The phylogeny of the Cicadina (Homoptera, Cicadina) based on comparative morphological data

A.F. Emel’yanov

Transactions of the All-Union Entomological Society
Morphological principles of insect phylogeny

The phylogenetic relationships of the principal groups of cicadine* insects have been considered on more than one occasion, commencing with Osborn (1895). Some phylogenetic schemes have been based only on data relating to contemporary cicadines, i.e. predominantly on comparative morphological data (Kirkaldy, 1910; Pruthi, 1925; Spooner, 1939; Kramer, 1950; Evans, 1963; Qadri, 1967; Hamilton, 1981; Savinov, 1984a), while others have been constructed with consideration given to paleontological material (Handlirsch, 1908; Tillyard, 1919; Shcherbakov, 1984).

As the most primitive group of the cicadines have been considered either the Fulgoroidea (Kirkaldy, 1910; Evans, 1963), mainly because they possess a small clypeus, or the cicadas (Osborn, 1895; Savinov, 1984), mainly because they do not jump. In some schemes even the monophyletism of the cicadines has been denied (Handlirsch, 1908; Pruthi, 1925; Spooner, 1939; Hamilton, 1981), or more precisely in these schemes the Sternorrhyncha were entirely or partially depicted between the Fulgoroidea and the other cicadines. In such schemes in which the Fulgoroidea were accepted as an independent group, among the remaining cicadines the cicadas were depicted as branching out first (Kirkaldy, 1910; Hamilton, 1981; Savinov, 1984a), while the Cercopoidea and Cicadelloidea separated out last, and in the most widely acknowledged systematic scheme of Evans (1946b**) the last two superfamilies, as the Cicadellomorpha, were contrasted to the Cicadomorpha and the Fulgoromorpha. At the present time, however, the view affirming the equivalence of the four contemporary superfamilies and the absence of a closer relationship between the Cercopoidea and Cicadelloidea (Evans, 1963; Emel’yanov, 1977) is gaining ground.

---

* The neologism “cicadine” is employed in this translation as both adjective and noun for the Russian term “tsikadovye” which Emel’yanov uses in the wide sense as a vernacular term for the Cicadina. [Tr.]

** Sic. Should be 1946a. [Tr.]

*** The numbers in the right-hand margin indicate the corresponding pages in the original text. [Tr.]

The range of features used for phylogenetic analysis remains very narrow up to the present time, and in some cases even each divergence has been supported by only a single feature (Hamilton, 1981). Kramer (1950) enlisted the greatest number of features but he was unable to reach sufficiently definite conclusions, although he did declare himself in general in favour of Kirkaldy’s concepts.

At the present time the phylogenetic scheme proposed by Kirkaldy and supported by Kramer is most widely acknowledged. However, the question of the polyphyletic origin of the cicadines still remains open. At the same time none of the proposed schemes, including Kirkaldy’s scheme, appears to have a convincing basis, both by reason of the scantiness and one sided nature of the data enlisted, as well as by reason of the simplified ideas concerning the character of evolution, which occasionally come into conflict with the observed facts of the distribution of the features within the different groups of cicadines.

One of the important conclusions, resulting from the distribution of features throughout and within the main groups of cicadines, is the inevitability of acknowledging various forms of reversibility in the evolution of individual features and structures, all the way to instauration, i.e. to the repeated appearance of a feature following a phylogenetic (macroevolutionary) stage of its absence. This reversibility emerges from the impossibility of constructing a phylogenetic tree in which even the most fundamental features were formed only once and, having disappeared, did not appear again. An acceptance of the principle or instauration assists in resolving many contradictions in the phylogeny of the cicadines, about which more will be said later.

This paper is devoted to elucidating the mutual relationship and origin of the principal groups of the contemporary cicadines, considered as superfamilies. Four superfamilies are accepted, the Cicadelloidea, Fulgoroidea, Cercopoidea and Cicadoidea, in the following composition:

Cicadelloidea	Cercopoidea	Fulgoroidea	Dictyopharidae

Aetalionidae Cercopidae Tettigometridae
Fulgoridea
Membracidae Clastopteridae
Delphacidae Nogodinidae
Ulopidae Machaerotidae
Cixiidae Issidae
Ledridae Aphrophoridae
Kinnaridae Tropiduchidae
Cicadellidae
Meenoplidae Lophopidae
Cicadoidea
Achilixiidae Eurybrachydidae
Tettigarctidae
Derbidae Flatidae
Cicadidae
Achilidae Ricaniidae

In the analysis of the features, naturally, their state in the most primitive groups is taken into consideration in the first instance. It should be kept in mind that many widespread concepts concerning the differences between the cicadine superfamilies in their level or organization are based on a comparison of advanced representatives of advances families; this applies especially to the Cicadelloidea and Fulgoroidea, in which the internal diversity is great.

Within the superfamily Cicadelloidea the families Aetalionidae and Ulopidae are accepted as the most primitive, the former as the origin of the line to the Membracidae, the latter - to the Cicadellidae. The family Aetalionidae is considered in its old scope without the additions of Hamilton (1971) that were taken from the Membracidae without sufficient grounds. The independence of the Ulopidae and Ledridae as families, which was acknowledged by Ribaut (1936) and not acknowledged by Evans (1946b), is demonstrated, in particular, by the absence in these of a buttonlike locking device on the hind coxae, which is characteristic of the Cicadellidae, including the Eurymelinae and Hylicinae (Figure 20).

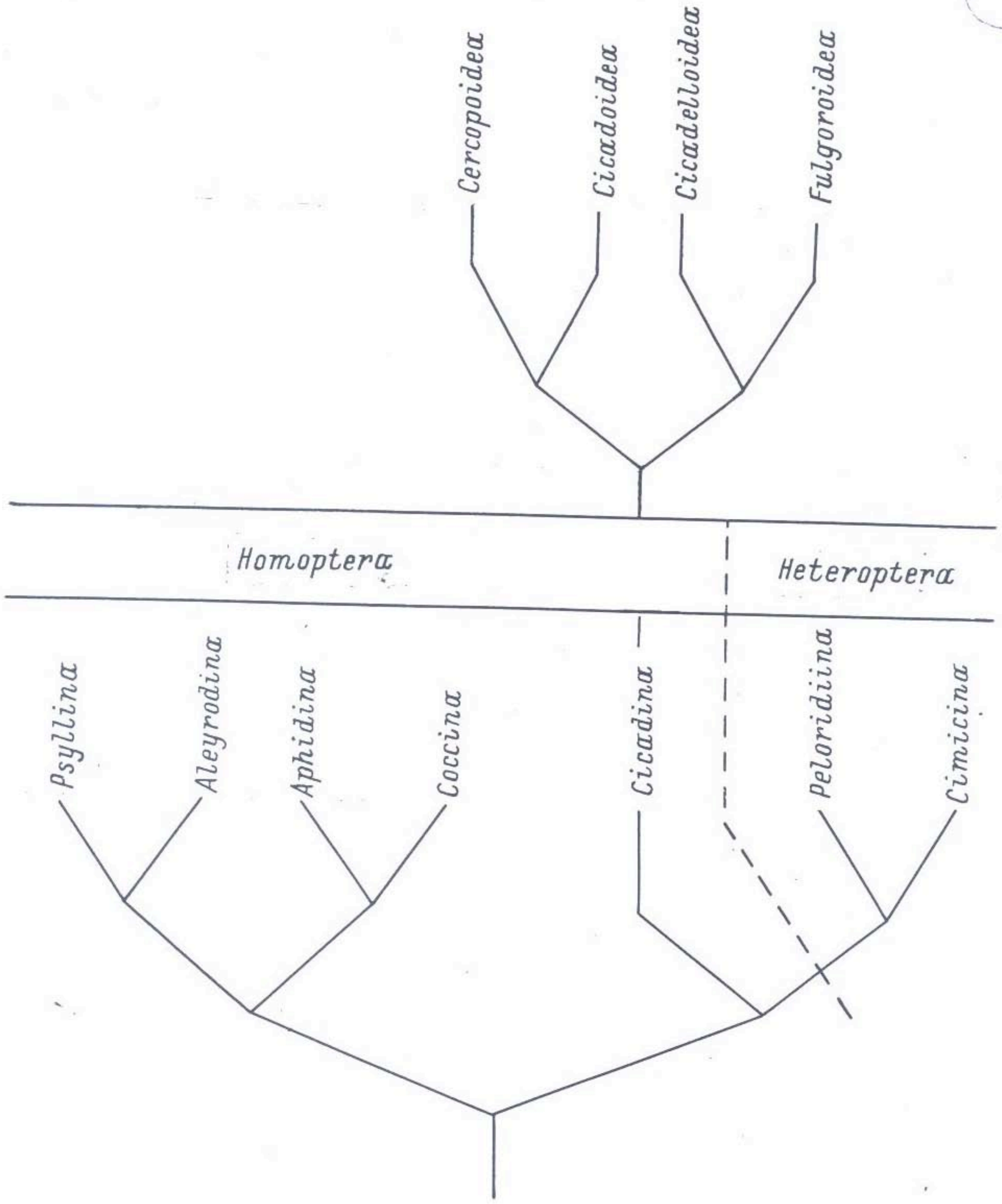


Figure 1. Reference scheme of the phylogeny of the Rhynchota and the proposed phylogeny of the Cicadina.

Within the superfamily Cercopoidea the least modified, apparently, are the Cercopidae, from which originated the more advanced Aphrophoridae and Machaerotidae, that are synapomorphous on the basis of the feature of the anastomosis of veins Pcu and A_1 on the hind wings; the Clastopteridae comprise either a sister or daughter group of the Cercopidae, or else may be a predecessor of the Aphrophoridae and Machaerotidae on their common stem. Among the Cicadoidea the Tettigarctidae and undoubtedly archaic, having several striking features of plesiomorphous resemblance with the Cercopoidea, which have been lost in the Cicadidae.

Among the Fulgoroidea the Tettigometridae are accepted as the most primitive, with features of a narrow secondary specialization; then follow the Delphacidae and Cixiidae, possessing an unchanged piercing-sawing ovipositor; the Delphacidae are depicted as a sister group to the Cixiidae and all of the other Fulgoroidea, except for the Tettigometridae.

In the subsequent presentation the system of evidence is constructed on the basis of the acceptance of the monophyly of the Rhynchota, which is not disputed by anyone, of the monophyly of the Heteroptera, which is also generally accepted, of the monophyly of the Sternorrhyncha, the doubts as to which are not well founded, and the monophyly of the cicadines, for which evidence is presented below.

A phylogenetic scheme for the Rhynchota (Figure 1) is accepted, in which the first branching occurs between the Sternorrhyncha and the common stem of the bugs and cicadines. This position is very important for shedding light on plesiomorphy in the cicadines as a whole, i.e. the synapomorphy of the cicadines and the bugs. Within the Sternorrhyncha branch the phylogeny as proposed by Schlee (1969a, b, c, d) is accepted, in which the jumping plant lice with the white flies and the coccids with the aphids are sister pairs, having a lower common origin. The bugs and the cicadines are accepted as sister groups, and some new evidence for this is presented below. The Peloridiidae are considered as the most primitive representatives of the Heteroptera, according to Schlee and others (Schlee, 1969b; Emel'yanov and Fal'kovich, 1983).

Synapomorphy of the bugs and cicadines

1) In contrast to the Sternorrhyncha, the bugs and the cicadines have a similar, well developed ano-jugal lobe of the hind wings. 2) The basal lobe of the clavus is drawn out in the form of a tectum. 3) The posterior margin of the pronotum forms a tectum which covers a considerable part of the mesonotum and the bases of the fore wings. 4) By their claval margins the folded fore wings are insered in oblique grooves, which border the interalar triangle

of the mesonotum, the so-called scutellum. 5) In flight the fore and hind wings are coupled by means of overlapping lip-like structures of the wing itself, while in the Sternorrhyncha on the hind wing the coupling is ensured by hook-like structures of chaetoid nature. Differences in the wing coupling in various Rhynchota are considered below (p. 38*). 6) The maxillary levers are attached to the lateral margins of the wings of the hypopharynx. 7) The salivary pump has only retractor muscles of the piston and has no dilator muscles of the sheath.

---

* Page reference to original text. In translation: p. 45 and following pages. [Tr.]

Evidence for the monophyly of the cicadines

There are several reliable synapomorphies of all the cicadines and several synautomorphies (Emel'yanov, 1980, p. 63), i.e. of features that are present in only some of the cicadines, which may be treated as synapomorphies, acquired by a common ancestor but subsequently lost by some of the descendants. The combination of mutually complementary synautomorphies may serve as additional evidence for the monophyly of the group.

Synapomorphies of the cicadines: 1) the coupling apparatus of the wings (see p. 38*); 2) the coeloconic sensillum on the maxillary sclerites (see p. 33**); 3) the displacement of abdominal spiracles I and II onto the laterodorsal surface of the abdomen, together with the narrowing of the corresponding tergites; 4) the peritoneal membrane, covering the filter chamber or the entire middle section of the gut in the absence of a chamber (Fick, 1981).

Synautomorphies of the cicadines: 1) lateral lobe of metapleural apodeme (absent in the Cicadoidea); 2) the metapisternal apodeme (absence in the Cercopoidea); 3) the filter chamber with the Malpighian tubules that are connected to it (absence in the Fulgoroidea); 4) the right-dorsal outgrowth of the anterior part of the mid-gut (absence in the Cicadelloidea); 5) the double row of teeth on the apex of the hind tibiae (absent in the Cicadelloidea, except for the Ledridae).

---

* Pagination in original text.
* - p. 45 in this translation.
** - p. 32 in this translation. [Tr.]

ANALYSIS OF THE PRINCIPAL EVOLUTIONARY FEATURES

1. **Head.**

1.1. Overall structural plan of head (Figure 2). The head is considerably and diversely modified in all of the groups of the Rhynchota and for this reason it is difficult to speak of the primitive state. Setting aside the cases of obvious secondary specialization, associated, for example, with the formation of the gula in the bugs or the disintegration of the head in the jumping plant lice, it may be concluded that the primitive head of the Rhynchota was characterized by a small, round, well demarcated loro-clypeal region, which jutted up into the frons in a shallow arch; at the same time the lora were turned towards the facial side, rather than laterally, and had a cone-shaped, convex form, as a result of which the boundary between the lora and the anteclypeus was concealed in a cleft; the antennae were situated in front of the eyes. A round loro-clypeal region is characteristic of many of the Sternorrhyncha and Coleorrhyncha, as are the coneshaped lora. The antennae are situated in front of the eyes in all of the Sternorrhyncha and Heteroptera.

In the cicadines one may distinguish several basic types of head, without mentioning especially the secondary cases. 1) Aetalionoid type. Clypeus small, fronto-clypeal boundary shallowly arcuate, lora cone-shaped, lying in the plane of the face. The outer margins of the maxillary plates and the genae from behind form the lateral carinate margin of the head. The antennae are located in front of the eyes. 2) the Ulopoid type of head is characterized by the fusion of the frons and clypeus, with the retention and reinforcement of the frontovertical sutures. It is also distinguished by a more considerable advance of the clypeus upwards in relation to the eyes, antennae and points of attachment of the manidibular levers. In other respects this type is similar to the predecing type. Inherent to the Ulopidae and Membracidae; possibly convergent. 3) The Cicadelloid type is characterized by a very considerable advance of the clypeus upwards and by the disappearance of all the boundaries of the frons. In addition there occurs a proliferation of the lateral margin of the

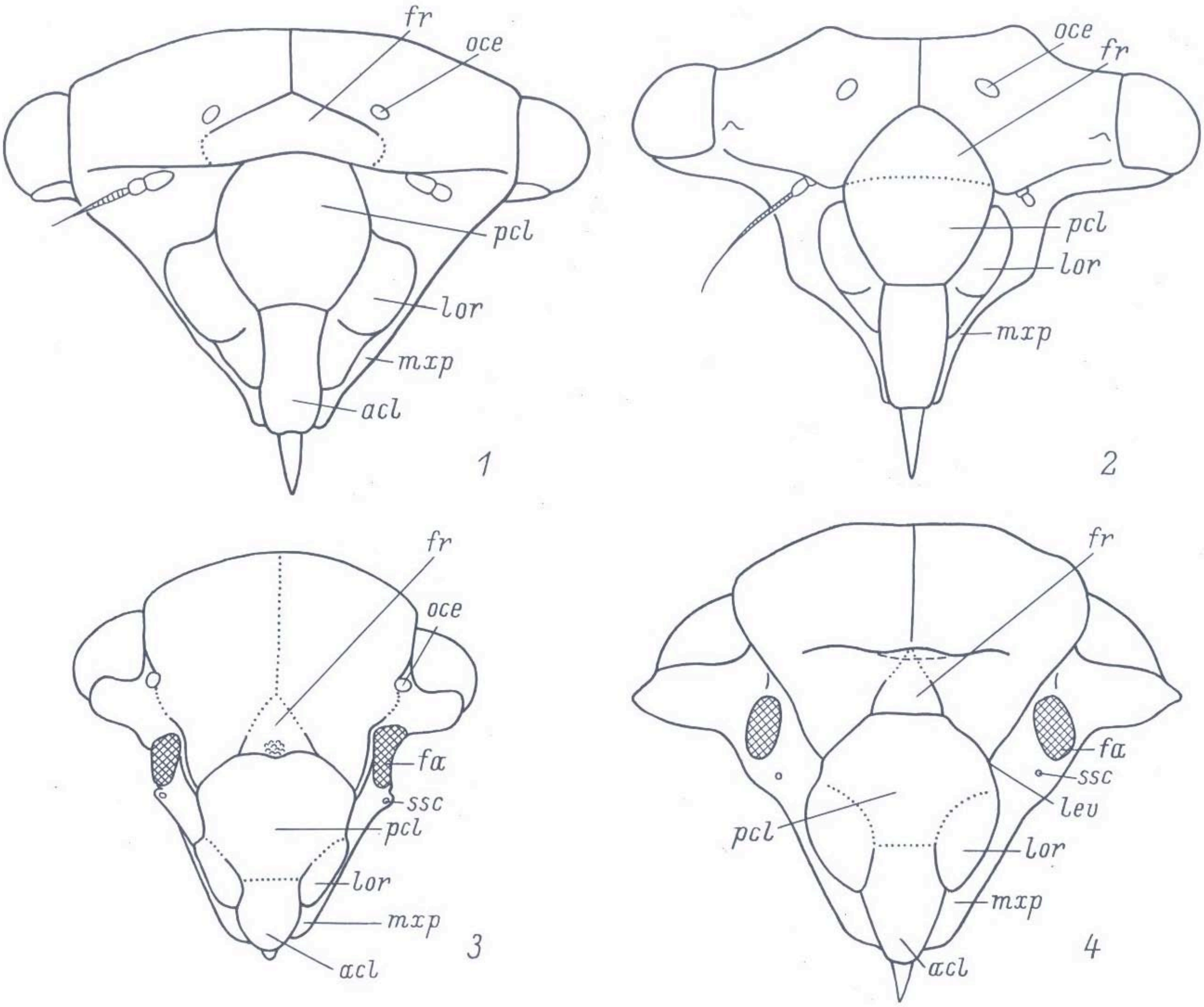


Figure 2. Head

1 - *Aetalion nervosopunctatum* Sign. (Aetalionidae); 2 - *Microcentrus carvae* Sign. (Membracidae); 3 - *Hilda* sp. (Tettigometridae), imago; 4 - *Tettigometra* sp. (Tettigometridae), 5th instar larva.
acl - anteclypeus, fa - antennal opening of head capsule, fr - frons, lev - site of attachment of mandibular lever, lor - lorum,

mxp – maxillary plate, oce – ocellus, pcl – postclypeus, ssc – coeloconic sensillum at base of maxillary lobe.

face, covering part of the propleura and fore coxae. In other respects this type is similar to the previous two types. 4) The Cercopoid type (Cercopoidea and Cicadoidea) is also characterized by a very strong advance of the clypeus upwards, with an outlet onto the vertical (upper) surface of the head and a well developed lateral margin, but this type is differentiated from the preceding type by the always pronounced frontoclypeal boundary and the more or less complete disappearance of the frontovertical sutures. 5) The Tettigometroid type is similar to the Aetalionoid type (1) on the basis of the cone-shaped lora, the lateral carina of the face and the weak advance of the frontoclypeal boundary upwards; in essence, they are almost equivalent on the basis of these features. The differences consist in that in the Tettigometridae the frons (metopion) is wider, the ocelli are more widely set apart, and the antennae are displaced downwards in relation to the eyes. 6) Fulgoroid type. In all of the Fulgoroidea, except for the Tettigometridae, the flat lora are turned to the side, the boundary between the lore and anteclypeus is not concealed in a cleft, the frontoclypeal boundary is primarily almost straight, the antennae are situated under the eyes, and the lateral carinae of the face are absent, though the posterior genal or postantennal carina of the Delphacidae and Cixiidae may apparently be considered as a rudiment of the lateral margin of the face.

Thus is may be seen that the structural features of the head of the Fulgoroidea, which are usually accepted as primitive, are not such and are not even all expressed in the primitive representatives of the superfamily. Such are the flat lora and the weak development of the clypeus. The positioning of the antennae in the Fulgoroidea is also a secondary phenomenon, it is not encountered in the other Rhynchota and is apparently associated with the proliferation of the vertical part of the head. It may also be seen that the hypertrophied clypeus of the cercopo-cicadoids and cicadelloids arose independently and cannot serve as an indicator of a direct relationship of these groups.

1.2. Ocelli. The original type, with 3 ocelli, is expressed in all of the Cicadoidea and in some of the lower Fulgoroidea: in some of the Cixiidae, in some of the Meenoplidae and in the Kinnaridae, although in the families Tettigometridae and Delphacidae there are only 2 ocelli. In all of the Cercopoidea and in most of the Cicadelloidea there are 2 ocelli, although in the latter the ocelli may secondarily disappear completely. The ocelli are reduced also in some of the short-winged Fulgoroidea and others. In the bugs there are usually two ocelli but they are absent in some of the advanced families (Miridae, Tingidae) even in the fully-winged forms, as well as in the parasitic families Cimicidae and Polyctenidae; 3 ocelli are not found in the bugs. Among the Sternorrhyncha 3 ocelli are found in the Psyllina and

Aphidina, 2 are found in the Aleyrodina, while in the Coccina there are no ocelli.

The tendency for the median ocellus to disappear is noteworthy. This disappearance apparently occurred repeatedly, and, possibly, through this is difficult to accept, its instauration also occurred.

The arrangement of the ocelli in relation to the eyes and to one another is variable, especially the disposition of the lateral ocelli. In the Cercopoidea and Cicadoidea the ocelli are set in quite close proximity to one another and at some distance from the eyes, while in the Fulgoroidea they are set apart from one another and close to the eyes; in the Cicadelloidea the situation, on the whole, is intermediate, if one speaks of the primitive groups. The arrangement of the ocelli on the dorsal or antero-ventral surface of the head in the Cicadelloidea varies considerably in a secondary manner, since the demarcation of the upper and facial surfaces of the head by a bend or carina is very variable and is often not homologous even within groups of low taxonomic rank. The low situation of the ocelli in the Fulgoroidea may also be explained by the strong development of the vertical part of the head capsule, enclosing the food reservoir.

In the Sternorrhyncha the ocelli are widely set apart, while in the bugs, for the most part, they are more closely situated. The situation in the Peloridiidae with fully developed wings has not been described. In the general features within the cicadines one may note a correlation between the distance between the ocelli and the width of the upper part of the clypeus.

1.3. Ecdysial sutures. According to the data of Hamilton (1981) the ecdysial sutures in most of the Rhynchota run in a similar fashion near the frontovertical boundaries, as in the Psocida; a small superficial deviation is apparently expressed in the Sternorrhyncha: the suture was displaced backwards towards the antennal cavities. Only in the Fulgoroidea do the sutures run in a substantially different fashion: behind the ocelli. This once more corroborates the idea that the so-called frons of the Fulgoroidea and the entire extensive upper part of the head do not provide evidence of a primitive nature for this superfamily. The exuviae of the Cercopoidea have not been described in the literature and they have not been studied by me; the exuviae of the Cicadelloidea have not been adequately studied.

1.4. Antennae (Figure 3). Three types of antennae are found in the imagines. 1) Not polymerized, composed of 9-11 segments in the Cicadoidea and some Proconiini (Cicadellidae, Cicadellinae). Evans' (1941) data on the 4-segmented nature of the antennae of the imago of the Terrigarctidae are refuted by the material: in the specimens of *Tettigarcta tomentosa* examined by me the antennae had precisely the same structure as in the Cicadidae. The non-polymerized antenna of the Proconiini has an especially secondary origin, since even in this advanced group it is expressed in only a few genera. 2) Flagellum polymerized and tapered commencing from its second segment (i.e. from the fourth antennal segment), the third antennal segment is small, round, bears specialized sensilla and is clearly set apart from the polymerized flagellum. The antenna of the Cercopoidea and Fulgoroidea is constructed in this fashion (Silvestri, 1934). 3) Flagellum integrated and polymerized as a whole; the basal segment of the flagellum is not distinguished; on the basal, thicker part of the flagellum are scattered characteristic coeloconic sensilla, similar to those found on the non-polymerized flagellum of the Cicadidae. The antenna in the Cicadelloidea is contructed in this fashion (Silvestri, 1934).

③

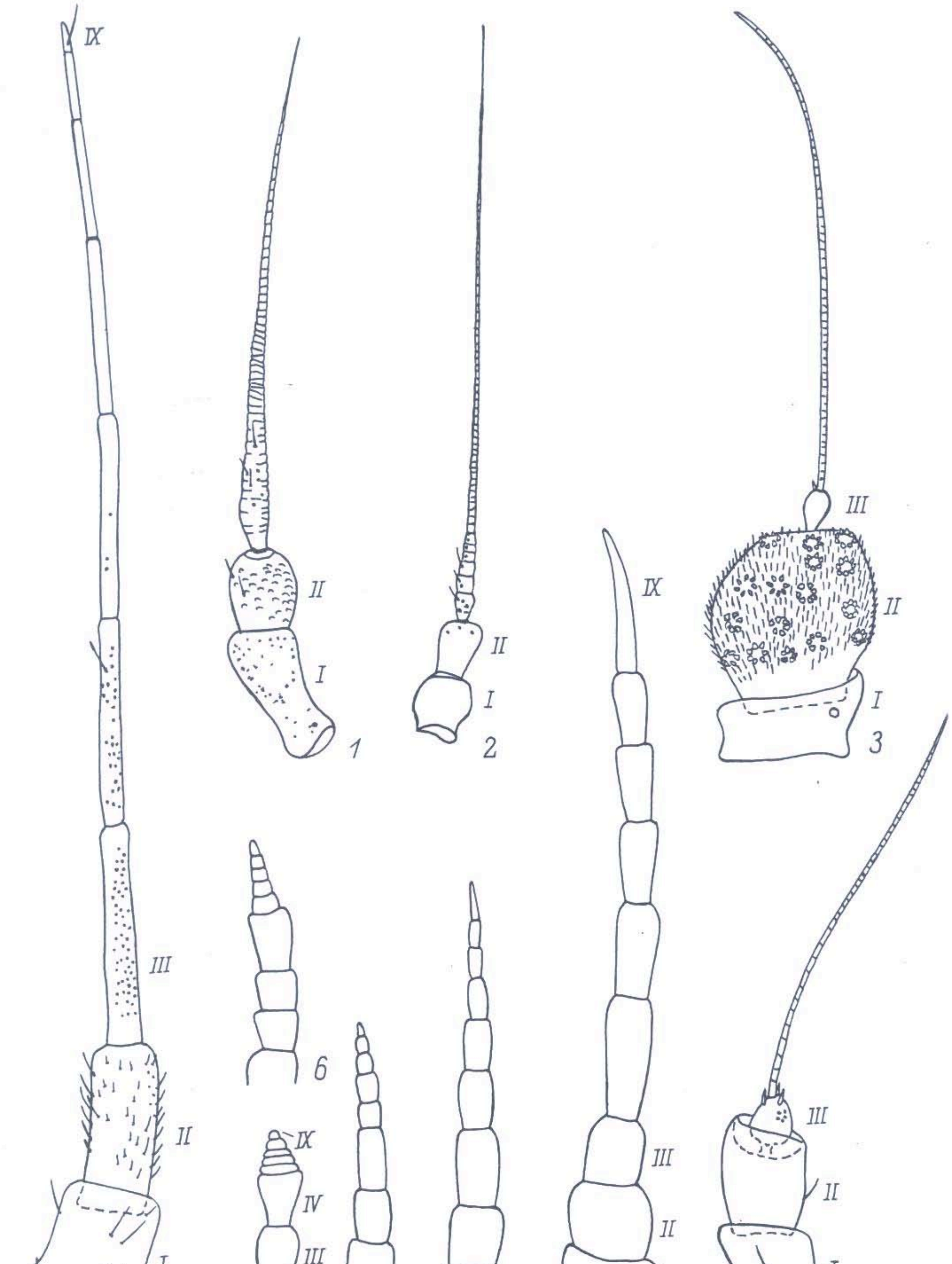


Figure 3. Antennae.

1 – *Centrotus cornutus* L. (Membracidae), imago; 2 – *Cicadella viridis* L. (Cicadellidae), imago; 3 – *Reptalus panzeri* Löw (Cixiidae), imago; 4 – *Cicada orni* L. (Cicadidae), imago; 5-9 – *Lepyronia quadrangularis* Say, larvae from instars I-V; 10- *L. coleopterata* L., imago. (According to: Doering, 1922; Silvestri, 1934). The primary segments are designated by Roman numerals.

In the larvae of the Cercopoidea and Cicadoidea are found non-polymerized homonomous 9-segmented antennae with a weakly distinguished scape and pedicel, including the Tettigarctidae (Evans, 1941; Doering, 1922; Kudryasheva, 1979). In the Cicadelloidea and Fulgoroidea the larval antennae are similar to the imaginal antennae, and in the Fulgoroidea the third segment in the younger larvae is markedly differentiated from the flagellum and in its dimensions resembles the first and second segments (Silvestri, 1934; Lindberg, 1939).

As a whole the cicadines are characterized by polymerization and tapering of the flagellum in the presence of a well developed or hypertrophied (Fulgoroidea) scape and pedicel. The variant of the Cicadoidea may be treated as a retention (recurrence) of the larval antennae in the imago. Thus, the antenna of the Cicadelloidea appears to be the most isolated form. It is difficult to explain the appearance of the cercopoid antenna by way of the differentiation of the base from the completely polymerized flagellum of the Cicadelloidea. It is more probable that the process of the polymerization of the flagellum in the common ancestor of the Cicadina commenced from the apex and was completed in different ways after the separation of the Cicadelloidea from the common stem of the other cicadines. The imaginalization of the larval antennae of the Cicadelloidea and Fulgoroidea may be an original state of all of the cicadines, if the non-polymerized antenna of the cercopo-cicadoid larvae was formed by instauration, which then in the Cicadoidea also passed on into the imago. A second variant postulates the independent transition of the imaginal antenna into the larvae in the Cicadelloidea and Fulgoroidea, the retention of the original state in the Cercopoidea and the larvalization of the antennae in the imagines of the Cicadoidea.

1.5. Rostrum (Figure 4). In the cicadines the rostrum is composed of from 3 to 5 segments. The primitive number of rostral segments in the Rhynchota is 3. In the psyllids and aleyrodids there are 3 segments, in the coccids there is a maximum of 3 segments with a subsequent reduction to 2 and 1. Koteja's (1974) contention that there are 4 segments in the Phenacoleachiidae is unconvincing and it based only on a count of the setae on the basal segment (according to Koteja – the two basal segments), but the chaetotaxy here, as is evident from Koteja's own data, is not sufficiently stable. In the aphids there are 4 segments; sometimes 5 are counted, if the more isolated apical sensory tubercle is accepted as a segment. Characteristic of the aphids is an oblique articulation between the second and third rostral segments. A very similar oblique articulation between the second and third segments is present also in the aleyrodids (Silvestri, 1934), which allows one to think that the 4-segmented rostrum of the aphids was formed from a 3-segmented rostrum by the division of the distal segment into two. Thus, in the Sternorrhyncha the rostrum is primitively 3-segmented. In the bugs the rostrum is usually 4-segmented, although, as was shown by Matsuda (1965), the second rostral segment in the bugs is homologous to the first segment in the homopterans, which is well shown by the basal apodeme of the rostrum, which in the bugs emerges from the second segment and passes through the first, while in the Homoptera it emerges from the base of the first segment. The formation of a supplementary basal segment of the rostrum in the bugs is associated with the mobilization of the head and the formation of the pharyngeal plate.

In the Cicadelloidea, Cercopoidea and Cicadoidea the rostrum is always 3-segmented, although the structure and proportions of the segments are specific for each individual superfamily. In the Cicadelloidea the rostrum is usually short; all of the segments are approximately uniform; at the base of the third segment ventrally a pair of supplementary sclerites are present. In the Cercopoidea the rostrum is also fairly short, but in it the 3rd segment is somewhat longer than the other two. In the Cicadoidea there are 2 basal segments, the second being somewhat swollen, while the third segment is strongly drawn-out and is markedly longer than the first two together. In the Fulgoroidea there are originally 3 segments (always so in the Tettigometridae and Delphacidae), with the first segment being comparatively short, while the other two are drawn-out and are approximately equal in length. In the higher Fulgoroidea the number of segments may range from 3 to 5. The basal segment is usually divided into two. In some of the Fulgoridae (Lieu, 1934) the rostrum is 5-segmented, since the second primary segment is also divided into two. In the higher Fulgoroidea the rostrum becomes three-segmented when the distal half of the primary first segment becomes membranized.

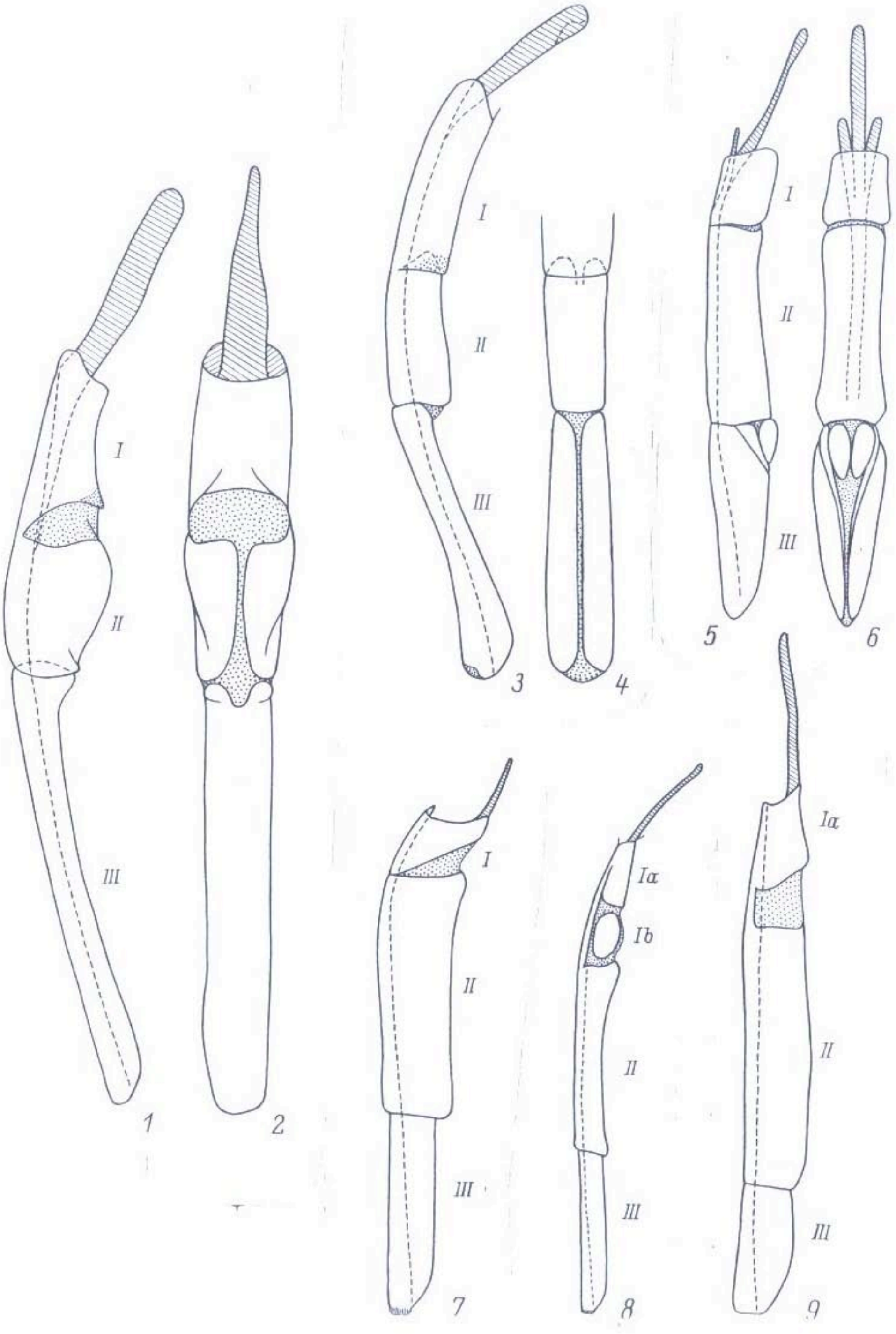


Figure 4.

1.6. Stylets of rostrum (Figures 5 and 6). As demonstrated by the data of Forbes and Raine (1973), Pollard (1972), Cobben (1978), Ekblom (1928) and others, most distinctive among the cicadines are the stylets of the Fulgoroidea, which preserve or regenerate a character resembling that of the Peloridiidae; in the Fulgoroidea the connection of the partitions between the ducts of the maxillary stylets is accomplished by means of a sliding tongue-and-groove suture. In the other cicadines this connection is accomplished by a strand that is T-shaped in cross-section, which is enveloped by the sides of the salivary duct. The conditions of the Cicadelloidea, Cercopoidea and Cicadoidea form a morphological series. In the Fulgoroidea the lower lip (slide) of the salivary duct is shorter and leaves a part of the left maxilla as a wall of the duct itself; in the other cicadines the lip extends to the T-shaped strand.

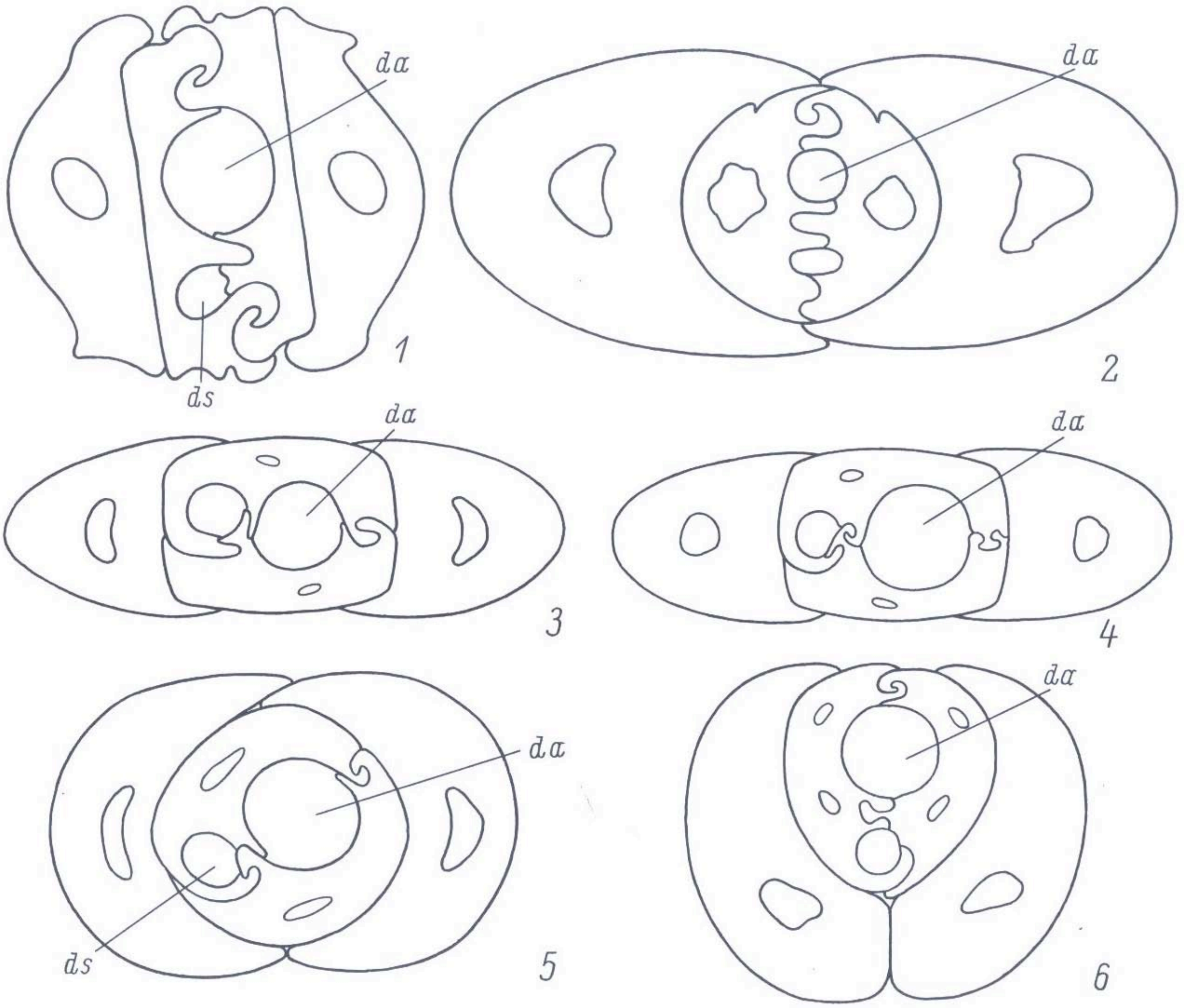


Figure 5.

Rostral stylets, schematic diagrams. View from apex of rostrum. 1 – Aphidina; 2 – Peloridiidae; 3 – Cercopidae; 4 – Cicadidae; 5 – Cicadellidae; 6 – Cixiidae. (According to: Parrish, 1967; Cobben, 1978). da – food duct, ds – salivary duct.

The character of the sliding coupling mechanisms of the maxillary stylets changes along the length of the rostrum, revealing a pattern, as one moves towards the tip, that is analogous to the phylogenetic series of complication of the coupling mechanisms, with a maximum in the distal part of the rostrum. The coupling mechanism at the base of the rostrum of *Macrosteles* (Cicadellidae) appears to be similar to the coupling mechanism of the Fulgoroidea and Peloridiina. In the stylets of *Macrosteles o*ne can see how the simplified groove could turn into the T-shaped closure with a reduction of the lower edge of the slot.

Another peculiarity of the maxillary stylets is their twisting along the longitiduial axis, reaching 45° in the Cicadelloidea (Ledridae, Cicadellidae) and 90° in the Cercopoidea and Cicadoidea. In the Fulgoroidea twisting has not been revealed. There is a clear parallel between the features of the reinforcement of the coupling mechanisms and the twisting.

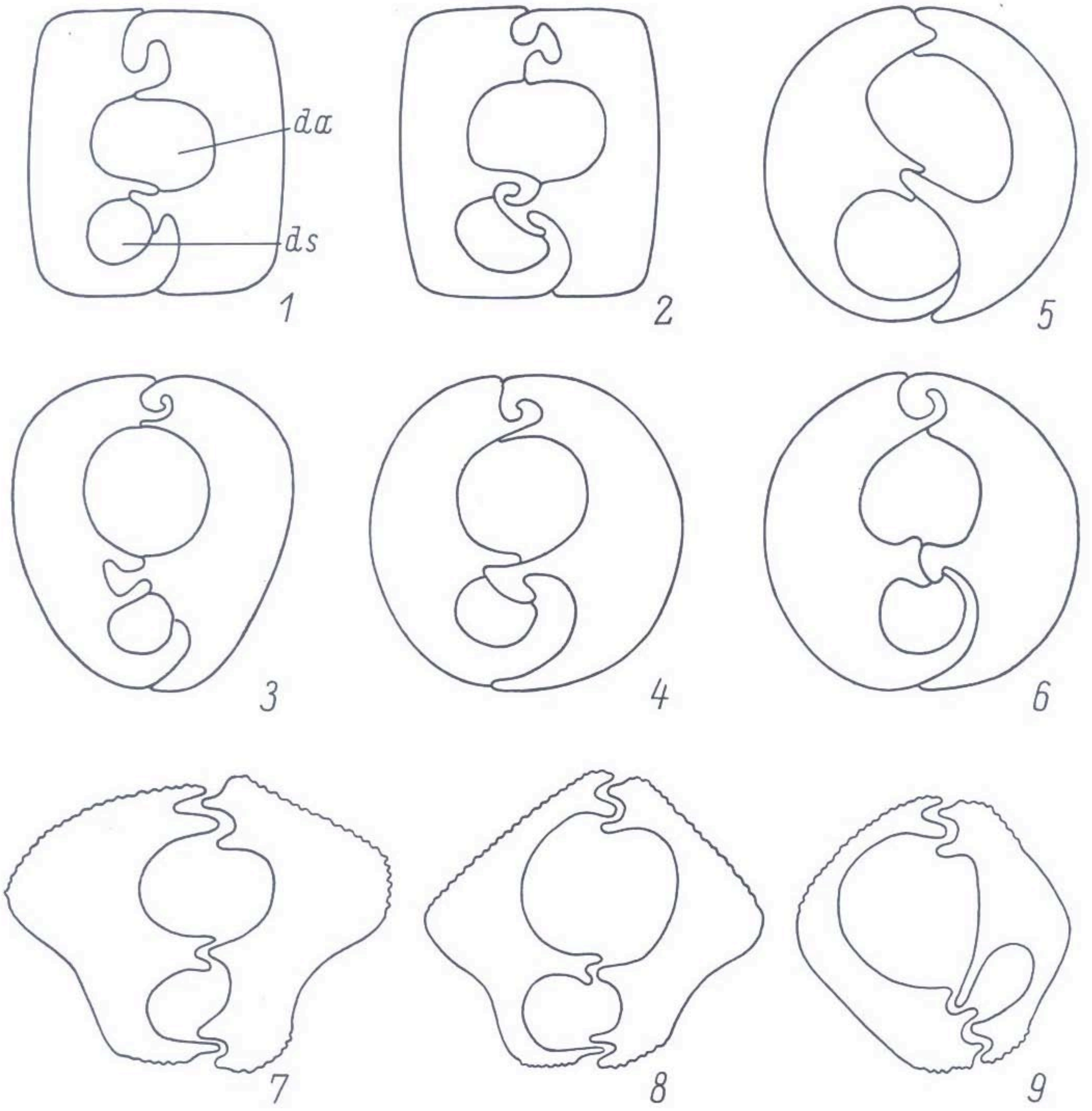


Figure 6. Maxillary stylets of rostrum. View from apex of rostrum.

1 - Cercopoidea; 2 - Cicadoidea; 3 - Fulgoroidea; 4 - Cicadelloidea; 5, 6 - *Eupteryx* sp. (Cicadellidae), (5 - at the base, b - at the apex); 7-9 - Nabidae, *Nabis flavomarginatus* Scholz. (7 - at the base, 8 - in middle part, 9 - at the apex). (According to: Ekblom, 1926; Pollard, 1972; Forbes and Raine, 1973; Cobben, 1978). Designations as in Figure 5.

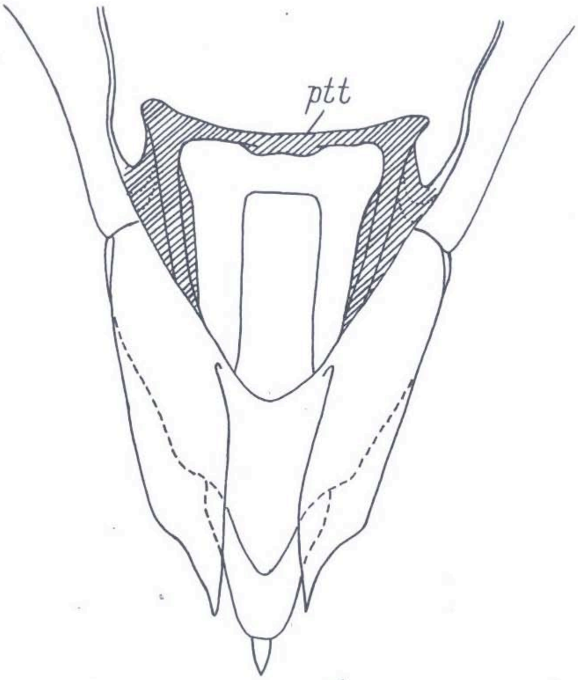
On the basis of the structural features of the mandidular stylets the Fulgoroidea stand by themselves, distinguished both from the Peloridiina and from the other cicadines.

The form of the maxillary stylets of the Fulgoroidea may be interpreted most simply as weakly autapomorphous on a plesiomorphous peloridiod basis. Unfortunately, the type of coupling mechanism under the salivary duct in the Peloridiina is still unknown, since Cobben’s photographs do not allow one to reliably discern this portion of the section of the rostrum. The structures of the rostrum of the Fulgoroidea may be explained as a consolidation, by way of retardation, of a stage similar to that which is expressed at the base of the rostrum of *Eupteryx* (Cicadellidae, Typhlocybinae).

