

Morphological characteristics of the antennal flagellum and its *sensilla chaetica* with character displacement in the sandfly *Phlebotomus argentipes* Annandale and Brunetti *sensu lato* (Diptera: Psychodidae)

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Using light microscope and scanning electron microscope, the external morphological characteristics of the antennal flagellum and its sensilla are described in the sandfly, *Phlebotomus argentipes* Annandale and Brunetti *sensu lato*, a well known vector of visceral leishmaniasis in India. A revised terminology is given for the antennal segments to bring phlebotomine more in line with other subfamilies and families while a description of antennal sensilla is provided for the first time in phlebotomine sandflies. Each flagellum consists of scape, pedicel, flagellomeres I to XIII and apiculus. The antennal segments contain scales and sensilla and the latter consist of *sensilla trichodea*, *s. basiconica*, *s. auricillica*, *s. coeloconica* and *s. chaetica* and their putative functions are discussed.

The *sensilla chaeticum* hitherto known as antennal ascoid in the phlebotomine sandflies was used to differentiate within and between species. Differences in its relative size to the flagellomere between the populations of *P. argentipes* collected from the endemic and non-endemic areas in Tamil Nadu state, southern India were established. These differences are considered to be a character displacement as means of premating reproductive isolating mechanism among the populations/members of species complex.

1. Introduction

The morphology of the antennal flagellum and its associated structure, the ascoid has been used widely for differentiating within and between species of phlebotomine sandflies (Parrot 1940; Fairchild 1955; Lewis and Lane 1976), of which some species cause leishmaniasis diseases in warm parts of the world. The number and shape of the antennal segments and their ascoids are conserved fairly in sandflies while they show great variation among the Psychodids especially in the Psychodines (Duckhouse 1978, 1987). However, the terminology used for various parts of the antennal flagellum in phlebotomines is obsolete and presents conflicting usage.

Among the blood sucking Diptera, the fine structure and function of different types of antennal sensilla were studied with the help of light microscopy and both scanning and

transmission electron microscopes in Blackflies (Mercer and McIver 1973), in *Culicoides* sp. (Wirth and Navai 1978; Wirth and Hubert 1989) and in mosquitoes (McIver 1982). They were known to serve for the detection of hosts stimuli, odour, CO₂ and of oviposition sites, water vapour, convection currents (McIver 1982). Among the phlebotomine sandflies, the antennal structures of *Phlebotomus papatasi* Scopoli was illustrated by Jobling (1987) using light microscopy and its two types of sensilla were described by Chaika (1975) using scanning electron microscopy. The sensilla of *Lutzomyia longipalpis* Lutz and Neiva described by Jefferies (1987) using scanning electron microscopy were restricted to the labrum and cibarium of the mouth parts. However, the structures and functions of the antennal sensilla in the phlebotomine sandflies remain unknown.

Phlebotomus argentipes Annandale and Brunetti *sensu*

Keywords. Antennal flagellum; character displacement; *Phlebotomus argentipes*; sensilla; visceral leishmaniasis vector

lato is well known as the vector of Indian visceral leishmaniasis and has been considered as species complex (Secombe *et al* 1993) i.e. members of species complex are morphologically identical or nearly so but different in behaviours, likely to be descendants of populations that were once members of a single species. Of the morphological characters of *P. argentipes*, the *sensilla chaetica* (= antennal ascoid) received special attention as it was shown

that differences in its relative length to the flagellomere II are shorter in the populations of visceral leishmaniasis endemic region while those elsewhere are longer (Lane 1988).

In this paper, using light microscope and scanning electron microscope, the external morphological characteristics of antennal flagellum and its sensilla in *P. argentipes* were described. Based on this study, their terminology were revised to adopt changes made in other subfamilies and fami-

