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MORPHOLOGY OF ANTENNAL SENSILLA IN *ACHILIXIUS SANDAKANENSIS* MUIR (HEMIPTERA: FULGOROMORPHA: ACHILIXIIDAE) WITH COMMENTS ON THE PHYLOGENETIC POSITION OF THE ACHILIXIIDAE

Ai-Ping Liang

Department of Entomology, Institute of Zoology, Chinese Academy of Sciences, 19 Zhongguancun Lu, Beijing 100080, P. R. China

ABSTRACT. – External morphology of antennal sensilla on adult male of *Achilixius sandakanensis* Muir (Hemiptera: Fulgoromorpha: Achilixiidae) was examined using scanning electron microscopy. Five major types of sense organs were found on the pedicel and the swollen flagellar base. These are microtrichia, cuticular denticles, plaque organs, coeloconic sensillum, and basal flagellar process. The 'Bourgoin's organ' on the apex of the swollen flagellar base, named by Cobben (1988), is considered as a coeloconic sensillum. The basal flagellar process is proposed as a strong apomorphy of the Achilixiidae and Cixiidae and the clear homology of this structure in the two families indicates that the Cixiidae is paraphyletic with respect to the Achilixiidae; Achilixiidae should therefore be treated as a subgroup of the Cixiidae following Liang (1999). The two achilixiid subfamilies, Achilixiinae and Bebaiotinae, which were previously placed by Emeljanov (1991) in the Achilidae, are moved to the Cixiidae.

KEY WORDS. – Antennal sensilla, basal flagellar process, ultrastructure, homology, phylogenetic position, Achilixiidae, Cixiidae, Fulgoromorpha.

INTRODUCTION

The Achilixiidae is one of the smallest of the twenty families of the hemipteran infraorder Fulgoromorpha. Currently the family includes only twenty-four described species in two genera: *Achilixius* Muir (sixteen species) from the Oriental region and *Bebaiotes* Muir (eight species) from the Neotropical region (Metcalf, 1945; Wilson, 1989).

The Achilixiidae is poorly defined and its monophyly has never been established. Muir (1923a, 1923b, 1924) characterized this family primarily by the possession of one or two pairs of processes arising laterally from the abdomen. But rather similar lateral abdominal processes are also present in the Bennini (including *Benna* Walker and *Bennarella* Muir) of the Cixiidae and the homology of this structure in the Achilixiidae and the bennine Cixiidae has been questioned by Fennah (1947), Hoch (1988) and Emeljanov (1991) (see Discussion below).

The phylogenetic relationship of the Achilixiidae to other fulgoromorphan groups has been uncertain and it has been variously linked with various families by various authors (Muir, 1923a, 1923b, 1930; Fennah, 1947, 1950; Metcalf, 1938, 1945; Emeljanov, 1990, 1991; also see Discussion below). New characters are needed to solve these problems.

The morphology of the antennal sensilla has provided many useful characters for the taxonomic and phylogenetic studies of Fulgoromorpha (see, for example, Hansen, 1890; Marshall & Lewis, 1971; Bourgoin & Deiss, 1994; Cheng & Yang, 1997). However, the antennal sensilla of the achilixiids are still undescribed except one published scanning electron micrograph showing the antennal sensilla of an undetermined *Achilixius* species by Wilson (1989).

The present paper gives a description of the external morphology, number, and distribution of the antennal sensilla that are found on the antenna of *Achilixius sandakanensis* Muir and provides a discussion on the phylogenetic position of the Achilixiidae in light of the new antennal characters revealed.

MATERIALS AND METHODS

Material. – Specimens used in this study were from the Natural History Museum, London (BMNH) and the Institute of Zoology, Chinese Academy of Sciences, Beijing, China (IZCAS). *Achilixius sandakanensis* Muir (Achilixiidae, Borneo: Sabah, BMNH) was examined externally by both SEM and light microscopy. *Bebaiotes nigrigaster* Muir (Achilixiidae, Ecuador, BMNH) was examined only by light microscopy. *Betacixius nigromarginalis* Fennah

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(Cixiidae, China: Sichuan, IZCAS), *Catonidia* sp. (Achilidae, China: Hainan, IZCAS), *Zathauma metasequoiae* Fennah (Achilidae, China: Hubei, IZCAS), *Proutista* sp. (Derbidae, Borneo, IZCAS) and several other species from the Cixiidae and Achilidae were examined by either SEM or light microscopy for comparison.

