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## An analysis of existing views on the taxonomic system of the tribe Macrosiphini

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**Abstract:** The tribe Macrosiphini WILSON includes about 41 percent of all known recent aphid species. This taxon is internally quite heterogeneous group. The analysis of various publications devoted to the tribe system, as well as publications containing phylogenetic trees built on the basis of molecular genetic data, including species from the tribe Macrosiphini. As a result of this studies, it makes possible with considerable confidence to assume the presence inside the tribe of several subtribes. It is obvious that the complex of different criteria must be used for constructing a stable system, which will represent the real evolution of the taxon.

**Key words:** Anuraphidina, Liosomaphidina, Myzina and Macrosiphina, evolutionary tendencies, molecular genetic data, phylogenetic trees.

### INTRODUCTION

Tribe Macrosiphini WILSON, 1910 contains about 2250 species assigned to 240 genera. It represents almost 41 percent of all known aphid species (FAVRET 2019). For more than 100 years of tribe existence, several attempts to divide the tribe into lower groups have been made. In this paper we have analyzed all taxonomic systems of the tribe Macrosiphini that have been proposed at the present time and made conclusions about possible solutions to problem of creating a modern system of the tribe.

For the first time the taxonomic group of aphids, which is close to the current tribe Macrosiphini, was identified by THOMAS (1879), who divided the family Aphididae into four subfamilies: Aphidinae, Pemphiginae, Chermesinae, and Rhizobinae (Fig. 1). According to his opinion, Aphidinae consisted of three sections: Siphonophorini, Aphidini and Lachnini. Therefore section Siphonophorini was the first taxonomic analogue of the current tribe Macrosiphini. The genera *Siphonophora*, *Phorodon*, *Megoura* and *Myzus* as well as, the genera *Drepanosiphum*, *Rhopalosiphum* and *Hyalopterus* were included in it. However, the name Siphonophorini is invalid because its type genus – *Siphonophora* KOCH, 1855 – is a junior homonym of *Siphonophora* BRANDT, 1837, genus from class Diplopoda.

OESTLUND (1887) divided the subfamily Aphidinae into three tribes: Callipterini, Aphidini and Nectarophorini, the latter tribe included the genera *Myzus*, *Rhopalosiphum*, *Macrosiphum*, and *Nectarophora* (Fig. 2). But Nectarophorini is *nomen oblitum* and was replaced by Macrosiphini WILSON, 1910 before 1961.

WILSON (1910) also divided the subfamily Aphidinae into three tribes: Trichosiphini, Aphidini and Macrosiphini (Fig. 3), and included in the last tribe 11 genera of which only 2 are not currently in this tribe. The name of the tribe which Wilson proposed 108 years ago is accepted as valid.

## RESULTS

At the present time the tribe Macrosiphini is recognized by all aphidologists. Consequently, such a numerous and morphologically diverse taxonomic group attracted the attention of researchers from the point of view of the possibility of its further fragmentation into smaller taxonomic groups. There are the three stages during this process which we can designate.

On the first stage basis for fragmentation was practically limited to morphological features. The first attempt was made by Mordvilko in 1914, who distinguished within the tribe Aphidea two subtribes: Aphidina and Macrosiphina (MORDVILKO 1914) (Fig. 4). The morphological criterion for this division was the height of the antennal tubercles and the length of the antennae. As a result, the genera close to *Anuraphis* and *Liosomaphis*, which are now a part of Macrosiphini tribe, were found in the subtribe of Aphidina in the Mordvilko's system. Mordvilko divided the subtribe Macrosiphina, which is the taxonomic analogue of Macrosiphini of WILSON (1910), into three groups: Macrosiphini, Myzini and Rhopalosiphini. Morphological criteria for the separation were the shape of the antennal tubercles (their inner side), the shape of the frons and median tubercle, the presence or absence of secondary rhinaria on the third antennal segment of the apterous viviparous females, and a reticulation on the siphunculi.

In 1928 Mordvilko improved the system increasing the taxonomic status of the tribe Aphidea to the subfamily Aphididae and, accordingly, the subtribes Aphidina and Macrosiphina to the tribes Macrosiphea and Aphidea, distinguishing them on the height of the antennal tubercles, as well as the absence or presence of marginal tubercles on the abdominal segments I and VII (MORDVILKO 1928) (Fig. 5). Within the Aphidea he separated two subtribes: Aphidina and Anuraphidina. The first one included, among others, many genera close to *Liosomaphis*, and the second tribe included genera close to *Anuraphis*. Tribe Macrosiphea was divided on the basis of the same as in 1914 morphological criteria into three groups: Macrosiphina, Myzina and Rhopalosiphina subtribes.

The succeeding system was proposed by OESTLUND (1923 [1922]), who divided subfamily Aphidinae into three series: Lachnea proper, Lachnea-Aphidea and Lachnea-Macrosiphea. He separated Lachnea-Aphidea from Lachnea-Macrosiphea on the basis of the setae shape (Fig. 6). Aphidea usually has short and pointed setae, and Macrosiphea usually has enlarged at the tip or capitate setae. As a result, genera close to *Anuraphis* and *Liosomaphis* were included in Lachnea-Aphidea similarly to Mordvilko's *Aphis*-close group. Oestlund divided the Lachnea-Macrosiphea group into two supertribe: Callipterea and Macrosiphea, and the latter one into three tribes: Myzini, Microsiphini and Macrosiphini, that was based on the shape of the antennal tubercles and setae, as well as the length of the siphunculi. Tribe Macrosiphini was divided into taxonomic groups of the lower order, such as subtribes, divisions and groups of genus, thereby creating a rather fractional tribe system. The main

shortcoming of the Oestlund system is that it was based largely on the North American material and, accordingly, could not account for the full range of morphological variability within the taxonomic groups.

Carl Börner several times returned to the development of both aphid systems in general, and the Macrosiphini tribe system in particular. In the paper of 1930 he distinguished subtribes Pterocommina and Aphidina within the tribe Aphidini, and divided the latter one into 5 groups (Fig. 7): Cryptosiphea, Aphidea, Liosomaphidea, Hyaloptera, and Macrosiphea, using morphological characteristics such as the length and shape of the cauda, the presence of the marginal tubercle on the abdominal segment VII, the presence or absence of marginal setae on the thorax and abdomen of the first-instar larvae, and the number of dorsal setae on pronotum of the first-instar larvae, as well as the shape and size of antennal tubercles, the shape of frons, the length of the antennae and the presence or absence of secondary rhinaria in apterae (BÖRNER 1930). So Börner was the first one who used morphological characteristics not only of imago, but also immature specimens for creating the system of Macrosiphini.

Just two years later BÖRNER (1932) published a new system in which the tribe Aphidini was divided into two subtribes: Coloradoina and Aphidina, and the latter consisted of 7 groups: Pterocommatea, Cryptosiphonea, Aphidea, Brachycaudea, Liosomaphidea, Brachycolea, and Dactynotea (Fig. 8). The differences between the groups were based on a combination of morphological characteristics such as the shape and length of the cauda, the shape of the frons, antennal and median frontal tubercles, the length of the antennae and the presence or absence of the secondary rhinaria on the 3<sup>rd</sup> antennal segment, the presence or absence of the marginal tubercles on the abdominal segments I and VII, the number of the marginal and medial setae on the pronotum of the first-instar larvae, the venation of wings and the shape of the ultimate rostral segment.