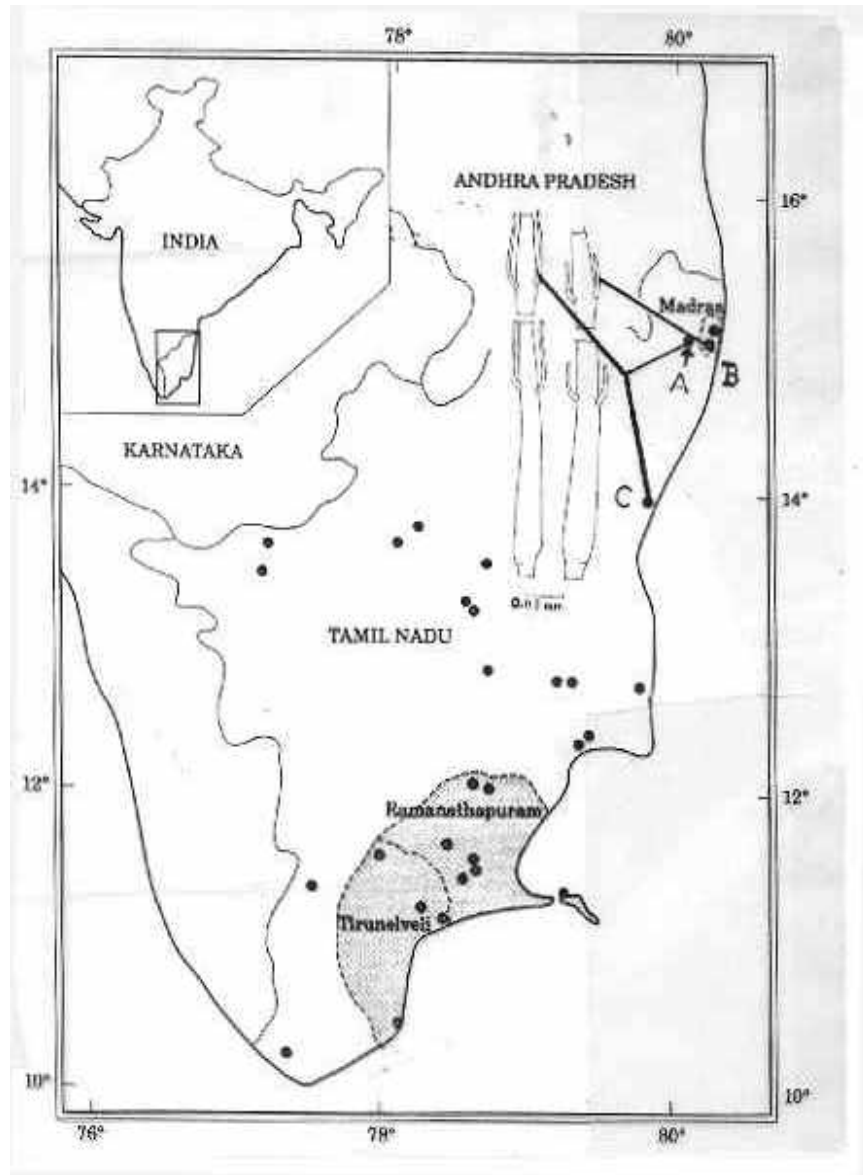


Figure 1. Map showing the visceral leishmaniasis foci (shaded) in the Tamil Nadu state, southern India and collections of the sandfly *P. argentipes* from Poonamalle village (A), Royapettah (B) of Chennai and Thuthipet of Pondicherry (C) and relative length of the *sensilla chaetica* on flagagellomeres I and II of *P. argentipes*.

lies. The evidence is provided for the structural differences in the *sensilla chaetica* for the existence of character displacement among the populations/species of *P. argentipes*.

2. Materials and methods

2.1 Sandflies

Materials used for this study were collected from 3 places in southern India (figure 1): [i] Royapettah, Chennai (= Madras) one of the known foci of visceral leishmaniasis in the Tamil Nadu state, the other foci being two rural districts, Ramanad and Tirunelveli. [ii] Poonamalle village, 30 km west of Chennai and [iii] Thuthipet village near Pondicherry Union Territory. Flies were collected using aspirator from cattle sheds, human dwellings from dawn to dusk and were stored dry in sealed glass tubes with silica gel.

2.2 Light microscopy

The head and its mouth parts of the fly were removed carefully from the body and treated with 0.5% KOH solution overnight, washed in distilled water and mounted on slides with Berle's fluid. Photographs were taken with a Polyvar phase-contrast light microscope using Kodak colour and black and white films.

2.3 Scanning electron microscopy

The head along with mouth parts of the flies were fixed in 4% glutaraldehyde in 0.1 M sodium cacodylate buffer/0.2 M sucrose (pH 7.4) at 4°C for 1 h, washed in buffer, dehydrated in graded acetone solutions at room temperature (70%, 80%, 90%, 100%, 100%: 10 min in each grade) and were dried using CPD750 critical point drier. They were mounted on aluminium stubs with double-sided cello tape and sputter-coated on an Eduardo S150 Sputter coater with a thin-layer of gold. The antennae and their sensilla were examined with JEOL25 III scanning electron microscope and photographed with Kodak Technical Pan film TP120.

