

Henryk SZELEGIEWICZ

**Studies on the Tribe *Pterocommatini* MORDV. (*Homoptera*, *Aphididae*).
Part I. Phylogeny and Generic Classification**

**Studia nad plemieniem *Pterocommatini* MORDV. (*Homoptera*, *Aphididae*).
Część I. Filogeneza i klasyfikacja rodzajowa**

**Изучение трибы *Pterocommatini* MORDV. (*Homoptera*, *Aphididae*).
Часть I. Филогенез и родовая классификация**

[With 61 text-figures]

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INTRODUCTION

The present paper was first planned as a taxonomic revision of the Polish species of the subfamily *Pterocommatinae* sensu MORDVILKO, 1948. However, the difficulties encountered during its realization forced me to abandon the original concept and to broaden the scope of the subject first to include all the European, than all actually known species; as it appeared in the course of the work undertaken, all existing so far revisions can hardly be relied upon. Thanks to the valuable collaboration of the many of my colleagues from many

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different countries it has been possible to collect a large material covering the whole geographical range of the group, and thus to revise the descriptions of almost all known at present species. The factual material thus collected proved to be a good start for further morpho-comparative studies on the group in question. The studies were later extended also to the primitive groups of aphids. Without such additional studies the proper understanding and interpretation of the processes of morphological changes would be completely impossible. The supplementing of the morpho-comparative analysis by zoogeographical one, as well as an thorough analysis of the existing host relations, permitted to revise the existing concepts on the systematic position and phylogeny of the group and to base the generic classification on more reliable, more objective bases. The results of my research also throw a new light on the existing taxonomic difficulties within certain genera, viz. *Pterocomma* BUCKT. and *Plocamaphis* OEST.

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I. SYSTEMATIC POSITION OF THE *PTEROCOMMATINI*

Up to now no generally accepted system of aphids has been claimed to exist. Among many attempts to classify these insects, only three have been accepted more generally, and namely the generally applied in America and England classification of BAKER (1920) and popular in Europe those of MORDVILKO (1948) and BÖRNER (1930, 1952).

BAKER's classification, based on a very superficial and sometimes erroneous knowledge of the aphids morphology, undoubtedly is the least correct one and certainly may in the least pretend to reflect the existing relationships within the group in question. This system is nowadays being dropped even in America where it has been so commonly employed. The MORDVILKO's and BÖRNER's systems are in general fairly similar, and BÖRNER considered his system as an attempt toward a further development and perfection of the MORDVILKO's system. Certain authors even speak of only one system, developed by MORDVILKO, BÖRNER and HILLE RIS LAMBERS. BÖRNER's system

was thoroughly criticized by SHAPOSHNIKOV (1956). In my hitherto published papers I used the classification of MORDVILKO (1948), which, in my opinion, more than any other reflects the phylogenetic relations between various groups of aphids, and, more than any other, approaches the natural system. Unfortunately, MORDVILKO gave only a tentative system, not free from errors and simplifications, which he was not able to correct¹, and which requires a further elaboration. The system in question is being perfected mainly by Soviet aphidologists (AIZENBERG, 1956; SHAPOSHNIKOV, 1956). Certain changes and corrections are proposed in this paper too.

The aphid species discussed in the present paper have been included by the older authors into two, distant genera (BUCKTON, 1879), separated on the shape of siphunculi. This completely artificial classification was maintained by MORDVILKO (1948) and even by NARZIKULOV (1962). MORDVILKO was the first who brought the mentioned genera closer (1908), by including them together with the genus *Chaitophorus* KOCH into a newly established by him group *Chaetophorini*. In 1914 MORDVILKO established a separate group for the mentioned genera — *Pterocommini*, which he put together with the groups *Chaitophorini* and *Trichosiphonini* as subtribe *Chaitophorina* within the tribe *Callipterea*. The taxonomic distinctness of the discussed group has not been questioned so far². However, its systematic position and the relationship with other groups were looked upon very differently, and these differences of opinion persisted up to now.

In America first WILSON (1915) published a review of the group in question, expressing also his opinion on its systematic position. WILSON raised the group to the rank of tribe, and transferred all at a time known species to the genus *Pterocomma* BUCKT. certainly regarding the existence of two separate genera as groundless. Following OESTLUND (1887) the mentioned author treated the tribe *Pterocommatini* as a transitional group between *Chaitophorini* and *Lachnini*.

BAKER, who in his review of the *Pterocommini* (1916) still agrees with WILSON, several years later (1920) in his fundamental work "Generic Classification of the Hemipterous Family *Aphididae*" comes off with a different view. In this work the author distinguished, besides the genus *Pterocomma* BUCKT., again the genus *Melanoxantherium* SCHOUT., and an overlooked so far genus *Fullawaya* ESSIG. He put together the first two mentioned genera as the subtribe *Pterocommina* and for the third one he established a new subtribe *Fullawayina*, giving as the only justification the lack of siphunculi in *Fullawaya*

¹ MORDVILKO's classification has been published after his death as a key to the *Aphidodea* of the European part of the U.S.S.R.

² An exception constitutes a Dutch aphidologist VAN DER GOOT (1913), who, still before the publication of the MORDVILKO's work, very rightly included the discussed group into his new tribe *Siphonophorina* (this tribe covers entirely the subfamily *Aphidinae* as such it is understood in the present paper) but does not create a new group for it.

ESSIG¹. He included the mentioned subtribes, together with other ones, into the tribe *Callipterini* (this tribe corresponds to the subfamilies *Phyllaphidinae*, *Chaitophorinae* and *Pterocomminae* in MORDVILKO's system). BAKER makes one group of *Chaitophorina*, viz. *Pterocommina* and *Fullawayina* as opposed to the remaining *Callaphidini*, which is clearly visible in his key to the identification of the subtribes of tribe *Callipterini* and the diagram picturing the phylogeny of *Aphididae*. BAKER considered subtribe *Fullawayina* as a most advanced and specialized stem of this group thus emphasizing the "loss" of siphunculi as fact of a considerable phylogenetic importance. I gave the BAKER's views a little more attention, because they persisted in the American literature almost unchanged until the present time. The subsequent authors (OESTLUND, 1922; GILLETTE et PALMER, 1931; HOTTES et FRISON, 1931, and others) did not alter a thing in the BAKER system, but only added new genera or species. It was PALMER (1952) who first introduced several changes by putting all the species of the subtribe *Pterocommina* into one genus (*Pterocomma* BUCKT.), but still maintained a completely unjustified division into *Pterocommina* and *Fullawayina*; however, he underlines the similarity of the group in question to *Aphidinae* ("*Aphini*" in PALMER's work).

BÖRNER (1930), distinguished only one genus (*Pterocomma* BUCKT.), included it into the tribe *Aphidini* (corresponding to the subfamily *Aphidinae* in the present paper) as a subtribe *Pterocommina*, as opposed to all remaining *Aphidini*, which he treated as the subtribe *Aphidina*. Unfortunately, as soon as in the supplement to his paper (p. 69–171) he changed his previous, right view, and, basing on the eye structure, divided the tribe *Aphidini* into subtribes *Brevicorynellina* (with one genus *Brevicorynella* NEVSKY) and *Aphidina*. The genus *Pterocomma* BUCKT. has been included by him into the second subtribe, in which several minor groups were made out, and among others a group *Pterocommea*. To the last mentioned group he numbered, however, basing mainly on the shape and length of cauda, besides the genus *Pterocomma* BUCKT., also several unrelated genera.

In 1952 BÖRNER raised *Pterocommatini* to a rank of subfamily, stating clearly that "... verwandschaftliche Beziehungen bestehen entgegen bisheriger Annahme weder zu den Lachniden noch zu den Chaitophoriden" (BÖRNER, 1952, p. 66). By contrast to his earlier work he did not consider this group as of equal rank to the remaining *Aphidinae* (*Aphididae* in BÖRNER's work), but divided these into several subfamilies. These subfamilies are a typical example of an artificial, "horizontal" classification, which does not reflect the phylogenetic relations. A fuller picture of his views can be found in "Handbuch der Pflanzenkrankheiten" (1957) where six genera have been listed as

¹ Isolation of the genus *Fullawayia* Essig into a separate subtribe is without any ground as in these aphids the siphunculi are present. Evidently BAKER overlooked the siphunculi though they are well visible also in the Canada-balsam slides which were used by BAKER and other American aphidologists.

belonging to *Pterocommatinae*. The genus *Fullawaya* ESSIG was separated by BÖRNER from the other ones, still upon the absence of siphunculi. This is incomprehensible as the only one microscopic slide possessed by BÖRNER and containing one single specimen of the mentioned genus shows the siphunculi very plainly. The subdivision of the genus *Pterocomma* BUCKT. into *Pterocomma* s. str. and *Clavigerus* SZEPL. (characterized by the shape of siphunculi) took place in both BÖRNER's works, this of 1952 and that of 1957. While this subdivision in the BÖRNER's catalogue seems to have been a consistent one (the subgenus *Clavigerus* SZEPL. contained only the species of the *salicis* group), the classification in the "Handbuch" (1957) can hardly be named a consistent one. Thus, for instance two allied species *P. bicolor* (OESTL.) and *P. steinheili* (MORDV.) were included into two separate subgenera.

MORDVILKO, whose early concepts on the classification of the group in question have been characterized above, did not change them in his subsequent papers (1928, 1934), but only raised certain groups to higher taxonomic ranks. In 1948 he placed the said group as a separate subfamily *Pterocomminae*, between the subfamilies *Chaitophorinae* and *Aphidinae*, thus marking its transitional character.

AIZENBERG (1956) treated *Pterocommatini* as a subfamily, and still paid attention to its transitional character between *Aphidinae* and *Chaitophorinae* (and even *Callaphidinae*). However, he emphasized its relationship with *Aphidinae*, accepting even a possibility of a union of these two groups.

HEINZE's paper (1961) devoted to the Middle-European species of the *Pterocommatinae* have brought no new concepts as compared with BÖRNER. The keys to the identification of species (particularly that to the identification of species of the genus *Pterocomma* BUCKT.) are hardly useful, since the author, basing on a too scanty material, completely omitted the morphological variation. However, HEINZE has for the first time noticed the particular location of siphunculi in the species of the genus *Plocamaphis* OESTL. and the form of stigmata in the genus *Neopterocomma* H.R.L.

It is fairly plain from the above given evolution of concepts on the systematics of *Pterocommatini* that the majority of the authors with the exception of VAN DER GOOT (1913) and BÖRNER (1930, 1952) recognized the similarity of the said group to the subfamily *Chaitophorinae*, and even to *Lachninae*, and placed it either together with the groups mentioned in one single taxonomic unit, or near these groups. However, as the years passed and the better knowledge of the aphid morphology was acquired, the phylogenetic relation of *Pterocommatini* with *Aphidinae* was more and more emphasized.

It is worthy of noting, that the mentioned authors, indicating the evident relationship of the discussed group with *Chaitophorinae* and even *Lachninae* or *Callaphidinae*, did not even try to look for the evidence to support their views, and they had noticed only the general similarity of *Pterocommatini* to the mentioned groups. How misleading such a "similarity" may be, is shown

clearly by the fact that other authors such as HILLE RIS LAMBERS (1935) had pointed out the resemblance of *Pterocommatini* to the genus *Anuraphis* DEL GU. (and thereby to the *Aphidinae*), and RUSSANOVA (1942) even described one of the forms of *Pterocomma pilosum* BUCKT., under the name *Anuraphis magnituberculata*, misled by the apparent "habitus" similarity. According to BÖRNER (1952) the said aphids are not even in the slightest degree directly related to the subfamily *Chaitophorinae*, not to mention *Lachninae* or *Callaphidinae*. This may be born out by a morphological analysis of these aphids. The hairiness of the body, which presumably strongly determined placing these groups near *Chaitophorinae* and *Lachninae*, is not of a particular importance, as it is not only confined to them but it is also to be found in all primitive species of nearly all subfamilies, including *Aphidinae* (for instance in the genus *Toxopterella* H.R.L.).

As it is being shown in the chapter devoted to the morphological analysis, *Pterocommatini* are characterized by the same morphological characters as the *Aphidinae*, except that these characters are to be found in certain combinations absent in *Aphidinae*. All processes of morphological changes peculiar to *Aphidinae* can be observed in *Pterocommatini* but they are more gradual and their direction in certain cases shows some peculiarities. The group in question belongs, because of its systematic position, to the same phylogenetic stem as *Aphidinae* and its separation into a parallel subfamily linking *Chaitophorinae* and *Aphidinae*, as it was done by MORDVILKO, seems to be completely groundless. While including this group into the *Aphidinae*, I consider it justified to treat it as a separate tribe, parallel to the tribes *Aphidini* and *Macrosiphini* which contain all remaining genera of the hitherto known subfamily *Aphidinae*¹. In such understood subfamily the tribe *Pterocommatini* constitutes a primitive secondary evolutionary branch which separated comparatively early from the group of common ancestors with the present subfamily *Aphidinae*. It may be supposed that the main stem of *Aphidinae* — the tribes *Aphidini* and *Macrosiphini* passed over onto the *Rosaceae* and *Caprifoliaceae* owing to its heteroecy and its plasticity toward the host-plants it spread over all angiospermae plants, and differentiated rapidly becoming the most rich in species groups of all existing ones. However, the ancestors of the nowadays living *Pterocommatini* probably retained their primitive connections with *Salicaceae* and their monoecy during their development cycle which checked the tempo of their evolution and reduced the tribe to one small, relict group.

Taking into consideration the above said the classification of the subfamily *Aphidinae* runs as follows:

¹ It was already AIZENBERG (see SHAPOSHNIKOV, 1956) who maintained one tribe system within the known subfamily *Aphidinae* agruing that the differences existing between the groups are, as compared with tribes of other subfamilies, not deep enough to justify the splitting.

- Subfamily: *Aphidinae* LATREILLE
 Tribe: *Pterocommatini* MORDVILKO
 Subtribe: *Pterocommatina* MORDVILKO
 Subtribe: *Paducina* subtr. nov.
 Tribe: *Aphidini* LATREILLE
 Subtribe: *Rhopalosiphina* BÖRNER
 Subtribe: *Aphidina* LATREILLE
 Tribe: *Macrosiphini* MORDVILKO¹

II. GENERAL MORPHOLOGY

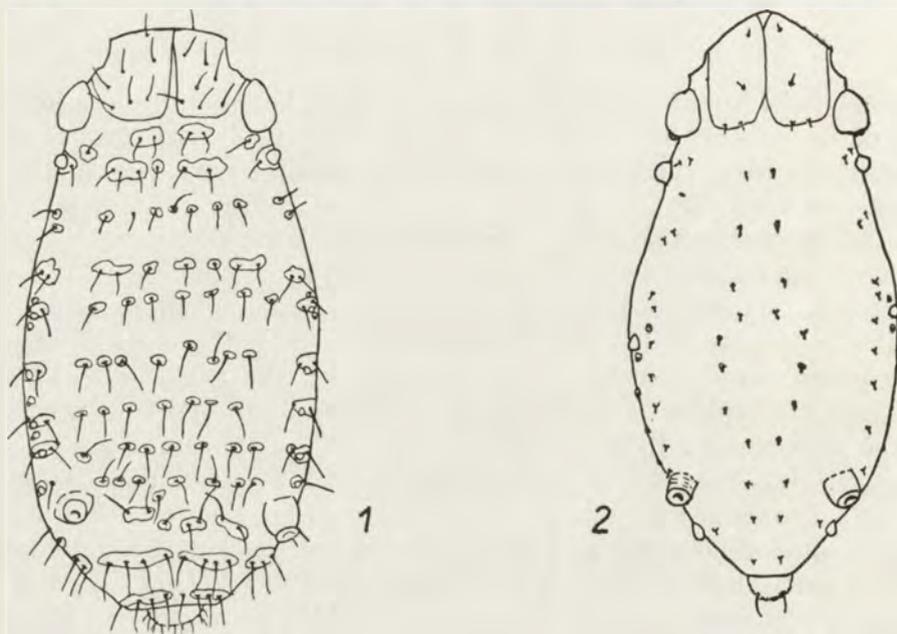
A superficial knowledge of the morphology of the group in question, overrating of the value of the "habitus" or certain morphological features treated in abstraction from the general evolutionary trends, gave rise in the past to many contradictory views both with regard to the systematic position of the group within the family *Aphididae* and to its phylogenetic relations with other groups of aphids. A complete lack of systematic criteria based on an thorough morphological analysis in a close relation with the evolutionary trends was not benefited the establishing of a satisfactory systematics of the group. Any such analysis compared with the evolution "charts" of other groups of aphids is indispensable for the purpose described above and only this may throw a light on primitiveness or secondariness of any discussed characters. Unfortunately, in the hitherto published papers only the diagnostic "key" characters were taken into account, and they were treated as equivalent to phylogenetic features. Therefore, in the present paper I drew my attention particularly to the atavistic characters and relict organs, and tried to uncover the main morphological changes which took place in the evolution, as well as factors which may have governed them. As it was already stated by SHAPOSHNIKOV (1956) the gradual morphological changes "play a decisive role in the interpretation of the systematic relations, but as they can not be used in the diagnosis they are overlooked by many authors" (SHAPOSHNIKOV, 1956, p. 233-234).

