Difficulties in building a molecular phylogeny of the issidoid planthopper lineages (Insecta: Hemiptera: Fulgoroidea)

V. M. Gnezdilov[1], Th. Bourgoin[2], F. Mozaffarian[3&*] and S. Manzari[3]

1. Zoological Institute, Russian Academy of Sciences, Universitetskaya nab.1, 199034, St. Petersburg, Russia, vmgnezdilov@mail.ru, vgnezdilov@zin.ru 2. UMR-7205 (ISYEB) MNHN-CNRS-UPMC-EPHE, Muséum National d'Histoire Naturelle, Sorbonne Universités, CP50, 57 rue Cuvier, F-75231 Paris cedex 5, France, bourgoin@mnhn.fr 3. Insect Taxonomy Research Department, Iranian Research Institute of Plant Protection, Agricultural Research, Education and Extension Organization (AREEO), Tehran, Iran, manzari@iripp.ir

*Corresponding author, E-mail: mozaffarian@iripp.ir, faribamozaffarian@gmail.com

Abstract

Four gene loci COI, 28S (D4D5 and 28SD6), and 18S (helix 17 up to helix 50) were sequenced successfully for 32 (COI), 29 (18S) and 30 (28S) species from a sampling of 36 species representing 29 genera of the families Issidae, Caliscelidae, Tropiduchidae, Nogodinidae, Ricaniidae, Dictyopharidae, Flatidae and Aphrophoridae. Analysis of the resulting molecular phylogenies shows a low support of the results presented, probably due to genes and species sampling bias not enough representative of diversity and evolution of issidoid lineages. While Issidae monophyly is not clearly recovered, monophyly of Western Palaearctic issid genera and Caliscelidae respectively seems well supported; however genus *Bubastia* Emeljanov appears to be polyphyletic and several other issid genera remain unplaced. The positions of some "problematic" taxa like the genera *Lollius* Stål, *Colpoptera* Burmeister and *Bladina* Stål are still unclear on the molecular trees and needs further study.

Key words: Issidae, Issina, Hysteropterina, Tropiduchidae, Caliscelidae, Caliscelini, Peltonotellini, Trienopini, Trypetimorphini, phylogeny, molecular sequence, Western Palaearctic

چکیده

مشکلات تهیه درخت تبارشناسی مولکولی زنجرک‌های رگه issidoid (Insecta: Hemiptera: Fulgoroidea)

ولادمیر گنزدیلف، تییغی بوغگوان، فریبا مظفریان و شهاب منظری

چهار ژن COI، 28S (D4D5 و D6) و 18S (helix 17 تا helix 50) به ترتیب برای ۳۲، ۲۹ و ۳۰ گونه با موفقیت توالی‌یابی شدند. این گونه‌ها به یک مجموعه ۳۶ گونه‌ای از ۲۹ جنس در خانواده‌های Issidae، Caliscelidae، Tropiduchidae، Nogodinidae، Ricaniidae، Dictyopharidae، Flatidae و Aphrophoridae تعلق داشتند. تحلیل تبارشناسی ملکولی نشان‌دهنده تأیید اندک نتایج است که احتمالاً به دلیل کم بودن تعداد جنس‌ها و گونه‌های مورد استفاده برای رگه Issidoid می‌باشد. تک‌نیا بودن خانواده Caliscelidae و همچنین جنس‌های غرب پالئارکتیک از خانواده Issidae تأیید شد، ولی این مساله در مورد کل خانواده Issidae اثبات نشد. جنس *Bubastia* Emeljanov به عنوان یک جنس چندنیایی نشان داده شد و جایگاه تعدادی دیگر از جنس‌های این خانواده روشن نشد. موقعیت بعضی تاکسون‌های مشکل‌زا مانند *Lollius* Stål، *Colpoptera* Burmeister و *Bladina* Stål در درخت تبارشناسی مولکولی همچنان نامشخص باقی ماند که نیازمند مطالعه بیشتر می‌باشد.

واژگان کلیدی: Issidae، Issina، Hysteropterina، Tropiduchidae، Caliscelidae، Caliscelini، Peltonotellini، Trienopini، Trypetimorphini، فیلوژنی، توالی مولکولی، غرب پالئارکتیک

Introduction

The classification of family Issidae Spinola, 1839, "*sensu lato*", as it was previously known (Melichar, 1906; Fennah, 1954; Metcalf, 1958) has been intensively modified since R.G. Fennah's attempts (Fennah, 1978, 1982). Major changes were the recognition of Acanaloniidae Amyot et Serville, 1843 and Caliscelidae Amyot et Serville, 1843, as separate families (Emeljanov, 1999, 2008; Gnezdilov, 2008a, 2012b, 2013c), the restriction of Issidae to only three tribes: Issini Spinola, 1839, Hemisphaeriini Melichar, 1906, and Parahiraciini Cheng et Yang, 1991 (Gnezdilov, 2009, 2013d) and the transfer of several sub-units to other families: Tropiduchidae (Trienopinae Fennah and Gaetuliina Fennah), Nogodinidae (Tonginae Kirkaldy and Colpopterini Gnezdilov), Ricaniidae (Pharsalinae Gnezdilov), and Caliscelidae (Adenissini Dlabola) (Gnezdilov, 2003a, b, 2007, 2008b, 2009; Gnezdilov & Wilson, 2006).

