

Leg sense organs of ticks

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INTRODUCTION

The forelegs of ticks are important sensory appendages bearing sensory hairs (SH), some of which are concentrated in Haller's organ. Numerous morphological and fine structural studies on tarsus 1 have revealed specific differences in tick chaetotaxy and morphology (Balashov & Leonovich 1976, 1978, Clifford & Anastos 1960, Homsher & Sonenshine 1975, 1977, Hoogstraal *et al.* 1983, Zumpt 1949). However, classical chaetotaxy does not seem to be a very powerful tool for discriminating tick species.

We have studied the foreleg tarsal sensory system from a functional point of view. By analyzing sensory hairs quantitatively with respect to the modality-specific structures, and the total input of the tarsal sensory system in terms of receptor neurons, we have assessed the relative importance of the different sensory modalities in ticks. This approach, called functional chaetotaxy, has shown that the contribution of the different sensory modalities to the total tarsal sensory input varies in the instars of *Amblyomma variegatum* (Hess & Vlimant 1983b). We have also compared the functional chaetotaxy of species differing in their systematic position, life cycle, and ecology. This approach, called comparative functional chaetotaxy, is useful in helping answer questions such as: Are the systematic position, life cycle, and ecology reflected in the morphology and fine structure of the tarsal sensory system of a tick species? Is the foreleg sensory system of a reptile-specific parasite such as the adult *Amblyomma nuttalli* structurally different from that of a closely related species, e.g. *A. variegatum* which feeds exclusively on warm-blooded vertebrates? Or, do adult one-host ticks such as *Boophilus microplus* have a reduced tarsal sensory system because they choose their hosts during the larval stage? Answers to questions such as these should help us solve problems associated with the physiology of host seeking and host specificity. The results of our comparative study on *Amblyomma variegatum*, *Amblyomma nuttalli*, *Dermacentor marginatus*, *Boophilus microplus*, *Ixodes ricinus*, and *Ornithodoros moubata*, are summarized and reviewed in this chapter.

Two other phenomena related to the sensory physiology of ticks are considered: i.e. the function of leg sense hairs located on other leg segments than the foreleg tarsi, and our discovery of intracuticular sensilla located ubiquitously on tick legs. It is unusual that researcher's have thus far limited their research to Haller's organ, tarsus 1, the palpal organ, and most recently the cheliceral sense organs, and have neglected the great number of sensory hairs on the legs and elsewhere. Even more astonishing is the absence of descriptions of the intracellular sensilla of tick legs prior to our study (Hess & Vlimant 1984) in spite of the known abundance of slit sense organs and lyriform organs in spiders, scorpions, and mites. It should be noted that authors erroneously interpreted gland openings on tick legs as campaniform sensilla or similar organs. Thus we have examined the structure of the sensory hairs on all segments of the four pairs of legs in *A. variegatum* and the intracuticular sensilla in the legs of *A. variegatum*, *I. ricinus*, and *O. moubata*.

16.2 STRUCTURE, FUNCTION, AND DISTRIBUTION OF SENSORY HAIRS OF TARSUS 1

Previously, the structure of the foreleg tarsal sensory hairs was described in detail, by means of transmission electron microscopy (TEM) or TEM and scanning electron microscopy (SEM) in the following species: *Alveonaspis lahorensis*, *Amblyomma americanum*, *Amblyomma variegatum*, *Argas arboreus*, *Argas tridentatus*, *Boophilus microplus*, *Hyalomma asiaticum*, *Ixodes persulcatus*, *Ixodes ricinus*, and *Ornithodoros moubata* (Axtell 1979, Chu-Wang & Axtell 1973, Foelix 1972, Foelix & Axtell 1971, 1972, Hess & Vlimant 1980, 1982, 1983a,b, Jorgensen 1985, Leonovitch 1977, 1978, 1979, 1980, Roshdy *et al.* 1972, Thonney 1980, 1986, Waladde 1979). Two important facts emerged from these studies: a) There is a restricted number of structural types of sensory hairs present including 11 in argasids, 12 in the Metastriata, and 13 in the Prostriata. b) In the different species, the sensory hairs are distributed over the tarsus in a comparable manner.

16.2.1 Structure and function of sensory hairs

The structure and microanatomy of tick sensilla follows the general scheme as defined for arthropods (Altner 1977, Altner & Prillinger 1980, Hess & Vlimant 1982, 1983a,b). Thus four categories based on modality-specific structural features can be distinguished: a) wall pore single-walled sensilla (wp-sw). b) wall pore double-walled sensilla (wp-dw). c) terminal pore sensilla (tp). d) no pore sensilla (np).

These categories may contain sensory hairs with an innervated socket (sensilla chaetica) or with a noninnervated socket (sensilla basiconica or sensilla trichodea). In the former, the innervation of the base is always double, i.e. two tubular bodies are present). The lack of socket-innervation does not exclude the flexibility at the base of the sensillum.

wp-sw Sensilla (Fig. 16.1) are characterized by a shaft pierced by numerous pores and the presence of pore tubules or pore strands represent-

ing stimulus conducting structures. The dendrites of the sensory cells are branched or unbranched. These sensory hairs are mono- or multimodal olfactory sensilla; additional possible modalities include thermo- and hygro-sensitivity.

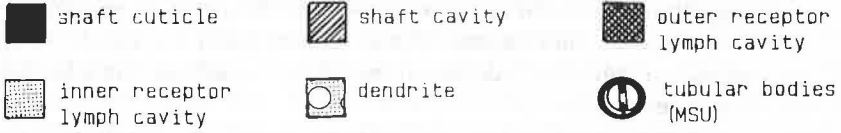
wp-dw Sensilla (Fig. 16.2) have a double setal wall with the receptor lymph cavities separated in the shaft. Stimulus conduction occurs through 'spoke canals' opening into surface grooves. The dendrites of the shaft innervating units (SIU) are unbranched. A specialized innervated mechanosensory socket may be present or absent. These sensory hairs are mono- or multimodal olfactory sensilla; additional possible modalities are mechano-, hygro and thermosensitivity.

tp Sensilla (Fig. 16.3) have a terminal or subterminal pore or slit which connects the inner receptor lymph cavity to the outside. The inner and outer lymph cavities are separated by a sheath (scolopale) or a cuticular wall. Most of the unbranched dendrites reach to the tip of the hair. The base is generally innervated and forms a mechanosensitive socket. Tp sensilla are mechanogustatory receptors (contact chemoreceptors), with other possible modalities being thermo- and hygro-sensitivity.

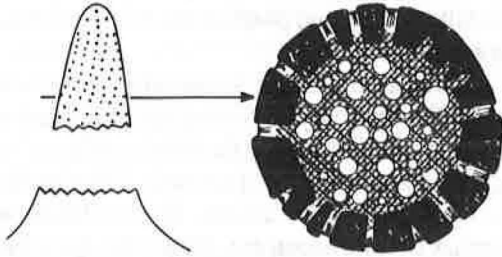
np Sensilla (Fig. 16.4) are characterized by an absence of pores or slits. They possess either an innervated socket or an innervated shaft, or both. They are mono- or multimodal with possible modalities being mechano-, thermo, and hygro-sensitivity.

All tick sensory hairs fit this classification scheme, and all four categories are present on tarsus 1. As in other arthropods, the four categories of sensory hairs include several different types as designated by different letters (Figs. 16.1–16.4). Although the categories are homologous among arthropods, the types are not identical. Consequently, a type wp-sw/A sensillum of *Periplaneta americana* is not necessarily structurally identical to the type wp-sw/A sensillum of *Amblyomma variegatum*. However both have features in common and both are olfactory. Among ticks, the different types can, however, be considered as structurally identical, but not necessarily have identical functional specificity. Thus a wp-sw/B sensillum have identical structural characteristics in both *A. variegatum* and *O. moubata*, and it contains olfactory units in both species, but the specificities of the receptor neurons in the two are not necessarily identical. The important question of functional specificity can only be evaluated by electrophysiological means and has not been resolved in most cases. Electrophysiological studies on some of the tarsal sensilla have confirmed functions hypothesized from structural studies. Np/C sensilla of *A. variegatum* contain mechanosensory and antagonistic thermosensitive receptor neurons (Fig. 16.5) (Hess & Loftus 1984), and the corresponding sensillum of *B. microplus* larvae also contains a cell sensitive to heat (Jorgensen 1985).