Twelve years later BÖRNER (1944) published the next system, which was extremely different from the former two. Within the family Aphididae he distinguished four subfamilies: Pterocommatinae, Aphidinae, Myzinae, Dactynotinae (Fig. 9). The subfamily Pterocommatinae included all aphids with a short and not narrowed basally cauda. As a consequence, in this subfamily, that was later divided into 4 tribes were combined genera closely related to *Pterocomma*, genera *Acaudinum* and *Cryptosiphon*, and genera close to *Anuraphis*. The subfamily Aphidinae differed from Myzinae and Dactynotinae by presence of the marginal tubercles on the segment VII. It was divided into two tribes: Rhopalosiphonini and Aphidini, and quite accurately corresponds to the current tribe Aphidini, divided into two subtribes Rhopalosiphina and Aphidina. For Myzinae and Dactynotinae identification Börner took into account the length of the antennae, the presence of obvious antennal tubercles, the secondary rhinaria on the 3<sup>rd</sup> antennal segment and the shape of the mesosternal furca. Each of these two subfamilies was divided into three tribes: Myzinae consisted of Myzini, Liosomaphidini and Phorodontini, and Dactynotinae included Phalaridini, Dactynotini and Megourini.

In 1952, Börner published a new version of the Aphididae family system, which was very fractional (Fig. 10). He divided Aphididae into five subfamilies: Pterocommatinae, Aphidinae, Anuraphidinae, Myzinae and Dactynotinae, and these subfamilies were separated into many tribes and subtribes (BÖRNER 1952). For example, Anuraphidinae was divided into three tribes and two subtribes, Myzinae to 7 tribes and 4 subtribes, and Dactynotinae to 4 tribes and 8 subtribes. For systematic difference between groups Börner used both relatively stable characteristics, such as the shape and position of the spiracular plates on the abdominal segments I and II, the shape of the cauda, the shape and reticulation on the siphunculi, the

length of the antennae, the shape of the antennal tubercles, the structure of the cuticle on the head, the shape of the frons, the presence of the ocular tubercle, mesosternal furca in apterae, and also the highly variable characteristics such as the pronotum, first tarsal and hind tibiae chaetotaxy of larvae, the presence of the marginal tubercles on some abdominal segments and their position, the number of setae on the genital plate, the presence of a wax powder and the rhinaria on the 3<sup>rd</sup> antennal segment, as well as a type of sclerotization and the structure of the digestive system. In this case, Börner again broadened the number of features and used for diagnostics not only morphological but anatomical characteristics too. The same family system with minimal changes was presented in a paper published by BÖRNER and HEINZE (1957).

After that, more works on the taxonomy of aphids were published concerning, to some extent, the tribe Macrosiphini. PINTERA (1969), without any explanation and indication of specific morphological features, divided it into three subtribes – Anuraphidina, Myzina and Macrosiphina (Fig. 11). NARZIKULOV (1970) also without indicating the genera and characteristics divided the subfamily Aphidinae into 4 tribes: Aphidini with subtribes Rhopalosiphina and Aphidina, Anuraphidini, Myzini with subtribes Liosomaphidina and Myzina and Macrosiphini with subtribes Macrosiphina and Neoanuraphidina (Fig. 12).

All these systems were created largely on a formal relation to the morphological characteristics; they did not take into account or neglected such evolutionary processes as regression and parallelism. So far even on the first stage was not possible to create completely natural system of tribe, but the analysis that was done allow to find some important characteristics such as: the shape of the frons, antennal and median frontal tubercles, the structure of antennae, the shape of cauda, the shape and the structure of siphunculi, the presence of the ocular tubercle and mesosternal furca in apterae, the presence of the marginal tubercles on some abdominal segments and their position and others.

At the second stage of creating the system more complex approach was used. It was based not only on a widening of characteristics, but also on their evolutionary analysis.

Shaposhnikov took these processes into consideration in his works on the taxonomic system of aphids to a much greater extent. In the publication on subtribe Anuraphidina (SHAPOSHNIKOV 1956) he gave a detailed phylogenetic assessment of the morphological characteristics of this group and described the trends in accordance with the characteristics changed during the evolution. Based on the findings in 1964 Shaposhnikov presented the system of Macrosiphini tribe which was divided into three subtribes Anuraphidina, Liosomaphidina, and Macrosiphina (SHAPOSHNIKOV 1964) (Fig. 13). Unfortunately, this system was created only on the basis of aphid species inhabiting the European part of the former USSR and did not include many groups from other regions. Although it was universal enough that allowed PASHTSHENKO (1988), for example, to use it for the elaborating the keys to the identification of aphids of the Soviet Far East.

The last work included another attempt to divide the tribe Macrosiphini into subtribes was published in 90-ties. SHAPOSHNIKOV *et al.* (1998) considered the system of the family Aphididae (including the tribe Macrosiphini) based on the evolutionary tendencies of changes in morphological characters, karyotypes, and the connection of aphids with their host-plants. Authors have made an attempt to reveal evolutionary tendencies within the family and then to ground supergeneric taxa utilizing these tendencies. They implied under the evolutionary tendencies not only directions of the changes, but also different ways of realization these changes within each taxon of the family. It was shown, for instance, that the sequence of the changes from a complete set of the marginal tubercles situated on tergites

I–VII of the abdomen to their total absence is specific for each supergeneric aphid taxa. This was basically the first and so far the only attempt of the comprehensive analysis for the various characteristics, such as morphological, biological and karyological ones, for the ascertainment of the lowest taxonomic groups within the tribe Macrosiphini. The authors concluded that the tribe has to be divided into four subtribes: Anuraphidina, Liosomaphidina, Myzina and Macrosiphina, the evolution of which was originally associated with the plants from apple tribe (Fig. 14). However, the work contained only a brief summary of the authors' conclusions with a minimum of evidence. And there was also no indication of which genera to which subtribes belonged. This made impossible to use it in practice by other researchers, and as a result, it did not have a significant influence on the existing point of views.

The third period in the improvement of the system of tribe was related to active use of DNA analysis in taxonomic studies. Von DOHLEN *et al.* (2006) published results of testing of the morphological hypotheses for tribal and subtribal relationships within Aphidinae using DNA sequences. Among other things the authors used the obtained data for the analysis of the Macrosiphini system proposed by BÖRNER and HEINZE (1957). They showed a significant discrepancy between their data based on DNA sequences and the system developed by Börner and Heinze. In addition, they justified the inclusion in Macrosiphini tribe species that belonged earlier to the subfamily Pterocommatinae. This viewpoint was supported later by HEIE and WEGIEREK (2009), but this conclusion is currently being questioned by a number of researchers also based on data of molecular biology (ORTIZ-IVAS & MARTÍNEZ-TORRES 2010, KIM *et al.* 2011, PAPASOTIROPOULOS *et al.* 2013).

At the same time, analysing the phylogenetic tree obtained by von DOHLEN *et al.* if instead of the Börner and Heinze system using the SHAPOSHNIKOV *et al.* (1998) system, we can see the following: Macrosiphini tribe divides into three groups, the first one corresponds to the subtribes Anuraphidina + Myzina, the second one to Liosomaphidina, the third one to Macrosiphina (Fig. 15). The only exception is the genus *Cavariella* attributed by SHAPOSHNIKOV *et al.* (1998) to Liosomaphidina.

Similar results are presented by PAPASOTIROPOULOS *et al.* (2013) (Fig. 16). Anuraphidina + Myzina (though not completely) were also combined on the phylogenetic tree, Liosomaphidina was quite clearly confined, but Macrosiphina here was broken into two clusters. Moreover, the genus *Capitophorus*, related, according to SHAPOSHNIKOV *et al.* (1998), to the tribe Macrosiphina, in this case turned out to be get closer to *Pterocomma* and *Cavariella*.

In the paper of NIETO NAFRÍA *et al.* (2013), which was devoted to the description of the new genus and aphid species and did not have a purpose to analyse the Macrosiphini system, the phylogenetic tree shows a division into the same three groups (Fig. 17), and only one species, *Myzus hemerocallis*, was found not in its "own" subtribe, and far from another species of this genus.