Distinguishing all these major issidoid lineages is currently built on morphological characters of male and female genitalia structure (Fennah, 1982; Emeljanov, 1999; Gnezdilov, 2003a, 2008b, 2012b, 2013b).

Most of them belong to the "issidoid group" which was recently established by Gnezdilov (2013a) to include five Fulgoroidea families: Issidae Spinola, 1839, Acanaloniidae Amyot et Serville, 1843, Caliscelidae Amyot et Serville, 1843, Nogodinidae Melichar, 1898, and Tropiduchidae Stål, 1866. Currently, this grouping remains a practical one and is not claimed to represent any monophyletic natural taxon as clearly based on parallel adaptative radiations to sub-arid and arid

landscapes with so-called Mediterranean type of vegetation leading to an issidoid habitus (issidisation) (Gnezdilov, 2013a): a box-like body shape, sub- or fully brachypterous forms.

In this study we aim to provide the first investigation about the phylogenetic relationships among these lineages and among the genera of the family Issidae "*sensu stricto*", and to test their monophyly on a molecular base. Moreover, because some of the major taxa analysed belong to different families, it will also give the opportunity to address the higher classification of the Fulgoromorpha in relation with classical studies (Asche, 1988; Emeljanov, 1991; Bourgoin *et al*., 1997) and more recent (Yeh *et al*., 1998, 2005; Urban & Cryan, 2007) on planthopper phylogeny.

Materials and methods

Taxon sampling

Specimens were collected from different parts of the world (Table 1) and preserved in absolute ethanol until molecular analyses. The specimens studied are deposited in the following museums:

BMNH – the Natural History Museum, London, United Kingdom;
CASC – California Academy of Sciences, San Francisco, USA;
MNHN – Museum national d'Histoire naturelle, Paris, France ;
ZIN – Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia.

DNA extraction, amplification and sequencing

DNA was extracted from single specimens using the DNeasy Tissue Kit (Qiagen) according to the manufacturer's *protocol with slight modification*, i.e. elution in 50 or 100 µl buffer AE (instead of 200 µl) depending on the size of the specimen. Extraction, sequencing protocol and primers follow Ceotto *et al*. (2008) and were conducted in MNHN and CBGP (INRA Montpellier).

Genes COI, 28S (D4-D5 and D6), 18S (helix 17 up to helix 50), were sequenced successfully for 32 (COI), 29 (18S) and 30 (28S) species) respectively. Sequences will be deposited in the NCBI GenBank.

Phylogenetic Analyses

The numbers of base pairs for amplified regions were as follow: COI: 602 to 666 bp, 28S, D4-D5 regions: 630 to 651 bp, 28S, D6 region: 668 to 741 bp, 18S: 775 to 1407 bp. The sequences were aligned using full multiple alignment option implemented in BioEdit version 7.2.5 programme (Hall, 1999) and then checked by eye and manipulated if necessary. The alignment performed for COI were checked in three frames by translating to amino acids (Artimo *et al*., 2012) to be sure the sequences of amino acids were not affected by dashes. The aligned sequences were appended and organized in three different data sets for analyses: (i) 28S, (D4-D5 and D6) and 18S (Helix 17 up to Helix 50) sequences for all taxa sampled (ii) plus the Cytochrome Oxidase I sequences, (iii) same as (ii) but restricted to Western Palaearctic species of Issidae. Parsimony analyses were conducted on the three datasets using PAUP* (Swofford, 1998). Heuristic searches were performed with 20000 random additions followed by branch swapping using tree-bisection-reconnection (TBR) holding a single tree. Gaps were treated as missing data. Bootstrap support was calculated using 1000 pseudoreplicates each of 1000 random additions.

Results

According to fig. 1 which is resulted from data set (i):

1. Issidae *s. str.* are divided into two clusters – Hysteropterina sensu Gnezdilov (2002) + *Thionia* St*å*l and Issina sensu Gnezdilov (2002) + *Hemisphaerius* Schaum (as a sister group to Issina).

2. The genus *Bubastia* Emeljanov appears to be a polyphyletic unit as *Bubastia ephialtes* Linnavuori and *B. taurica* Kusnezov fall in different clusters. Subgenus *Bubastia s. str.* (with type species *B. taurica*) falls in a sister position to the genus *Hysteropterum* Amyot et Serville.

3. *Hemisphaerius* is a sister group to subtribe Issina (bootstrap value is 58) which is separated from the Hysteropterina within Issidae, however its status is not clear and still would have to be confirmed.

4. *Thionia* is placed in the cluster of Hysteropterina. At the moment this may be treated as supporting the synonymy of Issini Spinola, 1939 and Thioniini Melichar, 1906 proposed by Gnezdilov (2009), but it does not mean that *Thionia* have to be placed within Hysteropterina.

5. *Colpoptera* previously placed in the Issidae (Gnezdilov, 2003b) is excluded from this family. It supports its possible placement within Nogodinidae as proposed by Gnezdilov (2012a).

6. Caliscelidae is a monophyletic group with a bootstrap value 98. Caliscelini and Peltonotellini are separated within Caliscelidae.

7. Trienopini is a sister group to Trypetimorphini (bootstrap value is 79).

8. Madagascan subbrachypterous ricanid *Nasatus* Stroinski, Gnezdilov & Bourgoin appears in a sister position to *Ricania* Germar (bootstrap value is 81).

