

Archepopovia yurii n. gen. n. sp. a new remarkable lace bug
from Baltic amber, with some notes on phylogeny and
classification of Tingidae (Heteroptera, Tingidae)

VIKTOR B. GOLUB, Voronezh *)

With 2 figures

Contents

Abstract	267
Zusammenfassung	267
I. Introduction	268
II. Systematic descriptions	268
III. Notes on the classification and the phylogeny of the Tingidae	272
Acknowledgements	279
References	279

Abstract

A remarkable new fossil lace bug of the subfamily Tinginae, *Archepopovia yurii* n. gen. n. sp. is described from in Baltic amber (Eocene). Based on morphological characters of extant and fossil taxa, phylogenetical aspects of the family Tingidae are discussed. As a result, the long established concept of a monophyletic family Tingidae comprising the subfamilies Tinginae and Cantacaderinae is confirmed as well as the monophyly of the superfamily Tingoidea with the families Tingidae and Vianaididae. A family rank of Cantacaderidae as proposed by LIS (1999) is not supported by the present analysis.

Zusammenfassung

Eine bemerkenswerte neue fossile Gitterwanze *Archepopovia yurii* n. gen. n. sp. (Fam. Tingidae, Subfam. Tinginae) wird aus dem Baltischen Bernstein (Eozän) beschrieben. Anhand morphologischer Merkmale rezenter und fossiler Taxa werden phylogenetische Aspekte der Familie Tingidae diskutiert. Als Ergebnis wird das lange anerkannte Konzept einer einzigen monophyletischen Familie Tingidae mit den Unterfamilien Tinginae und Cantacaderidae bestätigt. Darüberhinaus wird auch die

*) Author's address: Dr. VIKTOR B. GOLUB, Voronezh State University, Universitetskaya pl. 1, Voronezh 394693, Russia.

Überfamilie Tingoidea mit den Familien Tingidae und Vianaididae als monophyletisch angesehen. Die vorliegende Merkmalsanalyse widerspricht dem Vorschlag von LIS (1999), der Unterfamilie Cantacaderidae den Rang einer eigenen Familie zuzusprechen.

I. Introduction

So far nearly 30 fossil species of Tingidae have been recorded (GOLUB & POPOV, 1999, 2000a,b), and only the Cantacaderinae (Cantacaderini and Phatnomini) are fairly well known. Five of the six species described from the Baltic amber (Eocene) clearly belong to this family and only one, *Tingicader cervus* GOLUB & POPOV (1998), combines features of Cantacaderinae (Cantacaderini and Phatnomini) and Tinginae. Thanks to Mr. J DAMZEN and Mr. C. GRÖHN and with the help of Dr. W. WEITSCHAT it was possible to study two unique specimens from the Baltic amber containing a new tingid species which clearly belongs to the subfamily Tinginae, but shows some features of the Cantacaderinae as well. A comparative analysis of the morphological characters of recent and fossil (from Eocene) Cantacaderinae and Tinginae shows that some features commonly used for distinguishing between these two subfamilies, are met with simultaneously in Eocene representatives. The beginning of the differentiation of Tingidae into Cantacaderinae and Tinginae, which took place at least not later than in Eocene time, was in turn accompanied by the differentiation into Cantacaderini and Phatnomini.

II. Systematic descriptions

Suborder Heteroptera

Infraorder Cimicomorpha

Superfamily Tingoidea LAPORTE, 1832

Family Tingidae LAPORTE, 1832

Subfamily Tinginae LAPORTE, 1832

Genus *Archepopovia* n.gen.

Type species: *Archepopovia yurii* n.sp.

Derivatio nominis: Combined from *arche* (greek) = ancient and the name of my old friend and well known Russian heteropterologist and paleoentomologist YURI A. POPOV.

Diagnosis: Body surface slightly areolate. Head short, with 5 spines directed obliquely upward – 3 frontal and 2 occipital. Bucculae elongated forward and distinctly protruding beyond clypeal tip; converging at V-shaped angle and touching or almost touching by their apices, not curved towards each other. Antennae thin, 3rd joint very long: just a little shorter than width of body (relation 0.95). Pronotum with 3 low longitudinal carinae. Areolate vesicula (hood) of pronotum tectiform, relatively low, its anterior margin more or less emarginate, slightly projecting forward along midline. Areolate posterior pronotal process well developed, but rather short, elongated backwards along hemelytra approximately at one third of discoidal area, with obtusate apex, leaving one third of clavi uncovered from above. Scent-gland openings surrounded by well-developed peritreme (evaporatorium). Macropterous form. Hemelytra distinctly subdivided by raised veins into costal, subcostal, discoidal and sutural areas. Stenocostal area absent. Discoidal area with one additional elevated transverse vein