The olfactory function of wp-sw/A sensilla has been demonstrated unequivocally in several species. Hess & Vlimant (1980) reported cells reacting to short-chain fatty acids and 2,6-DCP (dichlorophenol) in *A. variegatum* sensory hairs of this type, and recently Schöni & Hess (in preparation) identified chemosensory neuron in the same sensilla which is specific for *o*-nitrophenol, a component of the aggregation-attachment

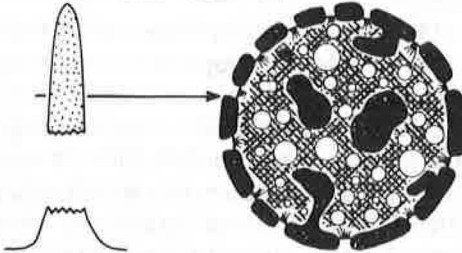


Type wp-sw/A: \odot_A



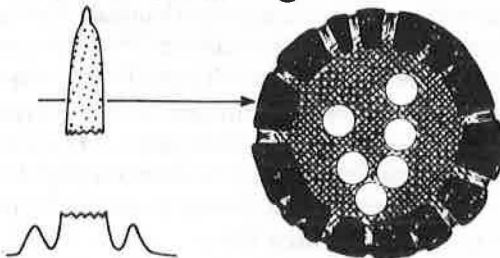
- s. basiconicum
- rel. size small to medium
- 1 to 3 groups of 4 or 5 SIU with ramifying dendrites

Type wp-sw/B: \odot_B



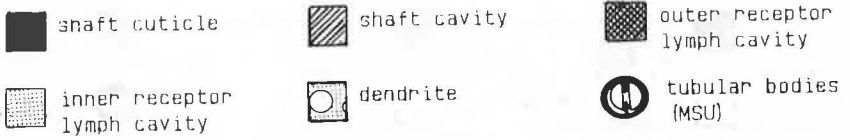
- s. trichodeum or basiconicum
- rel. size small to medium
- 3 to 5 SIU with ramifying dendrites
- cuticular framework forming basal ring in some species
- restricted to the capsule of Haller's organ

Type wp-sw/C: \odot_C

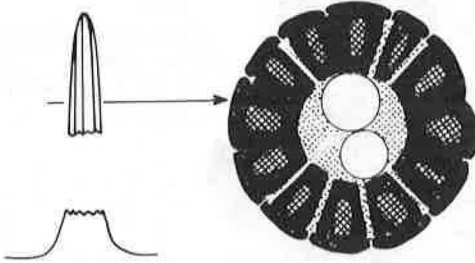


- s. trichodeum
- rel. size long
- 1 or 2 groups of 5 or 6 SIU with ramifying dendrites
- restricted to Prostriata

Fig. 16.1 — Characteristic structural features of tick leg sensory hairs. Wall pore single-walled (wp-sw) sensilla. SIUs shaft innervating units.

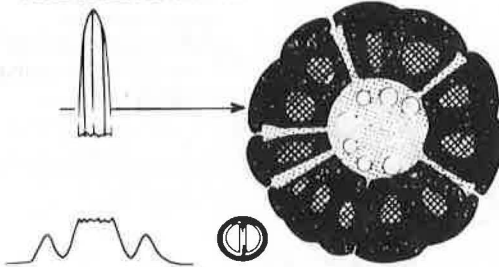


Type wp-dw/A: \emptyset_A



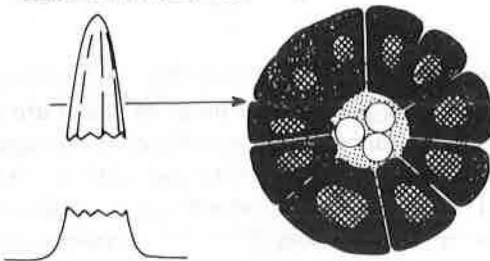
- s. trichodeum
- rel. size medium
- 1 or 2 SIU (and 4 in *O. moubata*) with unbranched dendrites

Type wp-dw/B: \emptyset_B



- s. chaeticum
- rel. size medium to long
- 3 to 8 SIU with unbranched dendrites

Type wp-dw/C: \emptyset_C



- s. basiconicum
- rel. size small
- usually 3 SIU (sometimes 2) with unbranched dendrites

Fig. 16.2 — Characteristic structural features of tick leg sensory hairs. Wall pore double-walled (wp-dw) sensilla. MSU: mechanosensory units, SIU: shaft innervating units.

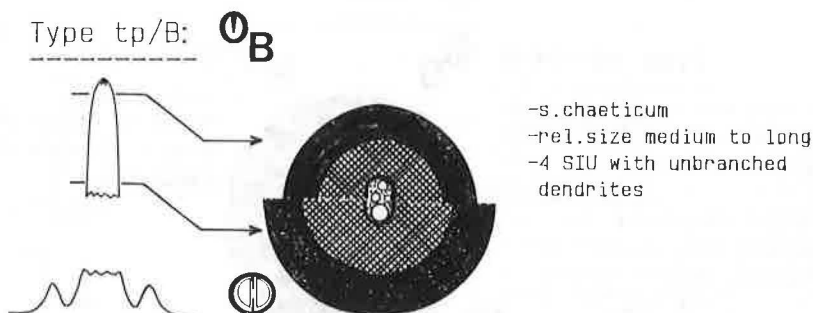
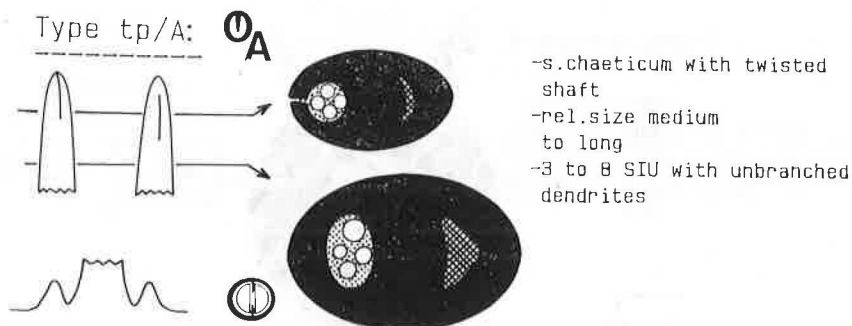
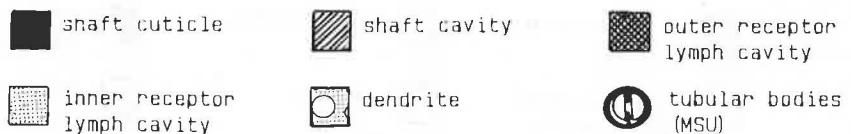
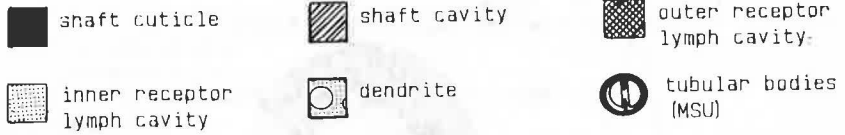


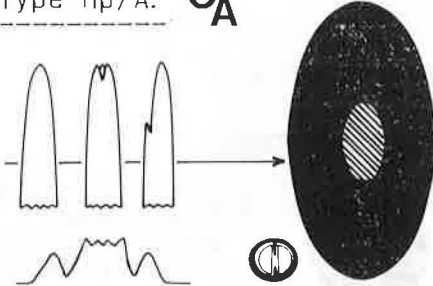
Fig. 16.3—Characteristic structural features of tick leg sensory hairs. Terminal pore (tp) sensilla. MSU: mechanosensory units, SIU: shaft innervating units.

pheromone of this species (Schöni *et al.* 1984) (Fig. 16.6). Waladde (1982) had already demonstrated the presence of neurons which are sensitive to 2,6-DCP and tick washes in the wp-sw/A sensilla of *A. variegatum*. In *A. americanum*, the corresponding sensory hairs also contain 2,6-DCP sensitive cells (Haggart & Davis 1981). More astonishing is the discovery of 2,6-DCP sensitive units in wp-sw/C sensory hairs of *I. ricinus*, a species which failed to respond to this pheromone in attraction experiments (Graf 1975, Thonney 1986).