9. The monophyly of Nogodinidae is not confirmed.

10. The clade of Issidae is proposed as a sister group to the clade Tropiduchidae+(Ricaniidae+Flatidae).

Two results remain problematic: separated position of *Kervillea conspurcata* (Spinola) from other Hysteropterina and paraphyletic Flatidae (*Metcalfa pruinosa* (Say) and *Phantia christophi* Rusiecka).

II. In all various dataset tested (figs 1-3), the monophyletic origin of Western Palaearctic fauna of the family Issidae is confirmed.

Discussion

Subtribes Issina Spinola, 1839 and Hysteropterina Melichar, 1906 are confirmed as monophyletic groups, except of the strange distinctive position of *Kervillea conspurcata* on fig. 1, while on figs 2 and 3 it is in frame of Hysteropterina. Two studied species of the genus *Bubastia*, *B. ephialtes* and *B. taurica,* are separated in different clusters which is in accordance with morphological structure of male genitalia (Gnezdilov, unpublished) showing we have in fact different taxa. In all our results and tests, Western Palaearctic Issidae monophyletic origin is supported. This is very important thesis for further study of evolution of the Issidae as a whole and the faunogenesis of Western Palaearctic region in particular.

The monophyly and 3-tribes composition of the family Issidae *s. str.* suggested by Gnezdilov (2009, 2013d) is not fully supported by the current results, as we had no any Parahiraciini involved, but obtained in the molecular analysis of Sun *et al*. (2015) except for the position of the Tongini Kirkaldy which might be an artefact. An interesting result of Sun *et al*. (2015) analysis is the suggestion of the sister-group relationships of Parahiraciini and Hemisphaeriini. Moreover, Caliscelidae isolated position from the Issidae in Sun *et al*.'s phylogeny (2015) still support them as a separate family as their position within Issidae is not tested in Sun *et al.*'s analysis.

Caliscelidae is a monophyletic group with possible separation of Caliscelini and Peltonotellini within Caliscelinae (fig. 1) as proposed by Emeljanov (2008). In Urban & Cryan's phylogeny the Caliscelidae is presented as a most recent group. However, current fauna of New World Caliscelidae is represented by one tribe, Peltonotellini Emeljanov (Gnezdilov, 2013c), a probable monophyletic group evolved from one Palaearctic ancestor recently (Gnezdilov, 2015). It is suspected that the use of Old World Caliscelini or Ommatidiotinae in those analyses might have provided a different result.

As in previously published molecular phylogeny of Fulgoroidea (Urban & Cryan, 2007), Tropiduchidae sensu Gnezdilov (2013b) including Elicinae (=Gaetuliina) and Tropiduchinae would be a monophyletic group, but more tropiduchid taxa should be included to confirm this result.

Nogodinidae in its current treatment (Gnezdilov, 2009, 2012a) is possibly a polyphyletic group, which is in agreement with Urban and Cryan's results (2007). Emeljanov (1991) did not find any autapomorphies for the families Nogodinidae and Issidae sensu lato. In his scheme, Flatidae and Ricaniidae are sister groups which is in agreement with the results of the current study (figs 1, 3).

Following Yeh *et al*. (2005) and according to Gnezdilov (2013a) the relationships between the families of issidoid group of Fulgoroidea families is one of the most difficult problems in current planthopper systematics and cannot be precisely defined now.

Table 1. Geographical information of the studied species.

Species name	**Locality**
Issidae *: Scorlupaster asiaticum* (Lethierry, 1878)	Southern Kazakhstan, 42º50´20.724´´N 71º10´12.900´´E, 29.VII.2006, V.M. Gnezdilov leg.
Issidae *: Agalmatium flavescens* (Olivier, 1791)	Italy, Tuscany, Livorno Province, Castellaccio vill., 6.IX.2004, V.M. Gnezdilov leg.
Issidae: *Agalmatium bilobum* (Fieber, 1877)	Central Mount Lebanon, near to Qartaba, 1000–1200m, VII. – VIII. 2004, H. Abdul-Nour leg.
Issidae *: Latilica maculipes* (Melichar, 1906)	Italy, Tuscany, Livorno Province, Castellaccio vill., 6.IX.2004, V.M. Gnezdilov leg.
Issidae *: Issus abdulnouri* Dlabola, 1987	Central Mount Lebanon, near to Qartaba, 1000–1200m, VII. – VIII. 2004, H. Abdul-Nour leg.
Issidae: *Issus coleoptratus* (Fabricius, 1781)	Slovenia, near Nova Gorica, 46º00´17.8´´N 13º040´40.0´´E, 300 m, 03.VII.2004,G. Seljak leg.
Issidae *: Mycterodus phoenicicus* Gnezdilov, 2008	Central Mount Lebanon, near to Qartaba, 1000–1200m, VII. – VIII. 2004, H. Abdul-Nour leg.
Issidae *: Libanissum talhouki* (Dlabola, 1974)	Central Mount Lebanon, near to Qartaba, 1000–1200m, VII. – VIII. 2004, H. Abdul-Nour leg.
Issidae *: Bubastia ephialtes* (Linnavuori, 1971)	Central Mount Lebanon, near to Qartaba, 1000–1200m, VII. – VIII. 2004, H. Abdul-Nour leg.
Issidae *: Bubastia obsoleta* (Fieber, 1877)	Slovenia, Nova Gorica, 25.V.2004, G. Seljak leg.
Issidae *: Bubastia taurica* (Kusnezov, 1926)	Russia, Krasnodar Territory, 2 km WNW of Gelendzhik, near Golubaya Bukhta vill., Doob Mt., 30.VII.2004, V.M. Gnezdilov leg.
Issidae *: Latissus dilatatus* (Fourcroy, 1785)	Slovenia, Nova Gorica, 45º59´31.6´´N 13º39´39´´E, 320 m, 03.VII.2004,G. Seljak leg.
Issidae *: Kervillea conspurcata* (Spinola, 1839)	Slovenia, Črnotiče, 30.V.2004, G. Seljak leg.
Issidae *: Hysteropterum reticulatum* (Herrich-Schaeffer, 1835)	Slovenia, Ravnica, 06.VI.2004, G. Seljak leg.
Issidae *: Hysteropterum vasconicum* Gnezdilov, 2003	Spain, Espot, 15.VI.2004, A. Maryańska-Nadachowska leg.
Issidae *: Hemisphaerius* sp. (Laos)	Laos, Région de Phongsaly, Long Nai Mai, forêt primaire, 21˚14.243' N 101˚54.448' E, 918 m, 01.X.2004, A. Soulier-Perkins leg.

