strict consensus							
Length	608	476	472	471	466	464	463
CI index	12	15	15	15	16	16	16
RI index	35	51	52	52	53	53	53

One cumulative cladogram was found by strict consensus rule for each of the six cases of the implied weighting as well as for the case of equal weighting and the

parameters are given in table 1. After comparing all of these cumulative cladograms with each other, the optimal one turned out to be that found by IW with $k = 6$ (fig. 3-5) and further analysis is based on this tree.

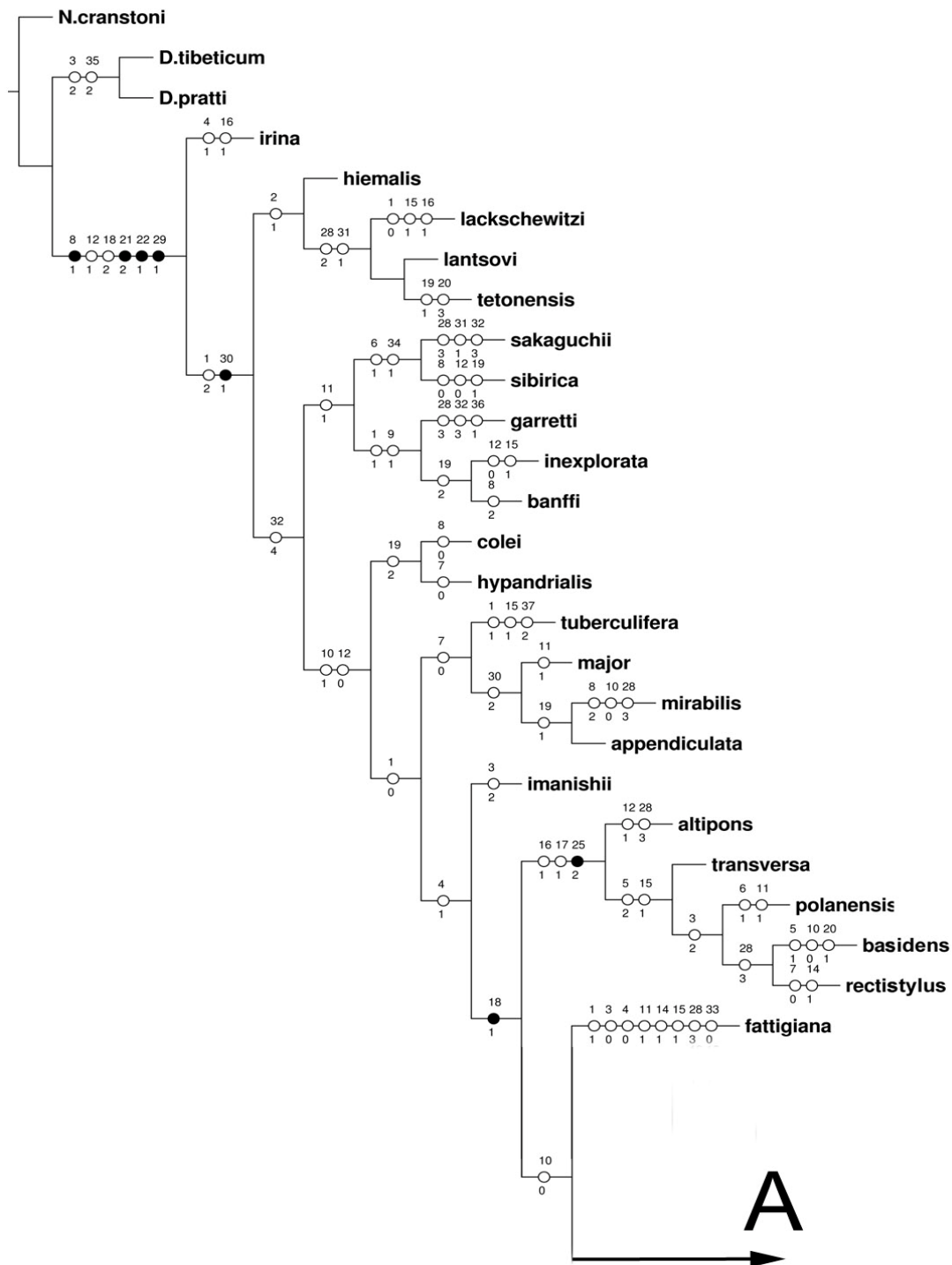


Figure 3. Strict consensus tree of the 4 cladograms acquired by IW ($k=6$) (unambiguous changes only). Black circles – apomorphies, digits above circles – numbers of the characters, below – state of the character (Continued in Fig. 4).