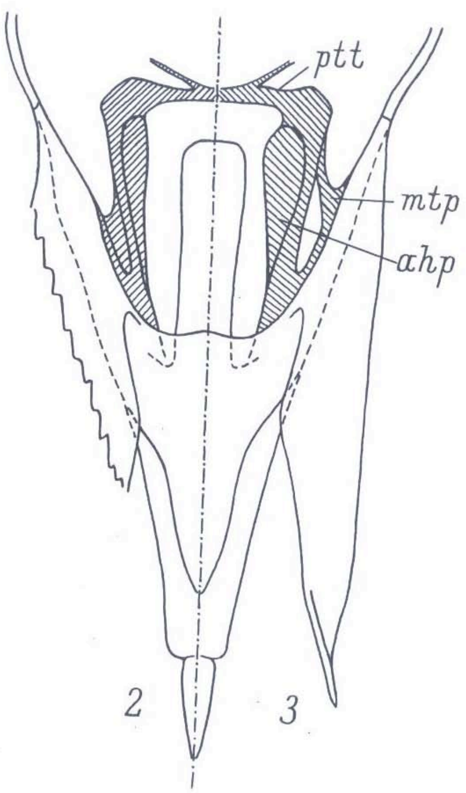
1.7. Tentorium (Figure 7). Among the Rhynchota a tentorium is developed only in the Homoptera; in several cases it is reduced or fused with the wings of the hypopharynx. In cases when there are no obvious secondary transformations the anterior arms extend from the head capsule above the epistomal suture near the boundary of the postclypeus and the lora, while the posterior arms extend above the subgenal suture in the posterior half of the region of the attachment of the maxillary plates. Among the Auchenorrhyncha the tentorium is most completely developed in the Cicadoidea (Myers, 1928; Evans, 1941; Kramer, 1950) and the Cercopoidea (Kramer, 1950); it is composed of a tentorial bridge, connecting the apices of the hypopharyngeal wings, the anterior arms and the free dorsal arms. In the Fulgoroidea the anterior arms lose their attachment to the wall of the head, they become thinner and weaker together with the dorsal arms and their common base, and are converted into strands that have no skeletal significance. At the same time the antennal muscles retain their attachment to the dorsal arms. In the Cicadelloidea the bridge of the tentorium becomes detached from the anterior and dorsal arms along the ecdysial suture, the common base of the anterior and dorsal arms disappears, the anterior arms retain their attachment and the antennal muscles remain in the anterior section. The reduction of the tentorium in the Fulgoroidea and Cicadelloidea is possible only in an independent fashion from the complete state; the break (detachment) of the tentorium occurs on different sides of the dorsal arms with their antennal muscles. However, taking into consideration that the break in the tentorium most probably occurs along the ecdysial sutures, it cannot be excluded that in the Fulgoroidea the site of attachment of the antennal muscles shifted from the dorsal arms onto the anterior arms behind the ecdysial suture, and then the similarity of the Cicadelloidea and Fulgoroidea in the break of the tentorium may prove to be an apomorphy of these two groups.

Kramer considered that in all of the cicadines, except for the Fulgoroidea, the posterior tentorial arms are absent and the tenorial bridge, becoming accreted with the apices of the hypopharyngeal wings, has lost its original connection with the occipital part of the head, while in the Fulgoroidea (Cixiidae, Dictyopharidae) the posterior arms are well expressed and set apart. It is remarkable that in the most primitive families of the Fulgoroidea, the Tettigometridae and Delphacidae, which Kramer did not consider, there are no isolated posterior arms of the tentorium and the connection of the hypopharynx with the tentorial bridge appears as in the other cicadines. A similar picture is found in the larvae of all the Fulgoroidea (verified in the Dictyopharidae and Fulgoridea). The isolated posterior arms of the tentorium appear as a result of the resorption of the middle part of the zone of contact of the arms with the wings of the hypopharynx. As a homologue of the posteror arms of the Fulgoroidea in the other cicadines Kramer considered the apodemal plate of the maxillary lobes and he did not assign these to the tentorium.

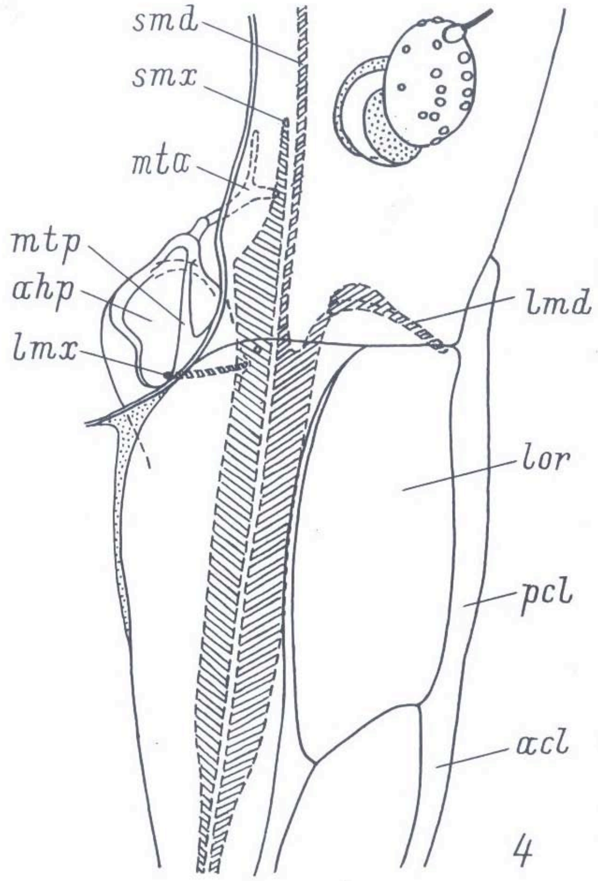
It is most probable that the posterior arms of the tentorium in all of the cicadines were originally entirely fused with the hypopharyngeal wings, and it is only in the imago of the higher Fulgoroidea that they become secondarily separated, though not completely, acquiring the structural plan found in the Psyllina.


ptt

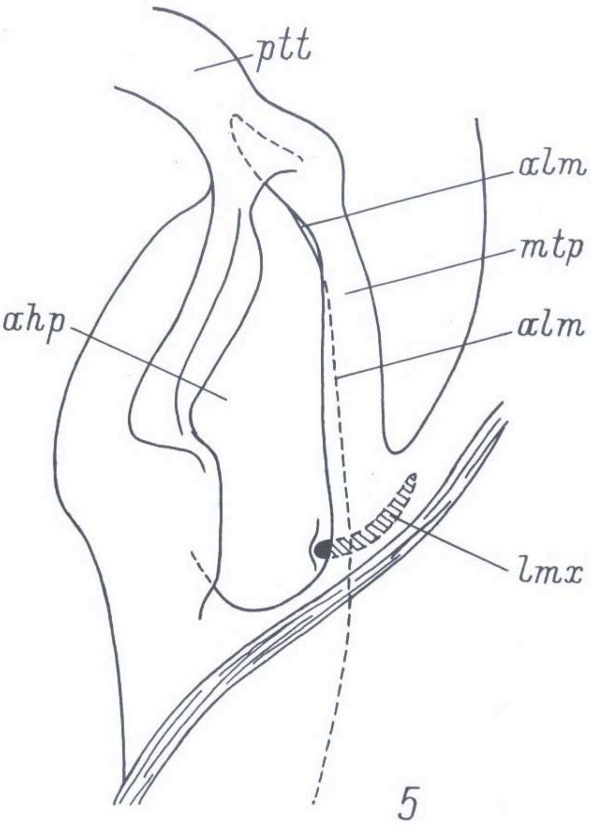
1


ptt
mtp
ahp

2 3


smd
smx
mta
mtp
ahp
lmx
lmd
lor
pcl
acl

4


ptt
alm
mtp
alm
ahp
lmx

5

Figure 7. Tentorium

1 – Delphacidae, *Delphax* sp., imago, 2, 3 – Dictyopharidae, *Elysiaca* sp. (2 – 5th instar larva, 3 – imago); 4, 5 – Dictyopharidae, *Saigona ussuriensis* Leth., attachment of maxillary lever (4 – general view from side, 5 – site of attachment in close view from behind and from the side).
acl – anteclypeus, aph – wings of hypopharynx, alm – anterolateral margin of hypopharynx, lmd – mandibular lever, lmx – maxillary lever, lor – lorum, mta – anterior arms of tentorium, mtp – posterior arms of tentorium, pcl – postclypeus, ptt – tentorial bridge, smd – mandibular stylet, smx – maxillary stylet.

The question of the composition of the tentorium and of its relationship with the hypopharyngeal wings within all of the Rhynchota is very complicated and, at the same time, important from the phylogenetic aspect both in itself as well as in connection with the site of attachment of the maxillary levers. Hypopharyngeal wings have been found, though not always correctly homologized, not only in the cicadines but also in the psyllids, as the “sehnenartiges Chitinband” (Weber, 1929a), in the aleyrodids, as the posterior arms of the tentorium (Weber, 1935), and in the bugs (Bekker, 1929; Rieger, 1976); at the same time they have apparently not been found or are rudimentary in the aphids and the coccids (Weber, 1928; Pesson, 1944). In the psyllids the posterior tentorial arms are free, while the apices of the hypopharyngeal wings are accreted with the tentorial bridge. It is considered (Spooner, 1939) that a tentorium is completely absent in the bugs. In the Peloridiidae the tentorium is represented by the bridge, which has become accreted with the apices of the hypopharyngeal wings, and by the anterior arms; there are no dorsal arms, as in the Sternorrhyncha. On the sides of the hypopharyngeal wings in the Peloridiidae (*Xenophyes cascus*) there are free apodemes, which in their position are very reminiscent of the posterior arms of the tentorium, though they are not directly associated with either the tentorial bridge or with the hypopharyngeal wings. Similar apodemes are also present in the bugs; thus E.G. Bekker (1929) described them in *Naucoris* as the site of attachment of the depressor muscle of the head.

It should be noted that neither these apodemes nor hypopharyngeal wings have been described in the Peloridiidae; in the literature the figures of the tentoria of the Peloriidae are either incomplete (Myers and China, 1929; Evans, 1981) or fantastic (Hamilton, 1981). The latter author depicted the hypopharyngeal wings as part of the outer wall of the head capsule, erroneously showing the posterior tentorial pits on the apices of formations that are actually the wings of the hypopharynx, and he confused the posterior wall of the hypopharynx with the gular plate which is absent in the Peloridiidae.

The great simplicity of the hypopharyngeal wings, and of the form and site of attachment on them of the maxillary levers, in the cicadines and in the bugs, compels one to think that in the bugs the posterior arms have been preserved in the composition of the hypopharyngeal wings, while the tentorial bridge and the other parts of the tentorium have disappeared. In the Peloridiidae there are no maxillary levers. In the bugs the apices of the hypopharyngeal wings are accreted by a short stalk with the occipital region of the head capsule; this stalk may correspond to the posterior arms of the tentorium, although it most probably bears a secondary character, since it is situated distally to the points of attachment of the maxillary levers, in which it is reminiscent of the secondary contacts of the wings in the cicadines (see below).

The absence of expressed hypopharyngeal wings and, consequently, of their accretion with the tentorium in most of the Sternorrhyncha may be secondary. It is very probable that the bugs and the cicadines are synapomorphous in the complete accretion of the posterior tentorial arms with the hypopharyngeal wings.

Along their entire posterior surface the hypopharyngeal wings of the Cicadelloidea serve for the attachment of the muscles of the salivary pump and at the same time their corresponding surface is turned quite severely backwards, i.e. it lies in the transverse plane to the body axis. In the Cicadoidea and Cercopoidea only the medial half of the posterior surface of the wings serves for the attachment of the muscles of the salivary pump, the outer boundary of the region of attachment of the muscles has the form of a high ridge, turned backwards, so that the surface of the attachment of the pump muscles is turned medially, i.e. it is situated in the longitudinal plane to the body axis. The same is found in the

Fulgoroidea, although in the latter in most cases, as has already been stated, the posterior arms of the tentorium (apodemal plates of maxillary lobes, according to Kramer) are free at the base. Originally in the cicadines the apices of the hypopharyngeal wings have no contact with the adjacent margin of the head capsule. This is the situation in the lower Cicadelloidea, including the Membracidae and some of the Cicadellidae. However in the Cercopoidea, Cicadoidea (Cicadidae) and many Cicadelloidea (Ledridae, some Cicadellidae) the lateral portions of the hypopharyngeal wings come into contact and become accreted in a point-like fashion with the lateral margins of the head capsule, near the occipital foramen. The contact appears repeatedly and in different portions of both components. In the Cercopoidea the accretion of the wing occurs opposite the point of attachment of the maxillary lever to the margin of the head, a little below the level of the eyes. In the Cicadoidea (Cicadidae) the contact was formed in the dorso-lateral corner of the wings above the point of attachment of the lever to the margin of the head, lying above the lower margin of the eyes; both components of the contact are not homologous to those in the cercopoids. In some of the Cicadelloidea the point of accretion of the hypopharyngeal wings to the wall of the head is similar (analogous) to that in the Cicadidae, although the maxillary levers are displaced upwards and are set closer to the site of accretion. In the Ledridae the points of accretion lie below the site of attachment of the levers. The question still remains open as to which state of the hypopharyngeal wings is primitive: longitudinal, as in most of the cicadines, or transverse, as in the Cicadelloidea.

1.8. Levers of maxillary stylets (Figure 7). In spite of the existing differences of opinion, in all of the cicadines, except for the higher Fulgoroidea, the maxillary levers have the same attachment to the lateral margins of the hypopharyngeal wing plates, extending from the site of divergence of the plates from the head capsule. Kramer refers to the sections where the maxillary levers are attached as the apodemal plates of the maxillary lobes and, consequently, he does not assign these to the hypopharynx. Kramer established such an attachment of the maxillary levers in all of the representatives which he studied: *Magicicada, Lepyronia, Aulacizes* (s. lato), *Ceresa* (s. lato) and *Scolops*. In the last case Kramer was apparently incorrect, since in another representative of this same family (*Saigona ussuriensis*) it was possible to establish without a doubt that the lever was attached to the wing, and not to the "apodemal plate" (Figure 7, 4, 5). It should be noted, however, that a separate passage of the posterior arms of the tentorium (of the apodemal plate), i.e. a window between the arms and the wing, occurs only in the imagines of the higher Fulgoroidea, commencing with the Cixiidae; in the Tettigometridae and Delphacidae, as well as in the larvae of all the Fulgoroidea there is no such window. The transition of the lever from the apodemal plate onto the wing may be associated with the formation of the window. The apodemal plate of the maxillary lobes corresponds well with the posterior arms of the tentorium in the Sternorrhyncha. It may be conjectured that in the cicadines and the bugs are hypopharyngeal wings in their lateral parts correspond to the posterior arms of the tentorium, onto which, from their base upwards, were displaced the maxillary levers. The question of the homology of the posterior arms of the tentorium and the lateral portions of the wings is complicated by the presence in bugs, along the sides of the hypopharynx, of apodemes which may also be accepted as posterior arms that become isolated in connection with the reduction of the rest of the tentorium; this view was accepted by Hamilton (1981).

In contrast to the bugs and the cicadines, in the Sternorrhyncha the maxillary levers are always attached to the wall of the maxillary plate, for the most part around the subgenal suture, but they are not always associated with the bases of the posterior arms of the tentorium. In the Psyllina the bases of the arms and the points of attachment of the levers are located on the anterior margin of the maxillary plates; in the Aleyrodina – on the middle of the margin, but the bases of the levers are moved markedly away from the subgenal suture and thus also from the bases of the arms; in the Coccina both the arms and the levers are attached side by side in the middle of the subgenal margin of the maxillary plates; in the Aphidina the arms are located in front of the margin, while the levers are located in the middle of the margin. In the Peloridiidae there are apparently no maxillary levers.

1.9. Mandibular levers. The site of attachment of the mandibular levers is of considerable comparative interest within all of the Rhynchota. In all of the cicadines they are attached on the epistomal suture at the boundary of the postclypeus and the lora. In all of the Sternorrhyncha, except for the psyllids (the lever is absent in these) and also in the bugs, at least in the Ochteridae (Rieger, 1976) and, apparently, in the Naucoridae (Bekker, 1929), the mandibular levers are attached at the boundary of the lora and maxillary plates. According to the data of Evans (1981) and Hamilton (1981), in the Peloridiidae the mandibular lever is also attached at the boundary of the base of the lora and the maxillary plate. As was shown by Weber (1935), the mandibular lever in the aleyrodids has a dual articulation with the head capsule: anteriorly at the boundary of the lora and the maxillary plates and posteriorly alongside the point of attachment of the maxillary lever. The first point is undoubtedly primitive, since near it, as in the other homopterans, is attached to the lever the protractor muscle; the second articular apophysis is devoid of muscles.

1.10. Subgenal suture. It is considered that a subgenal suture is developed in the Fulgoroidea, Cercopoidea, Aetalionidae and Ulopidae (Evans, 1946a, 1975; Kramer, 1950). However, it is often indistinct or questionable in these groups. Thus, in the lower Fulgoroidea (Tettigometridae, Delphacidae, Cixiidae) it is indistinct. At the same time in these groups a coeoloconic sensillum (Silvestri, 1934; Evans, 1973) is situated above the proposed line of the subgenal suture. Apparently the subgenal suture in the cicadines is a secondary formation, resulting from instauration, at least in the Fulgoroidea. The positioning of the coeloconic sensillum also differs within the limits of the maxillary lobe. In the Cercopoidea, Cicadoidea and most of the Cicadelloidea it lies to the sides of the lora and is displaced from the region of the subgenal suture; in the Eurymelinae (Cicadellidae) it is even shifted to the apex of the maxillary plates. In the first instar larvae of the Cicadidae this sensillum still has the form of an ordinary seta (Silvestri, 1922).

1.11. Cervicalia. Present in the Cicadoidea, absent in the other cicadines. Kramer (1950) described dorsal and lateral cervical plates in the Cicadidae, while Evans (1941) described lateral cervical plates in *Tettigarcta*. It is possible that these formations bear a secondary character and are associated with the dimensions.

2. Prothorax

2.1. Posterior lobe of the pronotum. Synapomorphy in the bugs and the cicadines. Strongly abbreviated and, as such, almost completely reduced in the Cicadidae; short in the Fulgoroidea but homologous over the length of the covered part of the mesonotum with that of the Cercopoidea and Cicadeloidea; it extends to the posterior ends of the parapsidal furrows. The lateral edges of this lobe in the bugs and many cicadines serve for immobilizing the base of the clavus (see section 5.4*).

2.2. Notopleural suture (Figure 8). Developed in the Fulgoroidea and not developed in the other cicadines. In the larvae, however, a notopleural suture is developed in the Fulgoroidea, Cercopoidea and Cicadoidea, and is not developed in the Cicadelloidea, including the Membracidae (the situation in the Aetalionidae is unknown).

In the bugs, as was shown by I.M. Kerzhner (1981) in the Nabidae, the notopleural suture is not developed in the imago, though traces of it are present. In the larvae of the bugs the notopleural suture is distinct, free, and it stretches as the larva grows between moults. A free notopleural suture is also found in the larvae of such very or comparatively primitive families as the Enicocephalidae, Ceratocombidae and Reduviidae; a distinct but non-stretching suture is found in the Leptopodidae; there is no notopleural suture in the Saldidae, Naucoridae, Notonectidae and Belostomatidae.

---

* Sic. Should be 5.9. [Tr.]

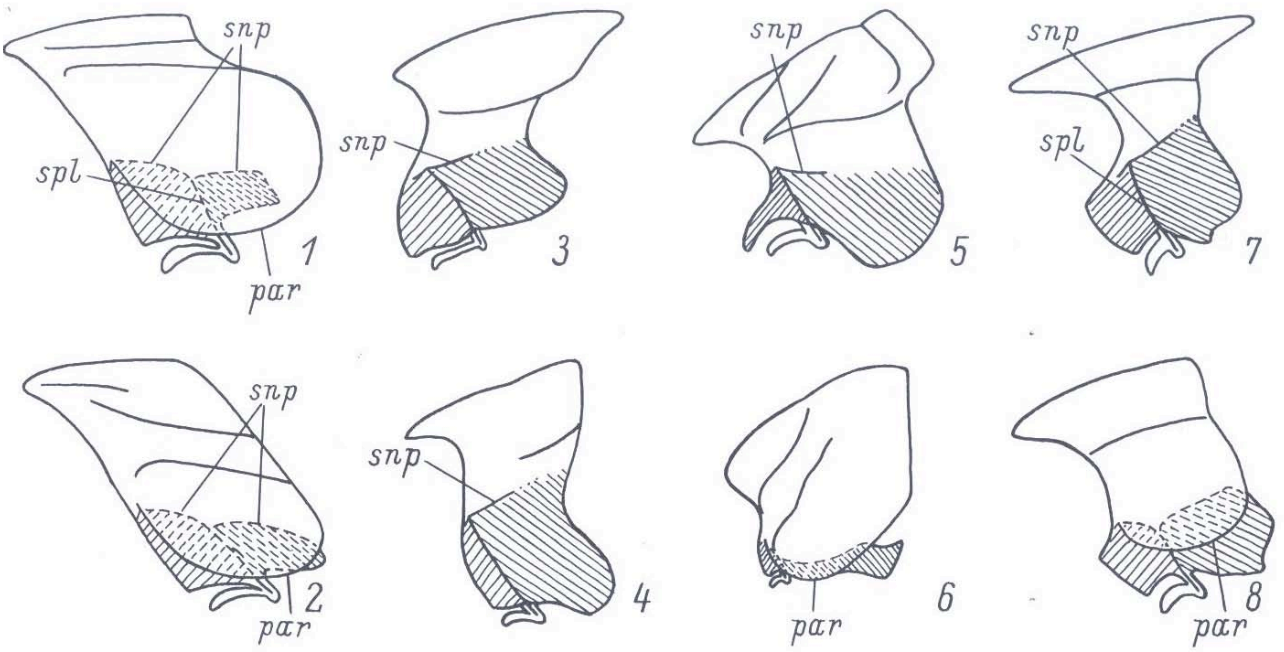


Figure 8. Notopleural region of the prothorax.

1, 2 – Dictyopharidae; 3, 4 – Cicadellidae; 5, 6 – Cicadidae; 7, 8 – Aphrophoridae; upper row – imagines, lower row – 5th instar larvae (oblique hatching to the right – episternum, to the left – epimeron); par - paranota, snp – notopleural suture, spl – pleural suture.

Thus is may be considered that in the Cicadelloidea imaginalization of the larva occurred with regard to the suture, while in the Fulgoroidea we find a larvalization of the imago. The primitive type of development of the notopleural suture has been preserved in the Cicadoidea and Cercopoidea.

2.3. Carinae and outgrowths of the pronotum (Figure 9). All of the cicadines have lateral carinae of the pronotum, which it would be more correct to call lateral carinae of the dorsum of the pronotum, since under them is located a section, also belonging to the pronotum, though it is directed laterally and borders with the propleura from below. There are no other permanent carinae in the Cercopoidea, Cicadoidea and most of the Cicadellidae. In the Fulgoroidea a fairly complex system of carinae is developed (Emel'yanov, 1980): besides the lateral carinae of the dorsum there are present a medial carina, lateral carinae of the disc, an upper carina of the paranota, which runs ventrally and parallel to the lateral carina of the dorsum, and some others. All

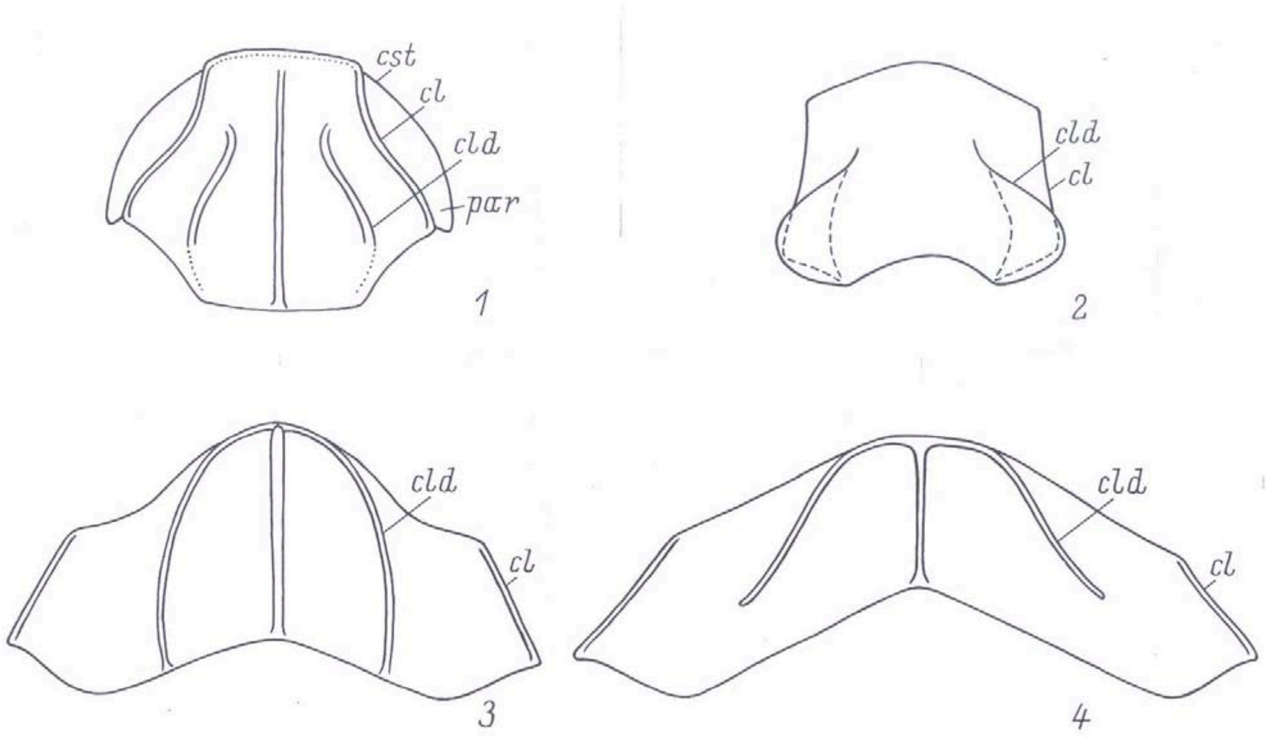


Figure 9. Pronotum. Dorsal view.

1 – *Aetalion quadratum* Fowl. (Aetalionidae); 2 – *Ledra aurita* F. (Ledridae); 3 – *Terauchiana sagitta* Kusn. (Delphacidae); 4 – *Changeondelphax velitshkovskyi* Mel. (Delphacidae).
cl – lateral carina on dorsum of pronotum, cld – lateral carina on disc of pronotum, cst – costal carina on proparanotum, par – paranota of pronotum.

of the mentioned carinae are frequently developed in many of the primitive Cicadelloidea. In some of the Aetalionidae (clearly in *Aetalion quadratum* Fowl.) only the upper carinae of the paranota are absent; in many of the Ulopidae the upper carinae of the paranota are present but the lateral carinae of the disc are indistinct. Incidentally, in these groups the paranotal lobes themselves are generally well developed with a distinct costal carina (*Aetalion quadratum*, *Myerslopia parva*, some Membracidae). The plan of the carinae in the Ulopidae and Aetalionidae is applicable to the Membracidae; the lateral horns of the pronotum of treehoppers are found to be homologues of the lateral carinae of the disc, as are the ear-sharped outgrowths in the Ledridae.

Thus, the Cicadelloidea and Fulgoroidea turn out to be (synapomorphously) similar on the basis of the plan of the pronotal carinae and the hypertrophy of the paranota.

3. **Mesothorax**

3.1. Epicostal carinae of mesopleura (Figure 10). On the mesothoracic pleura in the cicadines is present a so-called pleural alar sulcus, into which is inserted, at rest, the base of the costal margin of the fore wings. From below and the outer side this sulcus is bordered by the epicostal carina, which may be divided into three segments on the basis of the places of its passage: 1) episternal segment, which is set apart as the episternal lobe; 2) anterior epimeral segment, lying in front of the transepimeral suture, and 3) posterior epimeral segment behind the latter. The transepimeral suture is clearly expressed only in the Cicadoidea, but it can always be easily extrapolated from the pit of the pleural apophysis.

An episternal lobe is present only in the Cicadelloidea and Fulgoroidea, but in the Cicadelloidea both segments of the carina on the epimera are expressed, while in the Fulgoroidea only the posterior segment is expressed. In the Cercopoidea and Cicadoidea there is no episternal lobe, but its rudiment maybe discerned in the form of a tubercle in front of the pleural suture and displaced backwards by the base of the fore wing. In the last two superfamilies the anterior segment of the epimeral carina is more strongly developed, while the posterior segment is weakly developed.

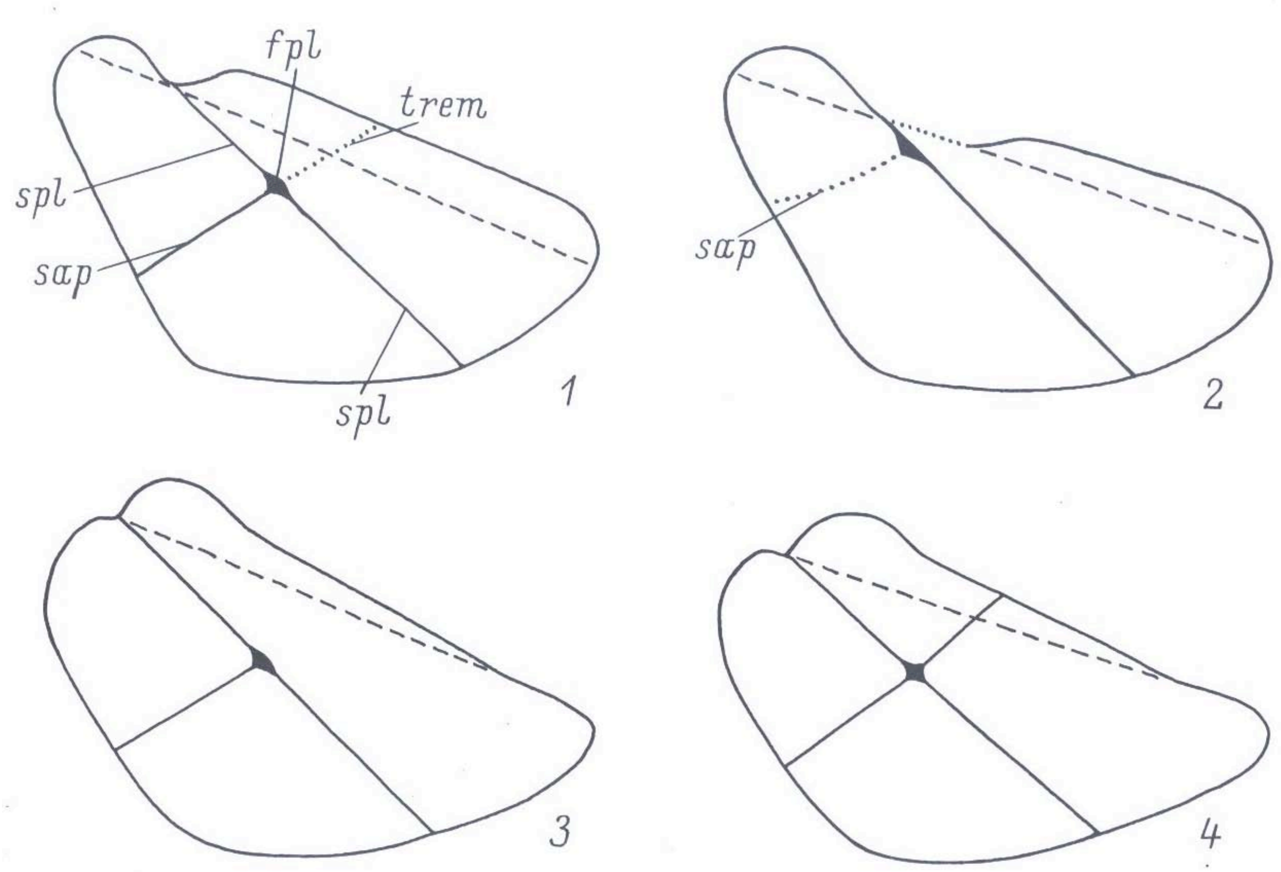


Figure 10. Epicostal carinae of the mesopleura. Schematic diagrams.

1 – Cicadelloidea; 2 – Fulgoroidea; 3 – Cercopoidea; 4 – Cicadoidea.
fpl – pit of pleural apophysis, sap – anapleural suture of episternum, spl – pleural suture, trem – transepimeral suture.

3.2. Parapsidal furrows. Present in all the cicadines but developed in different ways. In the Aetalionidae and Membracidae the parapsidal furrows are in the form of a concave linear trough in the completely sclerotized body wall; in the Cicadellidae, Ulopidae and Ledridae there are in the form of membranous, terminally enclosed strips. The interpolated or evident point of convergence of the parapsidal furrows is far removed from the anterior margin of the scutellum. The scutum is furnished with a sagittal inner carina.

In the Cicadoidea the parapsidal furrows are expressed as furrows on the outside and as carinae on the inside. The site of convergence of the parapsidal furrows is at some distance from the border of the scutellum. A sagittal inner carina is not developed on the scutum.

In the Cercopoidea the parapsidal furrows are expressed in the form of membranous strips, enclosed at both ends; the lateral margins of the strips are reinforced by inner carinae. The posterior ends of the parapsidal furrows are located more or less close to the border of the scutellum. A sagittal carina cannot be traced.

In the Fulgoroidea the parapsidal furrows are rudimentary, expressed as lines of a concave bend of the steep anterior part of the mesoscutum, covered by the lobe of the pronotum. Posteriorly (dorsally) they terminate far from one another; from their posterior ends commence the lateral carinae of the mesonotal scutellum (autapomorphy of the Fulgoroidea), which are expressed as convex folds; these carinae apparently have no genetic continuity with the parapsidal furrows. The sagittal carina of the scutellum is similar to the lateral carinae.

The structure of the parapsidal furrows is similar in the Cercopoidea and some of the Cicadelloidea (the Cicadellidae line). This similarity is most probably a result of convergence and instauration, since in the most primitive Cicadelloidea, the Aetalionidae and Membracidae, the furrows are not membranous. The second possibility, of an apomorphous independent character of the overgrowth of the parapsides in the Membracidae line and in the other three superfamilies, seems less probable.

The parapsidal furrows are quite well expressed in all of the Rhynchota; in the bugs they are apparently developed, for the most part, as external furrows corresponding to internal carinae.

3.3. Lateroparapsidal furrows. Not manifested in the Fulgoroidea. As a rule they are absent in the Cercopoidea, through occasionally traces are evident. In the Cicadoidea they are expressed as traces in the form of a linear bend. Evans (1941) did not indicate the furrows in *Tettigarcta*, but nor did any of the authors who described the morphology of the Cicadidae (Myers, 1928; Kramer, 1950). In the Cicadelloidea the lateroparapsidal furrows are most strongly expressed in the Membracidae line (Aetalionidae, Membracidae), where they appear as furrows from the outside and as carinae from the inside (Ross, 1957). In the Cicadellidae line (Ulopidae, Ledridae, Cicadellidae) the furrows are more moderately expressed, as lines of a concave bend, though sometimes they appear as strongly as in the Membracidae line.

The absence of the lateroparapsides in the Fulgoroidea places the latter close to the cercopo-cicadoids. In the bugs and in the Sternorrhyncha there are apparently no lateroparapsides, although in the males of some Coccina (*Pseudococcus citri, Eulecanium taxi*) one may discern them in Theron’s (1958) figures in a not quite usual position, because of the growth of the anterior part of the mesonotum.

3.4. Furcal pits. Secondary phanerosternia is expressed in the Fulgoroidea. Since the Homoptera are primitively characterized by cryptosternia, and among the Auchenorrhyncha the latter is absent only in the Fulgoroidea, it is natural to consider it here as secondary. In the Sternorrhyncha cryptosternia is also developed. The situation in aphids is of interest, since in the alate females the mesothorax is cryptosternous, while in the apterous forms it is phanerosternous with furcal pits that are widely set apart, in similar fashion to the Fulgoroidea. The metathorax in *Aphis faba*e is phanerosternous in both cases, which is apparently associated with its weak development and the weakness of the wing musculature with the diminished hind wings.

It seems that from the time of Hansen (1890) it has been accepted to assign very considerable importance to the widely set-apart middle coxae of the Fulgoroidea; this feature, however, which is in part associated with the phanerosternia, no longer so drastically differentiates the Fulgoroidea from the other cicadines. Widely set-apart middle coxae are present in the Aetalionidae and Membracidae, while in the Tettigometridae the mobility and disposition of the middle coxae is close to the aetalionoid type.

3.5. Segmentation of pleuron. An anapleural suture of the episternum and a transepimeral suture may be developed on the mesopleuron of cicadines. The complete picture is found in the Cicadoidea; in the Cicadelloidea only traces remain of the transepimeral suture, it is absent in the Cercopoidea, and in the Fulgoroidea it is also absent, with the exception of the advanced families Nogodinidae and Ricaniidae, where it apparently appears in a secondary fashion. The presence of the transepimeral suture in the Cicadoidea may also be secondary, associated with the enlargement of dimensions in this superfamily.

The primary and secondary states in the structure of the mesopleuron should be considered in interrelation with the other characteristics of its structure, including the epicostal furrow and its position. For this a comparison is necessary with the hemipterans and, ideally, with the Archescytinoidea. In the Sternorrhyncha an epicostal furrow is not expressed, but this may be a secondary state, since all of the lines of the sternorrhynchans are characterized by a simplification of the morphological structures associated with the wings and with flight. It seems that the Cicadelloidea stand closest to the primitive state; in these the epicostal carina is fully developed (all 3 elements, see section 3, 1) and traces of the transepisternal carina are present. The situation in the Cercopoidea and Cicadoidea is differentiated by the disappearance of the episternal lobe of the carina and by a weakening of its posterior part, lying behind the transepimeral suture (expressed or extrapolated). The state in the Fulgoroidea is characterized by a similarity with that in the Cicadelloidea, but with an absence of the middle portion of the carina, which is associated with the lowering of the costa of the fore wings and with the corresponding displacement of the carina to the pit of the pleural apophysis. The largest number of apomorphous features, counted from the original state of the Cicadina, are found in the structure of the mesopleuron in the Fulgoroidea.

3.6. Posterior alar process. Not separated in the Cercopoidea and Cocadelloidea, short in the latter; separated in the Cicadoidea (including the Tettigarctidae); absent in the Fulgoroidea, in which the third axillary sclerite has lost its connection with the notum.

4. **Metathorax**

4.1. Episternal apodeme. A distinct metepisternal apodeme is present in the imagines of cicadines (Emel'yanov, 1981); it is expressed in the Cicadelloidea, Fulgoroidea and Cicadoidea. The episternal apodeme, which is free in the Cicadelloidea and Cicadoidea (not described in the Tettigarctidae), is accreted into a single synapodeme with the pleural ridge in the Fulgoroidea.

4.2. An episternal apodeme in the larvae is developed in the Cicadelloidea and Fulgoroidea in a very similar form, as a single whole with the pleural ridge (Emel'yanov, 1981; Savinov, 1983); absent in the Cicadoidea and Cercopoidea.

4.3. The pleural apodeme of the metathorax has been considerably transformed in the cicadines; it is devoid of a free pleural apophysis and often bears supplementary lateral lobes, covering peculiar formations of indistinct origin and functional significance, possibly resonators (Emel'yanov, 1981); often accreted with the episternal apodeme (see section 4.1.). In the Cercopidea lateral lobes are present on both sides (on the side of the epimera and on the side of the episterna); in the Cicadelloidea and Fulgoroidea they are present only on the side of the episterna, and in this case the lobe is well developed in the Fulgoroidea and weakly developed (rudimentary?) in the Cicadelloidea, and among the latter it is not developed in some groups. In the Cicadoidea (Cicadidae) there are no lobes and, in contrast to the other cicadines, a secondary protruberance is hypertrophied opposite the apex of the cavity of the pleural apophysis.

4.4. The pleural apodeme in the larvae of cicadines has no apophysis in some cases (Cicadelloidea, Fulgoroidea), while in others it is furnished with a well developed apophysis (Cercopoidea, Cicadoidea). In both cases the ridge has a single structure without lateral lobes. In the absence of an apophysis the pleural ridge is united with the episternal apodeme and, based on all its characteristics, is secondary, while in the presence of an apophysis the ridge appears as a primitive, unchanged structure.

The relationships of the episternal and pleural apodemes in the larvae and the imagines (sections 4.1.-4.4.) are very interesting and evolutionary complex. In the Cicadelloidea the larvae possess a monolithic synapodeme, while its components in the imagines are separate; in the Cicadoidea the relationships in the imagines are similar to those in the Cicadelloidea, while in the larvae there is no episternal apodeme, while the pleural apodeme has the primitive appearance. In the Fulgoroidea a synapodeme is developed in both the larvae as well as the imagines; in the larvae it is the same as in the Cicadelloidea, while in the imagines it is similar to the cercopoid type, but supplemented by fusion with the episternal lobe. In the Tettigometridae in the last (5th) instar larvae of *Tettigometra*, which do not jump, and also larvae of the preceding instars, a weakly sclerotized episternal lobe is preserved and also a common fulgoroid structure of the metapleura. This characteristic in combination with the mobilized trochanter and the 3-segmented hind tarsus clearly testify to the fact that the larvae of the ancestors of the Tettigometridae jumped, as in all of the other Fulgoroidea. It allows us, however, to understand the appearance of the cercopoid imaginal apodeme without an episternal lobe: evidently this commenced with the situation that the larvae of the Cercopoidea ceased jumping, and ended with the fact that the jumping in the imagines was carried out by other muscles or by muscles which had changed the site of their attachment to the thoracic skeleton.

It seems that that “primitive” appearance of the pleural apodeme and the absence of an episternal apodeme in the larvae of the Cercopoidea and Cicadoidea are not primitive, and that the primitive stage in the formation of the morphofunctional jumping complex has not been preserved in any one superfamily.

Some fundamental transformations in the primitive metapleural apodeme apparently occurred back in the common paraneopteran ancestor, since a metapleural apophysis is not expressed in the bugs, nor in the Sternorrhyncha, nor in the psocopterans.

4.5. Astragal (Emel’yanov, 1981). Not developed in the Cicadelloidea; developed in the Fulgoroidea and Cercopoidea, and transformed into the covers of the sound apparatus in the Cicadoidea.

4.6. Posterior notal alar process. Normally developed in the Cicadelloidea (short) and the Fulgoroidea; separated in the Cercopoidea and Cicadoidea.

4.7. Furca. It seems that the forked sclerite of the Fulgoroidea corresponds to the furca, notwithstanding my previously expressed opinion (Emel'yanov, 1981). In this case the Fulgoroidea are differentiated from the other cicadines by the phanerosternous nature of the metathorax.

4.8. Trochantin. Has disappeared in the Fulgoroidea in connection with the accretion of the coxae to the thorax.

5. **Wings**

5.1. Wing-coupling apparatus (Figures 11-15). This is of two types in the cicadines: basic and supplementary (Ossiannilsson, 1950). The basic type consists of a fold along the sutural margin of the clavus, formed by the bending downwards and forwards of the posterior margin (a narrow peripheral membrane) of the forewing, and of a lobe on the anterior margin of the hind wing, bent upwards and backwards, lying in the region of the junction of C and ScR. The supplementary type consists of one or a series of hook-like spines, lying proximally to the basic lobe on the anterior margin of the hind wing and also fastening onto the posterior margin of the clavus of the forewing, but often on another part of the latter.

The basic coupling mechanism is homologous in all of the cicadines and differs little in its structure in the various groups (Figures 12-15). In the Cicadelloidea the lobe of the hind wing is narrow, while in the other cicadines it is wider.

The supplementary coupling mechanism is always developed in the Cercopoidea (Figure 14); there are usually only a few hooks here (sometimes 1) and they are seated on a forwardly protruding promonotory of the lobe on the antieror margin of the wing. In the Cicadidae there are no hooks, while in the Tettigarctidae there is only one well developed hook but there is no protrusion of the anterior margin of the wing. In the Cicadelloidea and Fulgoroidea hooks of the supplementary coupling mechanism are encountered only in some undoubtedly secondary groups, such as the Proconiini of the Cicadellidae and the Flatidae of the Fulgoroidea. In the primitive representatives of both these superfamilies (Aetalionidae, Tettigometridae, etc.) a supplementary coupling apparatus is absent. The appearance of the hooks of the supplementary coupling mechanism in these two superfamilies may be interpreted as instauration.

The coupling apparatus in the Sternorrhyncha (Weber, 1930) differs from that in the Auchenorrhyncha in that the posterior component is formed only in the form of curved spiniform setae that are set apart (Psyllina, Aleyrodina) or of similar setae that are set very close together (Aphidina); in the Cocicna the hind wings are reduced to the state of halteres, although the halteres bear one or several curved setae which fasten onto a special lobe at the base of the fore wing (Stickney, 1934; Ghauri, 1962; Kawecki, 1964; Giliomee, 1968; Afifi, 1968, et al.). The posterior component of the coupling apparatus of the Sternorrhyncha apparently corresponds to the supplementary couping mechanism of the Auchenorrhyncha.

The coupling apparatus of the bugs, including the Peloridiidae, differs strongly in many respects from both the sternorrhynchan as well as the cicadine type (Weber, 1930; Silvestri, 1934; China, 1962, et al.). In the bugs a long fold is located on the costal margin of the hind wing, while the coupling lobe is on the fore wing. In contrast to the cicadines, the anterior component is situated on the first anal vein (more precisely, on $Pcu+A_1$) rather than on the second, though right at the apex of the clavus, where these veins converge. A pecularity of the coupling mechanism on the fore wings of bugs also consists of the fact that, besides the forwardly turned monolithic lip, there is a supplementary structure lying opposite to the latter, composed of a comb of backwardly directed, very closely arranged short setae; at the same time the edge of the fore wing, which insets into the anterior coupling mechanism, has a T-shaped cross-section.

Proceeding from the assumption that the orthopterigia (i.e. the wing type with a widened anal lobe of the hind wings) of the bugs and the cicadines was formed once in their common ancestor and that the coupling mechanism of the bugs and the cicadines has a common origin, it is evident that the coupling apparatus in the bugs underwent reorganization and this could have occurred by way of: 1) a widening of the coupling lobe of the hind wings in the extended fold, with a simultaneous narrowing of the coupling fold of the fore wings into a lobe, by way of a stage of two moderately wide folds; 2) a displacement of the anterior lobe to the very tip of the clavus, and 3) its subsequent small regression backwards, now along the first anal vein, in connection with the weakening of the second (Figure 11). These changes could have been associated with the elongation of the scutellum (mesonotal triangle between the wings), corresponding with a shortening of that margin of the clavus, which enters into the interalar contact and where the anterior part of the coupling mechanism is located, and also with other changes in the proportions of the wings. Apparently also directly associated with the reorganization of the coupling apparatus is the fact that the clavi of the right and left wings in the Peloridiina and the primitive Cimicina overlie one another along the commisural suture, rather than butt up against one another, as in all of the cicadines. The inversion in the width of the coupling mechanisms was possibly facilitated by supplementary setae in the coupling mechanism on the fore wing.

Thus, it is difficult to evaluate the slight differences in the coupling mechanisms in the individual superfamilies of the cicadines as apomorphy or pleisiomorphy, all the more so since it is not clear how the monolithic posterior coupling mechanism of the cicadines (and bugs) originated.

5.2. Subcosta of fore wings at the basal cell. In the Cercopoidea at the base of the wing the subcosta is free, it runs in an arch and abuts onto the radius (fuses with the latter) distally to the basal cell (Figure 14). Among the Cicadoidea in the Tettigarctidae the relationship is similar but the subcosta lies much closer to the radius and fuses with the latter immediately past the basal cell (Figure 15). In the Cicadidae the subcosta is independent only before the basal cell, and in this case the base of the subcosta is not visible from above; it becomes gradually stronger distally and is transformed into a first-order vein before the fusion; at the same time the common trunk of ScR serves as a direct continuation of Sc, while R approaches the point of fusion from the side. In the Cicadelloidea and the Fulgoroidea the subcosta and the radius (on the upper surface of the wing)

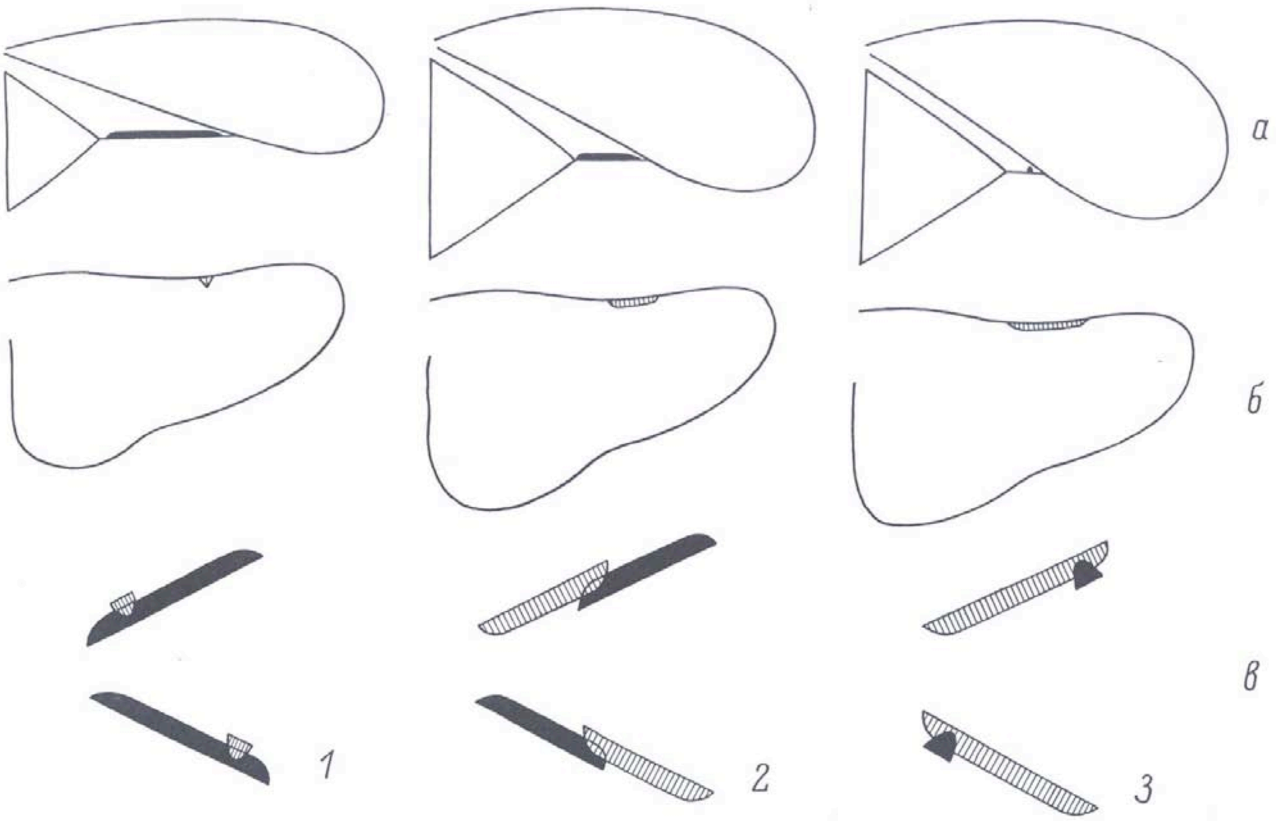


Figure 11. Hypothesis concerning the formation of the coupling apparatus in the bugs from the cicadine type. Schematic diagrams.