In the figure, taken from the paper, which was recently published by REBIJITH *et al.* (2017) and devoted to reconstructing the macroevolutionary patterns of aphids using nuclear and mitochondrial DNA sequences (Fig. 18), the same situation happens: 3 fairly well-defined groups corresponded to Anuraphidina + Myzina, Liosomaphidina and Macrosiphina by SHAPOSHNIKOV *et al.* (1998), and also the significantly separated *Pterocomma* + *Cavariella* group and an obscure position of the species from the genus *Pentalonia*.

At the same time in the number of studies (FOOTTIT *et al.* 2008, LEE *et al.* 2011, WANG *et al.* 2011, CHEN *et al.* 2015, etc.) the constructed phylogenetic trees do not substantially coincide with the proposed system of Macrosiphini. However, some of the articles referred to barcoding in which the COI gene was used. This gene usually gives high accuracy results for

identifying species but shows a weak suitability for constructing a phylogeny at a level above the generic. Another part of the research was based on the primary endosymbiont gene. It is known that these symbionts are transmitted vertically, but it is not known what happens to them during hybridization and whether the horizontal transmission is completely impossible.

## DISCUSSION

All attempts for the creation of Macrosiphini system did not lead to a single-meaning result, although there are a number of facts relating to various aspects of the aphids study, which confirm the heterogeneity of this tribe. It makes possible with considerable confidence to assume the presence inside the tribe of several subtribes.

Summarizing, analysis of published papers allowed us to make some theoretical and methodological conclusions. It seems to be doubtless that tribe Macrosiphini as it is taken now includes several groups of the lower rank or, it is still possible, the equal rank as it might be in the case of the group combining *Cavariella* and *Pterocomma*. However, confines of those groups and their particular rank cannot be determined for now. It is obvious that the complex of different criteria must be used for constructing a stable system, which will represent the real evolution of the taxon. Only complex research that unite the data from genetics, morphology and ecology of the members of the taxonomic group will lead to the solution of the problem.

## ACKNOWLEDGEMENTS

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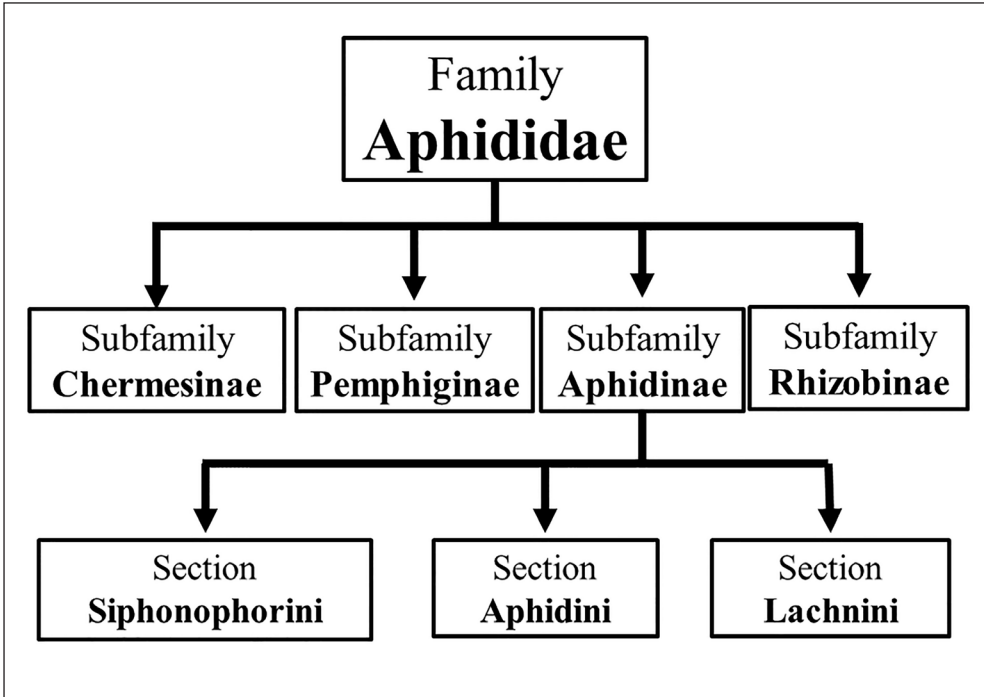


Fig. 1. The system of family Aphididae according to THOMAS (1879).

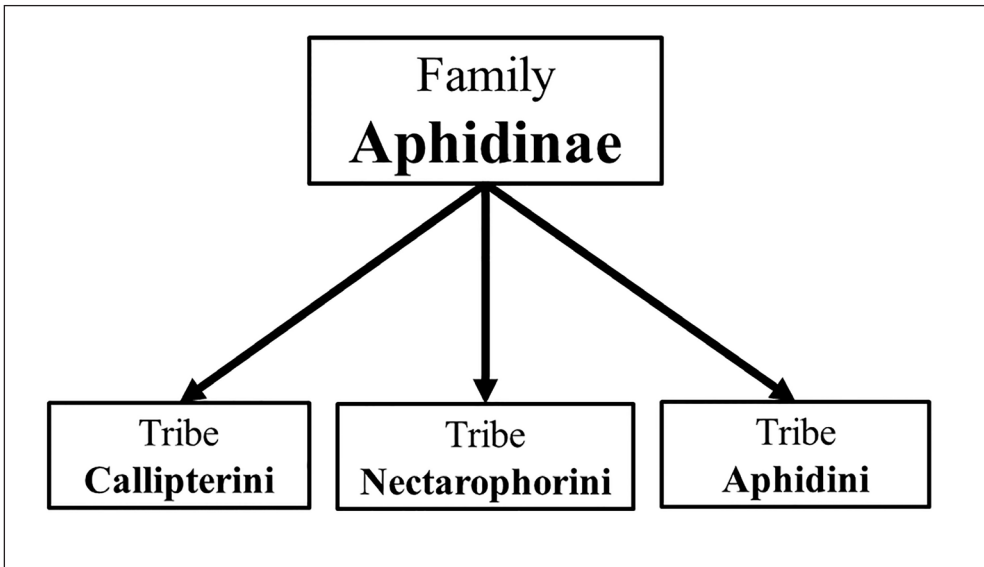


Fig. 2. The system of subfamily Aphidinae according to OESTLUND (1887).



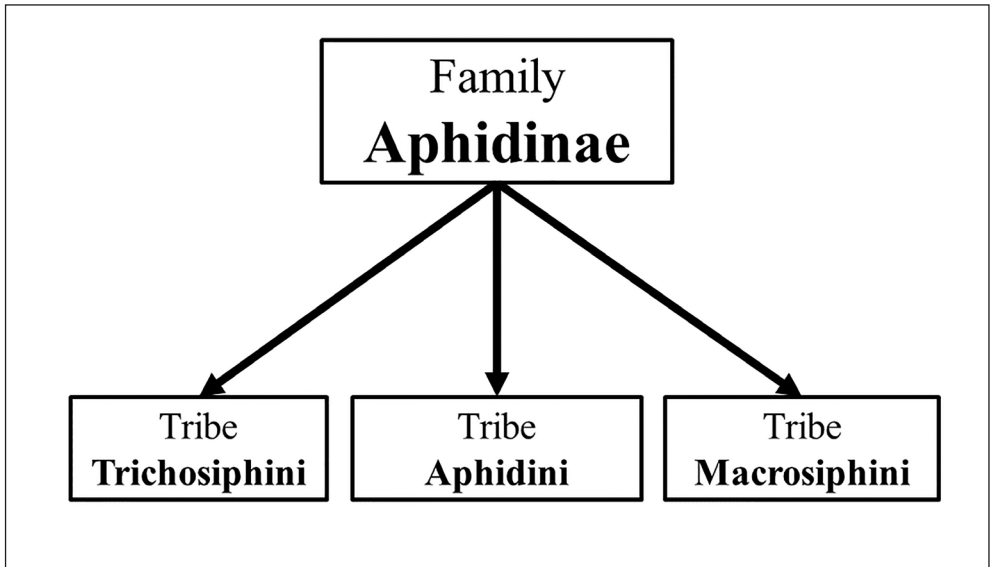


Fig. 3. The system of subfamily Aphidinae according to WILSON (1910).