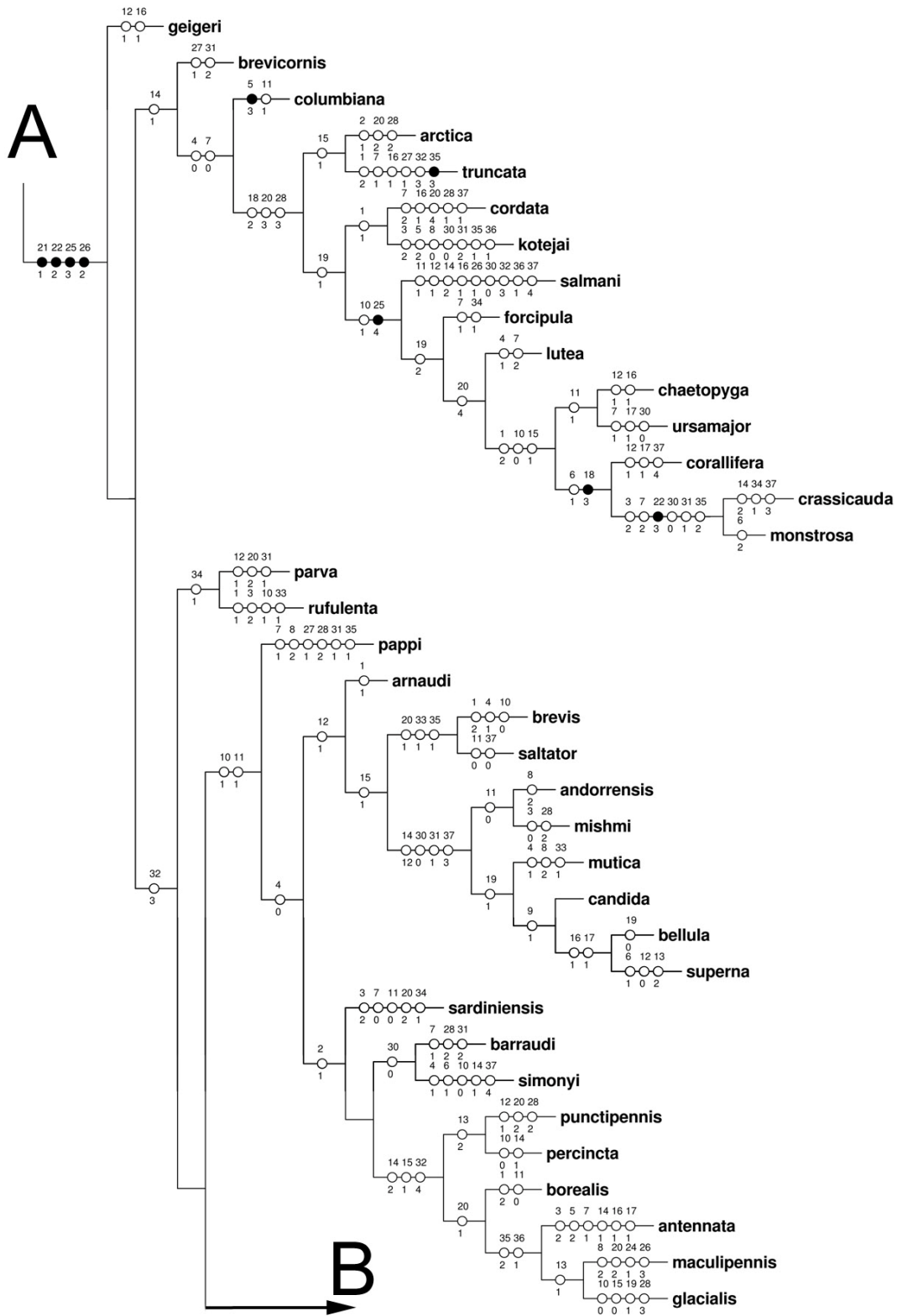


Figure 4. (Beginning in Fig. 3) Strict consensus tree of the 4 cladograms acquired by IW (k=6) (unambiguous changes only). Black circles – apomorphies, digits above circles – numbers of the characters, below – state of the character (Continued in Fig. 5)