1 – initial state, commissural margin of clavus long, claval fold wide, costal fold narrow; 2 – transitional state, the commissural margin of the clavus and, together with the latter, the fold have been abbreviated, the costal fold has been widened in compensation ; 3 – the commissural margin of the clavus has been severely abbreviated (in connection with the elongation of the scutellum and the widening of the body), the anterior fold has been transformed into a narrow hook at the apex of the clavus, where the $Pcu+A_1$ trunk runs into the margin of the wing, the costal fold of the hind wing has been greatly widened.
Upper row (a) – scutellum and fore wing in the rest position, dorsal view; middle row (b) – hind wing in the open state, dorsal view; lower row (v) – schematic diagram of the position of the components of the coupling mechanism in the extreme anterior (antero-ventral) and posterior (postero-dorsal) positions.

are not separated. The separation of the basal segments of Sc and R in the cercopocicadoids is, apparently, of a secondary character, since it is not found in the Sternorrhyncha nor in the Heteroptera, and is not encountered at all on the hind wings in the Rhynchota.

The freeing of the subcosta is in some way associated with the hypocostal carina and the carina along the subcosta (hyposubcostal) in the distal part of its free passage. These carinae are developed in the Cercopoidea. The hypocostal carina serves for the attachment of the hemelytra at rest. The hyposubcostal carina laterally bounds the costal margins of the hind wings at rest and possibly assists in their folding. In the Cercopidae, Machaerotidae and Clastopteridae the hypocostal carina passes into the hyposubcostal carina in such a way that the basal non-carinate part of the subcosta abuts onto the middle of the common costal-subcostal carina. In the Aphrophoridae these two carinae

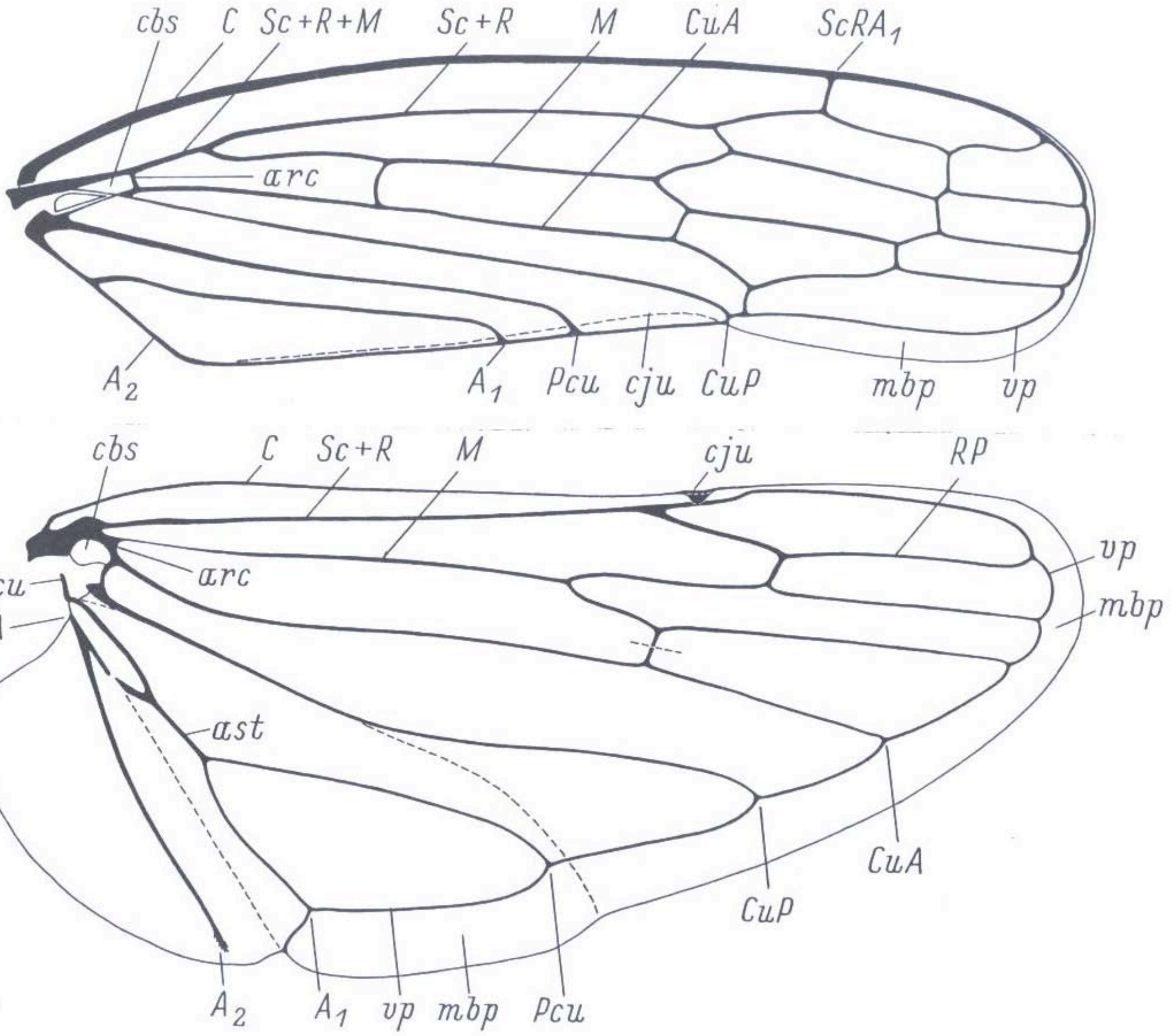
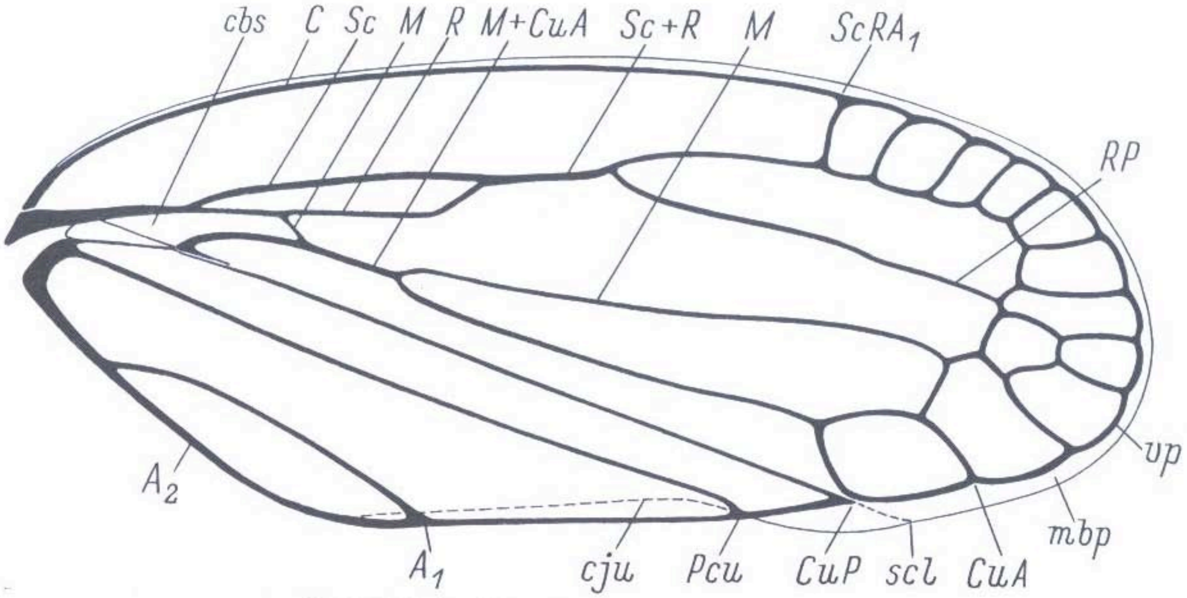


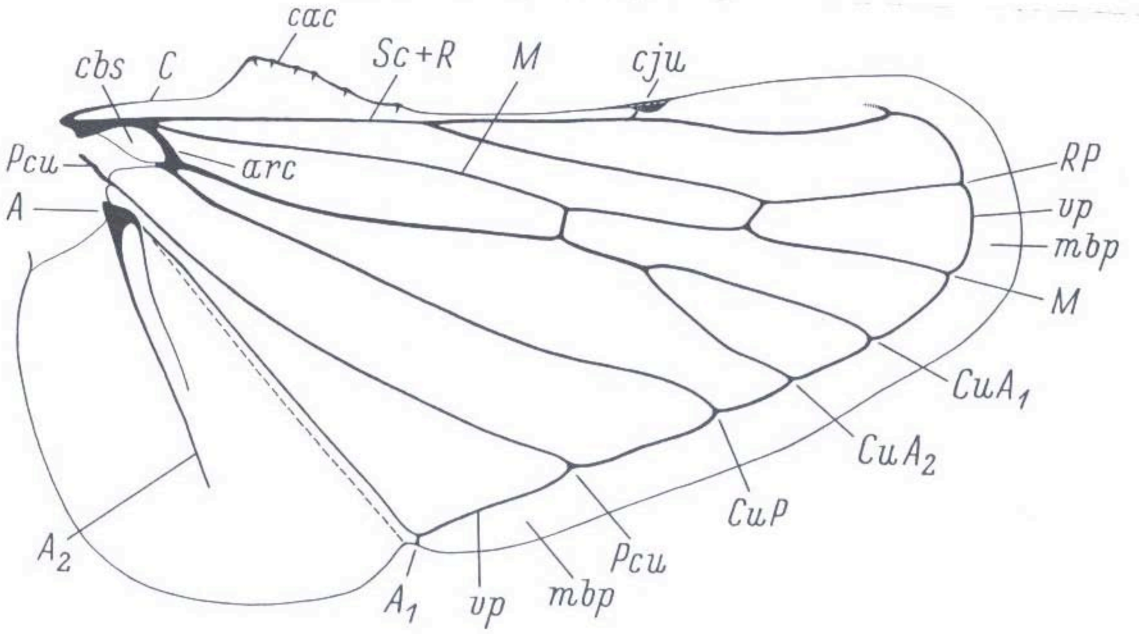
Figure 12. Venation of the wings in the superfamily Cicadelloidea, *Bothrogonia* sp. (Cicadellidae).
ast – anastomosis, cbs- basal cell, arc – arculus, cac – supplementary coupling apparatus of fore wing, lnd – nodal line, vp – peripheral vein, pst – pterostigma, cju – coupling fold of wing margin, scl – suture of clavus, mbp – peripheral membrane.

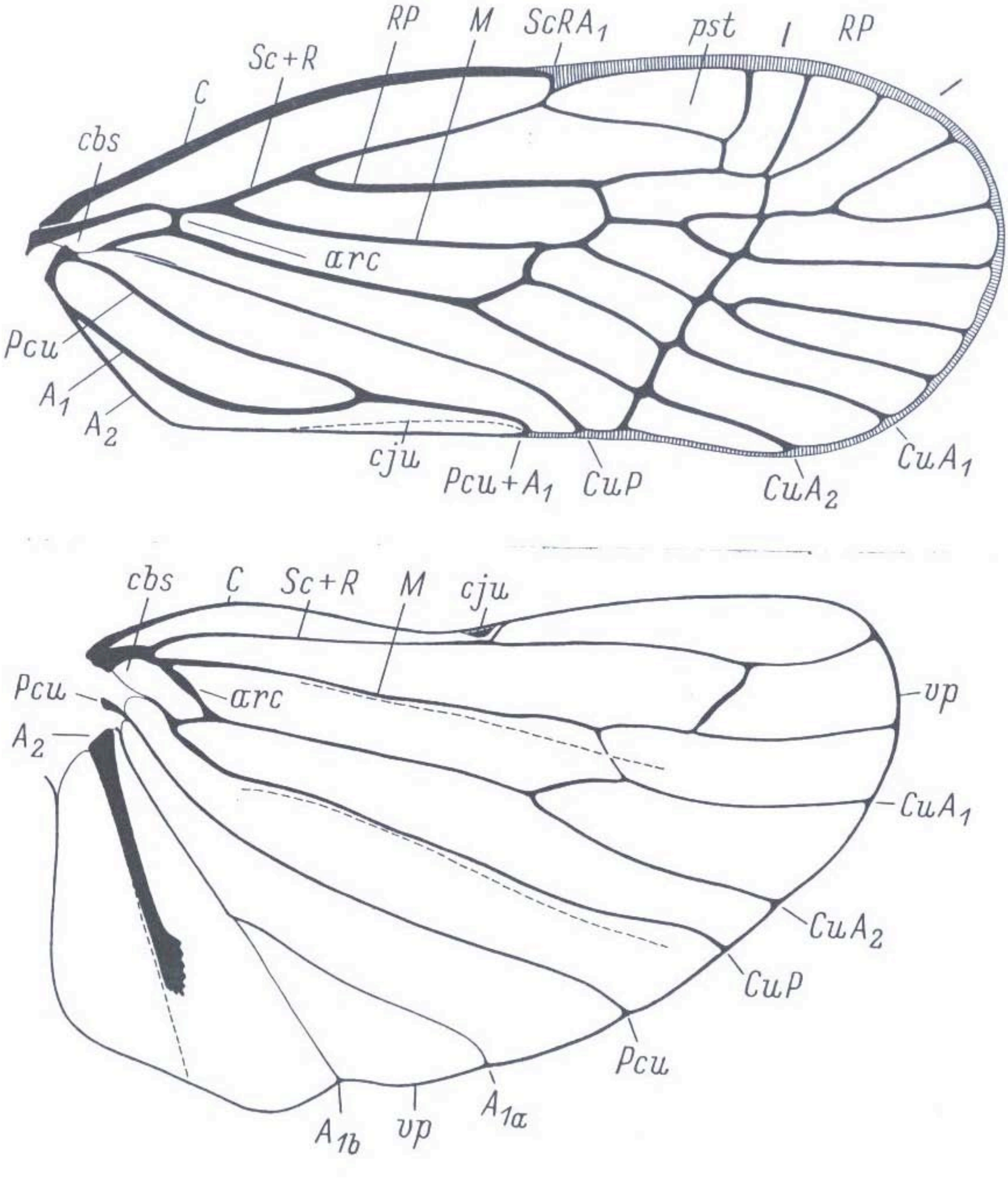
are clearly separated, at most there is a very much smoothed-out anastomosis, although at the same time the carina of the subcosta is continued proximally a little further than the traces of the anastomosis. In other cicadines there is no carina ventrally on the costa and subcosta, the protruding parts of the subcosta are round in cross-section.

The protrusion of the hyposubcostal carina, which in the Cercopoidea supports the costa of the hind wings, is homodynamic with the tooth on the arculus in the Fulgoroidea (the tooth is absent only in the Tettigometridae and Delphacidae), and in its positioning it is also close to this tooth; it is possible that they have a single origin. In the Cicadoidea there is no tooth or carina here, but the hind wings are reduced in these insects.

5.3. Peripheral membrane. The marginal fringe of the wing plane, lying outside the peripheral vein of the membrane, is called the peripheral membrane. Anteriorly the peripheral membrane passes into the anterior carina of the costa; posteriorly, on the fore wings, - into the coupling fold of the clavus. The peripheral membrane on the fore wings is often entirely or partially reduced. On the hind wings it is characteristically absent in the Fulgoroidea and present in the remaining (now-living) superfamilies. The absence of the peripheral membrane in the Fulgoroidea is often treated as a primitive feature, but without the presentation of evidence for this. In the Fulgoroidea to the outside of the peripheral vein there is a narrow vestige or rudiment of the peripheral membrane; it is true that is is never wide.


cbs
C
Sc
M
R
M+CuA
Sc+R
M
ScRA$_1$
RP
vp
mbp
A$_2$
A$_1$
cju
Pcu
CuP
scl
CuA


cac
cbs
C
Sc+R
M
cju
Pcu
arc
A
RP
vp
mbp
M
CuA$_1$
CuA$_2$
CuP
Pcu
A$_2$
A$_1$
vp
mbp



Figures 13 and 14.

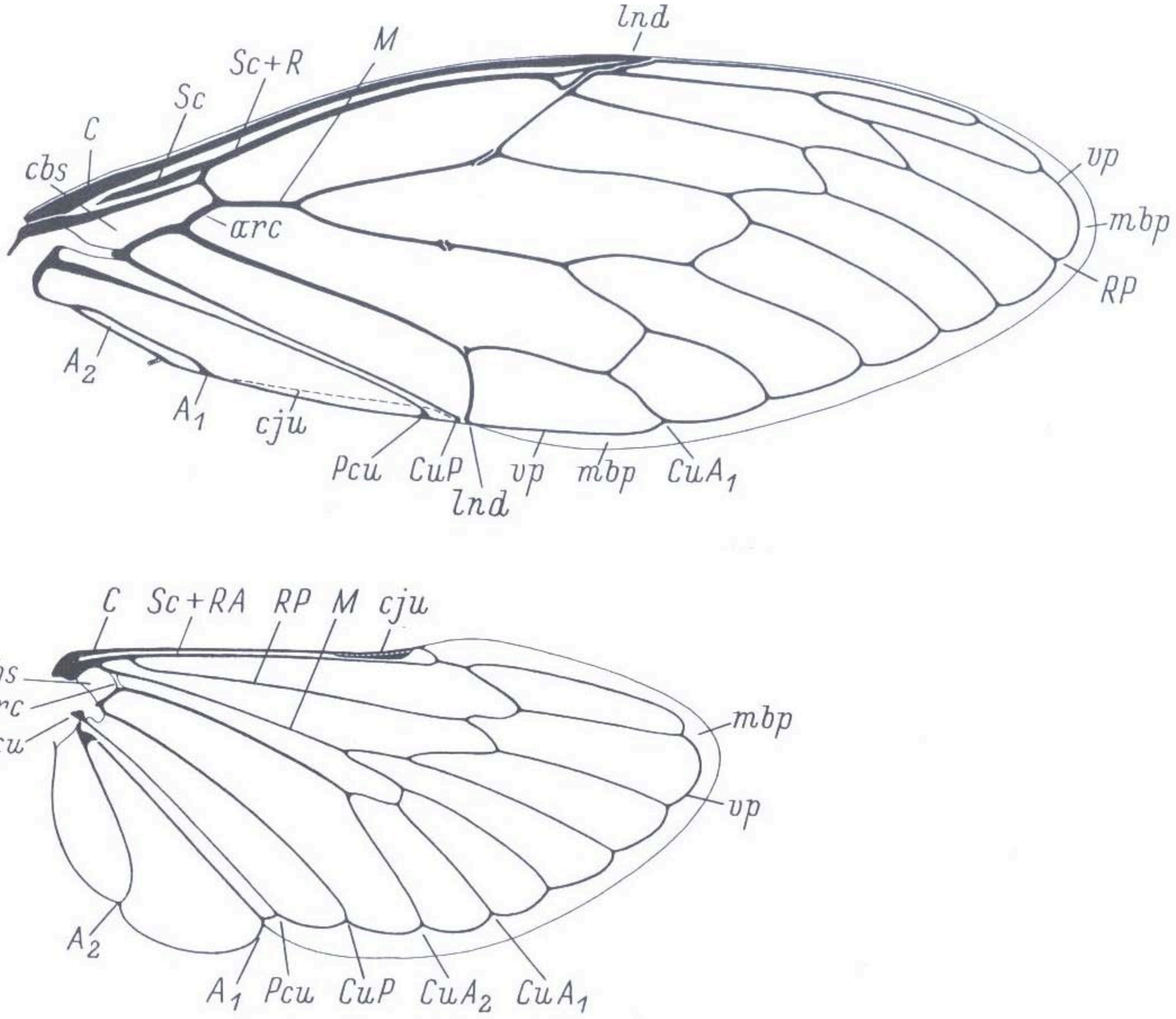


Figure 15. Venation of the wings in the superfamily Cicadoidea. *Tibicina intermedia* Fieb. (Cicadidae). Conventional designations as in Figure 12.

In contrast, in the other cicadines the peripheral membrane (on the hind wings) is reduced only extremely rarely; apparently only one example is known from the Cicadidae, with the two closely related genera *Lembja* and *Cystosoma* (Myers, 1928).

5.4. Arculus on fore wings (Figures 12-15). Developed in the groups which have a tendency to lighten the wings, when the function of wing rigidity is entirely dependent on the veins, while the covering function is secondary to the flight function, as in the Cicadoidea and Fulgoroidea. In the Cicadelloidea and Cercopoidea an arculus is not developed, and the neighbouring trunk veins in the region of the arculus are set more or less close together, which is also the case in the beetle-like Tettigometridae, in which the wing structure also in other respects resembles the cercopoid or cicadelloid type. Apparently the strongly developed arculus of the Fulgoroidea is not primitive on the fore wings, and the same is also possible in the Cicadoidea, since in the bugs with their dense hemelytra there is also no arculus.

5.5. Sutures at the base of the radiometial trunk-vein on the fore wings. From the axillary region along the margins of the radiomedial trunk on the upper surface there run deep grooves (anteradial and postmedial), whose existence is associated with the consolidation and corialization of the blade of the fore wings. On the strongly consolidated wings the arculus is usually weakened and is often completely inconspicuous, although the postmedial suture never intersects it. The anteradial suture in the Cercopoidea and Cicadoidea cuts off (but only on the upper surface!) the base of the free subcosta and extends to where it fuses together again, but does not intersect the subcosta. In the Cicadelloidea the anteradial suture extends to the first branching of the radius, as is the case also in the Tettigometridae. In the other Fulgoroidea there is no anteradial groove, but there is a short groove, parallel to the latter, displaced to the front in such a way that it commences from the base of the costal vein. In contrast to the other Cicadelloidea, in the Membracidae and anteradial suture, extending along the median, cuts the base of the free radius and sometimes (*Microcentrus, Heteronotus*) even penetrates onto CuA, which is associated with a point-like or extended anastomosis of M and CuA.

5.6. Cubital plate, or cubital triangle (Figures 16 and 17). Developed in all of the cicadines (Shcherbakov, 1984), although among the Fulgoroidea only in the Tettigometridae, where it is diminished. The structure of this plate is uniform in the cercopo-cicadoids, and differs from that in the cicadelloids and fulgoroids. In the cercopo-cicadoids the anterior-basal corner of the triangle is shifted distally, and the distomedial plate is wedged in between the triangle and the base of the clavus. In the fulgoroids (Tettigometridae) and cicadelloids, conversely, the postero-basal corner of the triangle is shifted distally, and the distomedial plate is wedged in between the radiomedial trunk and the cubital plate. This apparently, is one of the most reliable synapomorphies of the

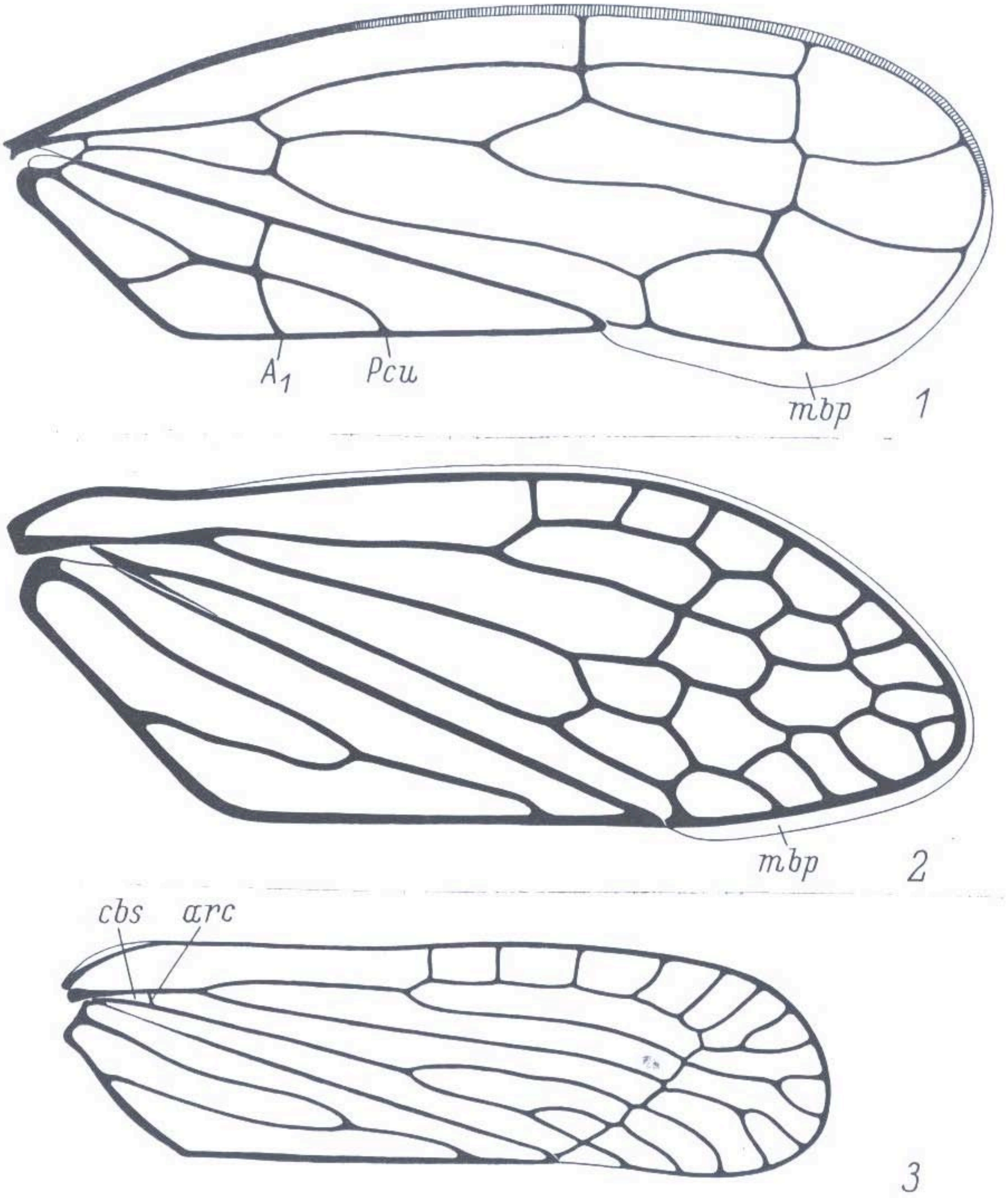


Figure 16. Additional examples of the venation (fore wing). 1 – *Japananus hyalinus* Osb. (Cicadellidae) ; 2 – *Tettigometra obliqua* Panz. (Tettigometridae); 3 – *Asiraca clavicornis* F. (Delphacidae). Conventional designations as in Figure 12.

Cicadelloidea and Fulgoroidea.

5.7. Nodal line. Evans considered the nodal line which is present in the contemporary Cicadoidea (Figure 15, 1) and Cicadellidae Hylicinae (Hylicidae according to Evans) as a direct legacy of such a line in the Mesozoic Prosboloidea, in connection with which he ascribed considerable importance to it as an indicator of the antiquity of the group that possessed this line. The nodal line gives additional flexibility to the stiff wings; it originates at the site of the approach of the subcosta (ScR_1) to the margin of the wing and it terminates at the apex of the clavus, in the same manner in all cicadines; these points are conditioned primarily by the fundamental construction of the wing itself, which does not allow for a weakening or break of the clavus and costal field basally to the topographically first cross-vein of ScR_1, that together with the costa and radius forms the frame of the costal field. However, the passage of the nodal line along the blade of the wing in relation to the venation differs in the different groups. In the prosboloids the line runs much more basally to the first branch of M_1, in the Hylicinae it runs along the point of branching, while in the Cicadoidea and Cicadoprosbolidae (an extinct group) it runs distally to this point. Even in the last case, however, the resemblance of these two groups cannot be called complete. The majority of the contemporary cicadines do not have

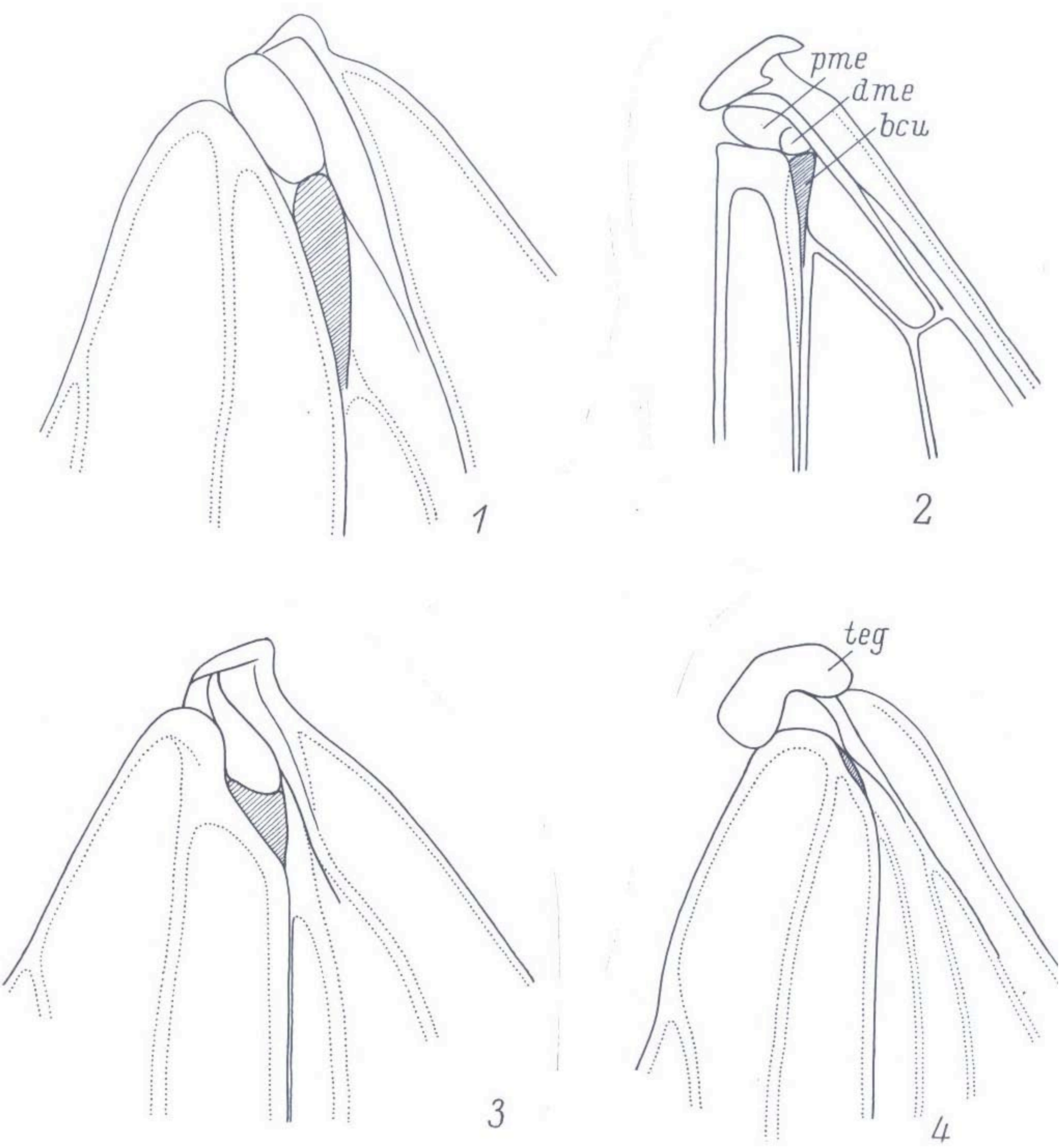


Figure 17. The basicubital plate of the fore wings. 1 – Aphrophoriae; 2 – Cicadidae; 3 – Cicadellidae; 4 – Tettigometridae; (*Euphyonarthex)*, basicubital plate hatched. bcu – basicubital plate, dme – distomedial plate, pme – proximedial plate, teg – tegula.

---

a nodal line. The line apparently appears independently every time that a functional necessity for it arises, and it cuts though those veins which turn out to be in its path, in accordance with the venation of the given group at the time of the appearance of the nodal line.

5.8. Venation of the clavus. Three types of venation of the clavus may be distinguished in the cicadines. 1) Veins Pcu and A_1 run independently into the margin of the clavus, vein A_2 (Figures 12 and 14). In this fashion is constructed the clavus in the Cicadelloidea, Cercopoidea and the Tettigarctidae of the Cicadoidea 2) Vein Pcu comes very close to or runs into CuP; a short segment at the very tip remains free; vein A_1 runs close to A_2 and merges with it shortly past the emergence onto the margin of the suture of the wings. The clavus in the Cicadidae is constructed in this fashion (Figure 15, 1). 3) In the Fulgoroidea vein A_1 runs into Pcu; in the distal part of the clavus there is only one vein (Pcu+A_1) which runs into the suture of the clavus (primitively), into the apex of the clavus or even into CuP near the apex of the clavus (Figures 13, 1; 16, 2, 3). D.E. Shcherbakov (1984) considers that the independent (as in the Archescytinoidea) passage of veins Pcu and A_1 along the clavus to its commissural margin in the Prosbolidae, Cicadelloidea, Cercopoidea and Cicadoidea is secondary, and arose from the reversed fork, characteristic of the Prosbolopseidae, owing to the bending-under of the posterior part of the first anal field and its inclusion in the coupling fold. With such an interpretation, in the distal part of the posterior margin of the clavus in the Prosbolidae there should be two veins, running one under the other, and there should not be an anastomosis of A_1 and A_2 in the place where A_2 emerges onto the posterior margin of the clavus, but Shcherbakov writes nothing about such relationships. If, following Shcherbakov, one assumes that the Prosbolidae arose from the Prosbolopseidae, then it is easier to visualize a fusion of the apical parts of veins A_1 and Pcu with vein A_2, which retains its extreme position and which supports the coupling fold, than to visualize a substitution of the posteromarginal vein with a retention of the fold. In the contemporary Cicadelloidea, Cercopoidea and Cicadoidea there are no traces at all of a parallel movement of veins A_1 and A_2 under the margin of the clavus. Although the Prosbolopseidae are known commencing from the Lower Permian, while the Prosbolidae are known only from the Upper Permian, one cannot exclude the possibility that the Prosbolidae inherited their venation of the clavus directly from the Archescytinoidea.

The reversed fork of the Prosbolopseidae and their descendants is characterized by a late (distal) fusion of Pcu and A_1 and by the confluence of their common trunk directly into the acute apex of the clavus. In the Fulgoroidea the fusion of Pcu and A_1 was primitively considerably earlier (more proximal) and the common apex of Pcu and A_1 clearly runs into the margin of the wing (vein A_2), without reaching into the apex of the clavus. The occurrence of the reversed fork in the Fulgoroidea may be visualized independently of the similar process in the Prosbolopseidae. A tendency towards the formation of a postcubital-anal reversed fork is observed in some of the Cicadellidae (*Hecalus, Japananus, Homalodisca, Flexamia* and others) and some of the Machaerotidae, and moreover the apex or Pcu+A_1 retains its position at some distance from the apex of the clavus, as in the lower Fulgoroidea, but not as in the Prosbolopseidae (Figure 16, 1).

5.9. Basiclaval tectum. In the cicadines and the bugs the basal margin of the clavus forms a tectum, which primitively participates in the clamping of the wings at rest. As I.M. Kerzhner (1981) showed, this lobe, which it is better to call the basiclaval tectum, at rest slides in between the underlying lateral part of the mesonotum and the overlying lobe of the pronotum. Kerzhner calls this lobe a rudiment of the anal lobe, which is incorrect, as this is a formation of the upper surface of the wing, rather than of its posterior margin.

In the cicadines this lobe is clearly developed in the Cicadelloidea, Cercopoidea and in the Tettigarctidae of the Cicadoidea; it is weakened in the Fulgoroidea and the Cicadidae, i.e. in those representatives in which the lobe of the pronotum is weakly developed. Incidentally, in many of the Cicadelloidea the basiclaval lobe does not slide in under the lobe of the pronotum (many Cicadellidae, brachypterous representatives of the Ulopidae).

The basiclaval lobe comprises a synapomorphy of the Heteroptera and Auchenorrhyncha.

5.10. Tegulae. Present only in the Fulgoroidea and only on the fore wings; secondarily absent in some of the brachypterous forms.

5.11. Relationship of the postcubitus and the first anal vein on the hind wings. The first anal vein usually runs immediately in front of the anojugal lobe, in front of the line or bending, and the base of the anal vein is intersected by this fold. In the superfamily Cicadelloidea the first anal vein in its middle part moves away from the fold and anastomoses with the postcubitus; often the free base of A_1 is weakened or disappears completely. A similar picture is observed in the superfamily Cercopoidea in the Aphrophoridae and Machaerotidae, but in the former the anastomosis is incomplete here, the merging parts of the veins remain separated by a thin furrow. The anastomosis in the Aphrophoridae is of a convergent character, in relation to that in the Cicadelloidea, and it is not developed at all in the other families of the Cercopoidea. In the remaining two superfmailies Pcu and A_1 are always independent in the Cicadoidea and in the overwhelming majority of the Fulgoroidea, with the exception of the family Tropiduchidae and a few other examples, where the anastomosis is clearly secondary; here it often appears as an ultimate anatomosis, rather than as an intermediate anastomosis, by which the Cicadelloidea and Aphrophoridae are characterized.

6. **Legs**

6.1. Coxae of middle legs, meracanthi (Figures 18-20). The meracanthus is a protrusion on the meron, possibly homologous to the stylus on the coxae of the Machilida. It is often developed on the middle and hind legs in many of the Homoptera (Emel’yanov, 1981), and was originally described in the Psyllina (Weber, 1928). The functional significance of the meracanthus

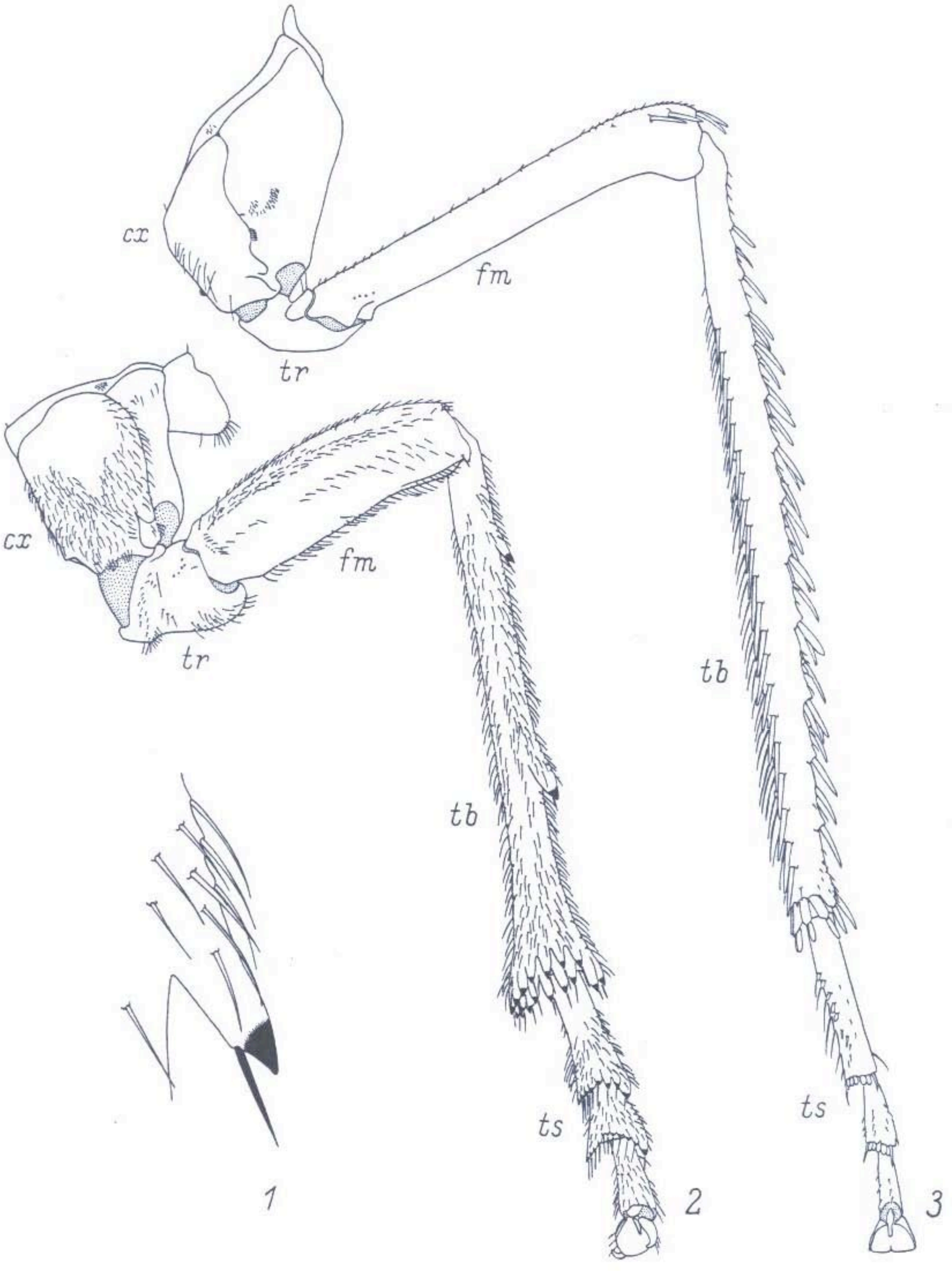


Figure 18. Hind legs. Ventral view.

1, 2 – Cercopoidea, *Aphrophora alni* Fall. (1 – lateral tooth on tibia, close up); 3 – Cicadelloidea, *Cicadella viridis* L. cx – coxa, tr – trochanter, fm - femur, tb – tibia, ts – tarsus.

apparently consists of the fact that it comprises a proprioceptive pair together with the yellow spot, a sensory area at the base of the femur, and controls the mutual positioning of the coxa and femur, which is especially important in jumping: the meracanthus and the spot on the hind legs come into contact when the legs are folded and they signal readiness for jumping. In the Psyllina, however, there is no yellow spot. In the Cicadelloidea and Cicadoidea there are no meracanthi on the middle coxae; in the Cercopoidea flat wedge-shaped meracanthi are well developed, while in the Fulgoroidea the meracanthi are rudimentary and conical.

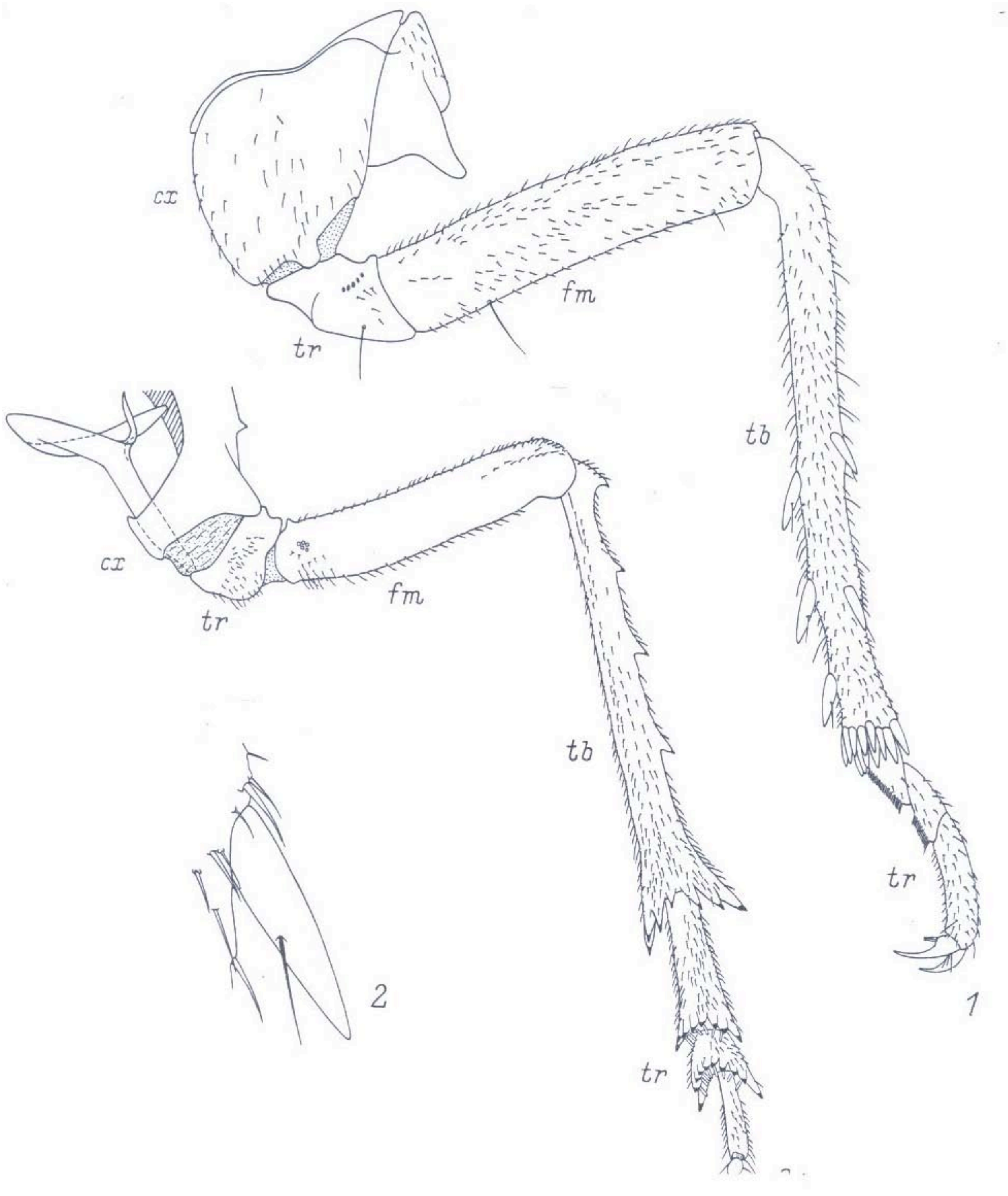


Figure 19. Hind legs. Ventral view.
1, 2 – Cicadoidea, *Melampsalia caspia* Kol. (2 – lateral spur on tibia, close up); 3 – Fulgoroidea, *Ototettix jaxartensis* Osh. Conventional designations as in Figure 18.

The question of the phylogenetic evaluation of the meracanthi in the cicadines is complex, since they may be developed on the middle and hind legs, or only on the hind legs, or they may be completely absent; moreover, meracanthi are absent in bugs but are present in psyllids on the hind coxae.

In the general form of the coxae on all the legs and in the absence of meracanthi the Cicadelloidea resemble the bugs. In the Cicadoidea meracanthi are usually present only on the hind legs, but they have a form that is very similar to the meracanthi on the middle coxae of the Cercopoidea. Among the Cicadidae there are genera in which the hind legs resemble the middle legs, in particular the hind coxae are devoid of meracanthi, repeating the structure of the middle legs (*Gaeana*).

6.2. Yellow spot-meracanthus complex on middle coxae. This complex is absent in the Cicadelloidea (primitively?) and Cicadoidea (secondarily? in connection with the loss of jumping), it is developed in the Cercopoidea and rudimentary in the Fulgoroidea: no spot, meracanthus vestigial or rudimentary. It is noteworthy that there are cases in which a meracanthus is present while the yellow spot is absent, but the reversed situation is unknown.

If jumping is accepted as the primitive state in all of the contemporary Rhynchota commencing with the Sternorrhyncha (the

Aleyrodina and Psyllina jump), then one may assume a one-time appearance (associated with jumping) of meracanthi on the hind coxae already in the Sternorrhyncha, but then it is difficult to understand why there is no meracanthus – yellow spot complex in the Aleyrodina, and only a meracanthus is present in the Psyllina.

If one assumes an independent appearance of meracanthi in the Psyllina (yellow body absent) and some of the Cicadina (yellow body primitively present), then among the Cicadina the coxae without meracanthi and femora without yellow bodies will be primitive, and similar in structure to those present in the bugs.