2.4 Terminologies used for various segments of antennal flagellum and its sensilla

Terminologies were adopted from McAlpine (1981) and Duckhouse (1987) for antennal segments and the nomenclatures from Altner (1977) and Wirth and Navai (1978) and McIver (1982) for various sensilla. For measuring variations of the *sensilla chaetica* in *P. argentipes*, the length of the chaeticum on flagellomere II was divided by that of its flagellomere. The ratio obtained was considered as short (0.5 less), medium-length (0.51–0.75) or long (over 0.75) (Lewis 1975). Figure 3 refers to the male

antennal structures and the remaining figures refer to the female.

3. Results

3.1 General morphology

Based on light microscopic studies, the gross morphology of the antennal flagellum and its sensory structures was described. A pair of filiform antennal flagella, 1.5 mm in length, arise from the frons of the head (figure 2). Each flagellum consists of 16 segments and its revised and old terminologies are listed below.

Terms used	Old terms
Scape	First or basal segment
Pedicele	Second segment
Flagellomere I	Third segment or post pedicel
Flagellomeres II to XIII	4th to 15th segments
Apiculus	16th or terminal segment

The scape is somewhat triangular in shape with the upper surface broadly sclerotized but its lower surface reduced to a narrow transverse, chitinized bar. Scape is larger in male than in female. A minute hair-like structure is found on its dorsal surface. The pedicel is globular or oval in shape and has attached to it one row of long hair-like structures and another row of shorter lanceolate scales with reduced ends. Flagellomere I measuring 0.23 mm in length is rod-like structure, longer than the remaining flagellomeres. In its basal half it is covered with many scales of an elongate oval type while the distal part has a very dense growth of long hairs. Flagellomeres II to XIII are also cylindrical in shape with their base slightly broader than the apex covering with the similar dense growth of hairs as the flagellomere I. A pair of stout spines are found arising at the junction of the middle and distal thirds of the segment. The female has a pair of spines in all the flagellomeres whereas the male has a pair of spines only in the flagellomere I to X and the remaining flagellomeres XI to XIII have a single spine. These spines were termed previously as ascoids in phlebotomine sandflies and non-phlebotomine moth flies. Apiculus is diminutive, conical or drop-shaped and often incorrectly regarded as an apiculus of 15th segment (Duckhouse 1965). In addition to hair-like structures and spines, the flagellomeres I to XIII contain sensory structures known as "hirsute glands" (Sinton 1923).

3.2 Structural characteristics

The SEM studies have shown that the presence of scales is limited to the pedicel and flagellomere I. However the