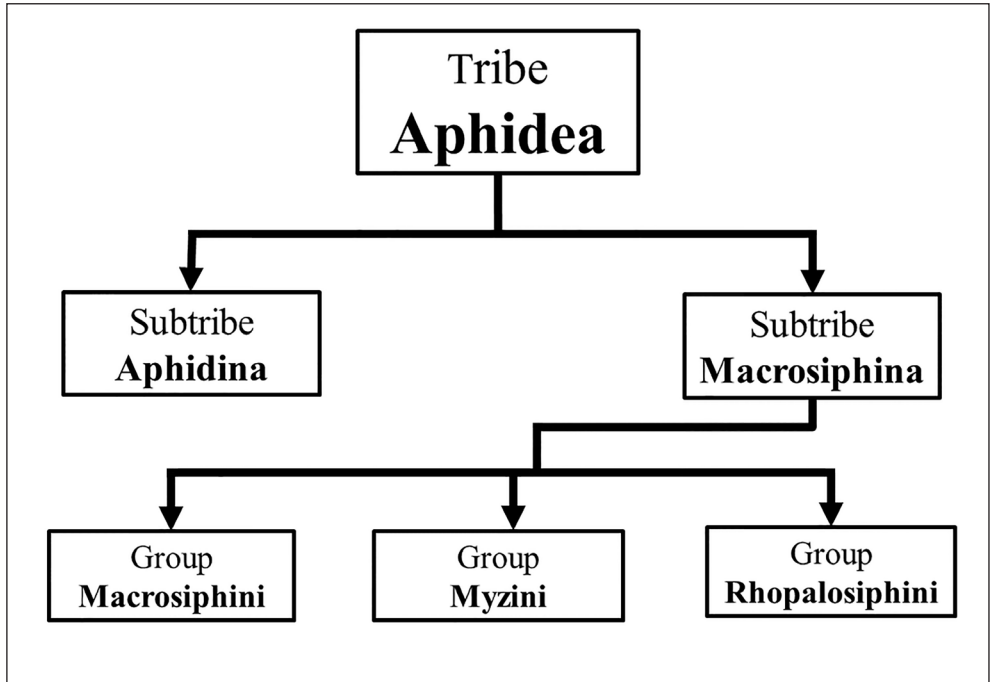


Fig. 4. The system of tribe Aphidea according to MORDVILKO (1914).

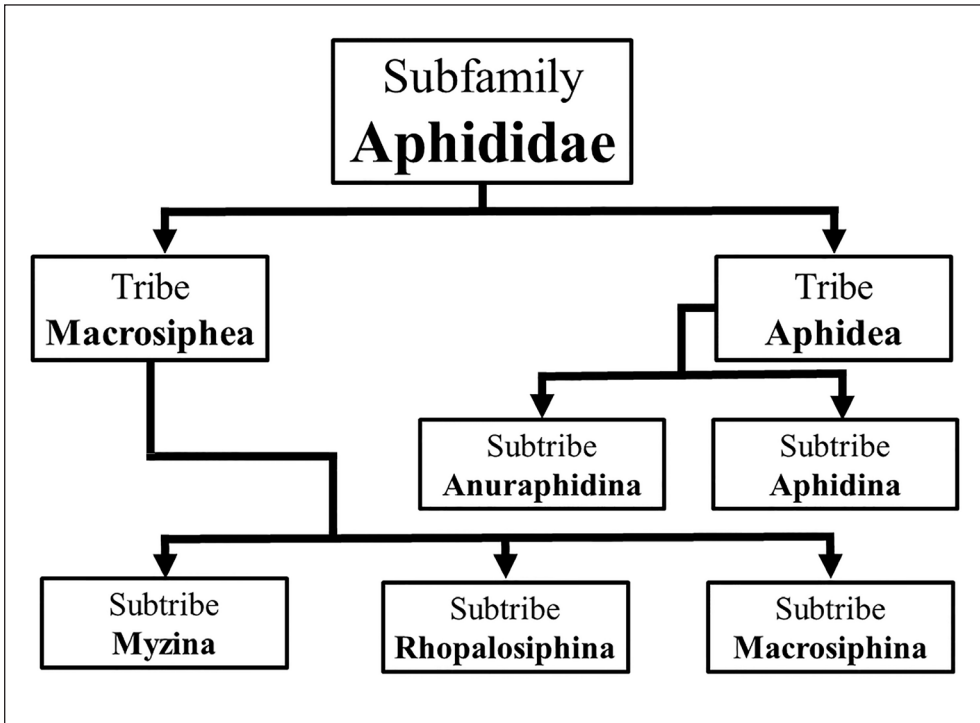


Fig. 5. The system of subfamily Aphididae according to MORDVILKO (1928).

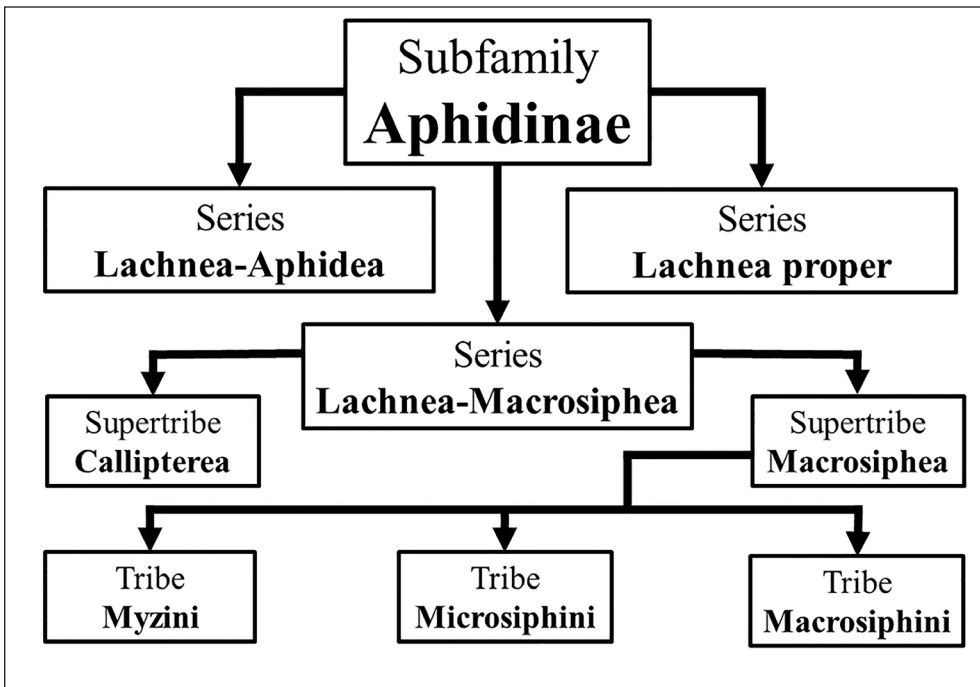


Fig. 6. The system of subfamily Aphidinae according to OESTLUND (1923 [1922]).