SEM. – Dry pinned male specimens were employed. For scanning electron microscopy (SEM), the head together with antennae was removed from the body and transferred to 10% KOH for 2 minutes, cleaned with fine brush, then washed in distilled water, mounted on aluminium stubs by double-sided sticky tape, air-dried at room temperature, and coated with gold-palladium using a sputter coater. Observations were made with a JEOL 5200LV and Zeiss DSM 950 scanning electron microscope, operated at accelerating voltages of 25 kV.

Terminology. – Morphological terminology follows that of Kramer (1950), Lewis & Marshall (1970) and Marshall & Lewis (1971).

RESULTS

1. Gross morphology of the antenna

As in other planthoppers, the antennae of *A. sandakanensis* are situated on the lateral region of the frons beneath the compound eyes. Each antenna consists of three segments: a small basal scape, a cylindrical pedicel and a long bristle-like flagellum (Fig. 1). The flagellum is composed of two distinct portions, a swollen, amphora-like base with smooth surface and a short petiole at the extreme base and a long, slender, non-segmented, apical extension (Figs. 1, 3, 4). The scape is without special characters, but the pedicel and the amphora-like flagellar base are distinctive in possessing sensory sensilla.

2. Antennal sensilla types and distribution

Five major types of sense organs are found; these are microtrichia, cuticular denticles, and plaque organs on the surface of the pedicel, and coeloconic sensillum and basal flagellar process on the apex of the amphora-like flagellar base (Figs. 1-4).

(1) *Microtrichia*
These are very fine and short hair-like structures. They are very few in number and are scattered on the surface of the pedicel. Their base is inserted into a well defined socket on a raised, broad, and round base (Figs. 1, 2). The microtrichia are common in the Fulgoromorpha, but in the Achilixiidae they are very sparse in number and are distinct in having a raised, broad and round base.

(2) *Cuticular denticles*
These are small, sclerotized, blunt denticles which are present in great numbers on the surface of the pedicel (excluding the extreme base) (Figs. 1, 2). They are about 5-8 mm long and are tooth-shaped with smooth surface and acute apex. They are somewhat regularly and circularly arranged around the digitate processes of the plaque organs (see below). The number of the denticles surrounding each plaque organ varies from 18 to 38, depending on the plaque diameter.

The cuticular tooth-like denticles are also found in the Cixiidae, Meenoplidae, Kinnaridae, Derbidae (part), and Tropiduchidae (part) but are absent in the Tettigometridae, Delphacidae, Derbidae (part), Dictyopharidae, Lophopidae, and Flatidae (Marshall & Lewis, 1971; Bourgoin, 1985; Bourgoin & Deiss, 1994; Liang, unpubl. data).

(3) *Plaque organs*
The plaque organs were first described by Lewis & Marshall (1970) in the *Pyrops candelaria* L. (Fulgoridae). In *A. sandakanensis*, there are approximately 20-22 plaque organs on the pedicel surface of each antenna (Fig. 1). They are evenly distributed on the pedicel surface (excluding the extreme base) and are of typical digitate, flattened, star-shaped. Each plaque possesses 12-18 digitate processes. The digitate processes are concentric around a bare, flat, central multiporous area of about 10 µm diameter and clearly tend to be arranged in pairs which are separated by the cuticular denticles. The digitate process is about 23-35 µm long, slender, compressed and concave laterally, and hollow centrally (Fig. 2).