Issidae *: Thionia* sp.	Panama, 22.IX.2006, canopée, D. Ouvrard leg.
Issidae *: Kodaianella bicinctifrons* Fennah, 1956	Laos, Région de Phongsaly, Long Nai Mai, forêt primaire, 21˚14.243' N 101˚54.448' E, 918 m, 01.X.2004, A. Soulier-Perkins leg.
Nogodinidae *: Colpoptera* sp.	Panama, 23.IX.2006, D. Ouvrard leg.
Nogodinidae: *Bladina* sp.	Panama, 24.IX.2006, D. Ouvrard leg.
Nogodinidae *: Lollius* sp.	Vanuatu, Santo I., Camp 2, Mont Tabwémasana, forêt, 15º20´38.9´´ S 166º44´41.4´´ E, 1065 m, 04.XI.2006, A. Soulier-Perkins & M. Attié leg.
Acanaloniidae *: Acanalonia* sp.	Panama, 25.IX.2006, canopée, D. Ouvrard leg.
Tropiduchidae *: Trienopa* sp. 1	Madagascar, Région Atsimo-Andrefana, Parc de Zombitse, zone sèche de la forêt de ?, 22º53.406´S 44º41.819´E, 817 m, 18.III.2006, A. Soulier-Perkins leg.
Tropiduchidae *: Trienopa* sp. 2	Madagascar, Région Amoron ï Mania, Forêt d'Ankazomivati à 35 km d'Ambositra, forêt d'altitude semi décidue, 20º47.002´S 47º10.964´E, 984 m, 24.III.2006, A. Soulier-Perkins leg.
Tropiduchidae *: Trypetimorpha occidentalis* Huang & Bourgoin, 1993	Northern Kazakhstan, 6 km W of Semiozernoe, 52º21´58.932´´N 64º00´37.116´´E, 17.VIII.2006, V.M. Gnezdilov leg.
Caliscelidae *: Caliscelis wallengreni*	Slovenia, Koper, 45º33´05.7´´N 13º45´41.2´´E, 24.IX.2005, G. Seljak leg.
Caliscelidae *: Peltonotellus quadrivittatus* (Fieber, 1876)	Slovenia, Opatje selo, 30.V.2004, G. Seljak leg.
Caliscelidae: *Peltonotellus melichari* Horváth, 1897	Slovenia, near Nova Gorica, 45º58´40.3´´N 13º41´41´´E, 410 m, xerothermic meadow, 03.VII.2004, G. Seljak leg.
Caliscelidae: *Afronaso gryphus* Gnezdilov & Bourgoin, 2009	Madagascar, Fianarantsoa Province, Parc National d'Andringitra, Plateau d'Andohariana, 35.9 km 205˚ Ambalavao, 22˚09´08´´ S 046˚53´57´´ E, 2000 m, 15.IV.2006, maxi winkler litter extraction in ericoid thicket, B.L. Fisher leg.
Caliscelidae: *Calampocus sphaeroides* Gnezdilov & Bourgoin, 2009	Madagascar, Fianarantsoa Province, Parc National d'Isalo Ambovo Springs, 29.3 km 4˚ N Ranohira, 22˚17´54´´ S 045˚21´06´´ E, 990 m, pitfall trap in Hapaca woodland, 9–14.II.2003, Fisher, Griswold *et al*. leg.
Ricaniidae: *Nasatus davidouvrardi* Stroinski, Gnezdilov et Bourgoin, 2011	Madagascar, RN4 entre Antananarivo et Mahajanga, fôret galerie de plateaux, près Mahatsinjo, 17º52.869´S 47º04.684´E, 1500 m, 08.XI.2005, Th. Bourgoin, A. Soulier-Perkins, D. Ouvrard & M. Attié leg.
Ricaniidae: *Ricania japonica* Melichar, 1898	Russia, Krasnodar Territory, 2 km WNW of Gelendzhik, near Golubaya Bukhta vill., Doob Mt., 30.VII.2004, V.M. Gnezdilov leg.
Flatidae *: Phantia christophi* Rusiecka, 1902	Southern Kazakhstan, Peski Mujunkum, 43º00´00.924´´N 72º06´05.112´´E, 30.VII.2006, V.M. Gnezdilov leg.
Flatidae: *Metcalfa pruinosa* (Say, 1830)	Italy, Tuscany, Livorno Province, Castellaccio vill., 6.IX.2004, V.M. Gnezdilov leg.