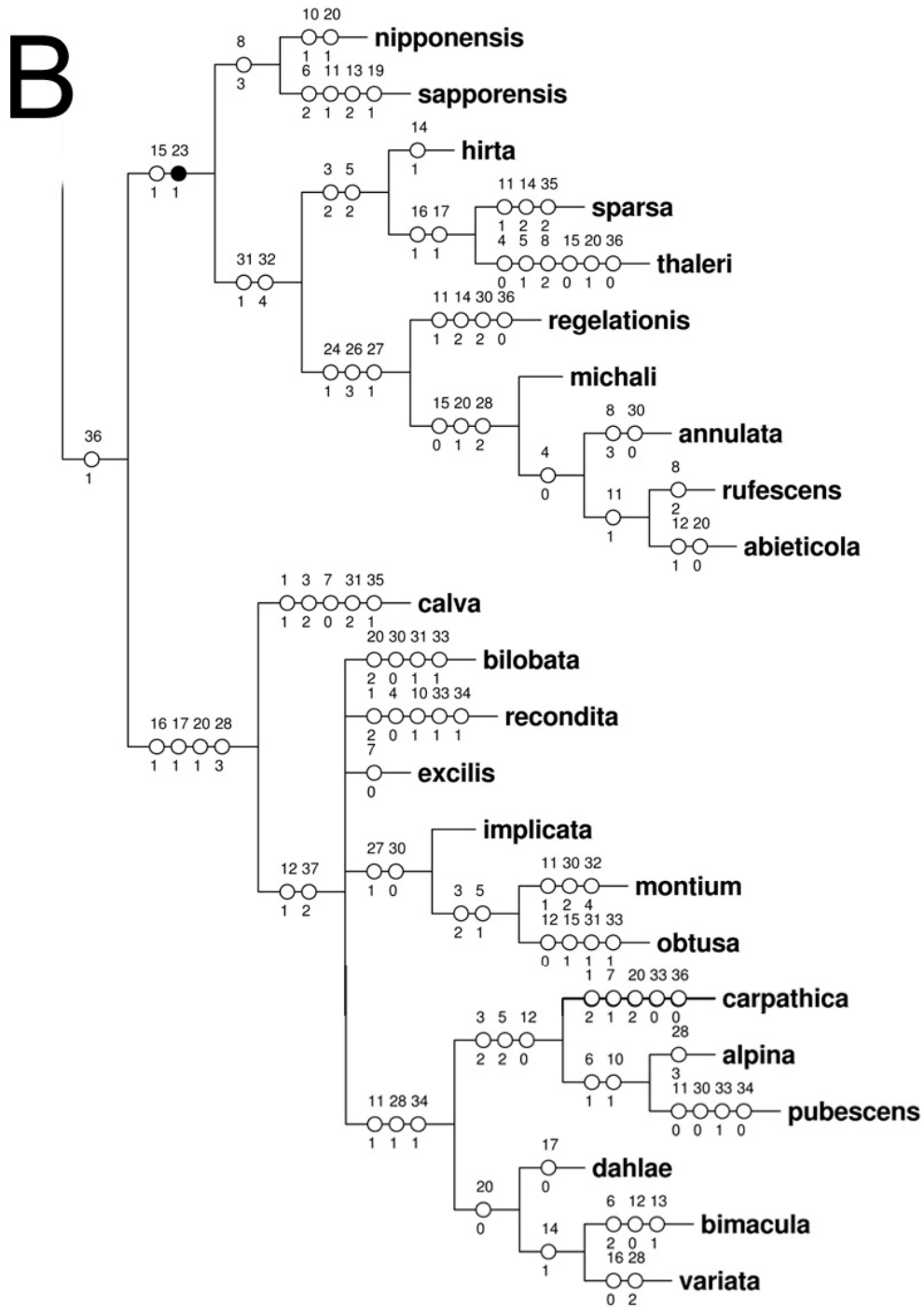


Figure 5. (Beginning in Fig. 3 and 4) Strict consensus tree of the 4 cladograms acquired by IW (k=6) (unambiguous changes only). Black circles – apomorphies, digits above circles – numbers of the characters, below – state of the character

Phylogenetic relations

For an easier view, a simplified cladogram is presented in fig. 6.

Majority of the most parsimonious trees found by different techniques had the species traditionally attributed to subgenus *Trichocera* at their base. This group is characterized by two apomorphies: 21.2 – membrane between the lateral apodemes and base of parameres forms a “hood” and 22.1 - parameres bent at base and as long as eedeagus or slightly longer than that. J. Starý also used these characters while defining the nominotypical subgenus *Trichocera s. str.* (Starý, 1998).

A group of five species, *T. rectistylus* group (*T. altipons*, *T. transversa*, *T. basidens*, *T. polanensis* and *T. rectistylus*) is separated from the rest of the subgenus *Trichocera* bei their chunky lateral apodemes (25.2).