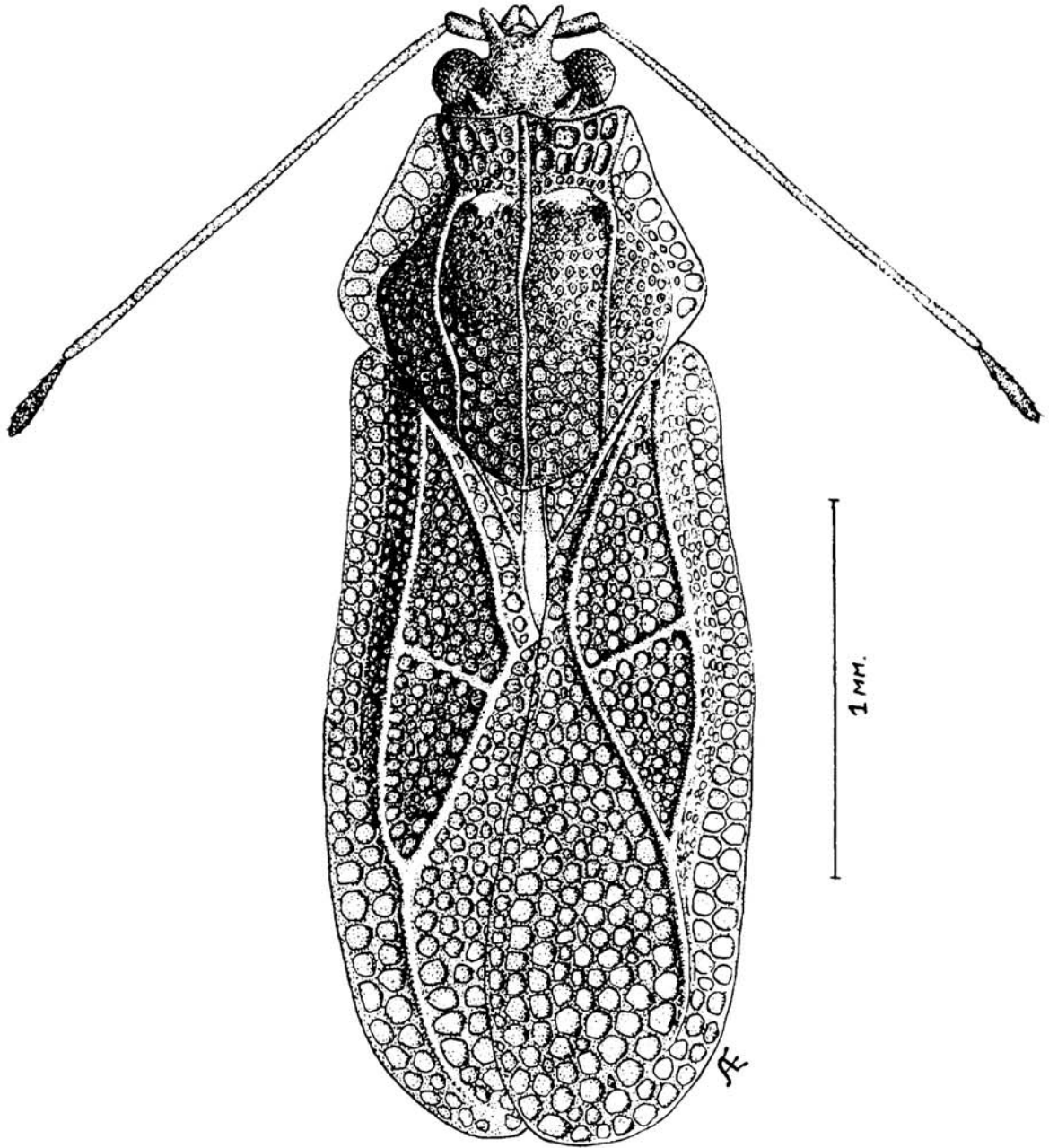


Fig.1: *Archepopovia yurii* n. gen. n. sp., reconstruction of the holotype, ♂, (macropterous form), in Baltic amber: coll. Geologisch-Paläontologisches Institut und Museum, Universität Hamburg, Nr.4302; (ex coll. C.GRÖHN Glinde, (Germany) Nr.2238).

placed obliquely in respect to longitudinal axis of body. Clavus distinctly separated from corium, areolate. Tarsal claws with well-developed basal hook-like process.

Comparison: The new genus demonstrates all the main characters of the subfamily Tinginae, i.e. the developed, although rather short areolate posterior pronotal process, the short head with 5 spines, one of which is the unpaired frontal spine placed before the eyes, and the hemelytra without stenocostal area and without numerous additional transverse veins.

According to some morphological features the new genus is close to the Palearctic genus *Tingis*. These features are: the head with 5 spines (3 frontal and 2 occipital ones); the converging bucculae that touch or almost touch each other at their tips; the 3 longitudinal carinae of the pronotum; the tectiform vesicula; the horizontal paranota spread out; the peritreme of the scent-gland opening distinctly present; the rather small cells of the pronotum and the hemelytra. On the other hand, the described new genus has peculiarities that separate it not only from the genus *Tingis* but also from other genera of the subfamily Tinginae and connect it with the tribe Phatnomini (Cantacaderinae). These peculiarities are as follows: bucculae elongated forward, their anterior apices not curved toward each other, although touching or almost touching (representatives of the genera Tinginae have anteriorly closed bucculae with arched curved anterior parts); the discoidal area with one additional elevated transverse vein (among the recent palearctic tingids such vein is present only in the genus *Monosteira*); clavi clearly separated by the suture from the corium, areolate, joining their inner sides in repose; the triangular posterior pronotal process rather short leaving about half of clavi length opened from above. In addition to the above, it differs from the genus *Tingis* by its very long 3rd antennal joint (all species of the genus *Tingis* have short 3rd antennal joints, in fact, shorter than the pronotum width and much shorter than the body width).

The new genus differs from the Cantacaderinae by: the short head, with five spines (the frontal paired spines, one unpaired frontal and paired occipital spines), without paired jugal, unpaired clypeal and additional dorsomedial spines which are typical of the Phatnomini. The posterior triangular process of pronotum is well developed, although it is rather short; (among the Cantacaderinae, the posterior pronotal process of the triangular or rounded form is present only in some Cantacaderini: *Cantacder*, *Pseudophatnoma* and *Teratocader*); the stenocostal area which is characteristic of the Cantacaderini is absent.