Dictyopharidae: *Dictyophara europaea* (Linnaeus, 1767)	Russia, Krasnodar Territory, near Gelendzhik, 27.VII.2004, V.M. Gnezdilov leg.
Aphrophoridae *: Lepyronia coleoptrata* (outgroup)	Central Mount Lebanon, near to Qartaba, 1000–1200m, VII. – VIII. 2004, H. Abdul-Nour leg.

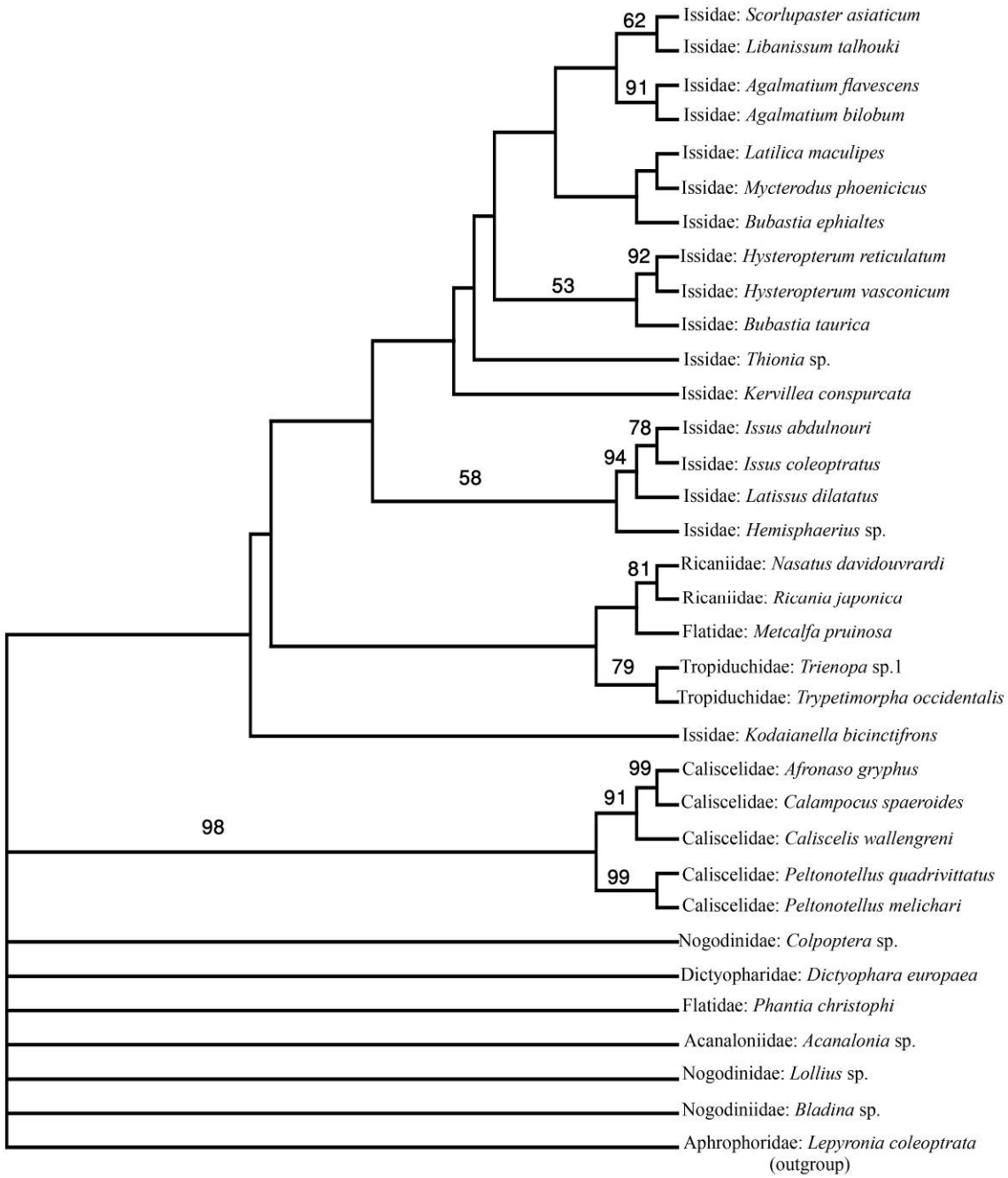

Fig. 1. Strict consensus tree resulted from the analysis of the sequences in regions18S, 28S. The range of bootstrap values (more than 50%) is written above branches. (Tree length: 1991, Consistency index (CI): 0.6801, Retention index (RI): 0.4863, number of trees: 27).