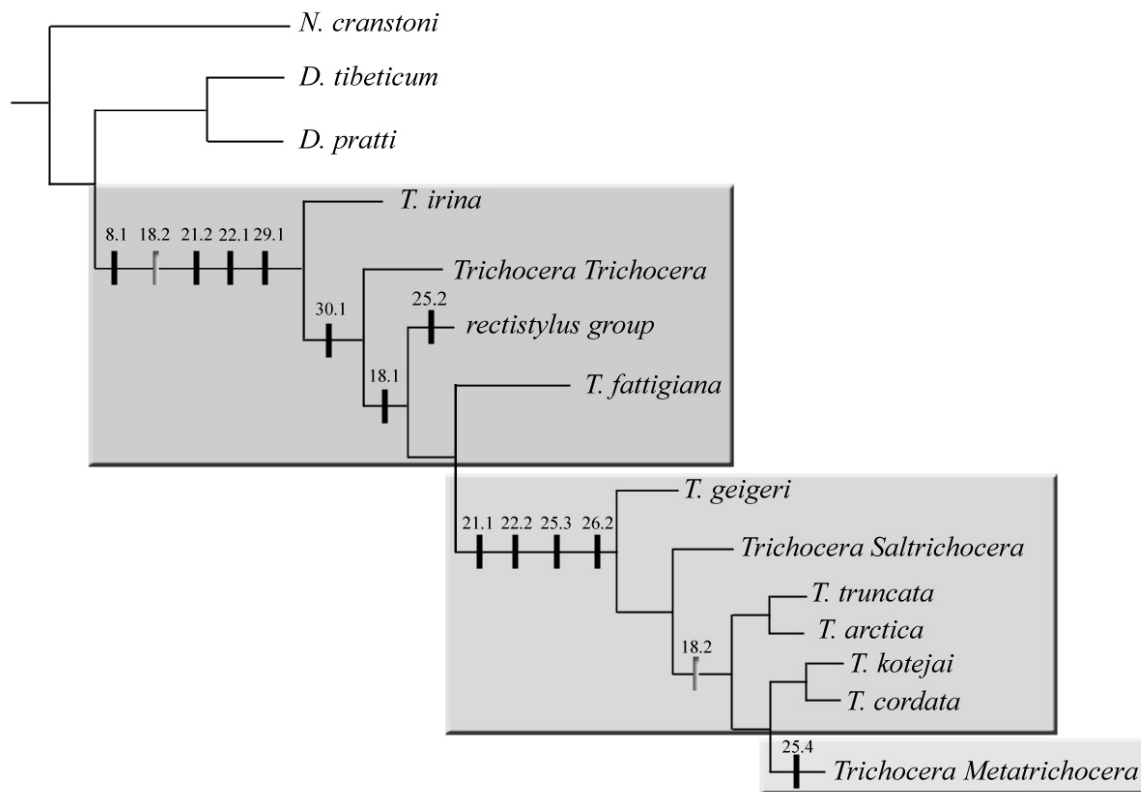


Figure 6. A simplified version of the cladogram given in fig. 3-4.

One synapomorphy – the unmerged gonocoxal bridge (18.1) connects the *rectistylus* group with part of the species of the subgenus *Saltrichocera*. Whilst the merged gonocoxal bridge (18.2) is a homoplastic character, because it is found in all other species of the subgenus *Trichocera* as well as in *T. arctica*, *T. truncata*, *T. cordata*, *T. kotejai* from *Saltrichocera* and also in part of the species from subgenus *Metatrachocera* (Fig. 4)

The clade of *Saltrichocera* is separated by the presence of long paremeres equally bent over entire length (22.2) and lateral apodemes, distanced from the basal apodemes and parameres (25.3). The lateral apodemes of this group are also clearly connected by membrane at the base (26.2) which tightly covers the edeagus (21.1). Three of these apomorphic characters (21.1, 22.2 and 26.2) are also shared by eight species attributed by us to subgenus *Metatrachocera* (*T. salmani*, *T. forcipula*, *T. lutea*, *T. chaetopyga*, *T. ursamajor*, *T. corralifera*, *T. crassicauda*, *T. monstrosa*) which in its way is defined by one autapomorphy - very narrow and long lateral apodemes (25.4). *T. crassicauda* and *T. monstrosa* have one more synapomorphy – very long parameres (22.3). Specimens of five more species (*T. gigantea*, *T. latilobata*, *T. mackenzie*, *T. schmidi*, *T. thaumastopyga*) were not checked during the studies, but these species are left in subgenus *Metatrachocera* based on the earlier published views of other authors, although their position may change after precise examination.

E. Krzemińska (2002) considered long and narrow lateral apodemes together with long slim paremeres and balloon-like gonocoxites to be characteristic to the species of subgenus *Metatrachocera*, but such enlarged gonocoxites (19.2) are also found in species from other clades, so the character is not specific to this one subgenus.

A clear group of ten species (*T. nipponensis*, *T. sapporensis*, *T. hirta*, *T. sparsa*, *T. thaleri*, *T. regelationis*, *T. michali*, *T. annulata*, *T. rufescens* and *T. abieticola*) separates in subgenus *Saltrichocera* by parameres wide at the base (23.1) (Fig. 5). Several of the species of this *T. regelationis* group have “untwisted” lateral apodemes (24.1) – character also witnessed in *T. maculipennis* (fig. 5).

None of the characters of the wing, antennae, thorax or legs led to forming of apomorphic groups, so features of these parts most probably are fit for the identification of separate species, but not for the analysis of phylogenetic relations.

During the analysis using the implied weighting, clear clades formed mostly based on the characters of male edeagal complex while features of gonostyles and gonocoxites were not as informative. Species with complicated gonostyles ended up in all three subgenera, e.g. *T. colei* and *T. hyandrialis* in *Trichocera*, *T. truncata* and *T. cordata* in subgenus *Saltrichocera*, while most of the rest in subgenus *Metatrachocera*. This leads us to conclusion that elaborate outgrowths of gonostyles evolved independently several times.

Description of the new species of *Trichocera*

During the research under the “Centro Nazionale Biodiversità Forestale, funds 2007” grant “Arthropod diversity in south-west Sardinia”, M. Bardiani, D. Birtele, P. Cerretti, G. Chessa, E. Minari, G. Nardi, M. Tisato, D. Whitmore and M. Zapparoli collected some winter gnat material that was later given to the author of this thesis for examination. The dominating species was found to be *Trichocera* (*Saltrichocera*) *annulata* Meigen, 1818 (420 males and 203 females), followed by *T. (S.) rufescens*

Edwards, 1921 (28 males and 56 females) and *T. (S.) saltator* (Harris, 1776) (13 males, 27 females), with 17 more specimens exhibiting some features not found in other known winter gnat species before.

Based on the enlarged first antennal flagellomere of the females, possessing flattened peg-like setulae (males have those too), form of the ovipositor and features of genital plate as well as peculiarities of the male gonocoxal bridge, form of the ninth sternite and features of the edeagal complex, new species of the winter gnats - *Trichocera (Saltrichocera) sardiniensis* Petrašiūnas, 2009 was described in volume 2108 of the journal "Zootaxa" (Petrašiūnas, 2009).