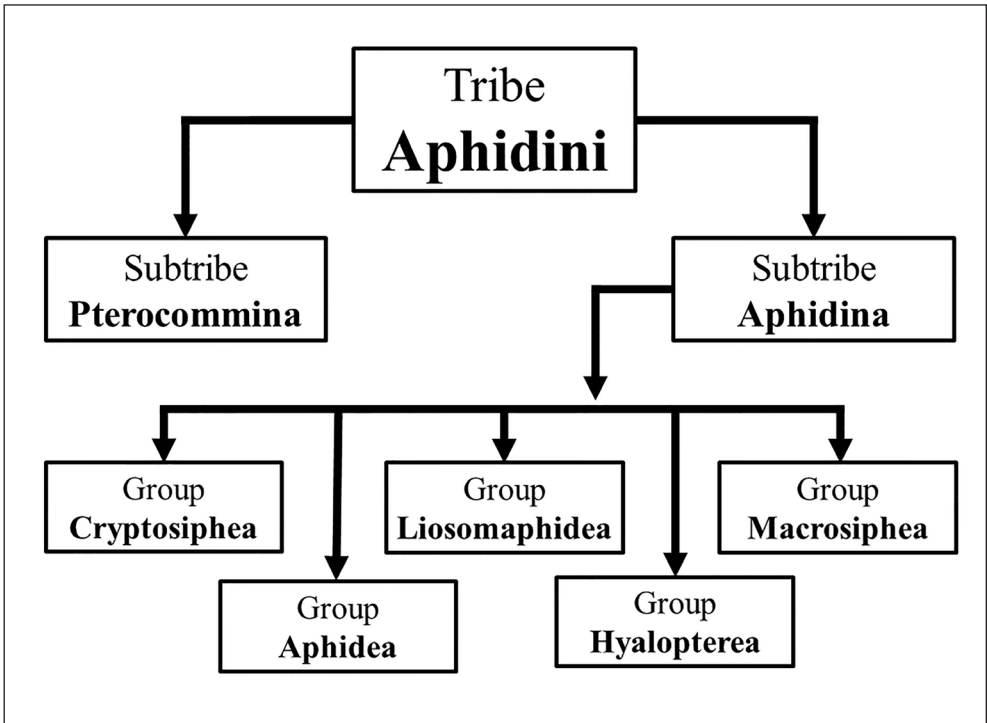


Fig. 7. The system of tribe Aphidini according to BÖRNER (1930).

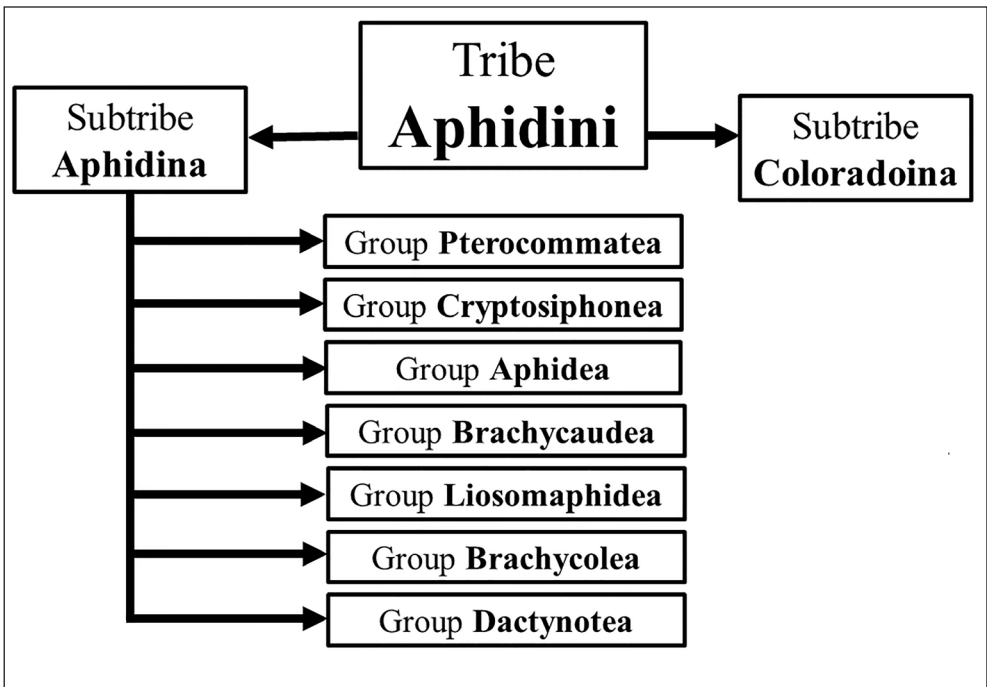


Fig. 8. The system of tribe Aphidini according to BÖRNER (1932).

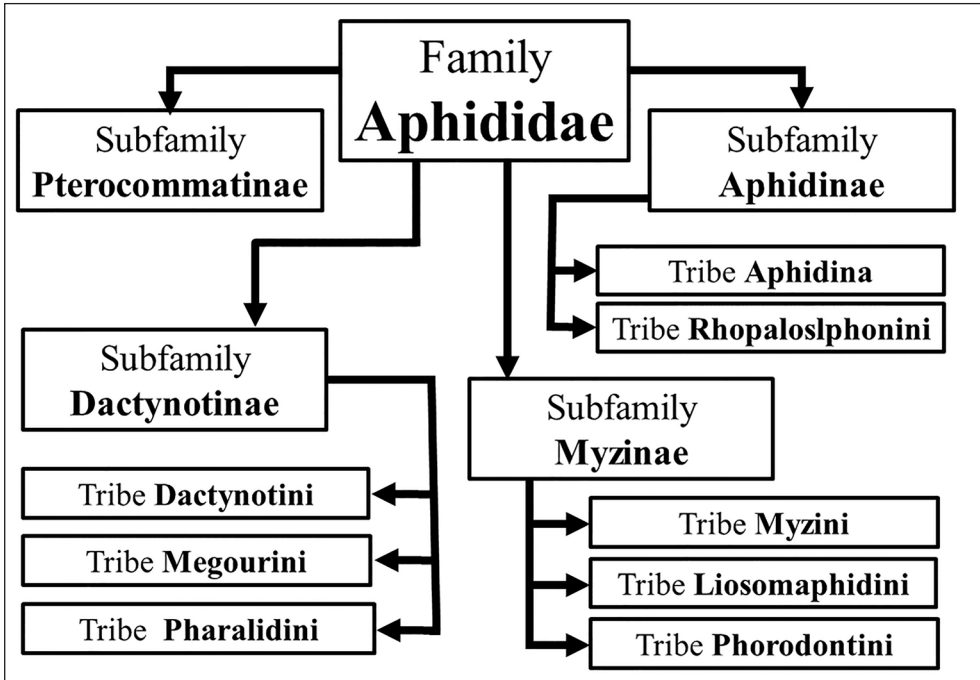


Fig. 9. The system of family Aphididae according to BÖRNER (1944).