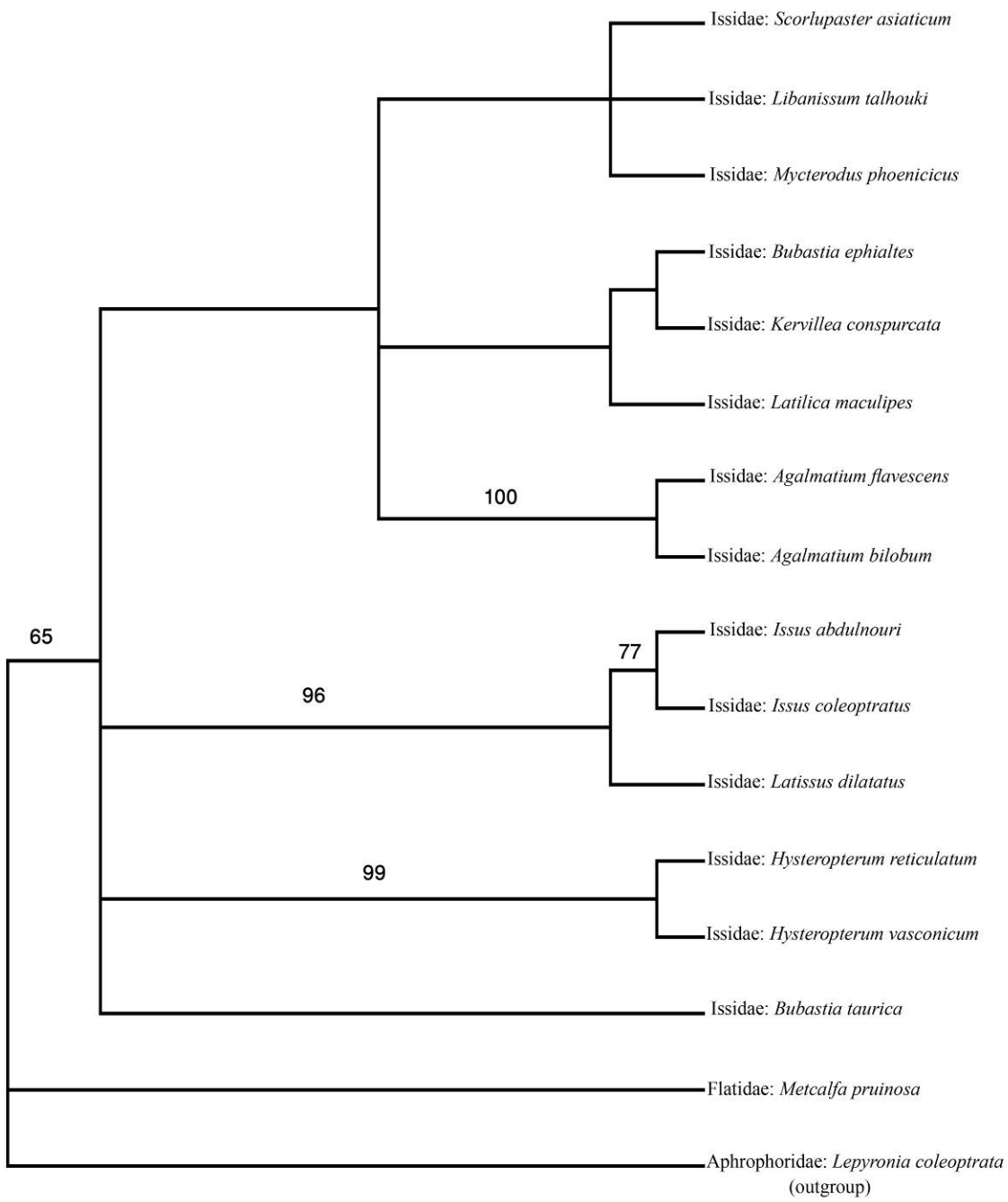

Fig. 2. Strict consensus tree resulted from the analysis of the sequences in regions COI, 18S, 28S on Western Palaearctic Issidae. The range of bootstrap values (more than 50%) is written above branches. (Tree length: 2122, Consistency index (CI): 0.6857, Retention index (RI): 0.3568, number of trees: 2).