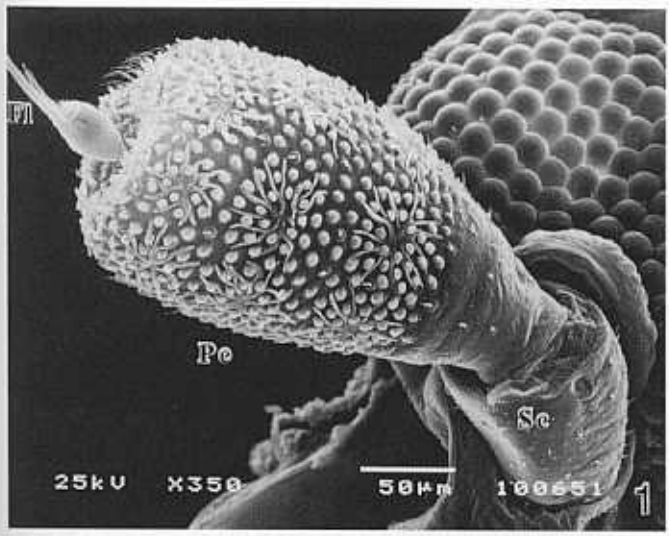
The flattened star-shaped plaque organs were also found in the Cixiidae (part), Meenoplidae, and Kinnaridae (Bourgoin & Deiss, 1994; Liang, unpubl. data).

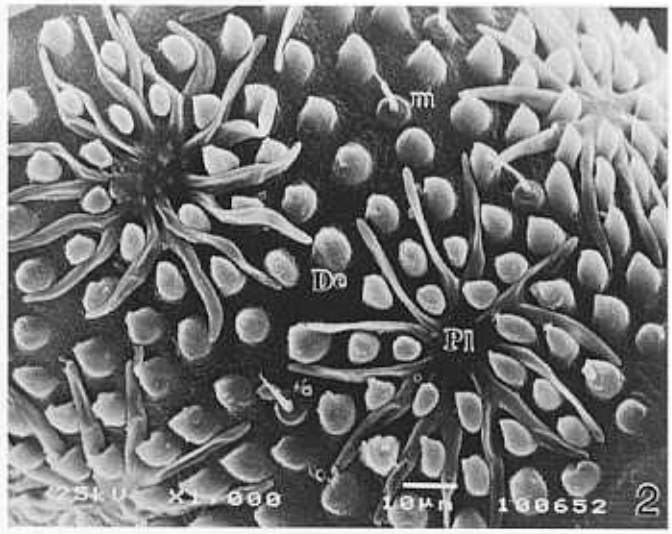
(4) *Coeloconic sensillum*
This is a sensory structure located at the apex of the swollen amphora-like flagellar base. It is composed of a shallow cavity with an opening which is surrounded by dorsally and inwardly directed tufts of hairs and with one or several central grooved pegs set on the inner wall of the cavity (Figs. 3, 4; the pegs are not obvious here in *A. sandakanensis*, but see Bourgoin, 1985: Figs. 16, 17; Liang, 2000: Fig. 9).

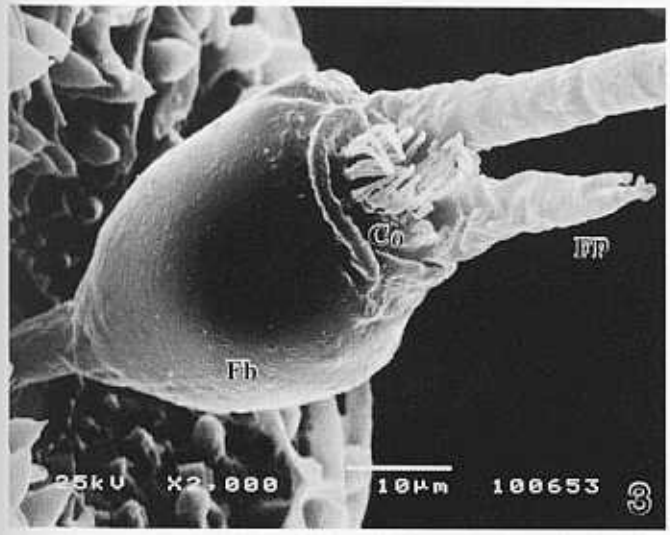
This structure was first described by Bourgoin (1985) as a 'basal sensory organ' of the flagellum. Cobben (1988) called it the 'Bourgoin's organ'. Baker & Chandrapatya (1993) described this structure as the 'flagellar atrium'. However, my comparative study of this structure in *A. sandakanensis* and species from several other fulgoromorphan families showed that it is actually a coeloconic sensillum (Liang, in prep.).