The new species resembles *T. (S.) antennata* most of all by short peg-like setulae on fused and enlarged female flagellomeres and general shape of the ovipositor. First flagellomere is also quite similar in males of both species by the form and peg-like setulae. On the other hand, *T. (S.) sardiniensis* differs from *T. (S.) antennata* by the form of female genital fork and by having only two bristles on supragenital plate. It also differs by males having distinct projection at inner base of gonostyles, almost straight IX sternite, different aedeagal complex and comparatively short, less curved tarsal claws. Finally, both males and females of *T. (S.) sardiniensis* have no setae on pleurons contrary to the state in *T. (S.) antennata*.

The newly described species is also very similar to recently redescribed (Dahl & Krzeminska, 2008) *T. (S.) borealis* Lackschewitz by the general view of male and female terminalia. Males of both species have distinct basal tubercle at inner base of gonostylus, straight margin of IX sternite with setae all along it, but the gonocoxal bridge in *T. (S.) sardiniensis* is low and broad compared to the high and narrow bridge in *T. (S.) borealis*. The base of parameres in *T. (S.) borealis* is wider, while basal apodemes narrower than those in *T. (S.) sardiniensis*. Male tarsal claws exceed half of fifth tarsomere in *T. (S.) borealis* whilst they reach only 1/3 of the tarsomere in *T. (S.) sardiniensis*. The shape of the ovipositor is rather similar in females of both species. Females of *T. (S.) borealis* and *T. (S.) sardiniensis* are also similar by having two setae on supravaginal plate, but vaginal apodeme in *T. (S.) borealis* has very short lateral portions compared to longer and parallel lateral portions in *T. (S.) sardiniensis*.

Investigations of the Lithuanian winter gnat fauna

A period of more active investigations of the Lithuanian winter gnat fauna was started in 2005 when the author of this work started his PhD studies. Before that, most of the data was collected during the period of 1985–1995 by S. Podėnas and the list of Lithuanian Trichoceridae comprised 11 species (Pakalniškis et al., 2000).

The author of this thesis published a record of one new for Lithuanian fauna winter gnat species – *Trichocera (S.) calva* Starý, 1999 in 2006, then five more species (*T. (S.) dahlae* Mendl, 1971, *T. (S.) recondita* Starý, 2000, *T. (S.) rufulenta* Edwards, 1938, *T. (S.) sparsa* Starý&Martinovský, 1996 and *T. (S.) geigeri* Starý&Krzemińska,

2000) were added to the list in the joint publication with P. Visarčuk in 2007, together with new data on distribution and seasonal activity of the winter gnat species in Lithuania. Later, data on findings of two more species - *T. (S.) bilobata* Starý, 1999 and *T. (S.) implicata* Dahl, 1976, found in vicinities of Vilnius, was published in 2008. Several specimens of *T. (S.) brevis* Krzemińska, 2002 were found in trap material from Švenčionys district, so altogether 22 species of Trichoceridae are known from Lithuania with two of them - *T. (M.) lutea* Becher, 1886 and *T. (S.) antennata* Starý, 1999 included in the list based on the Fauna Europaea database: 1. *Diazosma hirtipenne* (Siebke, 1863), period of activity: July-August; 2. *Trichocera (Metatrachocera) forcipula* Nielsen, 1920 (end of September – October); 3. *T. (M.) lutea* Becher, 1886; 4. *Trichocera (Saltrichocera) annulata* Meigen, 1818 (end of August – end of October); 5. *T. (S.) antennata* Starý, 1999; 6. *T. (S.) bilobata* Starý, 1999 (November); 7. *T. (S.) brevis* Krzemińska, 2002 (October); 8. *T. (S.) calva* Starý, 1999 (October - December); 9. *T. (S.) dahlae* Mendl, 1971 (end of September – November); 10. *T. (S.) implicata* Dahl, 1976 (November) 11. *T. (S.) maculipennis* Meigen, 1818 (February-May and October-November); 12. *T. (S.) parva* Meigen, 1804 (end of September - November); 13. *T. (S.) recondita* Starý 2000 (October - December); 14. *T. (S.) regelationis* (Linnaeus, 1758) (April – May, September - November); 15. *T. (S.) rufescens* Edwards, 1921 (September – November, single specimens in April); 16. *T. (S.) rufulenta* Edwards, 1938 (June - October); 17. *T. (S.) saltator* (Harris, 1776) (April – May, end of August – November); 18. *T. (S.) sparsa* Starý & Martinovský, 1996 (October - November); 19. *T. (S.) geigeri* Starý & Krzemińska, 2000 (October); 20. *Trichocera (Trichocera) hiemalis* (De Geer, 1776) (end of February – May, September – end of November) 21. *T. (T.) inexplorata* (Dahl, 1967) (October); 22. *T. (T.) major* Edwards, 1921 (September – December).