Therefore the new genus is included in the subfamily Tinginae. *Archepopovia* shows also some features of the tribe Phatnomini (Cantacaderinae).

Archepopovia yurii n.sp.

(figs.1-2)

Holotype: ♂ (?), (macropterous form) in Baltic amber; coll. Geologisch-Paläontologisches Institut und Museum, Universität Hamburg, Nr.4302; (ex coll. C.GRÖHN Glinde, (Germany) Nr. 2238).

Paratype: ♀ (macropterous form) in Baltic amber; coll. A. HERRLING, Bramsche, (Germany) Nr. 611.

Derivatio nominis: Named after the above mentioned heteropterologist Dr. Yuri POPOV.



Fig.2: *Archepopovia yurii* n. gen. n. sp., holotype, ♂ (macropterous form) in Baltic amber; coll. Geologisch-Paläontologisches Institut und Museum, Universität Hamburg, Nr.4302; (ex coll. C.GRÖHN Glinde, (Germany) Nr.2238).

Description: Rather strongly convex. Paranota rather narrow, in the most of length with 2 rows of rectangular or pentagonal cells in the greater part of the length with direct or emarginate margins. Triangular hind projection of pronotum rather short leaving the apical part of clavi open from above almost by half of the length; lateral margins of hind projection weakly S-like, curved: at the basis slightly emarginated while closer to the top - convex and rounded. Scent-gland openings with a distinct peritrema in form of a protruding oval ring.

Macropterous. Hemelytra and hind wings considerably overlap apex of abdomen from behind. Hemelytra distinctly divided by elevating veins. Costal area in greater part of length with 2 rows of predominantly pentagonal cells. Subcostal area in greater part of length with 3 rows of rather small oval or pentagonal cells. Discoidal area in broadest section with 6 irregular rows of rather small angled and rounded cells crossed by elevating transverse vein, located at an angle to the linear axis of the body, with exterior end directed forward. Sutural area in broadest place with 11 rows of angled cells; size of cells slightly increasing from base of area to top. Clavus clearly separated from corium by a sutura, with straight inner margin, at the level of the top of posterior protrusion of pronotum with 3 rows of cells in transverse direction. Hypocostal plate with 1 row of cells along whole length. In holotype and paratype legs moderately long (in holotype only hind legs could be measured). Tarsi with sharp claws curved almost at right angle with hook-like protrusion at the base.

Dimensions (in mm): Length of body from clypeus apex to apex of hemelytra 3.05 (holotype) and 3.42 (paratype), width 1.2 (holotype) and 1.22 (paratype); length of head from posterior margin of eyes to bucculae apex 0.3 (holotype) and 0.29 (paratype), width of head 0.57 (holotype) and 0.54 (paratype); width of vertex 0.29 (holotype), ratio of antennomeres 0.086 : 0.07 : 1.14 : 0.27 (holotype); pronotum length 1.04 (holotype) and 1.14 (paratype), maximum width of pronotum 0.97 (holotype) and 1.02 (paratype); hemelytra 2.21 (holotype) and 2.36 (paratype); length of discoidal area of hemelytra 1.33 (holotype) and 1.39 (paratype), maximum width of discoidal area 0.29 (holotype)

and 0.36 (paratype); length of hind femur 0.7 (holotype), length of hind tibia 0.76 (holotype), length of tarsi 0.11.

III. Notes on classification and phylogeny

Since the system of the family Tingidae is insufficiently studied on the suprageneric level, the genus *Archepopovia* is not referred to any of the Tinginae tribes.

At the present time the system of the family Tingidae, which is accepted by most hemipterologists, comprises two subfamilies, Cantacaderinae STAL, (1873), and Tinginae LAPORTE (1832). The former includes 2 tribes: Cantacaderini STAL, (1873), and Phatnomini DRAKE & DAVIS (1960). Several authors distinguished different sections and tribes in the subfamily Tinginae. They are Aidoneusaria DISTANT (1909), Acallyptini BLATCHLEY (1926), Ypsotinigini DRAKE & RUHOFF (1965), Lytadeini DRAKE & RUHOFF (1965) and others. Some of the more recent authors accept part of the distinguished taxa of the suprageneric rank (LIS, 1999; FROESCHNER, 2000), others consider Tinginae as a single one without dividing them into tribes (PERICART, 1983, PERICART & GOLUB, 1966).

In order to work out the questions of phylogeny and to improve the Tingidae system, LIS (1999) made a cladistic analysis of the morphological and the anatomical features of the highest taxa in the superfamily of Tingoidea and the genera in the Cantacaderini tribe. Based on the analysis she assigned an independent family status to the tribe Cantacaderini and that of a subfamily to the Phatnomini tribe. (LIS used the name Phatnomatini, which is not correct in the zoological nomenclature).

Part of the general features of Phatnomini and Tinginae, presented by LIS (1999), most probably have the character of synplesiomorphies and synapomorphies (partially – autapomorphies). By these features they can be distinguished from the Cantacaderini. They may be used in taxonomic and phylogenetic analyses as follows:

1. A free trochanter; in Cantacaderini it fuses with femur.
2. A reduced apodema between gonocoxopodit I and laterotergite VIII (a thickened carina serving for fastening muscles); in Cantacaderini it is well expressed and functional.
3. A pseudospermatheca that replaces the true spermatheca; in Cantacaderini the true rudimentary and not functioning spermatheca is preserved.
4. An additional sclerit in the pleural membrane of abdominal segments; in Cantacaderini such sclerit is absent.
5. Strongly sclerotized female genital plates (gonapophyses III, gonoplacs); in females of Cantacaderini these plates are weakly sclerotized.
6. A small genital camera; in Cantacaderini it is large.
7. A paired pseudospermatheca; in Cantacaderini a true rudimentary spermatheca is preserved.