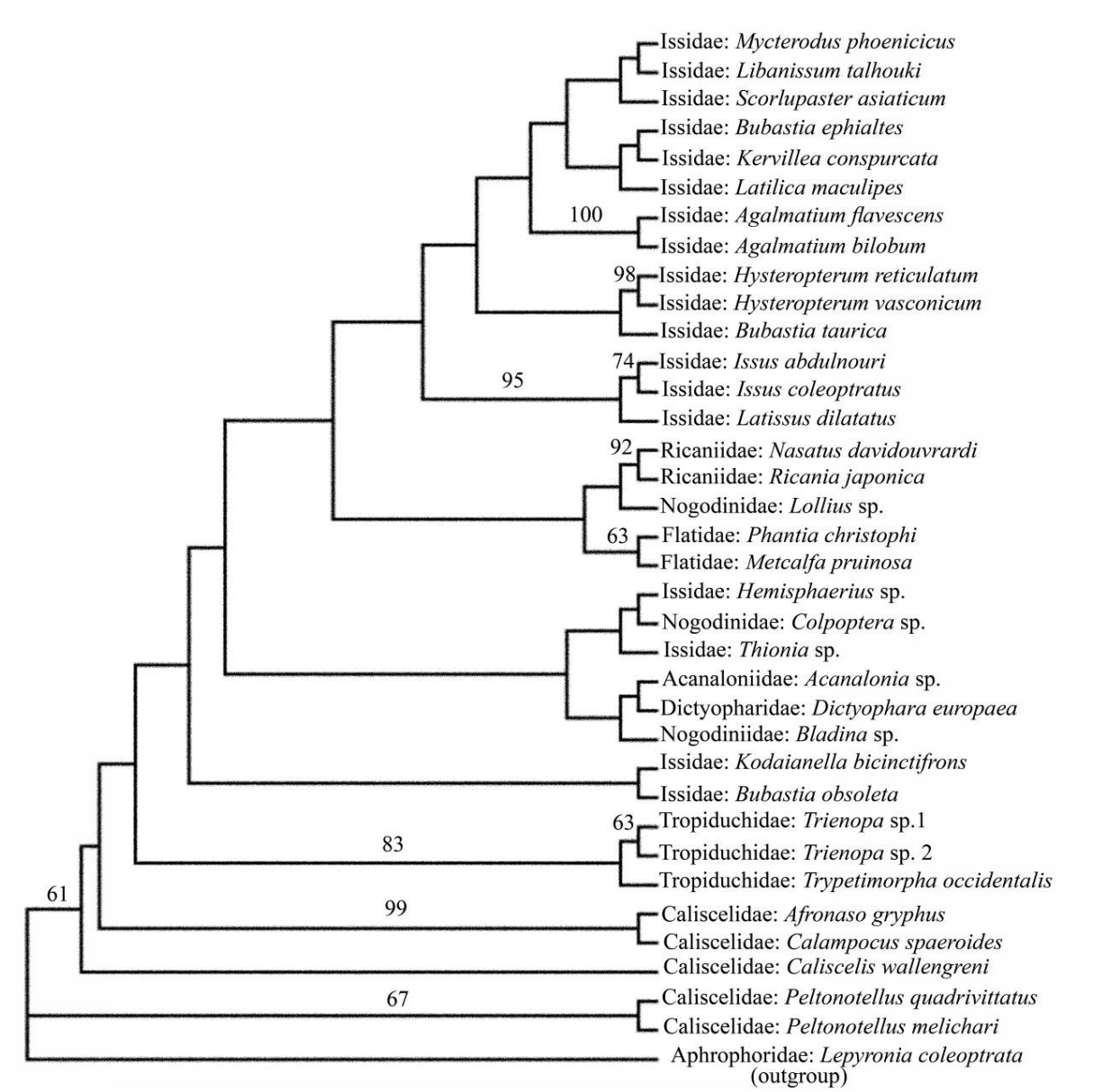

Fig. 3. Strict consensus tree resulted from the analysis of the sequences in regions COI, 18S, 28S. The range of bootstrap values (more than 50%) is written above branches. (Tree length: 4540, Consistency index (CI): 0.4907, Retention index (RI): 0.454, number of trees: 1).

References

Artimo, P., Jonnalagedda, M., Arnold, K., Baratian, D., Csardi, G., de Castro, E., Duvaud, S., Flege., V., Fortier, A., Gasteiger, E., Grosdidier, a., Hernandez, C., Ioannidis, V., Kuznetsov, D., Liechti, R., Moretti, S., Mostaguir, K., Redaschi, N., Rossier, G., Xenarios, I. & Stochinger, H. (2012) ExPASy: SIB bioinformatics resource portal. *Nucleic Acids Research* 40(W1),W597–W603.

Asche, M. (1988) Preliminary thoughts on the phylogeny of Fulgoromorpha (Homoptera : Auchenorrhyncha). *Proceedings of the 6th International Auchenorrhycnha Meeting, Turin, Italy, University of Turin Press* 47–53.

Ceotto, P., Kergoat, G.J., Rasplus, J-Y & Bourgoin, T. (2008) Molecular phylogenetics of cixiid planthoppers (Hemiptera: Fulgoromorpha): new insights from combined analyses of mitochondrial and nuclear genes. *Molecular Phylogenetics and Evolution* 48, 667-678.

Bourgoin, T., Steffen-Campbell, J.D. & Campbell, B.C. (1997) Molecular phylogeny of Fulgoromorpha (Insecta, Hemiptera, Archaeorrhyncha). The enigmatic Tettigometridae: evolutionary affiliations and historical biogeography. *Cladistics* 13, 207-224.

Emeljanov, A. F. (1991) An attempt of construction of phylogenetic tree of the planthoppers (Homoptera, Cicadina). *Entomologicheskoe Obozrenie* 69(2), 353–356. English translation published in *Entomological Review* 70(1), 24–28.

Emeljanov, A. F. (1999) Notes on delimitation of families of the Issidae group with description of a new species of Caliscelidae belonging to a new genus and tribe (Homoptera, Fulgoroidea). *Zoosystematica Rossica* 8(1), 61–72.

Emeljanov, A. F. (2008) New species of the genus *Peltonotellus* Puton (Homoptera, Caliscelidae) from Kazakhstan, Middle and Central Asia. *Tethys Entomological Research* 16, 5–12. (In Russian with English summary).

Fennah, R. G. (1954) The higher classification of the family Issidae (Homoptera: Fulgoroidea) with descriptions of new species. *Transactions of the Royal Entomological Society of London* 105(19), 455–474.

Fennah, R. G. (1978) The higher classification of the Nogodinidae (Homoptera, Fulgoroidea) with the description of a new genus and species. *Entomologist's Monthly Magazine* 113, 113–119.

Fennah, R. G. (1982) A tribal classification of the Tropiduchidae (Homoptera: Fulgoroidea), with the description of a new species on tea in Malaysia. *Bulletin of Entomological Research* 72(4), 631–643.

Gnezdilov, V. M. (2002) Morphology of the ovipositor in members of the subfamily Issinae (Homoptera, Cicadina, Issidae). *Entomologicheskoe obozrenie* 81(3), 605–626. English translation published in *Entomological Review* (2004), 82(8), 957–974.