Arrangement of the dorsal body hairs

The chaetotaxy was first used as diagnostic features by BÖRNER, who applied it first in the taxonomy of the family *Phylloxeridae* (1908) and then *Aphididae* (1930, 1952). The mentioned author appreciated both the arrangement of the dorsal hairs and their shape, as well as the number of hairs on

¹ This subtribe is usually sub-divided into following groups: *Anuraphidea*, *Myzea* and *Macrosiphea*, the division, unfortunately being, as the paper of HILLE RIS LAMBERS (1950) and those of SHAPOSHNIKOV (1951) had shown, an artificial, "horizontal" one, such which does not reflect the phylogenetic relationship.

the first tarsal joints. Other authors (HILLE RIS LAMBERS, 1947; PAŠEK, 1953) employed for diagnostic purposes also the chaetotaxy of the last joint of rostrum and that of the end of processus terminalis. BÖRNER, who considered the chaetotaxy as the foundation of his system, with no doubt overrated the importance and value of this structure (particularly the chaetotaxy of the tarsi), and by using it as a sole diagnostic criterion to all groups and overlooking the biological properties, certainly in many cases created completely artificial taxonomical units.



Figs. 1, 2. Chaetotaxy of first instar: 1 — primitive in *Pterocomma smithiae* (MONELL), 2 — secondary in *Aphis intybi* KOCH.

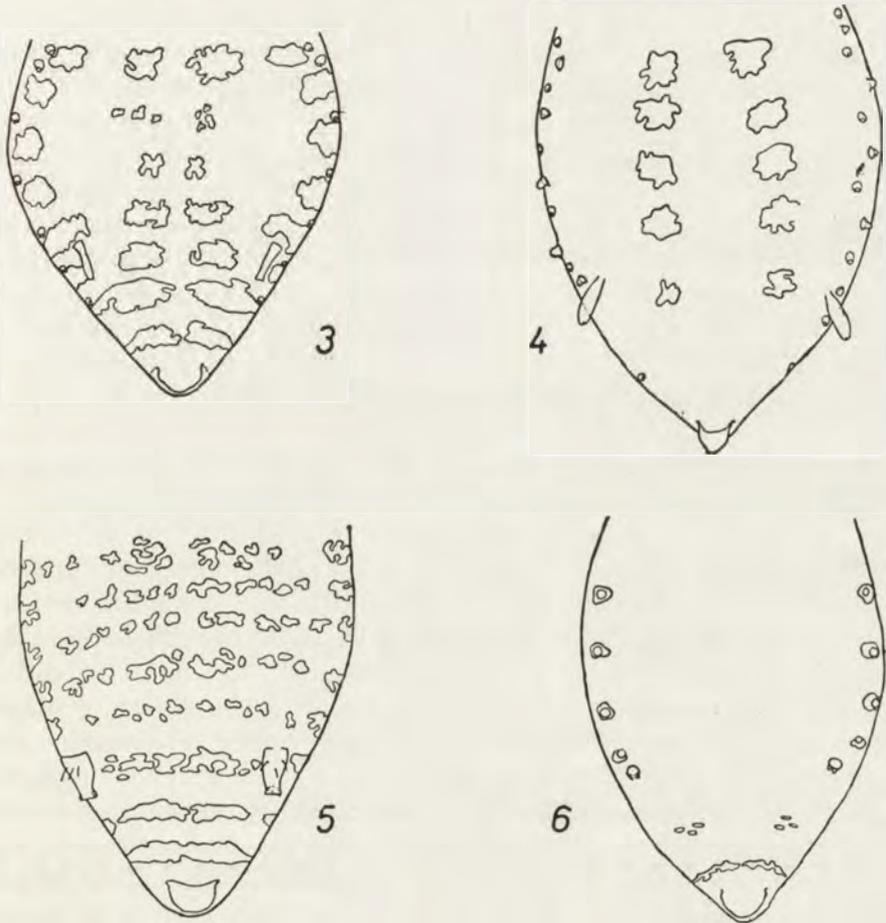
A certain phylogenetic importance evidently could be ascribed to the number and the arrangement of the dorsal hairs. BÖRNER (1930) distinguished two different types of arrangement of the dorsal body hairs. One (fig. 1), regarded generally as a primitive type, is characterized by a great number of hairs scattered without any order on tergites, and it is to be found in all primitive forms among the different groups. The second type (fig. 2) shows a small number of hairs on tergites (6 or more), which are arranged in regular longitudinal rows (two marginal, two pleural and two spinal ones). The straight hairs are also regarded by BÖRNER as primitive ones; they are acuminate and persisted in all now living aphids on the ventral side of body. Other types of hairs, such as bluntly terminated, bifid, flattened or broadened at the apex are regarded by BÖRNER as secondary ones.

The primitive type of hairs had been retained by all species of *Pterocom-*

matini, both in the arrangement and in the form. Only the larvae of *Paducia* HOTT. et FRIS. show a secondary type of hairs arrangement, different from that in the adults (HILLE RIS LAMBERS, 1952).

Degree of sclerotization of the dorsal side of body

The importance of this character in the taxonomy of aphids had been already emphasized by HILLE RIS LAMBERS (1938) and BÖRNER (1952). SHAPOSHNIKOV (1956) who studied this character in primitive *Macrosiphini*, regarded the cuticula sclerotized in the form of separate plates arranged in longitudinal rows, as a primitive feature. Such type of sclerotization corresponds to the location of the glandular plates from which, in his opinion, it had evolved.



Figs. 3-6. Different types of sclerotization of abdominal tergum in apterous viviparous females: 3 - *Pterocomma populeum* (KALT.), 4 - *Plocamaphis borealis* OSSIANN., 5 - *Stau-roceras chaetosiphon* BÖRN., 6 - *Fullawayia braggi* (GILL. et PALM.).

The fusion of the sclerites into transversal plates, or even the total sclerotization of cuticula, is regarded by him as a secondary character. It turned out, however, that the sclerotization degree depends not only on the evolution of a given group of aphids, and conditions under which the evolution occurred, but also on the influence exercised by the actually acting environmental factors, such as temperature, humidity, physiology of the host-plant etc., and that this may vary even within one species (HILLE RIS LAMBERS, 1949). Despite of the fact that characters mentioned constitute an easy and generally accepted taxonomic criterion, it should not be given too much phylogenetic importance, and we should never forget its close dependence on the habitat.

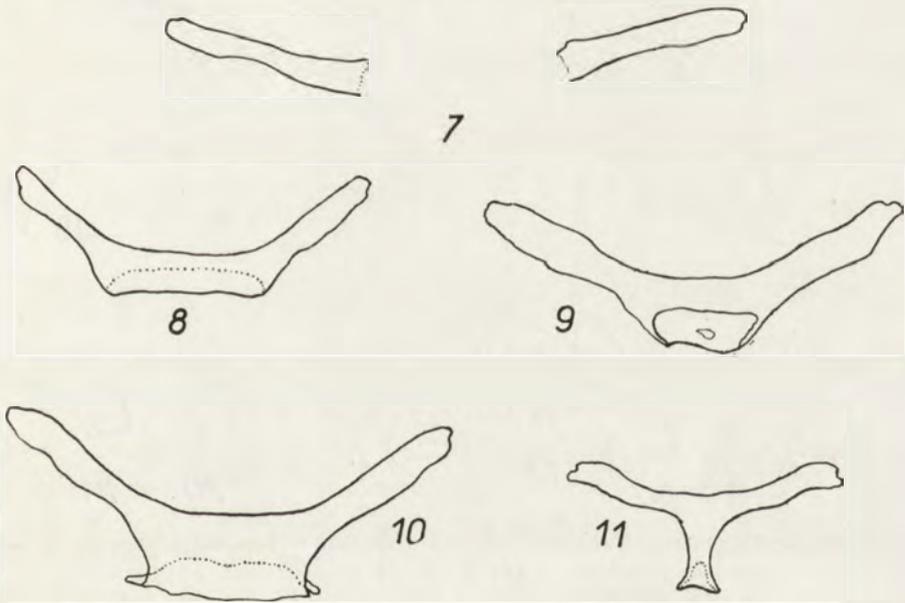
The most frequent type of sclerotization of the dorsal side of body, which may be observed in *Pterocommatini*, is that one in form of separate sclerites or plates covering the particular abdominal tergites (fig. 3) and less frequent in the form considered by SHAPOSHNIKOV as primitive (fig. 4). A secondary reduction of the sclerotization either in the form of splitting of the plates into minute, numerous sclerites (fig. 5) or their complete or almost complete disappearance (fig. 6) can be observed in the genera *Stauroceras* BÖRN. and *Fullawaya* ESSIG. This process is with no doubt correlated with the biology of these species. They live in the cracks of bark of tree trunks, under soil particles brought by ants, or completely underground, on the *Salix* roots. A similar phenomenon of plates reduction can be encountered in the species of *Chaitophorus* KOCH, which live in identical habitats. The strong sclerotization of the cuticula appears to have value as a certain kind of defensive device protecting the aphids from the loss of humidity and this may be observed particularly in the xerophilous species. The aphids living in the soil or in some hiding places are less endangered by the loss of water than those living in more exposed habitats. This may throw a light on the disappearance of plates and sclerites in these species.

The process of the reduction of sclerites is further advanced among the species living in the soil, on the roots of plants (*Fullawaya* ESSIG and certain *Plocamaphis* OESTL.) than in those aphids which lead a semi-hidden way of life, in the cracks of trunks (*Neopterocomma* H. R. L. and *Stauroceras* BÖRN.). This may be a further example of an influence of the habitat conditions on the evolution of certain morphological characters. The reverse evolutionary tendencies also may be observed in the group discussed. *Pterocomma smithiae* (MONELL) exhibits a strong, total sclerotic tergites, without membraneous part; particular tergites are, however, separated by membraneous sutures. A considerably further advance in sclerotization may be noticed in *Paducia* HOTT. et FRIS. where also the sutures are sclerotized, to the effect of forming of a sort of one single dorsal plate, covering the whole surface of body, save for head, pronotum and the VIIIth abdominal tergite, which have separate cover. The causes of this sclerotization in *Paducia* HOTT. et FRIS. are not known, in any case they cannot be brought down to their actual habitat conditions

(the species live on roots of *Salix* sp.). However, it may constitute a certain evidence that the present ecological niche has been occupied by them relatively recently. It should be emphasized that this view appears to be strongly contradicted by the reduction of eyes and antennae in those species — the changes brought about by the subterranean way of life or life in galls. The correct interpretation of these phenomena seems not to be possible as yet.

Marginal, pleural and spinal tubercles

They are cuticular processes on various tergites. According to their location (fig. 17), a pair of marginal, pair of pleural and a pair of spinal tubercles may be distinguished. BÖRNER regarded the marginal tubercles as a rudiment of posterior angles of the primeval paratergites, OESTLUND (1922) as structures which replaced the glandular plates and MORDVILKO (1914, 1934) and HOTTES (1928) consider them as transformed glandular plates.



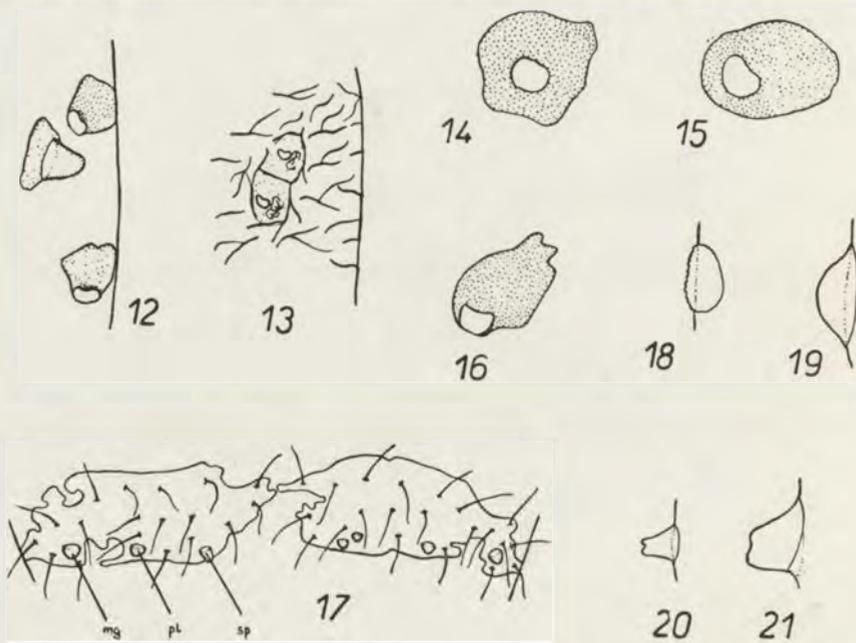
Figs. 7-11. Mesothoracic furca: 7 — *Neopteroomma asiphum* H. R. L., 8 — *Pterocomma populeum* (KALT.), 9 — *Pterocomma bicolor* (OESTL.), 10 — *Plocamaphis goernitzi* BÖRN., 11 — *Dactynotus obscurus* (KOCH).

BÖRNER's view is the least probable, as it does not explain the origin of the pleural and spinal tubercles which are of identical structure with the marginal ones. The most probable seems to be the conception given by MORDVILKO. The glandular plates are arranged similarly as the tubercles, into marginal, pleural and spinal pairs. They are to be found only in those primi-

tive species which are devoid of tubercles. So far nobody was able to find both structures together. The MORDVILKO's hypothesis is further supported by the fact that in their primitive form (for example in *Stauroceras* BÖRN.) the tubercles strongly resemble the wax glands and were often confounded with them; inside the marginal tubercles there are longitudinal hypodermal cells, which do not differ from those of the glandular plates (MORDVILKO, 1934).

In my opinion, the tubercles should be regarded as typical rudimentary structures which are just in a state of being reduced, and which play no functional role in aphids. The fact of their disappearance and their inconstancy within the species, and even within a morph, strongly supports this idea.

SHAPOSHNIKOV (1956), basing on MORDVILKO's presumption, regarded the six-row arrangement of tubercles as a primitive character, and the four-row,



Figs. 12, 13. Arrangement of spiracles in the first two abdominal segments: 12 — *Pterocomma populeum* (KALT.), 13 — *Myzus persicae* (SULZ.).

Figs. 14-16. Shape of spiracles: 14 — *Neopterocomma asiphum* H. R. L., 15 — *Plocamaphis goernitzi* BÖRN., 16 — *Pterocomma populeum* (KALT.).

Figs. 17. Arrangement of tubercles on the seventh abdominal tergite of *Pterocomma pilosum konoii* HORI (fundatrix); mg — marginal, pl — pleural, sp — spinal tubercle.