CONCLUSIONS

1. Both methods of equal and implied weighting yielded cladograms where clear groups formed by characters of male aedeagal complex, therefore these characters are considered a basis for distributing the species into subgenera.
2. Elaborate formations of male gonostyli are found in the species that ended up in all the subgenera during the phylogenetic analysis, so such formations must have developed independently several times.
3. The group of eight species (*T. chaetopyga*, *T. corallifera*, *T. crassicauda*, *T. forcipula*, *T. lutea*, *T. monstrosa*, *T. salmani* and *T. ursamajor*) with long parameres and very long and narrow lateral apodemes should be considered the core of subgenus *Metatrachocera* while enlarged male gonocoxites and elaborate formations of gonostyli are found in the species attributed to other subgenera and are not confined to this only subgenus.
4. Based on the performed analysis, seven species were transferred from subgenus *Metatrachocera* to subgenus *Saltrichocera* (*T. bifurcata*, *T. candida*, *T. cordata*, *T. glacialis*, *T. kotejai*, *T. ticina*, *T. truncata*), one species from *Metatrachocera* to *Trichocera* (*T. hypandrialis*) and seven more species from *Trichocera* to *Saltrichocera* (*T. arctica*, *T. arnaudi*, *T. auripennis*, *T. geigeri*, *T. idahoensis*, *T. tenuicercus*, *T. unimaculata*).
5. One new species of winter gnats – *Trichocera (Saltrichocera) sardiniensis* Petrašiūnas, 2009 – was described.
6. Structures important for identification of the species were illustrated for the first time for the females of four winter gnat species (*T. (S.) dahlae*, *T. (S.) candida*, *T. (S.) carpathica* and *T. (S.) truncata*) and male of *T. (S.) nipponensis* along with the type specimens of other fifteen species (*T. (S.) abieticola*, *T. (S.) arisanensis*, *T. (S.) auripennis*, *T. (S.) bellula*, *T. (S.) bisignata*, *T. (S.) glacialis*, *T. (S.) ocellata*, *T. (S.) percincta*, *T. (S.) punctipennis*, *T. (S.) reticulata*, *T. (S.) sapporensis*, *T. (S.) superna*, *T. (S.) szechwanensis*, *T. (S.) tenuicercus*, *T. (S.) variata*).
7. Nine winter gnat species new for the Lithuanian fauna were found and the total number of representatives of the family Trichoceridae in our country reached 22 species.

LIST OF PUBLICATIONS

Publications in editions included in the list of the Institute of Scientific Information (ISI):

- PETRAŠIŪNAS, A. 2006. New for Lithuania winter gnat (Diptera: Trichoceridae) species. *New and Rare for Lithuania Insect Species*, 17: 78-79. - ISSN 1648–8555.
- PETRAŠIŪNAS, A. 2008. Two winter gnat (Diptera: Trichoceridae) species new for the Lithuanian fauna. *New and Rare for Lithuania Insect Species*, 20: 56-57. - ISSN 1648–8555.
- PETRAŠIŪNAS, A. 2009. A new species of *Trichocera* Meigen (Diptera: Trichoceridae) from Sardinia. *Zootaxa*, 2108: 62-64. - ISSN 1175-5326 (print edition), ISSN 1175-5334 (online edition).
- PETRAŠIŪNAS, A. & VISARČUK, P. 2007. Updated checklist of Lithuanian winter gnats (Diptera: Trichoceridae). *Acta Zoologica Lituanica*, 17 (4): 276-280. - ISSN 1392-1657.

Conference abstracts:

- PETRAŠIŪNAS, A. 2008. Winter gnats (Diptera: Trichoceridae) in forensic entomology. *Proceedings of the sixth meeting of the European Association for Forensic Entomology*. Kolymbari/Crete. p.81.

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SANTRAUKA

Trichocera Meigen, 1803 genčiai šiuo metu priskiriama apie 110 rūšių, daugiausia paplitusių Holarktikoje (Hågvar & Krzemińska, 2007), bet kelios rūšys buvo įvežtos į kai kurias pietų Atlanto salas, Australiją (Dahl & Krzemińska, 1997). Didžiojoje šiaurės pusrutulio dalyje šios genties uodai aptinkami vėsaus, drėgno vidutinio klimato zonose rudens, žiemos ir pavasario mėnesiais. Suaugėliai paprastai laikosi turtinguose irstančios organikos biotopuose (Dahl & Krzemińska, 1997).

Ankstyvuojų žieminių uodų tyrimų laikotarpiu *Trichocera* genties atstovai dažniausiai buvo priskiriami įvairiems Tipulidae šeimos pošeimiams (Meigen, 1804; Latreille, 1809; (Rondani, 1856; Osten Sacken, 1869; Brunetti, 1911 ir kt), vėliau, daugiausia remiantis lervinių stadijų panašumu, buvo traktuojami kaip priklausantys Anisopodidae (tuo metu Rhyphidae) šeimai (Keilin, 1912; Bezzi, 1914; Alexander, 1921; 1924b), kol 1924 metais G. C. Crampton pateikė juos savarankiškoje Trichoceridae šeimoje.

Antroje XX amžiaus pusėje mokslininkai ėmėsi genčių ir pogenčių lygio klausimų. 1966 metais Dahl išskyrė naują *Metatrachocera* gentį, tipine rūšimi pasirinkdama *T. lutea* Becher, 1886 (Dahl, 1966a), o nominotipine *Trichocera* genties rūšimi liko *T. hiemalis* (De Geer, 1776). Visgi jau kitais metais po *Metatrachocera* genties paskelbimo, Alexander & Alexander (1967) traktavo ją kaip vieną iš dviejų *Trichocera* pogenčių, nors galutinai toks skirstymas bendrai pripažintas 1976 metais pasirodžiusiame „Pasaulio žieminių uodų kataloge“ (Dahl & Alexander, 1976).