We recently identified wp-sw/B sensilla within the capsule of Haller's organ with temperature-sensitive units and receptor cells specific to methyl salicylate (Fig. 16.7) (Hess & Blendermann, in preparation), another

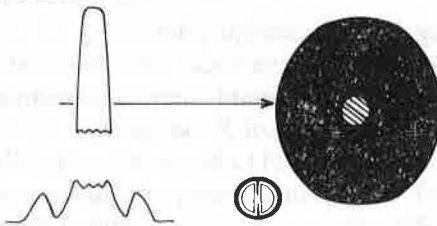


Type np/A: O_A



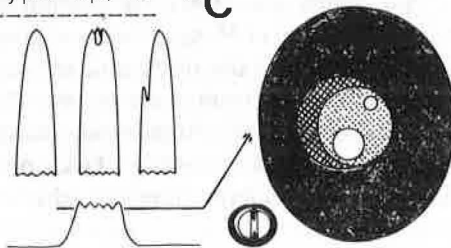
- s.chaeticum
- rel.size long
- no SIU
- gradual transition to np/B

Type np/B: O_B



- s.chaeticum
- rel.size medium to small
- no SIU
- gradual transition to np/A

Type np/C: O_C



- s.chaeticum
- rel.size medium or long
- 1 or 2 SIU with unbranched dendrites

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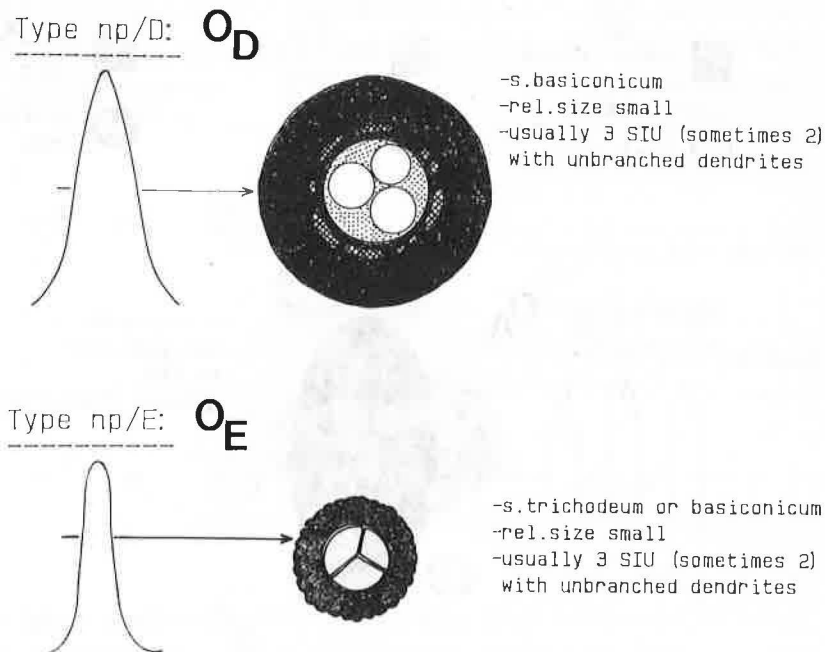


Fig. 16.4— Characteristic structural features of tick leg sensory hairs. No pore (np) sensilla. MSU: mechanosensory units, SIU: shaft innervating units.

component of the aggregation-attachment pheromone of *A. variegatum* (Schöni *et al.* 1984). Wp-dw sensilla have been tested electrophysiologically only by Haggart & Davis (1980) who found ammonia sensitive cells within wp-dw/A sensilla of the 'medial group' of *R. sanguineus*.

Tp sensilla have been demonstrated to be gustatory by Elizarov (1963) and Balashov *et al.* (1976). Some contain receptor cells that react to NaCl and water as well, and Waladde *et al.* (1981) identified neurons in tp/A sensory hairs that react to a decrease in temperature.

Other electrophysiological studies have been published which unfortunately do not allow the precise determination of the sensilla from which the recordings were made. For example, Elizarov (1963) demonstrated repellent sensitive neurons in Haller's organ of *H. asiaticum* and *Ixodes persulcatus*, and Sinitzina (1974) identified cells in the anterior pit of the same species reacting to *n*-valerianic acid and odours from white mouse, blood, and the respiration of man. Haggart and Davis (1981) found ammonia sensitive units at the same location in *R. appendiculatus*. In a study of CO₂ perception, the source of the electrical impulses was undetermined (Holsher *et al.* 1980).

16.2.2 Distribution of sensory hairs

A superficial look at the comparative functional chaetotaxy of tick foreleg tarsi reveals that the distribution of sensory hairs is similar in all tick species. To what extent are they actually comparable? To help answer this

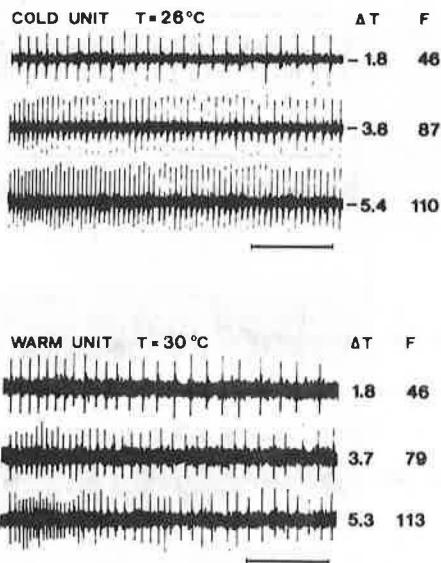


Fig. 16.5 — *A. variegatum* female: type np/C sensillum (dI.2). Impulse trains of a warm and a cold unit in response to abrupt temperature changes. Response magnitude for first 100ms indicated under F. Time scale: 200ms. Interstimulus conditioning time at T: 3min. Exposure to ΔT : 1.3s. (Hess & Loftus, (1984) by courtesy of Springer Verlag).

question, we need a system of designating sensory hairs which can easily be applied to all tick species and to all instars, to facilitate rapid vertical (stage) and horizontal (species) comparison. The system used in our laboratory assumes that the different types of sensory hairs are distributed in a comparable manner in all species, and takes into account the possibility of specific variations. It assumes homologous groups of setae in adults, but it is also relevant for nymphs and larvae. In most ixodids homologous groups of setae consist of the same types of sensilla and are arranged in a similar or identical manner. However, in some species or stages one or several groups may be modified or even missing. In others, two groups may fuse to form a combined group consisting of setae of the original groups. An example is the combined group dI/II in argasids which is composed of the sensilla of the original groups dI and dII, which are separated in ixodids.