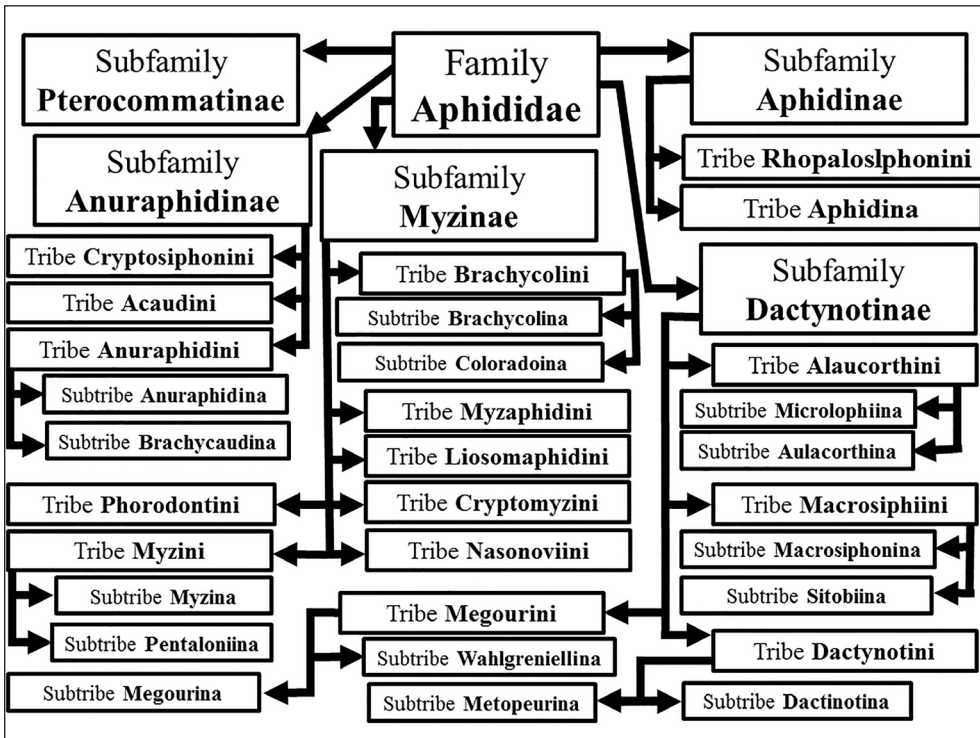


Fig. 10. The system of family Aphididae according to BÖRNER (1952).

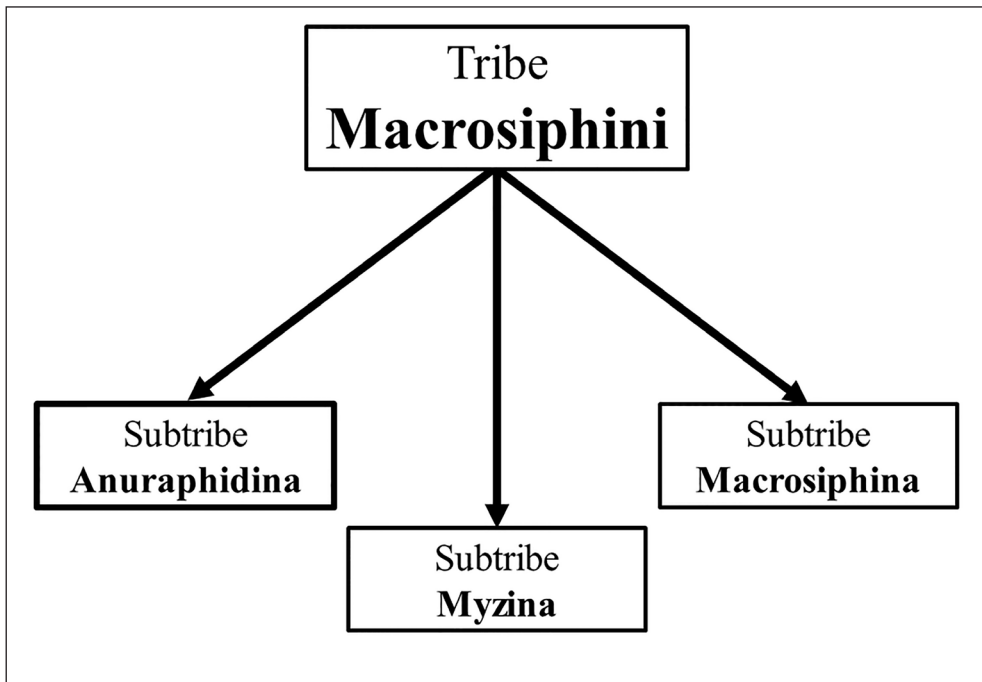


Fig. 11. The system of tribe Macrosiphini according to PINTERA (1969).

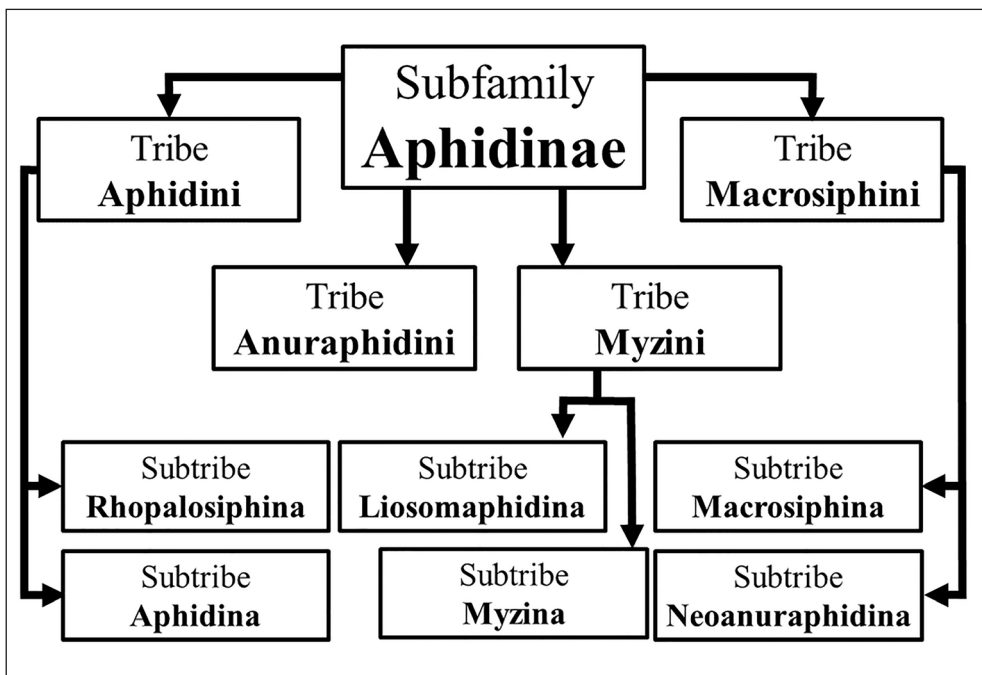


Fig. 12. The system of subfamily Aphidinae according to NARZIKULOV (1970).

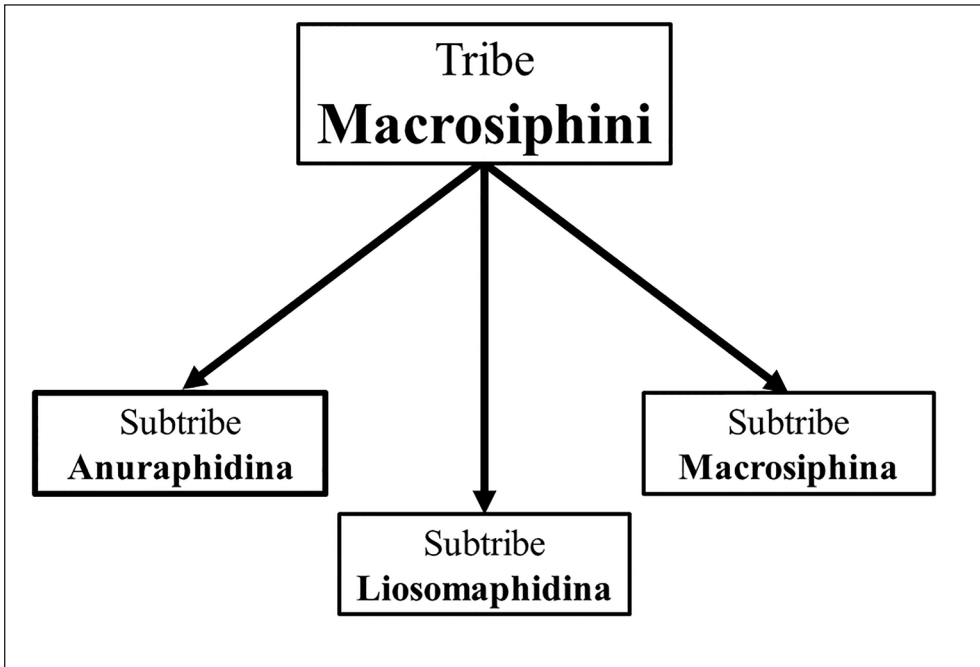


Fig. 13. The system of tribe *Macrosiphini* according to SHAPOSHNIKOV (1964).