At the same time LIS (1999) uses a number of other features separating Cantacaderini both from Phatnomini and from Tinginae for substantiating the independence of the Cantacaderini as a family and the Phatnomini as a subfamily. Yet these differences are either hardly appropriate or altogether inappropriate for differentiating taxa of such rank. Below we give a critical analysis of them.

1. The presence (Phatnomini) or absence (Cantacaderini, Tinginae) of the non-paired clypeal spine is principally unimportant: in *Tingicader cervus* GOLUB & POPOV (Phatnomini)

from the Eocene Baltic amber the absence of the clypeal spine and the preocular location of paired head spines (specific features in Cantacaderini) is accompanied by the absence of a stenocostal field of the hemelytra and the absence of the posterior projection of the pronotum (specific features in all Phatnomini) (GOLUB & POPOV, 1998).

2. LIS (1999) also states that in the whole tribe Tingini the bucculae join at the dorsal side. In reality the extensive tribe Tingini sensu DRAKE & RUHOFF (1965) includes a number of palearctic genera (*Campylosteira*, *Acalypta*, *Galeatus*, *Stephanitis*, etc.), some representatives of them having bucculae in front and along their dorsal surface which do not fuse.

3. Since Cantacaderini often have a posterior areolate protrusion of the pronotum (*Cantacader*, *Teratocader*, *Pseudophatnoma*), Tinginae are even closer to them than to Phatnomini which do not have a posterior protrusion.

4. In macropterous representatives of a number of genera of both Ypsotingini and Tingini sensu DRAKE & RUHOFF (1965) the clavus is well developed and divided by the vein Pcu from the corium, although it is covered by the posterior protrusion of the pronotum. When the protrusion is weakly developed (*Dictyonota*), a considerable part of the clavus is clearly seen from above.

5. LIS (1999) unites Phatnomini and Tinginae on the basis of them having 1 to 3 longitudinal carinae of the pronotum contrary to Cantacaderini which have from 3 to 5. The increase of the number of carinae up to five may be considered as an evolutionary tendency, which appears in a number of genera of Cantacaderini. However, for instance, in *Cantacader bomansi* there is only one medial carina (LIS, 1999). In Tinginae, the number of carinae (but not larger than 3) varies not only in different genera, but even within the limits of one genus. For instance, in all species of the subgenus *Derephysia* s.str. there are 3 carinae of the pronotum, while in species of the subgenus *D.* (*Paraderephysia*) there is only one.

The interruption of the lateral carinae of the pronotum at the level of the callous disc elevation is a specific feature of Cantacaderini. And here the anterior parts of the interrupted lateral carinae overlap the collar; the latter is usually weakly expressed. In all recent Phatnomini and Tinginae the lateral carinae are not interrupted and do not overlap the vesicular which is quite distinctly expressed. However, *Intercader weitschati* GOLUB & POPOV (Phatnomini) of Eocene time has 5 carinae, and the lateral carinae look like interrupted ones (similarity with Cantacaderini) and there are also displaced parts in the place where the vesicula is located in Tinginae (GOLUB & POPOV 1998: 239; fig.7; pl.II, fig.1), like in Cantacaderini.

6. The different size of the cells of the hemelytra between the subfamilies are not distinct. Not only in Cantacaderini, but also in many Phatnomini and Tinginae the cells are often very small, almost deeply punctuated.

7. One of the main morphological difference of Cantacaderini from Phatnomini and Tingini is the presence in the former of a stenocostal area of the hemelytra and a specific ostiolar-stenocostal system (DRAKE & DAVIS, 1960; FROESCHNER, 1996). This difference between both groups were already evident in the Eocene (GOLUB & POPOV, 1998).

FROESCHNER (1996) distinguished 3 degrees of complexity of the ostiolar-stenocostal system of Cantacaderini depending on the development of the stenocostal area. In the modern genus *Carldrakeana* the stenocostal area is hardly visible – it is seen only ventrally and represents a narrow trough across the hypocostal vein between two thickened subbasal veins and to the opposite of the peritrema top (FROESCHNER, 1996). Thus, there is no sharp

hiatus between the two forms of the hemelytra – with stenocostal area (Cantacaderini) or without it (Phatnomini, Tinginae).

8. LIS (1999) uses differences in the openings of the scent glands of the structure of the peritrema as a diagnostic feature of families and tribes and for a phylogenetic analysis. These differences are: in Cantacaderini the peritrema is slot-like with the opening of the scent gland directed upwards, in Tingini it has the form of a loop, and in Ypsotingini it is absent. In reality, the peritrema may be absent not only in Ypsotingini, but also in many Tingini - *Campylosteira*, *Acalypta*, *Galeatus*, *Dictyla* and others. Slot-like peritrema of Cantacaderini may be narrow or more or less widened, it may be located on the surface or more or less sunk into the covers (GOLUB & POPOV, 1998) and on the whole it probably reflects only the plesiomorphic state of this structure.

9. In Cantacaderini vein M of the hind wings is almost perpendicular to veins R and Cu, contrary to Tinginae and Phatnomini (in genera studied in this respect) where it is clearly located under a sharp angle towards Cu. However, this feature does not have alternative states: in different genera of Tinginae veins R and M. form different angles. Moreover, despite a generally rather great uniformity of the hind wing venation, in some genera of the subfamily Tinginae there are considerable deviations from the general type. For instance, in *Acalypta marginata* WOLF, vein R+M on the summit of forking and in *Elasmotropis testacea* H.-S. in the postcubital sector there are well developed additional transverse veins (personal observations). Such significant differences, nevertheless, cannot serve as a basis for separating the above genera even into the rank of tribes.