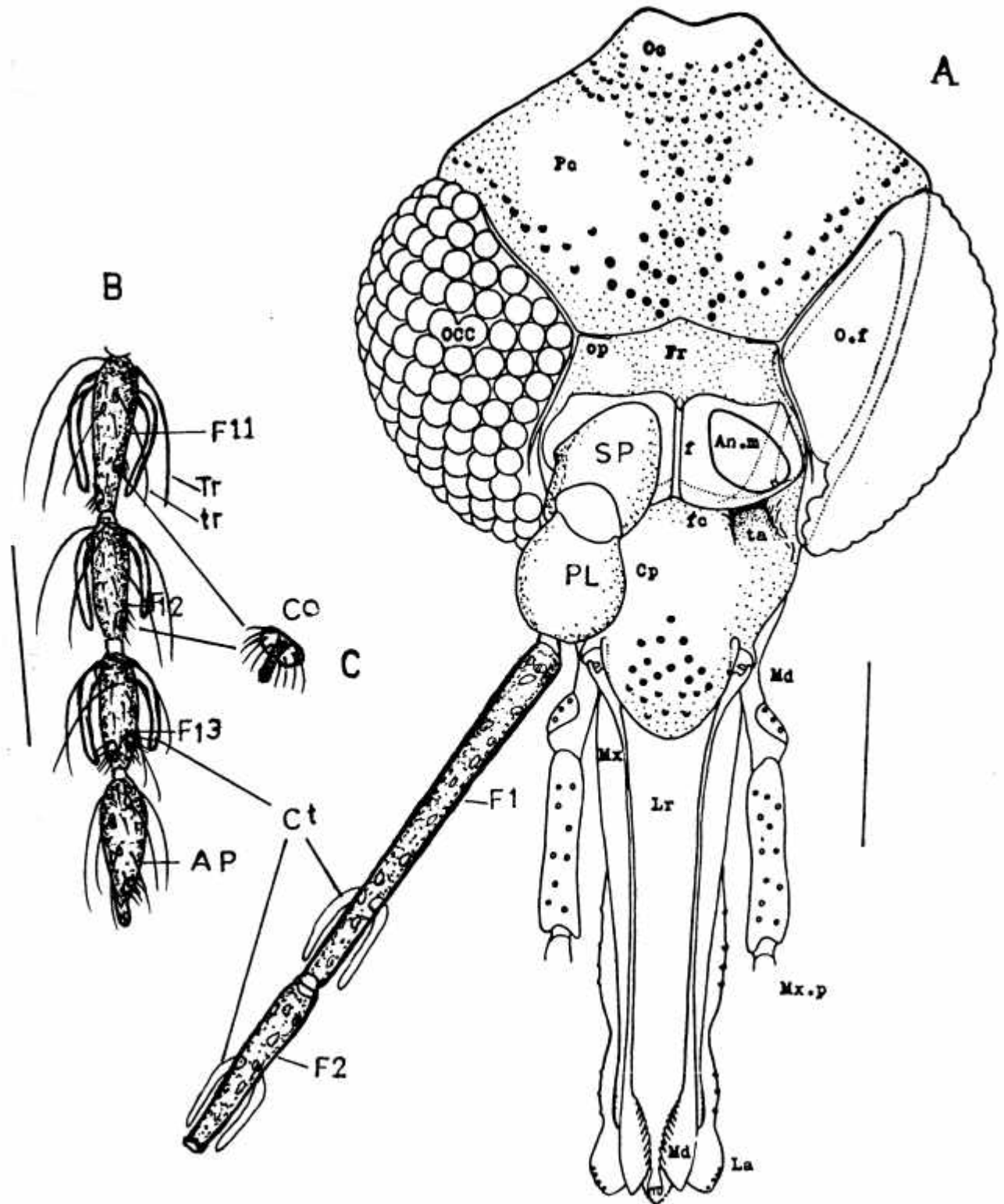
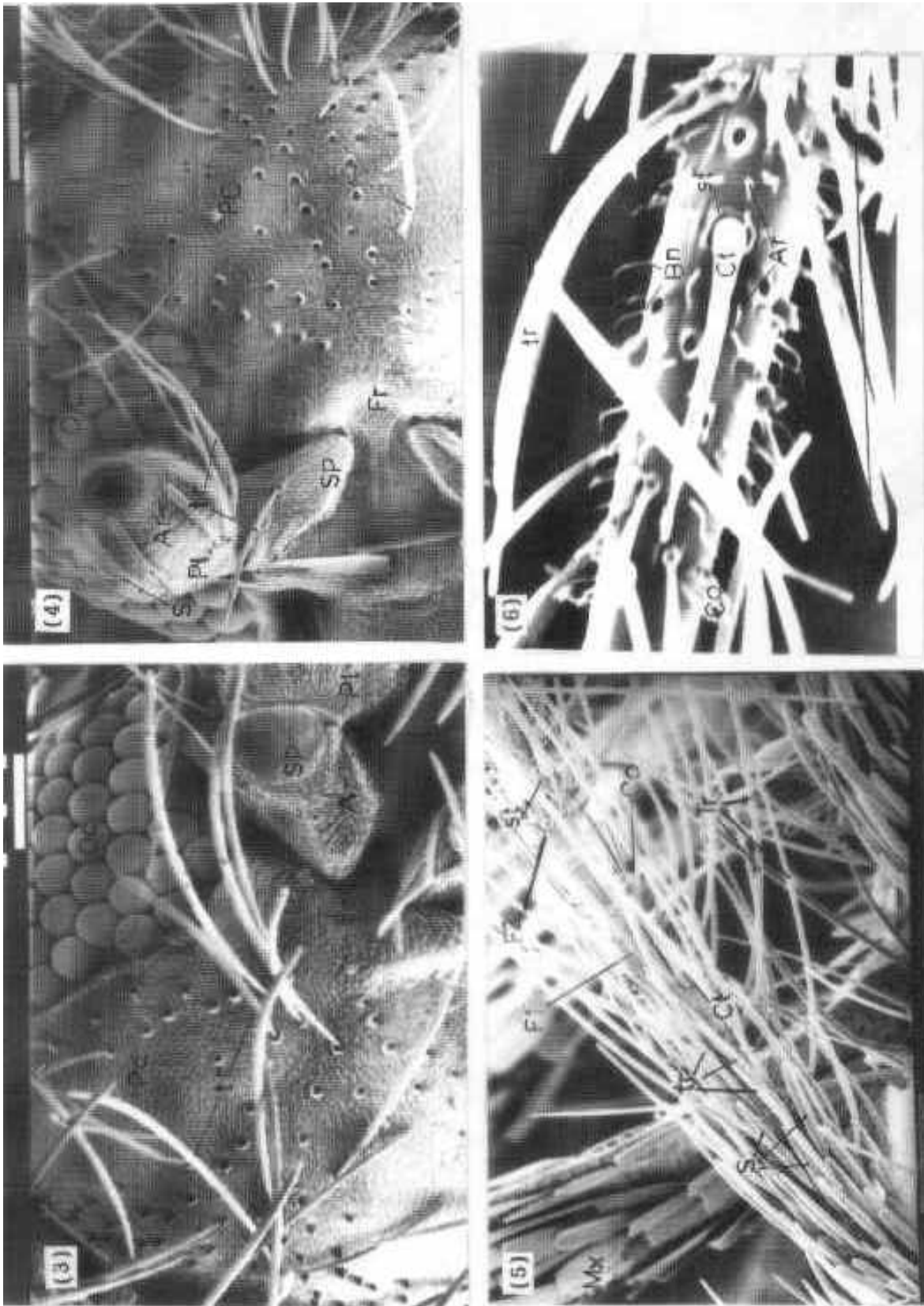