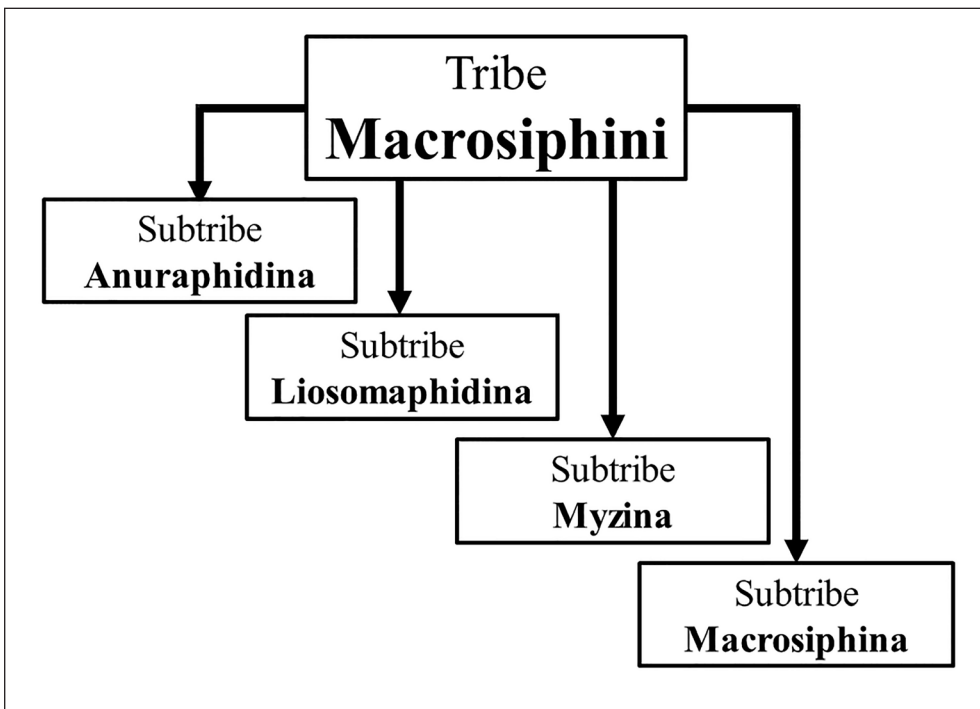


Fig. 14. The system of tribe *Macrosiphini* according to SHAPOSHNIKOV *et al.* (1998).

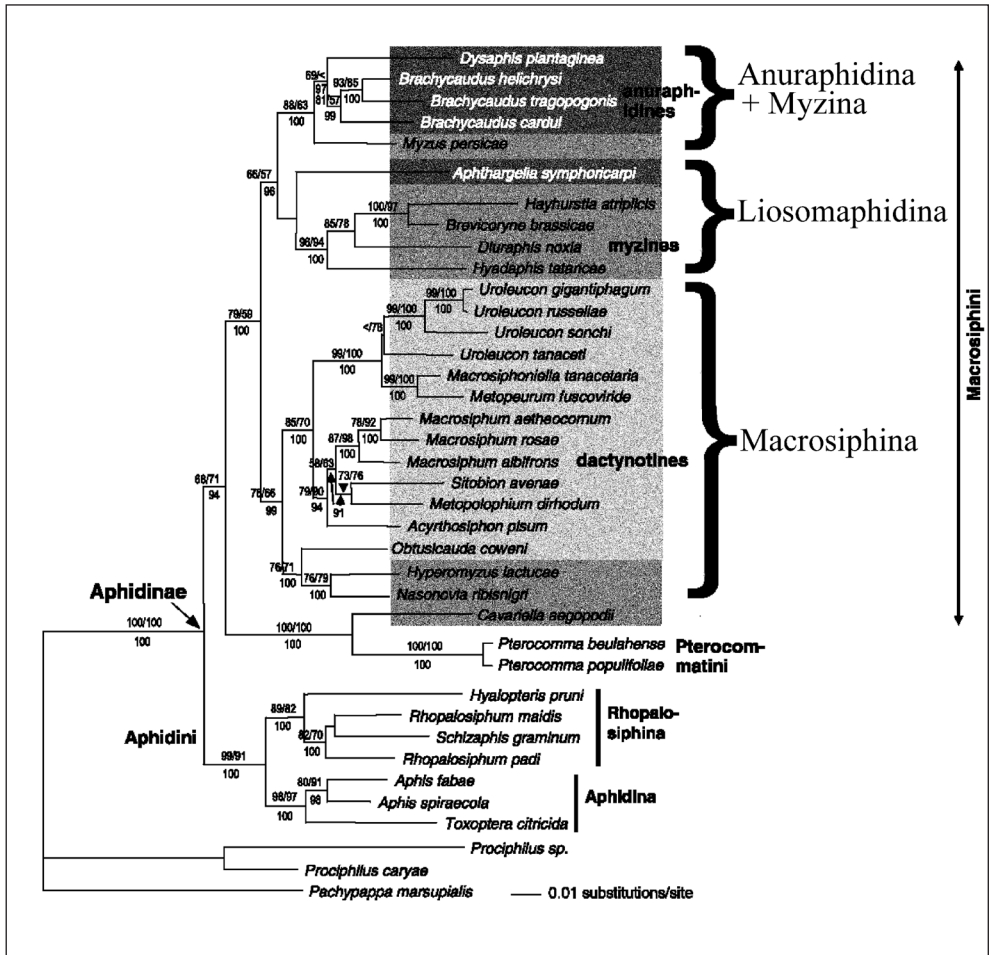


Fig. 15. Phylogeny of Aphidinae reconstructed from combined mitochondrial tRNA/COII and nuclear EF1 sequences (after von DOHLEN *et al.* 2006, with changes).