Our alphanumeric code of designation of the setal groups includes letters to indicate the topographical location of the group (d=dorsal, v=ventral, la=lateral-anterior, lp=lateral-posterior, C=capsule of Haller's organ) and a Roman numeral to number the groups in the disto-proximal direction. Thus, the group dI is the most distal group of sensilla on the dorsal face of the tarsus. When a cypher is added to the group-code it is possible to designate individual sensilla from anterior to posterior and from distal to proximal. Thus, for example, the sensillum dI.1 (a type wp-sw/A in all metastriates) is

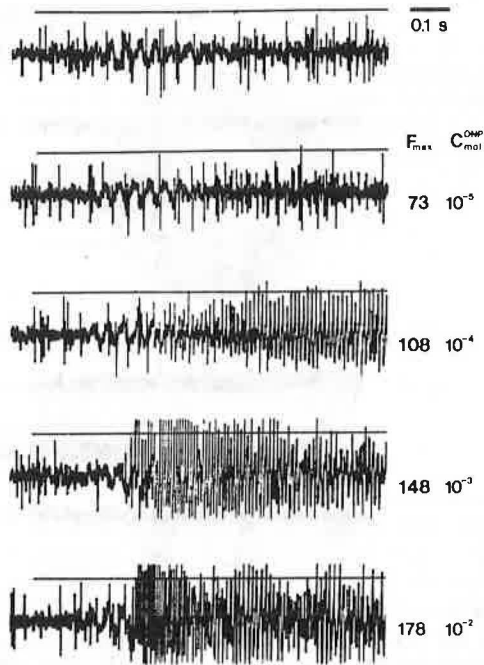


Fig. 16.6 — *A. variegatum* female: type wp-sw/A sensillum (group d II). Impulse trains of a unit in response to dry air control (upper trace) and to *o*-nitrophenol (ONP). Maximum response magnitude indicated under F_{max} . Molar concentration of the stimulating source indicated under C_{mol} . Horizontal bar represents stimulation (duration 1.5 s). Interstimulus time 3 min. (Schöni & Hess, in prep.).

the anterior sensillum of the group dI, and sensillum dI.2 (a type np/C sensillum in all metastriates) is posterior to dI.1.

Figs. 16.8–16.11 demonstrate the high degree of homology of the functional chaetotaxy of tarsus 1 among tick species. A closer look at the figures shows that metastriate ixodids strongly resemble each other; some species such as *A. variegatum* and *A. nuttalli* are identical. Prostriates (*I. ricinus*) differ from metastriates by having a more homogeneous ventral side lacking the group vIV, a higher density of sensory hairs, and the group dI composed of 2 np/C and 2 wp-sw/C sensilla. This latter type is restricted to prostriates. We suppose that the anterior np/C sensillum of the group dI represents the original lateral np/C sensory hairs (laI.1 of metastriates) shifted to a dorsal position in *Ixodes*. This dorsal shift of the sensillum laI.1 has also been observed on the larval tarsus of *A. variegatum* (Hess & Vlimant 1983a).

The tarsus of the foreleg of *O. moubata* is characterized by the fused group dI/dII with 3 wp-sw/A sensilla; the fusion of groups dIV and dV, and a striking small number of setae as compared to hard ticks. As will be seen later, the lack of sensory hairs is partly compensated by intracuticular

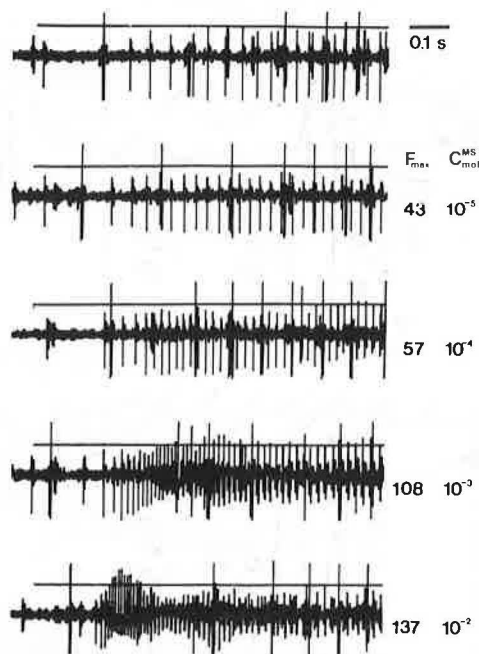


Fig. 16.7 — *A. variegatum* female: type wp-sw/B sensillum (capsule of Haller's organ). Impulse trains of a unit in response to dry air (upper trace) and to methyl salicylate (MS). Maximum response magnitude indicated under F_{max} . Molar concentration of the stimulating source indicated under C_{mol} . Horizontal bar represents stimulation (duration 1.5s). Interstimulus time 3 min. The unit producing high-amplitude spikes does not respond to the component. (Hess & Blendermann, in preparation).

sensilla. This situation seems to be characteristic of soft ticks. It would be interesting to determine if this represents a primitive condition or a highly differentiated stage.

Even more interesting than the morphological comparison of the groups of sensilla is the comparison of total tarsal sensory input in terms of receptor cell types and sensory modalities (Table 16.1). This method allows assessment of the real sensory potential and it standardizes differences occurring in the number of sensory hairs. In fact, a lower number of setae observed in a given species can be compensated for by a higher number of neurons per sensillum as observed in the capsule of Haller's organ.

Before we discuss in detail the total foreleg tarsal sensory input of the different species, we must point out the identical structure of the tarsal sensory systems of *A. variegatum* and *A. nuttalli*, which share a common column in Table 16.1.

Comparing the total number of sensory hairs among the different species studied we note that *I. ricinus* has the largest number (79), followed by the two species of *Amblyomma* (74), *D. marginatus* (64), and *B. microplus* (56). *O. moubata* has only 30 sensory hairs. When we compare, however, the

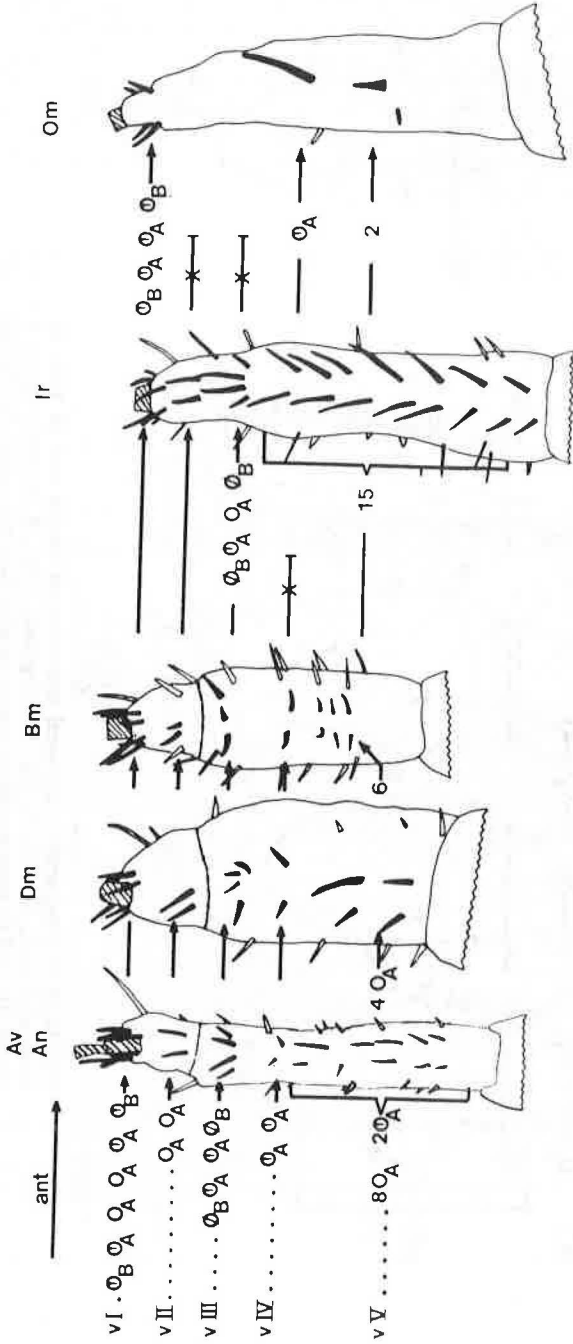


Fig. 16.9 — Comparative functional chaetotaxy of foreleg tarsi of adult *A. variegatum* (Av), *A. nuttalli* (An), *D. marginatus* (Dm), *B. micropius* (Bm), *I. ricinus* (Ir), and *O. moubata* (Om). Ventral faces with groups vI to vV (black sensilla). Not to scale. The symbols of the different types of sensory hairs are explained in Figs. 16.1–16.4. The figures should be read from left to the right beginning with the composition of the setal groups as found in *A. variegatum* and *A. nuttalli*. The arrows point to the corresponding groups in the other species, specific modifications in respect to the left species being indicated on the arrow.