6.3. Sensilla on trochanter of middle legs (Figures 21 and 22). Present on the trochanters of the fore and middle legs in a uniform complement of sensilla, characteristic of all of the Paraneoptera; these same sensilla are also developed on the hind legs, if the latter have not been too strongly transformed for jumping. The complex includes lateral placoid sensilla, anterodorsal basiconic

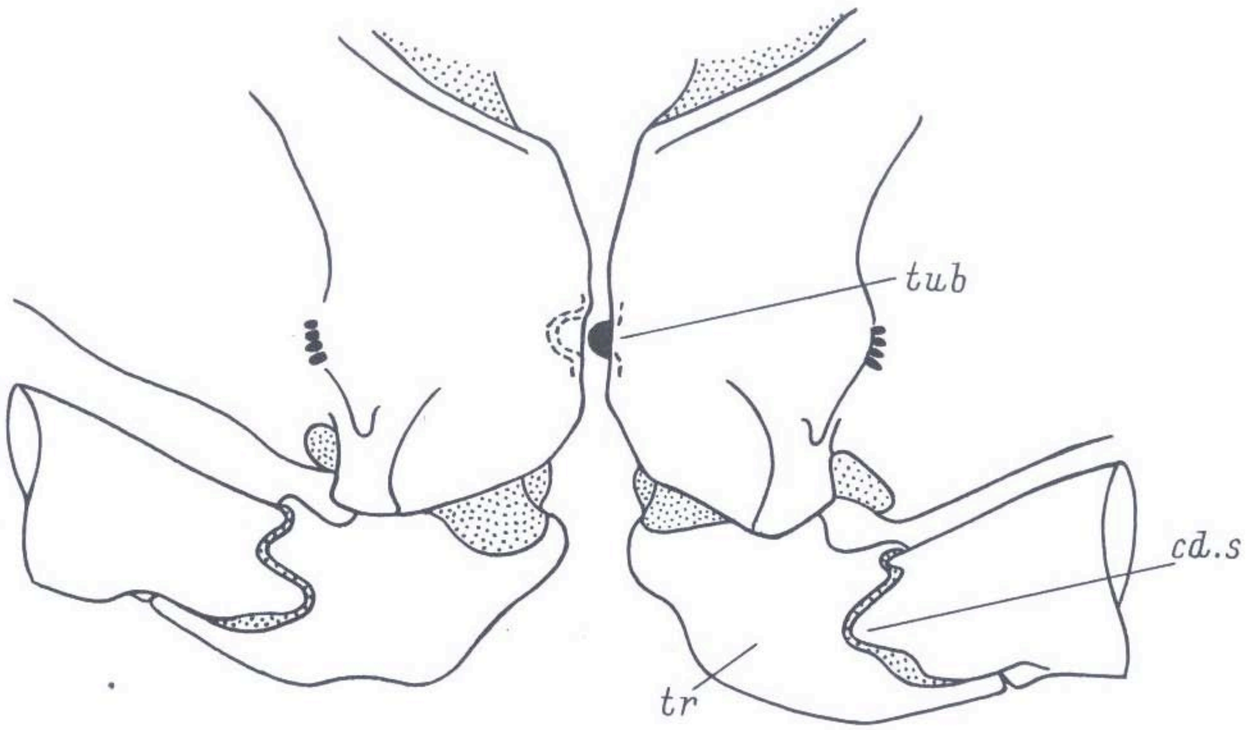


Figure 20. Clamping mechanism of the hind coxae in the family Cicadellidae.
Medial portions of coxae, trochanters and bases of femora of the hind legs of *Aphrodes* sp., ventral view.
cd. s – primitively-dorsal condyle of trochantero-femoral articulation, tr – trochanter, tub – tubercle of coxal clamping mechanism.

---

sensilla and two sturdy setiform proprioceptive sensilla, situated dorsally. Among the cicadines differences are found only in the dorsal chaetoid sensilla.

The dorsal chaetoid sensilla are polymerized in the imagines of the Cercopoidea and Cicadoidea, but in the Cercopoidea they are not polymerized in the larvae, in contrast to the Cicadoidea (it is not known what their condition is in the larvae of *Tettigarcta*). In the Fulgoroidea they are not polymerized, nor are they in the Cicadelloidea, except for the Aetalionidae (the condition in the larvae of the latter is unknown).

In the Cicadelloidea the chaetoid dorsal sensilla of the trochanter are developed on all the pairs of legs, as is the case also in the Cicadoidea; in the Cercopoidea and Fulgoroidea they are absent on the hind trochanteres in the imagines, but are present in the larvae of the Cercopoidea and of the Tettigometridae of the Fulgoroidea.

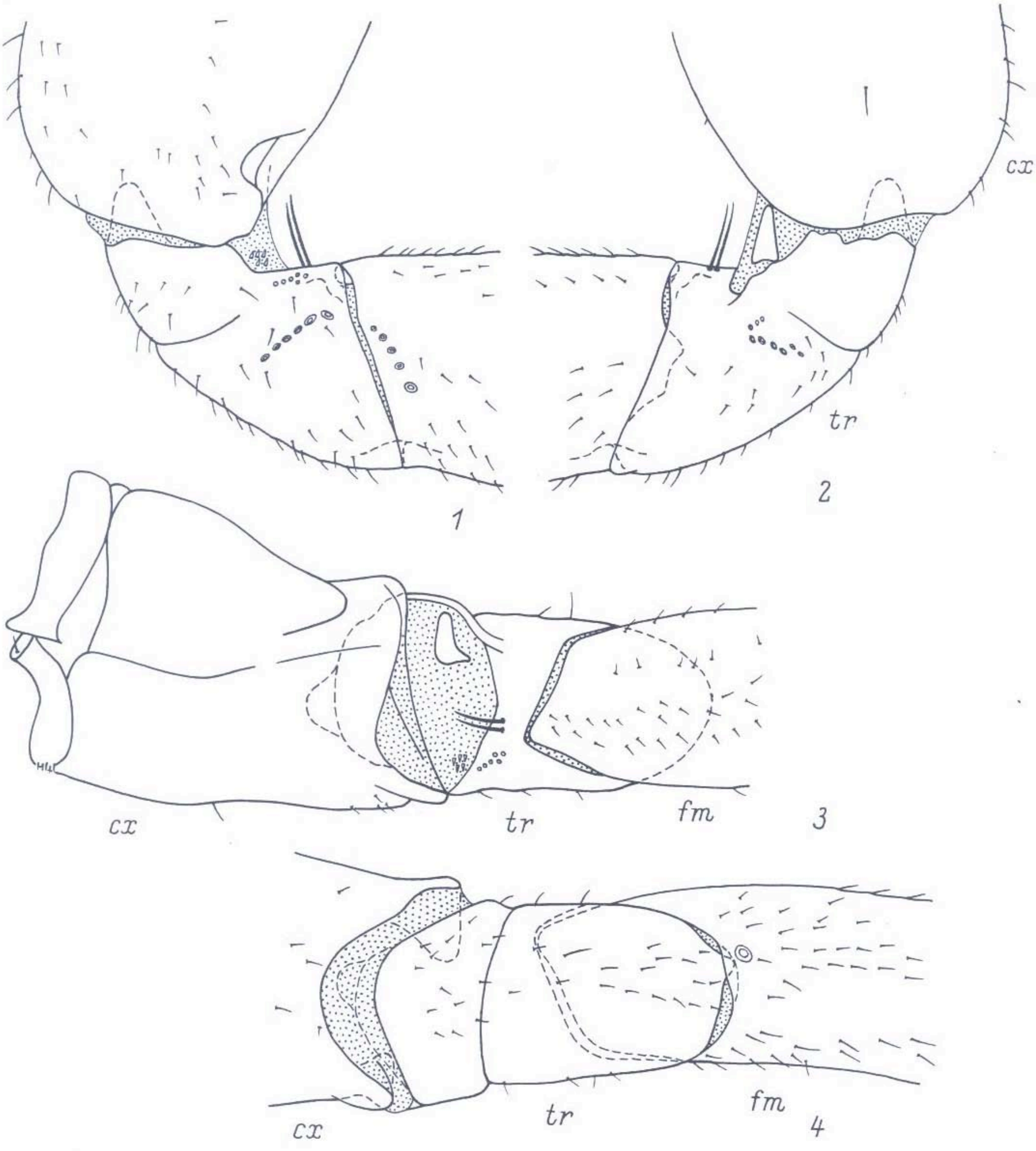


Figure 21. Sensilla on middle legs of *Saigona ussuriensis* Leth. Apex of coxa, trochanter and base of femur.
1 – anterior side, 2 - posterior, 3 – dorsal, 4 – ventral; cx – coxa, fm - femur, tr – trochanter.

As the plesiomorphous state one should consider two dorsal trochanteral chaetoid sensilla, as is found in the Psocida, Cimicida and Aleyrodina; only one seta is found in the Psyllina, Aphidina and Coccina.

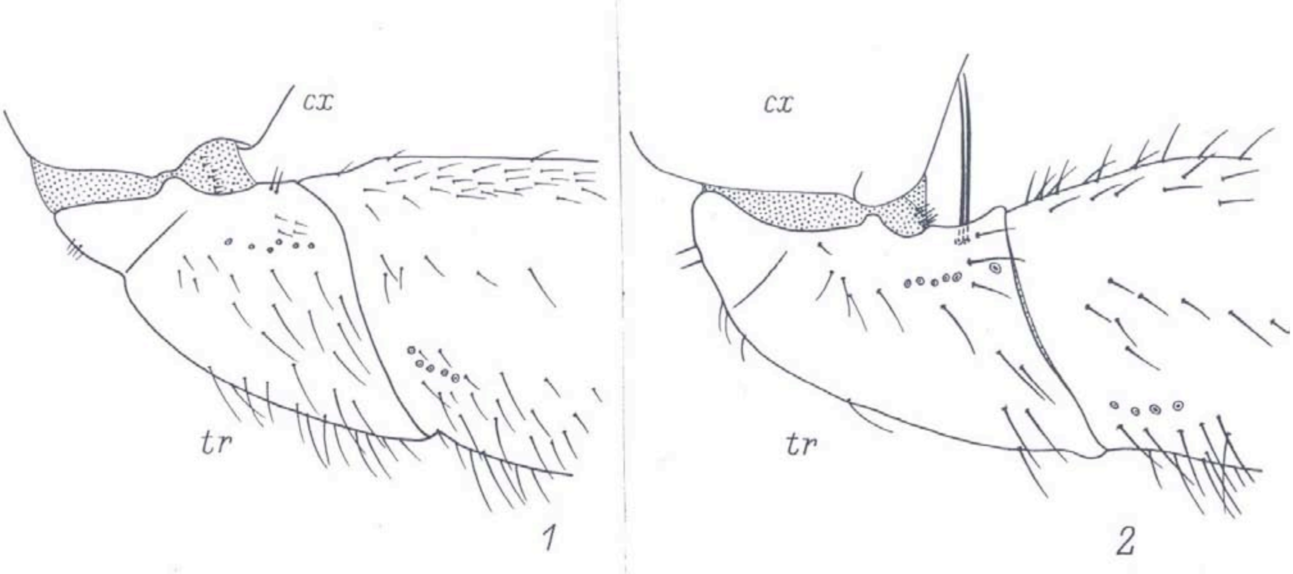


Figure 22. Sensilla on middle legs. Apex of coxa, trochanter and base of femur, anterior side.
1 – *Aphrophora* sp.; 2 – *Rhytidodus* sp. Designations as in Figure 21.

6.4. Sensilla on middle femur (Figures 21 and 22). Anteriorly on the femur, near the trochanteral margin just below the mid-line, is present a longitudinal row of placoid sensilla, usually four in number. Such is the case in the Cicadelloidea and Cercopoidea; in the Cicadoidea there are only two sensilla and they are reduced in size. In the Fulgoroidea the sensilla run practically across the femur, almost parallel to its trochanteral margin; furthermore, one isolated placoid sensillum is situated right on the ventral trochantero-femoral condyle. The condition of the Fulgoroidea is apparently apomorphous with regard to the direction of the row of sensilla and is undoubtedly apomorphous with regard to the sensillum located beside the condyle. The presence of these sensilla in other Rhynchota has not been clarified.

6.5. Placoid sensillum on second tarsal segment (Emel'yanov, 1982). A placoid sensillum is present on the dorsal surface of the middle tarsal segment (of all three pairs of legs). It is usually situated near the proximal condyle, but in some of the Cicadelloidea and in the Cicadidae it is located in the middle part on the upper side of the segment. In the Cicadelloidea this sensillum is moved up close to the condyle only in the Aetalionidae and Membracidae.

This sensillum has also been found in the bug *Adelphocoris* (Miridae) and is possibly widely distributed among the Rhynchota, but this question has not been studied. In *Adelphocoris* the sensillum is located on the middle of the segment.

6.6. Sensilla on apex of third tarsal segment. In the Fulgoroidea and Cercopoidea on the tip of the distal segment of the tarsus, ventrally to the sides of the pretarsus, is present a group of one basiconic and two campaniform sensilla, closely arranged in one line along the margin of the sclerotization; the basiconic sensillum lies dorsally. In the Cicadidae in this place are located one or two short setae, in the latter case they are slightly set apart; in the Cicadelloidea no such structure is present. The condition of the Cicadelloidea is apparently plesiomorphous, while the condition of the Cicadidae is apparently a result of reduction. The question of the genesis of these sensilla is complicated by the fact that in the Thripida there have also been found structures which are practically indistinguishable from the cercopoid and fulgoroid structures (Heming, 1972).

6.7. Pretarsus (Fennah, 1945; Doering, 1956; Emel'yanov, 1982). The principal types of pretarsus well characterize the superfamilies (Figures 23 and 24).

The pretarsus of the Cercopoidea is strongly differentiated. The claws of the Cercopoidea bear numerous, randomly positioned setae on their lateral surfaces and, in addition, ventrally along the edge of the arolium there is also a row of several, approximately four, setae. The upper inner margin of the claws, in the form of a border, extends onto the arolium. The lateral surfaces of the round arolium, adjacent to the claws, bear sclerotized bands, divided into three parts: the dorsolateral, distolateral and ventrolateral platelets. The dorsolateral platelets are accreted together proximally. The distal part of the arolium, which is softer, is evidently a sucker. On the arolium is present a central seta, seated on a strongly developed high base, and a group of setae on the dorso- and ventrolateral platelets. The larva is differentiated by its shorter and wider claws, which bear ventrolaterally a total of one seta on each side; there are no separate platelets on the

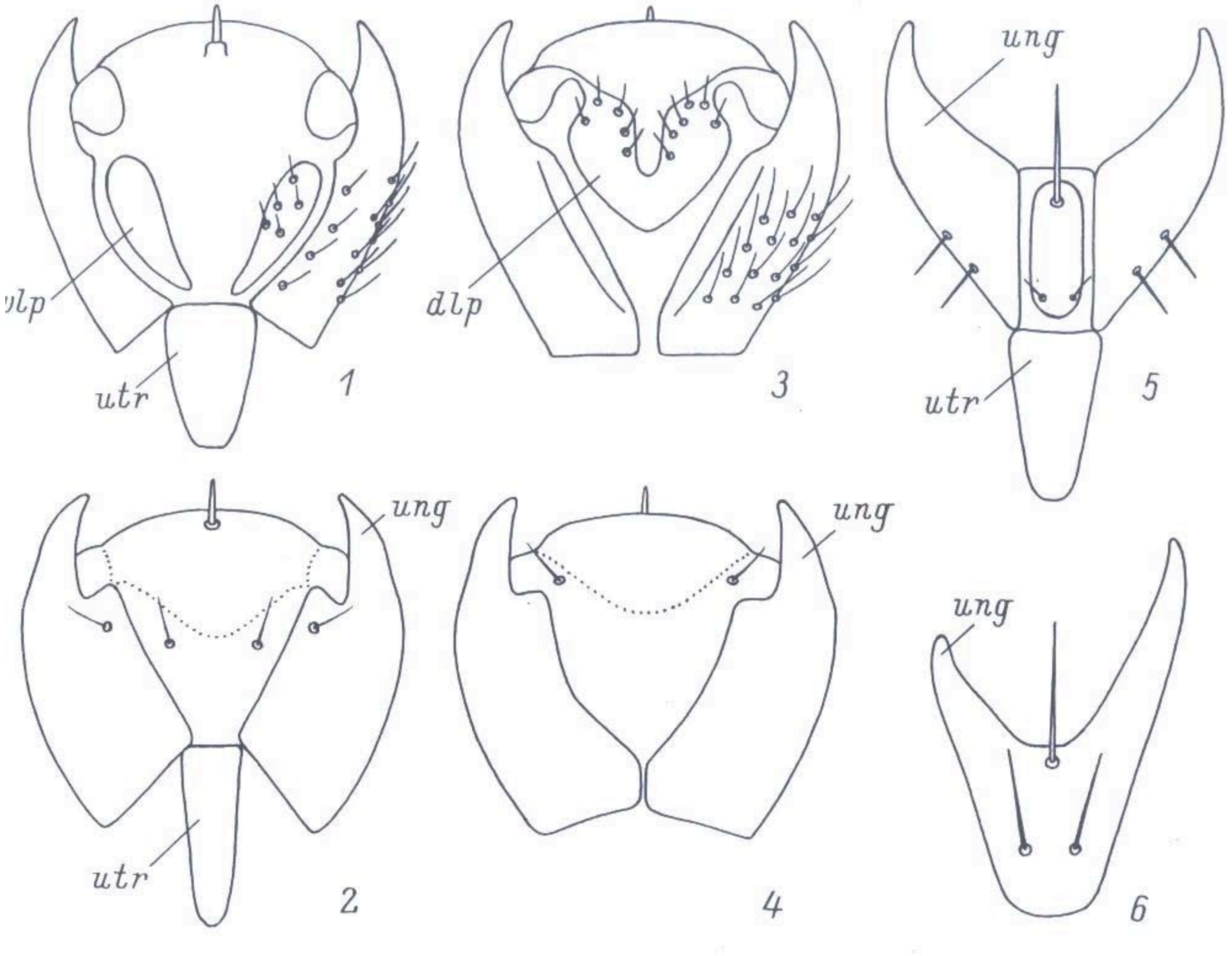


Figure 23. Pretarsus. Schematic diagrams.

1-4 – *Aphrophora* sp. (Cercopoidea) (1 – imago, dorsal view, 2 – imago, ventral view; 3-5th instar larva, dorsal view, 4 – same, ventral view); 5, 6 – *Tibicen plebejus* Scop. (Cicadoidea) (5 – imago, ventral view, 6-5th instar larva, ventral view).
dlp – dorsolateral platelets, ung – claw, utr – unguitractor, vlp – ventrolateral platelets.

---

arolium, and the groups of setae corresponding to the latter are each reduced to one seta; there are 5 setae on the arolium, including the central seta. The region of the sucker is distinct.

Most closely resembling the above description is the pretarsus of the Fulgoroidea. Here on the claws is present a row of setae, usually of 4, more rarely there are 5, 3, 2, 1 or no setae at all. On the arolium 1 or, more rarely, 2 pairs of setae are present ventrally; the central seta and dorsal setae are absent; only separate dorsolateral platelets are present. In the larvae the dorsolateral platelets are united, owing to proliferation, into a triangular plate which is distally notched in the middle, and which laterally borders the lobes of the claws; these lobes are absent in the imago.

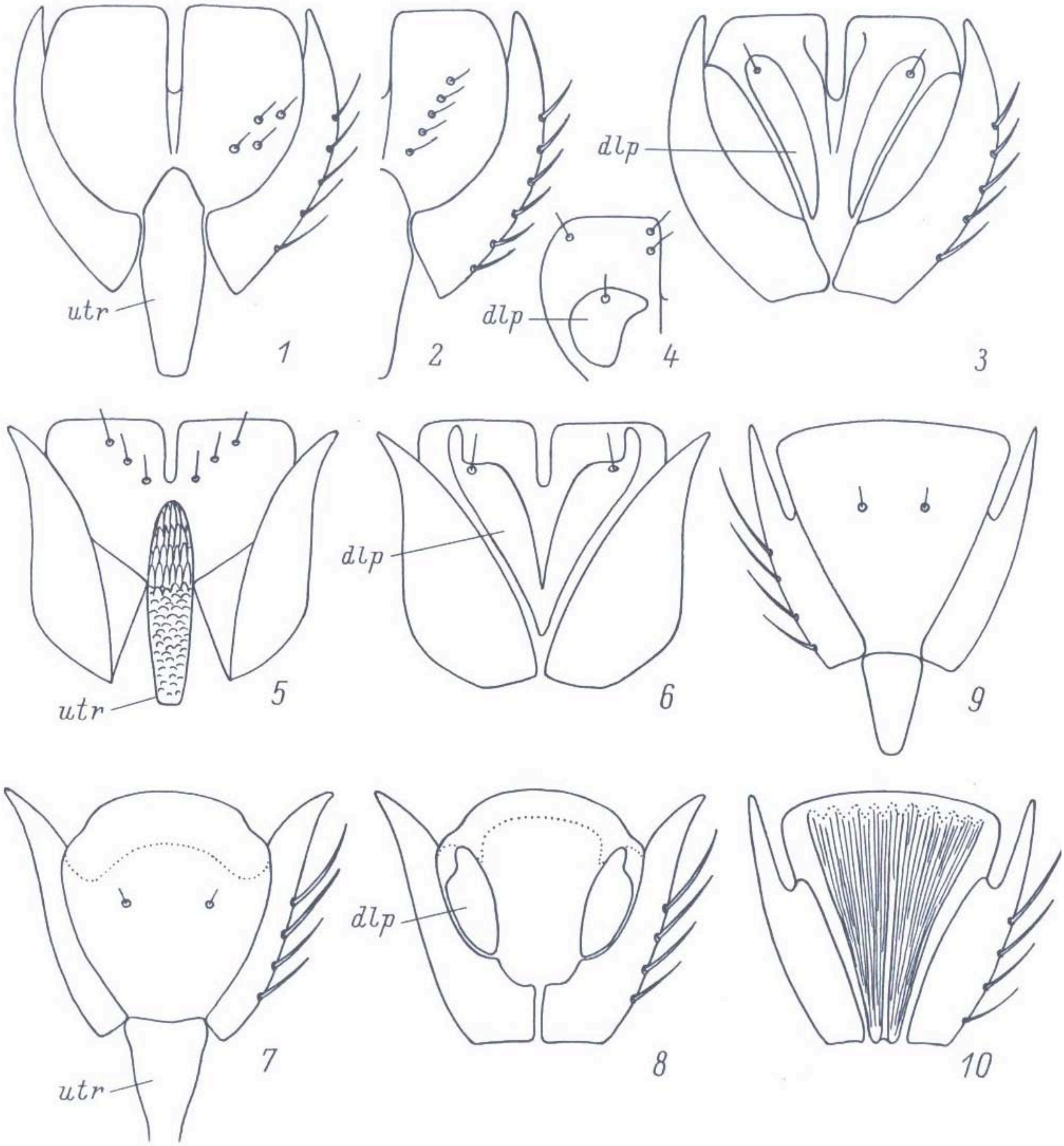


Figure 24. Pretarsus. Schematic diagrams.
1 – *Ledra* sp. (Ledridae), imago, ventral view; 2 – *Cicadella viridis* L. (Cicadellidae), same; 3 – *Ledra* sp., imago, dorsal view; 4 – *Platygonia* sp. (Cicadellidae), same, left half of arolium; 5, 6 – *Cicadella viridis*, 5th instar larva (5 – ventral view, 6 – dorsal view); 7, 8 – Dictyopharidae, imago (7- ventral view, 8 – dorsal view); 9, 10 – *Lycorma delicatula* White (Fulgoridae), 5th instar larva (9 – ventral view, 10 – dorsal view).
Contentional designations as in Figure 23.

In the Cicadidae are arolium is reduced, but between the claws is present a platelet which dorsally bears a large central seta, and ventrally a pair of small setae. On each claw there are 2 setae. In the Tettigarctidae the ventral setae are polymerized, while the central seta has been transformed into a group of platellae on a single strongly hypertrophied base. In the larvae of the Cicadoidea, including the Tettigarctidae (Evans, 1941), the claws are accreted at the base and there is no arolium. The atrophy of the arolium in the Cicadoidea is apparently associated with the underground way of life of the larvae, and also with the large dimensions of the representatives of this group.

The pretarsus of the Cicadelloidea is distinguished by a bifid, owing to a constriction, arolium (it bears only the dorsolateral platelets, adjacent to the lobes of the claws) and an unguitractor which is built up by its distal section, extending to the constriction. Setae are present on the claws, usually five on each claw, on the apices of the dorsolateral platelets, one on each, and in the region of the unexpressed ventrolateral platelets, several on each. The pretarsus of the larvae is similar, but devoid of setae on the claws.

It is difficult to establish the plesiomorphous state of the pretarsus. In the imagines of the Psyllina and Cimicina the arolium is bifid; in the Peloridiina it is entire and round; a round arolium of a type similar to that in the Cercopoidea and

Fulgoroidea is found in the thrips (Heming, 1971, 1972). It is possible that a round arolium is secondary, but is arises from the initial larval form. The weak change in the arolium in the ontogeny of the Cicadelloidea may be treated in two ways: as a progressive feature in the form of imaginalization of the larva or as a primitive feature; the former is more probable. There is no doubt as to the relationship of the Cercopoidea and Cicadoidea, manifested in the central seta.

6.8. State of coxothoracic articulation of the metathorax. Freely articulated hind coxae with the same mobility as that of the middle and fore coxae are present in the Cicadoidea; they are differentiated only by the presence of a sternal condyle. A coxothoracic articulation is preserved also in the Cicadelloidea and Cercopoidea, but here the joint has a very restricted mobility. In the Fulgoroidea the coxa has become completely accreted to the thorax and the sutures are inconspicuous. In the larvae of the Fulgoroidea the coxae are separated and a pleurocoxal condyle, with limited mobility, is clearly expressed; sternal condyles are absent, obviously in a secondary manner. Also secondarily simplified are the hind coxae of the larvae of the Tettigometridae (see section 6.3.).

6.9. Meracanthus and yellow spot on hind legs (see also sections 6.1. and 6.2.). In the Cicadelloidea there is no meracanthus on the hind coxae. In the Cicadoidea the meracanthus is flat, wedge-shaped, as on the middle coxae in the Cercopoidea, but in the Cicadoidea there is no yellow spot, and sometimes the meracanthus itself is also absent (*Gaeana*), and then the middle and hind coxae become very similar. In the Cercopoidea the entire meron is transformed into a coneshaped body with a sensory area at its apex; this is a homologue of the meracanthus. In the Fulgoroidea the meracanthus is conical with a soft sensory apex. In the Fulgoroidea and Cercopoidea a similarly developed yellow spot is present on the base of the femur. It is most probable that the Cicadelloidea did not have meracanthi and yellow spots, while the Cicadoidea have atavistically retained the meracanthi but have lost the yellow spots, along with the disappearance of the jumping function. Metatopy was observed in the relationship of the meracanthi, i.e. a transfer of features from one metamere onto another, in this case from one pair of legs onto another.

The Cercopoidea and Cicadoidea are similar in the strongly marked isolation of the meron by means of a deep furrow or constriction.

6.10. Subapical lobe-like protrusion on hind coxa near the anterior trochanteral condyle. Present in the Cicadelloidea and Cercopoidea (Figure 18), absent in the Fulgoroidea and Cicadoidea. Only in the Cercopoidea developed also on the fore and middle legs. The origin and distribution of this feature in groups related to the Cicadina has not been ascertained.

6.11. Trochanter and trochantero-femoral articulation of hind legs (Figure 25). The original structure of the trochanter can be seen on the middle legs. The coxo-trochanteral articulation primitively has a longitudinal axis, approximately parallel to the body axis, and accordingly the articulation of the trochanter with the femur has a vertical axis. The coxae are always markedly

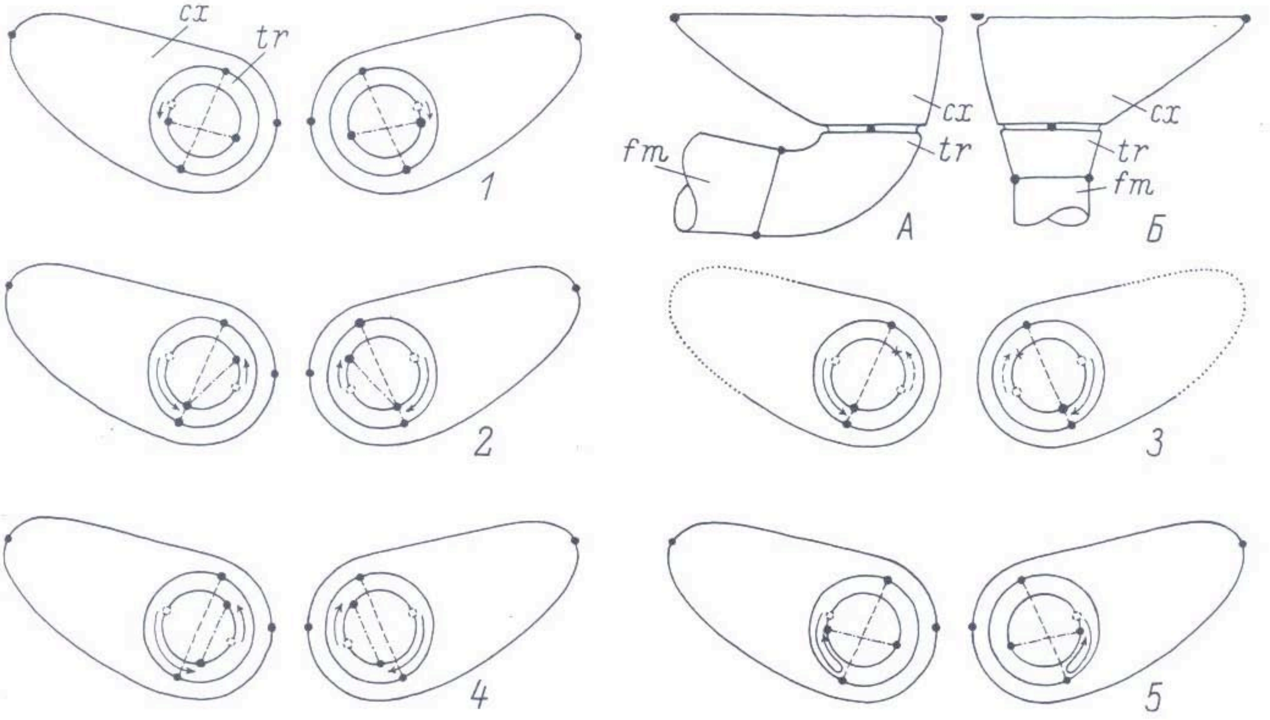


Figure 25. Schematic diagrams showing the relationships of the axes in the coxal and trochanteral articulations of the hind legs.

A – coxa, trochanter and base of femur, dorsal view, original structural scheme, preserved in a little-changed form on the middle legs; B – character of the simplification of the relationships presented in detail A to be shown in schematic diagrams 1-5; 1-5 coxa, trochanter and base of femur, view form behind according to the scheme in detail B: 1 – initial scheme, preserved with slight deviations on the middle legs, 2-5 – modifications of the initial scheme (1) in individual superfamilies (2 – Cercopoidea, 3 – Fulgoroidea, 4 – Cicadelloidea, 5 – Cicadoidea).
cx - coxa, fm - femur, tr - trochanter. The initial positions of the condyles are shown by the open circles, the actual positions – by the black circles; the arrows indicate the directions of displacement of the condyles in the phylogeny; the asterisk indicates the supposed site of the reduction of the condyle in the Fulgoroidea.

inclined backwards by their apices, and therefore the axes of the joints are also inclined away from the hypothetical initial directions. The dorsal trochantero-femoral joint has a cup on the trochanter and a lobe on the femur, while the ventral joint is expressed as a simple butt joint, reinforced by a tendon. The posterior side of the articulation on the femur is furnished with a small trapezoidal apodeme, which extends along the wall deep into the trochanter. Primitively the trochantero-femoral articulation has a very restricted mobility. In the jumping legs of the Homoptera this mobility is amplified.

The hind coxae of the cicadines are deflected backwards actually to the horizontal position, and in this case the primitive axis of the coxo-trochanteral joint has acquired an almost vertical position, while the axis of the trochantero-femoral joint is close to longitudinal; in connection with jumping, however, this axis has changed its primitive positioning. The initial transformation of the articulation for purposes of jumping comprises that the upper lobe of the femur is strengthened and displaced to a position opposite the lower (primitively anterior) condyle of the coxo-trochanteral articulation; the posterior trapezoidal apodeme on the proximal end of the femur forms a projection with its base, that rests up against a similar projection of the adjacent margin of the trochanter; a supplementary posterior articulation or support is formed. The primitively ventral joint changes little, but the trochanter grows out around it in a bulge, or lip, and its position is displaced upwards with respect to the actual orientation of the body, i.e. onto the primitively posterior side. Thus the axes of the coxo-trochanteral and trochantero-femoral articulations cease to be clearly expressed antagonists; they now become positioned in a subparallel fashion and not crosswise.

The described scheme (A, 1) in its pure form is not expressed in the contemporary cicadines. Coming closest to this scheme are the Cercopoidea (2), but here the trochanter is strongly abbreviated in the region of the lower condyles of the coxo-trochanteral and trochantero-femoral articulations, i.e. respectively, of the primitively anterior and primitively dorsal articulations.

Further transformations of the cercopoid trochanter and trochantero-femoral joint are found in the Fulgoroidea (3). Here the trochanter is abbreviated as a whole, similarly along all of its lateral walls. The primitively ventral trochanterofemoral joint is completely reduced and freed or replaced by soft intersegmental membrane. Thus the trochantero-femoral joint of the Fulgoroidea becomes monocondylar, robust and highly mobile. It is operated by muscles through the differentiated and hypertrophied primitively posterior (initially trapezoidal, see Figure 21, 2) apodeme on the base of the femur. The musculature of the articulation is described by Sander (1956).

The Cicadelloidea (4) have advanced further from the initial state (1) than the Cercopoidea. In the Cicadelloidea an abbreviation of the trochanter is not expressed but there has occurred a further displacement of the primitively dorsal condyle of the femur onto the ventral, i.e. primitively anterior, side of the trochanter. The protrusion that had occupied a primitively posterior position has become displaced to a position opposite the primitively anterior (i.e. ventral) condyle of the coxa. The primitively ventral trochantero-femoral joint has retained and consolidated its construction; on the femur, opposite the lip of the trochanter, a projection has been formed, which butts up against the joint.

An explanation for so strange a displacement of the dorsal trochanteral condyle may be found in the situation that in the Cicadelloidea, after the stage of a jumping mobilization of the joint approximately to the cercopoid level, there followed a secondary immobilization and then the wedge-shaped primitively dorsal condyle of the femur began to play the role of fixator (lock) of the trochantero-femoral joint; caught from the sides of its deepening trochanteral cup, this lock in the process of its establishment also became displaced onto the ventral (primitively anterior) side of the leg.

In the Cicadoidea (5), in connection with the loss of jumping, the structures under discussion reverted to a state that is similar to the state of the middle and fore legs, apparently by way of metatopy and instauration.

6.12. Adornment of lateral walls of hind tibiae (Figures 18, 19 and 26). The principal adornment of the tibiae consists of setae and teeth; sometimes there are no setae or, more precisely, they are polymerized and attenuated to the state of hairs, forming a sparse cover. The latter is characteristic of the Cercopoidea and Cicadoidea. The plesiomorphous condition, as is shown by a comparison with the bugs and book lice, is characterized by a covering of hairs and 4 rows of setae, demarcating the dorsal, ventral and lateral edges. The edges are clearly evident and are demarcated by ridges in the Cicadelloidea and Fulgoroidea, but are poorly evident or inconspicuous in the Cercopoidea and Cicadoidea. In the jumping forms the teeth and setae of the primitively antero-dorsal row (which turns out to be the external row according to its actual position) are developed most strongly.

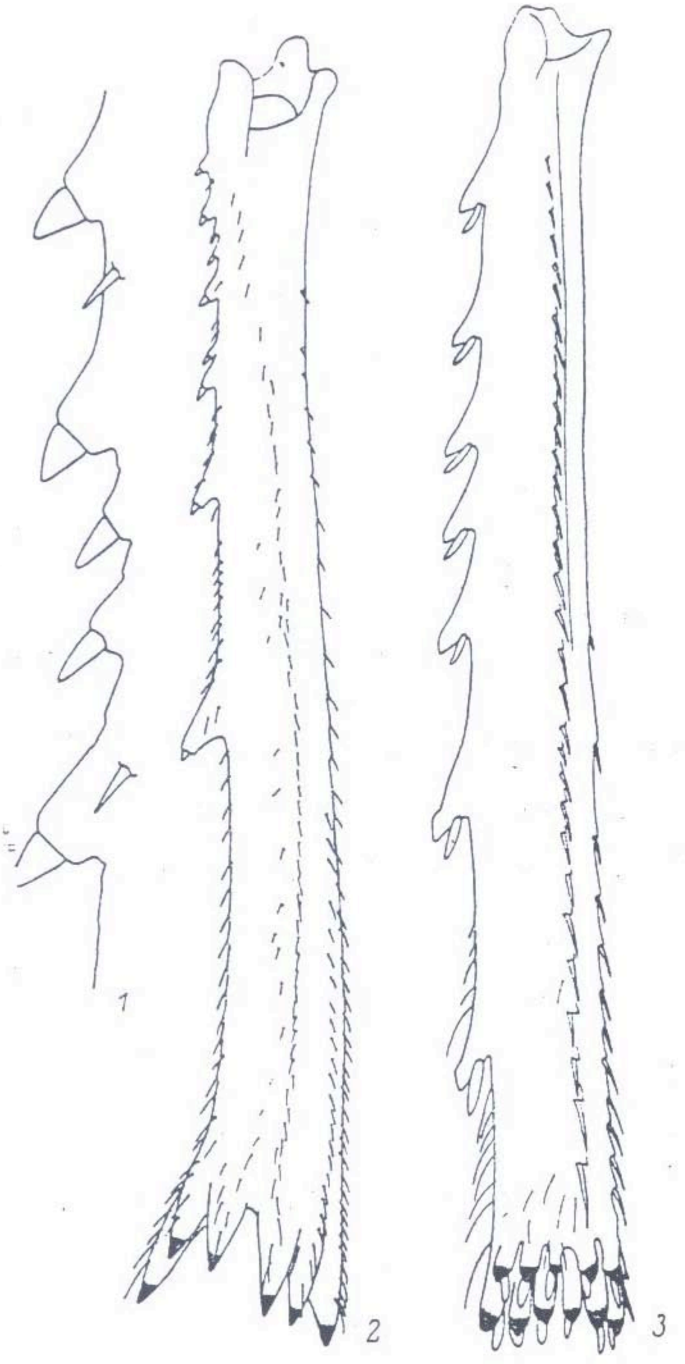


Figure 26. Hind tibiae. Ventral view.
1, 2 - *Oecleopsis artemisiae* Mats. (Cixiidae) (1 - teeth on outer margin in close-up); 3 - *Petalocephala* sp.) (Ledridae).

Characteristic of the Cicadelloidea are the thickened and comparatively few setae, seated along the 4 ridges on tubercle-like or tooth-like bases (Davis, 1975). The setae of the external (i.e. primitively antero-dorsal) row (row II of Davis) are more strongly developed, they are larger, thicker and shorter; their bases are more strongly developed and are clearly inclined towards the apex of the tibia in accordance with the overall slope of the setae. Only in the Aetalionidae is the hair covering preserved together with the setae. The bases of the main setae of the external row are sometimes hypertrophied into a tooth, bearing a seta on the middle of its distal margin; the apex of the tooth is formed by a tapering of the most elevated proximal portion of the base, which is initially adjacent to the seta. The described teeth are encountered sporadically in various groups of the more primitive Cicadelloidea, such as the Ledridae, Membracidae and the Eurymelinae of the Cicadellidae, and some others. The setiferous teeth of the Cicadelloidea have a trihedral form; the seta is seated on the short edge that is located transversely to the axis of the tibia.

The teeth of the Cercopoidea are strongly hypertrophied and oligomerized, usually to 2, though their number sometimes increases to 5-7 (*Sinophora*, Aphrophoridae). The teeth are situated only in the external row; they are large, conical, with a characteristic thin and long subapical seta, which is seated on the distal wall of the tooth.

In the Cicadoidea the tibial teeth on the (ambulatory) hind legs are similar in structure to the cercopoid teeth, but, having become detached at their base, they have become spurs and are situated not only in the antero-dorsal row but also in the row along the mid-line of the ventral edge. The ventrally positioned row is a clearly secondary formation; it was evidently formed by the displacement to the position of teeth (spurs), most probably from the postero-ventral row of the ridge.

The teeth of the Fulgoroidea are situated only along the external ridge; they vary in number from 2-3 or 5-7, and are sometimes absent. The teeth of the Fulgoroidea characteristically do not have the subapical seta, that is characteristic of the cercopocicadoids. The lateral teeth on the tibia of the Fulgoroidea arise from a short seta with a high base by way of integration. This is clearly evident in the teeth of the Cixiidae, where frequently (perhaps always) in the larvae the seta is still set apart in the form of a short and wide conical cap[1]; sometimes this condition is also preserved in the imago (Figure 26). The presence of sturdy setae, with an absence of teeth, in the Tettigometridae has the appearance of a previous (possibly instaurized) state, resembling the situation in the Cicadelloidea. The construction with a toothlike base and a thickened subapical

---

[1] D.E. Shcherbakov drew my attention to this circumstance.

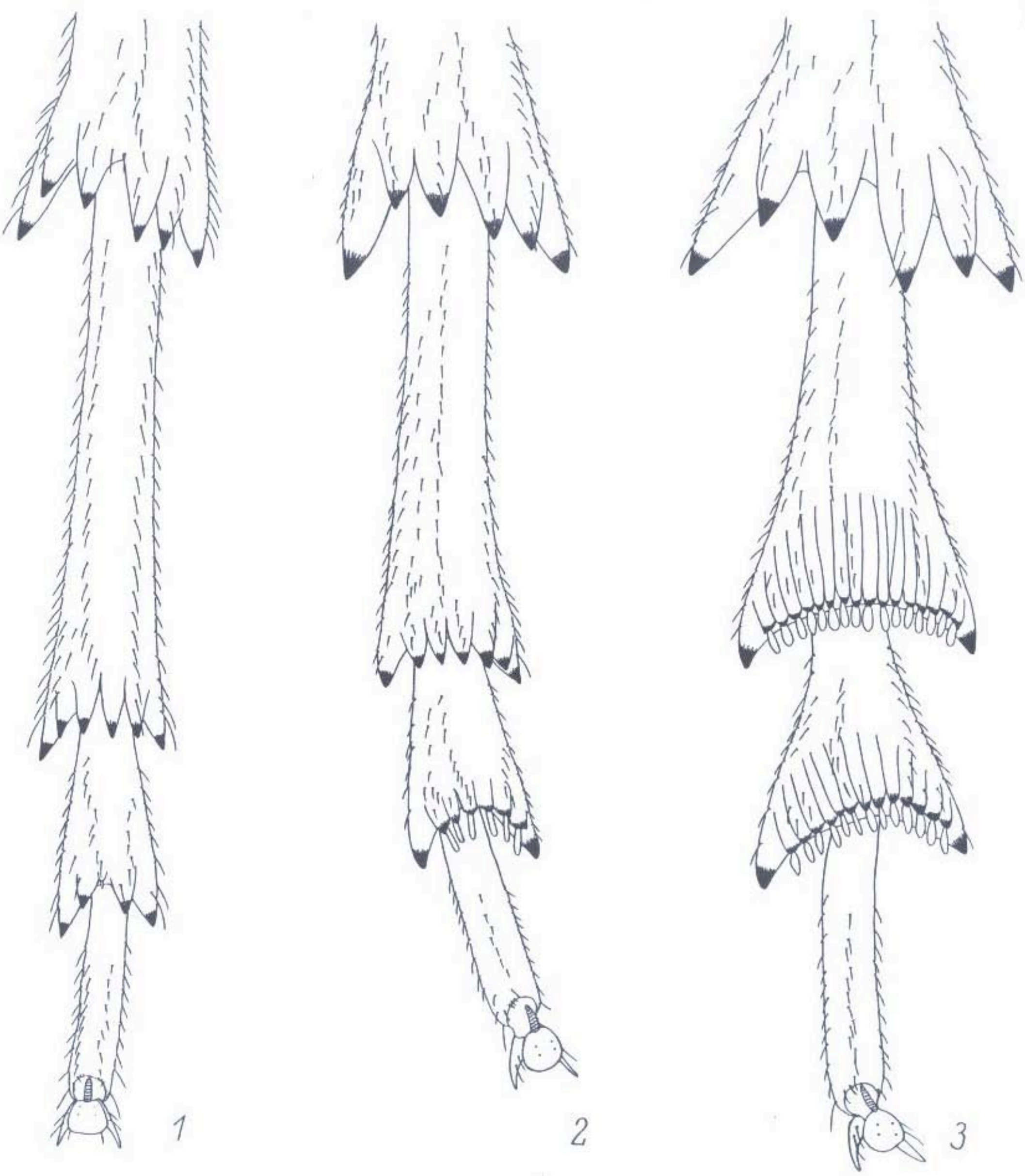


Figure 27. Hind tarsi in the family Cixiidae (tribe Pentastirini). Ventral view.
1 - *Oecleopsis artemisiae* Mats.; 2 - *Reptalus melanochaetus* Fieb.;

3 - *Pentastiridius* sp.

seta, characteristic of the Cicadelloidea, is also encountered, however, in the Fulgoroidea, but only on the hind tarsi, where teeth without a seta (with an incorporated seta) and teeth with an independent seta are known; often there are no setae on the first segment, while a seta is present on the second segment (Figure 27).

The teeth and setae of the external row on the hind tibiae play the role of defensive armament in kicking, and kicking is a by-product of the capacity for jumping. One of the primary functions of the setae, the sensory function, retreats into the background in the Cicadelloidea for the setae in the external row; in the Cercopoidea and Cicadoidea there occurs a division of functions: the tooth takes onto itself a mechanical power function, while the subapical seta retains only the sensory function. In the Fulgoroidea the dental seta has become fused with the tooth and has completely lost its sensory function.

Attracting attention to itself is the similarity of the Cicadelloidea and Fulgoroidea in the functions and structure of the dental setae (Figure 26), which should evidently be considered as their synapomorphy. The structure of the tooth with a slender subapical seta in the Cercopoidea and Cicadoidea represents an indubitable synapomorphy (Figures 18 and 19).

However, the homology of the subapical setae of the Cicadelloidea with those of the cercopocicadoids may prove to be wrong, if one supposes that the tips of the teeth of the Cercopoidea were formed, as in the Fulgoroidea, by way of the incorporation of an apical seta, while the specialized subapical seta became differentiated later from the non-individualized small setae at the base of the tooth. This supposition is less probable but it cannot be discarded at the present time. Another example of the transformation of a seta into a tooth is found in the larvae of the cicadas, in which a seta, located ventrally in the middle part of the femur, is developed in the first instar but is replaced in the second instar by a nonarticulated tooth (Silvestri, 1922; Kudryasheva, 1979).

6.13. Adornment of apices of hind tibiae. The hind tibiae of the Cicadelloidea bear one row of compactly displaced spur-like teeth on their apex ventrally (ventrally and anteriorly). The teeth are furnished with thickened subapical setae. The bases of the teeth are proximally separated from the surface of the tibia, which here forms a common margin, serving as a support for the teeth. The described margin, in the spaces between the bases of the teeth bears short setae on tubercle-like bases, one in each space (Davis, 1975). This is, as it were, a rudiment or vestige of a second row of teeth, which never attains development in the Cicadelloidea, except for the Ledridae, but this case is possibly secondary; in the contrast to the Cercopoidea and Fulgoroidea, and also to the other Cicadelloidea, the teeth do not spread out and the tibio-tarsal joint is not reinforced.

In the Cercopoidea the tibiae have on their apex 2 rows of uniformly developed teeth, bearing fairly slender subapical setae.

The second row is situated opposite the spaces in the first row. The teeth are spread in a dovetail.

In the Fulgoroidea the tibiae on their apices bear 2 rows of teeth that are spread in a dovetail, as in the Cercopoidea, but they never bear subapical setae. In the Fulgoroidea one may distinguish the teeth belonging to the primitively ventral and to the primitively anterior surfaces of the tibia (Emel'yanov, 1982).

In the Cicadoidea the teeth on the apices of the hind tibiae are arranged in 2 rows, as in the Cercopoidea and Fulgoroidea; they are strongly sclerotized but are not spread out, in which they resemble the situation in the Cicadelloidea.

16. 4. Tibiotarsal joint of hind legs. On the fore and middle non-jumping legs the tibiotarsal joint has a telescopic character; the somewhat narrower base of the tarsus is drawn in slightly into the wider apex of the tibia, condyles are not developed.

In the Cicadelloidea the tibiotarsal telescopic joint of the hind legs is reinforced dorsally by a wide condyle on the tarsus and a corresponding wide, moderately developed hollow on the tibia. In the Cercopoidea the joint has a sturdy dorsal condyle on the tarsus, which goes into a deep hollow on the tibia, which is completely covered from above.

The tibiotarsal joint of the Fulgoroidea is similar to the cercopoid one but is modified by the removal (reduction) of the upper wall of the tibial hollow. In the most primitive family of the fulgoroids, the Tettigometridae, the upper wall and, consequently, the hollow as such are still developed.

In the Cicadoidea the tibiotarsal joint is similar to the cicadelloid type. The weakening of the joint here is associated with the disappearance of the jumping function.

6.15. Hind tarsi. The first and second segments of the hind tarsi in the Cercopoidea and Fulgoroidea are similar and, like the tip of the tibia, they are widened in the form of a dovetail. A difference consists of the fact that in the Cercopoidea all of the teeth bear subapical setae, while in the Fulgoroidea the outer teeth never bear such setae; on the remaining teeth setae may be present or absent. The corresponding segments in the jumping Cicadelloidea and non-jumping Cicadoidea are not widened at their tips and do not bear lateral apical teeth, except for the Tettigarctidae, in which teeth are present but only on the anterior side.

The last three points (6.13.-6.15.) are in accord in drawing a picture of a reinforcement of the tibiotarsal fulcral and jumping complex proceeding from the Cicadelloidea to the Cercopoidea and Fulgoroidea, and of its subsequent reduction in the Cicadoidea.