Figure 2. Female head of *P. argentipes*. (A) The mouth parts and basal antennal segments (bar = 0.1 mm) (Christophers *et al* 1926). (B) Terminal antennal segments (bar = 0.1 mm). (C) Co-enlarged *s. coeloconica* (not to scale). Ap, apiculus; Co, *s. coelonicum*; Cp, clypeus; Ct, *s. chaeticum*, F1, flagellomere I; F2, flagellomere II; F11–13, flagellomeres XI–XIII; Fr, frons; La, labium; Lr, labrum; Md, mandible; Mx, maxilla; Oc, compound eyes; Pc, epicranium; Pl, pedicel; Sp, scape; Tr, long and sharp-tipped *sensillum trichodeum*; tr, short and blunt-tipped *sensillum*.



Figures 3 (3 and 4). Dorsal aspect of head and basal antennal segments of *P. argentipes*. (3) Male. The scape (SP), pedicel (PI) with short scales (S), short and blunt-tipped *s. trichodea* (tr) and a series of rows of *s. auricillica* (Ar) (bars = 5 μ m). (5 and 6). Antennal flagellomeres I and II of the female *P. argentipes*. (5) Flagellomere I with scales (S), long and sharp-tipped *s. trichodea* (Tr), short and blunt-tipped *s. trichodea* (Tr), short and blunt-tipped *s. trichodea* (Tr), *s. chaeticum* (Cl) surrounded by socket (St), *s. coelonicum* (Co), *s. basiconica* (Bn) (bar = 5 μ m). (6) Flagellomere II with *s. chaeticum* surrounded by the socket (St), *s. coelonicum*, *s. basiconica* (Bn), *s. auricillicum* (Ar) (bar = 15 μ m).

diversity of sensillum types has been observed from the entire surface of the flagellum. Based on their shapes and segmental distribution, there are 5 types of sensilla: *sensilla trichodea*, *s. basiconica*, *s. auricillica*, *s. coeloconica* and *s. chaetica*.

The scales measuring 10 µm in length are short, striated with their constricted base and blunt apex. Scales occur in a row along with the short *s. trichodea* (tr, see below for their classification) at the base of the pedicel and flagellomere I (figures 4 and 5). The scape has a single *s. trichodeum* (tr) on the mid-dorsal surface.

The *s. trichodea* are by far the most numerous type of antennal sensillum found in the entire flagellum. They are of 2 types viz., the long *s. trichodeum* (Tr) with long and pointed-tip and the short *s. trichodeum* with striated, blunt-tip (tr) (figures 3–5). The *s. trichodea* (Tr) measuring 20–30 µm in length occur at the base of flagellomeres while *s. trichodea* (tr) measuring 10–15 µm in length are distributed randomly on entire length of the flagellum and the head. According to Altner (1977), walls of the trichodeal sensilla are thin, transparent and grooved belonging to the porous type.

The *s. basiconica* (Bn) are 1–2 µm in length, smaller than the *s. trichodea* and are found on the entire flagellum (figure 6). Structurally *s. basiconicum* is similar to *s. trichodeum* i.e., of wall-pore type. The *s. auricillicum* is much smaller than the *s. trichodeum* and *s. basiconicum* and but structurally similar to *s. basiconicum*. The *s. auricillica* occur abundantly on the scape, pedicel and the head but they are sparse on the flagellomeres. Further *s. auricillica* are arranged in a series of rows over the scape and pedicel whereas they are distributed at random on the head and flagellomeres.

