

**The interlocking mechanism of maxillae and mandibles in Fulgoroidea
(Insecta: Hemiptera: Fulgoromorpha)**

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ABSTRACT. The paper shows a general model of the internal structure of mouthparts in Fulgoroidea (Hemiptera: Fulgoromorpha), in cross-section through the subapical segment of rostrum. The study comprised 10 representatives of 8 various planthopper families. This is a comparative analysis of the connecting systems between right and left maxillae in Fulgoroidea. In the internal structure of mouthparts, three locks between maxillae have been identified: dorsal, middle and ventral. Straight, hooked and T-shaped processes form these locks. In all examined representatives of various families, the shape of the processes in corresponding locks is the same. A stable number of processes in particular locks have been observed in studied representatives of Fulgoromorpha families (dorsal lock – 4, middle lock – 3, ventral lock – 2). The food and salivary canals are formed by both maxillae. In the examined species the closure of the salivary canal is similar at the family level. The interlocking mechanism between right and left maxillae is the same in representatives of various families. Mandibles in Fulgoroidea are not firmly connected with maxillae but only contiguous with their external wall.

KEY WORDS: Fulgoromorpha, Fulgoroidea, Cixiidae, Delphacidae, Achilidae, Derbidae, Dictyopharidae, Issidae, Caliscelidae, Lophopidae, mouthparts, internal connecting systems, processes of dorsal, middle and ventral locks, food and salivary canals.

INTRODUCTION

External and internal structure of particular rostral elements as well as their function in penetration of plant tissues in the Hemiptera suborders: Cicadomorpha (cicadas, froghoppers, spittle bugs, leafhoppers) and Fulgoromorpha (planthoppers) have been discussed in several works, e.g. by SNODGRASS (1921, 1927, 1938), WILLIS (1949), ARRORA & SINGH (1962), POLLARD (1968, 1969, 1972), SORIN (1966), FORBES & RAINE (1973), BACKUS (1985), TAVELLA & ARZONE (1993).

Most detailed, morphological studies of "homopteran" mouthparts were concerned with aphids (Sternorrhyncha: Aphididae) rather than leafhoppers and planthoppers (PONSEN 1972, FORBES 1977). Up to date, connecting systems between maxillae and mandibles in Fulgoromorpha have not been analyzed in detail. Only three species of Fulgoromorpha were examined with respect to cross-section of the mouthparts, i.e. *Muellerianella fairmairei* (PERRIS, 1875), and *Nilaparvata lugens* (STÅL, 1854) of Delphacidae, and *Cixius nervosus* (LINNAEUS, 1758) of Cixiidae. However, COBBEN (1978) and BACKUS (1985) did not analyse the interlocking mechanism of maxillae and mandibles. Scant data on the internal structure of the mouthparts in Fulgoromorpha are to be found in EMELJANOV (1987). More is known about internal connecting systems of maxillae and between maxillae and mandibles in Cicadomorpha: Cicadellidae and Heteroptera (BROŽEK & HERCZEK 2001, 2004) and in Sternorrhyncha (unpublished data). These data provide information about new characters of taxonomic importance, which can be applied to kinship analysis.

The aim of the present study is to establish a general model of the internal structure of the mouthparts and the types of connecting systems between maxillae and mandibles in Fulgoromorpha.

Material and methods

A list of examined species is given below:

Achilla marginatifrons (HAGLUND, 1899) – Achilidae: Achillinae, det. M. Boulard;

Ommatidiotus dissimilis (FALLÉN, 1806) – Caliscelidae, det. J. Szwedó;

Cixius nervosus (GERMAR, 1818) – Cixiidae, det. H. Ribaut;

Javesella pellucida (FABRICIUS, 1794) – Delphacidae: Delphacinae, det. J. Szwedó;

Peregrinus maidis (ASHMEAD, 1890) – Delphacidae: Delphacinae, det. G. Gouturier

Stiroma affinis FIEBER, 1866 – Delphacidae: Delphacinae, Poland, det. J. Szwedó;

Diostrombus gangumis VAN STALLE, 1984 – Derbidae: Derbinae: Cenchreini, det. G. Gouturier;

Dictyophara europaea (LINNAEUS, 1763) – Dictyopharidae: Dictyopharinae;

Trienopa paradoxa GERSTAECKER, 1892 – Issidae: Trienopinae, det. M. Boulard;

Lophops africanus (SCHMIDT, 1912) – Lophopidae, det. A. Soulier-Perkins;