10. A well developed clavus is characteristic not only of the Cantacaderini and Phatnomini, but also of many Tinginae. Its development usually directly depends on the degree of development of the hemelytra: in macropterous forms the clavus usually is well developed and separated from the corium (PERICART, 1983), in particular, in the species *Tingis* (PERICART 1983), *Dictyonota* (GOLUB, 1998) and others. In species with a short posterior protrusion of the pronotum, the clavus is clearly seen from above at a considerable stretch (*Dictyonota*).

11. A distinct tendency toward fusing of the abdominal segments can be seen within the subfamilies of Tingoidea. The degree of fusing in the subfamilies of Tingidae and even in the different genera of the subfamily Tinginae is different: in Cantacaderini and Phatnomini, only the abdominal segments II and III fuse (FROESCHNER, 1996; LIS, 1999); in Tinginae – usually II, III, and IV, and in *Stephanitis* – even from II through VI (PERICART, 1983); in Vianaididae, similar to Tinginae, the segments II, III, and IV are fused. Therefore it is probably not possible to use the degree of fusing of the abdominal segments as a diagnostic feature of the taxa of highest rank. At least it needs additional and careful studies of this feature in many Tingidae genera.

Based on the above arguments we support the long established concept that Tingidae is a single family both taxonomically and phylogenetically, comprising two subfamilies – the Cantacaderinae and the Tinginae. Nevertheless, the features presented by LIS, among others, are useful when analyzing the phylogenetic relationship of Tingidae and Vianaididae with the groups inside the family Tingidae.

The results of the analysis of morphological and some anatomical features of recent and fossil forms points to monophyly of not only the family Tingidae, but also the superfamily Tingoidea (Tingidae and Vianaididae).

Synapomorphies of Tingidae and Vianaididae of a morphological character, which are not met with in other families of Cimicomorpha, are as follows:

1. There is almost always an areolate-like structure of the hemelytra (except for the largest part of the membrana or even all of the hemelytra in Vianaididae).
2. Most often the hemelytra are divided by elevated veins Hc, R+M, R+M+Cu into areas.
3. Most often there are flattened lateral margins of the pronotum – paranota.
4. To certain extents there is a tendency towards reduction of the present spermatheca.

Other specificities of apomorphic character of the superfamily Tingoidea are: the herbivorous type of the rostrum and the almost smooth surface of the maxillae, the development of bucculae and the disappearance of the hind bridge, the reduction of the ocelli, the reduction of veins on the membrane of the hemelytra, the availability of a paired reservoir of the scent glands, the fusing of several abdominal segments, the development of a subgenital plate in females, backwards directed parameres, and some other. However, these special features are often developed in the process of evolution independently in different families of Cimicomorpha as a result of a distinct purpose of the given feature and so they are not reliable as synapomorphies.

Every family of Tingoidea manifests in its turn autapomorphies that to some extent reflect their independent evolution.

Autapomorphies of Tingidae: head spines in imago and nymphs; the absence of macrochaetae on the head; a complete areolate membrana; the development of carinae on the pronotum; the presence of hook-like protrusions at the basis of the claws in form of transformed pulvilli; the development of a pair of pseudospermatheca (the latter two features are present only in the Tinginae – the most advanced group of the Tingidae in evolutionary respect).

Autapomorphies of Vianaididae: Y-like peritrema of the scent gland openings; significantly elongated 2nd antennal joint; short head; the latter feature is well pronounced already in the Upper Cretaceous representatives (GOLUB & POPOV, 2000 a.).

The modern mirmecophilous brachypterous Vianaididae have acquired a number of special features and have undergone a reduction of the eyes (DRAKE & DAVIS, 1960). The modern macropterous specimen and the Late Cretaceous submacropterous and macropterous ones have preserved a number of initial morphological features of Tingoidea (SCHUH & STYS, 1991; SCHUH & SLATER, 1995; GOLUB & POPOV, 2000 a.).

The absence of a distinct posterior protrusion of the pronotum, commonly fine cells of the corium of the hemelytra, and distinctly separated clavus, often with a well seen vein Pcu, - all these are synplesiomorphic features of Vianaididae and Cantacaderinae pointing to their older age as compared with Tinginae. Between the two, Vianaididae have preserved more plesiomorphic features than Cantacaderinae and, on the whole, Tingidae: in the latter all or almost all membrana are not areolate, there are no spines on the head, at least in part of the fossil specimens there are some true chaeta-like pulvilli of tarsi and macrochaetae on the head (GOLUB & POPOV, 2000 a,b).

Most apomorphic features manifest themselves only as a tendency which is the main problem in the definition of phylogenetic links of subfamilies and Tingidae tribes.

The phylogenetic connections of the two largest taxa of Tingidae, and the subfamilies Cantacaderinae and Tinginae are revealed on the basis of a consecutive analysis of the plesiomorphic and apomorphic characters of the subfamilies and the tribes of Cantacaderinae.

The plesiomorphic morphological features of Cantacaderinae (there are more of them and as a tendency they manifest themselves more often than in Tinginae) include: the absence or a relatively weak development of the posterior protrusion of the pronotum; a clavus that is usually separated from the corium and often with a distinct vein Pcu along it; more often bucculae that do not connect in front or only touch each other by their frontal ends; always thin antennae; predominantly (but not always) small cells; in most cases elongated head. An elongated head in the oldest known fossils points to the plesiomorphic nature of the latter feature of Tingidae (POPOV, 1989), (pers. observations). The non-functioning rudiment of the spermatheca that has been detected in *Cantacader quadricornis* (CARAYON, 1954; pers. observations) and *Allocader cordatus* (LIS, 1999) may probably be considered an anatomic feature of an apomorphic character.