Vėliau *Metatrachocera* pogentė pasirodė esanti parafiletinė, kai E. Krzemińska (1996) išsiaiškino, jog viena iš rūšių, *T. (M.) garretti* Alexander, 1927, yra savo edeaguso kompleksu artimesnė *Trichocera* pogentės rūšims. Sekdamas ta mintimi, Starý (1998b) pertvarkė gentį taip, kad *T. hiemalis* rūšių grupė buvo patalpinta nominotipinėje pogentėje *Trichocera*, o visos likusios rūšys, nepriklausomai nuo gonokoksitų ir gonostilių ypatybių, atsidūrė pogentėje *Metatrachocera*.

Aprašydami naujas rūšis iš Japonijos, Nakamura ir Saigusa (1997) atkreipė dėmesį, kad Dahl ir kitų autorių pateikti *Metatrachocera* apibrėžimai nėra tikslūs ir remiantis išoriniais patinų genitalinio aparato požymiais pogentei priskiriamos skirtingos kilmės rūšys. Siekdama atskirti rūšis, turinčias paprastus gonokoksitus nuo turinčių sudėtingus darinius, E. Krzemińska pasiūlė naują *Saltrichocera* pogentę, į kurią dalį rūšių įtraukė vadovaudamasi tik originaliais aprašymais (Krzemińska, 2002a), nors juose ir nebuvo jokių iliustracijų, kuriomis galima būtų patikimai remtis. Be to, į pogentes buvo suskirstytos ne visos žinomos žieminių uodų rūšys, taigi reikėjo atlikti išsamesnę skirstymo į pogentes analizę bei naujai aprašyti rūšis, kurių yra tik originalūs aprašymai be jokių požymių iliustracijų.

Nors ir žadėjusi atlikti filogenetinę *Trichocera* genties analizę (Krzemińska, 2002a), E. Krzemińska jokių rezultatų nepublikavo, taigi šios genties rūšių ryšiai liko nenagrinėti, skirtingai nuo *Nothotrichocera* genties (Krzemińska, 2001a) ar *Paracladurinae* (Krzemińska, 2005a) pošeimio rūšių.

Žieminiai uodai yra gana sudėtinga grupė rūšių apibūdinimo požiūriu ir Lietuvoje išsamiau nagrinėti buvo XX amžiaus pabaigoje (Valenta & Podėnas, 1985; Podėnas, 1989; 1991; 1993; 1995 ir kt.). Kiek vėliau, suintensyvėjus tyrimams kitose Europos šalyse, buvo aprašyta visa eilė naujų mokslui žieminių uodų rūšių, taigi atėjo metas ir Lietuvos faunos sudėties patikslinimui.

Globaliu mastu sparčiai nykstant gyvūnų rūšims, didelė jų dalis dingsta dar neaprašytos, mokslininkų neatrastos, todėl viena svarbiausių užduočių yra ir naujų mokslui rūšių aprašymas bei atskirų šalių faunos inventoriniai tyrimai

Darbo tikslas

Atlikti taksonominę ir filogenetinę genties *Trichocera* Meigen, 1803 apžvalgą

Uždaviniai:

1. Ištirti Lietuvoje gyvenančių *Trichocera* genties žieminių uodų rūšinę įvairovę;
2. Ištirti kuo didesnio rūšių skaičiaus tipinę medžiagą, tinkamai iliustruoti dar neaprašytas ar blogai aprašytas svarbias identifikacijai struktūras;
3. Sudaryti požymių filogenetinei analizei sąrašą bei atlikti pačią analizę;
4. Atlikti rūšių skirstymo į pogentes analizę.
5. Sudaryti recentinių *Trichocera* genties rūšių pasaulio faunos taksonominį katalogą.

Ginami teiginiai. 1. Nauja genties filogenijos ir klasifikacijos versija. 2. *Trichocera* genties patinų edeaguso komplekso ypatybės yra pagrindas priskiriant rūšis pogentėms. 3. *Trichocera* genties patinų genitaliniame aparate sudėtingi gonostilių dariniai išsivystė nepriklausomai kelis kartus, o iki šiol naudotas pogentės *Metatrichocera* Dahl, 1966 apibrėžimas nėra tikslus.

Darbo naujumas ir reikšmė. Atrasta ir aprašyta viena nauja mokslui žieminių uodų rūšis. Patikrinta 96 nagrinėtų rūšių taksonominė pozicija ir to pasėkoje 15 rūšių perskirstytos iš vienu pogenčių į kitas. Pirmą kartą atlikta filogenetinė genties *Trichocera* analizė, pateikta nauja genties filogenijos ir klasifikacijos versija.

Parengtas atnaujintas sisteminis *Trichocera* genties pasaulio faunos katalogas, kuriame susiteminti duomenys apie 110 recentines rūšis, jų biologiją, paplitimą, tipinių egzempliorių saugojimo vietas etc. Pirmą kartą tinkamai iliustruota tipinė 15 rūšių medžiaga, keturių rūšių patelių bei vienos rūšies patino svarbios identifikacijai struktūros. Sudarytas raktas kai kurioms pasaulyje aptinkamoms rūšims apibūdinti. Identifikuotos devynios naujos Lietuvos faunai žieminių uodų rūšys.