7. **Abdomen**

7.1. Configuration of basal abdominal segments (I-III) (Figure 28). There is one common structural plan for the base of the abdomen (segments I-III) in the cicadines. Characteristic features are; a displacement of abdominal spiracles I and II in the dorsal direction; an abbreviation and weakening of segment I; an abbreviation of the second sternite in the medial part and its adjunction to segment III; its widening in the lateral portions with the formation of a distinctive swelling or thickening, enclosing the organ of hearing (its presence has been demonstrated in the Cicadoidea (Vogel, 1923) and Cicadelloidea (Vondracek, 1949) but, judging by external features, it is also present in the Cercopoidea and Fulgoroidea); the extension of the lateral anterior corners of tergite III with an envelopment from the side of tergite II; at the same time the lateral ends of sternite II (auditory capsules) have been pushed forward and lie in front of the lateral protrusions of tergite III and to the front and to the side of the lateral margins of tergite II. Tergite I is characterized by a shortening and partial membranization in its middle part. In the Cicadidae the anterior corners of tergite III are secondarily shortened, but in the Tettigarctidae they are still well developed. In the Fulgoroidea tergite II is more freely articulated with III and is not joined up on the sides with the sternite, i.e. with the auditory capsules.

In the males of some groups, in particular in the Delphacidae and especially in the Cicadidae, the anterior segments are more markedly transformed, in connection with the strengthening of the sound-producing apparatus, but all of these transformations are of a secondary character, are weakly expressed in the less advanced representatives and do not pertain to the females.

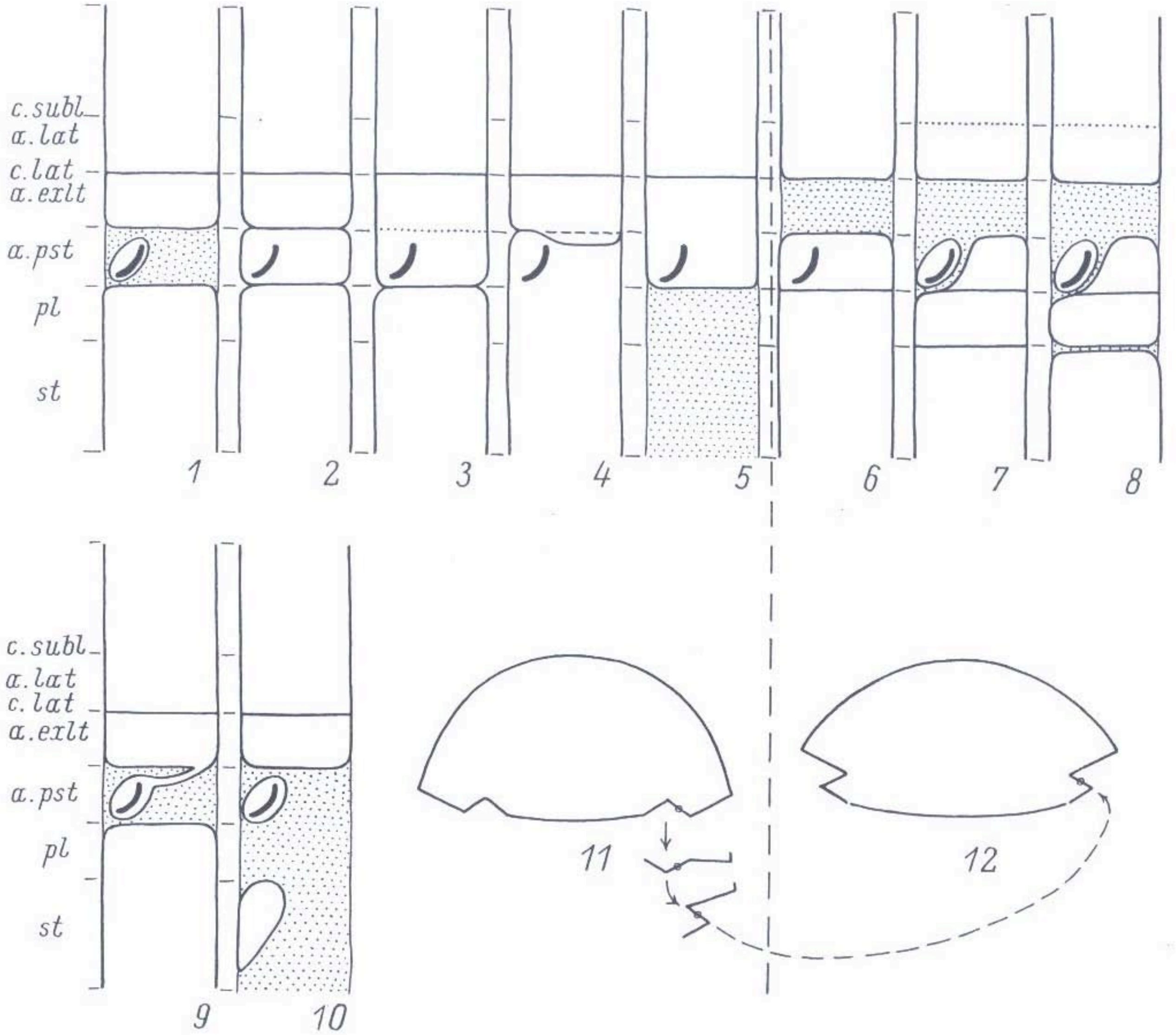


Figure 28. Schematic diagram of homonomous abdominal segments IV-VII. Schematic scan of heft half of segment.
1 - Ulopidae; 2 - Cicadellidae; 3 - Membracidae; 4 - Cicadidae; 5 - Tettigometridae, larva; 6 - Tettigometridae, imago; 7 - Cixiidae; 8 - Dictyopharidae; 9 - Cercopidae; 10 - Fulgoroidae, larva; 11 - cross-section of abdomen in the representatives illustrated to the

left of the dashed vertical line (1-5, 9, 10); 12 – cross-section of abdomen in the representatives illustrated to the right of the vertical dashed line. The arrows in figures 11 and 12 indicate the rearrangements in the pleural region during the transition from the first state to the second.
a. exlt –axtralateral area, a. lat – lateral area, a. pst – parastigmal area, c. subl – sublateral carina, c. lat – lateral carina, pl – pleurite, st – sternite.

7.2. Tympanal membranes. A very small stridulatopry tympanal membrane is present in the Cicadelloidea and Cercopoidea (Evans, 1946a; Ossiannilsson, 1949), and a large one in the Cicadoidea (Myers, 1928; Evans, 1941); it is located in the posterior part of abdominal tergite I close to the sides. In the Cercopoidea it is striated with fine grooves, and frequently also in the Cicadelloidea; in the Aetalionidae the membrane was noted by Evans (1946a, 1957), in the Cicadidae it is well known (Myers, 1928; Weber, 1930), and in the Tettigarctidae it was described by Evans (1941).

In the Fulgoroidea there is no membrane in the explicit form but in some case, for example in the females of *Delphax* (Delphacidae), in place of the tympanum there is found a shallow, more strongly pigmented depression. As is evident from the data of Ossiannilsson (1949), the dorsoventral muscle of abdominal segment 1 (Ia dvm_1, according to Ossiannilsson), which is homologous in all the cicadines, is well developed in the Cercopoidea, Cicadelloidea and Fulgoroidea, and it has a similar attachment ventrally and dorsally around the tympanum, and moreover in the Cercopoidea and

Fulgoroidea (Delphacidae) the attachment is localized on a homologous longitudinal fold (fo, in Ossiannilsson). It is interesting that in some of the Cicadelloidea (*Evacanthus, Oncopsis*) the dorsal attachment is accomplished by means of a funnel-shaped or mushroom-shaped tendon, as in the Cicadidae.

7.3. Relationship between auditory capsule and first two abdominal spiracles. This varies in the different superfamilies. In the Cicadoidea and Cercopidea the second spiracle is located anteriorly under the auditory capsule and not dorsally to the first spiracle, it is turned ventrally; in the Cicadelloidea and Fulgoroidea the second spiracle is turned dorsally, it is situated in front of and to the inside of the auditory capsule, and medically to the first spiracle. In the Cicadelloidea the spiracle is set close to the capsule, while in the Fulgoroidea these structures are markedly separated. In the Cicadelloidea in front of the auditory capsule on segment I, between the first spiracle and the lateral portions of tergite I, is present a convex formation, resembling a homologue of the auditory capsule (pil, in Ossiannilsson); in the Cercopoidea there is no such formation, but in the Cicadoidea this formation is comparable with the longitudinal convexity of tergite I in front of the auditory capsule. In the Fulgoroidea the corresponding region is membranous.

The less marked displacement of the anterior abdominal spiracles, especially of the second, onto the dorsal side in the Cercopoidea and Cicadoidea may be secondary, associated with the formation of the air cavity under the abdomen in the larvae by means of the stigmocalyptrae.

In the bugs, including the Peloridiidae, only the first abdominal spiracles, when they are not reduced, are displaced onto the dorsal side; in the Sternorrhyncha all of the abdominal spiracles are situated laterally and only the first are located very slightly or markedly dorsally to the following spiracles in a number of cases (Silvestri, 1934; Pflugfelder, 1941; Theron, 1958), and this manifests a similarity with the bugs but not with the cicadines.

7.4. Structure of the homonomous abdominal segment (IV-VII). The common and persistent elements of the little-varying abdominal segment are the lateral carina, running along the tergite, and the spiracles with their associated sclerotizations, the peritreme and parastigmal area. The lateral carina, which forms the lateral or ventrolateral margin of the abdomen, is homologous in all the cicadines and bugs. On the whole the following portions (areas) may be distinguished on the abdominal tergite; 1) lateral, lying medially to the lateral carina, its inner boundary is usually not expressed, but in several groups of the Fulgoroidea is denoted by the sublateral carina; 2) extralateral, lying below the lateral carina, usually turned downwards and lying below and to the inside of the lateral carina; 3) the parastigmal area with the peritreme near its anterior margin or in its anterior part, often not separated from the extralateral area. Further on is located the sternite, the lateral parts of which, the pleurites, apparently, may be separated off by a suture from the sternite proper in some of the Fulgoroidea. The lateral area of the cicadines corresponds to the dorsal laterotergite of the bugs, while the extralateral area together with the parastigmal area correspond to the ventral laterotergite according to I.M. Kerzhner's (1981) terminology.

In the Cicadelloidea the extralateral and parastigmal areas are either united but with traces of a boundary (Aetalionidae, Membracidae), or separated by a flexible suture (Cicadellidae, Ledridae and others), or else the parastigmal area is membranous while the peritreme is free (Ulopidae).

In the Cercopoidea the parastigmal area is membranous and the peritreme is free but connected by a narrow stalk with the extralateral sclerotization.

In the Cicadoidea all of the elements are sclerotized, but the lateral margin of the extralateral area forms the rudiment of a stigmocalyptra (ventral paranotum) above the rigid suture with the parastigmal sclerite.

The Fulgoroidea are characterized by a separation of the sclerotization of the extralateral and parastigmal areas, which, becoming indented along their suture (mutual boundary), form a lateral groove that covers the spiracle. The differentiation of the segment in the larvae is different: the lateral groove is absent in these and the spiracles are turned ventrally. The primitive state, apparently, may be found in the larvae and imagines of the Tettigometridae.

In the larvae of the Tettigometridae the tergites are sclerotized, while the sternites (with the pleurites) are not sclerotized. In the imagines of the Tettigometridae and Delphacidae a lateral groove is present, the extralateral areas are membranous, while the parastigmal areas are sclerotized and are accreted across the carina with the sternites, in which the pleural portions are not separated off. The differentiation of the segment in the Cixiidae is distinguished by the separation of the pleurites by means of a narrow flexible suture. Many of the Fulgoroidea are characterized by a joining together of the parastigmal sclerotization with the pleurite into a single sclerite with a carinate boundary of the elements; at the same time the sclerite may become disconnected from the sternites proper and from the completely free peritreme (Dictyopharidae, Fulgoridae). In the larvae of the Fulgoroidea the whole tergite is sclerotized, including the extralateral areas, but excluding the parastigmal areas; the pleurites and a considerable part of the sternite are membranous. In the higher Fulgoroidea

(Caliscelidae, Flatidae, Ricaniidae and others) cases are encountered of a reinforcement of the sclerotization and of a secondary fusion of the elements.

The similarity of some of the Cicadelloidea (Cicadellidae and others) with the lower Fulgoroidea in the isolated parastigmal area is associated in the other Cicadelloidea with another pleisomorphous similarity, but in this case with the Cercopoidea, based on the membranous parastigmal area. It is noteworthy that the membranous parastigmal in the Fulgoroidea is usually expressed only in the larvae of the more advanced families (Fulgoridae and others). The segment in the Cicadoidea is distinguished by a continuous sclerotization and by rudiments of the stigmocalyptera, well developed in the larvae of the Cicadidae. At the same time in the Cercopoidea, in which larval stigmocalyptera are also well developed, these are completely lacking in the imagines.

Apparently the primitive type of structure of the homonomous segment is expressed in the Cicadelloidea* and closely related families. From this state it is easy to pass on to the lateral furrow in the Fulgoroidea and to explain the relationships in the Cercopoidea and Cicadoidea, and in the other Cicadelloidea. The state of the coherence of the extralateral and parastigmal areas in the lower Fulgoroidea makes it difficult to accept the state of the Fulgoroidea as being the initial state for the other superfamilies. It is possible that the differentiation of the ventral laterotergite commenced from a stage of membranization of the parastigmal area, as in the imagines of the Cercopoidea and Ulopidae, and in the larvae of the Fulgoroidea. The lateral fold of the abdomen is an autoapomorphy of the Fulgoroidea.

---

* Sic. Should be Cicadellidae here. (Tr.)

7.5. Stigmocalyptrae. This name is employed for the covers above the abdominal spiracles (Boulard, 1969); these covers are formed by the margins of the extralateral sclerotization and are apparently homologous to the paranota. They are expressed in the larvae of the Cercopoidea and Cicadidae of the Cicadoidea; they are not expressed in the larvae of the Tettigarctidae (Evans, 1941), and are absent in the Cicadelloidea and Fulgoroidea. In the Cercopoidea they serve to protect the abdominal spiracles from becoming soiled and plugged up, in the first instance, by the liquid that is secreted by the larvae themselves to form the froth. They fulfill a similar function in the larva of the cicada *Muansa clypealis*, which leads an aquatic way of life (Boulard, 1969). The significance of the stigmocalyptrae in the larvae of cicadas that develop in the soil is unclear, all the more so since, according to the data of I.V. Kudryasheva (1979), they appear only in the 5th instar.

7.6. Areas of wax glands on tergites VI-VIII in the larvae. These are present only in the larvae of the Fulgoroidea (VI-VIII) and Cercopoidea (VII-VIII); in their position and form they are homologous, as Šulc (1911) considered long ago. The areas of wax glands in the Fulgoroidea are paired and occupy the greater part of tergites VI-VIII, while the wax areas of the Cercopoidea (glands of Batelli) occupy the same location on tergites VII-VIII. It is noteworthy that the reduction of the wax areas in the Fulgoroidea initially involves segment VI.

It is most probable that in the Cicadelloidea wax areas were never present on the tergites, while in the Cicadoidea they disappeared with the transition to an active underground way of life.

7.7. Ovipositor. In the Cicadelloidea, Cercopoidea, Cicadoidea and in some of the more primitive Fulgoroidea (Delphacidae and Cixiidae; in the Tettigometridae the ovipositor is reduced) the ovipositor is of the piercing-sawing type, it has the typical structure and is differentiated only by secondary features. The first valvifers may be arranged more transversely or more longitudinally; the second valvifers occupy a more or less vertical or an approximately horizontal position; the groove of the pygophore for the insertion of the ovipositor may be more or less deep with pronounced edges, or without pronounced edges, or scarely expressed at all. The Cercopoidea and Cicadoidea have horizontally disposed second valvifers; the Cicadelloidea and Fulgoroidea usually have vertically disposed second valvifers, but in the Aetalionidae (Cicadelloidea) they are obliquely situated, while in the Cixiidae (Fulgoroidea) they are horizontally disposed.

In the Cercopoidea the second valvifers are indistinctly separated from the pygophore at the articulation with the pygophore, while in the Cicadoidea the separation is distinct everywhere. In the Cicadelloidea the ovipositoral groove of the pygophore is distinct, with clearly marked borders, and the region of the articulation of the third valvulae (gonoplaques) occupies more than half of their length, while in the Cicadoidea and Cercopoidea this region occupies less than half of their length. In the Fulgoroidea the ovipositoral groove of the pygophore is shallow, without clearly marked borders; the third valvulae are widened at the base, ventrally they overlie the pygophore and, furthermore, they may be secondarily displaced forward from the site of attachment to the valvifer (gonocoxite); the region of the articulation of the third valvulae to the pygophore is very short, as in the Cicadoidea, but, in contrast to the Cicadoidea, the valvulae are long. Unlike the other cicadines, the ovipositor of the Fulgoroidea is devoid of a wide subgenital plate, it is abbreviated to a small plate that is partially or completely covered by the neighbouring sclerites. The main difference of the ovipositor of the Fulgoroidea from that of the other cicadines comprises the newly formed medial basal apodeme of the second valvulae (gonapophyses), it is preserved also in the modified ovipositor of the higher Fulgoroidea (Emel'yanov, 1979).

Most primitive among the Fulgoroidea appears the ovipositor of the Cixiidae; in these it is slightly displaced forward at its base and has horizontal second valvifers, while in the Delphacidae the valvifers are vertical, while the ovipositor is strongly displaced forward towards the base of the abdomen, so that the posterior pregenital sternites are bent at an angle.

The horizontal position of the second valvifers and their considerable length, in both the Cercopoidea and Cicadoidea, have a plesiomorphous character, since they are characteristic also of the non-transformed ovipositor of the bugs (Saldidae). The similarity of the more advanced Cicadelloidea and the Delphacidae of the Fulgoroidea in the vertical positioning of the second valvifer may be explained by functional convergence, by the necessity for reinforcing the sawing function.

In the Fulgoroidea there are many autapomorphous features, but one cannot comprehend on what basis they were formed, i.e. the point of separation of the Fulgoroidea from the other cicadines is unclear on the basis of the complex of structural features of the ovipositor.

7.8. Genitalia of the male (Figure 29). The genital segment (IX) of the male in the ciadines is called the pygophore when it is not divided, but if the tergal and sternal parts are distinguishable this name is retained only for the tergal part, while the sternal part acquires the name of genital valve. The latter may bear lobe-like proliferations of the posterior margin, which may or may not be separated off, that are called the genital plates. Dorsally and posteriorly the pygophore bears the anal tube (segment X), under which is situated an extensive intersegmental membrane, which includes the penis in its medial part and the harpagones in its lower (morphologically anterior) part.

Apparently the pygophore in cicadines was primitively not divided into dorsal and ventral parts, although this occurs in the advanced representatives of the Cicadelloidea and Cercopoidea, probably with the development and subsequent reinforcement of the mobility of the genital plates.

In the bugs there is no separation of the pygophore into dorsal and ventral parts, nor in the Aleyrodina; in the Coccina the genital region has been considerably transformed; in the Psyllina segment IX has been desclerotized dorsally but only above the anal tube, while in the aphids the situation remains unclear.

The genital plates are primitively present in the Cicadelloidea, Cercopoidea and primitive Fulgoroidea (Tettigometridae) in the non-separated form; they are absent or present only in the form of rudiments in the Cicadoidea, and are absent in most of the Fulgoroidea. Apparently the phallobase and aedeagus are primitively articulated (Cercopoidea, Fulgoroidea), but frequently become fused (Cicadelloidea, Cicadoidea). The aedeagus may evert to the outside its membranous internal wall; in the superfamilies Cercopoidea and Cicadoidea, and possibly also in other superfamilies, for example, in the Tettigometridae of the Fulgoroidea, according to Cobben (1965).

In the Cercopoidea the phallobase is unified, articulated with the aedeagus; the base of the aedeagus bears a small apodeme. The harpagones (styli) are situated to the sides of the phallobase and are connected to its lateral protrusions. The harpagones are covered ventrally by the genital plates. There is no articulation of the phallobase with the anal tube. The phallobase lies in the lower (morphologically anterior) part of the genital chamber. The pygophore is incised posteriorly to the sides of the genital plates. The genital plates are sometimes separated off from the genital valve (*Peuceptyelus* and others), apparently in a secondary fashion.

In the Cicadoidea the aedeagus and phallobase are accreted, and the latter is apparently partially reduced (upper part, see *Tibicina*). The pygophore is compact, without genital plates but with their rudiments on the lateral wals of the posterior margin, according to Ribaut (1936). The harpagones are retained only in the Tettigarctidae (Evans, 1931). The hooks and posterior lobe of the anal tube embrace the stem of the aedeagus and direct it. The phallobase is displaced downwards, as in the Cercopoidea. From below the genital block is covered by the spoon-like subgenital valve (sternite VIII).

In the Cicadelloidea the aedeagus is primitively and in almost all cases not separated from the phallobase. The phallobase, however, is separated into a basal upper part, which bears the aedeagus, and a lower part, which is articulated with the upper part

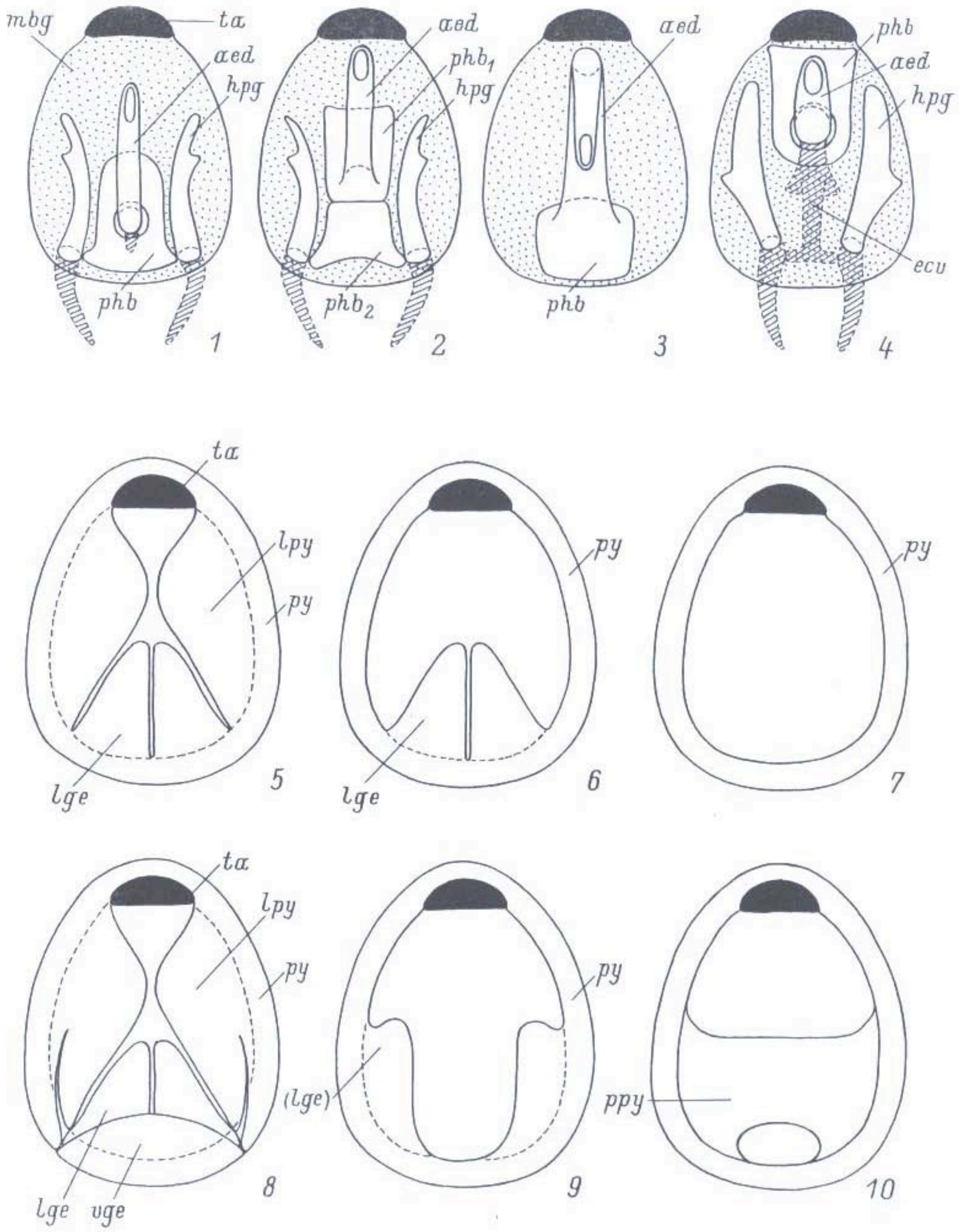


Figure 29.

General structural plan of the male genitalia according to the superfamilies. Schematic diagrams.

1 – 4 – relationship of penis and harpagones: 1 – Cercopoidea, 2 – Cicadelloidea, 3 – Cicadoidea (Cicadidae), 4 – Fulgoroidea; 5 - 10 – structure of the pygophore and its appendages, posterior view: 5 – original type of the Cicadelloidea, 6 – secondary type of the Cicadelloidea, 7 – type of the Cercopoidea, 8 – type of the Cicadidae (Cicadoidea), 9 – basic type of the Fulgoroidea, 10 – type of the Delphacidae (Fulgoroidea).

aed – aedeagus, ecv – endoconnective, hpg – harpagones (Styli), lge – genital plates, lpy – lobes of pygophore, mgb – genital membrane, phb – phallobase (phb_1 – phallobase in Cicadelloidea, phb_2 – connective in Cicadelloidea), ppy – commisure (bridge) of pygopore, py – pygophore, ta – anal tube, vge – genital valve.

and with the harpagiones (connective) (Snodgrass, 1935). Usually expressed in the Cicadelloidea are the parameres (lateral processes of the phallobase), which lie to the sides of the penis on the basal phallobase, and the upper appendage (or part of the phallobase), which separates the basal part from the anal tube, unfortunately termed the genital phragma. The parameres are separated from the phallobase or are accreted with the latter; sometimes they are accreted with the connective but articulated with the basal phallobase (*Cicadella, Doraturopsis, Aconura, Scaphoideus, Tetartostylus* and others). In the Cicadelloidea pairing of the gonopore is sometimes found in various representatives of unrelated groups: *Ulopa* (Ulopidae), *Japananus* (Cicadellidae, Scaphytopiini), *Neoaliturus* (Cicadellidae, Opsiini), *Notus* (Cicadellidae, Typhlocybinae). This may be interpreted as an instauration of the original pairing of the penis in insects. The lateral parts of the pygophore form lobes, the lobes of the pygophore, which cover the genital chamber from the sides. The genital plates in many representatives are apparently secondarily separated from the genital valve, which primitively was also not separated from the pygophore. With the most complete differentiation of the pygophore the lateral margins of the valves and the basilateral margins of the genital plates articulate independently with the lower margin of the pygophore in the narrow sense; these two articulations on the pygophore are separated by a blind membranous furrow or fold, which increases the flexibility of the pygophore and ensures a wide separation of its lobes when the genital valve is moved downwards with respect to the pygophore, and of the genital plates downwards and to the sides with respect to the valve. Such a construction is characteristic for the Cicadellidae of the subfamilies Deltocephalinae and Cicadellinae. In the family Membracidae the mobility of the lobes of the pygophore is provided for by their complete separation from the pygophore proper in the narrow sense.

In the Fulgoroidea the phallobase is separated from the aedeagus, and from above it is joined to the anal tube, i.e. the so-called genital phragma is included in its composition. The phallobase is not articulated with the harpagones, but the basal apodeme of the aedeagus, which is very strongly developed (synarmos* or endoconnective), is articulated endosomatically, not integumentally, by its process with the bases of the harpagones. The pyrophore is not differentiated; only in the Tettigometridae are present genital plates that are not separated off. The structure of the genitalia varies in its details. In the Delphacidae the genital membrane is sclerotized into a bridge in the region between the phallobase and the harpagones, which is also unfortunately called the genital phragma. In several groups the aedeagus is subjected to reduction, while in others the phallobase may be reduced; sometimes the phallobase envelopes the aedeagus in a muff-like fashion and acquires the name of phallotheca. On the phallobase in the families Cixiidae and Delphacidae outgrowths are often developed, which apparently are homologous to the parameres. Incidentally, parameres are also encountered in cicadas, for example in the genus *Cicadetta*.

All of the variants of the genitalia of the male may be derived from a type closely resembling the cercopoid type: Cicadoidea – by way of the reduction of the genital plates, and subsequently also of the harpagones, the accretion of the phallobase and aedeagus, the specialization of the outgrowths of the anal tube and the inclusion of sternite VIII in the genitalia; Fulgoroidea – by way of the hypertrophy of the basal apodeme of the aedeagus with a subsequent transfer of the connection by way of the shortening muscle into direct contact; Cicadelloidea – by way of the differentiation of the phallobase below (in front of) the aedeagus. Phylogenetically these events could have occurred in almost any order, since the structure of the genitalia of all the superfamilies, apparently except for the Cercopoidea, is full of apomorphous features; only the direct close relationship of the Cercopoidea and Cicadoidea is fairly clear. One should note also the similarity of the Fulgoroidea and Cicadelloidea in the close connection of the phallobase with the anal tube, while in both the Ceropoidea and Cicadoidea the phallobase is at some distance from the base of the anal tube and is (always?) separated from the latter by a membranous space.

---

* “sinarmoz” would be the direct transliteration of the Russian term. (Tr.)

7.9. Anal tube (segments X-XI and their appendages) (Figure 30). The structure of the anal tube in the cicadines is in most cases differentiated in the males and the females, being more specialized

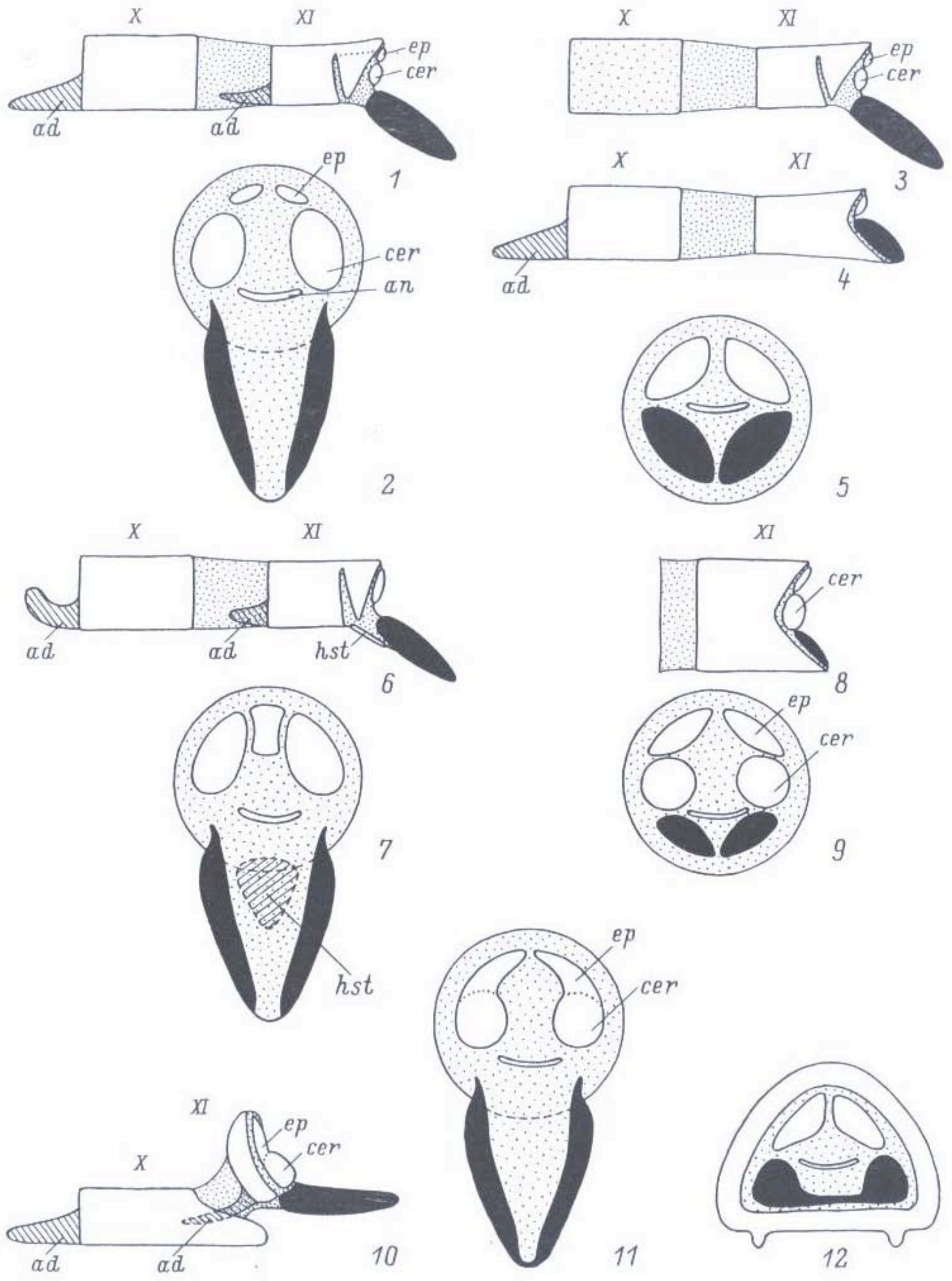


Figure 30.

Structure of the anal tube in females. Schematic diagrams. 1, 2 – Cicadellidae (1 – side view, 2 – apex, posterior view); 3 – Membracidae, side view; 4, 5 – Aetalionidae (4 – side view, 5 – posterior view); 6, 7 – Cercopidae (6 – side view, 7 – posterior view); 8, 9 – Cicadidae (8 – side view, 9 – posterior view); 10, 11 – Fulgoroidea, Dictyopharidae (10 – side view, 11 – posterior view); 12 – Fulgoroidea, Tettigometridae, posterior view, male. ad- apodeme, an – anus, cer – cercal sclerite, ep – supplementary sclerite, hst – hypostylar sclerite, sty – stylar sclerite, X, XI – corresponding abdominal segments.

in the females. The basic parts of the anal tube are retained in all cicadines but are modified in different ways. Segment X is usually the largest and is sclerotized without sutures along its entire cross-section, often more or less cylindrical, at its base on the sides ventrally is usually bears a pair of apodemes that are directed forward. Segment XI is quite narrow and short, it is separated from X by a membranous ring and is capable, to some degree or other, of being retracted into X; at its base below and to the sides, like X, it has a forwardly directed pair of apodemes. Segment XI, behind the tergite proper, bears dorsally and posteriorly a sclerite or paired sclerites, which Snodgrass (1935) considered to be the epiproct; below the epiproct on the sides and posteriorly are situated roundly-convex sclerites, which Snodgrass considered as rudiments of the cerci. On the lower part of the segment under the cerci, and articulated on the sides with the latter, is located usually an elongated digitiform structure, the anal style, with sclerotized lateral walls, which Snodgrass considered as the fused paraprocts. The anus is located above the style, between the cerci and under the epiproct. The anal style serves as a guide channel along which the liquid excreta are sprayed out.

Segment X in the males may bear, ventrally on its sides, a pair of teeth, the homology of which is unclear among the superfamilies; the teeth are present in all the Cicadoidea, in some Cercopoidea, in some Fulgoroidea (in particular in the Tettigometridae and

Delphacidae) and in some Cicadelloidea, though for the most part not in the primitive forms.

In the Cicadelloidea, if one digresses from the secondary details that apply mainly to the configuration of segment X, a characteristic feature is the complete telescopic retraction of segment XI into X, and in the females also of X into the pygophore (segment IX). On the basis of the structure off the anal tube in the Cicadelloidea (female) 3 types may be distinguished: the Cicadellidae type (Ulopidae, Ledridae, Cicadellidae), the Aetalionidae type and the Membracidae type.

Cicadellidae type. Females. Segment X is cylindrical and elongated. The membranous region between segments X and XI is equal in length to X; the diameter of XI is slightly less than that of X. The rings of segments X and XI are continuous; both segments have basal paired apodemes anteriorly (XI not in all representatives). Segment XI is longer on the dorsal side, it protrudes here backwards in a rounded or angular fashion. The lateral portions of the segment are incised by oblique sutures, which extend from below, from the posterior margin, upwards and a little towards the front; from above the sutures almost disappear; the dorsal part of segment XI is not separated off; sometimes the described lateral lobes may be separated from the dorsal part by longitudinal sutures. Above the anal style the posterior margin of the segment, which is truncated in a more or less straight line, bears paired, fairly flat sclerites in the plane of the wall on its sides; these sclerites are apparently the cercal sclerites, and underneath them are located very minute paired sclerites, which are not distinct in all representatives. Anal style, freely protruding backwards, with apically separated lateral sclerotizations.

In the males segment X is free and is not retractable, it is longer than in the females; at its base it is flattened dorsoventrally and devoid of apodemes. The region distally to segment X, including the intersegmental membrane, is amost the same in both sexes. In the males the lateral lobes are more clearly separated off from above by the longitudinal sutures.

Aetalionidae type. Females, Segment X is distinctly sclerotized, cylindrical; segment XI with a small protrusion behind dorsally and a large wedge-shaped protrusion behind ventrally; this protrusion apparently corresponds to the triangular stylar sclerite of the Cercopoidea (see below), but it is not separated off from the segment proper. Because of the lower protrusion the anal style is not expressed as an independent formation; its lateral sclerotizations lie dorsally above the wedge-shaped protrusion. Above the bases of the stylar sclerites are located the cercal sclerites; there are no supplementary sclerites on top. Segment XI displays traces of cicadelloid differentiation.

Membracidae type. Females. The Membracidae type is characterized by a similarity to the Cicadellidae type, but here segment X is completely membranous, although its borders with the intersegmental membrane can be seen when the anal tube is fully everted. Segment XI is constructed according to the same plan as in the cicadelloid type, and traces of its differentiation are usually evident.

Males, Segment X, as in the females, is membranous and is retracted into the pygophore.

The original structural plan for the anal tube in the Cicadelloidea was apparently closely related to the first type (Cicadellidae type) and from it originated independently the Membracidae type, by way of the reinforcement of the telescopic character and membranization of segment X, and the Aetalionidae type, by way of the sclerotization of the triangular membranous space ventrally at the base of the anal style, with the joining together of this sclerotization to the basal ring of the tergite, as a result of which the anal style ceased to exist as such. It is possible, however, that the original type differed from the cicadellid type by the presence of a small free hypostylar sclerite, which was subsequently lost by all of the cicadelloidea except for the Aetalionidae.

In the Cercopoidea the anal tube is almost nonretractable, segment XI is a little smaller than X and the membrane between the segments is not wide. The ring of sclerotization of segment X is continuous, ventrally with a basal incision and a small distal lobe (as in the Cicadidae, but smaller). The basal apodemes of segment X are simple; the ring of segment XI is usually separated ventrally, thought rarely (*Lepyronia*) it may be continuous. Behind the ring dorsally and on the sides is located a yoke-shaped sclerite, which, narrowing, extends downwards to the base of the sclerotization of the anal style; dorsally this sclerite is not separated from the basal ring along the mid-line. The posterior wall of segment XI dorsally is occupied by the convex rudiments of the cerci, between which is located a rectangular small sclerite that is drawn out from below upwards. Ventrally from segment XI extends the large anal style with its lateral sclerotizations, separated apically, as in the Cicadelloidea. Between the lateral sclerites on the anal style ventrally, at its base, lies the triangular independent hypostylar sclerite.

Differences between males and females are evident only in segment X and concern mainly the proportions, and occasionally also the outgrowths that appear only in the males.

In the Cicadoidea, although the anal tube on the whole is constructed in a uniform fashion, it is differentiated in the degree of sclerotization in different representatives. In the Tettigarctidae the anal tube in general has the same outlines as in the Cicadidae but it has not been precisely described (Evans, 1941). Evidently the sclerotization of the anal tube among the Cicadidae is expressed in different ways in the Cicadinae and Tibicinae; at any rate in *Magicicada*, studied by Snodgrass (1935), and also in *Melampsalta*, belonging to the subfamily Cicadinae, the sclerotization is comparatively weak, while in *Tibicina* of the subfamily Tibicinae it is markedly stronger, which allows one to better understand its differentiation.

In the males of the Cicadidae segment X ventrally bears a pair of study teeth and a lobe on the posterior margin below and behind them. The teeth and the lobe support and direct the stem of the penis. In *Tibicina* the teeth as such are not expressed and have become fused with the lobe into a single inverted guide channel. At the base of the anal tube in *Tibicina* there is some asymmetry in its attachment to the pygophore, apparently associated with copulation with an asymmetrical penis. Segment XI is weakly sclerotized and pigmented. Dorsally and ventrally the ring proper of the segment is fused with triangular lobes that are directed backwards and are adpressed to one another; the lower lobe, which corresponds to the anal style and the postero-ventral part of the segment itself, is a little larger. Between the bases of the lobes on the sides are situated the round convex rudiments of the cerci (Snodgrass, 1935). The adjoining surfaces of the lobes are constructed in a similar fashion: along the sagittal line they have grooves, which together form an extension of the anal canal. To the sides of the membranous grooves and adjoining walls of both lobes are sclerotized, and this sclerotization forms a single whole with the sclerotization of the outer walls of the lower and upper lobes. The weaker sclerotization of segment XI in *Melampsalta* (apparently expressed in the same fashion as in *Magicicada*) shows that the ring proper of segment XI is well expressed ventrally and on the sides but has almost disappeared dorsally, and that the upper surface of the upper lip and the lower surface of the lower lip in *Melampsalta* are membranous, though the configuration is the same as in *Tibicina*. Clearly distinguishable in the pure form in *Melampsalta* are the lateral (dorsolateral) sclerites of the anal style, which has been transformed into the lower lobe, and the ventrolateral sclerotizations of the upper lobe, which Snodgrass considered as homologues of the epiproct.

In the female of *Melampsalta* segment X is in the form of a continuous but simple ring, while segment XI is of the same form as in the male, although there is evident a narrow rudiment of sclerotization of the lower wall of the lower lobe, apparently corresponding to the hypostylar sclerite of the Cercopoidea.

In the Fulgoroidea, in both the females and the males, segment X is sclerotized along its entire cross-section, it is sometimes dorsoventrally flattened and the site of attachment of the comparatively small segment XI is displaced dorsally. In the female of *Asiraca* (primitive Delphacidae) a basal apodeme of segment X is present. Segment XI is short, separated ventrally and always bears fairly large basal apodemes; in other respects it is not differentiated, though sometimes only on top it is secondarily separated along the mid-line. The posterior wall of segment XI ventrally bears a well developed free anal style without a hypostylar sclerite and with apically accreted lateral sclerotizations. On the sides above the style are situated the cercal sclerites, with a convex surface and narrow flat strips above, which run along the posterior margin of the segment to the point where they meet one another dorsally; these are possibly homologous to the epiproct or to the small upper sclerites of the Cicadelloidea.

8. **Anatomy**

8.1. Filter chamber. A striking feature of the structure of the gut in the majority of the Homoptera is the filter chamber (FC). In principal the FC is formed by the close conjunction of two remote portions of the gut, as a result of which a loop is formed.

The functional signfiicance of the FC consists of the situation that the excess of water and sugars, contained in the food of the Homoptera, are eliminated from the organism by the shortest path through the junction of the walls of the intestinal loop, while the protein and fatty components are assimilated over a longer pathway in the loop of the gut (Berlese, 1908; Licent, 1912; Kershaw, 1914;

Godochild, 1966; Gouranton, 1968). The sugars secreted by homopterans are known as honeydew. The physiological aspect of the activity of the FC has been poorly studied, and up to the present time there is no unified opinion on the majority of questions concerning its operation.

A filter chamber has been found in all (that have been studied in this respect) aleyrodids and psyllids, in the overwhelming majority of coccids, in a substantial number of aphids and in all cicadines except for the majority of the Fulgoroidea (Figures 31 and 32). The structure of the FC in different groups has a varying degree of complexity and also, in part, a homologously differing composition of the components.

The question of the origin and homology of the FC has been posed and resolved in different ways. There is a widespread opinion that the formation of the FC is non-homologous and independent in different lines of the Homoptera (Evans, 1963; Goodchild, 1966; Klimaszewski and Glowacka, 1977, and others). The diversity in the opinions and concepts concerning the polyphyletic nature of the FC is associated with the great diversity of the latter, with the difficulties in homologizing the basic parts of the intestine, and with the absence of precise concepts concerning the pathways of possible evolutionary transformations of the FC.

The initial simplest type of chamber, which Ponsen (1979) called “the parallel FC” but which it would be better to call “the linear FC”, in its most archaic form has apparently been preserved in the aleyrodids (Weber, 1934, 1935), but even here we already find an imbedding of one component (the posterior one) into a longitudinal fold of the other, wider (anterior) component. In the psyllids the linear type has been modified: the anterior component is swollen, while the posterior component bends around in loops over its surface but is not embedded in folds (Klimaszewski and Glowacka, 1977).

In the coccids two main types of FC are found: a dual FC and a rectal FC (Berlese, 1908; Pesson, 1944, 1951; Bielenin, 1963, and others; for review see Ponsen, 1979). In all of the coccids the rectum is included in the composition of the FC, but in the case of the rectal FC the posterior end of the mid-gut does not participate in the contact. The rectal component envelopes the anterior portion of the mid-gut, which is bent in a loop, in a cup-shaped fashion. The dual FC is differentiated by the fact that the rectal cup envelopes a primiarily linear FC.

Various variants of the FC are developed in aphids: a rectal FC of a simpler type than in the coccids (Ponsen, 1981); a tunnel-type rectal FC in which the anterior component passes through the posterior one, which embraces the anterior one from all sides (Ponsen, 1977, 1979), and, finally, a simple linear FC of a secondary character, formed by descending and ascending branches of the mid-gut (Ponsen, 1979); this secondary FC occurs together with the primary tunnel-type FC. In many aphids the FC is completely absent (Eriosomatidae, Phylloxeridae, some Aphididae) or only a secondary linear FC is developed (Ponsen, 1979).

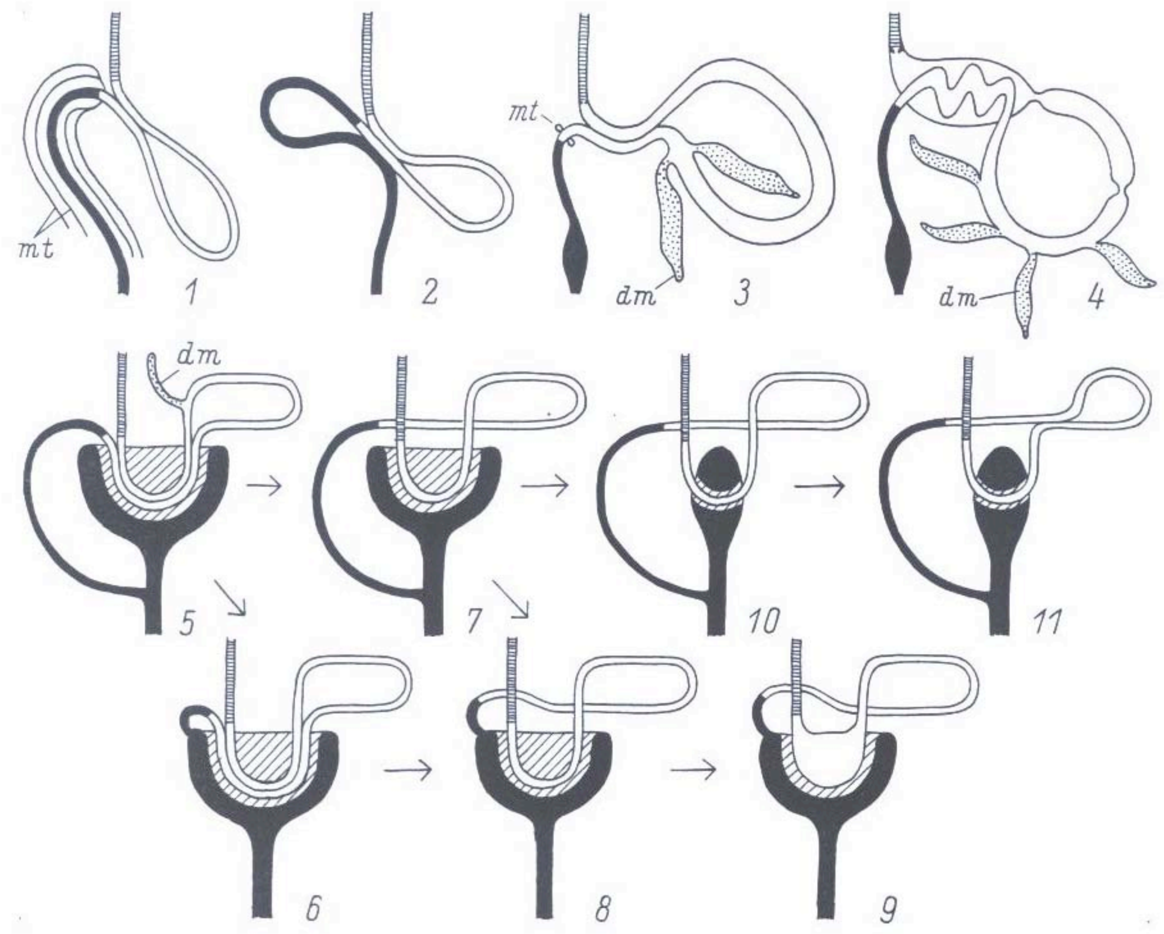


Figure 31. Different types of filter chamber in the Sternorrhyncha. Schematic diagrams.
1 – primitive plan; 2 – schematic diagram of dual filtration chamber; 3 – Aleyrodina; 4 – Psyllina; 5 – Aphidina and Coccina, initial plan; 6 – dual filter chamber with an abbreviated connection of the component parts of the hind-gut; 7 – rectal filter chamber (a freeing of the posterior component of the mid-gut from the contact has occurred); 8 – rectal filter chamber with abbreviated connection of the component parts of the hind-gut; 9 – rectal fitler chamber with swollen mid-gut component; 10 – tunnel-type rectal filter chamber, which is a derivitave of state 7; 11 – tunnel-type rectal fitler chamber, supplemenmted by a secondary

linear filter chamber. Types 5-9 characteristic of the Coccina, 10 and 11 – of the Aphidina.

dm – miod-gut diverticula, substituting for the Malpighian vessels in the Sternorrhyncha, mt – true Malpighian vessels, horizontal striation – fore-gut, solid black and oblique striation – hind-gut.