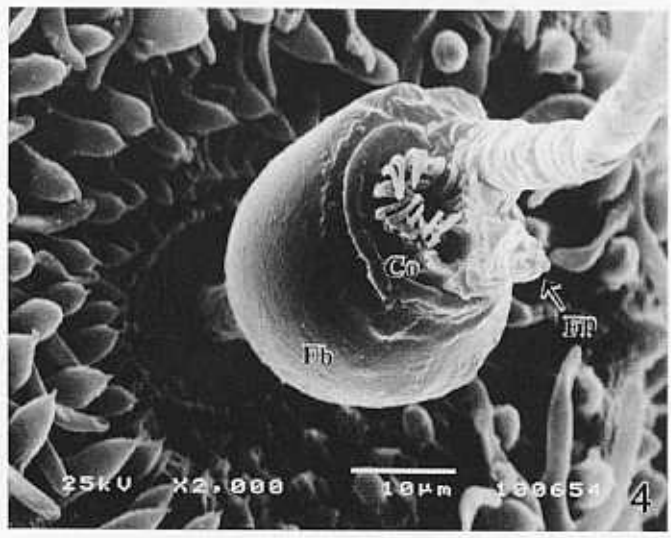
The tufts of hairs surrounding the opening of the swollen amphora-like base were also seen in the Cixiidae (part), Achilidae, Derbidae (Fig. 6), Meenoplidae, Kinnaridae, and Flatidae (part) but was not found in Tettigometridae, Dictyopharidae, Fulgoridae, Tropiduchidae, and Lophopidae (Bourgoin & Deiss, 1994; Liang, 2000, in prep.).

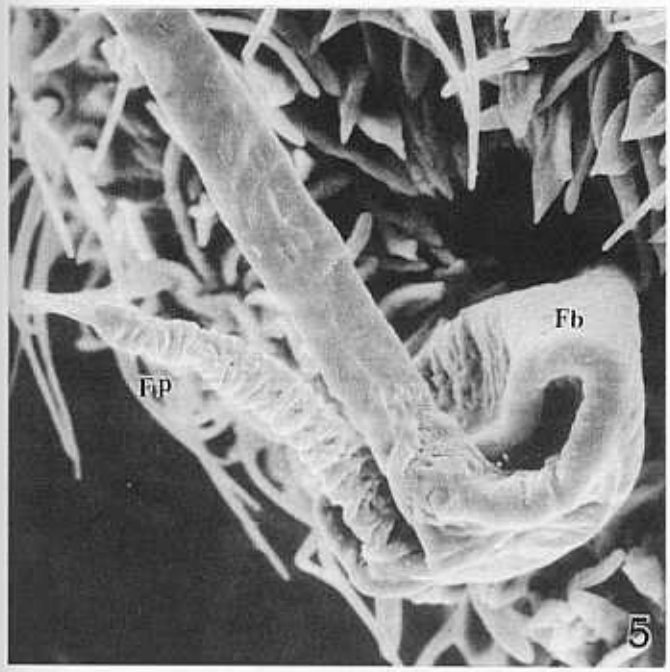
(5) *Basal flagellar process*
This is an elongate, filamentous process with digitate tip which is located at the apex of the swollen amphora-like flagellar base opposing the coeloconic sensillum and being