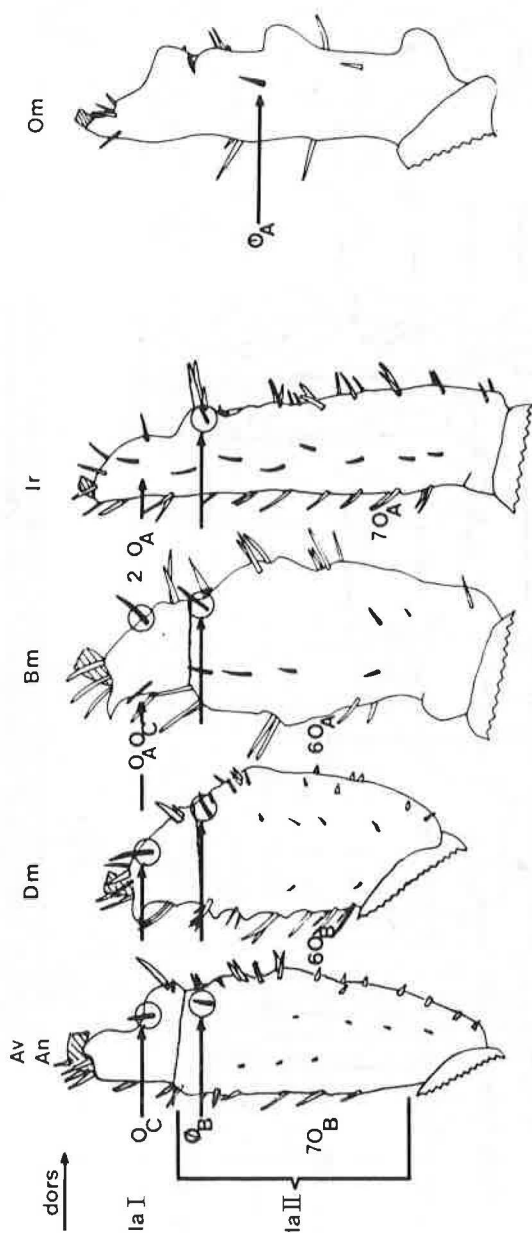


Fig. 16.10 — Comparative functional chaetotaxy of foreleg tarsi of adult *A. variegatum* (Av), *A. nuttalli* (An), *D. marginatus* (Dm), *B. microplus* (Bm), *I. ricinus* (Ir), and *O. moubata* (Om). Lateral anterior faces with groups IaI and IaII (black sensilla). Not to scale. The symbols of the different types of sensory hairs are explained in Figs. 16.1–16.4. The figures should be read from left to the right beginning with the composition of the setal groups as found in *A. variegatum* and *A. nuttalli*. The arrows point to the corresponding groups in the other species, specific modifications in respect to the left species being indicated on the arrow.

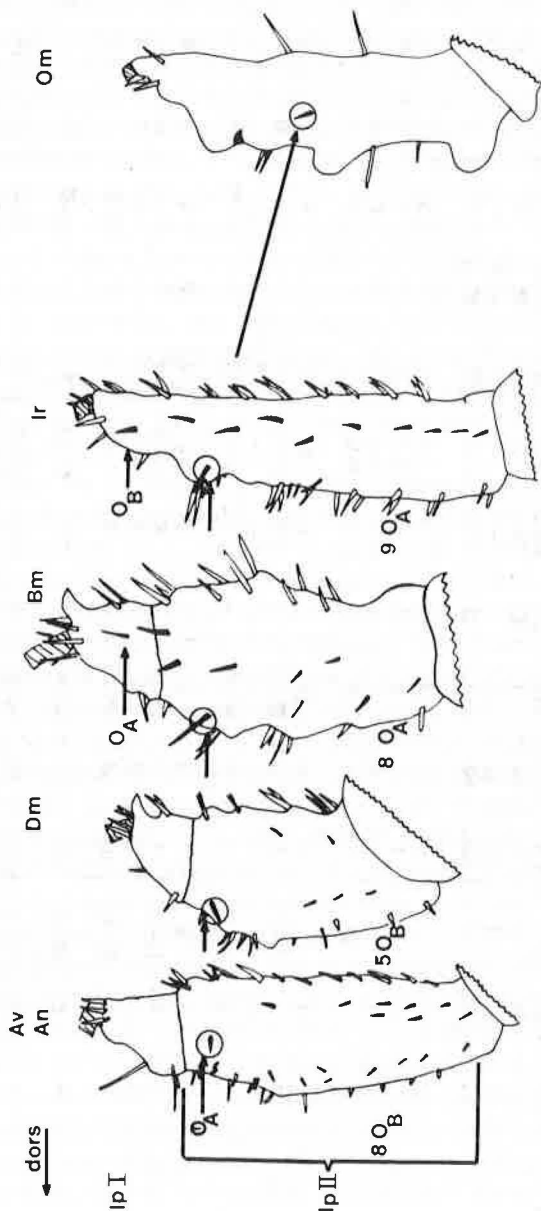


Fig 16.11 — Comparative functional chaetotaxy of foreleg tarsi of adult *A. variegatum* (Av), *A. nuttalli* (An), *D. marginatus* (Dm), *B. micropilus* (Bm), *I. ricinus* (Ir), and *O. moubata* (Om). Lateral posterior faces with groups IpI and IpII (black sensilla). Not to scale. The symbols of the different types of sensory hairs are explained in Figs. 16.1–16.4. The figures should be read from left to right beginning with the composition of the setal groups as found in *A. variegatum* and *A. nuttalli*. The arrows point to the corresponding groups in the other species, specific modifications in respect to the left species being indicated on the arrow.

Table 16.1 — Numbers of sensory hairs (SH) of the different types and corresponding numbers of mechanosensory units (MSU) and shaft innervating units (SIU) occurring on one foreleg tarsus of 6 species of ticks. For information about the functions of the different types refer to the text.

Types of SH	<i>A. variegatum</i>			<i>D. marginatus</i>			<i>B. microplus</i>			<i>I. ricinus</i>			<i>O. moubata</i>		
	SH	MSU	SIU	SH	MSU	SIU	SH	MSU	SIU	SH	MSU	SIU	SH	MSU	SIU
Np/A	12	24	0	8	16	0	25	50	0	43	86	0	3	6	0
Np/B	23	46	0	22	44	0	—	—	—	—	—	—	—	—	—
Np/A+B	35	70	0	30	60	0	25	50	0	43	86	0	3	6	0
Np/C	2	4	4	2	4	4	2	4	2-3	2	4	3	1	2	1
Np/D	1	0	3	1	0	3	1	0	2-3	1	0	2	1	0	2
Np/E	2	0	6	2	0	6	2	4	4-6	2	0	6	2	0	6
Np/C+D+E	5	4	13	5	4	13	5	4	8-12	5	4	11	4	2	9
Wp-sw/A	2	0	19	2	0	19	2	0	20	1	0	6	3	0	16
Wp-sw/B	7	0	21-25	5	0	21-35	4	0	21-35	7	0	21-35	0	0	18
Wp-sw/C	—	—	—	—	—	—	—	—	—	2	0	17	—	—	—
Wp-sw/A+B+C	9	0	40-54	7	0	40-54	6	0	41-55	10	0	44-58	8	0	34
Wp-dw/A	4	0	6	4	0	6	2	0	4	4	0	4	3	0	7
Wp-dw/B	4	8	16-28	4	8	16-28	4	8	16-28	4	8	12-20	—	—	—
Wp-dw/C	2	0	6	2	0	6	2	0	6	2	0	6	2	0	4
Wp-dw/A+B+C	10	8	28-40	10	8	28-40	8	8	26-38	10	8	22-30	5	0	11-13
Wp-sw+wp-dw	19	8	68-93	17	8	68-94	14	8	67-93	20	8	66-88	13	0	45-47
Tp/A	13	26	39-78	10	20	40-70	10	20	40-70	9	18	27-45	8	16	32-64
Tp/B	2	4	8	2	4	8	2	4	8	2	4	8	2	4	8
Tp/A+B	15	30	47-86	12	24	48-78	12	24	48-78	11	22	35-53	10	20	40-72
Grand totals	74	112	128-193 112	64	96	129-185 96	56	86	123-183 86	79	120	112-152 120	30	28	94-128 28
Total number of sensory cells	240-305			225-281			209-269			232-272			122-156		

total number of the sensory cells innervating the sensilla instead of the number of sensilla, the two species of *Amblyomma* surpass *I. ricinus*. This reversal is due mainly to the *Amblyomma* species having more contact chemoreceptors containing multiple shaft innervating units (SIU) while *I. ricinus* possesses a higher number of monomodal mechanosensory sensilla (type np/A with 2 mechanosensory cells each).