Gnezdilov, V. M. (2003a) Review of the family Issidae (Homoptera, Cicadina) of the European fauna, with notes on the structure of ovipositor in planthoppers. *Chteniya pamyati N.A. Kholodkovskogo (Meetings in memory of N.A. Cholodkovsky), St. Petersburg* 56(1), 1–145. (In Russian with English summary).

Gnezdilov, V. M. (2003b) A new tribe of the family Issidae (Homoptera, Cicadina) with comments on the family as a whole. *Zoosystematica Rossica* 11(2), 305–309.

Gnezdilov, V. M. (2007) On the systematic positions of the Bladinini Kirkaldy, Tonginae Kirkaldy, and Trienopinae Fennah (Homoptera, Fulgoroidea). *Zoosystematica Rossica* 15(2), 293–297.

Gnezdilov, V. M. (2008a) To the taxonomy of higher Fulgoroidea (Hemiptera). *Bulletin of Insectology* 61(1), 119–120.

Gnezdilov, V. M. (2008b) On the taxonomy of the tribe Adenissini Dlabola (Hemiptera: Fulgoromorpha: Caliscelidae: Ommatidiotinae), with the description of a new genus and a new species from Vietnam. *Acta Entomologica Slovenica* 16(1), 11–18.

Gnezdilov, V. M. (2009) Revisionary notes on some tropical Issidae and Nogodinidae (Hemiptera: Fulgoroidea). *Acta Entomologica Musei Nationalis Pragae* 49(1), 75–92.

Gnezdilov, V. M. (2012a) Revision of the tribe Colpopterini Gnezdilov, 2003 (Homoptera, Fulgoroidea, Nogodinidae). *Entomologicheskoe obozrenie* 91(4), 757–774. English translation published in *Entomological Review* (2013), 93 (3), 337–353.

Gnezdilov, V. M. (2012b) On the composition and distribution of the family Acanaloniidae Amyot et Serville (Homoptera, Fulgoroidea). *Entomologicheskoe obozrenie* 91(3), 643–647. English translation published in *Entomological Review* (2013), 93 (1), 69–72.

Gnezdilov, V. M. (2013a) Issidisation of fulgoroid planthoppers (Homoptera, Fulgoroidea) as an evidence of parallel adaptive radiation. *Entomologicheskoe obozrenie*, 92(1), 62–69. English translation published in *Entomological Review* (2013), 93(7), 825–830.

Gnezdilov, V. M. (2013b) Contribution to the taxonomy of the family Tropiduchidae Stål (Hemiptera, Fulgoroidea) with description of two new tribes from Afrotropical Region. *Deutsche Entomologische Zeitschrift* 60(2), 179–191.

Gnezdilov, V. M. (2013c) Modern system of the family Caliscelidae Amyot et Serville (Homoptera, Fulgoroidea). *Zoologichesky Zhurnal*, 92(10), 1309–1311. English translation published in *Entomological Review*, (2014), 94(2), 211–214.

Gnezdilov, V. M. (2013d) Modern classification and the distribution of the family Issidae Spinola (Homoptera, Auchenorrhyncha, Fulgoroidea). *Entomologicheskoe obozrenie* 92(4), 724–738. English translation published in *Entomological Review*, (2014), 94(5), 687–697.

Gnezdilov, V. M. (2015) A new genus and new species of the family Caliscelidae (Hemiptera: Auchenorrhyncha: Fulgoroidea) from Thailand with notes on evolution of the family. *Proceedings of the Zoological Institute RAS* 319(1), 120–125.

Gnezdilov, V. M. & Wilson, M. R. (2006) Systematic notes on tribes in the family Caliscelidae (Hemiptera: Fulgoroidea) with the description of new taxa from Palaearctic and Oriental Regions. *Zootaxa* 1359, 1–30.

Hall, T. A. (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* 41, 95-98.

Melichar, L. (1906) Monographie der Issiden (Homoptera). *Abhandlungen der K. K. Zoologisch-botanischen Gesellschaft in Wien* 3(4), 1-327.

Metcalf, Z. P. (1958) *Fulgoroidea. Issidae. General catalogue of the Homoptera. Fasc.4. Pt.15.* 561 pp. Waverly Press.

Sun, Y., Meng, R. & Wang, Y. (2015) Molecular systematics of the Issidae (Hemiptera: Fulgoroidea) from China based on wingless and 18S rDNA sequence data. *Entomotaxonomia* 37(1), 15–26.

Swofford, D. L. (1998) PAUP, Phylogenetic analysis using parsimony (and other methods), version 4. Sinauer Associates, Sunderland, Massachusetts, USA.

Urban, J. M. & Cryan J. R. (2007) Evolution of the planthoppers (Insecta: Hemiptera: Fulgoroidea). *Molecular Phylogenetics and Evolution* 42, 556–572.

Yeh, W. B., Yang, Ch. T. & Hui, Ch. F. (1998) Phylogenetic relationships of the Tropiduchidae-group (Homoptera: Fulgoroidea) of planthoppers inferred through nucleotide sequences. *Zoological Studies* 37(1), 45–55.

Yeh, W. B., Yang, Ch. T. & Hui, Ch. F. (2005) A molecular phylogeny of planthoppers (Hemiptera: Fulgoroidea) inferred from mitochondrial 16S rDNA sequences. *Zoological Studies* 44(4), 519–535.