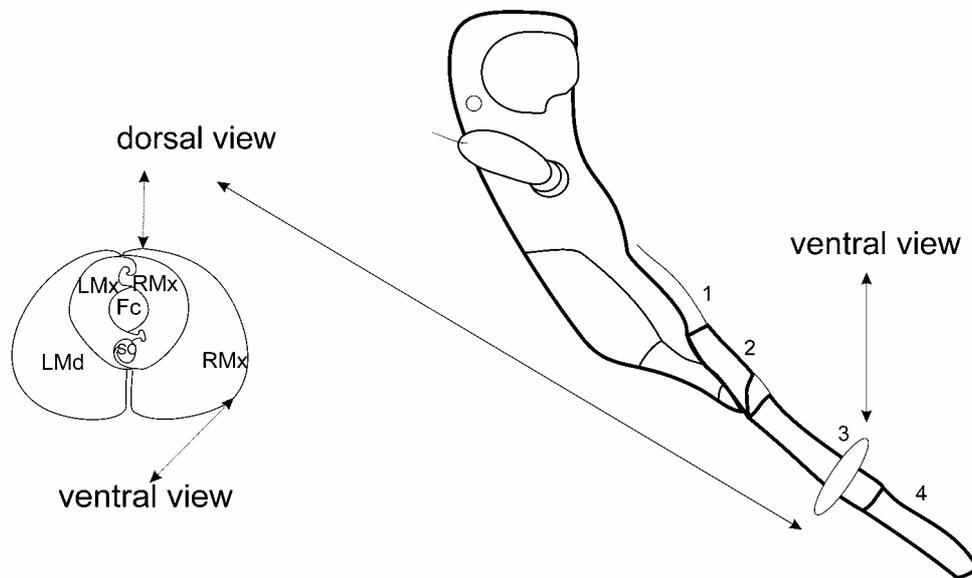


Fig. 1 – Head of the planthopper in lateral view and dorsal view of mouthparts at the point of cross section.

Material for analysis was obtained from the collection of the Museum National d'Historie Naturelle in Paris: *Peregrinus maidis*, *Cixius nervosus*, *Achilla marginatifrons*, *Dictyophara europaea*, *Trienopa paradoxa*, *Lophops africanus*, and *Distrombus gangumis*; and from the collection of the Department of Zoology, Faculty of Biology and Environmental Protection, University of Silesia in Katowice: *Stiroma affinis*, *Javesella pellucida* and *Ommatidiotus dissimilis*. The basal part of head with a part of rostrum was glued vertically onto the stage of a scanning microscope. Thus prepared material was dusted with gold and photographs were taken in SEM, Jeol SM III. The obtained documentation helped to reconstruct the rostrum from the point of cross-section. The structure of mouthparts was analysed in cross-section through the subapical rostral segment of adult specimens. This segment is usually well-developed and present in all adult planthoppers. According to other researchers, the internal structure of rostrum is irregular, so it was essential that comparison of the same structural elements in the studied groups be conducted with reference to the same level of cross-section (FORBES 1976).

Figure 1 presents dorsal view of the mouthparts of planthopper and the point of cross-section through the subapical segment of mouthparts.

Figure 2 present a general model of connecting systems between maxillae and mandibles in Fulgoroidea.

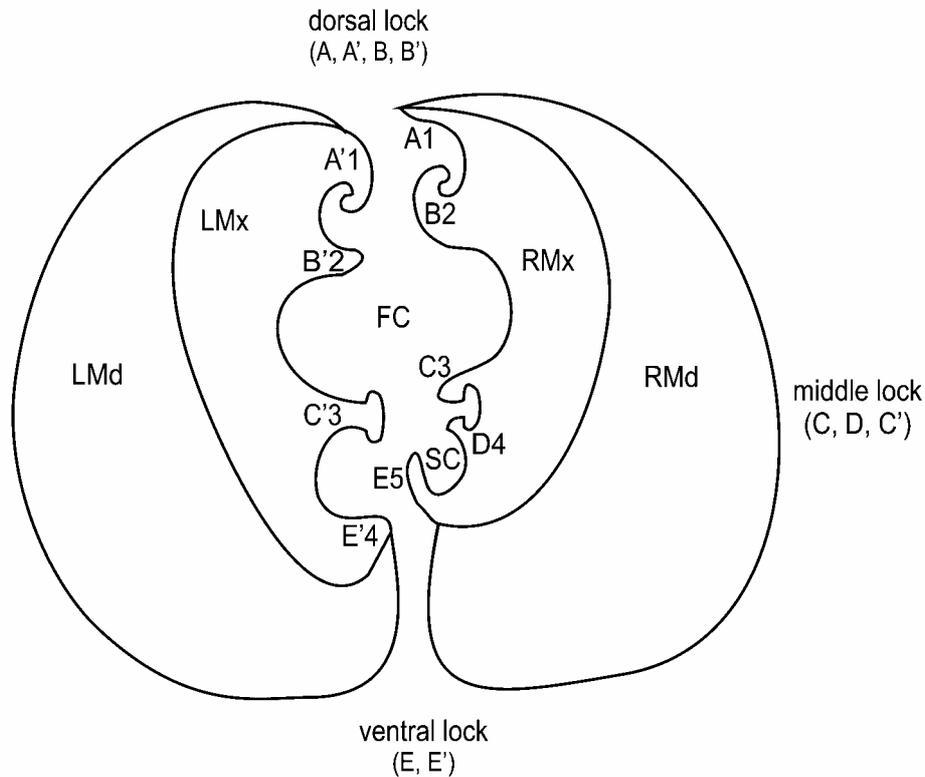


Fig. 2 – general scheme of connecting system between maxillae and mandibles in Fulgoroidea.