Figs. 18-21. Types of marginal tubercles: 18 — *Stauroceras chaetosiphon* BÖRN., 19 — *Pterocomma pilosum konoii* HORI, 20 — *P. bicolor* (OESTL.), 21 — *Plocamaphis goernitzi* BÖRN.

and particularly the two-row arrangement as a secondary feature. The large, flat tubercles or only slightly convex ones are considered by him as original ancestry type, while the diminishing of tubercles and their "bulging" (fig. 18-21) as a secondary phenomenon. The process of reduction and differentia-

tion of marginal tubercles takes a different course in different groups of aphids and even in different species or morphs it may prove to have its own direction, although a general common pattern is always visible. As yet these problems have been studied only in the tribes *Aphidini* and *Macrosiphini* (SHAPOSHNIKOV, 1956) and in the subfamily *Anoeciinae* (ZWÖLFER, 1957).

While marginal tubercles persisted in all *Pterocommatini* as well as in other groups of aphids, pleural ones are to be found only on certain tergites in the species of *Paducia* HOTT. et FRIS. and exceptionally on the VIIth or VIIIth abdominal tergite in *Pterocomma pilosum konoï* HORI in TAKAHASHI. The spinal tubercles persisted unchanged in *Neopterocomma* H. R. L., partly in *Paducia* HOTT. et FRIS. and exceptionally on the last two abdominal tergites in *Pterocomma pilosum konoï* HORI in TAKAHASHI.

The phylogenetic reduction of marginal tubercles in *Pterocommatini* follows always a certain pattern. First disappear the tubercles of the VIIIth tergite which are no more present in the recent species. Next the tubercles of meso- and metanotum (they can be found only in certain morphs of some species) undergo a reduction, so that only those on pronotum and first seven abdominal tergites remain. The species of *Neopterocomma* H. R. L., *Stauroceras* BÖRN., *Fullawaya* ESSIG, *P. pilosum konoï* HORI in TAKAHASHI and certain morphs of *P. populeum* (KALT.) show just such a degree of reduction, which is, besides, common for the whole subfamily *Aphidinae* and the subfamily *Anoeciinae*, and even may turn out as peculiar to all tubercle-bearing aphids.

As I stated above, the further reduction of the marginal tubercles takes a different course in the remaining two genera of *Pterocommatini*, e. i. *Pterocomma* BUCKT. and *Plocamaphis* OESTL. While in *Pterocomma* BUCKT. a somewhat irregular process can be observed, that in *Plocamaphis* OESTL. seems to be of a regular type.

In the "regular" process of reduction the tubercles disappear gradually and successively, and first from the posterior abdominal tergites. The reduction of tubercles on a given tergite is a total one and constitutes a constant character for a given species or species group. Thus in *P. martini* RICHARDS a full set of tubercles can be still observed, but in the species of *floculosa* group the tubercles persist only on pronotum and first six abdominal tergites, while in *amerinae* group they occur only on pronotum and first four abdominal tergites. The only tubercles which remained in *P. terricola* HOTT. et FRIS. seems to be those on the pronotum and first three abdominal tergites.

The process of a "irregular" reduction of marginal tubercles is characterized by first disappearance of a pair on the fifth abdominal segment, followed by a reduction of those on the sixth and seventh, later one by vanishing of those on first four abdominal segments, and finally by their total reduction on abdomen, while sometimes they may occasionally be retained on pronotum.

One can see, therefore, that the process of reduction of marginal tubercles

in *Pterocommatini* shows, at its final course, a definite peculiarity and does not resemble that in others *Aphidinae*, and its "regular" type shows certain similarity with that in *Anoeciinae*. The course of tubercles reduction in *Pterocomma* BUCKT. ("irregular" type) exhibits certain analogies with the similar process in *Macrosiphini*.

The shape of mesothoracic furca

By this term we understand the double cuticle ingrowth inside the meso- and metathorax, which occurs only in the adults. The metathoracic furca is always double, composed of two apodemal cones. The shape of mesothoracic furca is variable within the groups, and it is because of its differentiation that it has been used by BÖRNER as a diagnostic feature. BÖRNER's opinion has been expressed in his catalogue (1952). In winged morphs both cones of furca are connected by a kind of a bridge and inserted on a special shaft (fig. 11). Such a type of furca is regarded by BÖRNER as a primitive, original type. In the apterous morphs the shaft is shortened, so that the fused arms of furca are inserted directly on the sternite (fig. 8-9), without its partition. In the more advanced species the furca lose their bridge (fig. 7) and becomes similar to the metathoracic furca. According to BÖRNER this process is caused by the enhanced reproduction function of the apterous morphs and the reduced furca may be the measure of changes which they had acquired. Thus the particular small groups of aphids are all characterized by a similar type of furca which may play a certain role in the diagnosis.

The interpretation of BÖRNER contains, however, a basic contradiction. If process mentioned occurs in morphs of all species, than it must have taken place independently in various groups, the result being that each of them must have evolved a different furca "pattern". As the analysis of a large material of various groups had shown, this is not the case, and the said feature is not even typical for genera. An investigation of the mesothoracic furca in the wingless morphs of the subfamily *Aphidinae* had also shown that the primitive species already had attained the highest degree of its reduction. Quite unexpectedly, however, a "primitive" type of mesothoracic furca appears in the most advanced, and phylogenetically beyond a doubt the youngest species of *Aphidinae*, and a similar phenomenon can be met with in other subfamilies. As it is little doubt that these forms derived from those with the most simple type of furca (e. g. *Macrosiphum* PASS. from the "*Anuraphis*" group — see HILLE RIS LAMBERS, 1950; SHAPOSHNIKOV, 1951), the simplification must have been here a secondary process, which is clearly incompatible with the principle of irreversibility of the evolution.

By applying the BÖRNER's interpretation to the morphological analysis of the mesothoracic furca in *Pterocommatini*, we arrive to the identical conclusion. All primitive genera and species should, in the light of his hypothesis,

have the most complicated and the most specialized one — the most primitive type of mesothoracic furca. BÖRNER's interpretation, treating the process of changes of the organ mentioned separately from its function, certainly turns end for end.

The process of differentiation of the mesothoracic furca is with no doubt strongly connected with the locomotory function which it performs, as they are the point of attachment of the leg muscles. In primitive forms, usually little agile, the furca is very simple and this type of structure can be considered as a primitive, original one. In more agile, more specialized species this organ becomes more "compact" owing to the development of legs muscles which need stronger attachment point. It must be emphasized that the differentiation process of the mesothoracic furca runs independently in various morphs of the same species and usually is the least advanced in the least agile fundatrices, and conversely, the most developed in the wingend morphs. Such an interpretation of the differentiation process of the organ mentioned excludes the possibility of using it as a diagnostic feature, however, it may be very useful in the consideration of the phylogeny of small groups (at most within a genus).

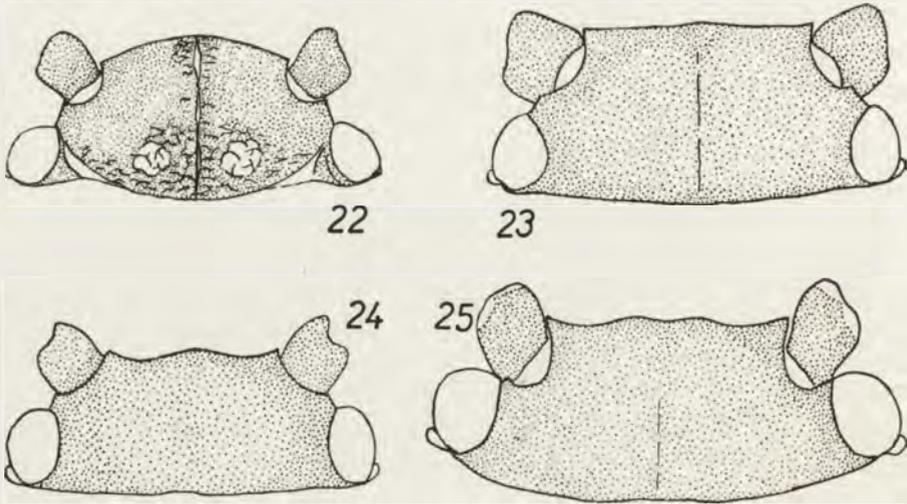
Arrangement and shape of stigmata

In accordance with the general tendency towards the reduction of the size of the body, the first abdominal segment, as a rule its sternite, undergoes also a certain changes (MORDVILKO, 1914). The greatest reduction may be observed in the subfamily *Aphidinae* which is the youngest phylogenetically group of aphids. Depending on the degree of reduction of the first sternite, two first stigmata may get closer together and this was used by BÖRNER (1952) in his diagnosis of groups within the subfamily *Aphidinae*. A thorough study of this process was given by SHAPOSHNIKOV (1956) and IVANOVSKAYA (1960) who distinguished two trends in the evolution of *Aphidini*, correlated with the process of disappearance of the marginal tubercles.

It is little doubt that *Pterocommatini* are a very primitive group in this respect. They show only a slight degree of reduction of the first abdominal segment, and accordingly the first stigmata are well set apart (fig. 12), a condition regarded by BÖRNER as a normal one.

The shape of the stigmata and their position on the plates show greater diversity. The oval stigmata situated in the centre of the plates are considered as being of primitive type, and the other ones may be easily derived from them (SHAPOSHNIKOV, 1956). Such a type of stigmata is to be found only in the genus *Neopterocomma* H. R. L., which in many respects is regarded as a primitive one among the *Pterocommatini*. In other genera all three types of stigma (oval, round and reniform) are present, and their occurrence shows no regularity. However, a regularity can be noted in the location of the stig-

mata. Here a process takes place of shifting the stigma from the centre of the plate to its posterior margin (fig. 14-16).



Figs. 22-25. Head: 22 — *Neopteroomma asiphum* H. R. L., 23 — *Fullawaya braggi* (GILL et PALM.), 24 — *Pterocomma populeum* (KALT.), 25 — *Plocamaphis goernitzi* BÖRN.

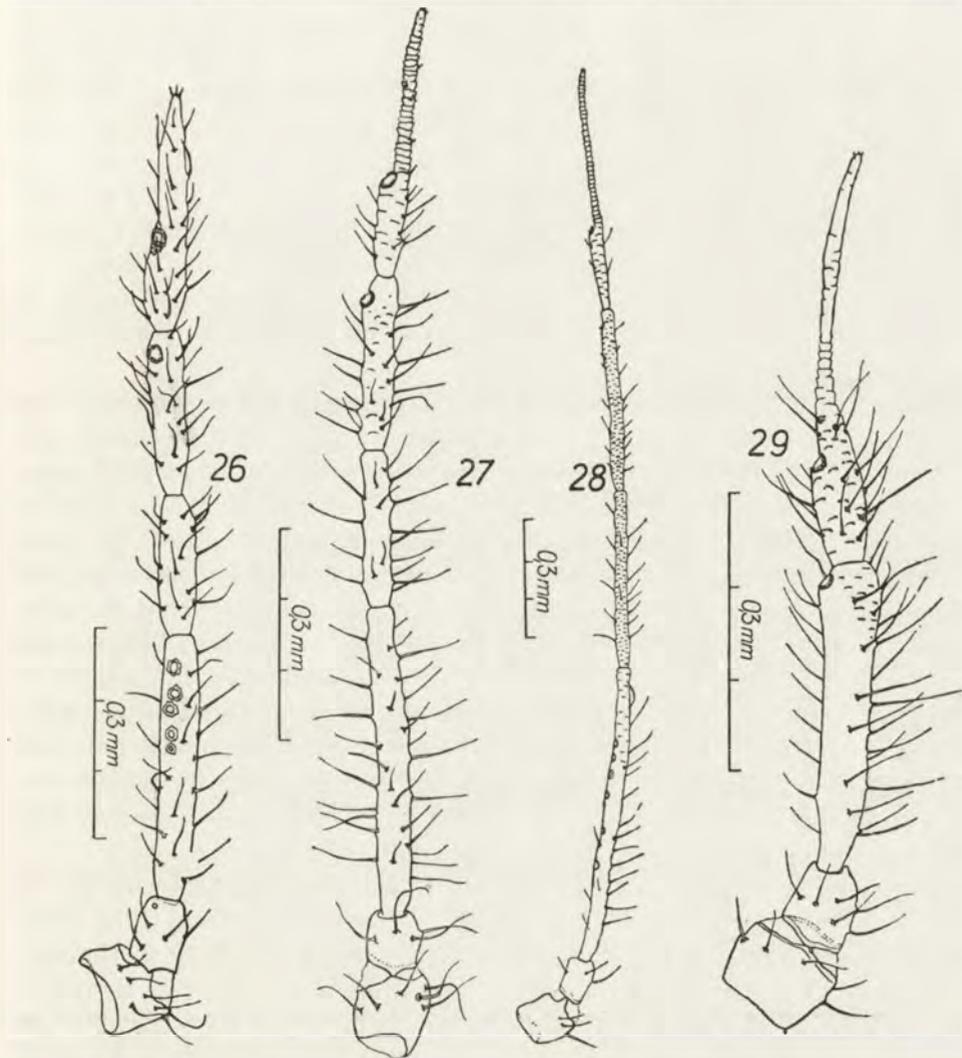
Head and antennae

The antennae contain most of the sensory organs which play a considerable rôle in a search for a suitable host-plant, a suitable feeding-site, sexual partner, etc. Therefore the best developed antennae, possessing numerous rhinaria are to be found in males and winged viviparous females, while the feebly developed ones are possessed by fundatrices.

The six-jointed antennae are generally regarded as typical for the whole suborder *Aphidodea*. SHAPOSHNIKOV (1956) correctly considers the short, 6-jointed antennae, possessing a short processus terminalis, and situated on a feebly convex frons, without antennal tubercles, as an ancestral, original type. Such type of antennae can be found in the majority of primitive forms. Depending on their mode of life and the environmental conditions under which they live, their antennae structure may vary more or less. In general this change can be brought down to two principal processes: one, induced by life in galls or below ground, is the reduction of the joints number and their "twisting" and "broadening", the other — a principal developmental process — is the elongation of the whole antenna, narrowing of the flagellar joints, and the elongation of the processus terminalis, which cause the differentiation of frons and first of all the very strong growth of the antennal tubercles.

In *Pterocommatini* a fairly primitive type of antennae generally prevails. They are 6-jointed in the majority of species, fairly broad and short, strongly

hairy, terminated by a fairly short processus terminalis and situated on a flat or only feebly convex frons (*Neopteroomma* H. R. L., *Fullawaya* ESSIG, *Stauroceras* BÖRN. and certain species of *Pterocomma* BUCKT.). In the species of *Neopteroomma* H. R. L. the epicranial suture of the head still persists (fig. 22), and certain traces of it are also to be found in *Fullawaya* ESSIG (fig. 23) and *Stauroceras* BÖRN. In certain number of species of *Pterocomma* BUCKT. a beginning of the frons differentiation (fig. 24) in the form of appearance of the median process can be observed, and in the species of the genus *Plo-*



Figs. 26-29. Antennae (apterous viviparous females): 26 - *Stauroceras chaetosiphon* BÖRN., 27 - *Pterocomma populeum* (KALT.), 28 - *Plocamaphis borealis* OSSIANN., 29 - *Paducia aterrима* H. R. L.

camaphis OESTL. possessing the longest and the most slender antennae among *Pterocommatini* (fig. 28) certain traces of antennal tubercles may be seen (fig. 25). Only in the genus *Paducia* HOTT. et FRIS., both in the winged morphs and in the wingless ones, strongly reduced, 4-jointed antennae on a flat frons are to be found (fig. 29).