Naujai iliustruota tipinė medžiaga bei atskirų rūšių patelių bei patinų identifikacinės struktūros sudaro pagrindą imantis išsamesnių žieminių uodų tyrimų mažai tyrinėtuose kraštuose (Indija, Mongolija, kt.) bei leidžia tiksliai nustatyti konkrečias rūšis.

Žinios apie atskirų žieminių uodų rūšių aktyvumo laikotarpius gali būti praktiškai naudojamos teisminėje entomologijoje kai šaltuoju metų laiku irstančiuose kūnuose gali būti aptinkamos tik žieminių uodų lervinės stadijos.

Tyrimų duomenys papildė žinias apie Lietuvos entomofauną ir galės būti panaudojami atnaujinant leidinį „Lietuvos dvisparnių katalogas“. Sukaupta nemaža žieminių uodų kolekcija iš įvairių pasaulio šalių (tame tarpe keliolika paratipų) padidino Vilniaus universiteto Zoologijos muziejaus (MZVU), kuriame jie yra saugomi, mokslinę vertę.

Išvados:

1. Vienodo sureikšminimo bei numanomo sureikšminimo būdais gautose kladogramose aiškios grupės susiformavo pagal patinų edeaguso komplekso ypatybes, todėl jos ir laikytinos pagrindiniais požymiais skirstant rūšis į pogentes.
2. *Trichocera* genties patinų genitaliniame aparate sudėtingi gonostilių dariniai stebimi rūšyse, priskirtose visoms trimis pogentėms, taigi jie išsivystė nepriklausomai kelis kartus.
3. 8 rūšių grupė (*T. chaetopyga*, *T. corallifera*, *T. crassicauda*, *T. forcipula*, *T. lutea*, *T. monstrosa*, *T. salmani* ir *T. ursamajor*), turinti ilgus lenktus paramerus bei ilgas ir siauras lateralines apodemas, turėtų būti laikoma sudarančia *Metatrachocera* pogentę, o stori gonokoksitai ir sudėtingi gonostiliai nėra vien šios pogentės požymiai.
4. Remiantis atlikta filogenetine analize, septynios rūšys perkeltos iš *Metatrachocera* pogentės į *Saltrichocera* pogentę (*T. bifurcata*, *T. candida*, *T. cordata*, *T. glacialis*, *T. kotejai*, *T. ticina*, *T. truncata*), viena rūšis iš *Metatrachocera* į *Trichocera* (*T. hypandrialis*) bei dar septynios rūšys iš *Trichocera* į *Saltrichocera* pogentę (*T. arctica*, *T. arnaudi*, *T. auripennis*, *T. geigeri*, *T. idahoensis*, *T. tenuicercus*, *T. unimaculata*).
5. Aprašyta nauja mokslui žieminių uodų rūšis – *Trichocera* (*Saltrichocera*) *sardiniensis* Petrašiūnas, 2009.
6. Pirmą kartą iliustruotos 4 žieminių uodų rūšių patelės - *T. (S.) dahlae*, *T. (S.) candida*, *T. (S.) carpathica* ir *T. (S.) truncata*, iliustruotas *T. (S.) nipponensis* rūšies patinas bei 15 rūšių tipiniai egzemplioriai (*T. (S.) abieticola*, *T. (S.) arisanensis*, *T. (S.) auripennis*, *T. (S.) bellula*, *T. (S.) bisignata*, *T. (S.) glacialis*, *T. (S.) ocellata*, *T. (S.) percincta*, *T. (S.) punctipennis*, *T. (S.) reticulata*, *T. (S.) sapporensis*, *T. (S.) superna*, *T. (S.) szechwanensis*, *T. (S.) tenuicercus*, *T. (S.) variata*).
7. Identifikuotos 9 naujos Lietuvos faunai žieminių uodų rūšys, o bendras mūsų šalyje aptinkamų Trichoceridae šeimos uodų rūšių skaičius pasiekė 22.

CURRICULUM VITAE

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Education:

1996-2000 B. Sc., Biology (Ecological biology), Vilnius university
2000-2002 M. Sc., Biology (Zoology), Vilnius university
2005-2009 Ph.D. studies, Zoology, Department of Zoology, Faculty of Natural Sciences, Vilnius university

Study visits:

17–22 March, 2008 Natural History Museum, Wien, Austria.
2–30 June, 2008 Natural History Museum, London, Great Britain, through the EU SYNTHESYS grant „Evaluation of morphological features of genus *Trichocera* (Diptera: Trichoceridae) for later use in phylogenetic analysis“ (GB-TAF-4047).
17–24 November, 2008 Zoological Institute of Russian Academy of sciences, St. Petersburg, Russia
24 January - 4 February, 2009 J. Starý personal collection, Olomouc, The Czech Republic
4–8 April, 2009 Institute of Systematics and Evolution of Animals Polish Academy of Sciences, Krakow, Poland

Employment:

September 2001 - June 2002 Computer classroom supervisor, Faculty of Natural Sciences, Vilnius university
July 2002 - May 2004 Manager, “Gritpėdžiai ir ko“
October 2004 - August 2007 Laboratory assistant, Department of Zoology, Faculty of Natural Sciences, Vilnius university
September 2007 - Lecturer, Department of Zoology, Faculty of Natural Sciences, Vilnius university