Figures are presented in apical view from the base to the apex of rostrum. The dorsal and ventral parts (dorsal, middle and ventral locks) of rostrum are marked in relation to the body axis. Orientation of maxillae and mandibular stylets, the position of the processes and the location of the salivary and food canals were established after POLLARD (1972).

RESULTS

The studied representatives of planthoppers have three arms on the inner surface of right and left maxillae: dorsal, middle and ventral arm. In their apical part, the arms bear processes of various shape. Terms used to describe these processes derive from their size and position (Fig. 2). If in the locks of maxilla there are two processes one above the other, these structures are called the upper (Fig. 2: A, A') and the lower processes (Fig. 2: B, B'). Unlike a T-shaped process (Fig. 2: C'), a hooked process (Fig. 2: C, D, E) is bent to one

side, while a straight process (Fig. 2: D') is not deflected.

The number of processes on the arms of right and left maxillae is different. On the right maxilla there are five processes, while on the left maxilla there are four. The relative placement of processes on the arms of right and left maxilla forms complex connecting structures, the locks. Representatives of Fulgoromorpha have three locks: dorsal, middle and ventral.

The dorsal lock comprises four processes (Fig. 2): upper – hooked (A') and straight (A); and lower – straight (B') and hooked (B). Two hooked processes (A') and (B) interlock. Straight processes (A) and (B') form a cover for the interlocking hooked processes. They prevent the unhooking of hooked processes when maxillae are moving. They may also prevent various elements from penetrating into the lock between the inner faces of hooked processes.

The middle lock is composed of three processes (Fig. 2): a T-shaped process (C') and two hooked processes (C, D). Hooked processes (C, D) interlock with the T-shaped process (C'). The glide path for the T-shaped process is formed by hooked processes, which prevent the maxillae from opening.

The ventral lock comprises only two processes (Fig. 2): a straight process (D') and a hooked process (E).

The food canal is formed by both maxillae and is placed centrally in subdorsal portion. It is usually oval in cross-section due to concave inner walls of maxillae.

The salivary canal is formed by both maxillae. Process (E), which belongs to the ventral lock, is short, and the left maxilla forms a lateral wall closing the salivary canal (Fig. 2).

The canals differ in size. The diameter of the food canal was found to be much greater than that of the salivary canal.

Mandibles are placed laterally in relation to maxillae. The concave, smooth surfaces of mandibles are contiguous with the convex walls of maxillae (Fig. 2).

Cixiidae

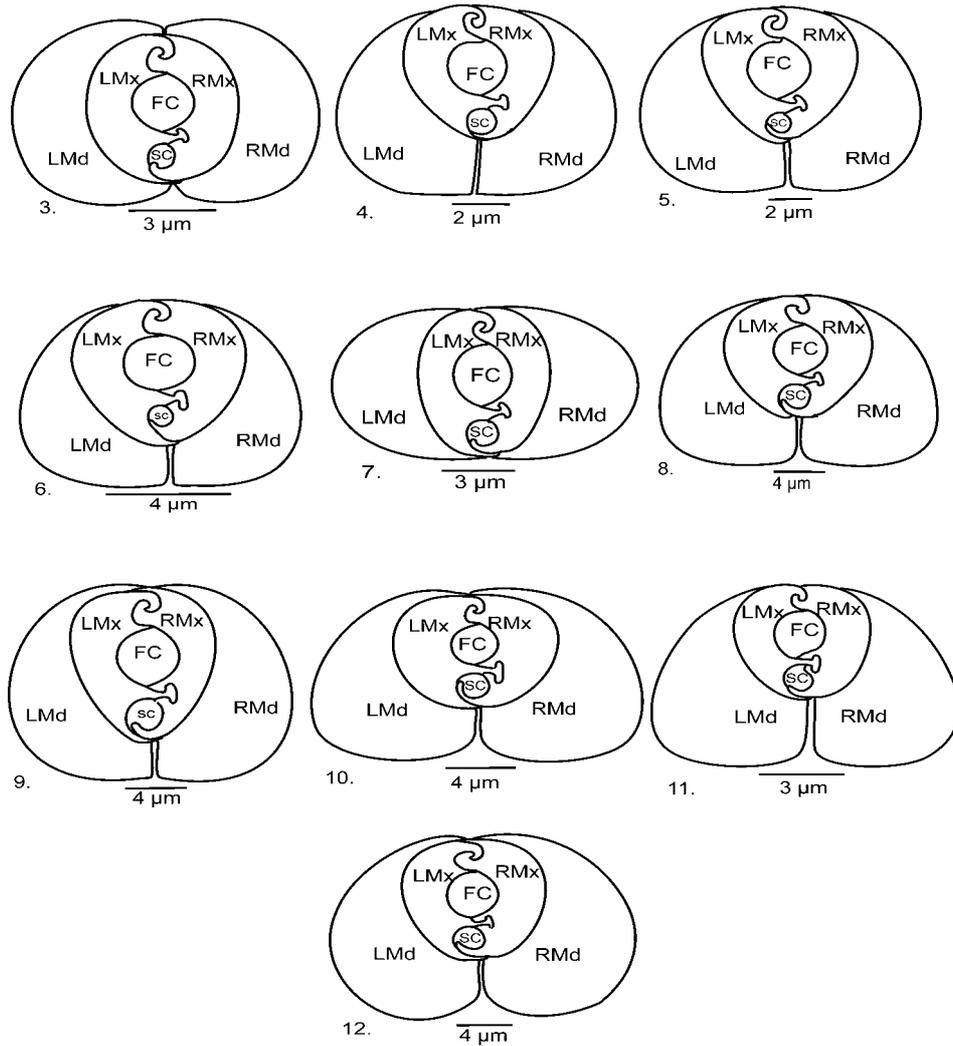
In representatives of the family Cixiidae the dorsal lock is formed by four processes. On the left maxilla, there are processes: upper hooked and lower straight. On the right maxilla, there are two processes: upper straight and lower hooked (Figs 3 & 13).