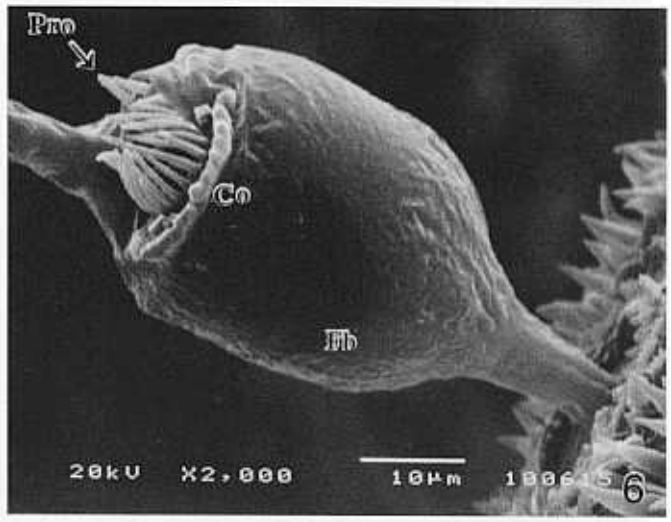












Figs. 1-6. Scanning electron micrographs of antennal sensilla of planthoppers. 1-4. *Achilixius sandakanensis* Muir (Achilixiidae): 1. antenna, showing the scape (Sc), pedicel (Pe) and flagellum (Fl); 2. surface of pedicel, showing microtrichia (m), cuticular denticles (De), and plaque organs (Pl); 3. swollen, amphora-like, flagellar base (Fb), showing coeloconic sensillum (Co) and basal flagellar process (Fp) with digitate tip; 4. same. 5. *Betacixius nigromarginalis* Fennah (Cixiidae), swollen, amphora-like, flagellar base (Fb), showing basal flagellar process (Fp) with digitate tip. 6. *Proutista* sp. (Derbidae), swollen flagellar base (Fb), showing tufts of hairs surrounding the opening of the coeloconic sensillum (Co) and the 'three short conical protuberances (Pro)'

next and paralleled to the bristle-like flagellar extension (Figs. 1, 3, 4). My SEM and light microscope examinations have shown that this process is also present in *Bebaiotes nigrigaster* Muir (Achilixiidae, Ecuador, BMNH), *Betacixius nigromarginalis* Fennah (Cixiidae) (Fig. 5), an undetermined species of *Bennarella* Muir (Cixiidae, Guiana, BMNH) and in the nymph of *Myndus* sp. nr. *taffini* Bonfils (Cixiidae, Solomon Islands, BMNH). It should be emphasized that this structure has not been seen in *Catonidia* sp. (Achilidae, China: Hainan), *Zathauma metasequoiae* Fennah (Achilidae) and the other achilids examined.

This structure was first noticed by Fennah (1975) in the cixiids based on light microscope observations. Fennah (1975) named it an 'arista' and used the relative length of this 'arista' in separating taxa.

Following Fennah (1975), Shih & Yang (1996) presented a scanning microscopic study on the morphology and the variation of this structure in the Cixiidae. They called the structure the 'antennal second projection' and reported that this 'projection' was seen throughout Cixiidae, except *Duilius halinus* and *Euryphlepsia yamia*.

In this paper I call this structure the basal flagellar process. This basal flagellar process was only seen in Achilixiidae (Figs. 1, 3, 4) and Cixiidae (Fig. 5) and was not found in any other fulgoromorphan families. The shape and position of this process looks very similar in Achilixiidae and Cixiidae.

It should be noted that a very similar structure, with three short conical protuberances that emerge from a shallow pit which is located at the same position as the above basal flagellar process, has been reported in the Tropiduchidae (see Al-Abbasi, 1988: Figs. 5, 6) and Delphacidae (see Shih & Yang, 1996, Fig. 9) and has also been observed in *Proutista* sp. (Derbidae) (Fig. 6) in the present study and in the Achilidae, Meenoplidae, Kinnaridae and Flatidae (Liang, in prep.).