In the cicadines a primary FC is present in three out of the four superfamilies: Cicadelloidea, Cicadoidea and Cercopoidea. Characteristic of these superfamilies is a hypertrophy of the clypeus; apparently, however, the Cicadelloidea acquired this feature independently of the other two superfamilies (see point 1.1). A distinctive feature of the FC of the cicadines is the peritoneal membrane which covers the FC; a similar such membrane freely covers the whole of the mid-gut in the Fulgoroidea that have lost the primary FC. Only in the Typhlocybinae (Cicadelloidea) is this membrane secondarily absent. The FC of cicadines is characterized by the imbedding of the posterior component in folds of the widened anterior component and by the inclusion within it of Malpighian vessels (tubules – MT), which run back along the mid-gut. In its simplest form such an FC is found in the majority of the Cicadelloidea (except for the Typhlocybinae), but even in this case there are complications, affecting the contact of the mid-gut with the oesophagus. A fold of the widened anterior part of the mid-gut covers the posterior part of the mid-gut and the MT; the fold is comparatively small and weakly curved. The studies devoted to the FC of cicadelloids (Membracidae; Kershaw, 1913b, 1914;

Mukharji, 1961; Kopp and Yonke, 1972; Khan et al., 1978; Cicadellidae: Saxena, 1955; Munk, 1967; Mukharji, 1961) are for the most part incomplete, they do not give the full picture and the omissions are different in the different studies; furthermore, some studies without substantial omissions pertain to secondary cases, in which, as one may think, individual primary structures have secondarily disappeared. This determines that the total picture of the FC in cicadelloids has a somewhat hypothetical nature. This question will be considered in more detail in the analysis of the evolution of the FC in all of the homopterans. In the cicadelloids the anterior end of the hind-gut is always involved in the FC.

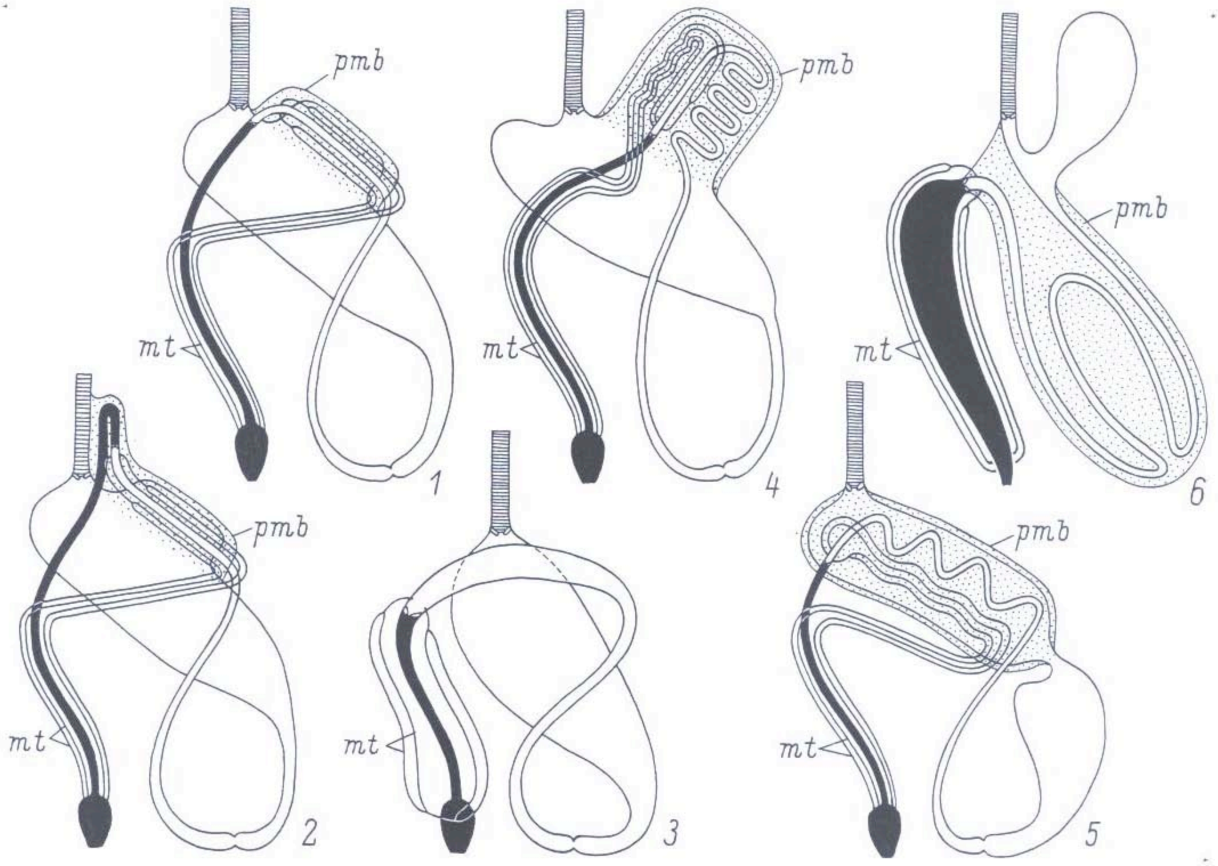


Figure 32. Filter chamber and its derivatives in the Cicadina. Schemetic diagrams.
1 – 3 – types of filter chamber in the Cicadelloidea (1 – type of Cicadellidae Deltocephalinae, 2 – type of Membracidae, 3 – type of

Cicadellidae Typhlocybinae); 4 – type of Cercopoidea; 5 – type of Cicadoidea; 6 – structure of intestine in the Fulgoroidea. P mb – peritoneral membrane (indicated by punctuation). Remaining designations as in Figure 31.

In the Cercopoidea and Cicadoidea the FC is more markedly isolated, it has not contact with the oesophagus, but the posterior component together with the MT meander considerably in folds of the anterior component, which, in contrast to the cicadelloids, is isolated from the following widened part of the mid-gut by a narrowing (constriction). In the Cercopoidea the anterior component of the FC has the appearance of a lateral diverticulum, connected by a narrow neck with the stomach (the widened part of the mid-gut behind the FC), while the entry and exist of the posterior component are set close together, apparently in a similar manner to the Cicadelloidea. In the Cicadoidea the anterior component is drawn-out, it does not look like a lateral diverticulum, and the entry and exit of the posterior component are set apart at a distance, lying at opposite ends of the FC.

A constriction-sphincter is present in the frog-hoppers (Gadd, 1902; Gouranton, 1968, and others) and tree-hoppers (Kersaw, 1913b), and in the leaf-hoppers (Gouranton, 1968); in the cicadas it separates the wide descending section from the narrow ascending section (Kershaw, 1914). The anterior (so-called descending) section of the mid-gut in all of the Clypeata is widened in its entirety or only in its anterior part; behind it lies a pronounced constriction, the intermedial sphincter, after which commences the ascending section which approaches the FC. The descending segment in the widened part, called the stomach, ventrally produces a forward protrusion which is connected with the oesophagus by a muscular strand.

The FC of the Typhlocybinae (Willis, 1949; Saxena, 1955; Berlin and Hibbs, 1963; Helms, 1968) has a (secondarily) simple structure, a linear contact of two components, without a covering peritoneal membrane, approximately as in the psyllids and even simpler. In the typhlocybids there is also no muscular strand connecting the stomach with the oesophagus. However, the relationship of the MT with the mid-gut and their contact in the region of the FC are retained.

8.2. Classification of filter chambers. Ponsen (1979) recently published a review and classification of filter chambers, distinguishing 5 types, including one hypothetical type. Ponsen’s classification has an important deficiency in that it was consistently constructed on the basis of a formal feature, without consideration of the homology of the parts that form the FC and without consideration to the history of the formation; in particular, he makes no distinction at all between primary and secondary FCs, even if they existed in one species, and he assigns no great significance in the classification to the difference between the dual FC and the simple (rectal) FC of coccids. Ponsen distinguishes: 1) the parallel filtration system (FS), 2) the concentric type, 3) the coccid type, and 4) the cicadid type. Ponsen’s approach to the classification of filter chambers shows that he does not accept the monophyletic hypothesis and, as he disregards the homologies, he obliquely acknowledges a polyphyletic nature of the appearance of the FC in different groups of homopterans. Ponsen’s position is apparently in part determined by errors in the homology of the parts of the intestine, that were accepted by previous authors, from which arises the impression of a motley and disordered status in the means of formation of the FC.

In the parallel filtration system Ponsen includes cases of a simple, more or less flat contact of two portions of the intestine, not covered by supplementary membranes. Here he includes the FC of aleyrodids, psyllids, some aphids, some fulgoroids and the Typhlocybinae. Among these filter chambers there are such in which portions do indeed run parallel to one another (aleyrodids, aphids, fulgoroids), but there are also such in which the posterior component runs athwart the swollen anterior component (Typhlocybinae) or forms loops on an also expanded anterior portion (psyllids). In the case of the aleyrodids, psyllids and Typhlocybinae the beginning and end of the mid-gut come into contact, while in the case of the aphids and fulgoroids the middle portions of the mid-gut form the contact; furthermore, in the Typhlocybinae, apparently, the MT also always participate in the contact (Helms, 1968). The contact of the beginning and end of the mid-gut may be considered as the original state of the primitive FC, while the contacts of the middle portions are secondary and undoubtedly arose independently in the aphids and the fulgoroids. Thus, Ponsen's first type is composite and heterogeneous.

To the concentric type, encountered only in aphids, Ponsen assigned the cases in which the anterior component (beginning of mid-gut) passes along a tunnel right through the posterior (rectal) component. This type is apparently homogenous and monophyletic.

In the coccid type Ponsen included two significantly different variants of the FC; a two-component variant, (anterior part of mid-gut plus rectum) and a three-component variant (anterior part of mid-gut, posterior portion of mid-gut and rectum). A common feature in these is that the mid-gut components are enveloped by the rectal component. These two types should in no way be confused.

To the cicadid type Ponsen all of the FCs of the cicadines, with the exception of the fulgoroids and Typhlocybinae, which were assigned, as has been stated above, to the parallel type. The cicadid FCs are distinguished by a peritoneal membrane, the participation of the MT and the imbedding of the posterior component in folds of the expanded anterior component. Ponsen's conception of this type is too broad, since on the basis of the structural details the cicadoid, cercopoid and cicadelloid types differ quite significantly, in particular in that the basic cicadelloid plan is characterized by a contact of the posterior part of the mid-gut and the beginning of the hind-gut with the oesophagus, with a retention of the contact with the anterior portion of the mid-gut.

Taking the genesis into consideration, one should distinguish the primary FCs, which have a continuity with the original type, and the secondary FCs, which arose independently in several cases beside the primary forms and, in connection with this, on a different homologous basis. Practically all of the secondary FCs retain the primitive structure and are similar to the first, linear type of the primary FCs.

1) Linear FCs. The tubular portions of the intestine, forming the FC, run parallel to one another, 1.1) The primary FCs combine the beginning and end of the mid-gut. 1.2) The secondary FCs may combine approximately the same portions as in the Fulgoroidea, or others, as in the Aphidina. Ponsen calls this type the parallel type, including also the following type, which cannot, in essence, be called parallel.

2) Flatly-meandering FCs. Loops of the posterior portion of the mid-gut pass over the swollen anterior portion. Characteristic of the psyllids and typhlocybids: in the latter case this type has a secondary origin as a result of reduction.

3) Dual cup-shaped FCs. The linear FC is enveloped by a cup-shaped outgrowth of the hind-gut, so that 3, rather than 2, components come into contact. Represented in several coccids.

4) Rectal cup-shaped FCs. These represent the result of a development of the preceding type, when the middle component (posterior portion of the mid-gut) withdraws from the contact, and the FC again becomes ordinary. Characteristic of many coccids; encountered in aphids.

5) Rectal tunnel-type FCs. Derived from the preceding type of the closing-over of the rectal component above the mid-gut component, so that the mid-gut passes through a tunnel in hing-gut. Characteristic of some aphids. The process of the closure of the lips of the rectal component and of the resorption of the contacting walls between them (but not around the mid-gut) during the ontogenetic process was traced by A.K. Mordvilko (1895) in *Trama troglodytes*.

Nest follow the covered Malphigio-intestinal FCs of the cicadines (the preceding types were uncovered intestinal types).

6) Oesophageal-intestinal FCs, in which the distal loop lies adjacent to the oesophagus and there is no constriction of the

intestine behind the FC; characteristic of the Cicadelloidea, except for the Typhlocybidae, and some others.

7) Diverticular FCs, in which the anterior component is separated off by a constriction from the base of the tract of the intestine (Cercopoidea).

8) Straight-flow-through FCs, in which the main tract passes through the FC (cicadas).

The first two types correspond to Ponsen’s parallel FC type, the 3rd and 4th correspond to Ponsen’s coccid type, the 5th – to Ponsen’s concentric type, and the 6th-8th – to the cicadid type.

In the fulgoroids there is no primary FC and the whole mid-gut, which is laid out in loops, is freely enclosed in a sac of the peritoneal membrane (Kershaw, 1910, 1913a; Lieu, 1934; Miller, 1940; Goodchild, 1963, 1966; Mishra, 1980; Fick, 1981); only the anterior dorsal diverticulum, a homologue of the anterior component of the FC, is directly covered by this membrane, which has become accreted here. In some fulgoroids a secondary linear FC appears within a peritoneal sac (Mishra, 1980); it is possible, however, that this kind of FC is widely distributed among the fulgoroids but has not been found, since it is easily separated during preparation.

8.3. Origin and evolution of the filter chamber. The adaptive meaming of the filter chamber, as has been stated, is associated with the feeding on the liquid contents of the vascular system of higher plants, when there is an excess of water and sugars in the food liquid, with a deficiency of proteins and lipids. Cases of the simplification and reduction of the FC are associated with a transition to feeding on the cell sap, which has a more or less balanced food composition (aphids, Typhlocibinae).

The following common considerations supoort a monophyletic formation of the FC: an FC is present in all the main branches of the Homoptera; at its basis there is always a contact of the beginning and end of the mid-gut, and the direction of flow of the food in the FC components is always counter-current. The cases of the absence of a filter chamber in individual representatives or fairly large groups (many Aphidina, Fulgoroidea) are obviously secondary. The considerations relating to the non-homologous character of the intestinal portions that are combined into the FC are based, in part, or an incorrect determination of their homology, while the differences are partially removed by the historically (phylogenetically) successive following transformations originating from the FC.

The boundary of the fore- and mid-gut is marked by the cardiac valve (not always developed in aphids), while the boundary of the mid- and hind-gut is marked by the phloric valve, immediately in front of which enter the Malpighian tubules; in aphids, however, there are no MT and the pyloric valve is often absent (see: Ponsen, 1979), which makes it difficult to determine the boundary of the mid- and hind-gut. The variable character of the participation of the hind-gut in the FC, even in closely related representatives among the aphids, psyllids and others, compels one to think of possible errors in the determination of the boundary and of a low evolutionary stability of this feature. The finding of true MT in one of the representatives of the aleyrodids (Chandhury and Gupta, 1970) allows one to categorically reject the homology of the mid-gut diverticula with the MT in the Aleyrodina and in the Psyllina, which is widely accepted in the literature (Weber, 1935). In this way is eliminated the question of a strange disposition of these conjectured MT diverticula (with respect to the hind-gut – they are dispersed along the mid-gut and not localized at its posterior end at the boundary of the hind-gut). In their structure also the diverticula do not resemble typical MT: they are more sac-like than tubular, with a wide lumen and a narrow orifice. However, the MT of coccids also have an atypical disposition, though their structure nevertheless does not deviate from the typical; these are narrow tubules with a narrow lumen and with few cells in the cross-section. The MT of coccids are arranged within the loops of the mid-gut (from 4 to 2 in number), like the diverticula of the aleyrodids and psyllids, but unlike the typical and indubitable MT of the cicadines and the rudimentary MT of the aleyrodids, which lie behind the posterior (mid-gut) component of the FC at the boundary with the hind-gut. If the monophyletic nature of the primary FC is acknowledged, then two explanatory hypotheses are possible.

1) The Malpighian tubules of coccids are not homologous with the true MT but are homologous with the mid-gut diverticula of aleyrodids and psyllids, which have become similar to the MT in association with a substitution of functions. Incidentally the MT of coccids are also arranged on the intestine in a chain-like, rather than a ring-like, fashion, which is not characteristic of the true MT. 2) The MT turned out to be in the posterior zone of contact of the FC and were displaced either forwards, as in the coccids and aphids, or backwards, as in the cicadines, psyllids and aleyrodids. Subsequently the MT in psyllids and aphids were reduced, as also in most of the aleyrodids.

The alternative to these hypotheses is the acceptance of a polyphyletic formation of the FC on at least two occasions: separately in the coccids and aphids, and separately in the aleyrodids, psyllids and cicadines. With such a point of view, however, the MT cannot be homologized with the diverticula of the aleyrodids and psyllids.

Taking into consideration the stability of the position of the MT in the insect class as a whole, the first assumption, which rejects the homology of the true MT with the similar homodynamic formations in coccinds, appears to be the most probable one.

Proceeding from the last assumption, the evolution of the FC may be depicted as a unified process.

1) The formation of a primitive linear FC in parallel with the formation of the rhynchotal beak in the primitive Archescytinoidea, which were becoming adapted to feeding on the contents of the vascular system of Late Paleozoic (? gymnospermous) plants.

2) The modification of the linear FC in the Aleyrodoidea, with the posterior narrower component became embedded in a groove of the wider anterior component.

3) The modification of the linear FC in the Psylloidea, with the posterior, more slender component meanders (moderately) over the surface of the sacculately expanded anterior component.

4) The inclusion of a rectal contact into the linear FC of the primitive type in the ancestors of the coccids and aphids.

5) The slipping-out of the middle component (posterior end of mid-gut) from the dual FC, so that the latter is transformed into a rectal FC, as in some coccids and aphids.

6) The transformation of the rectal FC in aphids into the tunnel-type by way of the fusion of the lips of the rectal cup around the anterior component in some aphids.

7) The primary FC of the cicadines (Prosboloidea?) was formed by way of the imbedding of the posterior component into a fold of the expanded anterior component, and in this case the MT also became included within the fold. The FC as a whole acquired its peritoneal membrane, apparently of embryonic origin, which was previously resorbed on hatching. The data of Kershaw (1913a) and Müller (1940) permit us to propose a derivation of this membrane from the vitelline membrane (splanchnopleure).

8) The posterior component behind the fold doubled up and came into contact with the posterior end of the osophagous under the peritoneal membrane, as in the majority of the contemporary Cicadelloidea (except for the Typhlocybinae). At this stage, evidently, the anterior end of the hind-gut became included, in one way or another, in the composition of the FC.

9) The posterior component menaders over the anterior component, which has become differentiated into a side sac which is connected by a narrow neck with the mid-gut, that is expanded into a stomach, as in the Cercopoidea. The anterior component of the FC acquires the function of a pump.

10) The anterior component becomes elongated, losing its isolation from the direct passage
from the osophagous into the stomach; the entry and exit of the posterior component become set apart, as in the Cicadidae. In the Tettigarctidae, apparently, the moving-apart has not yet occurred.

Kershaw(1914) thought that the sacculate FC of cercopids was secondary, while the elongated (straight-flow-through) type of the cicadids was primary, but in the primitive cicadoids of the Tettigarctidae, as may be judged from the figures, the FC is still similar to the cercopoid type (Evans, 1941).

12)* The posterior component loses its connection with the anterior component; the FC disintegrates. The anterior component, acquiring the name of “food reservoir” (FR), retains the form of step 9. The peritoneal membrane is differentiated over the whole mid-gut. The FR retains the function of a pump (Mukharji, 1961). This is the state in the Fulgoroidea. Pesson (1951) considered the FR of fulgoroides as a homologue of the ventral spur of the mid-gut sac of other cicadines, but Myers (1928, p. 442) was undoubtedly right in homologizing the FR with the anterior dorsal outgrowth of the stomach, i.e. the rudiment of the FC.

8.4. Salivary glands. Composed of the principal and the accessory glands. The principal gland, in its turn, is divided into anterior and posterior parts, which are sometimes completely separated and connected only by a duct. Such a situation is found in the cicadas (Bugnion, 1980) and similarly, thought not as clearly, in the larvae of the Cercopoidea (Kershaw, 1914). Just as clearly, but by not so extended a duct, are separated these parts also in the Fulgoroidea (Kershaw, 1910; Lieu, 1934). In the imagines of the Cercopoidea the anterior part is diminished and broadly connected with the posterior part, which usually bears digitiform, sometimes fairly long outgrowths (Kershaw, 1914; Nuorteva, 1956). In the Cicadelloidea the principal gland is botryoidal, without a clear-cut differentiation into sections (Nuorteva, 1956). The accessory gland has a long efferent duct, its main part in the Cercopoidea and Cicadoidea is also tubular, but below the transition into the duct it is swollen in a spherical or morula-like fashion. In the Cicadelloidea the gland is swollen in a sausage-shaped manner, sometimes with a tapered tip (Nuorteva, 1956). In the Fulgororidae it is kidney-shaped (Bugnion, 1908: Keshaw, 1910; Lieu, 1934).

8.5. Mapighian tubules (MT). A great diversity exists in the methods by which the individual tubules are connected with one another: from 4 that discharge independently, through intermediate variants to a single common duct (see Table 1), and moreoever the order of the junctions in the latter case may be symmetrical or

---

* Sic. There is no step 11) in the Russian text. (Tr.).

alternating (“braid-like”). The apices of the MT may be free, but lying close to the rectum in the Fulgoroidea, independent, but attached to the wall of the rectum in the Cercopidea, Cicadoidea and some Cicadelloids, or connected in pairs in two loops or all 4 in a cruciform fashion in the majority of the Cicadelloidea; furthermore, in the Typhlocybinae (Cicadellidae) the cruciform junction may be secondarily disconnected from the rectum. The described features are combined quite freely with one another in the different representatives, drawing a picture of homologous series. Thus, among the Membracidae are found examples of 4 separate apices (*Tricentrus albomaculatus* Dist.), 2 loops (*Oxyrhachis taranda* F.) and a common cross (*Gargara genistae* F.), and the same is found in the Cicadellidae, where free apices are rare (*Cicadella viridis* L. and a few others), two loops are infrequent (*Euscelis plebejus* Fall., *Allygus modestus* Scott, *Iassus lanio* L. and others), while a cruciform junction is the most common. In the Ulpoidae (*Ulopa reticulata* F.) a cross has been recorded, and a cross is apparently also present in the Ledridae (Licent, 1912).

Table 1

Variants of the junction of the Malpighian tubules.

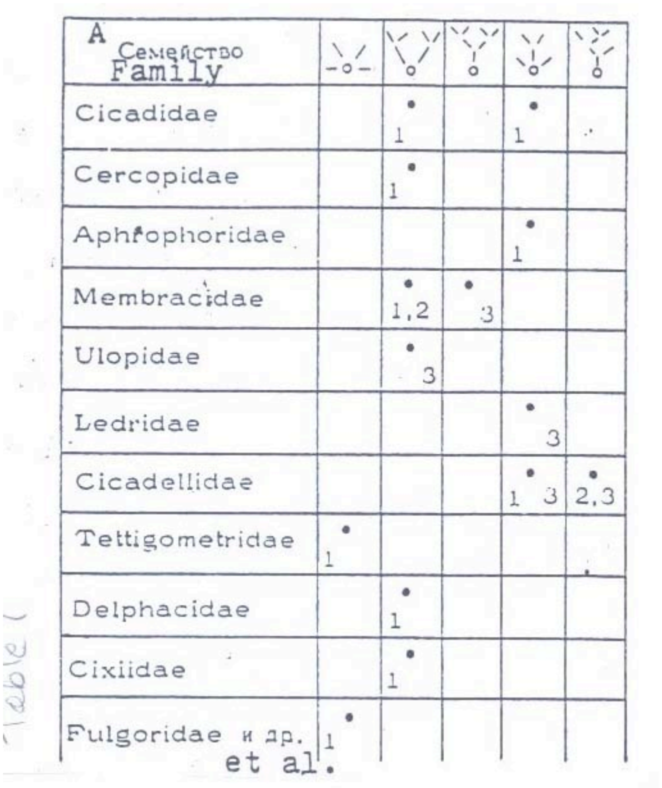


Table (

A Семейство Family					
Cicadidae		• 1		• 1	
Cercopidae		• 1			
Aphrophoridae				• 1	
Membracidae		• 1,2	• 3		
Ulopidae		• 3			
Ledridae				• 3	
Cicadellidae				• 1 3	• 2,3
Tettigometridae	• 1				
Delphacidae		• 1			
Cixiidae		• 1			
Fulgoridae и др. et al.	• 1				

A – Family
* Note. • - presence of feature, 1 – apices of Malpighian tubules independent, 2 – apices joined in pairs into two loops, 3 – all apices joined together in a cruciform fashion.

Common to all of the superfamilies is found to be a symmetrical variant with two efferent, apparently lateral ducts; furthermore a fourth variant with three ducts, if one follows Mukharji (1961) and Helms (1968) is considering that the two dorsal tubules have fused, is a primary derivative of the four-duct type, not derived by way of the usual transformations directly from the second variant. It is noteworthy that the variant with 4 ducts is characteristic only of the primitive but somewhat aberrant family of the Tettigometridae, and of the higher Fulgoroidea. In spite of its superficially primitive nature, it is apparently secondary. A rectilinear evaluation of the original nature and derivative state in such cases does not have completely convincing force. It is evident, from the states that are repeated in closely related representatives of various comparately unrelated groups, that some sort of order exists in the transformations of the MT and that the transformations proceed by jumps along previously used evolutionary parthways, having a closed circular character. For example, only variants 2 and 4 exist in the Cicadoidea and in the Cercopoidea, only variants 4 and 5 in the Idiocerinae and Deltocephalinae, and variants 1 and 2 in the Fulgoroidea. The absence of variant 3+1 is characteristic. From the table it can be seen that the transformation of the MT apices in the families Membracidae and Cicadellidae also proceed in parallel in a circle.

8.6. Integration of the main ganglia of the CNS. Differences are found in the region of the thoracic ganglia (Kershaw, 1910; Myers, 1928; Pflugfelder, 1937). In the Cercopoidea all of the thoracic ganglia are incompletely united; in the Cicadoidea and Cicadelloidea only the pro- and ptero-throracic, while in the Fulgorooidea all the thoracic ganglia are completely fused. The abdominal ganglia in the ciadines are always completely fused with the metathoracic ganglion (Pflugfelder, 1937, and others). In the Peloridiidae the degree of fusion is similar to that in the cercopoids (Pendergrast, 1962), while in the Sternorrhyncha it resembles that in the fulgoroids (Pflugfelder, 1937, 1941).

8.7. Gonads of male. The diversity in the structural details of the gonads in individual representatives and the scantiness of studied examples make it difficult to distinguish the group features. The number of the seminal tubules is amenable to a more reliable count (see review: Emel'yanov and Kuznetsova, 1983). Apparently, stages of polymerization and oligomerization alternated in the evolution of the group. It is possible that the starting point was an oligomerous state of 3+3, since in the related groups of the Paraneoptera the numbers are low (1, 2, 3) for the most part, but in the Heteroptera, apparently, the initial number was 7+7. In the Cicadelloidea the number 6 predominates, in the Cercopidea – more than 10 and up to 35, in the Fulgoroidea – from 3 and 6, with a polymerization of up to 20 noted in the higher groups (Issidae). There is a lack of data on the Cicadoidea, in which, judging by Myers' (1928) data, there is a no division in the testes into segminal tubules in the proper sense.

8.8. Gonads of female. The differentiation of groups on the basis of the structure of the female gonads (see review: Emel'yanov and Kuznetsova, 1983) is as difficult as in the males. It may be noted that the females overtake the males in increasing the number of tubules; only in the Cercopoidea has a reversed relationship been noted. The greater number of follicles in females, as compared to males, is mostly weakly expressed in the Cicadelloidea.

In the Cicadoidea the number of tubules is found to range from 70 to 80 (Myers, 1928).

8.9. Number of genital openings in the female. In cicadines the copulatory and egg-laying openings are often separate; it is possible, however, that no single system persists in any one group, since this is the case in those groups that have been better studied. In the Cicadelloidea, judging by the only observation (*Euscelis*), one opening is developed (Kunze, 1959). In the Cicadoidea and Fulgoroidea both cases are known (Boulard, 1965). Among the Cicadoidea there is one opening in *Tettigarcta* and *Tettigades*, while among the Fulgoroidea there is one opening in the majority of the Delphacidae (Asche and Remane, 1982), though with the exception of the Sternocraninae (Bouard, 1965; Asche and Remane, 1982), in which 2 openings are found. Apparently there is always one opening in the Tettigometridae but, in connection with the reduction of the ovipositor, it is unclear whether this is a secondary or primary condition. In the Fulgoridea (Boulard, 1965), as well as in the Dictyopharidae and, apparently, in all the other Fulgoroidea with a raking-kneading ovipositor there are two openings. Only a single observation is available for all of the Cercopoidea: 2 openings were found (Boulard, 1965). With the exception of the Cicadoidea and the Delphacidae, this question has scarcely been studied at all. The original number of openings remains unclear at the present time.

9. Egg

Cobbben (1965) considered several interesting and phylogenetically important characteristics of the eggs of the Cicadina but in most cases the individual features were not followed up in all of the superfamilies. The eggs may be with or without a micropylar protuberance, with or without an internal porous layer of the shell, with or without aeropyles, with one or with several micropyles; hatching may occur through a longitudinal slit that opens out or with the aid of an operculum, and, finally, the embryo may undergo a 180°rotation along the egg-body axis or may not rotate at all during embryonic development. Furthermore, during laying, the eggs in the Cicadelloidea and the Delphacidae (Fulgoroidea) are also rotated in 180° along the longitudinal axis, which produces one result, in combination with the embryonic rotation, in the Cicadelloidea, and the opposite result in the Delphacidae, without the embryonic rotation. According to Cobben there is no egg rotation in the Cercopoidea; he says nothing about the Cicadoidea, and considers egg rotation as a secondary feature.

A micropylar protuberance is present in many Fulgoroidea, including the Tettigometridae, and the same applies to the aeropyles and the internal porous layer of the shell. All three of these features are absent in the Delphacidae and Cixiidae, which embed their eggs in the substrate; the Delphacidae – in plant tissues, the Cixiidae – in the soil. The eggs of the Cicadelloidea, Cercopoidea and

Cicadoidea, which for the most part are embedded in plant tissues, also have no protuberance, no aeropyles and no porous layer. However an aeropyle is present in the bugs, as is also a porous layer of the shell; on the other hand, an aeropyle and a porous layer are found, as the only known example among the Cicadomorpha, in *Wagneripteryx germari* on the anterior side of the egg. Hatching through a longitudinal slit is primary in all of the superfamilies, and only in the Fulgoroidea has it been superseded by opercular hatching in a few individual branches. Embryonic rotation disappears in the Delphacidae, although it still occurs in *Asiraca*. The number of micropyles varies: in the Cercopoidea and Fulgoroidea there is only 1; in the Cicadoidea – 2-3, while in the Cicadelloidea it varies from 1 to 8 in different representatives. Cobben considers 1 micropyle as the original feature, although there may be more than 1 microphyle even in the primitive groups (*Ledra*), and there are 7-10 micropyles in the Peloridiidae; apparently the number of micropyles is not strictly fixed, at least among the Cicadelloidea. The correlated features of aeropyle-porous layer, apparently, are susceptible to instauration.

10. Mycetomes

10. 1. Symbionts of a common group of types, based both on their development and inheritance, as well as in their relationship with the organism of the host, are characteristic of all the cicadines, and more widely of all of the Homoptera; they have been

found in the Peloridiidae and some bugs, such as the Cimicidae and Lygaeidae (H.J. Muller, 1940, 1962, 1967; Buchner, 1965), as well as in the biting lice, the sucking lice and, apparently, the thrips (Buchner, 1953, 1965; Bournier and Louis, 1971). This compels one to conjecture a phylogenetically more ancient formation of the mycetomic symbiosis in the group Paraneoptera.

As a rule, the symbionts in one organism (in one species) exist at the same time in the form of several developmentally independent varieties, usually 2-3, more rarely 1 or 4, 5 and even 6. The prevailing opinions in the literature proclaim an independent penetration into the host organism and an independent formation of the symbiosis in the phylogeny of all of these forms (H.J. Müller (1940, 1962, 1967; Buchner, 1965). The mycetomic symbiosis has been examined in greatest detail in the cicadines by H.J. Müller (1940) in the Fulgoroidea, but less detailed and extensive observations on other groups show, in the main, a similarity in the major features with the condition found in the Fulgoroidea.

As was shown by H.J. Müller (1962, 1967), symbionts are presnt in those groups of phytophagous insects which feed specifically on food that is poor in the vitamins of the B group, originating from the phoem vessels. Among the Homoptera some groups secondarily lack symbionts, such as, for example, the Typhlocybinae, which feed on the contents of cells, and in these insects also the filter chamber has become degraded; similar cases are also known among the coccids and aphids (Buchner, 1953).

It was throught previously that some symbionts belong to the bacteria, while others belong to the yeast fungi, from which also the symbiotic organs acquired the name of mycetomes, but it is now considered that all of the symbionts have a bacterial nature (Gromov, 1978).

The mycetomes, and in other cases the individual mycetocytes or free symbionts, are situated in the cavity of the abdomen. The mycetomes may be paired or unpaired; they are supplied by special tracheae, the terminal branches of which densely entwine them. In the typical cases the symbionts are located within special cells, the mycetocytes, or very rarely among the cells of the fat body. For the most part the mycetocytes have been transformed into a syncytium. Besides the principal mycetome, the individual varieties of symbionts usually also have in the females a filial mycetome, which serves for infecting the developing eggs of the host. On the basis of the pathways and methods of inheritance, the symbionts are divided into 3 types: inherited through a germarium mycetome, though a rectal mycetome, or directly from the visceral (principal) mycetome without intermediate stages; the last two types enter the egg through the posterior pole, while the first enters through the anterior pole. Within the egg the symbionts form a common cluster, the symbiotic ball. All of these relationships have been elucidated in only a few cases; in the majority of the “Cicadomorpha” the pathways of the infectious forms have not been explained, except for type a, common to all of the Cicadina.

10. 2. Transformation of symbionts in the ontogeny of homopterans. According to Müller’s nomenclature the symbionts of different morphological types acquire a designation based on letters of the Latin alphabet. Following H.J. Müller (1940), consideration is given below to the development of *Dictyophara europaea* and its symbionts, whish are characteristic of these and other cicadines and which are, for the most part, widely distributed among the Fulgoroidea.

Five days from the commencement of the development of the egg, the blastoderm is formed. The symbiotic ball comes into contact with the blastoderm, and the latter overgrows its posterior half; simultaneously, a vitellophage, reaching the anterior pole of the ball, transforms the blastema of its anterior half also into blastoderm (7-8th day). At the same time the blastoderm differentiates into the germ band and the serosa. The posterior end of the band abuts onto the symbiotic ball. During invagination, which proceeds from behind, the symbiotic ball is moved along its top to the anterior pole of the egg (8-12th day), and within it occurs a sorting of the symbionts. The a-symbionts penetrate into the epithelium of the ball, which has a blastodermal origin; the x-symbionts penetrate into the vitellophage layer, while the m-symbionts remain inside. Anteriorly the mycetome becomes separated from the embryo, which begins to bend over dorsally and posteriorly. At this time are laid down the segmentation, limbs, and fore- and hind-guts. After this proceeds the reversion of the embryo. With the reversion, the provisional mycetome (=symbiotic ball) comes into contact through the a-mycetome with the embryo dorsally, near the gonads and the apex of the proctodeum. The mycetome becomes covered separately by a membrane from the embryo. After the reversion, the dorsal wall of the embryo, overgrowing the yolk, closes, and the m-symbionts disperse in the body cavity, penetrating into the body cells that lie dorsally to the mid-gut.

At the time of the reversion the proctodeum has the form of a tube, at the apex of which proliferate the 4 Malpighian tubules and a group of cells of the mid-gut rudiment. A similar group of cells is present at the apex of the stomodeum. With the closure of the dorsal wall of the embryo, the embryonic membrane that underlies the yolk with the rudiments of the mid-gut; the proctodeal rudiment moves the yolk forward and itself elongates in an intercalary fashion and, bending in loops, connects up at its apex with the stomodeal rudiment. The formation of the loops of the mid-gut bears the character of a recapitulation of the filter chamber, which has been lost in the superfamily Fulgoroidea.

Following isolation, the x-mycetome becomes divided sagitally into a pair of mycetomes, which in the females retain for a long time their commissure, that is adpressed below to the mid-gut. Though the commissure some of the symbionts penetrate into the lumen of the mid-gut, forming there a temporary mycetome, from which, during hatching, the symbionts penetrate into the rectal valve and form there a permanent mycetome. The a-mycetome remains entire during the course of late embryogenesis.

Growth of the mycetomes occurs mainly in the larval stage, and also some changes in form. The x-mycetome becomes extended; the round a-mycetome becomes transformed into a sausage-shaped structure and then divides into two; the my-symbionts, multiplying, form the indistinct m-organ which underlies the loops of the mid-gut from behind and from below. The mycetomes become overgrown by tracheae. The a-organs of the future females come into contact with the oviducts, and in these places develop infectious tubercles, which produce in the imagines the symbionts that migrate into the egg.

10.3. General analysis of symbiotic relationships.

The presence of only a few types of pathways of the inherited transmission of the symbionts and the great similarity in the development of the individual mycetomes, that are characteristic of the different types of symbionts, cast some doubt on the hypothesis of a multiply recurring establishment of the symbionts into the organism of the various cicadines and homopterans as a whole, and such a hypothesis is also poorly correlated with the monophyletic concepts. The profound differentiations of the host organism, directed towards servicing the symbiont, cannot be one-sided and compel one to assume, with a fairly high degree of reliability, such complex reciprocal coordinated reactions of the symbionts, which also must pass along a major evolutionary pathway by this time within the organism of the host. It is difficult to imagine that such a pathway could be independently realized repeatedly in a similar form.

Evidence against a multiply recurring establishment of independent forms into one host is also provided by the picture of the mutual incompatibility of certain types of symbionts, which cannot be linked with the successive phylogenetic development. Thus, with rare exceptions, symbionts x and H are not encountered together, nor are symbionts a and f, and moreover the presence in any species of symbiont x of the first pair always coincides with the presence of symbiont a of the second pair.

The above discrepancies in the hypothesis of multiply recurring establishment compel one to look for an explanation of this phenomenon by means of another hypothesis, namely the hypothesis of a monophyletic origin of the symbionts of the cicadines and other homopterans.

On the basis of the types of ontogenetic cycle (cycle in the ontogeny of the host) the symbionts may be divided into 3 types: the varieties that are inherited through the follicular mycetome and the anterior pole of the egg (m); those inherited directly through the cuneiform-cellular follicle, when the infectious forms are formed from the contact with the gonads (a), and those inherited through the cuneiform-cellular follicle, when the infectious forms are induced from the contact with the developing gut (x). In this case all 3 types form mycetomes: the first type forms a follicular mycetome, the other two form cavity-type mycetomes. There is much in common in the structure of the mycetomes.

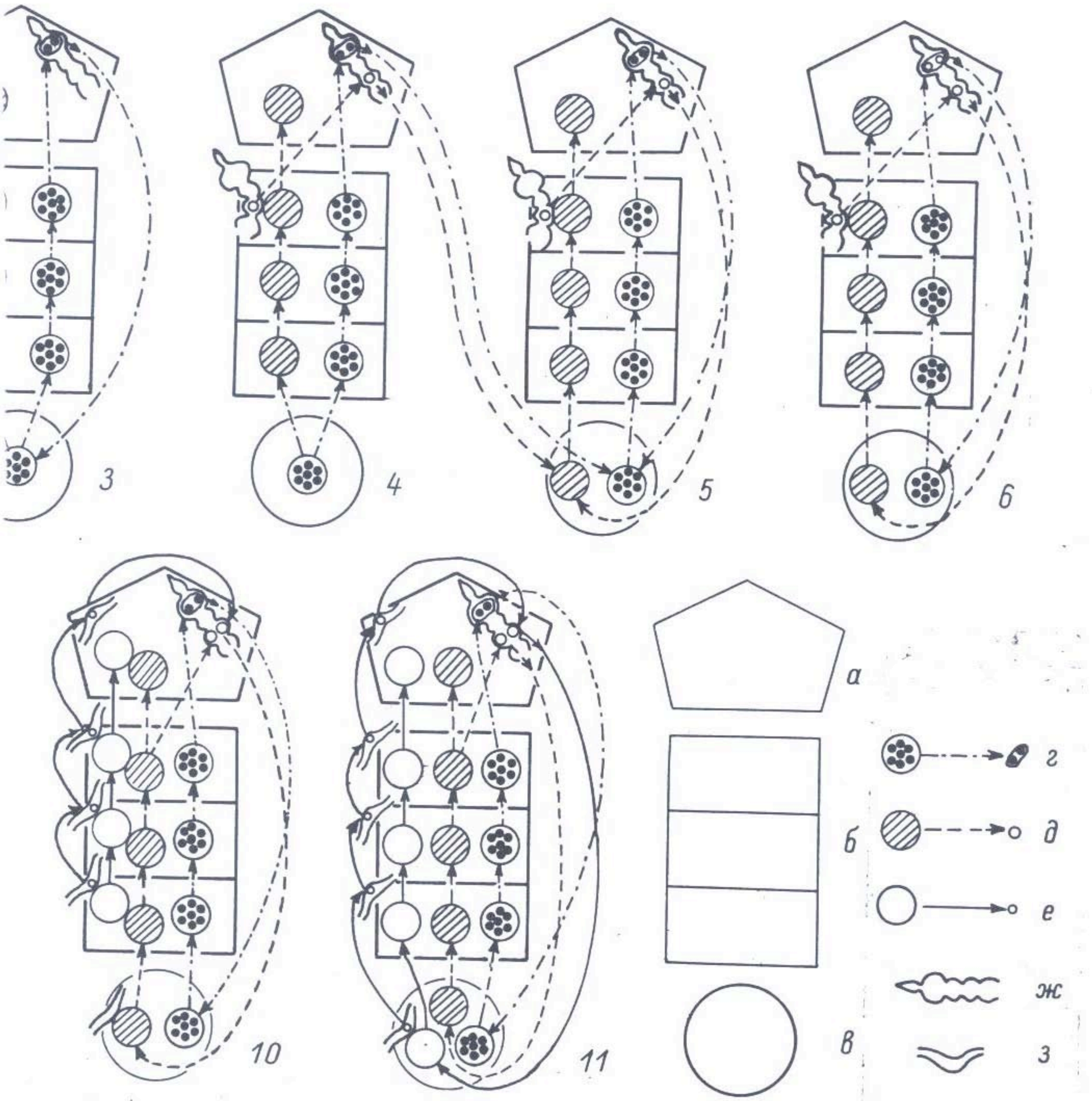
If one proceeds from Müller's concept of a multiply recurring establishment and tactily supposes that the evolution of the symbiosis moves along in a more or less uninterrupted fashion, i.e. in proportion to time, then one should accept as the oldest established forms those symbionts that have the closest and most complexly diverse relationships with the host organism. And so it is that Müller considers: as the youngest – the m-symbionts (Begleitsymbiont), as older – the a-symbionts (Nebensymbiont), and as the oldest – the x-symbionts (Hauptsymbiont). Subsequently Müller (1962) revised these opionions somewhat, and began to consider that the a-symbionts, as the most widely distributed, were the oldest forms. Muller's ideas on the simplicity of the m-type are based on the fact that the symbionts of this type retain their bacterial-like appearance with no change throughout the entire ontogenetic cycle of the host, without passing through any complex transformations and without forming a true mycetome in the body cavity of the host. However, Müller pays no attention to the follicular mycetome and to the method of infection through the nutritive protoplasmic cords, which can scarcely be called simple.

Naturally, the initial stage of the arising or arisen symbiosis proceeded under conditions when the host organism was still minimally adapted to the symbiont and when the symbiont was minimally changed by the host. Of the contemporary varieties of symbionts, the closest to this type are the m-symbionts, which have a bacterial-like (i.e. little modified) appearance and do not undergo substantial transformations of their form during the ontogeny of their host. Obligate symbiosis arises or is significantly consolidated with the elaboration of methods of reliable and direct inheritance, and for this reason it may be assumed that a relationship with the gonads in the cycle may be a primitive feature. Symbionts m and a correspond to this condition. At the same time symbionts a and x have similar mycetomes and a uniform type of inheritance through the follicular epithelium and the lower (posterior) pole of the egg. This allows one to assume that they are directly related and that both have a more secondary cycle, with a change in form at different stages. On the basis of the above, it may be assumed that the symbionts of the m-type demonstrate the oldest type-variant of ontogeny, and that the method of the inheritance of the symbionts through the nutritive cords is older and original. The capacity for forming a complete mycetome, manifested by the m-symbionts in the ovariole, allows one to think that this capacity did not arise secondarily in the visceral symbionts, since it is most probable that the mycetome became directly adapted precisely in its functional location, and that the mycetome under the germarium is more likely a supplementary utilization in another location of an already developed capacity. In the coccids the infection through the anterior pole proceeds without a germarium type mycetome. It is possible that the m-symbionts lost their leading role among the symbionts; their function ceased to be the most important for the host organism when the ax-symbionts were formed, whicih to some degree replaced the function of the first m-symbionts, and then the visceral part of the cycle of the m-symbionts was reduced, confined to the early stages of colonization of the fat cells. A new variety of symbionts could have been developed initially as a blind alley of development in the ontogeny of the host, having important significance to the host and being renewed every time form the principal inherited symbiont, or, which is the same or almost the same, in association with a specialization of the symbiont in late ontogeny, when an infectious stage should have closed the cycle of inheritance, becoming separated off in the early stages of the ontogeny. In other words, the blind-alley specialization of the form development arose as an anaboly and was subsequently shifted to the beginning of the ontogeny as a retardation. In such case the present m-symbiont, figurately speaking, escaped from the visceral mycetome, leaving its ax-modifications. Obviously, a main stage in the evolution, which entailed a separation of the varieties, was the moment when the new ax-symbiont acquired the capacity to be inherited independently and the m-ax relation proved to be duplicated by a simpler mechanism that did not require such complex transformations of the form of the symbiont in the ontogeny. In this moment one may conjecture a reduction of the m-ax relation. The induction of the transition of the ax-symbionts into the follicle could have arisen primarily from a contact of the ax-mycetomes with the ovarioles, and then the symbionts, as it were, simply migrated into the second (or third) generation of mycetocytes, whch comprises the follicular epithelium. The induction itself occurred by analogy with the reaction of the m-symbionts to substances in the ovariole, like the primary reaction to the migration into the egg. Initially it might have been active, later the moments of induction and the moment of migrataion into the follicle could have moved apart, as occurs in the a-symbionts. Such a separation may provide the opportunity and the time for a transformation into a form that has the capacity to infect. The primary stage in the differentiation of ax into a and x may be imagined as, intially, a differentiation of the mycetomes themselves, when the migrant forms liberated by the anterior and posterior ax-mycetomes proved to be somewhat different, but were inherited together in the egg by a single pathway. Generally speaking, the arising mycetomes are always associated with locations of active cell multiplication; evidently, a part of the ax-symbionts, let us say, from an embryonic anterior particular mycetome might have shifted over to an induction of migrating forms in an earlier stage of the ontogeny of the growing mid-gut, in place of the gonads, and for this reason the fate of the x-symbionts turned out to be associated with the intestine into which they migrate, like into a mycetome, and even prior to the appearance in it of a lumen. Here the induction changed over to the growth substances of the intestine. The subsequent differentiation of the R-mycetome is an adaptation to existence in a functioning intestine, the work of which commences with hatching. The displacement of the mycetome to the hind-gut was brought about by the situation that the mid-gut is enclosed in a peritoneal sac, together with which digestion is accomplished, and here the mycetome would prove to be in the wrong place, both inside and outside the intestine. All of the complex movements of the x-symbionts are associated with the intestine, except for the stage of the transition into the follicle. The interrelations of the a symbionts and the x symbionts in the embryogenesis of dictyopharids demonstrate the primariness of a, in that the a symbionts inculcate themselves into the blastoderm, i.e. into the outer part of the embryo, while the x symbionts penetrate into the protoplasm of the vitellophages, lying within the egg; then, following the reversion, the composite mycetome comes into contact with the embryo once more, initially with mycetome a.

In this fashion one may conceive the basic history of the splitting up to the symbionts (Figure 33). Each basic type (germarium type, follicular and intestinal) may also, in principle, become differentiated into supplementary types (obviously, for the most part these are secondary transfollicular types) and this may explain the tetra-, penta- and hexasymbiotic cases. One should consider as a special case the follicular m-symbionts that are found as a secondary phenomenon in *Dictyophara europaea*.

From observations on the combined frequency of occurrence and frequency or replacement of the individual varieties of symbionts it may be concluded that some varieties, as has already been mentioned above, as it were substitute for one another; thus, for example, the x-type substitutes for H, and in this case H ostensibly has nothing in common with x and does not form mycetomes. In such cases it may be conjectured that H is a degenerated, for some reason or other, form of x, which however retains its method of inheritance. In general, the frequency of occurrence and frequency of replacement of the individual varieties compels one to assume that they have not definitively lost the capacity for changing into one another, even though they are inherited independently, and for this reason, sometimes with the loss (inclusion and exclusion) of some stabilizing factor in the host organism, they are capable of changing over from one to another, at least in the supplementary pairs x and H, a and f, and in this case a transition from x+a to H+f is possibly determined by a single factor. Those cases of the joint existence of the antagonists (rare) H and x, or a and f, or of the combinations x+f and H+a should be considered as supplementary, new and secondary differentiations.