The middle lock is formed by three processes. On the left maxilla, there is a T-shaped process. On the right maxilla, there are two hooked processes (Figs 3 & 13).

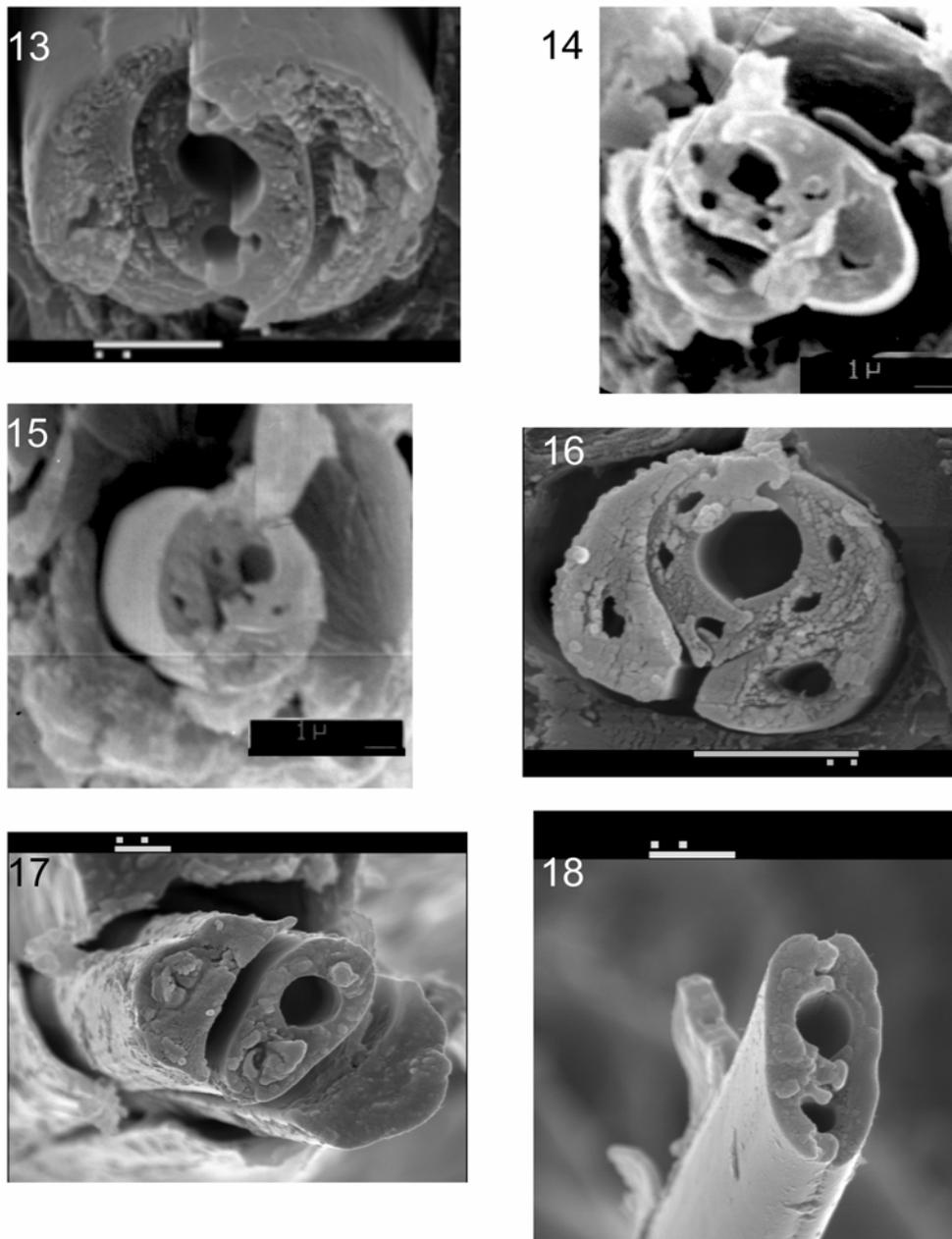
The ventral lock is formed by only two processes: straight and hooked. On the left maxilla, there is a straight process which interacts with the hooked process of the right maxilla (Figs 3 & 13).