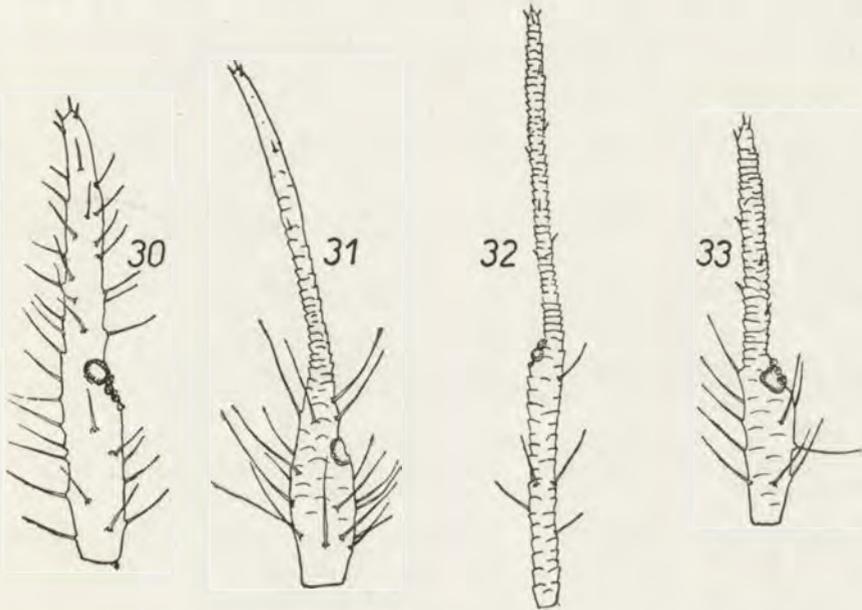
Antennae bearing secondary rhinaria (fig. 26, 28) are found in apterous morphs of many species of *Pterocommatini* and the presence of these structures in the apterous morphs is regarded by SHAPOSHNIKOV (1956) as an archaic feature, the opinion, which, being correct with regard to the primitive subfamilies, should be revised when the subfamily *Aphidinae* is concerned. In this subfamily the secondary rhinaria can be met with mainly in the most phylogenetically advanced species (*Macrosiphini*). Their occurrence in the primitive forms (*Anuraphidea*) should not always be regarded as an atavism, as is often caused by the appearance of alatiform apterae, which are so common in the *Anuraphidea*, that most of the found morphs show more or less intermediate character, and in certain species there are no typical apterous morphs. The alatiform apterae in *Pterocommatini* have not been described so far. Therefore, we may suppose that the presence of secondary rhinaria in the apterous viviparous females of this group is of a plesiomorphous character.

The processus terminalis was formed by narrowing of the terminal portion of the last antennal joint (starting from the distal margin of the primary rhinarium) and is to be found in its most advanced, perfect form, in phylogenetically younger groups. The degree of its development has long been used as a taxonomic criterion in separating higher taxonomic units, and the ratio of its length to the length of the base of last antennal joint had been applied in the identification of species. PAŠEK (1953), used the chaetotaxy of the apex of processus terminalis in the taxonomy of *Lachninae*, and ascribed to it a great phylogenetic importance. In the taxonomy of *Pterocommatini* the length of the processus terminalis has been long employed as a specific feature. BÖRNER (1940) and HILLE RIS LAMBERS (1947) used for the diagnostic purposes also the type of pilosity of processus terminalis and the way by which it is separated from the basal part. The last of two mentioned characters may also have, in my opinion, a certain phylogenetic value.

In the majority of species of *Pterocommatini* the processus terminalis is covered, similarly as in other *Aphidinae*, by not numerous, short and thick hairs, different from those on the remainder part of the last joint. Only in the species of *Staurocera* BÖRN. and *Fullawaya* ESSIG the hairs of the processus terminalis and those of the basis of the last antennal joint are alike (fig. 30). As the similar is to be found in many primitive forms of phylogenically old groups of aphids, this character should be regarded as a plesiomorphous feature. When studying in this respect all the species of *Pterocommatini* one may observe every possible gradation from the primitive type of pilosity (fig. 30)

in *Stauroceras* BÖRN. and *Fullawaya* ESSIG, through feebly differentiated (fig. 31) to the strongly differentiated type (figs. 32, 33). *Pterocommatini* are then the only group in the subfamily *Aphidinae* where the process of differentiation of pilosity on the processus terminalis is not yet terminated. Similarly the separation of the processus terminalis from the base is not yet complete and have, too, every gradation of change from the unseparated one (*Stauroceras* BÖRN.), through its indistinct separation (*Paducia* HOTT. et FRIS. and certain species of *Pterocomma* BUCKT.) to its very distinct separation, can be seen. The correlation of these two phenomena is very peculiar.

The chaetotaxy of the apex of processus terminalis has not been studied in *Pterocommatini*, however, it seems to be constant feature in the subtribes. In all species of *Pterocommatina* the sensory setae are four in number except in *Paduciina* where they are only three in number.



Figs. 30-33. Processus terminalis: 30 - *Stauroceras* BÖRN., 31 - *Paducia* HOTT. et FRIS., 32 - *Plocamaphis* OESTL., 33 - *Pterocomma* BUCKT.

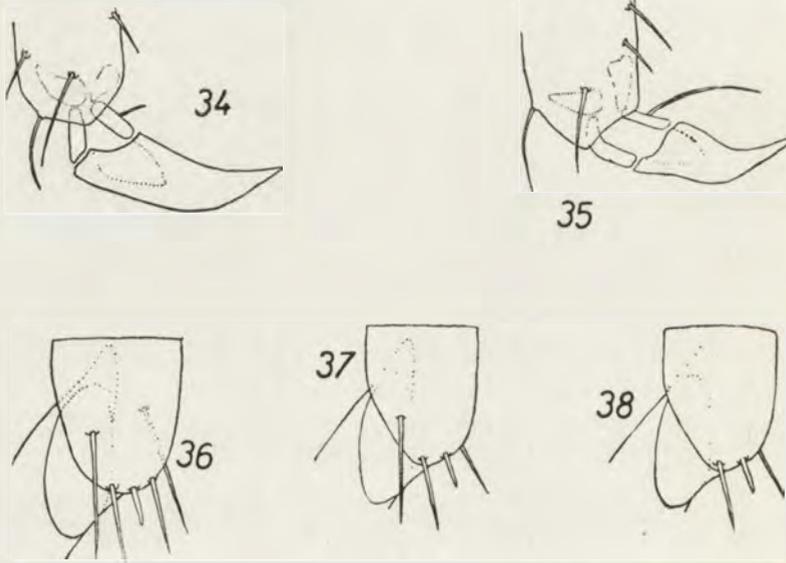
Rostrum

In the aphids taxonomy such characters as the length and shape of rostrum, and the length of its last joint, have been applied. The first of the enumerated features is of a distinctly adaptative character and its structure depends on the kind of organ of a plant which a given species inhabits. This character is, nevertheless, fairly constant within the species, and therefore it may possess a certain diagnostic significance. The structure of the last rostral joint,

particularly the number of hairs on it, have only recently been applied in the taxonomy of aphids. The chaetotaxy of last rostral joint has rather not been popular as a diagnostic character at least as far as *Pterocommatini* are concerned, none the less I regard it as an important taxonomic feature, which may be very useful in separating closely allied species.

Legs

They have in *Pterocommatini* only little taxonomic value and no phylogenetic importance. A certain systematic value may be ascribed to the pigmentation of legs, particularly that of tibiae, to the chaetotaxy of first tarsal joints and the length and shape of the empodial hairs. To separate the oviparous females of closely related species the swelling of the hind tibia and the number and arrangement of their pseudosensoria also have been used. However, these features in certain species of *Pterocommatini* proved to be very variable.

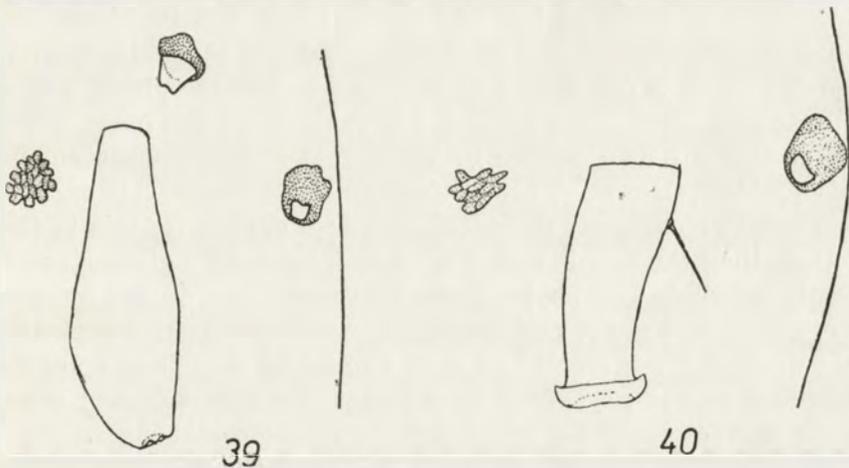


Figs. 34, 35. Empodial hairs: 34 — *Plocamaphis* OESTL., 35 — *Pterocomma* BUCKT.
Figs. 36–38. Chaetotaxy of first tarsal joints.

BÖRNER (1930, 1952) much overrated the value of the chaetotaxy of first tarsal joints applying it not only to diagnostics of genera but also higher taxonomic units. As the subsequent authors have shown, this character can be at most employed in the identification of species, and in *Pterocommatini* even within the species it may exhibit a certain degree of variation [e. g. in *Pterocomma smithiae* (MONELL)].

Siphunculi

These are paired organs of various length and form situated either on six or fifth abdominal segment or between them. Upon irritation they secrete a sticky wax substance which coagulates quickly. The function of siphunculi has not been sufficiently explained. Certain authors regarded them as protective organs. Most probably they have some secretory significance similar to that of wax glands. In the aphid systematics the siphunculi are of a great importance and their structural details proved to possess a considerable diagnostic value. Although we may not be clearly aware of their role in the life of aphids, they may serve as certain phylogenetic indicators. This is possible owing to their correlations with other structures. As long, however, as the function of this organ remains unknown, the phylogenetic value of the structure of siphunculi should be interpreted very cautiously. The siphunculi evolved in many of groups independently and their absence in the species of the family *Phylloxeridae* is generally accepted as a plesiomorphous character. According to certain authors, a lack of siphunculi in *Pemphiginae* should be regarded as a primitive character, too. In their most primitive form the siphunculi are merely two annular pores. The general trend is toward the elongation and swelling of these organs. Therefore short siphunculi are considered a plesiomorphous, and long ones an apomorphous feature. The siphunculi either covered by a microsculpture similar to that of the body cuticle or with short hairs are also considered as primitive, while the glabrous ones, devoid of hairs as secondarily evolved; similarly the cylindrical form of siphunculi is regarded as original, and swollen, clavate one as secondarily acquired.



Figs. 39, 40. Position of siphunculi: 39 — *Plocamaphis* OESTL., 40 — *Staurocera* BÖRN.

In *Pterocommatini* a great diversity of siphunculi can be observed both with respect to their length and their shape. The most primitive type is found

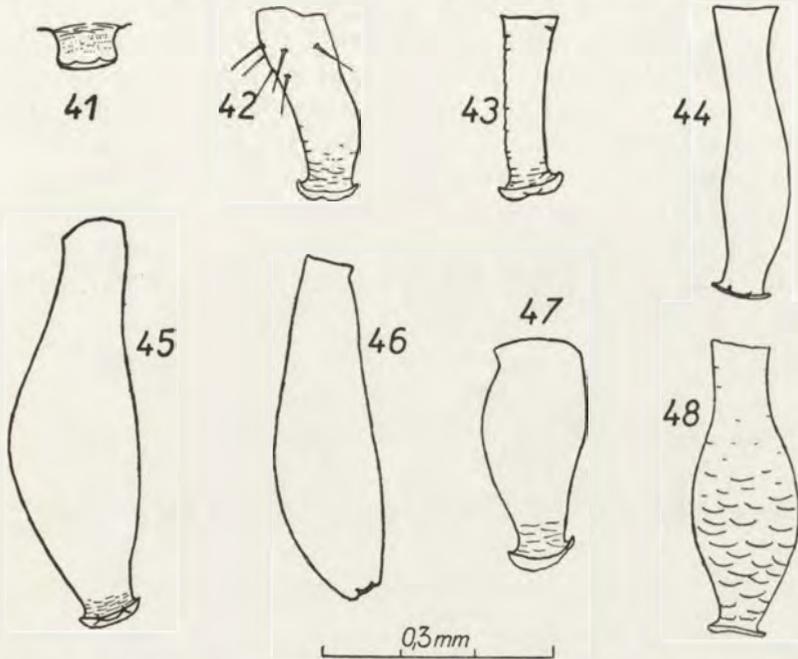
in *Neopterocomma* H. R. L. and *Fullawaya* ESSIG. In both these genera the siphunculi are feebly developed and devoid of flange; in *Fullawaya* ESSIG they are shaped as flat, feebly raised rings, in *Neopterocomma* H. R. L. — as small, cylindrical processes (fig. 41), while in certain morphs (males and fundatrices) of the latter genus their lack altogether. In the majority of species in *Pterocommatini* they are well developed and have either a cylindrical or more or less clavate form (figs. 42–48). The shape of siphunculi was long employed in the taxonomy of *Pterocommatini* as a generic character. It was still used by BÖRNER (1952) and NARZIKULOV (1962), although BÖRNER gave it merely subgeneric value. A study of an ample material reveals that this feature has actually but a very small diagnostic utility, as a tendency toward swelling of siphunculi is to be found in each species of *Pterocomma* BUCKT. and in certain species both types of siphunculi may be encountered in the same morphs. The splitting of the genus *Pterocomma* BUCKT. into two separate subgenera on the base of the shape of siphunculi has no ground, since the species of this genus differ from one another merely by the degree of swelling of the siphunculi, and any such a classification would not be a consistent one (compare BÖRNER, 1952 and BÖRNER et HEINZE, 1957).

Cauda

This is a more or less elongated process at the end of abdomen of various shape and length. It has been long rated very highly as an excellent diagnostic feature, as applied to both higher and lower taxonomic units. The shape and particularly the length of cauda were ascribed phylogenetic value as it was looked upon as transformed last abdominal tergite and its elongation considered an evolutionary process. A short and very broad cauda, therefore resembling a normal tergite, is commonly regarded as a plesiomorphous, and an elongated one as an apomorphous feature. The function of this organ is very little known and there is no evidence in taxonomic literature that anyone dealt with this problem. However, the systematic value which this organ appears to possess cannot be properly estimated unless we explain its role in the life of aphids. Only than the primitiveness or secondariness of a given structure may be correctly inferred. The phylogenetic conclusions are drawn, unfortunately, all too often superficially, and frequently without proper knowledge of the vital role which a given organ performs, and which may bear upon its evolution. It would be not too much to say that the morphological evolution is determined and directed by functional, physiological changes.