The *s. coeloconica* known as “hirsute glands” (cf. Sinton 1925) occur generally on the upper part of the flagellomeres and apiculus. These sensilla are variously referred to as papillae, pegs in pits and *sensilla ampullacea* depending on their size, location and number on the antenna flagellum of mosquitoes (McIver 1982). They are easily recognized even in light microscope due to the “fence-like sensory hairs that surrounds the centrally placed cuticular spine” (figures 6–8). *S. coeloconica* are found progressively more in numbers towards the tip of the flagellomeres. This type of sensillum belongs to the porous, double-walled sensilla as defined by Altner (1977).

The *s. chaetica* are thick-walled, bristles with a socket-like, circular structure surrounding the base – a characteristic feature of *s. chaeticum* (figure 6). They are of the terminal pore type (Altner 1977). *S. chaetica* are typically sharp-tipped, long spine-like structures which were earlier referred to as antennal spines and ascoids in phlebotomine sandflies (cf. Parrot 1940; Lane 1988) whereas their length and shape in non-phlebotomine Psychodids of mothflies are extremely diverse from the button-shape to a long whip-like structure

(Fairchild 1952; Duckhouse 1987).

Using light microscope, differences in the number and pattern of distribution of scales and types of sensilla were found in both the males and the females. However, *s. basiconica* and *s. auricillica* were unable to be seen with light microscopy. The males appeared to have the same number and types of scales and *s. trichodea* as the females. The males have more number of *s. coeloconica* especially towards the distal flagellomeres and apiculus than the females. Differences in the number of *s. chaetica* between male and female as described above is characteristic of sexual dimorphism in *P. argentipes*.

3.3 *P. argentipes* and its intraspecific variation in the *s. chaetica*

Figure 1 shows the relative length of *s. chaetica* on the flagellomeres II from the specimens examined from 3 places viz., (A) Poonamalle, (B) Royapettah and (C) Pondicherry: it is small [$\bar{x}=0.42 \pm 0.04$ (SD), $R=0.36-0.51$, $N=18$] from Royapettah, Chennai and it is medium or long [$\bar{x}=0.67 \pm 0.05$ (SD), $R=0.59-0.76$, $N=21$] from Poonamalle, Chennai and Thuthipet, Pondicherry.