Among the cicadines all the variants of the germarium symbionts, replacing one another in the different groups, should be considered as the result of a coupled phyletic differentiation of one initial type of symbiont (m in the Fulgoroidea); the same applies to the intestinal and gonadal transfollicular symbionts as derivatives of a and, in part, of m. Concerning the m-symbionts in *Dictyophara europaea*, it may indeed be conjectured that they have simply changed over onto the inheritance pathway that is characteristic of the ax-types, or that, on the whole, it is a form that has been restored from a or x after a phylogenetic period when the primary m-symbiont became lost. The second hypothesis would explain why the ovarial mycetome is empty.


3
4
5
6
10
11
а
б
в
г
д
е
ж
з

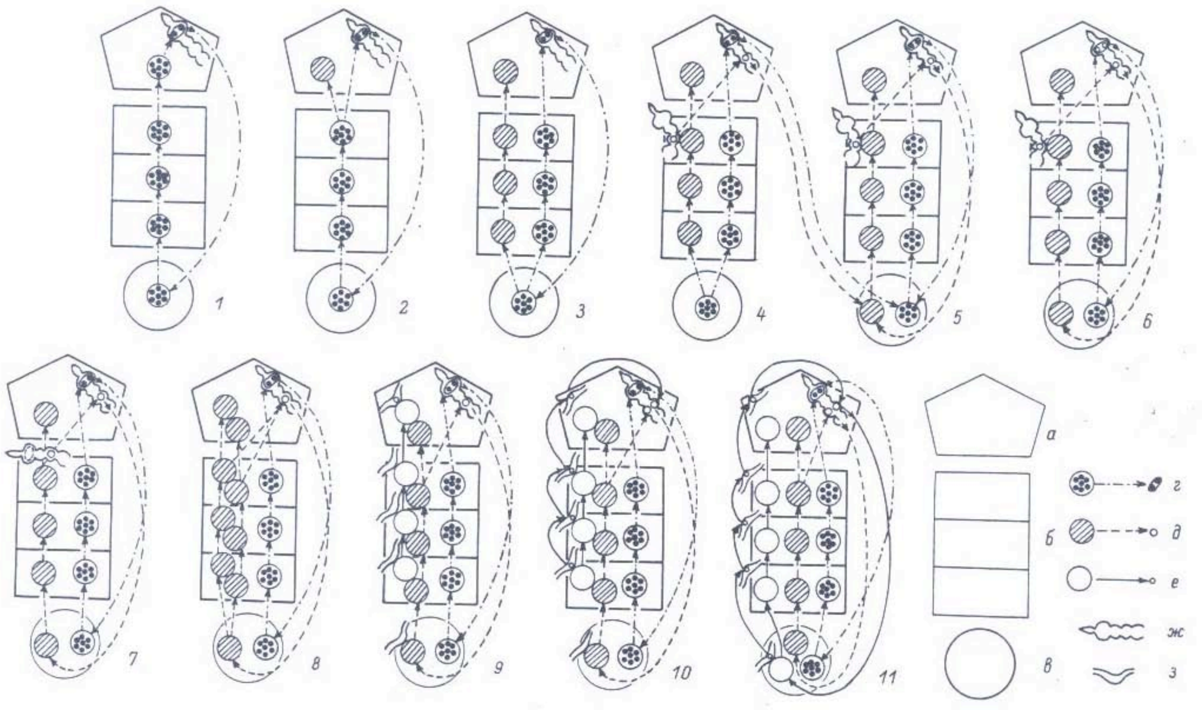


Figure 33. Conjectured transformations of the cycle of the mycetomal symbionts in the phylogeny.
1- primary cycle; 2 – formation of specialized visceral mycetome with transformed symbionts in the imago of the host, the infectioius non-transformed form of the symbionts passes into the germarium from the visceral mycetome prior to the transformation of the symbionts that fill the mycetome; 3 – the partition of the visceral mycetome in the early stages of the ontogeny of the host into a transformed non-inheritable part and a part that retains the symbionts in a non-transformed form for their subsequent transition into the germarium and then into the egg, during the development of which they once again separate off the transformed form; 4, 5 – induction of the transition of part of the tranmsformed symbionts into the follicle and then into the egg, due to the contact of the developing ovariole of the host with the transformed mycetome; transitional state with duplicate pathway for the inheritance of the transformed symbionts; 6 – subsequent isolation of the pathways for the inheritance of the primary and secondary symbionts due to the loss by the primary symbionts of the capacity to transform themselves into the secondary forms; 7 – shift of the moment of the departure of the infectious forms of the secondary symbionts into the early stages of the ontogeny of the host; 8 – the partition of the secondary mycetome into two equivalent parts; 9 – the differentiation of the separated parts – the formation of tertiary mycetomes from part of the secondary mycetomes, and the coming into contact of the tertiary mycetomes with the developing mid-gut; 10 – the transition of the tertiary mycetomes to an independent inheritance through an intestinal infectious mycetome; 11 – the loss by the secondary symbionts of the capacity to transform

themselves into tertiary mycetomes, and the complete separation of the cycles of inheritance of the three forms.
a, b, v – egg, larva and imago of the host, g – primary symbionts and their path in the cycle of the host, d – secondary symbionts and their path, e – tertiary symbionts and their path, zh – ovarioles of host, z – portion of mid-gut of host.

The phenomenon of mycetomal symbiosis, characteristic of the Homoptera, apparently occurred in some Psocida that are now extinct, since in contemporary booklice neither mycetomes nor mycetocytes in the larvae and imagines, nor a symbiotic ball in the egg, have been found up to the present time. However mycetocytal and mycetomal symbiosis is present in various Cimicida, in the Nirmida and Pediculida, and an embryonic mycetome has been found in the Thripida (Bournier and Louis, 1971). In the sucking lice, during embryogenesis, is found a homopterous like stellate guiding cell with protoplasmic rays, as it were pulling the symbiotic ball on the crest of the embryonic invagination from the posterior pole to the anterior pole.

The original bacteria must have been parasites or commensals that had gotten into an ancient paraneopteran (psocopteran), most probably with the food, and that were renewed in each new organism from the external environment after hatching from the egg. Directly after this the inheritance must have become transovarial, and this, apparently, was directly related with the endocytobiosis and with the possible transition from one cell into another (parasitism). Buchner (1960) considered that the primordial invasion occurred through the cavity of the gut.

The Nirmida and Pediculida are characterized by a mono-symbiont condition and, for the most part, by a cavity-type mycetome or separate mycetocytes and considerable, partially parallel variations in the embryonic pattern of transformation of the symbionts. Characteristic of the Nirmida are individual mycetocytes that are collected into nidi among the fat body; the Pediculida, for the most part, are characterized by membraneless mycetomes, made up to mycetocytes; the transition into the base of the ovariole is accomplished by free symbionts; whereas the elephant louse (*Haematomyzus*) and the biting lice are characterized by the constant finding of symbionts in the mycetocytes, in the louse the mycetome is in close contact with the gonads and the whole passes into the base of the oviduct, in the biting lice the mycetocytes with the symbionts migrate one at a time. In both groups the transition of the symbionts into the gonads occurs during the moult to the imago. Apparently the most primitive method is found in the elephant louse.

In the bugs cases of paraneopteran symbiosis are known in the Cimicidae and Lygaeidae, and are probably possible in some other families; disymbiont forms are encountered, and the infection of the eggs proceeds mainly through the anterior pole, but in its details the picture varies in different representatives. Cobben

(1968) doubs whether there are symbionts in the egg of the bed bug, as Buchner had postulated, but Cobben does not provide an interpretation of the structures which he calls “embryonic cells” (according to Buchner, these are the embryonic mycetome) and describes these, in addition to the Cimicidae and Lygaeidae, also in representatives of several other families: Reduviidae, Nabidae, Anthocoridae, Saldidae, Gerride, Ochteridae and Nepidae.

The Homoptera, like the bugs, are characterized by a polysymbiont condition, although monosymbiont forms are not rare; cases are also known of a secondary absence of symbionts in individual subordinate groups. Reviews of the symbiotic relationships in homopterans have been given in several studies by Buchner (1953, 1965), H.J. Müller (1962), Houk and Griffiths (1980) and Strümpel (1983).

In the Sternorrhyncha from 1 to 3 symbionts are usually found (Psyllina – 2, Aleyrodina – 1, Aphidina, Coccina – up to 3), intercellular and intracellular in individual mycetocytes and in mycetomes. The infection occurs for the most part through the posterior pole, but in the coccids it occurs more frequently through the anterior pole. The transmission of the infectious form of the symbionts is usually accomplished in the free form with the flow of the haemolymph, but sometimes with the direct contact of a visceral mycetome with the gonads, and also in some coccids within an itinerant mycetocyte. All of these phenomena have parallels in the sucking and biting lice. The mycetomes may be paired and unpaired; each variety of symbiont has its own separate mycetome, though occasionally a mycetome is dual (i.e. with sections for the different symbionts), but for the most part one variety of symbiont is located in the mycetome or mycetocytes, while the other is intercellular. The symbionts usually colonize some of the cells of the fat body, more rarely the haematocyte, gut wall and follicular epithelium, prior to penetration into the egg.

In the cicadines the polysymbiont condition clearly predominates, and most frequently 2 symbionts are found. The infection proceeds both through the anterior pole (some Fulgoroidea, some Membracidae) and through the posterior pole; the latter pathway is clearly predominant, and more over the infectious form initially settles in the follicular epithelium; infection through the anterior pole is found only in combination with infection through the posterior pole. The transmission of the infectious form is free or by means of the itinerant mycetocytes – t in *Euscelis*, according to J. Müller (1972). The transmission of the infectious form into the ovariole is free. The mycetomes are paired and unpaired, separate according to the varieties and combined (clearly in the Cicadelloidea). Sometimes a segmentation of the mycetomes is found (Aetalionidae, Membracidae). Forms associated with the gut are present among the Cicadelloidea (Membracidae: *Cymbomorpha*; Cicadellidae: *Cicadula*) and are the norm in the Fulgoroidea (Rx-symbionts). The combined (dual, according to Buchner) mycetomes of the larvae and imagines may be interpreted as an inhibition of the division of the embryonic combined mycetome.

H.J. Müller (1962) reported features that differentiate the symbionts and their abodes in the Fulgoromorpha and Cicadomorpha, and in the superfamilies Cercopidea, Cicadoidea and Cicadelloidea among the second subdivision. Characteristic of the Fulgoroidea, according to Müller, are: 1) the presence of only monosymbiont mycetomes; 2) lying in the posterior part of the abdomen; 3) the presence of imbedded infectious tubercles of the a-organ.; 4) the presence of x symbionts (with a rectal affiliation); 5) the presence of type f “nebensymbionts”; 6) an abundance of “begleitsymbionts”, including also mycetomeforming forms; 7) a rarity of accessory symbionts, and 8) some peculiarities in the combinational possibilities of type H. Of the listed features only 2), 3) and 4) are features that do indeed stand in contrast to all of the so-called Cicadomorpha; the rest pertain only to a comparison of the Fulgoroidea with the Cicadelloidea and are not found in the Cercopoidea and Cicadoidea; thus, in the last two superfamilies the mycetomes, though often set close together, are not fused, and there are no symbionts of the t type, to which the f type symbionts are contrasted. Bearing in mind that a clear-cut confrontation of the narrowly distributed “begleitsymbionts” and accessory symbionts is a matter of convention, we come to reject points 7) and 8).

Reasoning within the context of the monophyletic hypothesis of the formation of symbionts, it may be thought that in the evolution of the Cicadelloidea there occurred some reversible changes according to the following scheme:

, while in the Fulgoroidea this scheme was:

. The multiple repetition of these homologous combinations in different branches of the corresponding subdivisions demonstrates their instaurational nature on the basis of Vavilov's homologous series. Among the Fulgoroidea all three combinations have been found in the Delphacides and Issides, and two out of the three combinations (only a few examples have been studied) are found in the Fulgoroides and Cixiides. Among the Cicadelloidea both variants have been found in almost all of the families examined by Müller (the systematic scheme accepted by Müller is more fragmented than that accepted in the present study): Jassidae, Cicadellidae, Deltocephalidae and Membracidae; only in the Ledridae and Ulopidae was this not so, since only one example of each was studied. The later data of J. Müller (1969) show that both variants are also encountered in the Ledridae.

In the Cicadoidea the second symbiont is called w, in the Cercopoidea – b_c, and moreover in the Cicadoidea, besides the a+w combination, there has also been registered an a+H combination, which apparently means that the w symbionts changed to H.

In his scheme of the symbiont changes H.J. Müller considers only the so-called essential symbionts of the “haupt” and “neben” categories, and does not specifically take into account the symbionts of the third and fourth, “begleit” and accessory categories, and for this reason there do not appear here, in particular, the m-symbionts of the dictyopharids, which Müller assigned to the “begleit” category.

Analyses of the structure of the mycetomes and of the superficial form of the symbionts, in isolation from the methods of their hereditary transmission, cannot lead to fully valid phylogenetic results. At the same time the entire path of the infectious forms and the methods of their induction have been studied in only a very few representatives up to the present time. The data published to date permit us to propose a different approach to the interpretation of the genesis of the individual forms, which in the future will possibly give more concrete results. It is characteristic that the a-symbionts in all of the cicadines form the infectious form in the so-called infectious tubercles, arising from direct contact with the oviducts, while the m-symbionts are directly associated with the ovarioles; moreoever the m-symbionts in some forms are inherited through the anterior pole, while in others they are inherited through the posterior pole. Extremely significant in this connection is the character of the relationship of the visceral mycetome with the gonads in the Aleyrodina, where the mycetome in the larva is in contact with the ovarioles, whereas with the moult to the imago it is displaced to make contact with the oviducts. Direct contact with the gonads has been noted in the psyllids. In the coccid *Sticticoccus sjoestedti* (Stictococcidae) the mycetocytes come into direct contact with the growing ovarioles and infect them from the posterior pole.

In discussions on the age of the symbionts attention is always paid to the bacterial-like form (of the majority) of the supplementary, not so widely distributed, so –called complementary symbionts (of the “begleit” and accessory types), seeing in this an indicator of their recent colonization of the insect. However, first and foremost this is a form that is less closely connected with a specific place within the organism, it has become secondarily despecialized and set free, and is consequently capable of moving to new places within the organism and of entering into new relationships, in a similar fashion to the infectious forms of the principal symbionts, which also have a more primitive bacterial-like appearance. It may even be said that in their origin such accessory forms are former infectious forms of the principal symbionts, that have become isolated in their life cycle.

The free forms of the symbionts, i.e. not located within cells of the host, most probably are, in general, a secondary phenomenon; this is indicated, in particular, by the occurrence of entirely endocytic pathways of the existence of the symbionts only in the more primitive forms. At the same time, besides the variant of the direct contact of the visceral mycetocytes and mycetomes with the gonads, there is also encountered the transmission to the gonads of separated-off itinerant mycetocytes by way of the flow of the haemolymph. Exocytic forms of symbionts that completely lack mycetomes are not encountered, and the forms that live endocyticly only in the ovariole or in the provisional mycetome in the developing egg are obviously secondary, all the more so since the induction of their migration into the ovariole occurs without contact and without the infectious tubercles.

Judging by the position in the symbiotic ball, symbionts a and x in the Fulgoroidea correspond only to a in the Cicadomorpha, since they are located in the cortex of the ball, while m is located inside the ball, and on the basis of this feature it is similar to t, the induction of the infectious forms of which does not proceed from a contact in infectious tubercles but is caused by the appearance of the infectious forms of a. The frequency of occurrence of the secondary forms of symbionts should not be the main indicator of their phylogenetic significance.

Judging by which pole of the egg is used for entry by the infectious form, the m-symbiont of dictyopharids may also be compared with the t-symbiont in the species in which the germarium mycetome is empty, or with the supplementary forms that enter the egg of the Cicadelloidea from the anterior pole. Most probably both t and the anterior-pole forms among the Cicadelloidea ($_2$ and

$_3$ in *Enchophyllum quinquemaculatum*, in *Cymbomorpha*) are the product of a splitting of some primary variant, that is similar to m in the dictyopharids; apparently this is an ancient variant which changed the first infection through the anterior pole to infection through the posterior pole, retaining in this case the possibility of returning to infection through the anterior pole. From the primary posterior-pole symbiont are descended all of the following posterior-pole forms, i.e. the essential symbionts: a, x, t, b, w, f and H.

In summing up all that has been said about the mycetomes and symbionts it may be concluded that, besides types a and H which are common to all of the Cicadina, the specific types t, f, w and b are peculiar to each superfamily; the value of these latter types for explaining the order of divergence of the superfamilies is close to zero (at the present time), since all these types are autapomorphous in each individual superfamily. No symbiont types have been found that confront the superfamilies in a 2:2 ratio; only 1:3 ratios are found when in three of the superfamilies the feature is negative (the given type of symbiont is absent) and only in one it is positive, i.e. the ratio that provides the least phylogenetic information; the reciprocal case occurs only for the H symbionts, present in three superfamilies and absent in one (Cercopoidea), but there is scarcely any doudt that this is associated only with the poor coverage of studies of the Cercopoidea with regard to the symbionts, and that H will be found in this group. The distribution of the H type is most interesting from the phylogenetic point of view, since it contradicts straight-line monophyletic concepts. From polyphyletic positions, H.J. Müller considers it as a young and aggressive colonist which is pushing out the old symbionts, in the first place the symbionts of the “neben” type, i.e. t in the Cicadelloidea, w in the Cicadoidea and x in the Fulgoroidea. What the natural source, or external reservoir, might be, from which H would pass into a leafhopper, is not discussed by anyone; this question is not posed at all. From monophyletic positions, H is a form of existence of those symbionts with which, as a rule, H is not encountered, i.e. t, w and possibly b, and also, finally, a and x in the Fulgoroidea.

Type H may be interpreted as an inhibited infectious form which has become vegetative but does not form a complete mycetome. Drawing attention to itself is the diversity of the places colonized by H, and the spectrum of its degrees of integration, from individual mycetocytes to membraneless mycetomes, and also its colonization in various epithelia, including the epithelia of other mycetomes and of the mid-gut (J. Müller, 1969).

The principal landmarks in the formation of paraneopteran symbiosis are seen in the following manner.

1) An assembly of mycetocytes or a primitive membraneless mycetome on a base of cells of the fat body. Direct contact with the germarium. The symbionts penetrate into the immature oocytes and nutritive cells; from the latter they later pass into the mature egg cells along the nutritive cords and accumulate at the lower pole close to the germ band that is being laid down, or in the place where it will be laid down. These are the primary symbionts that are designated in the scheme by the letter ∀ .

2) Through direct contract with the germarium the infectious form penetrates only into the nutritive cells, from where, along the nutritive cords, it penetrates from the anterior pole into the more mature egg cells and migrates to the lower pole, where it becomes surrounded by periplasm from the wall of the egg.

3) The installation of some of the symbionts into the cells of the forming membrane of the ball and the adjacent cells of the blastoderm. Formation of a facultative penetration into the egg from the lower pole also through the direct contact of a visceral mycetome with the follicle. Appearance of the capacity for amphipolar infection.

4) Isolation from the ∀ symbionts of the a symbionts which penetrate into the egg only from the posterior pole and colonize the membrane of a symbiotic ball of only blastodermal origin. Transition of a to heterochronous induction of its infectious form

from contact with the oviducts. The ∀ symbionts remain free within the symbiotic ball.

5) The formation of part of the membrane of the symbiotic ball by the vitellophages, rather than by the blastoderm. The formation of t symbionts from some of the symbionts that are installed in the membrane of the ball, but in that part which has a vitellophage origin and is directed towards the anterior pole of the egg. This is, as it were, a late variant of a or its parallel variant that has retained a closer link with the initial type. The formation from the vitellophage rudiment of a visceral mycetome of t, which becomes induced to produce the infectious form from an infectious tubercle of a by way of a combined mycetome. The t-mycetome sends out infectious itinerant mycetocytes by way of the flow of the haemolymph. Some of the symbiotns remain free within the symbiotic ball and retain their independence in the unified visceral mycetome. All of the forms are inherited independently but they retain the facultative capacity to change into one another through ∀ . This stage is the initial one for all the cicadines.

6) The appearance of the apparently evolutionary reversible H form, which after the breakdown of the embryonic t mycetome changes over as if to an infectious phase, although it colonizes not the gonads but the vegetative organs (fat body, intestine), from where in the following stage appear the true infectious forms that penetrate into the egg cell.

7) In the Cercopoidea and Cicadoidea there occurs a phyletic divergence of type t into types b and w, respectively, with a retention of the capacity to change over into the H form.

8) In the Fulgoroidea a separation of the visceral mycetomes into individual ones occurs. Mycetome t is transformed into mycetome x due to a transition to induction from contact with the mid-gut; this also denotes a considerable emancipation from a in the cycle of development. At the same time x loses its capacity to change into H, if a has not changed into form f, at the same time the a mycetome apparently acquires the evolutionarily reversible capacity to change into the f form. The f form opens up the possibility for a seemingly evolutionarily reversible transition of the x form into the H form with a return of the dependence of the former x on the former a.

9) The supplementary forms of symbionts in the various Cicadina, some inherited through the posterior and others through the anterior pole, are apparently restored forms of , which at some time implemented a change in the pole of infection. They apparently splinter off from symbionts of the “neben” group, but possibly also from the “haupt” group; the occurrence of a hexasymbiont form may be imagined as the result of a splintering off a pair of supplementary symbionts from a “haupt” and a pair from a “neben” symbiont; in each pair one form penetrates into the

egg from the anterior pole, while the other penetrates from the posterior pole.

LIST OF GROUPS OF ELEMENTARY ALTERNATIVE FEATURES

The review conducted above, of the principal morphological differences between the superfamilies, permites us to provide a list of the revealed alternative groups) for the most part – pairs) of features. The list was compiled on the basis of (evaluated) elementary features, i.e. of features that cannot by further dismembered without a loss of their essence. The real sense of this concept is evident from the list itself. The morpho-functional complexes of evolutionary features (complex features) will be considered separately later.

The order in each individual group of features is taken as such which a priori it appears to be by way of the primary successive development (occurrence), but the definitive actual evaluation of a primary or secondary condition of the alternative (replacing one another) features is not anticipated by this.

Following the name of the group, there is presented in parentheses the number of the paragraph in the chapter on the “Analysis of the principal evolutionary features”, in which these features are discussed and characterized. In parentheses beside each alternative feature are given the abbreviated names of the superfamilies, the more primitive representatives of which (appearing more primitive) possess this feature: Cd- Cicadoidea, C1 – Cicadelloidea, Cr – Cercopoidea, Fl – Fulgoroidea.

1. Carinate lateral margin of head (1.1).
    1.1. Not expressed (Fl). 1.2. Expressed (Cl, Cr, Cd).
2. Medial ocellus (1.2).
    2.1. Present (Cd, Fl). 2.2. Absent (Cl, Cr).
3. Distance apart of lateral ocelli (1.2).
    3.1. Narrow (Cl, Cr, Cd). 3.2. Wide (Fl).
4. Location of antennae (1.4).
    4.1. In front of eyes (Cl, Cr, Cd). 4.2. Under eyes (Fl).
5. Postclypeus (1.1).
    5.1. Very small (Cl, Fl). 5.2. Large (Cr, Cd).
6. Segmentation of antennae of imago (1.4).

…

[Rest of item 6 and items 7-83 on pages 86-88 of Russian text, are not included in this translation, at client’s request. – Tr.]. [Subsequently translated by I Dworakowska at request of M.D. Webb (see below)].

84. Genital plates of male (7.8).
    84.1. Present (Cl, Cr, Fl). 84.2 Absent (Cd).
85. Separation of aedeagus from phallobase (7.8).
    85.1. Separated (Cr, Fl). 85.2. Not separated (Cl, Cd).
86. Location of phallobase in genital chamber (7.8).
    86.1 Below (Cr, Cd). 86.2. Above (Cl, Fl).

87. Division of phallobase (7.8).

87.1. Entire (Cr, Cd, Fl). 87.2. Divided into two (Cl).

88. Endosoma of aedeagus (7.8).

88.1. Not eversible (Cl, Fl). 8.2. Eversible (Cr, Cd).

89. Endoconnective (7.8).

89.1. Absent (Cl, Cr, Cd). 89.2. Present (Fl).

90. Anal rod (7.9.).

90.1. Free (Cl, Cr, Fl). 90.2. Fused with abdominal segment XI (Cd).

[Translation by I. Dworakowska of characters 6-83

6. Segmentation of antennae of adult (1.4).

6.1. Primary (Cd). 6.2. Secondary (Cl, Cr, Fl): 6.2.1. First segment of flagellum not separated (Cl), 6.2.2. First segment of flagellum separated (Cr. Fl).

7. Segmentation of antennae of larvae (1.4).

7.1. Primary (Cr, Cd). 7.2. Secondary (Cl, Fl). 7.2.1. First segment of flagellum not separated (Cl), 7.2.2. First segment of flagellum separated (Fl).

8. Segmentation of rostrum (1.5).

8.1. Only three segments (Cr, Cd, Fl). 8.2. Between 2nd and 3rd segment are on ventral side accessory sclerites (Cl).

9. Maxillary stylets (1.6).

9.1. Contact of stylets between ducts sliding tongue and groove suture (Fl). 9.2. Contact in form of a strand that is T-shaped in cross-section (Cl, Cr, Cd).

10. Outline of maxillar stylets [in cross section] (1.6).

10.1. Outer outline round (Cl. Fl). 10.2. Outer outline square (Cr, Cd).

11. Twisting of maxillar stylets (1.6).

11.1. Not twisted along axis (Fl). 11.2. twisted along axis (Cl, Cr, Cd). 11.2.1. twisted at 45° (Cl), 11.2.2. twisted at 90° (Cr, Cd).

12. Mandibular stylets (1.6).

12.1. Situated parallel at sides, almost not touching each other (Cl, Cr, Cd). 12.1. Shifted ventral where touching each other on long distance (Fl).

13. Tentorium (1.7).

13.1. Complete (Cr, Cd). 13.2. Incomplete (Cl, Fl). 13.2.1. Connection between anterior branches and bridge lost (Cl), 13.2.2. Connection between anterior branches and head capsule lost (Fl).

14. Subgenal suture (1.10).

14.1. Present (Cl, Cr). 14.1. Absent (Fl, Cd).

15. “Coeloconical” sensilla of maxillar lobe (1.10).

15.1. below subgenal suture (Cl, Cr, Cd). 15.2. above subgenal suture (Fl).

16. Cervical sclerites (1.11).

16.1. Present (Cd). 16.2. Absent (Cl, Cr, Fl).

17. Hind shield like extension of pronotum (2.1).

17.1, Developed (Cl, Cr, Cd). 17.2. Almost absent (Fl).

18. Notopleural suture of prothorax in adult (2.2).

18.1. Free and complete (Fl). 18.2. incomplete and not free (Cl, Cr, Cd).

19. Notopleural suture of prothorax in larvae (2.2).

19.1. Free and complete (Fl, Cr, Cd). 19.2. incomplete and not free (Cl).

20. Paranota of pronotum (pronotal paranota) 2.2.

20.1. Absent (Cl, Cr, Cd). 20.2. Present (Fl).

21. Episternal part of epicostal keel of mesopleurit (3.2).

21.1. Present (Cl, Fl). 21.2. Absent (Cr, Cd).

22. Parapsidal furrows of mesonotum (3.2).

22.1. Membraneous (Cr). 22.2. Sclerotized (Cl, Cd, Fl).

23. Hind ends of parapsidal furrows (3.2).

23.1. Situated far from margin of scutellum (Cl, Cd, Fl).

23.3. Situated near margin of scutellum (Cr).

24. Median inner crest of mesoscutum (3.2).

24.1. Not developed (Fl). 24.2. Developed (Cl, Cr, Cd).

25. Lateroparapsidal furrows of mesonotum (3.3).

25.1. Present at least rudimentarily (Cl, Cr, Cd). 25.2. Absent (Fl).

26. Furcal pits of mesosternum (3.4).

26.1. Cryptosternal (Cl, Cr, Cd). 26.2. phanerosternous (Fl).

27. Span of mesal coxae (3.4).

27.1. More narrow (Cr, Cd). 27.2. More broader (Fl, Cl).

28. Transepimeral suture of mesothorax (3.5).

28.1. Present (Cl, Cd). 28.2 . Absent (Cr, Fl).

29. Anapleural suture of episternum of mesothorax (3.5).

29.1. Present (Cl, Cr, Cd). 29.2. Absent (Fl).

30. Hing wing process of mesonotum (3.6).

30.1. Present (Cl, C, Cd). 30.1.1. Not sepatated (Cl, Cr,) 30.1.2. Separated (Cd).

30.2. Absent (Fl).

31. Episternal apodeme of metathorax of adult (4.1).

31.1. Free(Cl, Cd). 31.2. Fused with a metapleural apodeme (Fl). 31.3. Absent (Cr).

32. Episternal apodeme of metathorax of larvae (4.2).

32.1. Absent (Cr, Cd). 32.2. Present, fused with pleural crest (Cr, Fl).

33. Pleural apodeme methotorax of adult (4.3).

33.1. Without lateral lobes (Cd). 33.2. With lateral lobes (Cl, C, Fl).

34. Pleural apodeme of metathorax of larvae (4.4).

34.1. With apophysis (Cr, Cd), 34.2. Without apophysis (Cl, Fl).

35. Astragal [caudal projection of metathorax?] (4.5).

35.1. Absent (Cl). 35.2. Present (Cr, Cd, Fl).

35.2.1. Normal (Cr, Fl), 35.2.2. Transforemd into tympanal covers (Cd).

36. Hind notal wing process of metathorax (4.6).

36.1. Not separated (Cl, Fl). 36.2. Separated (Cr, Cd).

37. Furca of metasternum (4.7).

37.1. Primary (initial form) (Cl, Cr, Cd). 37.2. Transformed into bifurcated sclerite (Fl).

38. Metatrochantin (4.8).

38.1. Present (Cl, Cr, Cd). 38.2. Absent (Fl).

39. Main coupling of wings (5.1).

39.1. Broad (Cr, Cl, Fl). 39.2. Narrow (Cl).

40. Accessory wing coupling (5.1).

40.1. Present (Cr, Cd). 40.2. Absent (Cl, Fl).

41. Situation of Sc from above at base of fore wing (5.2.)

41.1. Free (Cr, Cd). 41.2. Fused with radio-medial stem (Cl, Fl).

42. Peripheral membrane of hind wings (5.3)

42.1. Absent (Fl). 42.2. Present (Cl, Cr, Cd).

43. Arculus opn fore wing (5.4).

43.1. Present (Cd). 43.2. Absent (Cl, Cr, Fl).

44. Relative position Pcu and A1 on fore wing (5.8).

44.1. Independent (Cl, Cr, Cd). 44.2. Fused distally (Fl).

45. Basiclaval love (5.9).

45.1. Well developed (Cl, Cr). 45.2. Weakened (Cd, Fl).

46. Relative position Pcu and A1 on hind wing (5.11).

46.1. Independent (Cr, Cd, Fl). 46.2. Coalescent (Cl).

47. Basicubital plate (cubital triangle) (5.6).

47.1. Extended along corium at base (Cr, Cd). 47.2. Extended along clavus at base (Cl, Fl).

48. Postmedial suture of fore wing. (5.5).

48.1. Not transversing arculus (Cl, Cd, Fl). 48.2. Transversing arculus (Cr).

49. Nodal line (5.7).

49.1. Absent (Cl, Cr, Fl). 49.2. present (Cd).

50. Meracanthus of mesocoxa (6.1).

50.1. Present (Cr, Fl). 50.2. Absent (Cl, Cd).

51. Compelx meracanthus - yellow spot on mesocoxa (6.2).

51.1. Present (Cr). 51.2. absent (Cl, Cd, Fl).

52. Seta-like sensillae of mesotrochanter in adult (6.3).

52.1. Not polymerized (Cl, Cr, Fl). 52.2. Polymerized (Cd).

53. Seta-like sensillae of metatrochanter in larvae (6.3).

53.1. Present (Cl, Cr, Fl). 53.2. Absent (Cr, Fl).

54. Seta-like sensillae of metatrochanter in adult (6.3).

54.1. present (Cl, Cd). 54.2. Absent (Cr, Fl).

55. Sensillae of bases of meso-femur (6.4).

55.1. in a longitudinal row (Cl, Cr, Cd). 55.2. in a transverse row (Fl).

56. Placoidal sensilla on second tarsomere (6.5).

56.1. basally (Cl, Cr, Fl). 56.2. In the midlength (Cd).

57. Sensillae on the apex of 3rd segment of tarsus (6.6).

57.1. A complex developed (Cr, Fl). 57.2. Reduced (Cl, Cd).

58. Ungutractor of claws (6.7.).

58.1. Simple (Cr, Cd, Fl). 58.2. overgrown developed (Cl).

59. Shape of arolium (6.7).

59.1. roundish (Cr, Fl). 59.2. Biolobed (Cl). 59.3. reduced (Cd).

60. Unparted seta on arolium (6.7).

60.1. Absent (Cl, Fl). 60.2. Present (Cr, Cd).

61. Setae on claws (6.7).

61.1. Two groups of setae (Cr). 61.2. One group of setae (Cl, Cd, Fl).

62. Ventrolateral plates of arolium (6.7).

62.1. Present (Cr). 62.2. Absent (Cl, Cd, Fl).

63. Coxothoracic articulation (junction) of metathorax (6.8).

63.1. Developed (Cr, Cd, Fl) 63.2. obliterated and disappeared (Fl).

64. Meracanthus of hind coax (6.9).

64.1. absent (Cl). 64.2. present (Cr, Cd, Fl).

65. Yellow spot of hind femur (6.9).

65.1. Absent (Cl, Cd). 65.2. present (Cr, Fl).

66. Meron separated (6.9)

66.1. Slightly (Cl, Fl). 66.2 definitely (Cr, Cd).

67. Subapical lobe-like protrusion on hind coxa (6.10).

67.1. Present (Cl, Cr). 67.2 . absent (Fl, Cd).

68. Subapical lobe-like protrusion on meso and procoxa (6.10).

68.1. present (Cr). 68. 2. absent (Cl, Cd, Fl).

69. Trochantero-femoral junction (6.11).

69.1. by two condyles (Cl, Cr, Cd). 69.2. in one condyle (Fl).

70. Cross section of hind tibia (6.12).

70.1. roundish (Cr, Cd). 70.2. Quadrangular (Cl, Fl).

71. Lateral teeth of hind tibia (6.12).

71.1. With thick seta (Cl, Fl). 71.2. With thin subapical seta (Cr, Cd).

72. Teeth on apex of hind tibia (6.13).

72.1. Flared (Cr. Fl). 72.2. Not [flared] (Cd, Fl).

73. Teeth on apex of hind tibia (6.13).

73.1. In one row (Cl). 73.2. In two rows (Cr, Cd, Fl).

74. Teeth on apex of (pro and) mesotibia in larvae (6.13).

74.1. absent (Cl, Fl). 74.2. present (Cr, Cd).

75. Tibiotarsal junction of hind legs (6.14).

75.1. Weak (Cl, Cd). 75.2. Strong (Cr, Fl).

76. Armature of apices of 1st-2nd segments of hind tarsi (6.15).

76.1. without [lateral] teeth (Cl). 76.2. with [lateral] teeth (Cr, Cd, Fl). 76.2.1. Lateral teeth without subapical setae (Fl). 76.2.2 . Lateral teeth with subapical setae (Cr). 76.2.3. not clear (Cd).

77. Tympanal membrane (7.2.)

77.1. looking like a dark patch (Fl). 77.2. looking like a striated field (Cl, Cr, Cd).

78. Situation of 2nd abdominal spiracles (7.3.).

78.1. Facing lateral (Cr, Cd). 78.2. facing dorsal (Cl, Fl).

79. Structure of homonous segment of abdomen (7.4.).

79.1. extralateral field sclerotized and not hidden in cleft together with the parastigmal field (Cl, Cr, Cd).

79.2. The field membraneous and hidden in cleft together with the parastigmal field (Fl).

80. Stigmocalyptrae of larvae (7.5.).

80.1. absent (Cl, Fl). 80.2. present (Cr, Cd).

81. Fields of waxglands on VI-VIII abdominal tergites in larvae (7.6).

81.1. absent (Cl, Cr, Cd). 81.2. present (Fl).

82. Meidan basla apodeme of the II valvae of ovipositor (7.7.).

82.1. absent (Cl, Cr, Cd). 82.2. present (Fl).

83. Subgenital sternite of female (7.7.)

8.3.1. Big (Cl, Cr, Cd). 8.3.2. small (Fl.).

PHYLOGENETIC ANALSIS OF ALTERNATIVE PAIRS OF FEATURES

90 pairs of features were taken into account. Features were selected that are known from the literature or that were elucidated on the material; only those features were taken into consideration that are quite reliably known in all 4 superfamilies, including, as far as possible, also the primitive representatives, especially if the corresponding features are not adequately stable in the evolutionary sense in one or other of the superfamilies. Of course, the list should not be considered as absolutely complete, and one should expect the finding of new important features of the external morphology, for example in the axillary region of the

wings, as well as in many other regions, as a result of a more through analysis of the available diversity. Much information may be provided by a study of the anatomy, in particular of the musculature, which has practically not been mentioned at all in the present paper, on the one hand, in expectation of the publication of all of A.V. Savinov’s materials on the muscles of the thorax, and on the other, in connection with the fragmentary nature of the literature data, which often does not permit comparison of all the superfamilies. Another important and little utilized source is the larval morphology and, to an even greater degree, the larval anatomy.

Out of the total of the considered pairs of features, a large number are such for which it has not been possible, as yet, to clearly elucidate the plesiomorphous state, in part because of the inadequate coverage of studies of related groups (bugs, sternorrhynchans, thrips, booklice), and in part because of the very nature of the evolutionary process.

As far as possible the accounting of the features was conducted in an unbiased fashion, but it should be noted that initially I was inclined towards variant 1 (Emel’yanov, 1977), while the majority supported variants 4 (Strümpel, 1983; Popov, 1980; Shcherbakov, 1984) and 6 (Kirkaldy, 1910; Pruthi, 1925) (Figure 34).

1. General analysis. Among the considered pairs of features the majority, or 55 pairs, are such that divide the superfamilies in a ratio of 1:3; there remain 35 features that divide the superfamilies in a 2:2 ratio. Specifically, according to the groups, they are distributed in the following manner: Cl, Fl – Cr, Cd: 22; Cl, Cr – Cd, Fl: 4; Cl, Cd – Cr, Fl: 9; Fl – Cl, Cr, Cd: 27; Cl – Cr, Cd, Fl; 9; Cr – Cl,Cd, Fl: 8; Cd – Cl, Cr, Fl: 11. Two groups of pairs are fairly clearly distinguished: of more than 20 (Cl, Fl – Cr, Cd (22) and Fl – Cl, Cr, Cd (27), and of less than 10 (11) (all of the rest). Moreoever, in both the 2:2 group and in the 1:3 group there is, in each case, a clearly predominant pairing. In the Fl – Cl, Cr, Cd pairing there is a distinct predominance of autapomorphies of Fl (there are no fewer than 18 of them); the synapomorphies of Cl, Cr and Cd, however unusual, are few (features 9, 11, 24, 42 and 77) and may be the result of reduction. In the 2:2 group the situation is different: here the Cl, Fl – Cr, Cd case is characterised by a parity in the distribution of synapomorphies and symplesiomorphes, which is clearly indicative of the primariness of this division. Since such a point of view seems unexpected, we will compare it with other variants that are more widely accepted and for which arguments have been presented in the literature. Taking into consideration that the close relationship of the Cercopoidea and Cicadoidea is quite clear and that one cannot, without obviously stretching reality, derive other groups from within these two superfamilies (place

other groups between them on the tree), one may exclude from the tentative analysis those variants of the tree in which the Cercopoidea and Cicadoidea are not arranged beside one another as a terminal branching (i.e. trees 2, 3, 5, 6, 7, 8, 9, 10, 11, 12, 14 and 15); trees 9 and 12 could be analyzed but for this it would be necessary to postulate several major reversions in the sister (on these trees) groups of the Cicadelloidea and Fulgoroidea. There remain numbers 1, 4 and 13 as the most probable candidates for the true state. At the same time the isolation of the Fulgoroidea, practically entirely built up on autapomorphies, by itself allows these to be placed in any place on the tree, and it is only in combination with the primary pair Cl, Fl - Cr, Cd that the phylogeny comes fully into view. Thus, the analysis carried out undoubtedly points to tree 13.

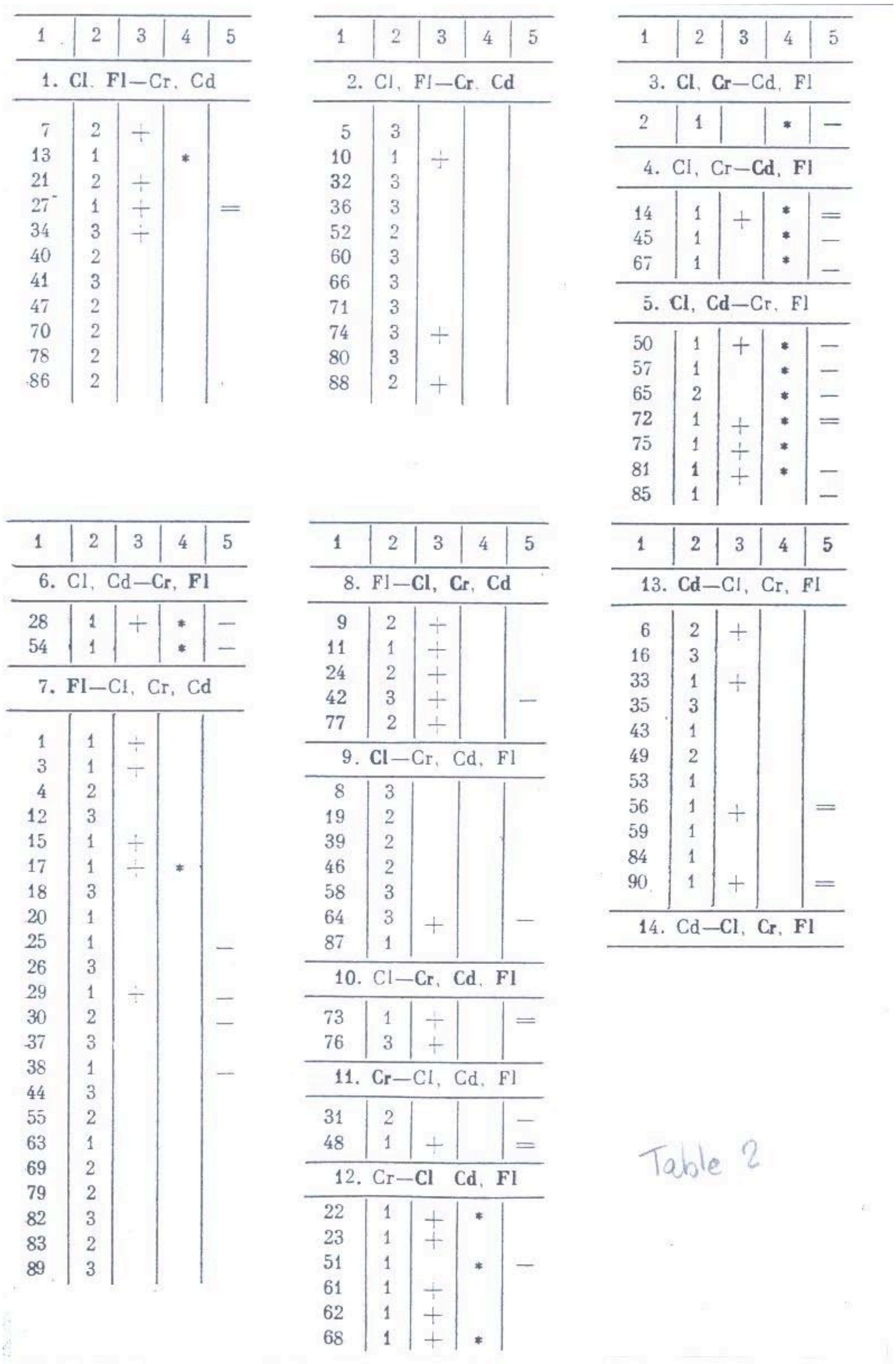
Figure 34. Possible variants of the phylogenetic relationships among the superfamilies of cicadines. 15 possible variants of the successive dichotomous emergence of four groups from a common ancestor.
Cd – Cicacoidea, Cl – Cicadelloidea, Cr – Cercopoidea, Fl – Fulgoroidea. The most probable schemes, 1, 4 and 13 are traced with a bold line.

2. Comparison of divisive features in potential sister groups. There are 7 such groups among the four superfamilies (Table 2).

Initially consideration is given to the groups that divide the superfamilies in a 2:2 ratio, and then to the 1:3. The features have been differentiated on a three-point scale, and additional observations were made on apomorphous features of a possibly convergent character (dubious and false apomorphies), on features which apomorphy was of a negative character, and on features with an unexplained plesiomorphous condition.

2.1. Cl, Fl – Cr, Cd. Thse groups are divided by 22 features, among which there is a predominance of features of high evolutionary significance, i.e. those that arose, as may be thought, by way of the successive complication or addition of structures and which, therefore, do not easily lend themselves to simple reversion or to simple suppression; a convergent

Table 2.



1	2	3	4	5
1. **Cl**. **Fl**—Cr. Cd				
7	2	+		
13	1		*	
21	2	+		
27	1	+		=
34	3	+		
40	2			
41	3			
47	2			
70	2			
78	2			
86	2			
2. Cl, Fl—**Cr**. **Cd**				
5	3			
10	1	+		
32	3			
36	3			
52	2			
60	3			
66	3			
71	3			
74	3	+		
80	3			
88	2	+		
3. **Cl**, **Cr**—Cd, Fl				
2	1		*	—
4. Cl, Cr—**Cd**, **Fl**				
14	1	+	*	=
45	1		*	—
67	1		*	—
5. **Cl**, **Cd**—Cr, Fl				
50	1	+	*	—
57	1		*	—
65	2		*	—
72	1	+	*	=
75	1	+	*	
81	1	+	*	—
85	1			—
6. Cl, Cd—**Cr**, **Fl**				
28	1	+	*	—
54	1		*	—
7. **Fl**—Cl, Cr, Cd				
1	1	+		
3	1	+		
4	2			
12	3			
15	1	+		
17	1	+	*	
18	3			
20	1			
25	1			—
26	3			
29	1	+		—
30	2			—
37	3			
38	1			—
44	3			
55	2			
63	1			
69	2			
79	2			
82	3			
83	2			
89	3			
8. Fl—**Cl**, **Cr**, **Cd**				
9	2	+		
11	1	+		
24	2	+		
42	3	+		—
77	2	+		
9. **Cl**—Cr, Cd, Fl				
8	3			
19	2			
39	2			
46	2			
58	3			
64	3	+		—
87	1			
10. Cl—**Cr**, **Cd**, **Fl**				
73	1	+		=
76	3	+		
11. **Cr**—Cl, Cd, Fl				
31	2			—
48	1	+		=
12. Cr—**Cl** **Cd**, **Fl**				
22	1	+	*	
23	1	+		
51	1		*	—
61	1	+		
62	1	+		
68	1	+	*	
13. **Cd**—Cl, Cr, **Fl**				
6	2	+		
16	3			
33	1	+		
35	3			
43	1			
49	2			
53	1			
56	1	+		=
59	1			
84	1			
90	1	+		=
14. Cd—**Cl**, **Cr**, **Fl**				

Table 2

appearance of such features is also not very probable. In Table 2 are given the estimates of the complexity of the features according to the three-point scale, and estimates are presented of the possibility of their convergent occurrence. In this table also are indicated the features for which it was not possible, for some reason or other, to determine consistently a plesiomorphous condition. From this table it is evident that most of the alternative features that were revealed for the Cl, Fl – Cr, Cd pairing have soilid and high estimates. Moreover, although the Cr, Cd pair obtains a large index (23) of the autapomorphous condition, which is not surprising, the second pair of Cl, Fl, which is so dissimilar in external appearance, also obtains a very high index of the autapomorphous condition - 13.

2.2. Cl, Cr – Cd, Fl. The association of Cd and Fl, which is unnatural from the point of view of all the authors that have published phylogenies, has only three dubious synapomorphies. The contrasted grouping of Cl and Cr has even fewer – 1, although a close relationship of the last two groups has been widely accepted in the past and has not been completely rejected at the present time. All 4 pairs of features that divide these groups may be interpreted as convergent and, in part, apomorphous features, since they bear a negative character (no ocelli, no suture, no protrusion, etc).

2.3. Cl, Cd – Cr, Fl. This pairing has more divisive features (9), but here also all the apomorphous features may be interpreted as coincidences based on absences, except for the 72nd and 75th, where an obvious convergence can be established in association with the absence or weakening of jumping in these groups.

2.4. Consequently, on the basis of the 2:2 confrontations one may clearly assign preference to the Cl, Fl – Cr, Cd pairing, where the number, quality and distribution of the apomorphous features indicate a high rank of the hiatus.

2.5. Fl – Cl, Cr, Cd. This confrontation collected the greatest number of features – 27, and in this case 22 apomorphies fall on Fl, and only 5 on Cl, Cr, Cd, which, it can be said, are considered as a monophyletic group by all systematists. The quality of the synapomorphies of Cl, Cr, Cd, in general, is also low. The most difficult question is related to feature 42 – the peripheral membrane of the hind wings. If the absence of the membrane in the Fulgoroidea is primary, and not the result of a later reduction, then this makes the Cl, Cr, Cd group synapomorphous on the basis of the presence of such a membrane. This main support for phylogenies 4, 5 and 6 stands out in sharp conflict with the distribution and quality of the apomorphies of Cl, Fl – Cr, Cd. The available set of features undoubtedly speaks in favour of tree 13.