BROADBENT (1951) stated that the origin and development of cauda is strongly correlated with defecation process, and more precisely, with a mechanism preventing the contact with excrements. This seems to be confirm by my own observations. The fluid, condensed faeces consists for the most part of saccharides, and is, therefore, a sticky and fast coagulating substance. Spe-

cimens drenched even slightly in its excrements die very quickly of choke. Living in numerous and compact colonies they have been forced to evolve a special protective apparatus. These are of three kinds. The aphids living

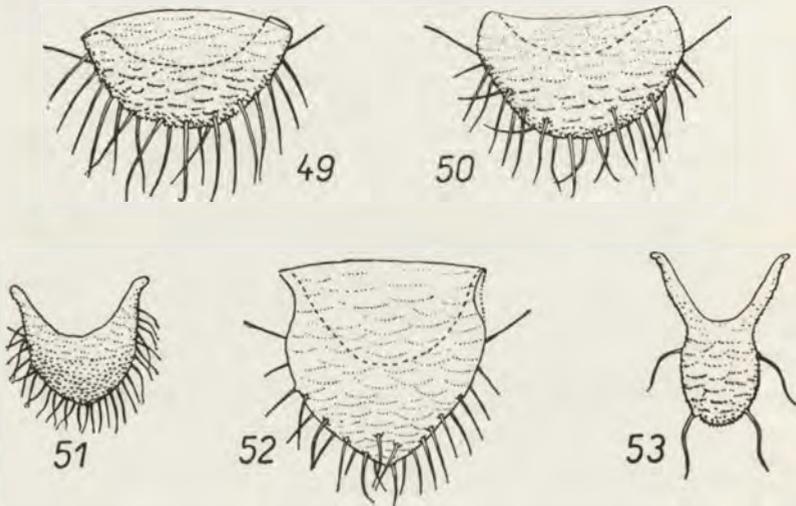


Figs. 41-48. Siphunculi: 41 - *Neopterocomma asiphum* H. R. L., 42 - *Stauroceras chaetosiphon* BÖRN., 43 - *Pterocomma populeum* (KALT.), 44 - *P. bicolor* (OESTL.), 45 - *P. salicis* (L.), 46 - *Plocamaphis goernitzi* BÖRN., 47 - *Pterocomma smithiae* (MONELL), 48 - *Paducia aterrma* H. R. L.

in galls, and therefore concentrated in a very cramped space, exude abundantly a sort of a wax secretion, which covers evenly both specimens surface and the drops of excrements. The said secretion forms a sort of a wax membrane round the drop, the effect being that they never splash when the gall opens, or at most break into several small drops. A well developed cauda is never found in such gall residents. In aphids which live underground on the roots of plants or in cracks of tree trunks (and which do not secrete wax) a more or less strong symbiotic coexistence can be observed. Neither these species have a strongly developed cauda, and they do not give out their excrements until their abdomen is irritated by ants. Certain aphids (because their association with ants) developed a special "trophobiotic" organ described very accurately by ZWÖLFER (1957), serving to hold the drops of excrements while they are being licked by ants. It is worth noting that even in those groups of species which may be considered as typical caudate, the organ in question is always reduced in forms which passed to subterraneous hidden way of life and entered into a certain symbiosis with ants. The most strongly developed

cauda is to be found in species living exposed on plants and which are not attended by ants. It is because the cauda performs a role of an protective apparatus preventing the contact with excrements. The mechanism of the organ in question was described very accurately by BROADBENT (1951).

One should, of course, always bear in mind this functional role of cauda when asserting its taxonomic value. A clear example of ignorance in this respect is placing the genus *Cryptosiphum* BUCKT. by BÖRNER (1930, 1952), mainly because of the apparent "primitiveness" of cauda, with the *Anuraphidea* group (*Anuraphidinae* in BÖRNER's work). It is little doubt, however, that the genus in question living in galls and exuding wax abundantly¹ lost its cauda in a secondary process, which is strongly supported by the presence of other features comm onto all long-caudate species of the *Aphidina* (IVANOVSKAYA, 1960).



Figs. 49-53. Cauda: 49 - *Pterocomma smithiae* (MONELL), 50 - *Pterocomma salicis* (L.), 51 - *Neopteroomma asiphum* H. R. L., 52 - *Plocamaphis goernitzi* BÖRN., 53 - *Paducia aterrima* H. R. L.

Pterocommatini are characterized generally by a short, broad cauda (figs. 49-52). Although the majority of the species of this group lead a hidden way of life and are strongly associated with ants, the primitive character of their cauda is doubtless, which seems to be born out by its primitive chaetotaxy. However, even in this group an elongation of this organ may be observed, a feature correlated certainly with other progressive changes. One may find here all possible gradation, from a very short type (figs. 49, 50), distinctly shor-

¹ These aphids have lost their wax glands in the course of evolution and the mechanism of the wax secretion is here different and consists in an exudation of a very fine dust through the whole cuticle - an example illustrating the irreversibility of evolution.

ter than its width at base, through a slightly longer than its basal width (figs. 51, 52), to a definitely elongated form such as in species of the genus *Paducia* HOTT. et FRIS. (fig. 53). A certain deviation from the trend described above is the cauda of the species of the genus *Neopterocomma* H. R. L. Although owing to its other features this genus is considered as the most primitive one, its species display a sort of cauda which is noticeably longer than wide at base (fig. 51). However, this incompatibility can certainly be explained if habits of the species as well the fact that also its subanal plate underwent an elongation are taken into account. These aphids shows an exceptionally strong association with ants¹ and this prompted the evolution of a very primitive "trophobiotic organ".

It seems that a feeble development of cauda in the majority of *Pterocommatini* has been caused either by their trophobiotic relations with ants, or, as in certain species, by a stronger secretion of wax (i. g. in *Plocamaphis* OESTL.).

The above said leads to the following conclusions:

1. No character of *Pterocommatini* allows for placing it near the *Chaitophorinae*, and all the more so near to *Lachninae* or *Callaphidinae*;
2. The majority of characters and the evolution trends within the group indicate a certain relationship with *Aphidinae*;
3. A peculiar pattern of adaptative changes and a set of morphological characters not encountered in other *Aphidinae* separate this group from all the *Aphidinae*;
4. The majority of morphological features appear to be plesiomorphous — an evidence of the "primitiveness" of the group.

III. GENERAL BIOLOGY AND HOST RELATIONS

A thorough study on the biology of species of the tribe *Pterocommatini* is still lacking. Little, if anything, can be said about life cycles of many species. Also our knowledge pertaining to the host relations is very incomplete since in many cases only as much as the generic names of the host plant are recorded. The observations given below have been gathered mainly either during my 6-year field investigations or short-time laboratory rearing carried out in the years 1959–1960, and they were intended primarily to throw a certain light on the food selectiveness of the species of the genus *Pterocomma* BUCKT.

All described so far species of *Pterocommatini* are closely associated with trees and shrubs of the plant family *Salicaceae*. They are monoecious and holo-cyclic.

A "pure" monophagism is a rare phenomenon in *Pterocommatini*, and it is observed only in *Pterocomma tremulae* BÖRN., *Neopterocomma verhoeveni* H. R. L.,

¹ HILLE RIS LAMBERS (1956) points out that when not attended by ants the aphids die covered by their sticky fecal fluid.

and may be in *Pterocomma beluahensis* (COCK.). The great majority of species are associated with several plants of the same genus, which is particularly true with regards to the species associated with *Salix* L. This kind of oligophagism seems to be, however, a secondary phenomenon, and it is probably due to the great biological plasticity of plants mentioned (willows give many interspecific and fertile crosses). This seems to be born out by more true monophagism of species associated with *Populus* L. and by the fact that the particular willow inhabiting species are always confined to a subsection of the plant genus *Salix* L. (an exception may be here the species associated with a relict section *Salices Pleiandrae*, which live usually on all species of this section comprising in Middle Europe, however, only four species). Moreover, the oligophagous species always displays a certain preference toward one particular host plant, e. g. *Pterocomma jacksoni* THEOB. occurs most frequently and most abundantly on *Salix repens* L., and is only seldom to be found on *S. caprea* L. and other willows belonging to the same group.

Among the 38 species and subspecies of *Pterocommatini* known so far, 29 species are associated with willows, and only 9 with poplars. Moreover, all species living on poplars belong to the genus *Pterocomma* BUCKT. which owing to its morphological and biological properties should be regarded as an apomorphic group. The representatives of all genera, either all or at least the most primitive ones, occur on willows of the section *Salices Pleiandrae*¹. No species of the group discussed is to be found on willows belonging to the sections *Humboldtiana* and *Salices (Diandrae) Dinectariae*. Most species are associated with the youngest evolutionary section of *Salix* L. — *Salices (Diandrae) Mononectariae*.

Until recently it was generally believed that particular species of *Pterocomma* BUCKT. can live both on poplars and willows, and the majority of authors of East Europe still wrongly record *Pterocomma populeum* (KALT.) both from *Salix* L. and *Populus* L. It was probably BÖRNER (1952) who first recognized that the aphids living on willows belong to a different species — *P. pilosum* BUCKT. As the species mentioned, and particularly its subspecies *konoii* HORI differ morphologically only very slightly, I carried out several experiments with host change (both in field and in the laboratory). The specimens of *P. pilosum konoii* HORI in TAKAH. would always choose a willow if given a choice of two different host plants², and they would bring forth their larvae still in the same day. Put into a cage with a branch of *Populus nigra* L. only they wandered restlessly around and after few days died, without accepting the food and displayed no intention whatsoever to bring forth offspring. The specimens transferred in the field from a willow onto a poplar disappeared from

¹ This does not concern the species of *Paducia* HOTT. et FRIS., of which it is nothing known except that they live on the roots of *Salix* sp.

² Keep in a cage with twigs of both plants cultivated on a nutrition fluid.

it already on the second day. Similarly acted the specimens of *P. populeum* (KALT.) transferred to a willow. I used apterous viviparous females in all these experiments and they have been repeated several times.



Figs. 54. Geographic distribution of the genera *Paducia* HOTT. et FRIS. (■) and *Fullawaya* ESSIG (●).

It is clear from the foregoing that the "willow" species of *Pterocomma* BUCKT. cannot live on poplars any more than the "poplar" species on willows. This, however, is only certain with respect to the European species¹. We cannot say anything about the Nearctic species, particularly *Pterocomma smithiae* (MONELL) which was recorded in North America both from willows and poplars. No essential morphological differences have been found between the specimens of this species collected on willows and those collected on poplars.

The particular species of *Pterocommatini* usually show a certain association with a definite plant organs. The species of *Paducia* HOTT. et FRIS., *Fullawaya* ESSIG and *Neopterocomma verhoeveni* H. R. L., as well as certain species of *Plocamaphis* OESTL. always live on the roots or underground parts of willows.

¹ I have also investigated in this respect the behaviour of *P. steinheili* (MORDV.), *P. alicis* (L.) and *P. jacksoni* THEOB.

Neopterocomma asiphum H. R. L. and *Stauroceras chaetosiphum* BÖRN. live in the cracks of tree trunks, often covered by soil particles brought by ants. *Pterocomma salicis* (L.) live mainly on the fairly thick branches of willows, while *P. steinheili* (MORDV.) on rather thinner ones. The association with a given plant organ is not always very close and the colonies of a certain species may live on different plant parts, for instance *P. populeum* (KALT.) may live either on the short, young shoots growing of the trunk, or at base of the branches, or on the thin ones, and *P. pilosum* BUCKT. may be found on trunks as well as on branches.

The above analysis brings the following conclusions:

1. The species of the tribe *Pterocommatini* are mainly associated with willows;
2. The association with poplars is of a secondary character;
3. The most species of *Pterocommatini* occur on the willows belonging to the evolutionary youngest section — *Salices* (*Diandrae*) *Mononectariae*;
4. The primitive forms of *Pterocommatini* live on willows of the *Salices Pleiandrae* section;
5. No association either with the oldest section of contemporary willows (section *Humboldtiana*), or with a Tertiary group of the mountainous willows of the *Salices* (*Diandrae*) *Dinectariae* section has been observed;
6. A prevailing group among the discussed aphids are the "narrow" oligophagous species, occurring most often on willows of one or two closely allied subsections;
7. The willow inhabiting species cannot live on poplars and vice versa (however, only European species has been studied in this respect);
8. Particular species of *Pterocommatini* display a close dependence on the certain parts of the host plant.

IV. GEOGRAPHIC DISTRIBUTION

The distribution of aphids has not been subject of a thorough study, and the geographic ranges of particular species are known only very fragmentarily, with quantitative relations never having been considered. Fairly complete data exist only with respect to the distribution of larger taxonomic groups, and they point out to greatest abundance in groups and forms in the northern hemisphere — in the Holarctic Region. The southern hemisphere shows considerably poorer fauna, and, aside from two old subfamilies and several smaller groups of tribe or genus rank, this is the home for cosmopolitic species mainly, often dangerous pests which spread widely owing to the human economic activities.

The *Pterocommatini* are distributed, similarly as the majority of aphids, exclusively in the northern hemisphere. Although their host plants occur in

the southern hemisphere as well¹ not a single species of this group has been recorded from there. The only record of their occurrence in Argentina (BLANCHARD, 1935), pertains to *P. populeum* (KALT.), which has been introduced into the area from Europe together with Lombardy poplar which is only propagated by cuttings.



Fig. 55. Geographic distribution of the genera *Stauroceras* BÖRN. (■) and *Neopterocomma* H.R.L. (○ = *N. asiphum* H.R.L., ● = *N. verhoeveni* H.R.L.).

Little is known of the distribution of particular species of the *Pterocommatini* and this is due on one hand, to the long time confusing of various closely related species, and, to the extreme rareness and sporadic occurrence of certain species, on the other. Thus the genera *Fullawaya* ESSIG and *Paducia* HOTT. et FRIS., described over a half century ago, are known only from three or four localities (fig. 54). Similar case is with certain European species, although the

¹ Few willow species of the phylogenetically old *Humboldtiana* section are found in Central America and South America, as well as on the continent and islands of Africa and Asia.

fauna of Europe has been studied very intensively, particularly its dendrophilous forms. The genus *Stauroceras* BÖRN., described over 20 years ago, is known only from three localities (fig. 55) in southern Germany, and one of these findings (SZELEGIEWICZ, 1961) appears to be a very doubtful record, since based on only one, badly preserved larval specimen. Of *Neopterocomma asiphum* H. R. L., described over 30 years ago, only three stations were known until recently (Germany and western Ukraine, U.S.S.R.), and *N. verhoeveni* H. R. L. is known only from two localities in Holland (fig. 55)¹. More of similar examples can be given. The insufficiently known distribution of the species is with no doubt due to a hidden, subterranean life (this is almost certain as far as *Fullawaya* ESSIG and *Paducia* HOTT. et FRIS. are concerned), but in many instances it may be a result of the true rareness of species concerned.

Of the 6 hitherto known genera of *Pterocommatini*, two (*Fullawaya* ESSIG and *Paducia* HOTT. et FRIS.) occur only in the Nearctic Region, further two (*Neopterocomma* H. R. L. and *Stauroceras* BÖRN.) are known only from the western part of the Palearctic Region, and remaining two (*Pterocomma* BUCKT. and *Plocamaphis* OESTL.) are common for both regions mentioned. It is worthy of noting, that the genera regarded as plesiomorphous occur in only one zoogeographic region and are confined to a very limited distribution area, while the widely distributed genera are plainly apomorphous. It is striking that there are no endemic genera in Eastern part of the Palearctic Region from where only some endemic species or subspecies of Holarctic genera have been recorded.

But even species belonging to the widely distributed genera may occupy a very limited area. Only one species — *Pterocomma salicis* (L.), has been found in both zoogeographic regions. This species, known in Europe as a serious osier pest, belongs to the commonest species and is here widely distributed. Little, however, is known about its distribution in North America. It is also possible that the species has been introduced from Europe. This question is difficult to solve because *P. salicis* (L.) was often confused with the North American species *P. bicolor* (OESTL.). The North American specimens of *P. salicis* (L.) are morphologically identical to the Europeans ones, which would suggest that this species does not belong to the Nearctic native elements. Neither its distribution in the Palearctic Region had been sufficiently studied (fig. 60); there are no data with regard to Asia. From Japan, the best explored territory in Asia, the species has not been recorded, and most probably it does not occur there. The species is also lacking in the records from the Middle East and from the Middle Asia it has been only recently recorded (NARZIKULOV, 1962). There is no published data with regard to Siberia, but that the species is certainly living there is indicated by the fact, that it is not rare in Northern Mongolia (SZELEGIEWICZ, 1963). East of the Baikal Lake and in Eastern Mongolia

¹ On this map are marked four unpublished so far finding-places (three from Poland and one from Slovakia) of *Neopterocomma asiphum* H.R.L.

lives already a different subspecies — *P. salicis rohdendorfi* HOLM. et SZEL. in litt.

The Nearctic species are distributed as a rule in the whole North America from Mexico to Canada, and only *P. groenlandicum* H. R. L. has a fairly limited range (fig. 56). *C. beluahensis* (COCK.) seems to have a limited distribution



Fig. 56. Geographic distribution of *Pterocomma groenlandicum* H. R. L. (●) and *P. beluahensis* (COCK.) (○).

too, because it was reliably recorded only from the Rocky Mts. (fig. 56). However, as the species had been too much confused in the past, it is difficult to state this with a certainty.