In the metastriates we observe a decrease in the number of sensory hairs in *B. microplus* and *D. marginatus* as compared to the *Amblyomma* species. This seems to be related to the size of the segments. The smaller the tarsus of a metastriate ixodid, the lower the number of sensory hairs in the proximal groups dVI, vV, IaII and IpII. Unlike metastriates, the small prostriate ticks such as *I. ricinus*, have well developed proximal groups providing them with a larger number of monomodal mechanosensory sensilla. In *I. ricinus* as well as in *B. microplus*, the typical short and blunt-tipped np/B sensilla are replaced by the longer np/A setae. This probably represents an adaptation towards a higher sensibility to mechanical stimulation and air currents. *O. moubata* has only 3 monomodal mechanosensory hairs, indicating a poorly developed sense of touch.

When we examined the putative hygro-thermosensitive sensilla np/C, np/D and np/E, we found 5 in hard ticks and 4 in soft ticks. The latter lack the np/C sensillum IaI.1. The innervation of *B. microplus*, *I. ricinus*, and *O. moubata* np/C sensilla differs from other ticks in that one or both of their np/C setae possess only one SIU, suggesting that either the warm or the cold temperature sensitive unit is lacking. This has also been observed in immatures of *A. variegatum* (Hess & Vlimant 1983a). In *B. microplus*, the number of neurons associated with np/C, np/D, and np/E sensory hairs seems to be more variable than in the other species. In general, the total thermo-hygro-sensitive potential is difficult to assess as tp and wp sensilla possess an unknown number of neurons reacting to temperature and humidity (Waladde *et al.* 1981, Hess & Blendermann, in preparation). We believe that thermo-hygro-sensitivity in argasids is reduced as compared to ixodids because soft ticks have fewer neurons related to np-thermoreceptors and olfactory chemosensory hairs.

Analysis of the olfactory wp-sw sensilla of the different species is a good example of why it is insufficient to compare only the number of setae among the species. Such differences in no way inform us about the real sensory potential provided by this category of sensory hairs. The best example is the innervation of the capsule of Haller's organ (wp-sw/B sensilla) of hard ticks. The number of sensory hairs varies between 4 and 7, but the total number of neurons innervating these sensilla is the same in all species. This is explained by the fact, that in the smaller metastriates, some of the capsule-sensilla have apparently fused. This becomes evident when we examine the fine structure of the sensory hairs. Fused sensory hairs are equipped with 2 separated bundles of 3-5 dendrites, but the total number of bundles in the capsule is 7 in all species. Fusion of olfactory sensory hairs is also observed in the type wp-sw/A of the group dII. The ticks we studied have only one wp-sw/A sensillum there, while in *Amblyomma americanum* (Foelix & Axtell

1972), some representatives of the genus *Dermacentor* (Arthur 1962), and *Haemaphysalis* (Roshdy *et al.* 1972) there are 2. Fine structural analyses of these wp-sw/A sensilla reveal the presence of 3 bundles of neurons with a total of 14 neurons except *B. microplus* with 15. These 3 bundles are distributed on two sensilla as in *A. americanum* or they share a common shaft as in *A. variegatum*. We believe that the presence of 3 bundles indicates a primitive state of 3 wp-sw/A sensilla in the group dII.

I. ricinus has only one wp-sw/A sensillum but possesses 22 additional wp-sw/C sensory hairs (restricted to this genus) with a slightly higher total of wp-sw-neurons as compared to the metastriates.

In conclusion, of all ticks studied, prostriates have the highest number of neurons associated with wp-sw sensilla, while argasids have the least.

Concerning the wp-dw sensory hairs, *B. microplus* differs from the other hard ticks by the absence of the 2 single-innervated sensilla of the group dIV (Hess & Vlimant 1982), and in *I. ricinus* the innervation of wp-dw/B sensilla is slightly reduced as compared to the other hard ticks. In *O. moubata* and other argasids this type is apparently lacking.

Considering wp-sw and wp-dw sensory hairs together, it can be concluded with some certainty, that ixodids possess a better olfactory sense than argasids if we assume identical proportions of olfactory and thermo-hygro-sensitive neurons in all species.

Concerning contact chemoreception (tp sensilla) the metastriate hard ticks appear best equipped, followed by *O. moubata* and *I. ricinus*. Compared to species of *Amblyomma* the smaller metastriates lack some tp/A sensilla related to the reduction of the proximal setal groups, while *I. ricinus* lacks tp/A sensilla on the ventral face of the tarsus. There is no difference in tp/B sensilla in all of the 6 species.

We hypothesize that taste is better developed in metastriates, than in postriates and argasids.

Thus far we have only compared the absolute numbers of the different types of foreleg tarsal sensilla and their innervation among species. We can also determine the relative importance of the different sensory modalities for each of them (Table 16.2). We observe that the ixodids differ greatly from the argasids in this respect. The latter have relatively few seta-associated mechanosensory units, and a higher percentage of thermo-hygro-sensitive and gustatory neurons.

Among ixodids, Metastriata and Prostriata differ somewhat in the relative importance of taste and mechanosensitivity.

The relative importance of olfaction is similar in all observed ticks. It is difficult to estimate the biological value of this comparison, but it could indicate that hard ticks and soft ticks have different modes of host seeking.

Comparison of larval ticks revealed identical functional chaetotaxy in all the ixodid species studied (Fig. 16.12) and showed that *O. moubata* larvae are very similar to hard ticks in this respect. Interestingly, almost all of the sensory hairs are present in the latter species, but not all of them are differentiated. This is explained by the fact that larval *O. moubata* and other larval argasids do not feed.

Table 16.2 — Estimation of the relative importance of sensory modalities of six species of ticks expressed in % of the total foreleg tarsal sensory hair input.

	Mechano- sensory neurons (%)	Thermo- hygro sensitive neurons (%)	Olfactory neurons (%)	Gustatory neurons (%)
<i>A. variegatum</i>	41	5	30	24
<i>A. nuttalli</i>				
<i>D. marginatus</i>	40	5	30	25
<i>B. microplus</i>	36	5	34	26
<i>I. ricinus</i>	47	4	31	18
<i>O. moubata</i>	21	7	34	38

		v I 2,1... \emptyset_B \emptyset_B 4,3... 6,5... \emptyset_A \emptyset_A	
d I 1..... \emptyset_A	lp I	v II	la I 1... \emptyset_C
d II 1..... \emptyset_A 2,3,4. \emptyset_E \emptyset_E \emptyset_D 5,6 \emptyset_C \emptyset_C			
basitarsal scissure			
C 1,2..... \emptyset_B \emptyset_B 3,4..... \emptyset_B \emptyset_B	lp II 1.. \emptyset_A	v III 4,3,2,1... \emptyset_B \emptyset_A \emptyset_A \emptyset_B	la II 1.. \emptyset_B
d III 1,2.. \emptyset_A \emptyset_B		v IV	
d IV 1,2... \emptyset_A \emptyset_A	2.. \emptyset_B	v V 2,1... \emptyset_A \emptyset_A	2.. \emptyset_B
d V			
d VI 1,2... \emptyset_B \emptyset_B			

Fig. 16.12 — Map of larval functional chaetotaxy of foreleg tarsi of *A. variegatum*, *A. nuttalli*, *D. marginatus*, *B. microplus* and *I. ricinus* with dorsal (d), lateral posterior (lp), ventral (v), and lateral anterior (la) setal groups. Compare also with Figs 16.8–16.11. The symbols are explained in Figs. 16.1–16.4.