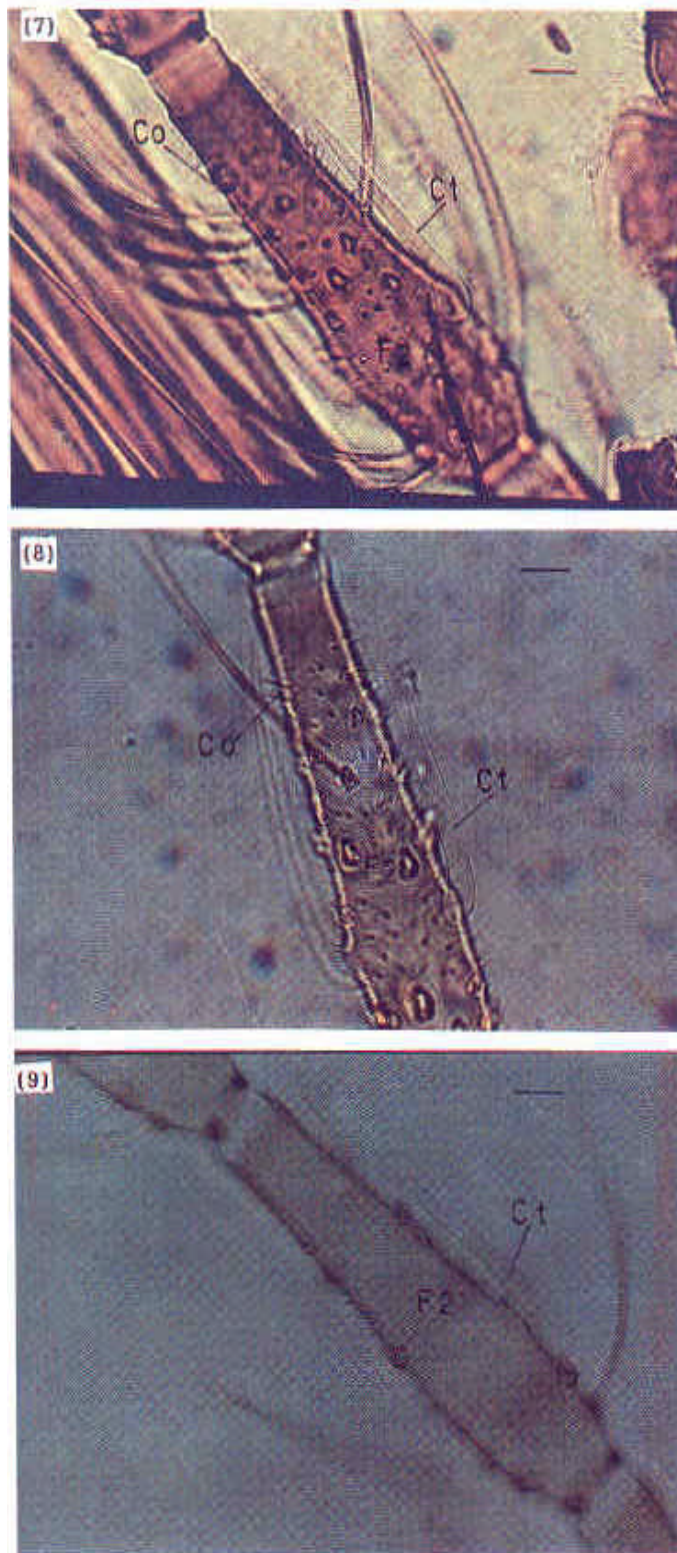
4. Discussion

4.1 Morphology of the antennal flagellum

The number and shape of the flagellar segments are the important taxonomic characters in the phlebotomine sandflies and non-phlebotomine Psychodids mothflies (Fairchild 1955; Duckhouse 1987). The number of flagellomeres with apiculus found in each subfamilies of the Psychodidae are as follows:

Bruchomyiinae	
<i>Eutonnoiria</i> sp.	111 segments
<i>Bruchomyia</i> sp.	24–29
<i>Nemapalpus</i> sp.	14
Horaiellinae	14–15
Phlebotominae	14
Trichomiinae	14
Psychodinae	14

A reduction in the number of antennal segments is a trend among the Diptera. The presence of higher number of antennal segments is considered as plesiomorphy in the lower group of flies like Nematocera and Orthorrhapha whereas a fewer number of segments as found in Cyclorrhapha is treated as an apomorphy (Yeates 1994). Accordingly the subfamily Bruchomyiinae except *Nemapalpus* sp. is a primitive taxa but it was considered by



Figures 7-9. Relative length of *s. chaeticum* on flagellomere II of the female *P. argentipes* collected from three different localities [(7) Royapettah, Chennai, (8) Thuthipet, Pondicherry and (9) Poonamalle near Chennai]. (Bar = 0.01 mm.)

Hennig (1972) as a paraphyletic group due to lack of true relationship with other Psychodids. *Horaiella prodigiosa* with 15 flagellomeres is questionable because the apiculus with its terminal projection could possibly have been considered as two separate segments. The remaining taxa of all Psychodids including Phlebotomines have invariably 14 flagellomeres.

The structure of the scape, pedicel, flagellomeres and apiculus is fairly conserved in phlebotomine sandflies and shows great variation among other Psychodids. The scape of *P. argentipes* and other sandfly species is usually shorter, narrower than pedicel. The scape is generally longer and stouter in Psychodinae than the pedicel while their flagellomeres are flask-shaped but these have arisen independently in many groups. The length of the flagellomere I is primitively much longer in *Idiophlebotomus*, *Spelaophlebotomus* of Phlebotomine, Sycoracinae and Trichomyia (Trichomiinae) group A than the maxillary palps (Duckhouse 1972; Lewis and Lane 1976). Further study on the comparative aspects of the antennal flagella will be very useful and rewarding and that could reveal the true relationship among Psychodids.

4.2 Phlebotomine sandfly sensilla

The sensillum types described in the antennal flagellum of *P. argentipes* were found to be like *Culicoides* sp., mosquitoes and other insects. But the structure of *s. coeloconica* and *s. chaetica* appeared to show both similarity and difference with other known insect antennal sensilla. The *s. coelonica* are similar to those in *P. argentipes*, *Culicoides* sp. and Lepidopterous insects with fence-like hairs that surround the centrally placed cuticular spine, whereas it is simple as a peg in a pit which lacks fence-like hairs in mosquitoes. There are 2 types of *s. chaetica* found in Diptera. A long form of numerous *s. chaetica*, the fibrillae was found in whorls especially at the basal flagellomeres in mosquitoes and a few in *Culicoides* sp. A few of the short *s. chaetica* are located at the distal end of the flagellomeres in mosquitoes (McIver 1982). Both types of *s. chaetica* are located in well-developed sockets. The latter type belongs to *P. argentipes*.