The food canal is formed by both maxillae and is placed centrally in subdorsal portion. The salivary canal is formed by both maxillae. The process on the right maxilla which belongs to the ventral lock is short, and the left maxilla forms a lateral wall closing the salivary canal. Mandibles are placed laterally in relation to maxillae. Mandibles are enlarged

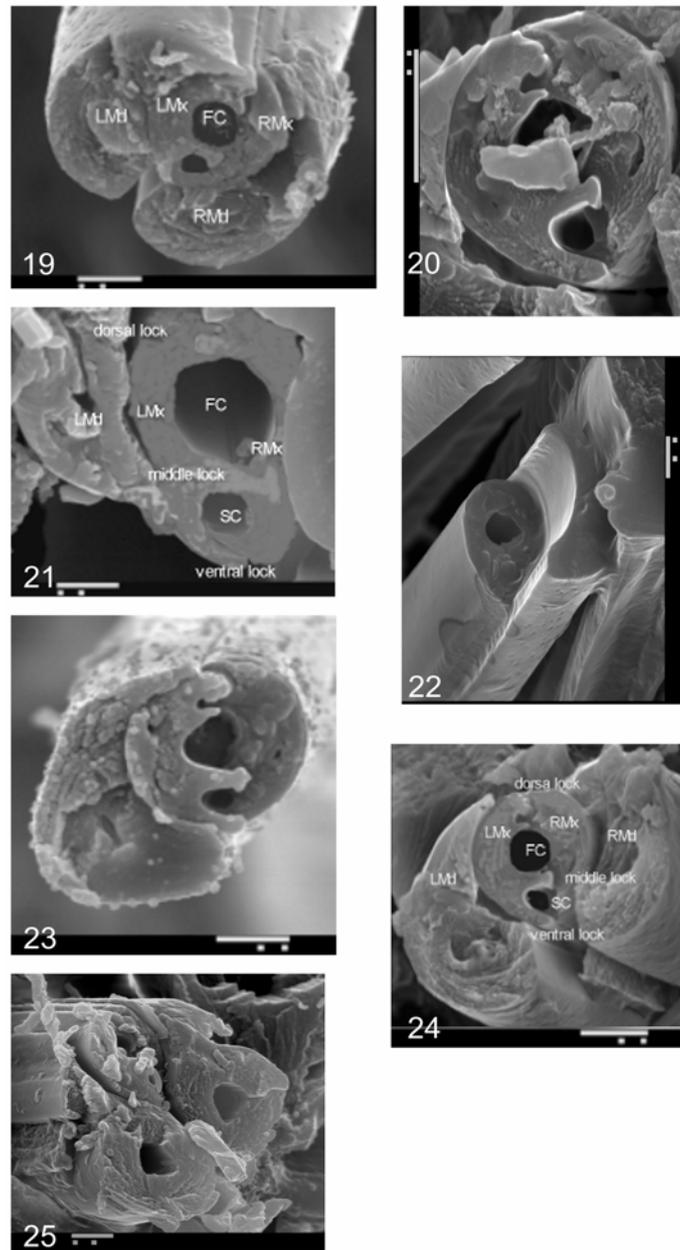
laterally and surround the dorsal lock from above and the ventral lock from beneath (Figs 3 & 13).



Figs 3–12. Cross section through by subapical segment of the rostrum in Fulgoromorpha. 3 - *Cixius nervosus* (Cixiidae), 4 - *Stiroma affinis* (Delphacidae), 5 - *Javesella pellucida* (Delphacidae), 6 - *Peregrinus maidis* (Delphacidae), 7 - *Achilla marginatifrons* (Achilidae), 8 - *Diostrombus gangumis* (Derbidae), 9 - *Dictyophara europea* (Dictyopharidae), 10 - *Trienopa paradoxa* (Issidae), 11 - *Ommatidiotus dissimilis* (Caliscelidae), 12 - *Lophops africanus* (Lophopidae).