We can now attempt to answer the questions asked at the beginning of this chapter, i.e. do systematic position, life cycle, and ecology affect the structure of the foreleg tarsal sensory system? Comparison of the six species which differ greatly in these respects, and the integration of observations already published by other authors demonstrate, that important modality-related differences in the tarsal sensory components are not expressed in the species but at a higher systematic level. We observe characteristic differences between argasids and ixodids and between the *Metastricata* and *Prostricata*, but there is no difference between *A. variegatum* and *A. nuttalli* parasitizing warm-blooded vertebrates or reptiles respectively. On the other hand, it is true that adult *B. microplus* have a reduced tarsal sensory system when compared to species of *Amblyomma*. It is not easy to determine if this is due to *B. microplus* not needing to seek a host for feeding, or to the general trend of reduction in the tarsal sensory system observed in the smaller *metastricates*. Because most of the missing sensilla in *B. microplus* belong to the proximal groups and because a reduction in sensory hairs occurs in *D. marginatus* as well (a small three-host tick), we strongly suggest the second hypothesis.

The lack of structural and morphological differences among related tick species with completely different life cycles demonstrates that we have to concentrate on the physiology of sensilla if we wish to understand the function of the tarsal sensory system in host detection. It is possible, or even probable, that electrophysiological experiments will confirm the results of our structural study, i.e. the absence of differences among related species and an absence of highly specific host cues. Thus we could conclude that, at least in some closely related species such as *A. variegatum* and *A. nuttalli*, physiological (in contrast to ecological) host specificity is determined not at the level of sensory input but at the level of integration of the sensory information. These ticks may possess an intrinsic 'portrait' of their hosts composed of a more or less accurate mosaic of stimuli. This mosaic could also include repellents.

Our detailed knowledge should, however, not lead us to overestimate the role of the foreleg tarsi. Other legs, other appendages, and the whole body also possess an important number of different sensory organs.

16.3 LEG SENSORY HAIRS ELSEWHERE THAN ON TARSUS 1

Zolotarev (1962) was correct when he commented on the 'absence of clarity' in the literature concerning the nomenclature of tick leg segments. For this reason we will discuss the nomenclature used in designating tick leg segments before presenting and discussing other results. We will use the nomenclature of Grandjean and Evans who subdivide the legs of *Anactinotrichida* (to which the *Ixodida* belong) into coxa, trochanter (Tr), femur (Fe), genu (Ge), tibia (Ti), tarsus (Ta), and an apotele (ambulacrum) (Grandjean 1954, Evans *et al.* 1961, Van der Hammen 1976, Krantz 1978).

The femora and tarsi of ixodid adults are subdivided into a basi- and telofemur, a basi- and telotarsus by the adesmatic basifemoral (Fig. 16.14) and basitarsal scissures (Fig. 16.15) respectively. In *metastricate* ticks, the

basitarsal scissure is less visible on the forelegs than on legs 2–4, and in the Prostriata and argasids it appears to be absent on tarsus 1. In immatures, distinct secondary segmentation seems to be lacking.

Near the proximal end of the foreleg tarsi and of each of the tibiae and genua of ixodid adults there are incomplete ventral fissures designated Foreleg Tarsal Fissure, Tibial Fissure, and Genua Fissure respectively. These scissures and fissures are mechanosensory organs which will be discussed in the next section.

All segments of the four pairs of legs bear sensory hairs. We studied these sensilla in *A. variegatum* by SEM and some by TEM in order to determine their modality.

The respective numbers of sensory hairs are approximately the same on the homologous leg segments of the four pairs of legs except tarsus 1, and no differences were observed between males and females. Moderate individual variations will not be discussed here.

On tarsi 2–4 the dorsal face is occupied by 2 distal np/A and 5–6 proximal np/B sensilla. The lateral anterior and lateral posterior faces bear 5–6 np/B sensory hairs. The most distal of these are longer and therefore could be considered as np/A as well. On the ventral face we found about 13 sensory hairs, 7 of which are arranged around the apotele. One 'vI'-sensillum is of the tp/A type; all the other ventral setae belong to the type np/A. A total of 31 np/A and B and 1 tp/A were observed on each of the tarsi 2–4.

The dorsal tibial face bears 10 np/B and a distal pair of gustatory tp/A sensilla (Fig. 16.13). The lateral anterior and posterior faces bear about 7 np/B sensilla each, the most distal being longer than the others. The ventral face bears 8 np/A sensory hairs. There are a total of 32 np/A and B and 2 tp/A sensilla for each tibia.

The genu, which is a relatively long segment, has a dorsal face with about 13 np/B and 2 distal tp/A sensilla, 10–11 np/B sensory hairs on each of the lateral faces and 6 ventral np/A setae. A total of 40 np/A and B, and 2 tp/A were found for each genu.

The femur has 11 dorsal np/B sensilla arranged in pairs. In the second pair we find a single tp/A sensory hair in the anterior position. The lateral faces bear 8–11 np/B sensory hairs on the telofemur and 1–2 on the basifemur. The ventral face has about 7 np/A sensilla of which 2 are located on the basifemur. A total of 40 np/A and B and 1 tp/A were found for each femur.

In nymphs, 1 tp/A sensillum is located on the dorsal faces of tibia, genu, and femur; the other sensory hairs are of the np/A and B types.

This study confirms that tarsus 1 is a highly specialized leg segment bearing 12 different types of sensory hairs. The other segments are equipped with np/A and B, and tp/A sensilla only, the former representing the largest number. Investigation of the total number of neurons associated with leg sensory hairs clearly indicate, however, that the 'other' leg segments play an important role in the sensory physiology of the tick. In adult *A. variegatum*, the total mechanosensory input provided by setae located on the legs is 2480 MSU (224 on the foreleg tarsi, 2256 on the other leg segments). The number

of putative thermo-gustatory SIU associated with tp/A sensilla is 216–432 (78–156 on the foreleg tarsi and 138–276 on the other segments). Thus 91% of the total seta-related mechanosensory input and 63% of the neurons associated with putative thermohygro-gustatory tp/A neurons are located on leg segments other than the foreleg tarsi.

We conclude, that the sensory hairs of the 'other' leg segments play an important role in taste and possibly in the detection of temperature differences, sense of touch and of substrate vibrations. An important role for np sensilla in the detection of air currents in *A. variegatum* seems improbable because np/A sensilla are too rigid and np/B sensilla too short. In *I. ricinus* these sensory hairs are much finer.

16.4 INTRACUTICULAR LEG SENSILLA

As in other chelicerates, the legs of ticks bear intracuticular sensilla distributed on all segments in addition to sensory hairs. During the last 3 years we have discovered and analyzed ten different structural types of such organs. They are mechanoreceptors that act as strain detectors since they possess tubular bodies. Some of them represent structural intermediates between arachnid slit sense organs and insect campaniform sensilla. One of these sensilla, called the *Distal Tarsal Slit Sense Organ* (DTSSO), has been described in detail (Hess & Vlimant 1984). In this chapter, we will not present and discuss the structural details of each of the ten types of sensilla (the corresponding papers are in preparation), but we will confine ourselves to describing their frequency and distribution on the legs of *A. variegatum*, *I. ricinus* and *O. moubata*.