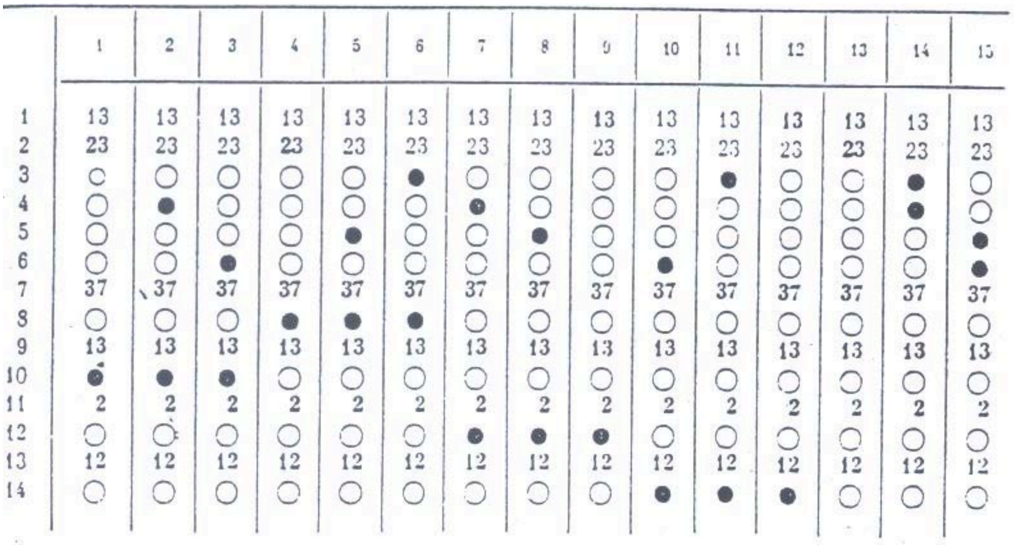
2.6. Cl- Cr, Cd, Fl. 9 features were found for this confrontation: 7 apomorphies of Cl and 2 apomorphies of Cr, Cd, Fl, and moreover the latter are not indisputable, which also allows one to reject variants 1, 2 and 3. The teeth on the apex of the hind tibiae (feature 73), arranged in one row, possibly comprise a secondary state, since the primordium, or rather the rudiment, of a second row is present in Cl, and moreover in the Ledridae a second row also develops or is re-established. The situation is more complex with the absence of the lateral teeth on segments 1 and 2 of the hind, jumping tarsi, for which no exceptions are known, but this too may be associated with the attenuation of jumping in this superfamily.

2.7. Cr – Cl, Cd, Fl. The Cercopoidea are set in confrontation to the other cicadines on the basis of 8 features, and in this case there is among them not one of a reliable plesiomorphy, and no less surprising is the poverty of autopomorphies. The most striking autapomorphy is the absence of an episternal lobe of the metathorax, and this may be, if so desired, interpreted as a plesiomorphy. The anatagonism of Cr – Cl, Cd, Fl clearly cannot be a contender for the primary condition.

2.8. Cd – Cl, Cr, Fl. This confrontation is outstandingly one that is composed entirely of autapomorphies of the Cicadoidea, most of which it is impossible to interpret in a different manner. However, features 6 and 33 seemingly indicate a profoundly primitive condition: the primitive segmentation of the antennae in the imago and the absence of extensions in the pleural apodeme of the metathorax, which preserve a more or less primitive appearance. However, the primitively segmented antenna in the imago was formed due to a retardation of the larval antenna, possibly in the same way as the pleural apodeme, although the resemblance of the apodeme to the primitive appearance may be a result of convergence (Emel'yanov, 1981); one way or another the discussed simplifications are associated with a loss of the jumping capacity by the cicadas.

2.9. An examination of Table 3 shows that with the grouping of the superfamilies in a 1:3 ratio in no single case are there found reliable synapomorphies for any three of the superfamilies, while autapomorphies are found in all, but in different numbers. In comparing the superfamilies in a 2:2 ratio only two variants demonstrate reliable synapomorphies and these variants reflect one another in a mirror-like fashion. It is also noteworthy that the autapomorphes of the individual superfamilies do not exceed in any significant fashion the synapomorphies of Cl, Fl and Cr, Cd, with the exception only of the autapomorphies of the Fulgoroidea.

Table 3



	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	13	13	13	13	13	13	13	13	13	13	13	13	13	13	13
2	23	23	23	23	23	23	23	23	23	23	23	23	23	23	23
3	○	○	○	○	○	●	○	○	○	○	●	○	○	●	○
4	○	●	○	○	○	○	●	○	○	○	○	○	○	●	○
5	○	○	○	○	●	○	○	●	○	○	○	○	○	○	●
6	○	○	●	○	○	○	○	○	○	●	○	○	○	○	●
7	37	37	37	37	37	37	37	37	37	37	37	37	37	37	37
8	○	○	○	●	●	●	○	○	○	○	○	○	○	○	○
9	13	13	13	13	13	13	13	13	13	13	13	13	13	13	13
10	●	●	●	○	○	○	○	○	○	○	○	○	○	○	○
11	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
12	○	○	○	○	○	○	●	●	●	○	○	○	○	○	○
13	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12
14	○	○	○	○	○	○	○	○	○	●	●	●	○	○	○

Comparative estimate (in point totals from Table 2) of different phylogenetic variants in relation to the number of quality of the discontinuities in the development of individual features.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	13	13	13	13	13	13	13	13	13	13	13	13	13	13	13
2	23	23	23	23	23	23	23	23	23	23	23	23	23	23	23
3	Φ	Φ	Φ	Φ	Φ	M	Φ	Φ	Φ	Φ	M	Φ	Φ	M	Φ
4	Φ	M	Φ	Φ	Φ	Φ	M	Φ	Φ	Φ	Φ	Φ	Φ	M	Φ
5	Φ	Φ	Φ	Φ	M	Φ	Φ	M	Φ	Φ	Φ	Φ	Φ	Φ	M
6	Φ	Φ	M	Φ	Φ	Φ	Φ	Φ	Φ	M	Φ	Φ	Φ	Φ	M
7	37	37	37	37	37	37	37	37	37	37	37	37	37	37	37
8	Φ	Φ	Φ	M	M	M	Φ	Φ	Φ	Φ	Φ	Φ	Φ	Φ	Φ
9	13	13	13	13	13	13	13	13	13	13	13	13	13	13	13
10	M	M	M	Φ	Φ	Φ	Φ	Φ	Φ	Φ	Φ	Φ	Φ	Φ	Φ
11	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
12	Φ	Φ	Φ	Φ	Φ	Φ	M	M	M	Φ	Φ	Φ	Φ	Φ	Φ
13	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12
14	Φ	Φ	Φ	Φ	Φ	Φ	Φ	Φ	Φ	M	M	M	Φ	Φ	Φ

Note. The numbers 1-15 in the upper line correspond to the numbers of the trees in Figure 34. The numbers 1-14 in the left-hand column correspond to the numbers of the combinations of superfamilies in Table 2. Marked in semi-heavy type are the point totals of those features which are not discontinuous in the given phylogenetic variant; the circles mark the columns in which reliable apomorphies were not registered: - M features (ought to be) continuous, Φ - features (ought to be) discontinuous.

Thus, the analysis of the available material leaves no possibility of an option. In comparison with tree 13, trees 1 and 4 require a double genesis of the synapomorphies of Cl and Fl (6 items, 13 point total), while tree 12 (Savinov, 1984b) requires a double genesis of the synapomorphies of Cd and Cr (8 items, 23 point total). Nobody has yet proposed tree 9, which is similar to tree 12 in the number of disruptions of continuity of the features. Variants 5 (Evans, 1963), 6 (Kirkalby, 1910; Pruthi, 1925; Ross et al., 1982) and 11 (Quadri, 1967) require one to assume the greatest number of disruptions of continuity in the development of the features and for this reason are the least probable, based on the available data.

COMPARISON OF SUPERFAMILIES ON THE BASIS OF THE FEATURES

1) The Cicadoidea and Cercopoidea are tied together by the greatest number of distinctive common features (synapomorphies): the uniformly developed clypeus, extending onto the vertical surface of the head; the similarly developed maracanthi on the middle and, in part, also hind coxae; the similar spines on the hind tibiae; the isolated subcosta in the basal part of the fore wings from above; the central sensillum on the arolium; the similar larvae with abdominal paranota (stigmocalyptra); the non-polymerized antennae in the larvae (9-10 segments); the way of life of the larvae, associated with the soil (all the Cicadoidea and the Cercopidae of the Cercopoidea), and the similar filter chamber, separated from the second section of the mid-gut by a constriction.

The absence of jumping in the Cicadoidea is secondary: their hind coxae retain the additional (jumping) condyle on the ventropleurite (Emel'yanov, 1981) and the lateral kicking teeth on the hind tibiae, while in the primitive family Tettigarctidae on the hind tarsi are also retained lateral teeth (which in their origin had a jumping-supporting function) on the first and second segments, through, it is true, only on one side. In the Tettigarctidae are retained several other plesiomorphous features, which bring them close to the Cercopoidea: the lobe of the pronotum, the arolium and the hook-chaetoid of the supplementary coupling apparatus, features that have disappeared in the Cicadidae.

The autapomorphies of the Cicadoidea which may be treated as secondary comprise of the non-polymerized antennae and the point of attachment of the maxillary lever.

2) Next in turn, the Cercopoidea have many features in common with the Fulgoroidea. Like the comparison of the Cercopoidea – Cicadoidea pairing, the comparison of Cercopoidea – Fulgoroidea manifests a mainly progressive character of the features on the Fulgoroidea with a large scale and volume of the differences. The features of similarity are most striking in the structure of the hind legs and of the sides of the metathorax. The structural plan of the hind tibia are tarsus is very superficially synapomorphous: the apical teeth on the tibia and first two tarsal segments; the lateral teeth on the tibia, and the tibio-tarsal articulation are the same in the Cercopoidea and in the Tettigometridae of the Fulgoroidea. The wax glands of the larvae of the Cercopoidea (Batelli glands) and Fulgoroidea are synapomorphous, as Šulc (1911) reported long ago. The metapleural apodemes of these two superfamilies are symplesiomorphously similar (Emel’yanov, 1982). Furthermore, in the Fulgoroidea meracanthi are present on the

middle and hind tibiae, which brings them close in equal measure to the Cercopoidea and Cicadoidea, though this feature more probably bears a plesiomorphous character, since meracanthi are also present in the Psylloidea. It is possible that the meracanthi of the Psylloidea are convergent.

Among the lower Fulgoroidea there are groups, the larvae of which are associated with the soil, although this relationship is either facultative (Tettigometridae) or is clearly secondary (Cixiidae), since the larvae move only along crevices and jump well (!), commencing from the first instar, but nevertheless an association of the Fulgoroidea with the soil-surface environment and with the lower layer of the vegetation is very probable (Emel'yanov and Fal'kovich, 1983).

The Fulgoroidea have very many distinctive features, commencing with the weakly developed clypeus and the absence of a filter chamber, and finishing with the tegulae of the fore wings, the hind coxae that are accreted to the thorax and the absence of a peripheral membrane on the hind wings. Features of simplification exist in the Fulgoroidea alongside a large number of secondary advances, in part autapomorphous and in part synapomorphous with the other superfamilies. The absence of the filter chamber in the Fulgoroidea bears a secondary character, and moreoever their so-called food reservoir, in its position and form, corresponds well to the anterior component of the filter chamber of the Cercopoidea, while in the Cicadelloidea the anterior component is not separated from the expanded part of the free mid-gut.

Apparently the very small clypeus of the Fulgoroidea is associated with the reduction of the filter chamber and with the transition of part of the suctorial functions of the clypeus to the food reservoir. A suction effect by means of the food reservoir was found by Mukharji (1962). Primitive Fulgoroidea – Tettigometridae have several symplesiomorphies with the Cercopoidea, which have disappeared in the other Fulgoroidea: the lobe of the pronotum, the dorsally covered tibiotarsal articulation of the hind legs, and the flat, as in other cicadines, disposition of the cone-shaped lora. All of this induces one to conjecture that the clypeus of the Fulgoroidea was initially larger, for example, like in the Aetalionidae, but was then reduced in size by way of a retardation of the early stages of development (Emel'yanov and Fal'kovich, 1983).

3) The superfamily Cicadelloidea possesses several features that appear more primitive than features in the three superfamilies considered above, and also alongside its distinctive features. However, many of the features typical of the Cicadelloidea are absent in the most primitive representatives of this superfamily, such as the Ulopidae and Aetalionidae.

The jumping legs of the Cicadelloidea are devoid of lateral teeth on the tibiae or they bear only rudiments of these, often polymerized (Ledridae, Eurymelinae). Conversely, the setae on the lateral edges of the hind tibiae in these insects are hypertrophied and thickened, which does not occur in other cicadines. One saltatorial muscle in them is located in the coxa, and therefore the coxae are enlarged, while the metathorax is comparatively small. The coxae are without traces of meracanthi. The hind tarsus does not have lateral supporting teeth without setae on the first and second segments, and differs little from the tarsi of the anterior pairs of legs. The trochanter of the hind legs, against a background of a generally primitive condition, has certain adaptations that are incompatible with the apomorphies of the Cercopoidea and Fulgoroidea: its femoral articulation is more strongly twisted than in the other cicadines, and it has additional support by means of special opposing, lip-like processes on the trochanter and femur.

The male genitalia of the Cicadelloidea are characterized by the presence of the so-called connective, which corresponds to a set-apart lower portion of the phallobase (Snodgrass, 1935); in other cicadines the phallobase is not differentiated, i.e. it has the primitive form. The polymerized flagellum of the antennae in the Cicadelloidea, in contrast to the other cicadines, also includes the third segment. Ventrally at the base of its distal segment the rostrum of the Cicadelloidea bears special platelets (Kramer, 1950), which Evans (1937), possibly mistakenly, considered to be rudiments of the glossae. The tentorium of the Cicadelloidea is divided up in a distinctive fashion (Kramer, 1950).

The hypertrophied clypeus is often cited as being a synapomorphy providing evidence of the advanced nature of the Cicadelloidea and of their close relationship to the cercopocicadoids, but this hypertrophy is convergent, and in the primitive cicadelloids (Ulopidae, Aetalionidae) it is no more strongly expressed than in the Paleozoic prosboloids. The form of the head, and the degree and character of the development of the clypeus vary very considerably in the Cicadelloidea.

GENERAL PATTERN OF EVOLUTIONARY DEVELOPMENT OF THE CONTEMPORARY CICADINES

On the basis of the analysis presented above, the evolution of the contemporary cicadines may be represented as a series of progressive transformations in each branch, accompanied by a regression or weakening of individual structures (Figures 1: 34, 13). The given phylogeny does not yet allow us to clearly resolve the question of the actual appearance and taxonomic position of the common ancestor of the contemporary superfamilies, i.e. more precisely, it does not answer the question of whether the contemporary superfamilies are derived from different groups of the Prosbolomorpha or whether there was a common ancestor that had already emerged from the Prosbolomorpha and had become the first Cicadomorpha; most probably, however, there was a common ancestor, the presence of which makes it lawful to set up all of the contemporary cicadines, as the Cicadomorpha, against their ancestors, as the Prosbolomorpha. Establishing the actual appearance of the Prosbolomorpha and the range of development of the latter may help to decide the question.

The prosboloids, at least those of the line that produced the cicadomorphs, were apparently phanerozoic sucking phytophages, with dense leathery fore wings; they possessed a single poorly directed jump of the psyllid type, a well developed filter chamber, inherited from the archescitinoids, a clypeus that was developed approximately as in the Aetalionidae, and a capacity to stridulate by means of musculature at the base of the abdomen and metapleural resonators of the cercopoid type. The larva led a free way of life in the same location as the imago, apparently in the crown of (gymnosperm) trees, and did not possess the capacity to jump. Lying at the base of the food specialization of all cicadines is polyphagy; oligophagy developed on the basis of the latter.

The formation of the Rhynchota (in practice in the form of the early Archescytinoidea) is associated with the appearance of plants that possessed a well developed vascular system, the fluid in the vessels of which was procured with the aid of the rostrum; this character of feeding brought to life the filter chamber. The loss of the filter chamber in the Rhynchota is usually associated with a transition to feeding on avascular plants, on the cell sap or on completely different diets; detritophagy, predation, etc., as in the bugs.

The formation of the cicadines was accompanied by the appearance of a peritoneal covering of the filter chamber, the differentiation of the antennae, which is expressed in a strengthening of the scape and pedicel, on the one hand, and in a thinning and polymerization of the flagellum, on the other, and by a transformation or substitution of the basic coupling mechanism of the hind wing.

The cercopocicadoid branch is much more monomorphous in its evolutionary and morphological aspects than the Cl, Fl branch, and moreover it does not contain clearly primitive forms that are close to the common ancestor of the branch. In particular, a strongly specialized state of the head with a uniformly hypertrophied clypeus is characteristic. The Cr, Cd group is apparently associated in its appearance with a transition to sucking the xylem (xylembibition). From the very beginning such a transition entailed a hypertrophy of the clypeus and a considerable development of the filter chamber. The Cr, Cd branch is characterized by an association with the soil-surface and soil layers, and also by not very mobile, non-jumping larvae. The cicadellofulgoroid branch is very polymorphous, in its evolutionary and morphological aspects, in all of its principal branches, both among the cicadelloids and among the fulgoroids. In particular, the structure of the head and the degree of development of the clypeus are very diverse. In the primitive cicadelloids the clypeus is very weakly developed. The Cl, Fl group is characterized by the primary type of feeding of the Rhynchota, i.e. phloembibition. The more nutritive contents of the vascular system of the phloem, in comparison with the xylem, did not require an obligate and drastic hypertrophy of the clypeus, nor also an inordinate developement of the filter chamber. The cicadelloids with the most strongly developed clypeus, the Cicadellinae, as shown by new data, are xylembibitors. It may be thought that among the lower Cicadelloidea have been preserved the least advanced cicadines: the Ulopidae and Aetalionidae. A paradoxal situation exists with the development in the ontogeny of the Cicadelloidea of the metapleural synapodeme: it is developed only in the larvae and disintegrates in the imagines. The similarity in the structure of the larval synapodeme in the Fulgoroidea and Cicadelloidea is striking. These circumstances induce us to conjecture that the Cl, Fl, branch was initially characterized by jumping larvae, and that the jumping larva was the key adaptation that moulded this branch. In such case, however, it is also impossible to represent the formation of the Cl, Fl branch as having occurred in the crowns of trees, as a jumping larva is adaptive only on low vegetation and in the soil-surface layer. In a definite sense, jumping is a more important adaptation for the larva than for the flying imago. Generally speaking, it is also impossible to exclude such a variant in which only the larvae initially started to jump. In any case, the flying imagines had less need for a strong jump than did the larvae. It is very probable that the contemporary cicadines, Cicadomorpha (in the Cl, Cr, Cd, Fl composition), separated off from the Prosbolomorpha owing to their descent from the crowns of trees to the soil-surface layer and to their acquisition of larval jumping. The vegetation of the lower layers of the mesophytic forest is poorly known, and on the basis of the literature it is not possible to compile a clear picture. Contemporary clubmosses, horsetails, ferns and cycads allow us to imagine such vegetation. Young seedlings of the upper layer could also provide a food base for the cicadies with a primarily jumping larva.

The remnants of saltatorial structures, such as the isolated episternal apodeme of the metathorax, in the cicadas permit us to see here a similiarity with the Cicadelloidea and to assume that the larvae of the ancestors of the cercopocicadoids also jumped, until they changed over to a more cryptic and less mobile way of life on the soil surface. Thus, it seems more probable to me that the first Cicadomorpha had a jumping larva and that the cercopocicadoids lost larval jumping in connection with their transition to a somewhat immobile way of life on the soil surface and in association with roots, with the elaboration of the froth.

A basic trend in the evolution of the locomotory apparatus in the Cicadelloidea branch consists of an improvement in the coordinative possibilities of the jumping without an augmentation of the jump itself, and possibly even with a weakening of the latter and its utilization in conjunction with the wings. The differentiated multivalent jump of the cicadelloids apparently made it unnecessary to possess the cumbersome proprioceptive meracanthus-yellow spot pair, which operated only on a maximal forward jump from a standard initial position; such unaimed primitive jumping is characteristic of the contemporary Cercopoidea. The supporting-saltatorial structures on the apex of the hind tibia and tarsus in the Cicadelloidea are weakly developed, and are more primitive in their appearance than in the Fulgoroidea and Cercopoidea: the tibiotarsla articulation is scarcely reinforced at all in comparison with the other pairs of legs, and there are no lateral apical teeth on the first and second tarsal segments. If this is not a result of reduction, then the structural similarity of the hind legs of the Fulgoroidea and Cercopoidea is entirely convergent. The contemporary flourishing of the Cicadelloidea is associated exclusively with flowering plants, as is also the abundance of dentrobionts among the Cicadelloidea; dendrobiosis led to a secondary loss of jumping in the larvae of many branches of the Cicadelloidea, while in the Aetalionidae – Membracidae line it became the determinant adaptation; the lowering locomotory activity in this line is correlated with the development of pronotal outgrowths of a cryptic nature.

Relict associations of contemporary cicadines with preflowering vegetation have not been found. Among the cicadelloids individual cases are known of oligophagy on horsetails, ferns and *Ephedra*, while more cases are associated with conifers, but all of these are clearly secondary phenomena in progressive groups. Associations with ferns and conifers are also known among the fulgoroids but here also they are rare and secondary.

The question of the origin of the contemporary superfamilies is closely associated with the question of their age. For the superfamilies Cicadelloidea, Cercopoidea and Cicadoidea a Jurassic of Late Triassic age is acknowledged (Shcherbakov, 1984). Much remains unclear here at the present time, but the question of the time of appearance of the Fulgoroidea is the most controversial.

D.E. Shcherbakov (1984) clearly separates off the contemporary Fulgoroidea, within the infraorder Fulgoromorpha, from the other contemporary cicadines, which are assigned by him to the Cicadomorpha together with the Prosboloidea and many other extinct groups. Within the composition of the Fulgoromorpha, according to D.E. Shcherbakov, are included two superfamilies: the Coleoscytoidea, known from the Early Permian, and the Fulgoroidea, known from the Late Permian. Thus, if this is true, the ancestors of the Fulgoroidea in our sense, from among the groups that have been discovered, can only be the very early Prosbolopseidae, which are very remote from the contemporary Cercopoidea, Cicadoidea and

Cicadelloidea. D.E. Shcherbakov considers the last three families as being closely related, having diverged only in the Mesozoic as descendants of the families Hylicellidae, Chiliocyclidae and others.

However, the Paleozoic Fulgoromorpha sensu Shcherbakov (Coleoscytoidea and Fulgoroidea, that are grouped around *Surijokocixius*, which D.E. Shcherbakov considers as a separate family, but which E.E. Bekker-Migdisova assigns directly to the Cixiidae) do not display features that would allow them to be assigned with confidence to this particular taxon, while at the same time they retain many of the most characteristic features of the Prospoloidea that are not characteristic of the recent cicadines as a whole or of the cicadellofulgoroid branch, such as: the wide and sharply bent (along its outer margin at the base) costal area with the bent hypocostal carinae; the short and wide, posteriorly obtusely-angled scutellum, and the free subcosta in front of the basal cell. Nor have there been found such characteristic features of the Fulgoroidea as the tegulae; in some cases the point of junction of vein Pcu+A_1 into the elytral suture has not been reliably traced (*Surijokocixius*), while in others, if this has been traced, the form of the clavus and the claval veins have an arrangement that is completely atypical of the Fulgoroidea (*Coleoscyta*). In those cases when the outlines of the pronotum have been preserved, the latter does not have the characteristic shallow notch in the middle part of the posterior margin nor the lateral notches where the tegulae should be located. As to the Coleoscytidae, this is so aberrant a group that one may even doubt that it belongs among the cicadines. As an indication of its affiliation to the Fulgoroidea might be accepted the wide and short basal cell, but such a cell is usually correlated with light-weight non-leathery wings, in which the veins take onto themselves a skeletal role.

As to the Fulgoroidea, the most primitive family of the Tettigometridae has leathery wings with weakly prominent veins and a basal cell, compressed to the limit, without an extended arculus. The more advanced family of the Delphacidae, already with light-weight elytra, still has a very small basal cell and a short arculus. A large basal cell and a long arculus are formed only in the more highly developed Fulgoroidea. At the same time none of the contemporary families, including the Tettigometridae and Delphacidae, retain the prosboloid costal area, scutellum and free subcosta in front of the basal cell. Thus there is no reliable evidence for the existence of the Fulgoroidea in the Paleozoic.

Another group that has been assigned to the Fulgoroidea is that of the Mesozoic Fulgoridiidae, including the genus *Eofulgoridium*, which does not even belong among the cicadines, since those insects have a completely free subcosta; they are most probably caddis-flies or moths, also characteristic of which is the fusion of the postcubitus and anal veins in a reversed fork.

Following the rejection of the above-enumerated forms, which are extremely dubious and controversial with regard to their systematic affiliation, the age of the Fulgoroidea seems to be more equal to the age of the other contemporary superfamilies, possibly except for the younger Cicadoidea, since the oldest family that has been assigned to the Fulgoroidea, the Cicadoprosbolidae, may most probably turn out to be a dead-end branch of the late Prosboloidea.

The most primitive family of the Fulgoroidea, the Tettigometridae, possesses non-jumping larvae, capable of living in ants’ nests, hiding in the axils of leaves, etc. However, the 3-segmented hind tarsi of the older larvae of the Tettigometridae allow one to think that the latter lost their capacity to jump. All of the remaining Fulgoroidea jump beautifully, commencing from the first larval instar. The most striking pecularity of the Fulgoroidea is their loss of the filter chamber and the dimishment of the clypeal reigon, induced by this loss. This may be associated with the transition of the ancestor of the Fulgoroidea to myco- or bryophagy, i.e. a transition to feeding on avascular plants. The organization of the mid-gut of the Fulgoroidea (Müller, 1940), located freely within a peritoneal sac, looks like a consolidated embryonic stage, when a peritoneal membrane encloses the yolk together with the rudiments of the mid-gut (Müller, 1940); at the same time the convergence of the beginning and end of the mid-gut (i.e. preparation to the formation of a filter chamber) during embryogenesis is clearly an act of recapitulation. Furthermore the food reservoir of the mid-gut of the Fulgoroidea corresponds in its position to the anterior component of the filter chamber of the cercopoids, as has already been noted by Kershaw (1914). The similarity of the cercopoids and fulgoroids based on their wax glands and certain other features was pointed Šulc (1911) also a long time ago.

The bugs are also distinguished by the absence of a filter-chamber, while the oldest representatives of this stem, the Peloridiidae, are bryophages or lichenophages. Among the lower fulgoroids there are several families whose larvae are inclined towards mycophagy (Cixiidae) or adhere to mycophagy in an obligate manner (Achilidae, Derbidae). The primary phytophagy of the Rhynchota and the primary formation in them of a simple filter chamber are in good accord with the distribution of these features in all of the primitive Rhynchota, except for the Heteroptera, but it is impossible to derive this order by by-passing the phytophagous Archesctytinidae, and therefore it should be considered that the bugs ancestrally lost the filter chamber. The recent proposal of Cobben (1978) that the first Rhynchota were predtors is not at all in accord with the phytophagy of all of the Homoptera and with the derivation of the bugs from a common ancestor with the Homoptera, i.e. from the Archescytinoidea.

The cercopocicadoid stem was already clearly associated in its formation with the habitation of the larvae in the soil, with the feeding on roots, and with the locomotion initially along crevices, as in the Cercopidae, and later by the active building of tunnels, as in the Cicadoidea. The larvae of the ancestors of the cercopocicadoids ceased jumping. The formation of froth in the older Cercopidae is carried out only on the emergence from the soil at the time of the imaginal moult.

From the common ancestor with the cercopoids, which had a soil-dwelling larva, the cicadoids have proceeded along the line of profound specialization, both as larvae and as imagines: increase in size, prolongation of development, intensification of fossorial activity of the larva, strengthening of active flight, intensification of singing, loss of jumping, and foetalization of the antennae and fore legs in the imago.

Traces of former jumping and features of similarity with the Cercopoidea are especially clear in the Tettigarctidae: in these a large pronotal lobe is still developed, the harpagones (styli) are retained, as are the lateral teeth on the first and second segments of the hind tarsi (on one side). The spurs on the hind tibiae, which are developed in the majority of the Cicadoidea, are also a legacy of a jumping stage in the evolution of the ancestors of the Cicadoidea.

The morphological evolution of the cicadines is complex to decipher and abounds in examples of parallelisms and of reversions in reductions, which create the (false) impression of a disordered and non-adaptive condition of the individual changes, on the one hand, and of the impossibility of constructing a non-conflicting phylogeny, on the basis of the crudely understood principle of the irreversibility of evolution, on the other. The very richness and diversity of the forms, even within groups of low taxonomic rank, indicates that evolution possesses much greater possibilities (degrees of freedom) than those which we have already noted and been able to explain.

Below are considered the most important conclusions on the modes of macroevolution, which deviate from the generally accepted modes.

SOME MODES OF MACROEVOLUTION, OBSERVED IN THE COURSE OF THE ANALYSIS OF CICADINE PHYLOGENY

1. Metatopy. One of the forms of the transformation of the organization of a species in macroevolution may be called the jump-transition* of particular structures, the jump-transition onto repetitive homologous, or generally in some way equivalent parts of the body. This possibility exists in practically every type of organism owing to the latent or explicit polymerism, metamerism and repetition of various structures, which in metazoans was primarily determined by a very profound polymerization – by the laying down

of the cells, as has already been described by A.N. Severtsov (1939). Even in the most differentiated organisms there are many polymerous structures: hairs, cilia, tubercles on the skin, vertebrae, limb girdles, and digits; in the lower organisms metamerism is universally and ubiquitously expressed.

The mechanism which provides for the possibility of some metatopies at the microevolutionary-individual level has acquired the name of homeosis in the mechanics of development.

The differentiation of polymerous structures and their stabilization in number and location obviously complicate the ontogeny and, in the first instance, build-on additional structural components to the ontogeny; structures, which start to develop in the ontogeny as equivalent and uniform, later diverge along different paths (anaboly plus deviation), but, evidently, in many cases, if not always, the overall basis of the arrangement is preserved. Apparently this circumstance also determines the possibility of jump-transitions (metatopies) in macroevolution, which basically have variability and individual errors in the

---

* “jump-transition” is used here to translate the Russian term “pereskok”, the colloquial meaning of which is “skip” or “jump”. (Tr.).

ontogenetic programme of realization of the repetitive structures. Three types of metatopy may be distinguished.

1.1. Segmental or intersegmental metatopy. Examples. Occurrence of paranota on the pronotum of *Myerslopia parva*, occurrence of paranota on the abdominal segments in the larvae of the Silphidae, and of legs on the abdominal segments in the Megaloptera, occurrence of meracanthi in several groups of homopterans, occurrence of limitations of the parapsidal and lateroparapsidal furrows on the pronotum in the cicadas. Similar processes on the segmented appendages with the change in the number of segments in the club on the antennae, in particular in the lamellicorn beetles; the jump-transition of the lateral teeth on the tibia onto the first tarsal segments on the hind legs in representations of the genus *Nilaparvata* (Delphacidae), and others.

1.2. Inter-row metatopy. The distinctive character of this type consists of the jump-transitions of structures from one row to another in the presence of such, for the most part longitudinal, rows that are not directly associated with the metamerism, and also in reticulate and otherwise polymerically arranged structures. Examples of structures: costae on tibiae of cicadines, veins on wings, longitudinal rows of setae and maculae on abdomen, and others. An example of inter-row metatopy (see p. 54*, paragraph 6.12) may be the change in the position of the lateral teeth

---

* p. 78 in this translation. (Tr.)

(spurs) on the hind tibiae in the cicadas, as compared with the spittlebugs. Inter-row metatopy on the hind tibiae is also found among the treehoppers.

1.3. Arbitary or ungraded metatopy. Characteristic, in the first instance, of integumental structures: sensilla, setae, glands, etc. Thus, the placoid sensilla in various groups of insects are located in quite different places which do not coincide in the different groups, namely in those places where there is a need for them. The assumption of remote macroevolutionary migrations of separate specific individualized sensilla seems in most cases to be an artificial stretching of reality, just like the attainment of the observed cases by way of a differentiated reduction of a more or less uniform “sensillary” integument, which is acceptable only for unspecialized hairs.

From another aspect, metatopies may be subdivided into saltatorial, when the structure appears in the new place and disappears in the old, and expansional, when the structure invades new parts or metameres and persists on the old.

There are numerous examples of metatopy in the plant kingdom; for example, cases of cauliflory may be ascribed to metatopy.

Of course, the features of structures that are subjected to metatopy pass through several stages in their evolution, from a single or local occurrence to generalization, then to localization by way of the building up and blocking-off of additional structures, and finally to metatopy; with a primordially multiple laying-down of the structures, the chain of events commences from the second link.

2. Instauration, or re-establishment, of features that have disappeared (from the phenotype of the species) in the course of macroevolution.

The question of the reversibility of evolution has been debated since the time of the publication of the widely known Dollo's law (Dollo, 1893, 1912; Suchkin, 1915; Sergeev, 1935; Shishkin, 1967, 1968; Gabuniya, 1974, and many other authors). Even earlier, Wallace and Darwin expressed their views on the question of reversibility (see: Orlov, 1981). In contrast to Dollo, their statements concern micro- and macroevolution without segregation, in particular they apply to the question of the reversion of breeds of domestic animals to the wild type, which is more of a macroevolutionary or borderline character.

At different times Dollo presented two different formulations of his law.

1) As a complete exclusion of reversibility (Dollo, 1893): “… the organism cannot return even partially to the preceding state, which had already been realized in several of its ancestors” (citation according to: Gabuniya, 1974, p. 231).

2) As an exclusion of reversibility only at the level of the organism as a whole, not extending to its separate small parts (Dollo, 1912): “the organism never returns precisely to its previous state, even in the case when it finds itself in conditions of existence identical to those it had passed through” (citation according to: Gabuniya, 1974, p. 234).

Although the second formulation is much more realistic and, as can be seen from L.K. Gabuniya’s (1974) analysis, more precisely reflects Dollo’s views, the majority of contemporary evolutionists, who are adherents of the synthetic theory of evolution, accept Dollo’s law in its first formulation, which bears an orthogenetic nuance and is not in full accord with the actual facts (results) of evolution. Thus the possibility or impossibility of the reversibility of features became the topic of the criticism of Darwinism from non-materialistic standpoints.

Cases of the re-establishment of individual features in evolution (i.e. cases of reversibility in their evolution) have been repeatedly demonstrated by various authors (Sergeev, 1935;

Shishkin, 1968, 1973, and others), although such data, as a rule, do not get into the compendia and text-books. At the same time antiDarwinists make use of cases of the re-establishment of features for criticizing contemporary evolutionary doctrine and Darwinism (see, for example, Lyubishchev’s articles). The possibility and even necessity of the phenomenon of reversibility in the evolution of features ensues from N.I. Vavilov’s law of homologous series, but this law has not been adequately appraised and understood by Darwinists, including such leading figures as I.I. Shmal’gauzen; recently B.M. Mednikov (1981) wrote a valid article concerning this matter.

It may be thought that many biologists-materialists, not seeing a rational (Darwinian) explanation for the phenomena of reversibility, refrained from commenting on them or denied them, citing an inadequate precision of repetition or the possibility of simple convergence.

Objectively observed phenomena of reversibility, which at first glance are improbable without the intervention of a teleological force, are, however, amenable to a completely materialistic explanation.

If we turn to the real picture of the results of evolution, as has been done in the present study, and attempt to construct and substantiate in detail the phylogeny of some group of low taxonomic rank, up to tribe or family, then we will come up against facts which cannot be explained without an acknowledgement of reversibility or of ubiquitous convergences and parallelisms that have no common genotypic basis and are induced only by the requirements of a similar external environment. For clearity we need to illustrate the above with an example.

In two close but not directly related families, the Cixiidae and Dictyopharidae, the monophyletic nature of each of which has been reliably proven, there are present three mutually-exclusive types of setae, occupying a strictly stabilized and homologous position on the first and second segments of the tarsi on the fore and middle legs (there are always two setae on each of the mentioned segments). The setae may be simple and blunt, or hyaline and sharply-tipped (actuellae), or hyaline and bluntly-tipped (platellae). These three types are very distinct and characteristic, and they do not have transitional forms. All three types, as has already been said, are present in some or other representatives in both families (Emel’yanov, 1981). As is obvious from simple deductions, it is impossible to monophyletically derive more than one of the homotopic alternative features that are expressed in two and more sister groups. Thus, we must assume that some features (platellae, acutellae) repeatedly appaeared in a convergent manner, but this is in poor accord with a materialistic understanding of randomness, or else we must assume that these features have a single origin, but that in the course of the phylogeny they may disappear from the phenotype and then reappear again. It is easy to multiply such examples and they are known to every attentive taxonomist-evolutionist.

I propose the term instauration (from instauratio-restoration) for this phenomenon in the evolutionary reversibility of features, when over a certain interval of macroevolution the feature completely disappears from the phenotype of a species or wider taxon, and then appears again in some descendants (other species, genera or tribes) in a very similar form, allowing one to speak of a retention of its genotypic traits.

Of course, in the hereditary mechanisms, determining and implementing individual development in its micro- and macro-evolutionary transformations, there are prerequisites, in part already known or understood in their general features from the standpoint of contemporary genetics, which set the conditions or open up the possibility for instauration. Before passing on to a specific discussion of these, it is necessary to define several concepts.

Concepts concerning the identity of features and structures that are assumed to be instaurational should be neither extremely stringent not extremely diffuse. To the feature being analyzed we should apply the same measures which thevariation of the feature presents in every monophyletic branch in which it exists continuously, i.e without instauration. It is appropriate to note here that the subject of homology is the phenotype, rather than the genotype, and that during evolution some change may occur in the genotype of a phenotypically unchanged feature (replacement of phenocopies by genocopies et al.). It is wrong in principle to look for the most stringent features of the homology in the genotype, rather than in the morphology (i.e. in the phenotype), as for example N.N. Vorontsov (1966) has proposed. In establishing the repetition of the state of a feature (organ, part of organ) in evolution, we must also consider its sameness and not only from abstract standpoints of an ideal (absolute) identity, when even the states of a feature of a single individual that are sequential in time are no longer identical, but rather from the standpoints of congruence within the limits of the specific individual variability of actual species and wider taxa, as we have just discussed. More “precise” comparisons are devoid of biological sense and are pure scholasticism. The criticism of A.S. Sergeev by M.A. Shishkin slips down to this level (Sergeev, 1935; Shishkin, 1968, 1973). A non-absolute reversional repetition of a feature, differing from the original one, that is homologous in closely related species, and even with a lesser similiarity but bearing all the features of homology, is no less surprising and to no lesser degree requires a rational explanation, which will obviously, in essence, be the same in both cases.

Figure 35. Schematic diagrams illustrating simple and instaurational heterobathmia in the example of a transformation of 5 different features.

A – pattern of evolution, leading to simple heterobathmia; B – pattern of evolution, leading to instaurational heterobathmia. 1-5 – number of features. Thick line, running from root of tree – plesiomorphous state, thin line – apomorphous state, thick line, running from dot, above thin line – instaurational state, indistinguishable from plesiomorphous state. Above are shown: by figures without parentheses – plesiomorphous features, by figures in parentheses – instaurational features.

In many cases repetition (instauration) involves certain common features which are not readily amenable to a precise accounting but which also cannot be explained by simple convergence or parallelism without stretching reality. For example, in several quite different cicadines in separate groups of the rank of genus or tribe, belonging to different families or or subfamilies of one family, there occurs a bifurcation (doubling) of the aedeagus (Ulopidae: *Ulopa*; Cicadellidae, Typhlocybinae: *Notus*; Deltocephalinae; Opsiini; Scaphytopiini; *Japananus*), although an unpaired aedeagus is characteristic of the order Homoptera as a whole and of all of the Rhynchota. At the same time it is known (Matsuda, 1976) that the aedeagus of insects, in its origin, is a paired structure.

To substantiate the complete impossibility of reversibility, examples are usually cited of the substitution of homodynamous organs (the fins of fishes and the flippers of mammals, the secondary armour of some skulls et al.), which substitution is incompatible with reversibility and which occurred after large-scale reorganizations of ordinal and similar rank. By themselves the examples of irreversibility do not refute the possibility of reversibility; these phenomena may co-exist, but it is important to point out here that the cases of reversibility, as a rule, have a much more modest morphological and evolutionary scale and that the main path of evolution is determined by new formations and not by the repetition of an already traversed path. Instaurations are possible in trivial macroevolution and are practically inconceivable in megaevolution.

The system of the morphofunctional integrity of an organism and the system of its integrity in ontogeny, which together also, in essence, create the organism, have a history that is equal to the history of life on the earth. All of the basic properties of a living being, which are manifested in every organism (species) and which have a 90% share in determining it, took shape as long ago as the unicellular level or with the formation of multicellularity. The possibility of any small and minute evolutionary transformations was achieved and refined by selection in the deep antiquity of evolution. The general properties of a living being, having once become an achievement of evolution, are preserved in any genotype in any of its evolutionary transformations, and it is these properties that in the first instance ensure the possibility of newer and particular transformations, which are usually perceived as purely new formations: in such a species there appeared a new feature, let us suppose, a bony plate on the skull or a “new” seta on the antenna. Let us consider the example with the seta (in an insect).

The seta of insects is a particular structure of the integument. The integument of insects bears a great diversity of various setae, all or at least the greater part of which are homologous. Any portion of the integument is capable of bearing (forming) setae; it they are absent somewhere, then this is a consequence of differentiation or suppression. Apparently there are no completely bare (i.e. without setae) insects at either the species level or, all the more so, at any higher phylogenetic level. In the line that led to the arthropods, setae appeared no later than in the annelids, and if we will look into this genetico-morphofunctional process and apparatus which, let us suppose, led to the formation of a seta in the first annelids, then we will see that an important part of it was formed (and has existed continuously from those times) even earlier with the formation of multicellularity and tissue organization, when there became determined (genotypically) systems of cell interaction, mutual transposition and their differentiation during the individual development in situ in the tissue and in the organism. Every multicellular organism clearly bears these properties, and there are no mutations, except lethal ones, that can distort them. Reasoning in a similar fashion, we may proceed to the sources of all life.

Thus, returning to the case of the appearance of a new seta, it can be ascertained that only its actual location is new here, but the mechanism for determining the location of the seta is also old, having been elaborated long before for determining the location of setae and generally of any isolated but repetitive integumental structures, or even of tissues in general.

The common initial prerequisite and cause of reversibility is the coordination of (ontogenetic) development, which is equal to the length of the evolution and the coordination that accumulated along the paths of the complication of the living organism and which occurred mainly by way of the addition and supplementation of structures, and not by way of substitution. One of the manifestations of this is the law of homologous series. The adaptive nature of the reactions of an organism to the external conditions and their coordination with one another is the most ancient and constant self-improving property that was laid down in the genotype as a whole and is not fully decomposable into the properties of individual genes; this property of the genotype as a system is an integral result of the work of natural selection over the entire course of evolution from the genesis of life to every recent species.

The possibility of instauration lies in that some of the features, that have become useless or harmful, are eliminated from the phenotype not by the destruction of the genes which determine the feature, but rather by the blocking of the final links of the morphogenetic chains determining it, by means of modifier genes. Pleiotropism of the genes and the many-sided correlated nature of the processes in the organism obviously make such a path easier and more adaptive. In the course of subsequent evolution under new conditions such blockings may be removed, and the features which returned once more to the phenotype were again subjected to selection.

The morphogenetic system which determines the formation of a feature practically always had a quantitative component in addition to the qualitative component. This quantitative aspect is initially contained in any differentiation, while the actual expression is determined by the adaptive nature, and consequently any reaction of the organism extends beyond the frame of the immediate or current adaptive state, and a change in the conditions shifts the frame of the adaptive portion of the more general reaction; this is also a result of the prolonged evolution of the reactions of the living organism to the conditions. These systems in combination make up homologous series, the borders of which are formed by deformities. But a deformity in one species may be an adaptation in another.

Examples of the opening up of blocked phenotypes and of the expansion of the spectrum of homologous series, by this means, is given to us by the breeds of domestic animals, for example of dogs. A striking example is provided by the breeding of silver foxes (Belyaev, 1979), which has revealed a set of forms homologous with dogs, both based on their external appearance as well as their behaviour, which is not manifested in the wild. Thus a hook-shaped tail or pendant ears in the dog and in the fox are neither a convergence not a parallelism; they comprise an identical link in a homologous series, formed directly or indirectly by selection in the history of the Canidae, of the mammals, etc.. An illustration of the same order is provided by the so-called atavisms and monstrous forms of pathogenic origin, for example the malformations of flowers under the influence of big-bud virus. Interesting and also showing this is the experimental induction of additional setae on the head in *Drosophila*, which was achieved by artificial selection for a strong expression of setae. Many systems of the deployment of some features have an open, essentially unrestricted character. Thus, for example, the row of teeth on the apex of the hind tibiae in the Fulgoroidea is formed in stages during the ontogeny: 2, 4, 6-7, 8; the retardation of this process leads to a decrease in the definitive (imaginal) number of teeth, while acceleration leads to an increase with no clearly tangible limit; cases are known in which the number of teeth was more than 20.

One of the pecularities of ontogenetic growth, allometry, also offers a direct path to instaurations, if in the evolution of any branch the organisms twice alter the direction of change of their dimensions. In this case once again the meristic features are affected most graphically. Of course, phyletic allometry is manifested in its clearest form on structures of secondary adaptive significance.

3. Instaurational heterobathmia. The acknowledgmenet of instauration phenomena entails some reconsideration of the concept of heterobathmia (Figure 35). When we compare contemporary monophyletic groups and establish the phenomenon of heterobathmia, then under this name we merge two groups of phenomena: a mosaic arrangement of features that arose as a result of evolution without instauration and a mosaic arrangement that arose as a result of the participation of instauration, considering all of these as heterobathmia without instaurations. It may be thought that, if we will establish the phenomenon of heterobathmia for the organism as a whole, then we will often encounter heterobathmias in the formation of which instaurations also participated, but if we will restrict ourselves to changes in any individual organs, etc., then here cases of simple of primary heterobathmia will also be frequenty encountered.

The acknowledgement of instauration phenomena entails a reconsideration of such phylogenetic concepts as apomorphy and plesiomorphy; it diminishes the accuracy of their contents and demonstrative force in the construction of phylogenetic trees, and makes it difficult to determine the direction of evolution of a feature over small intervals in the scale of genus, family, etc.

Compensation for the above-mentioned deficiencies should apparently be sought first of all by way of the enlistment of as large as possible a number of independent features of relationship. Taking into consideration that, on the whole, evolution moves forward, i.e. along the path of new formations, and that in this way new formations predominate over reversions, this path should nevertheless lead to objective results.

REFERENCES

1. Bekker, E. Contribution to the structures of the head of the Rhynchota. Part 1: Structure of the head of *Naucoris cimicoides* L.- Zoologischeskii zhurnal (Zoological Journal). 1929. vol. 9, no. 2, pp. 3-54.

2. Belyaev, D.K. Destabilizing selection as a factor of variability in the domestication of animals. - Priroda (Nature). 1979. No. 2. pp. 36-46.

3. Vorontsov, N.N. Homologous variability. - Probleny kibernetyki (Problems in cybernetics). 1966. No. 16. pp. 221-229.

4. Gabuniya, L.K. Lui Dollo (1857-1931). (Louis Dollo (1857-1931)). Moscow, 1974. 264pp.

5. Gadd, G.G. Structure of the intestinal duct of the larvae of Aphrophora *spumaria* L. - Trudy Imperatorskogo Sankt-Peterburgskogo obshchestva estestvoispytatelei (Transactions of the Imperial Society of Naturalists in Saint Petersburg). 1902. vol. 32, no. 4. pp. 65-95.

6. Gromov, B.V. Bacteria - intra-cellular symbionts of animals. - Uspekhi mikrobiologii (Advances in microbiology). 1978. No. 13, pp. 50-72.

7. Emel'yanov, A.F. Homology of wing structures in the cicadines and the primitive Polyneoptera. - Trudy Vsesoyuznogo entomologicheskogo obshchestva (Transactions of the All-Union Entomological Society). 1977. vol. 58. pp. 3-48.

8. Emel'yanov, A.F. The problem of the demarcation of the families Fulgoroidae and Dictyopharidae (Homoptera, Auchenorrhyncha). - Trudy Zoologicheskogo instituta Akademii Nauk SSSR (Transactions of the Zoological Institute of the Academy of Sciences of the USSR). 1979. vol. 82. pp. 3-22.

9. Emel'yanov, A.F. Phylogeny and evolution of dictyopharid planthoppers of the subfamily Orgeriinae (Homoptera, Dictyopharidae). - Chteniya pamyati N.A. Kholodkovskogo (Lectures in memory of N.A. Kholodkovskii). Leningrad. 1980. pp. 1-96.

10. Emel'yanov, A.F. The structure and origin of the endopleural formations on the metathorax in cicadines (Homoptera, Auchenorrhyncha). - Entomologischeskoe obozrenie (Entomological Review), 1981. vol. 60, no. 4. pp. 732-744.

11. Emel'yanov, A.F. The structure and evolution of the tarsi in the dictyopharid planthoppers (Homoptera, Dictyopharidae). - Entomo. obozrenie. 1982. vol. 61, no. 3. pp. 501-516.

12. Emel'yanov, A.F. and Kuznetsova V.G. The number of testicular follicles as a phylogenetic and taxonomic feature in the dictyopharid planthoppers (Homoptera, Dictyopharidae) and other cicadines. - Zoologischeskii zhurnal (Zoological Journal). 1983. vol. 62, no. 10, pp. 1583-1586.

13. Emel'yanov, A.F. and Fal'kovich, M.I. Concerning the book "Istorischeskoe razvitie klassa nasekomykh" ("Historical development of the class Insecta"). - Entomol. obozrenie. 1983. vol. 62, no. 1. pp. 205-222.

[The rest of the bibliography, on pages 105-109 of the Russian text, is not included in this translation at client's request. Tr.].