Figs. 13–18. Cross section through by subapical segment of the rostrum in Fulgoromorpha: 13 - *Cixius nervosus* (Cixiidae), 14 - *Stiroma affinis* (Delphacidae), 15 - *Javesella pellucida* (Delphacidae), 16 - *Peregrinus maidis* (Delphacidae), 17, 18 - *Achilla marginatifrons* (Achilidae).



Figs 19–25. Cross section through by subapical segment of the rostrum in Fulgoromorpha: 19, 20 - *Diostrombus gangumis* (Derbidae), 21, 22 - *Dictyophara europaea* (Dictyopharidae) 23 - *Trienopa paradoxa* (Issidae), 24 - *Ommatidiotus dissimilis* (Caliscelidae), 25 - *Lophops africanus* (Lophopidae).

Delphacidae

In representatives of the family Delphacidae the dorsal lock is formed by four processes. On the left maxilla there are processes: upper, hooked and lower straight. On the right maxilla there are two processes: upper straight and lower hooked (Figs 4, 5 & 6).

The middle lock is formed by three processes. On the left maxilla, there is a T-shaped process. On the right maxilla, there are two hooked processes (Figs 4, 5 & 6).

The ventral lock is formed by only two processes: straight and hooked. On the left maxilla, there is a straight process, which interacts with the hooked process of the right maxilla.

The food canal is formed by both maxillae and is placed centrally in subdorsal portion. The salivary canal is formed by both maxillae. The process on the right maxilla which belongs to the ventral lock is short, and the left maxilla forms a lateral wall closing the salivary canal (Figs 4–6, 14–16).

Mandibles are placed laterally in relation to maxillae. Mandibles are better developed in their ventral part and surround the ventral lock from beneath. (Figs 4, 5, 6, 14, 15 & 16).

Achilidae

In representatives of the family Achilidae the dorsal lock is formed by four processes. On the left maxilla, there are processes: upper hooked and lower straight. On the right maxilla, there are two processes: upper straight and lower hooked (Figs 7, 17 & 18).

The middle lock is formed by three processes: straight and hooked. On the left maxilla, there is a T-shaped process. On the right maxilla, there are two hooked processes (Figs 7 & 17).

The ventral lock is formed by only two processes. On the left maxilla, there is a straight process, which interacts with the hooked process of the right maxilla (Figs 7 & 17).

The food canal is formed by both maxillae and is placed centrally in subdorsal portion. The salivary canal is formed by both maxillae. The process on the right maxilla which belongs to the ventral lock is short, and the left maxilla forms a lateral wall closing the salivary canal.

Mandibles are placed laterally in relation to maxillae. Mandibles are enlarged laterally and surround the dorsal lock from above and the ventral lock from beneath (Figs 7 & 17).

Derbidae

In representatives of the family Derbidae the dorsal lock is formed by four processes. On the left maxilla, there are processes: upper hooked and lower straight. On the right maxilla, there are two processes: upper straight and lower hooked (Figs 8, 19 & 20).

The middle lock is formed by three processes. On the left maxilla, there is a T-shaped process. On the right maxilla, there are two hooked processes (Figs 8, 19 & 20).

The ventral lock is formed by only two processes: straight and hooked. On the left maxilla, there is a straight process, which interacts with the hooked process of the right maxilla (Figs 8, 19 & 20).

The food canal is formed by both maxillae and is placed centrally in subdorsal portion. The salivary canal is formed by both maxillae. The process on the right maxilla which belongs to the ventral lock is short, and the left maxilla forms a lateral wall closing the salivary canal.

Mandibles are placed laterally in relation to maxillae. Mandibles are better developed in their ventral part and surround the ventral lock from beneath (Figs 8, 19 & 20).

Dictyopharidae

In representatives of the Dictyopharidae four processes form the dorsal lock. On the left maxilla, there are processes: upper hooked and lower straight. On the right maxilla, there are two processes: upper straight and lower hooked (Figs 9, 21 & 22).

Three processes form the middle lock. On the left maxilla, there is a T-shaped process. On the right maxilla, there are two hooked processes (Figs 9, 21 & 22).

Two processes form the ventral lock: straight and hooked. On the left maxilla, there is a straight process, which interacts with the hooked process of the right maxilla (Figs 9, 21 & 22).

The food canal is formed by both maxillae and is placed centrally in subdorsal portion. The salivary canal is formed by both maxillae. The process on the right maxilla, which belongs to the ventral lock, is short, and the left maxilla forms a lateral wall closing the salivary canal.

Mandibles are placed laterally in relation to maxillae. Mandibles are better developed in their ventral part and surround the ventral lock from beneath (Figs 9, 21 & 22).