The Palearctic species may be divided into two groups. To the first one belong some widely distributed species such as the discussed previously *P. salicis* (L.), and *P. pilosum* BUCKT. s. l. which is distributed from England to Japan and from Scandinavia to the Middle East, as well as *P. populeum* (KALT.) a widely distributed species in the whole Europe (except the extreme North), in the northern Africa, in the Middle East, Western Siberia and Mongolia (fig. 57). The second group comprises species with a limited geographic range, including, apart from the species of *Neopterocomma* H. R. L. and *Stauroceras* BÖRN., also the species of *Pterocomma* BUCKT. such as *P. steinheili* (MORDV.) (fig. 58), *P. jacksoni* THEOB. (fig. 59) and *P. tremulae* BÖRN. all of them occur-

ring either in the whole of Europe or only in the part of it, as well as *P. salijaponicum* SHINJI (fig. 60) and *P. yezoensis* HORI, occurring exclusively in the Far East.

It is little known about the distribution of the species of *Plocamaphis* OESTL., since the majority of them have been, until recently, confused with the Nearctic species *P. flocculosa* (WEED), and recently even including into a collective species *P. goernitzi* BÖRN. This is, besides, due to a rare and scanty occurrence of these species, of which only few specimens had been collected. Judging upon the existing data they may be very local forms with strongly limited distribution areas.

It is notheworthy that *Pterocommatini* include several vicarious forms. Thus the Nearctic species *Plocamaphis flocculosa* (WEED) has its West Palearctic counterpart — *P. goernitzi* BÖRN. and an East Palearctic one in *P. coreanum* OKAM. et TAKAH., while *Pterocomma populeum* (KALT.) is replaced in the North America by a close species — *P. pseudopopuleum* PALM. Similar pairs of closely related species are *P. pilosum* BUCKT. and *P. media* BAKER, as well as *P. bicolor* (OESTL.) and *P. steinheili* (MORDV.). Even the whole genera substitute each other in various regions as it is the case with Palearctic *Neopterocomma* H. R. L. and Nearctic *Fullawaya* ESSIG.

The foregoing analysis leads to the following conclusions:

1. *Pterocommatini* are confined exclusively to the Holarctic Region, despite much wider distribution of their host plants;
2. The limited distribution areas of the majority of genera and species, as well as an extreme rarity of certain forms speak for the relict character of this group;
3. There are three origin centres of *Pterocommatini*: a Nearctic, a West Palearctic and an East Palearctic, the latter being the least distinct;
4. The Nearctic and West Palearctic radiation centres shows a great relationship expressed, among others, in a strong vicarism of forms.

V. REMARKS ON PHYLOGENY

The studies upon the evolution of various taxonomic groups constitute one of the most important fields of systematics. However, to approach a true picture of a phylogenetic development it must involve many different fields of research such as paleontology, chorology, comparative morphology, and as far as aphids are concerned, host relations.

Fossil aphids are known already from Permian time, however, they belong to an extinct family *Permaphidopseidae*. The first, undoubtedly contemporary species are not known until Cretaceous. The Tertiary forms (Lower Oligocene and Miocene) display already a great differentiation in their morphology and we can see among them almost all nowadays living subfamilies and even the smaller groups. No fossils of *Pterocommatini* have been found as yet. The fact,

however, that representatives of the *Aphidinae* are known from the Cretaceous period, and fossils of the *Aphidini* are numerous in the Oligocene, indicates that the separation of the two evolutionary stems in *Aphidinae* must have taken place considerably earlier, most probably in the Eocene or even in the Upper Cretaceous.

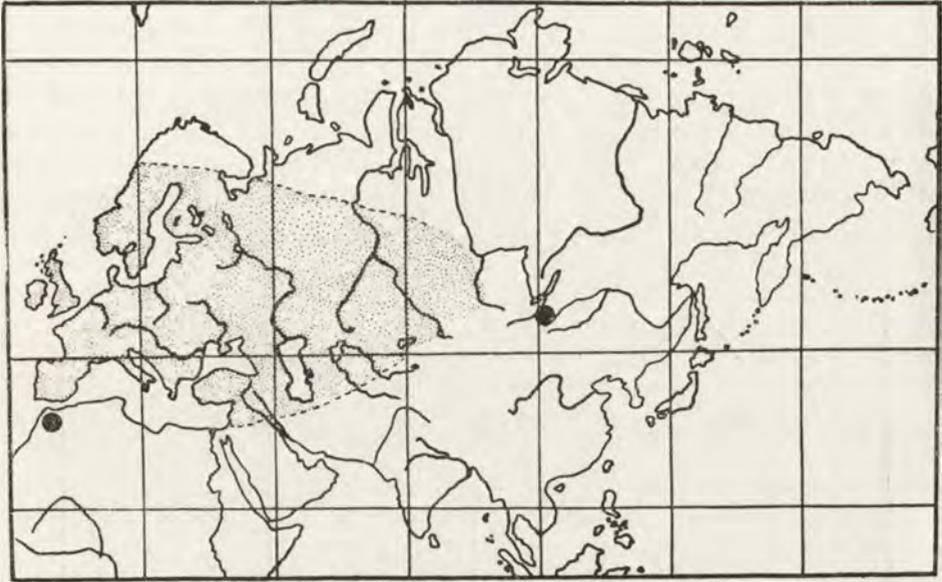


Fig. 57. Geographic distribution of *Pterocomma populeum* (KALT.).

A certain light on this problem may throw the zoogeographic data as well as the host plants of these aphids. The fact that *Pterocommatini* do not occur in the southern hemisphere where the willows as a group had originated (SZAFFER, 1959) and where still the phylogenetically oldest of these plants may be found (the section *Humboldtiana*), as well as the fact that all recent genera of *Pterocommatini* are associated with the pleiandric willows (which had their maximum development in the Paleogene) and that the development of the tribes *Aphidini* and *Macrosiphini* is with no doubt associated with the *Rosaceae* — all this seems to support the idea that the differentiation of the two mentioned groups (*Pterocommatini* and the other groups of *Aphidinae*) among the "Preaphidinae" took place not later than at the turn of the Cretaceous and the Paleogene.

The time and place of origin of the *Pterocommatini* are closely related problems. A zoogeographical analysis indicated three origin centres of the discussed group: Nearctic, West Palearctic and East Palearctic. The latter is the least distinct, and is probably of a secondary character with regard to the Nearctic and partly also to the West Palearctic center (only endemic species or subspecies of the phylogenetically youngest groups have originated here).

It may go back only as early as the end of Pleistocene and the beginning of the Holocene or even later, which makes it less interesting. The remaining two origin centers show a certain similarity in their strongly marked vicarism, an indicator of their original homogeneity. Taking the foregoing into account one may set up a hypothesis that the *Pterocommatini* evolved in the western part of the area occupied in the Eocene by a so called Arctic-Tertiary flora (Alaska, Canada, Greenland, Northern Europe over 57° of the northern latitude). As the climate got colder, they were driven along with their host plants to the south, and after the disappearance of the land bridge between North America and Europe they evolved in vicarious species and genera. They reached Eastern Asia by two ways. The earlier arrival took probably place from the North America and the emigrants gave rise to the endemic species of the Far East, and the later one from Europe and this migration, obviously to late for the formation of species, produced only geographic races.

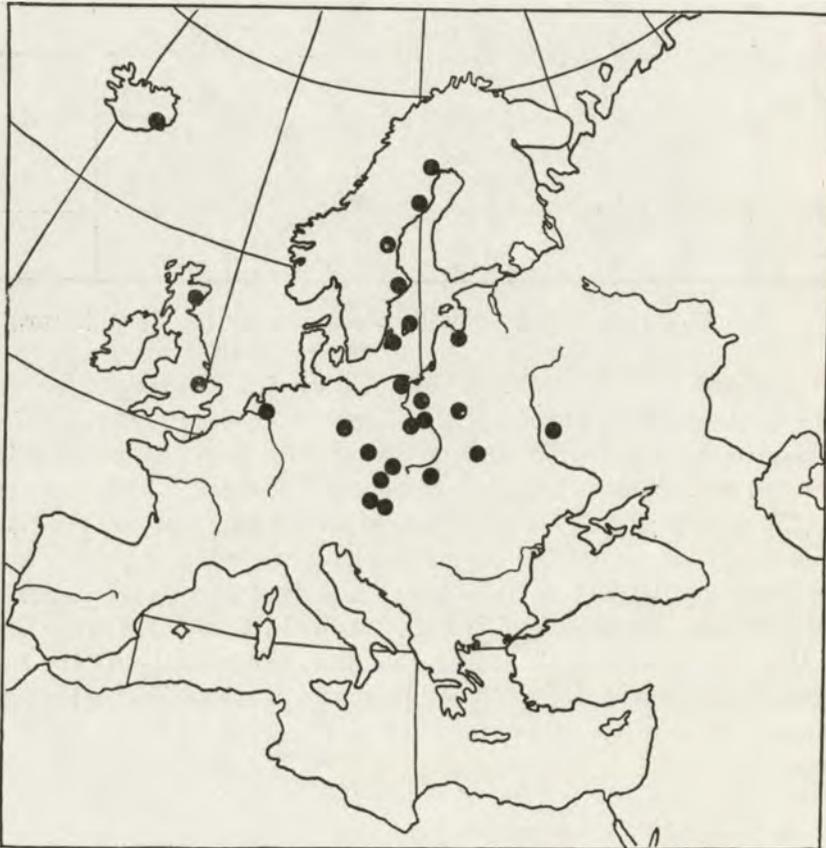


Fig. 58. Geographic distribution of *Pterocomma steinheili* (MORDV.).

The differentiation of *Pterocommatini* took place probably at a fairly early period. The fact that all nowadays existing genera are associated either wholly

(*Fullawaya* ESSIG, *Stauroceras* BÖRN.) or partly, through their most primitive species (*Neopterocomma* H. R. L., *Pterocomma* BUCKT., *Plocamaphis* OESTL.) with the ancient willow section *Salices Pleiandrae*, indicates that they might have occurred probably not later than in the Tertiary. For Tertiary (and more exactly Paleogene) was the period of greatest radiation of pleiandric willows, which since then shows a gradual decline (in Middle Europe only four species of this section survived).

Before I pass over to discuss the relationship within the *Pterocommatini*, I will try to explain why their evolution slowed down and how they became a relict group in the recent fauna. It seems that, apart from such factors as monoecy and the long-lasting associations with their host plants, mentioned on p. 256, the habit of these aphids contributed strongly in slowing their evolutionary process. It is probable that as the climate from Miocene on cooled down and, which is more important, became drier, the aphids were forced to give up their exposed habits and to go below ground where on the willow roots they found the proper humidity¹ and were protected from the environmental influences. A new relatively stable environment has not afforded strong evolutionary stimuli and caused the evolution of the group to slow down. In connection with this their rank of organisation has not advanced and the species retained their plesiomorphous features. A long-lasting evolution in a relatively stable environmental conditions leads consequently to a diminishing of polymorphism², and first of all to the disappearance of the alatae viviparous females. This process (it occurred in the genera *Neopterocomma* H. R. L. and *Stauroceras* BÖRN.) reduces the dispersal power of a species and leads to a steady diminishing of its distribution area, and can finally cause its total extinction. To such "dying out" species belong among the *Pterocommatini* undoubtedly *Stauroceras chaetosiphon* BÖRN. The species of these genera of *Pterocommatini* which retained until the present time the subterranean or semisubterranean way of life (*Fullawaya* ESSIG, *Stauroceras* BÖRN., *Paducia* HOTT. et FIRS., *Neopterocomma* H.R.L.) belong to the most rare species and have strongly limited geographic range³. Only the species of two genera (*Pterocomma* BUCKT. and *Plocamaphis* OESTL.) gave up entirely their subterranean habits what contributed decisively to their relatively recent and rapid evolution. In *Pterocomma* BUCKT. where almost all species returned to the exposed way of life the morphological differentiation is evidently greater

¹ SHAPOSHNIKOV (1951, 1956) considers "a danger of the humidity deficit" as one of the main evolution agents in aphids.

² MORDVILKO characterized the polymorphism in aphids as follows: "Je grösser der Polymorphismus, desto besser die Anpassung an die Existenzbedingungen bei jeder Form der Individuen." (MORDVILKO, 1933).

³ The reduced distribution area of species which still have retained their alatae morphs is probably due to a strong association of these aphids with ants. The latter, to ensure the permanence of a set up colony of aphids, bite off their wings, preventing their flying off.

than in *Plocamaphis* OESTL. where certain species remained below the soil surface on plant roots. This would prove that the speciation in *Plocamaphis* OESTL. occurred relatively recently, probably in Holocene. This may be also supported by the host plants of these aphids which were found to belong mostly to the section *Salices* (*Diandrae*) *Mononectariae* which is of Quaternary origin (SZAFFER, 1959).



Fig. 59. Geographic distribution of *Pterocomma jacksoni* THEOB.

Looking at the morphological characters of the *Pterocommatini* from the point of view of their evolutionary trends and comparing with them those of other groups, primitive as well as advanced ones, we may classify as plesiomorphous the following features: 1) the strong pilosity of the body and appendages; 2) the presence of large and flat spinal and marginal tubercles as well as rudiments of the pleural ones; 3) the short and thick 6-jointed antennae with secondary rhinaria; 4) a short, feebly developed processus terminalis with a primitive type of pilosity; 5) head with a flat frons and a distinct epicranial suture; 6) mesothoracic furca developed in form of separate horns;

7) short cylindrical siphunculi without a flange; 8) short and broad cauda with numerous hairs; 9) long empodial hairs, and 10) first tarsal joints with at least 5 hairs.

In the recent *Pterocommatini* the plesiomorphous characters occur together with the apomorphous ones. Basing on the morphological criteria one may distinguish three small groups of unequal taxonomic rank.

The first group comprises the genera *Neopterocomma* H. R. L., *Fullawaya* ESSIG and *Stauroceras* BÖRN. Their species have a very limited distribution and belong to the most rarely encountered aphids of the tribe *Pterocommatini*. Apart from their relict character these genera display many plesiomorphous features. Most of these features had been retained by the genus *Neopterocomma* H. R. L., and it may be regarded as the most primitive and phylogenetically the oldest group. This may be supported by such characters as the primary rhinaria without ciliated margins, a full set of spinal and marginal tubercles and the peculiar type of spiracles, the characters which distinguish this genus from all the other ones of the discussed tribe. Moreover, one may find here such typical plesiomorphous features as the presence of the epicranial suture, short, cylindrical siphunculi without any flange, a separated mesothoracic furca, first tarsal joints with 5 hairs, as well as the presence of the rudimentary gonapophyses. The only apomorphous features of this genus are the reduction of wings in the males, a partly reduction of the secondary rhinaria on the antennae, a specialised type of cauda and subanal plate, and the presence of a well developed processus terminalis which retained partly a primitive kind of chaetotaxy.

The genera *Fullawaya* ESSIG and *Stauroceras* BÖRN. retained considerably less of plesiomorphous features and by their apomorphous characters they come closer to the species of the second group. The first of the said genera retained such plesiomorphous characters as the epicranial suture, the secondary rhinaria on the antennae, a primitive chaetotaxy on the processus terminalis, short siphunculi without any flange and a complete set of marginal tubercles which, however, underwent a certain transformation. The reduction of eyes and the disappearance of the dorsal sclerotization are plainly of adaptative value and are a result of a long-lasting subterraneous way of life. The genus *Stauroceras* BÖRN. retained only few of plesiomorphous features. They are a full set of not transformed, primitive marginal tubercles, a feebly developed processus terminalis with a primitive type of chaetotaxy retained, the presence of the secondary rhinaria on the antennae and a peculiar type of the mesothoracic furca and of the tarsal chaetotaxy. The form of siphunculi, which have retained some hairs, show here a decisively secondary character and come closer in this respect to that of the genus *Pterocomma* BUCKT.