The structure of the individual sensillum and its presumable function as represented here by *P. argentipes* conforms to other known insect sensilla functions. The pedicel contains auditory sense organ, Johnston's organ within which the arrangement of scolophores, neural connections, enveloping cells were detailed by Christophers *et al* (1926). It is equally well developed in both male and female (Sinton 1925). In mosquitoes, the *s. trichodea* are olfactory chemosensilla (cf. McIver 1982) and their long point-tipped ones may mediate attractive odours such as

those from a human hand and the blunt-tipped may be sensitive to vapours of commercial repellents and of chemicals known to be used in the location of suitable oviposition site. In moths (Hallberg *et al* 1994), morphological differences between *s. trichodea* were interpreted as an adaptation to the concentration differences between the different pheromone components. So do they possibly in *P. argentipes*. The *s. basiconica* perform olfactory function while the function of *s. coeloconica* is responsive to odours, water vapour and convected heat. *S. chaetica* are mechanosensilla in mosquitoes (McIver 1982), *Culicoides* (Wirth and Navai 1989) and contain contact chemoreceptors in lepidopterous moth (Hallberg *et al* 1994). Hence they represent tactile/taste functions. The structures and functions of *s. trichodea*, *s. basiconica* and *s. coelonica* are remained unknown among the non-phlebotomine Psychodids, although the morphological characteristics of *s. chaetica* are extensively employed in the taxonomy of the family Psychodidae. They are bladder or disc-like in Bruchomyiine, simple and spine-like in Sycoracine, Horaielline and Trichomiine and show extreme diversity in Psychodine (Fairchild 1952; Jung 1956).

In Phlebotomine sandflies, *s. chaetica* form an important character to differentiate between the species (Parrot 1940) and were used to differentiate the closely related species of leishmaniasis vectors especially among the populations/species of *P. argentipes* (see below) and *P. papatasi* and *P. bergeroti* (Lane and Fritz 1986).

The internal structural characteristics of antennal sensilla and their sensory roles were known in many species of mosquitoes (cf. McIver 1982) and of the Lepidoptera of economic importance (Hallberg *et al* 1994). Using transmission electron microscopy and electrophysiology, the internal enveloping cells of sensilla viz., thecogen, trichogen and tormogen, neural connection, the presence and absence of wall pores, concentration of pheromone, and action potential were demonstrated. A similar study on the antennal sensilla of *P. argentipes* and other sandfly vectors of leishmaniasis would throw more light on host recognition, mate selection and blood feeding and that would allow or support the development of control strategies especially using pheromone/kairomone traps for leishmaniasis vector control.

4.3 Use of sensilla chaetica in the identification of leishmaniasis vector, *P. argentipes sensu lato*

Visceral leishmaniasis is confined to north-eastern and southern India and also adjoining Nepal and Bangladesh. However the geographical range of its vector *P. argentipes*, extending from Iran and Afghanistan in the west to Malaysia and Indonesia in the south-east (Lewis 1987), greatly exceeds that of the disease. Because of its vast geographi

cal distribution and the prevalence of the disease in a few places, suggest that they consisted of different populations which may be sufficiently distinct for *P. argentipes* to be considered as a species complex (cf. Lane 1988). Ilango *et al* (1994) described 2 morphological species of *P. argentipes* based on the *s. chaetica* variation from the same place in Madras, southern India.

Given the structural and functional significance of the *s. chaetica*, the relative differences observed between the samples in this study and also in Patna, Bihar (Lane and Rehman 1980) are possibly due to genetic rather than environmental (diet, ambient temperature) factors. It is unlikely that the latter factors have had any impact on the length and size of the *s. chaetica* as the samples of this species represented a more less similar habitats. Further the sandflies are able to fly only short distance and the distance between the samples is of considerable importance. The distance between A and B is 25 km and A, B and C 150 km. Hence B is sympatric to A whereas A, B are allopatric to C. Possibly this divergence is tenuous evidence for character displacement. According to Brown and Wilson (1956) character displacement exists between two closely related species when their allopatric populations are very similar and their sympatric populations are quite distinct in one or more characters. The disparate characters could be either morphological, physiological or behavioural. In this study the pattern of variation in the relative size of *s. chaetica* provides support for the divergence within a complex of species and that could be considered as a satisfactory character for the identification of vector species of *P. argentipes* from the non-vectors.

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