The presence of several or many additional elevating cross veins on the hemelytra is the autapomorphic feature of the whole subfamily Cantacaderinae (synapomorphic for the tribes Cantacaderini and Phatnomini).

In addition to the above features synplesiomorphic with Phatnomini, Cantacaderini also show the following plesiomorphies: the complete absence of medial spines on the head; a slot-like peritrema of the scent gland opening; the weak sclerotization of the gonapophyses III (gonoplacs); the absence of an additional sclerit in the membrane of the abdominal segments; a well developed and functioning apodema between laterotergite VIII and gonocoxopodite I and some others. At the same time some autapomorphies are quite distinct. The presence of a stenocostal area of the hemelytra formed by its front margins and misplaced backwards by Sc vein is most important. The following can also be considered autapomorphies and tendencies of autapomorphic character of Cantacaderini: the presence (often, but not always) of additional lateral carinae on the pronotum in its hind half, where in such case one can discover five of them; the interruption of the lateral carinae at the level of the callous disc elevation of the pronotum; the presence of a small posterior projection of the pronotum in representatives of some modern genera (*Cantacader*, *Pseudophatnoma*); and the trochanter fused with the femur.

Features shared by Tinginae and Cantacaderini (possibly these are autapomorphies of each of the groups) are as follows: the development of the posterior projection of the pronotum (in Cantacaderini not in all genera) and the absence in representatives of a number of genera of Tinginae (*Campylosteira*, *Acalypta*, *Dictyonota*, etc.) of only paired head spines (although, contrary to Cantacaderini, they are located in front of the eyes).

The common morphological and known anatomical characters of Tinginae and Phatnomini in a phylogenetic aspect are as follows:

Synplesiomorphic – the absence of a stenocostal area in fossil (beginning at the end of the Lower Cretaceous) and modern forms of both groups; a free trochanter, and a small genital camera (plesiomorphia?).

Synapomorphic (possibly some of them – autapomorphic of each group) - tendencies towards the development of unpaired frontal head spines; a reduced apodema between the laterotergite VIII and the gonocoxopodite I; the availability of a pair of pseudospermatheca; the presence of an additional sclerit in the pleural membrane of the abdominal segments; strongly sklerotized female genital plates (gonapophyses III, gonoplacs).

The presence of a non-functioning rudiment of a true spermatheca in Cantacaderini (DRAKE & DAVIS, 1960, LIS, 1999; pers. observations) and a paired ectodermal pseudospermatheca in Phatnomini (LIS, 1999) and Tinginae (CARAYON, 1954; DRAKE & DAVIS, 1960; pers.

observations) could probably be considered as correspondingly plesiomorphic and apomorphic states of sperm-receiving organs of females in these groups. Most probably these states represent certain stages of one evolutionary line: particle reduction of the true spermatheca in Cantacaderini as well as in the family Joppeicidae which is close to Tingidae (DAVIS & USINGER, 1970), a full reduction of spermatheca in Tinginae, Phatnomini, Vianaididae (DRAKE & DAVIS, 1960), as well as in Thaumastocoridae (DRAKE & SLATER, 1957) and its replacement in Phatnomini and Tinginae by secondary sperm-receiving organs: a pair of pseudospermatheca representing protrusions at the base of the oviductus.

On the whole, Tinginae have more general features with the Phatnomini than with the Cantacaderinae. However, each of these groups has some apomorphic morphological features which do not allow to take Tinginae out of Phatnomini.

Apomorphies of Phatnomini: the presence of additional transverse veins on the hemelytra (synapomorphy with Cantacaderini); the development of a non-paired clypeal spine on the medial line of the head, often even of paired clypeal, and the tendency towards a general increase of the number of head spines, often up to nine (autapomorphy). One should probably consider the tendency towards an increase of the sizes of the cells of the pronotum and the hemelytra an autapomorphy as well. It reflects itself already in the Eocene genus *Tingicader* (alongside its contemporary small-cell species *Archeopopovia yurii* from the Tinginae subfamily) and the recent genera *Daillea*, *Oranoma*, and *Distocader*.

Autapomorphies of Tinginae: the development of a cell-like hind outgrowth of the pronotum that covers the clavi either completely or their larger part; a short and broad head characteristic of most Tinginae; a distinct tendency towards an increase of the size of cells of the surfaces up to very large in *Galeatus*.

Hence, the possible origin of Tinginae may be considered as one of the most complicated questions of the family's phylogeny.

To a considerable degree, the Eocene genus *Tingicader* GOLUB & POPOV (1998) may help understand the origin of the Tinginae, since it has a set of morphological features of all the three discussed taxa (Fig.2). *Tingicader cervus* has the distinct major plesiomorphic character of all Cantacaderinae, i.e. a direct hind margin of the pronotum. The stenocostal area is absent (plesiomorphy) thus making it differ from the Cantacaderini that existed already in Eocene with a well developed area and brings it close to Phatnomini and Tingini. The availability of 4 head spines in front of the eyes is similar to Cantacaderini (probably synapomorphy). Additionally, this species has features that are characteristic of Tinginae: apomorphic – a short and broad head (two times wider than long), plesiomorphic – the absence of additional protruding transverse veins on the hemelytra. The pronotum of *T. cervus* (except its hind margin) has paranota that are wide in front and covered by hair-bearing spines, similar to those of a number of recent species of Tinginae. A high carina-like vein R+M and comparatively large cells of the pronotum and the costal area of the hemelytra are also more characteristic of Tinginae than of Cantacaderinae.