The second group includes only two genera, *Pterocomma* BUCKT. and *Plocamaphis* OESTL., which present two final stages of the two different evolutionary lines. In both genera there is a strong tendency toward the elonga-

tion and swelling of the siphunculi as well as differentiation of frons and elongation of the processus terminalis and the reduction of the number of hairs on the first tarsal joints, the disappearance of marginal tubercles, etc. These processes occurred in the mentioned genera independently and had a different course. Both genera belong to the richest in species groups of *Pterocommatini* and they are the most widely distributed groups among this tribe. In both genera the winged males are still present.

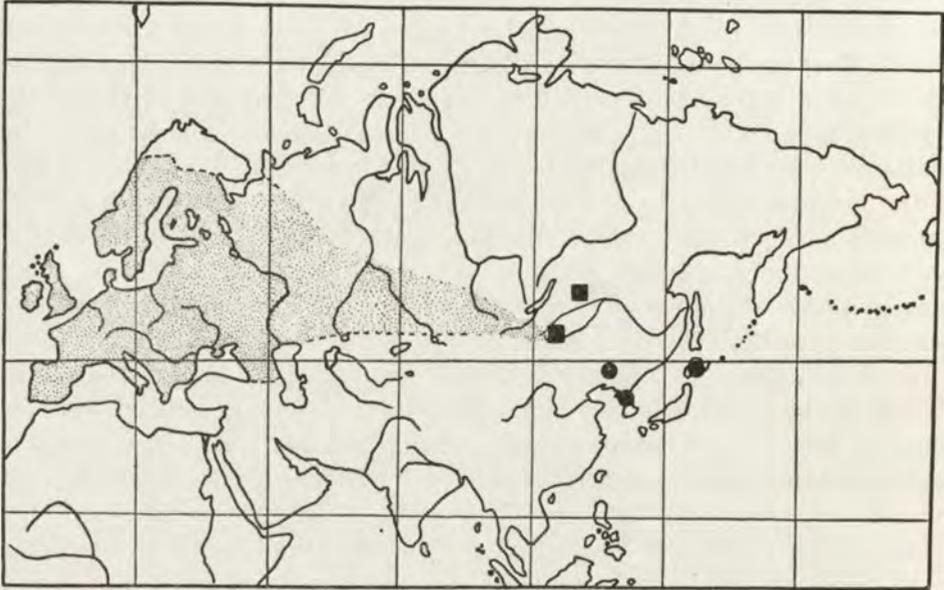


Fig. 60. Geographic distribution of *Pterocomma salicis salicis* (L.) (stippled), *P. salicis rohdendorfi* HOLM. et SZELEG. (■), and *P. salijaponicum* SHINJI (●).

The genus *Paducia* HOTT. et FRIS., the only representative of the recognised by me third group, occupies by its morphological characters a unique position among the *Pterocommatini*. It was HOTTES and FRISON (1931) who first in the description of the genus suggested its separation as a tribe noting its peculiarities of cauda and antennae. HILLE RIS LAMBERS (1952) basing on the features of cauda of the adults and on the chaetotaxy of the embryos, regards the genus even as a very primitive group of *Aphidini*. It is difficult to agree with this view since the primitive *Aphidini* show an entirely different type of siphunculi. The host relation of the *Aphidini* with the plant family *Salicaceae* is distinctly of a secondary character and hitherto no primitive species of the *Aphidini* is known to be associated with these plants. The majority of morphological characters in *Paducia* HOTT. et FRIS. such as the hairiness of the body in adults, the shape of antennae and siphunculi place this genus

into the tribe *Pterocommatini*. The chaetotaxy of first tarsal joints deny not such classification, since in *Pterocommatini* a distinct trend toward diminishing of hairs number on the first tarsal joints may be observed, and the type of chaetotaxy in *Paducia* HOTT. et FRIS. may be regarded as a final stage of this process. The only characters which separate the discussed genus from the other *Pterocommatini* are the shape and chaetotaxy of cauda and the chaetotaxy of embrions. Certainly the strong sclerotization of the body can hardly be considered as a distinct feature, since similar tendencies, although in a lesser degree, are peculiar to *Pterocomma smithiae* (MONELL), and the reduction of the joint number in antennae was probably caused by the peculiar way of life of these aphids (the American species of the genus *Chaitophorus* KOCH living under identical habitat conditions on the willow roots show the similar reduction of antennal joints). Nevertheless the systematic position of this genus remains still slightly enigmatic. May be a thorough study of their life cycles as well as knowledge of their host plants would throw a little more light on this problem.

The first two of the discussed groups of the *Pterocommatini* are undoubtedly closely allied and constitute two different stages of the same evolutionary process. Therefore, I place them into one subtribe — *Pterocommatina*, as distinct from the third group with only one genus, *Paducia* HOTT. et FRIS., and which I rank as a subtribe *Paduciina*. This subtribe constitutes certainly a separate evolutionary trend among the *Pterocommatini*. The existing relationships are pictured in fig. 61, which is presenting a hypothetical phylogenetic tree of the tribe *Pterocommatini*.

Aphids are typical plant parasites and their evolution is to be considered jointly with that of their hosts. Little attention has been devoted so far to the study of the rules of aphids evolution as well as to the evolution of the host-parasite relations in aphids (MORDVILKO, 1929, 1933, 1934; BÖRNER, 1939; HILLE RIS LAMBERS, 1947, 1950; SHAPOSHNIKOV, 1951, 1956; F. P. MÜLLER, 1956). The previous investigations proved, however, that the so called parallel evolution is a very rare phenomenon among the aphids. A slight evidence of such evolution may be encountered only in the tribe *Macrosiphini* where of two groups one is closely associated with the *Rosaceae* and the other

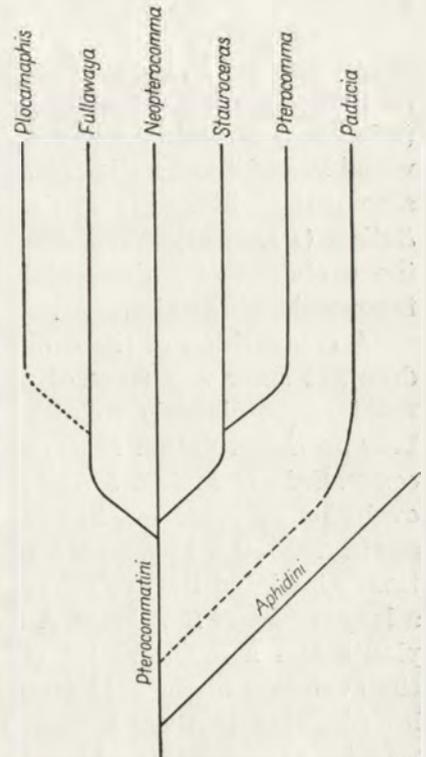


Fig. 61. Hypothetical phylogenetic tree of the tribe *Pterocommatini*.

with the *Caprifoliaceae*, and their evolution must have been closely linked with these plant families (HILLE RIS LAMBERS, 1950).

The *Pterocommatini* are associated strongly with the plant family *Salicaceae* and their evolution is linked mainly with that of the genus *Salix* L., which is, for its part, fairly well known, and its course from the Upper Cretaceous up to the Holocene is well documented by numerous paleobotanic data. Willows originated most probably in an area with a tropical climate and in their evolution a distinct change from the ecological tropical types to the temperate and cold ones, is evident. According to SZAFER (1959) the oldest group of arborescent pleiandric willows originated in the Cretaceous time and differentiated strongly in the Paleogene. In the end of Paleogene and in the beginning of Neogene a further radiation of willows took place and the section *Salices* (*Diandrae*) *Dinectariae* appeared. Finally in the Quaternary, the extremely variable Pleistocene climate stimulated a new wave of evolutionary processes among the willows giving rise to the youngest and most numerous in species *Salices* (*Diandrae*) *Mononectariae* section. The last, not completed phase in the evolution of willows still produces new forms — a cause of the present taxonomic difficulties.

A comparison of the evolution of the *Pterocommatini* with that of willows does not show any trace of a parallel evolution. Thus the appearance of the montaneous diandric willows might have served as new host plants did not bear on the evolution of the aphids group in question (no species of the *Pterocommatini* are known from these willows). A certain convergence of the two evolutionary processes, however, may be noted in the Quaternary. It is little doubt that the appearance of the *Salices* (*Diandrae*) *Mononectariae* at this time stimulated the evolutionary processes in the *Pterocommatini* by supplying a large series of new hosts. A colonisation of the superterraneous parts of these plants and a much varied climate of the Quaternary influenced decisively the evolution of the said group. Further, more recent transformations of willows leading to their specific uniformity, do not account in any important way for the evolution of the *Pterocommatini*, only by colonisation of new host plants (e. g. *Populus* L.) and by the adaptation to different plant organs could a certain differentiation be achieved. These factors are producing still new, difficult to identify forms to mention only the apparently not finished processes within such species as *Pterocomma pilosum* BUCKT. and *P. populeum* (KALT.). Still to be explained is the role played by the geographic isolation. The parthenogenetic reproduction of the *Pterocommatini* together with their rarity leads to an appearance of local isolated clones. This may also be regarded as a certain speciation factor within the group in question and this is born out by the occurrence of many vicarial forms of subspecific rank living on the same species of host plant, an extremely rare phenomenon among aphids.

VI. GENERIC CLASSIFICATION OF THE *PTEROCOMMATINI*Tribe: *Pterocommatini* MORDVILKO, 1914

Diagnosis: First instar antennae 4-jointed, covered by hairs on their whole length. Hind tibiae without "Rastralhaare"; first tarsal joints bearing two hairs. Cauda very hairy (exception: *Paducia* HOTT. et FRIS.).

Body of the apterous viviparous females as well as other morphs covered by long fine hairs. Dorsal hairs very numerous, not arranged in longitudinal rows. Arrangement of spiracles on the first two abdominal segments normal. Pronotum and abdominal segments usually with marginal tubercles, sometimes with spinal ones. Frons usually flat, antennae with a fairly short processus terminalis. Siphunculi fairly short, cylindrical or slightly swollen. Cauda short, rounded, usually with numerous hairs. First tarsal joint with 5, 5, 5 or 5, 5, 4(3), exceptionally 3,3,3 hairs. Wing venation normal, rarely one of the median veins is reduced. Males winged or wingless. Oviparous females usually with thickened hind tibiae, covered more or less by numerous pseudosensoria. All species living monoecious on the *Salicaceae*.

Key to the identification of subtribes

1. Antennae 6-jointed (fig. 27). Cauda short, at most slightly longer than broad at base (figs. 49-52), covered by numerous hairs. *Pterocommatina* MORDV.
- Antennae 4-jointed (fig. 29). Cauda elongate, distinctly longer than broad at base, at most with 6 hairs on its apical part (fig. 53). *Paduciina* subtr. nov.

Subtribe: *Pterocommatina* MORDVILKO, 1914

Diagnosis: Dorsal hairs in the first instar numerous, more than six on each tergite. Dorsal cuticle of abdomen of apterous viviparous females membranous, with only small sclerotic plates, exceptional fully sclerotized, but then always with free, separate tergites. Processus terminalis with 4 apical hairs. Cauda very short, broadly rounded or pentagonal. First tarsal joints with 5,5,5 or 5,5,4(3) hairs.

Key to the identification of genera

1. Empodial hairs normal, long (fig. 35). Siphunculi situated in the middle between the intersegmental sclerite and the spiracles (fig. 40), and usually with a distinct flange; when devoid of flange then very short. 2.
- Empodial hairs very short, rudimental (fig. 34). Siphunculi situated closer to the intersegmental sclerite than to the spiracles, always without flange (fig. 39). *Plocamaphis* OESTL.

2. Siphunculi long, distinctly longer than broad at base, always with a flange (figs. 43, 44). 3
- Siphunculi short, at most slightly longer than broad at base, always without any flange (fig. 41) 4
3. Processus terminalis distinctly separated from the basal part of the last antennal joint, and covered with very short hairs (fig. 33), exceptionally with several longer ones situated just over the primary rhinarium. Antennal joint III without secondary rhinaria (fig. 27); if present they are arranged on the whole length of joint or only in its basal part. Siphunculi without hairs, if exceptionally present than the siphunculi always distinctly swollen in the distal part. *Pterocomma* BUCKT.
- Processus terminalis conical, not distinctly separated from the basal part of the last antennal joint, and covered on its whole length by normal, long hairs (fig. 30). Antennal joint III bearing always secondary rhinaria, confined to the distal part (fig. 26). Siphunculi cylindrical, always covered with several hairs (fig. 42). *Stauroceras* BÖRN.
4. Primary rhinaria with ciliated margins. Spinal tubercles absent.
. *Fullawaya* ESSIG
- Primary rhinaria without ciliated margins. Head, thorax and abdomen with flat spinal tubercles. *Neopteroomma* H. R. L.

Genus: *Neopteroomma* HILLE RIS LAMBERS, 1935

1935. HILLE RIS LAMBERS, D. Arb. morph. taxon. Ent., 2: 52.

Type species: *Neopteroomma asiphum* HILLE RIS LAMBERS, 1935.

Diagnosis: Body broadly oval in outline or broadly spindle-shaped; dorsal side regularly convex, underside flat. Colour of body grey-brownish to purple; body covered by a fine wax dust. Tergum of abdomen membranous with small darkly pigmented marginal and spinal sclerites; surface of sclerites anteriorly wrinkled, and on the last abdominal tergites with a trace of microsculpture. No pleural tubercles. Spinal tubercles indistinct, flat, present on head, thorax and the first eight or seven abdominal tergites. Marginal tubercles similar to the spinal ones, occurring on pronotum and the first six or seven abdominal segments. Dorsal hairs not very numerous, particularly on the middle tergites. Spiracles fairly large, almost round, situated in the middle of the stigmal plates. Head with a distinct epicranial suture, frons feebly convex. Antennae usually without secondary rhinaria, at most with 4 rhinaria on antennal joint III; primary rhinaria without ciliated margins. Processus terminalis short, covered by very short hairs, sometimes with long, normally developed hairs at base. Eyes slightly reduced. Rostrum long, reaching up to the middle of abdomen or more. Siphunculi very short with thick walls, without a flange, glabrous; absent in fundatrices and males. Cauda pentagonal, slightly longer than broad at base, with numerous hairs. Subanal plate triangular, elongated. Gonapophyses three in number, strongly reduced. First

tarsal joints with 5,5,5 hairs. Males wingless. Oviparous females with hind tibiae not swollen and covered by a small number of pseudosensoria concentrated in their basal part. Pseudosensoria may usually appear in the autumn in apterous viviparous females too. Alatae viviparous females not known.

The genus contain two species, *N. asiphum* H. R. L., 1935 and *N. verhoeveni* H. R. L., 1956, distributed in Europe and living partly hidden, on *Salix* sp. The colonies of these aphids are always attended by ants.

Genus: *Fullawaya* ESSIG, 1912

1912. ESSIG, E. O. Pomona Journ. Ent., 4: 716.

Type species: *Fullawaya saliciradicis* ESSIG, 1912.

Diagnosis: Body broadly oval, dorsum regularly convex, underside flat; the whole body surface covered by a fine waxy dust. Colour of body yellowish to yellowish brown with dark brown patches. Abdominal tergum membraneous with small, feebly sclerotic and darkly pigmented marginal plates; surface of the plates almost glabrous, without any trace of microsculpture. Spinal and pleural tubercles absent. Marginal tubercles large, convex, present on pronotum and the first seven abdominal tergites. Dorsal hairs very numerous. Mesothoracic furca formed as two horns connected with each other by a broad and low bridge. Spiracles large, oval, situated in the posterior part of stigmal plates. Head with feebly marked epicranial suture, frons flat. Antennae always with secondary rhinaria; primary rhinaria with ciliated margins. Processus terminalis rather long, covered on its whole length by long hairs. Eyes slightly reduced. Siphunculi very short, in form of slightly elevated rings, without a flange. Cauda broadly rounded, with numerous hairs. Subanal plate normal, rounded. Gonapophyses strongly reduced, persisting only as three groups of gonochaetae. Chaetotaxy of first tarsal joints: 5,5,5. Males apterous. Oviparous females with slightly swollen hind tibiae covered by thiny pseudosensoria, which are arranged on the whole length of tibiae.