Issidae

In representatives of the family four processes form the dorsal lock. On the left maxilla, there are processes: upper hooked and lower straight. On the right maxilla, there are two processes: upper straight and lower hooked (Figs 10 & 23).

Three processes form the middle lock. On the left maxilla, there is a T-shaped process. On the right maxilla, there are two hooked processes (Figs 10 & 23).

Two processes form the ventral lock: straight and hooked. On the left maxilla, there is one straight process, which interacts with the hooked process of the right maxilla (Figs 10 & 23).

The food canal is formed by both maxillae and is placed centrally in subdorsal portion. The salivary canal is formed by both maxillae. The process on the right maxilla that belongs to the ventral lock is short, and the left maxilla forms a lateral wall closing the salivary canal.

Mandibles are placed laterally in relation to maxillae. Mandibles are better developed in their ventral part and surround the ventral lock from beneath (Figs 10 & 23).

Caliscelidae

In representatives of the family four processes form Caliscelidae the dorsal lock. On the left maxilla, there are processes: upper hooked and lower straight. On the right maxilla, there are two processes: upper straight and lower hooked (Figs 11 & 24).

Three processes form the middle lock. On the left maxilla, there is a T-shaped process. On the right maxilla, there are two hooked processes (Figs 11 & 24).

Only two processes form the ventral lock: straight and hooked. On the left maxilla, there is a straight process, which interacts with the hooked process of the right maxilla (Figs 11 & 24).

The food canal is formed by both maxillae and is placed centrally in subdorsal portion. The salivary canal is formed by both maxillae and is placed centrally. The process on the right maxilla that belongs to the ventral lock is short, and the left maxilla forms a lateral wall closing the salivary canal.

Mandibles are placed laterally in relation to maxillae. Mandibles are better developed in their ventral part and surround the ventral lock from beneath (Figs 11 & 24).

Lophopidae

In representatives of the family of Lophopidae four processes form the dorsal lock. On the left maxilla, there are processes: upper hooked and lower straight. On the right maxilla, there are two processes: upper straight and lower hooked (Fig. 12).

Three processes form the middle lock. On the left maxilla, there is a T-shaped process. On the right maxilla, there are two hooked processes (Fig. 12).

Only two processes form the ventral lock: straight and hooked. On the left maxilla, there is a straight process, which interacts with the hooked process of the right maxilla (Fig. 12).

The food canal is formed by both maxillae and is placed centrally in subdorsal portion. The salivary canal is formed by both maxillae. The process on the right maxilla that belongs to the ventral lock is short, and the left maxilla forms a lateral wall closing the salivary canal.

Mandibles are placed laterally in relation to maxillae. Mandibles are best developed in their ventral part and surround the ventral lock from beneath (Figs 12 & 25).

DISCUSSION

An interesting aspect of the inner structure of mouthparts in the studied species is the high structural similarity observed in different families of Fulgoromorpha. One of the characteristic

features of planthoppers is the different number of processes constituting each of the three locks (dorsal lock – 4 processes, middle lock – 3 processes and ventral lock – 2 processes). Another model was observed in Cicadomorpha (BROŹEK & HERCZEK 2001), where there are only two locks: dorsal and ventral (and the locks are formed by four processes each). Fulgoromorpha and Cicadomorpha have long been regarded as sister groups – a claim supported by YOSHIKAWA & SAIGUSA (2001) and BOULARD (2002). It appears, however, that these two groups should perhaps receive a different treatment (BROŹEK et al. 2003; BOURGOIN & CAMPBELL 2002). A close relationship between Fulgoromorpha and Cicadomorpha does not seem to be supported by the characters of the internal connecting systems of the mouthparts. The presence of three locks in the mouthparts has been observed in both Heteroptera (BROŹEK & HERCZEK 2004) and Sternorrhyncha (BROŹEK, in press). The number of locks in Fulgoromorpha, Heteroptera and Sternorrhyncha offers an interesting insight into the phylogenetic relationship among these groups. Some authors have suggested the possibility of a sister-group relationship between Fulgoromorpha and Heteroptera (GOODCHILD 1966; HAMILTON 1981; BOURGOIN 1986, 1993; BOURGOIN et al. 1997; SWEET 1996; SORENSEN et al. 1995; CAMPBELL et al. 1995).

A position of the food canal is stable, i.e. central in the dorsal part of the rostrum. It has been observed that the shape and size of the food canal are similar in all the analyzed species of Fulgoromorpha (Figs 2–24). The stable central position of the food canal has also been observed in other groups of Heteroptera (BROŹEK & HERCZEK 2004) and in Sternorrhyncha.