Most probably, the ancestor forms of Tinginae (their representative – *Tingicader cervus*) have separated from the general line of the family much earlier, before Cantacaderini acquired the stenocostal area and Phatnomini the medial head spines, while both latter groups show additional transverse veins of the hemelytra.

The development and individual stages of evolution of the Tingoidea, reconstructed by GOLUB & POPOV (1999) based on a comparative analysis of the morphological features of

fossil and recent representatives of Tingidae and Vianaididae alongside additions concerning the origin of Tinginae are as follows:

Judging on the fossil remnants from Mongolia, the most ancient Tingoidea or their direct ancestors already existed in the Early Cretaceous with two forms: *Sinaldocader drakei* POPOV, 1989 (Cantacaderinae, Phatnomini) and *Golmonia pater* POPOV, 1989 (Cantacaderinae, Golmoniini). Both species have the major morphological specific features of Tingoidea – deep punctation or very small cell structure of the surfaces and, at least in *G. pater*, an elongated head (POPOV, 1989). A review of the Early Cretaceous fauna of Tingoidea has shown that it was even richer (POPOV & GOLUB, in litt). Therefore, the development and the initial stages of the superfamily's evolution most probably can be referred to the Early Cretaceous.

In the late Cretaceous fauna of the North American a well-developed family Vianaididae was already common. It includes full-wing species with cell-like and deep punctated structure of the surfaces (GOLUB & POPOV, 2000 a).

The formation of the main morphological features of Vianaididae (evidently of Tingidae as well) was practically completed by the end of the Mesozoic, and there are no observations of a significant progressive evolution of the characteristic morphological structures of the Vianaididae, such as proportions of antennal joints, etc. Only in brachypterous forms, due to their cryptic way of life, the eyes have been reduced and the body has acquired a coleoptera-like form. North America or possibly only its southern part may be considered an area of differentiation of the superfamily into Tingidae and Vianaididae. Later on, the group penetrated to South America, while the north boundary of the family's area retreated southward to the 25th – 30th paleolatitudes. Most probably this penetration took place in the beginning of the Oligocene due to cooling and differentiation of the climate in the northern hemisphere.

Cenozoic Tingidae are known since Eocene time: Cantacaderini, Phatnomini (GOLUB & POPOV, 1998), and Tinginae (*Archeopovia yurii* n.gen. n.sp.) have been recorded from the Baltic amber. The first two groups were already well formed: the differences for instance between the Eocene *Paleocader strictus* GOLUB & POPOV and numerous recent species of the genus *Cantacader* hardly surpass the differences between the species of one genus. At the same time there were forms that show features of both Cantacaderini and Phatnomini, as well as *Intercader weitschati* GOLUB & POPOV. Judging on the relatively short hind outgrowth of the pronotum of *Archeopovia yurii*, the subfamily Tinginae was, at least partially, in the stage of formation of the main features in Eocene time. The differentiation of the Tingidae into the main recent groups of the family, Cantacaderini, Phatnomini, and Tinginae, has probably taken place in this period or even earlier.

Recent genera are already represented in the Tingidae fauna of the Oligocene-Miocene of both hemispheres: in the Palearctic – *Derephysia* and *Dictyonota*; in the Neotropic – *Eocader* and *Leptopharsa* (GOLUB & POPOV, 2000 b, c). It is interesting that most recent species of both first genera are found among the arid and subarid Tingidae fauna of the Palearctic. In Oligocene-Miocene, the southern part of Eurasia was characterized by a gradual aridization of the climate (SINITSYN, 1965, 1980) and the spreading of primary Mediterranean subarid biota (flora and fauna) beginning from the central foci to the north and west (EMELIANOV, 1979). Probably in this period, in the vast spaces of the middle part of Eurasia – from the south of West Europe (in Spain there is a typical location of *Derephysia penalveri* (GOLUB & POPOV) up to the Far East of Russia (Primorsky Krai with a typical location of

Dictyonota petrifacta GOLUB & POPOV) there formed autochthonous palearctic xerophilous and meso-xerophilous Tingidaefauna.

Acknowledgements

I wish to express my gratitude to Mr. Carsten GRÖHN (Glinde, Germany) and Mr. Jonas DAMZEN (Vilnius, Lithuania) for the loan of their materials. I am also especially indebted to A.A. EUSYUNIN (Moscow State University) for the excellently fulfilled original drawing. I greatly appreciate to Prof. Dr. Izyaslav KERZHNER and Prof. Dr. A.F. EMELIANOV (St. Petersburg) and also Dr. Yuri POPOV (Moscow) for the help in the preparation of this article. I am grateful to Dr. Wolfgang WEITSCHAT (Hamburg) for taking the color foto of the amber inclusion and also for his help and encouragement in publishing this paper and for the availability of these inclusions. The work was accomplished using the entomological collections of recent (Zoological Institute RAS, St Petersburg) and fossil (Paleontological Institute RAS, Moscow) bugs, and also materials of the Laboratory of Biodiversity and Monitoring of the Biological Research-education Center of the Voronezh State University. This work is a part of a project supported by grants from the Ministry of Education of the Russian Federation (Grant No. E00-6.0-33).