The genus contains two species, *Fullawaya saliciradicis* ESSIG, 1912 and *F. braggi* (GILLETTE et PALMER, 1929), which live on the roots of willows and are distributed in North America.

Genus: *Stauroceras* BÖRNER, 1940

1940. BÖRNER, C., ed. BÖRNER, Naumburg, p. 4.

Type species: *Stauroceras chaetosiphon* BÖRNER, 1940.

Diagnosis: Body broadly spindle-shaped, dorsum regularly convex, underside flat. Colour of body greenish-grey to brownish; body surface covered by a fine wax dust. Abdominal tergum membraneous with thiny darkly pigmented small sclerites densely transversing the tergites; the surface of these sclerites almost glabrous with only a trace of microsculpture. Spinal and ple-

ural tubercles absent. Marginal tubercles large, flat, scarcely visible, appearing as they were wax glands; they occur on pronotum and first seven abdominal segments. Dorsal hairs rather short, numerous. Mesothoracic furca formed as two separated horns. Spiracles small, reniform, situated in posterior part of stigmal plates. Head sometimes with a distinct trace of epicranial suture, frons flat. Antennae always with several large secondary rhinaria arranged in the distal part of joint III; primary rhinaria with ciliated margins. Processus terminalis short, almost not separated from the basal part of last antennal joint and covered on its whole length by long hairs. Eyes normal. Rostrum long, reaching more than half of abdomen; last rostral joint slightly acuminate. Siphunculi rather long, cylindrical and slightly bent, with a distinct flange and several hairs in the basal part. Cauda broadly rounded with numerous hairs. Subanal plate normal, rounded. Chaetotaxy of first tarsal joints: 5,5,5. Gonapophyses reduced, formed by three groups of gonochaetae. Males apterous. Oviparous females with slightly swollen hind tibiae and covered by not particularly numerous pseudosensoria. Alatae viviparous females not known.

Only the type species is known. It lives at the base of willow trunks, always visited by ants, and occurs in Middle Europe.

Note: In the very short original description (BÖRNER, 1940) and in my redescription of this species (SZELEGIEWICZ, 1961) it has been stated that the genus in question is devoid of marginal tubercles. However, whereas on the badly preserved slides of BÖRNER these tubercles are not visible, they can be observed on the alcohol specimens from BÖRNER's collection. They only are slightly flatter than those in other species and are more shifted onto the ventral side. They are also visible after mounting in slides.

Genus: *Pterocomma* BUCKTON, 1879

1879. BUCKTON, G. B. Monograph British Aphid., 2: 142.

Synonyms: *Cladobius* KOCH, 1856 nec DEJEAN, 1836; *Aphiodes* PASSERINI, 1860 nec RONDANI, 1848; *Melanoxanthus* BUCKTON, 1879 nec ESCHOLTZ, 1836; *Clavigerus* SZÉPLIGETI, 1880; *Melanoxantherium* SCHOUTEDEN, 1901; *Aristaphis* KIRKALDY, 1905.

Type species: *Pterocomma pilosa* (sic) BUCKTON, 1879.

Diagnosis: Body broadly oval, oval, or egg-shaped, abdominal tergum regularly convex (in the *populeum* and *salicis* groups) or with strongly convex, abdomen (in the *bicolor* group). Underside always flat. Colour of body brownish, olive-brownish, yellow-brownish, green-brownish or reddish-brownish; dorsal body surface covered by a fine wax dust, concentrated mainly between the segments, less frequently evenly covering the whole surface of tergum. Abdominal tergum membranaceous with sclerotic and dark pigmented marginal and spinopleural plates, only exceptionally sclerotised on the whole surface of tergites. Surface of sclerotic plates glabrous with traces of microsculpture. Spinal and pleural tubercles not present, rarely in *P. pilosum* BUCKT., s. l. occurring unilateral on the six and seventh abdominal tergites. Marginal tu-

bercles usually well developed, mammiform or conical, occurring on pronotum, first four abdominal tergites and irregularly on the six and seventh abdominal tergites. Sometimes (in *P. populeum dubium* BÖRN., *P. pilosum pilosum* BUCKT. and in *P. groenlandicum* H. R. L.) they lack altogether. Dorsal hairs long, fine and numerous. Mesothoracic furca formed as two horns jointed with each other by a broad and low bridge or inserted on a short and broad shaft. Spiracles large, oval or reniform, situated in posterior part of stigmal plates. Head always without epicranial suture, frons flat or with a distinct median protuberance and feebly developed antennal tubercles. Antennae without secondary rhinaria (in the *populeum* and *bicolor* groups) or with rhinaria on third and exceptionally on fourth antennal joint (in the *salicis* group); primary rhinaria with ciliated margins. Processus terminalis usually short, well separated from the base of the last antennal joint, covered on its whole length with very short hairs, exceptionally with several long hairs on its very base. Eyes normal. Rostrum either short, reaching up to middle or hind coxae or long, reaching the first or more abdominal segments. Siphunculi rather long, always with a distinct flange, almost glabrous, either cylindrical, or, in the middle or in the distal part, more or less strongly swollen. Cauda broadly rounded, usually shorter than broad at base. Subanal plate normal, rounded. Gonapophyses strongly reduced, retained only as three gonochaetae; their median group sometimes divided secondarily into two small groups. Chaetotaxy of first tarsal joints: 5,5,5 or 5,5,4, exceptionally 5,5,3. Males alatae, rarely (in the *salicis* group) apterous. Oviparous females usually with hind tibiae more or less strongly swollen and covered by a various number of pseudosensoria; exceptionally (in *P. jacksoni* THEOB.) without pseudosensoria.

The genus includes numerous species living on the superterraneous parts of willows and poplars and distributed over the whole Holarctic Region. Here belong the following species (synonyms also listed, and the original spelling retained): *Pterocomma americanum* nom. nov. (= *P. populifoliae* auct. nec FITCH); *Cladobius beluahensis* COCKERELL, 1904; *Melanoxanthus bicolor* OESTLUND, 1887; *Pterocomma dubium* BÖRNER, 1940; *Pterocomma fraxini* THEOBALD, 1921; *Pterocomma groenlandica* HILLE RIS LAMBERS, 1952; *Pterocomma jacksoni* THEOBALD, 1921; *Pterocomma media* BAKER, 1917; *Pterocomma morio* HILLE RIS LAMBERS, 1947; *Anuraphis multituberculata* RUSSANOVA, 1942; *Pterocomma konoi* HORI in TAKAHASHI, 1939; *Pterocomma pilosa* BUCKTON, 1879; *Aphis populea* KALTENBACH, 1843; *Aphis populifoliae* FITCH, 1851; *Pterocomma pseudopopulea* PALMER, 1952; *Pterocomma ringdahli* WAHLGREN, 1940; *Aphis rufipes* HARTIG, 1841; *Cladobius rufulus* DAVIDSON, 1909; *Aphis salicis* LINNAEUS, 1758; *Melanoxantherium salijaponicum* SHINJI, 1924; *Aphis saliceti* HARRIS, 1842; *Chaitophorus smithiae* MONELL, 1879; *Cladobius steinheili* MORDVILKO, 1901; *Pterocomma tremulae* BÖRNER, 1940; *Pterocomma turanicum* NEVSKY, 1929 (ut subsp.); *Aphis viminalis* HARTIG, 1841; *Pterocomma yezoensis* HORI, 1929.

Genus: *Plocamaphis* OESTLUND, 1922

1922. OESTLUND, O. W. 19th Rpt. State Ent. Minn., p. 122.

Type species: *Melanoxanthus flocculosus* WEED, 1891.

Diagnosis: Body oval or broadly spindle-shaped, abdominal tergum regularly convex, underside flat. Colour of body yellow-brownish to olive-brownish; body surface covered by a dense wax coating, less frequently (in species living subterraneously) only slightly powdered. Abdominal tergum with only marginal and small spinal plates; the spinal plates present up to the fifth abdominal tergite; surface of the sclerotic plates rugose. Spinal and pleural tubercles absent. Marginal tubercles well developed, conical; they occur always on pronotum (rarely also on meso- and metanotum) and on the first three or first four or five abdominal segments. Dorsal hairs long and fine, rather numerous. Mesothoracic furca situated on a distinct broad shaft. Spiracles normal, situated on the posterior margin of the stigmal plates. Head without epicranial suture, frons with a feebly median and antennal tubercles. Antennae long and rather slender, always with secondary rhinaria on joint III. Processus terminalis long, covered by very short hairs. Eyes normal, in the species living on roots slightly reduced. Rostrum short, reaching only up to the hind coxae, less frequently longer. Siphunculi situated closer to the intersegmental sclerite than to the spiracles and usually fairly long, narrowed at base and swollen in the distal part, less frequently very short and broadest at base, always without a flange. Cauda pentagonal, usually slightly longer than wide at base. Subanal plate elongate, rounded. Gonapophyses strongly reduced, retained as three groups of gonochaetae. Chaetotaxy of first tarsal joints: 5,5,5 or 5,5,4. Empodial hairs rudimentary, very short. Males apterous or winged. Oviparous females with only slightly swollen hind tibiae covered by a small number of pseudosensoria.

The genus contains numerous species, which are associated with willows and distributed over the whole Holarctic Region. They are: *Aphis amerinae* HARTIG, 1841; *Pterocomma bituberculata* THEOBALD, 1912; *Plocamaphis borealis* OSSIANNILSSON, 1959 (ut subsp.); *Plocamaphis brachysiphon* OSSIANNILSSON, 1959 (ut subsp.); *Melanoxantherium coreanum* OKAMOTO et TAKAHASHI, 1927; *Melanoxanthus flocculosus* WEED, 1891; *Plocamaphis goernitzi* BÖRNER, 1940; *Plocamaphis macrosiphon* OSSIANNILSSON, 1959 (ut subsp.); *Plocamaphis tericola* HOTTES et FRISON, 1931; *Plocamaphis martini* RICHARDS, 1963.

Subtribe *Paduciina* subtr. nov.

Diagnosis: Dorsal hairs in first instar arranged in longitudinal rows, in adults dense and scattered irregularly. Abdominal tergum strongly sclerotized, forming a uniform plate, reaching from mesonotum up to the seventh abdominal tergite inclusively. Antennae 4-jointed. Cauda elongate, with only few

hairs on its distal part. Chaetotaxy of first tarsal joints: 3,3,3. Processus terminalis with three apical hairs. The subtribe contains only one genus:

Genus: *Paducia* HOTTES et FRISON, 1931

1931. HOTTES F. C., FRISON T. H., Bul. Nat. Hist. Surv., 19: 167-168.

Type species: *Melanoxantherium antennatum* PATCH, 1913.

Diagnosis: Body broadly oval, dorsal side strongly convex, underside flat. Colour of body dark, almost black. Dorsal cuticle glabrous, shining with traces of microsculpture on eighth tergite only. Spinal tubercles very small, always present on head (one pair on epicranium and three pairs ventrally) and on the seventh abdominal tergite, less frequently also on pronotum and the sixth abdominal tergite. Pleural tubercles scattered irregularly on pronotum and on seventh abdominal tergite. Marginal tubercles large, in apterous morphs flat, in the alatae ones convex, always present on pronotum and the first seven abdominal tergites, less frequently on meso- and metanotum. Dorsal hairs numerous, sometimes bent at apex or bifid. Mesothoracic furca in form of two horns connected by a wide and low bridge. Spiracles small, reniform, situated on the posterior edge of stigmal plates. Head without epicranial suture, frons flat. Antennae without secondary rhinaria; primary rhinaria with ciliated margins. Processus terminalis long, conical, with several long hairs at base. Eyes slightly reduced. Rostrum short, not reaching beyond hind coxae. Siphunculi long, narrowed at base and apex, swollen in the middle, with a broad flange; walls of the siphunculi thick, covered by a distinct microsculpture of minute scales forming just behind the flange an indistinct reticulation. Cauda long, composed of a conical basal part and a round distal part separated by an indistinct narrowing; distal part bearing 4-6 hairs. Males not known so far. Oviparous females with barely swollen hind tibiae and few pseudosensoria.

The genus contains two little known species, *Paducia antennata* (PATCH, 1913) and *P. atterima* HILLE RIS LAMBERS, 1952, distributed in North America and Greenland and living on roots of willows.

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STRESZCZENIE

W oparciu o analizę morfologiczno-porównawczą, zoogeograficzną i powiązań z roślinami żywicielskimi autor koryguje stanowisko systematyczne dotychczasowej podrodziny *Pterocommatinae* i włącza ją jako plemię *Pterocommatini* do podrodziny *Aphidinae*. Praca zawiera także nową klasyfikację rodzajową plemienia *Pterocommatini* oraz poglądy autora na filogenezę tej grupy mszyc rozpatrywaną na tle ewolucji ich roślin żywicielskich. Autor traktuje omawianą grupę mszyc jako prymitywną, boczną gałąź rozwojową ewolucyjnie najmłodszej podrodziny mszyc. Między innymi przedyskutowane zostały takie zagadnienia, jak okres i miejsce powstania *Pterocommatini* oraz przyczyny, które zahamowały w trzeciorzędzie ich rozwój i wpłynęły decydująco na reliktowy charakter tej grupy we współczesnej faunie. Zasadniczy trzon pracy stanowi rozdział poświęcony morfologii *Pterocommatini*, w którym

dokonano szczegółowej analizy cech morfologicznych tych mszyc, porównując je z kierunkami przemian morfologicznych u innych, pokrewnych grup mszyc. Szczególną uwagę zwrócono na plezjomorfizmy, narządy szczątkowe oraz na uchwycenie prawidłowości i kierunków przemian morfologicznych w obrębie tej grupy. Autor dał tu oryginalne interpretacje takich mało badanych dotąd procesów, jak różnicowanie się widełek śródtułowia, wyrostka końcowego oraz ogonka, naświetlając ich znaczenie w badaniach nad filogenezą mszyc. Praca zawiera klucze do oznaczania podplemion i rodzajów, szeroko potraktowane diagnozy rodzajów oraz wykazy należących do nich gatunków.

РЕЗЮМЕ

Опираясь на морфо-сравнительный, зоогеографический анализ и связь с кормовыми растениями, автор корректирует систематическое положение группы родов близких к *Pterocomma* БУСКТ. и включает их как трибу *Pterocommatini* в подсемейство *Aphidinae*. Настоящая работа включает тоже новую систему трибы *Pterocommatini* а также мнение автора на филогенез этой группы тлей рассматриваемой на фоне эволюции их кормовых растений. Автор считает эту группу как примитивную побочную ветвь развития эволюционно самого молодого подсемейства тлей. Кроме того были обсуждены следующие вопросы: период и место появления *Pterocommatini* а также причины которые затормозили в третичном периоде их развитие и оказали решительное влияние на реликтовый характер этой группы в современной фауне. Основной частью работы является глава посвященная морфологии *Pterocommatini* в которой проведен анализ морфологических признаков этих тлей сравнивая их с направлениями морфологических перемен у иных родственных групп тлей. Особое внимание обращено на плезиоморфные признаки, остаточные органы, на закономерности и направления морфологических изменений в пределах этой группы. Автор дает оригинальную интерпретацию таких мало исследованных до сих пор процессов, как дифференцирование вилок среднегруди, шпика последнего членика усиков и хвостика, выясняя их значение в исследованиях над филогенезом тлей. Работа содержит определители подтриб и родов, а также широкие диагнозы родов и сводки принадлежащих к ним видов.

Redaktor pracy — prof. dr J. Nast