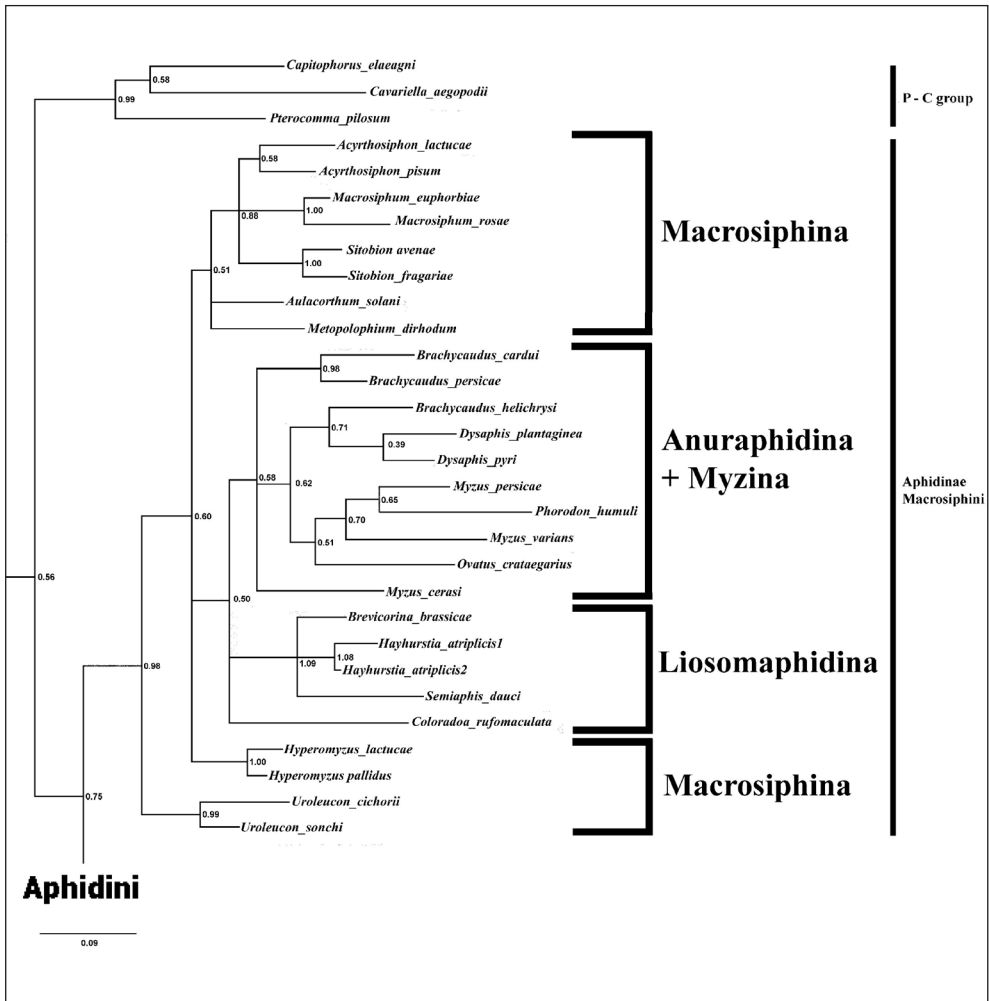


Fig. 16. BI analysis tree obtained from the combined data set (after PAPANOTIROPOULOS *et al.* 2013, partly with changes).



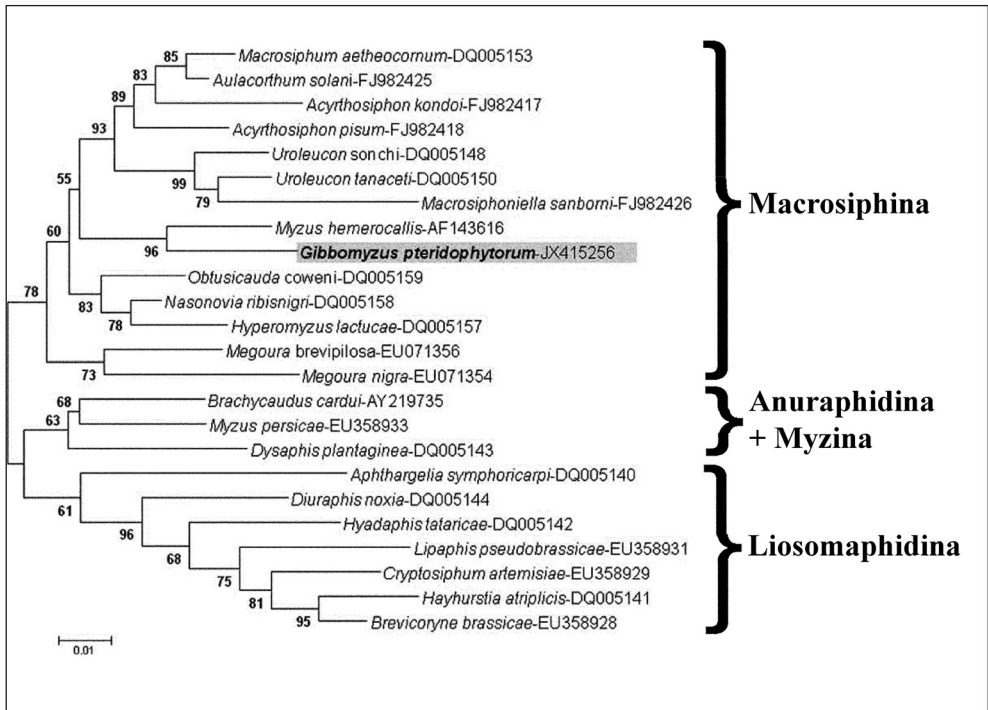


Fig. 17. Maximum likelihood tree obtained for elongation factor-1 alpha (EF1a) sequences from different Macrosiphini species (after NIETO NAFRÍA *et al.* 2013, with changes).

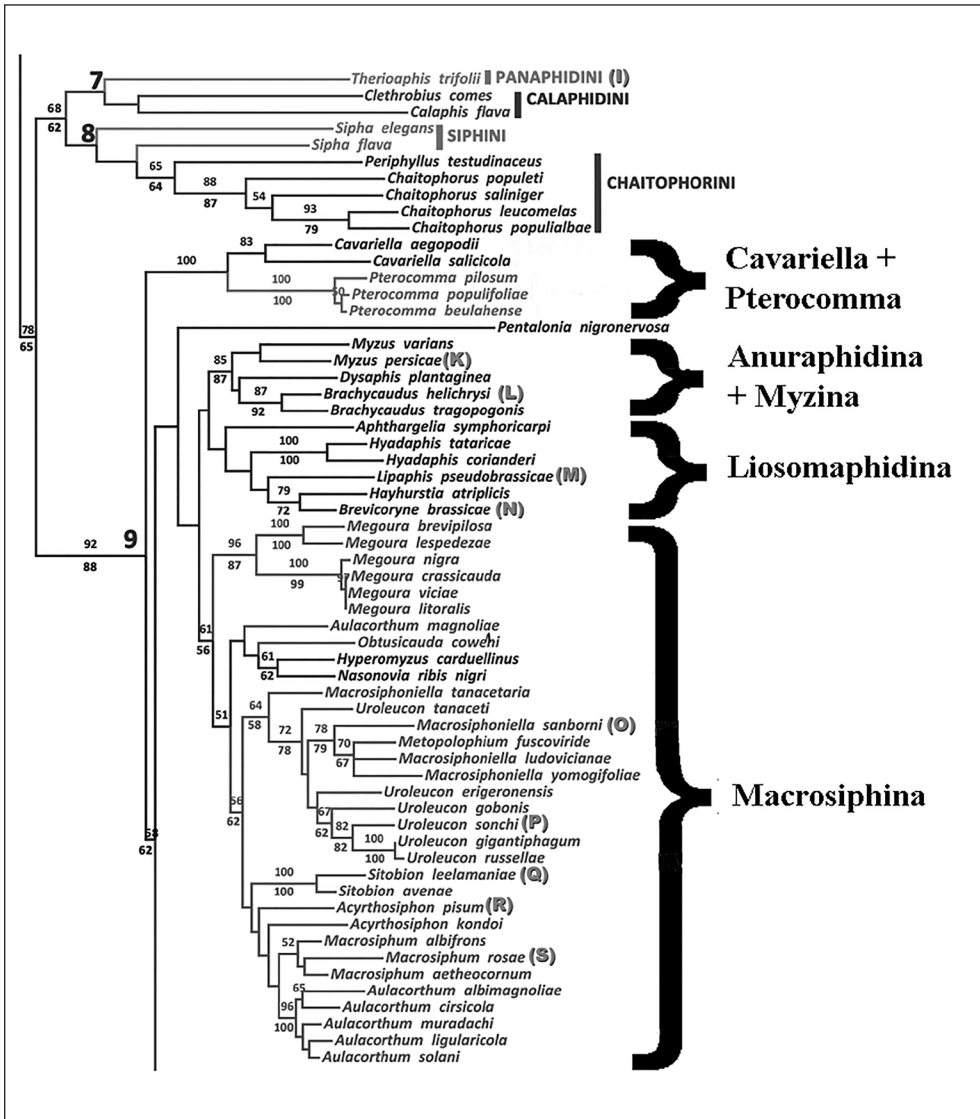


Fig. 18. Phylogenetic tree inferred from the concatenated dataset based on Maximum likelihood and Maximum parsimony (after REBIJITH *et al.* 2017, with changes).

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