References

- BLATCHLEY, W. (1926): Heteroptera or true bugs of eastern North America, with special References to the faunas of Indiana and Florida. – Nature Publ. Co., Indianapolis, 1116 pp.
- CARAYON, J. (1954): Organs assumant les fonctions de la spermatheque chez divers Heteroptera). – Bul. Soc. Zool. France, **79** (2): 189-197.
- DAVIS, N.T. & USINGER, R. (1970): The biology and relationships of the Joppeicidae (Heteroptera). – Ann. entomol. Soc. Amer., **62** (2): 557-587.
- DISTANT, W. (1909): New Oriental Tingidae. – Ann. Soc. Entomol. Belgique, **53**: 113-126.
- DRAKE, C. & DAVIS, N. (1960): The morphology, phylogeny, and higher classification of family Tingidae, including the description of a new genus and species of the Vianaididae (Hemiptera: Heteroptera). – Entomologia Amer. 1960. N.S., **39**: 1-100.
- DRAKE, C. & RUHOFF, F. (1965): Lace bugs of the World: Catalog (Hemiptera: Tingidae). - U.S. Nat. Mus. Bull., **243**: 1-634.
- DRAKE, C. & SLATER, J. (1957): The phylogeny systematics of the family Thaumastocoridae (Hemiptera: Heteroptera). – Ann. entomol. Soc. Amer., **50** (4): 353-370.
- EMELIANOV, A.F. (1979): Phylogeny and evolution of the subfamily Orgeriinae (Homoptera, Dictyopharidae). – The 32nd annual readings devoted to the memory of N.A. KHOLODKOVSKI, Public House “Nauka”, Leningrad: 1-95.
- FROESCHNER, R.C. (1996): Notes Systematics and Morphology of the Lacebug Subfamily Cantacaderinae. – Proc. Entomol. Soc. Wash., **70**: 245-254.
- FROESCHNER, R.C. (2001): Lace Bug Genera of the World, II: Subfamily Tinginae: Litadeini and Ypsotingini (Heteroptera: Tingidae). – Smiths. Contr. Zool., **611**: 1-28.
- GOLUB, V.B. (1998): New and little known lacebugs of the genera *Acalypta* Westw. and *Dictyonota* CURT. from the East and Central Palaeartic (Heteroptera: Tingidae). - Zoosystem. Rossica, **7** (1): 163-170.
- GOLUB, V.B. & POPOV, Yu.A. (1998): Cantacaderid lace bugs from the Baltic amber (Heteroptera: Tingidae, Cantacaderinae). – Mitt. Geol.-Paläont. Inst. Univ. Hamburg, **81**: 223-250.
- GOLUB, V.B. & POPOV, Yu.A. (1999): Composition and evolution of Cretaceous and Cenozoic faunas of bugs of the superfamily Tingoidea (Heteroptera: Cimicomorpha). – AMBA projects AM/

- PFICM/1.99: Proc. First Intern. Palaeoentomol. Conference, Moscow 1998: 33-39.
- GOLUB, V.B. & POPOV, YU.A. (2000a): A remarkable lace bug from Upper Cretaceous New Jersey amber (Heteroptera: Tingoidea, Vianaididae), with some phylogenetic commentary. – In: Studies on fossils in amber, with particular reference to the Cretaceous of New Jersey (ed. D. GRIMALDY). BACKUYS Publishes, Leiden, The Netherlands: 231-239.
- GOLUB, V.B. & POPOV, YU.A. (2000 b): New cantacaderid lace bugs from Dominican amber (Heteroptera: Tingidae, Cantacaderinae). – Acta Geologica Hispanica, **35 (1/2)**:165- 69.
- GOLUB, V.B. & POPOV, YU.A. (2000 c): New Cenozoic Lace Bugs (Heteroptera: Tingidae). – Palaentol. Journal, **34**, Suppl. **3**: 5290- 5297.
- LAPORTE, F. (1832): Essai d'une classification systematique de l'ordre des Hemipteres (Heteroperes LATR.). – In: GUERIN-MENEVILLE F.E. Mag. Zool. T.2, suppl. **52-53**, Paris. 88h, 5 tabl., 1-16.
- LIS, B. (1999): Phylogeny and classification of Cantacaderini [= Cantacaderinae stat. Nov.] (Hemiptera: Tingoidea). – Ann. Zool. (Warszawa), **49 (3)**: 157-196.
- PERICART, J. (1983): Hemipteres Tingidae euro-mediterraneens. – Fauna de France. T. **69**: 620 pp.
- PERICART, J. & GOLUB, V.B. (1996): Superfamily Tingoidea Laporte, 18832. – In: Catalogue of the Heteroptera of the Palaearctic Region. – Neth.Entom.Soc., Vol. **2**. Cimicomo.I. Wageningen: 3-78.
- POPOV, YU.A. (1989): New fossil Hemiptera (Heteroptera + Coleorrhyncha) from the Mesozoic of Mongolia. – N. Jb. Geol. Paläont. Mh., **3**:166-181.
- SCHUH, R.T. & SLATER, J.A. (1995): True bugs of the world (Hemiptera: Heteroptera): classification and natural history. – CORNELL University Press, New York, 1336.
- SINITSYN, V.M. (1965): Ancient climates of Eurasia. Part 1. Paleogene and Neogene. – Publ. House of Leningrad. Univ., 165 pp. (in Russian).
- SINITSYN, V.M. (1980): Natural condition and climate within the USSR in the earl and Middle Cenozoic (ed. N.N. VERZILIN). – Publ. House of Leningrad. Univ., 104 pp. (in Russian).
- STAL, C. (1873): Enumeratio hemipterorum. 3. – Kgl.sv. Vet.-Akad.Handl., Bd. **11 (2)** 167 pp.