The 'three short conical protuberances' (Fig. 6) and the 'basal flagellar process with digitate tip' (Figs. 1, 3, 4, 5) are very similar in form and position and are very likely a homologous character. The 'three short conical protuberances' are seen in many fulgoromorphan families, including the relatively primitive Delphacidae, Achilidae, Meenoplidae, Kinnaridae, and Derbidae and the more advanced Tropiduchidae and Flatidae (Liang, unpubl. data), and may represent a relatively primitive state. The elongate, filamentous basal flagellar process with digitate tip, found only in Achilixiidae and Cixiidae, is most likely a derived state or an apomorphy.

DISCUSSION

The antennal sensilla of *A. sandakanensis* are very similar to those found in the relatively primitive fulgoromorphan families, e.g. Cixiidae, Meenoplidae, and Kinnaridae (Asche, 1988; Emeljanov, 1990), in the pedicel surface with digitate flattened star-shaped plaque organs and numerous blunt cuticular denticles and the swollen amphora-like flagellar base with smooth surface and the tufts of hairs surrounding the apical opening (see Marshall & Lewis, 1971; Bourgoin & Deiss, 1994; Shih & Yang, 1996; Liang, unpubl. data). This supports the view that achilixiids belong to the relatively primitive fulgoroids.

The relationship of Achilixiidae to other fulgoroid families has never been resolved since its erection. Muir (1923) considered that the 'nature of the aedeagus [of Achilixiidae] places it in the Cixiine group ... otherwise placed near Achilidae in the Meenopline group' and later in 1930 he confined himself to saying that the family has 'a cixiid connection' and proposed the following phylogenetic relationship hypothesis: Achilixiidae + (Derbidae + (Tropiduchidae + (Cixiidae + Delphacidae))). Metcalf (1945) suggested that the family was closest to the bennine Cixiidae based on the presence of abdominal processes in both groups. However, Fennah (1947) believed that this shared character is of little phylogenetic significance since it has probably arisen independently and later, in 1950, he placed the Achilixiidae in a group with three other families, Achilidae, Kinnaridae and Meenoplidae on the basis of what he described as the 'fundamental characters': simple egg, subterranean nymphal life, reduced or obsolete ovipositor, tubular phallobase and greatly reduced or obsolete phallus, long second posterior tarsal segment, rostrum with long apical segment and the primitive forewing venation. Wilson (1989) analysed these characters used by Fennah (1947, 1950) and concluded that most of them are plesiomorphic. Emeljanov (1990) considered Achilixiidae to belong to Achilidae, and later in 1991 he formally downgraded Achilixiidae to two subfamilies, i.e. Achilixiinae and Bebaiotinae, and placed them in the Achilidae, based mainly on comparison of wing venation with Achilidae, Derbidae, Meenoplidae and Kinnaridae. Emeljanov (1990) believed that the abdominal processes in *Achilixius*, *Bebaiotes*, *Benna* and *Bennarella* all result from convergent evolution. Emeljanov's (1990, 1991) action has been accepted by some subsequent workers (e.g., Wilson et al., 1994).

The present investigation has found that the Achilixiidae and the Cixiidae share the same very specialized and characteristic flagellar structure, the basal flagellar process (Figs. 1, 3, 4, 5), which is unique among all the fulgoromorphan families (Fennah, 1975; Shih & Yang, 1996; Liang, unpubl. data). It may be postulated that this process has evolved twice, once in each family, but as it appears exactly the same in form, placement and possible function in both families and is unlike that of any other fulgoromorphan family, it seems most parsimonious to accept a common, homologous origin for this process, and to accept that it has arisen only once during the course of fulgoroid evolution.

The lack of the evidence in supporting the monophyly of the Achilixiidae and the clear homology of the basal flagellar process in Achilixiidae and Cixiidae indicate that the Cixiidae is paraphyletic with respect to the Achilixiidae; Achilixiidae should therefore be treated as a subgroup of Cixiidae, as

suggested recently by Liang (1999). The two achilixiid subfamilies, Achilixiinae and Bebaiotinae, which were previously placed by Emeljanov (1991) in the Achilidae, are here moved to the Cixiidae.

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