The salivary canal is placed in both maxillae in all the studied representatives of various families, and the size of the canal is similar. A unique feature of this group is the type of closure of the salivary canal. In representatives of the examined families, the salivary canal is closed by a short process of the right maxilla (Figs 2–8, 10–12), and by the wall of the left maxilla. On the basis of COBBEN's (1978) photograph it can be established that in *Muellerianella fairmairei* (PERRIS, 1857) (Delphacidae) the salivary canal is closed in a similar way. A different situation can be observed in *Nilaparvata lugens* (STÅL, 1854) (Delphacidae), where, according to Fig. 7.7 in BACKUS (1985), the salivary canal is entirely closed by a very long process of the right maxilla. This type of closure of the salivary canal in heteropteran groups (BROŹEK & HERCZEK 2004) is reminiscent of Fulgoromorpha. Another type of closure of the salivary canal is observed in Cicadellidae. In this group, the upper process of the ventral lock, which is placed on the left maxilla (BROŹEK & HERCZEK 2001), closes the salivary canal.

In the analysed species of Fulgoromorpha, no connection has been found between maxillae and mandibles. Mandibles lie close to maxillae, which is also true of Cicadomorpha. In contrast to Fulgoromorpha and Cicadomorpha (BROŹEK & HERCZEK 2001), in Heteroptera maxillae and mandibles are connected by processes (COBBEN 1978; BROŹEK & HERCZEK 2004).

In the examined representatives of Delphacidae, Derbidae, Dictyopharidae, Issidae, Caliscelidae and Lophopidae, mandibles are better developed in the ventral part. On the basis of Fig. 7.7 of *Nilaparvata lugens* (Delphacidae) in BACKUS (1985) and on the basis of COBBEN's (1978) data on *Muellerianella fairmairei* (Delphacidae), it can be established that also in these two species mandibles are better developed in their ventral part. Only in Cixiidae and Achilidae

mandibles are laterally enlarged (Figs 3 & 7). Resemblance between the shape of maxillae and mandibles in Cixiidae and Achilidae may result from their phylogenetic relationships.

According to BOURGOIN (1986), the clades Cixiidae and Achilidae are probably closely related. However, ASCHE (1987) and EMELJANOV (1991), based on morphology, argue that the nearest group to Cixiidae is Delphacidae. It was also supported by female genitalia structures (BOURGOIN 1993) and molecular data (BOURGOIN et al. 1997, YEH et al. 2005). ASCHE (1987), EMELJANOV (1991) BOURGOIN (1993), BOURGOIN et al. (1997) agreed that Meenopliidae is a sister group to Kinnaridae, Fulgoridae is a sister group to Dictyopharidae, Achilidae and Derbidae are closely related. Based on the molecular research the relationship between Meenoplidae and Delphacidae is distant (YEH et al. 1998), which is in disagreement with studies of nymphal characters (CHEN & YANG 1995). YANG & FANG (1993), based on nymphal characters divided Fulgoroidea into 2 groups Delphacidae–Meenopliidae–Cixiidae–Achilidae–Derbidae, with the rest in an individual group. CHEN & YANG (1995) divided them into five family groups (I: Tettigometridae-group – Tettigometridae; II: Ricaniidae-group – Ricaniidae, Lophopidae, Eurybrachidae, Hypochtonellidae, Gengidae; III: Tropiduchidae-group: Tropiduchidae, Flatidae, Nogodinidae, Issidae, Acanaloniidae, IV: Fulgoridae-group: Fulgoridae, Dictyopharidae; V: Cixiidae-group: Delphacidae, Meenoplidae, Kinnaridae, Cixiidae, Achilidae, Achilixidae, Derbidae). YANG & CHANG (2000) based on nymphal features and male genital structures, proposed sister groups Achilidae and Achilixidae, Cixiidae and Derbidae, Fulgoridae and Dictyopharidae, Kinnaridae and Meenopliidae as sister group to Delphacidae. According to YEH et al. (2005) Delphacidae and Cixiidae are sister groups, Derbidae is sister group to Tropiduchidae, Fulgoridae to Dictyopharidae, and Meenoplidae to Lophopidae. All these families form basal lineage of Fulgoroidea, where relationships among Meenoplidae, Delphacidae–Cixiidae, Lophopidae and Achilidae cannot be clearly resolved. Several groups among families in the derived lineages are revealed, including Derbidae–Tropiduchidae, Dictyopharidae–Fulgoridae, and Eurybrachidae–Ricaniidae, but relationships among the remaining families were poorly resolved (YEH et al. 2005).

Different morphological characters appear to reveal different relative phylogenetic positions of particular families, molecular results are also ambiguous. Thus, the only conclusion generally accepted in Fulgoroidea systematics is that the Fulgoridae and Dictyopharidae are sister groups, the families Cixiidae, Achilidae and Delphacidae – and Derbidae, Kinnaridae and Meenoplidae – are recognized as a cluster of closely related planthopper groups lying near the common stem. The study of the internal structure of the mouthparts allows adding more important data for studies on Fulgoroidea phylogeny.

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