The intracuticular sensilla are located in the cuticle or are associated with moving cuticular elements joined by membranes. All of them consist of the basic elements described for the DTSSO (Hess & Vlimant 1984), i.e. inner and outer receptor canals separated from each other by a fibrous cup (Fig. 16.19, 16.20). Either of the receptor canals may be reduced, depending on the type of sensillum. Externally, the outer receptor canal is closed by the covering membrane epiostracum which represents a specialized part of epicuticle (Figs. 16.15, 16.16, 16.18–20). The outer canal of some types of intracuticular mechanoreceptors contains globular cuticular particles (Figs 16.19, 16.20). The fibrous cup which acts as a stimulus transducer is penetrated by two structurally different tubular bodies protected by a scolopale (Fig. 16.20). The tubular bodies are specialized mechanosensory dendritic endings that respond to compressional forces. In most sensilla, the receptor elements are associated with slits and membranes that represent mechanical filters (Barth & Blickhan, 1984). Sensilla integrated in scissures and fissures probably represent composed organs. The ten types of mechanosensory organs differ in their arrangement of these components and their location on the segments. When normal preparative techniques are used the sensilla are invisible even when using SEM, because most are covered by cuticular lipids and dirt (Hess & Vlimant 1984).

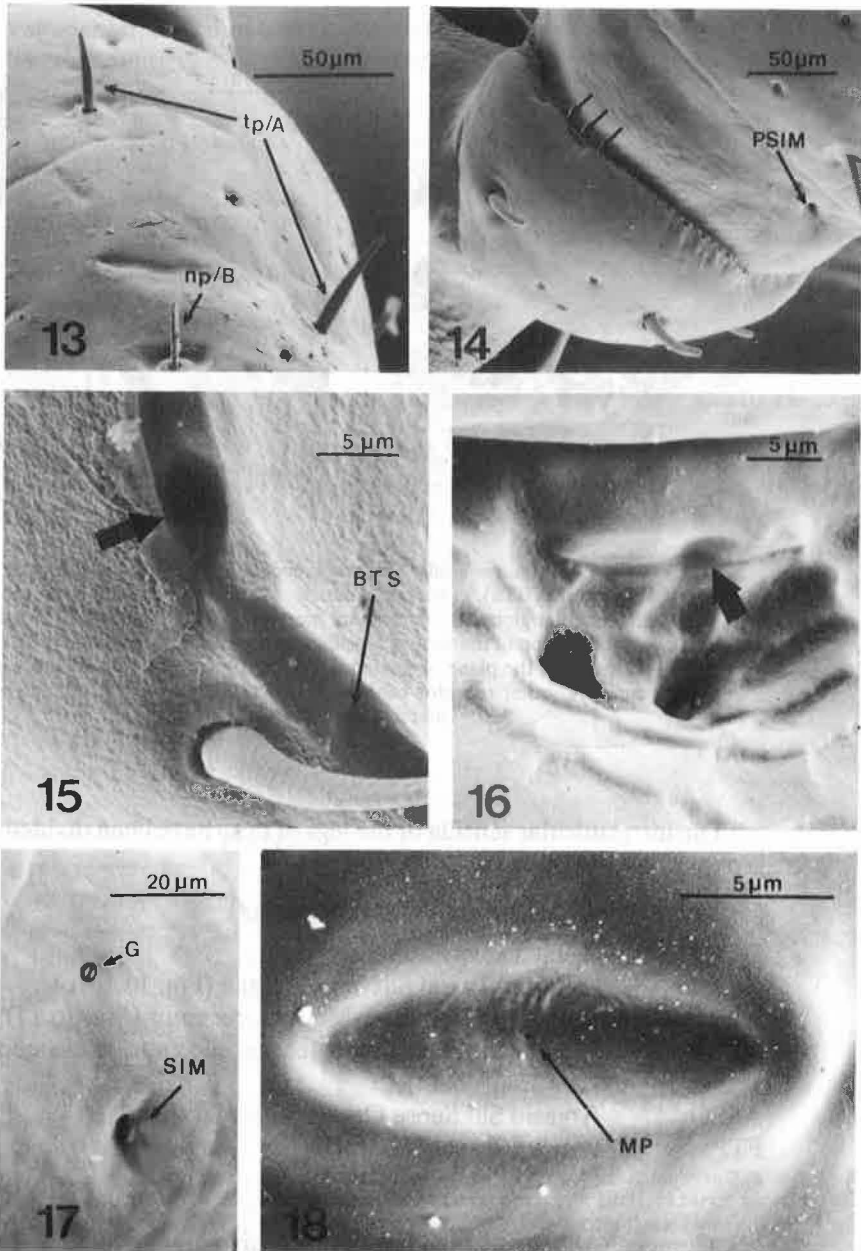


Fig. 16.13 — *A. variegatum* adult: Distal end of tibia with one np/B and two tp/A sensilla. The latter are easily recognizable by their twisted shafts. Fig. 16.14 — *A. variegatum* adult: Basifemur and telofemur are separated by the Basifemoral Scissure (BFS) which is equipped with numerous mechanoreceptors (arrows); PSIM: simple intracuticular mechanoreceptor associated with a pore; see also Fig. 16.21.

Fig. 16.15 — *A. variegatum* adult: The Basitarsal Scissure (BTS) of the legs 2–4 is equipped with two lateral and one ventral mechanosensory sensilla. Arrow: depression (covering membrane) of the anterior lateral mechanoreceptor; see also Fig. 16.21. Fig. 16.16 — *I. ricinus* adult: Proximal Tarsal Slit Sense Organ (PTSSO). The arrow indicates the central depression of the covering membrane invaginated into the fibrous cup; see also Fig. 16.22. Fig. 16.17 — *A. variegatum* adult: Simple Intracuticular Mechanoreceptor (SIM) and gland opening (G); see also Fig. 16.21. Fig. 16.18 — *O. moubata* adult: Argasid Slit Sense Organ (ASSO) with a central moulting pore (MP); see also Fig. 16.23.

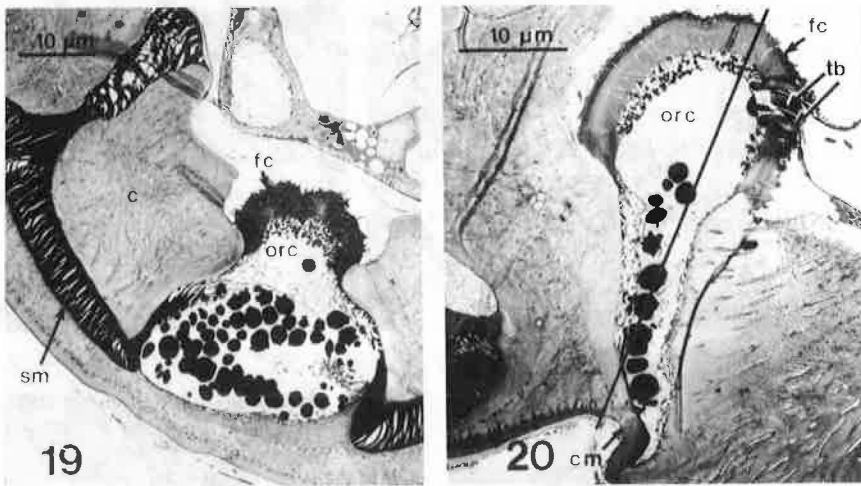


Fig. 6.19 — *A. variegatum* adult: Transverse section of the ventral sensillum of the Basitarsal Scissure (BTS). c: basitarsal cuticle; Fc: fibrous cup; orc: outer receptor canal with cuticular globules; sm: scissure membrane. Fig. 16.20 — *A. variegatum* adult: Sagittal section of the ventral sensillum of the Basitarsal Scissure (BTS). The black line indicates the plane of section of Fig. 16.19. cm: covering membrane; fc: fibrous cup; orc: outer receptor canal with cuticular globules; tb: tubular bodies piercing the fibrous cup.

The intracuticular sensilla of the legs of ticks have been divided into two groups:

(1) single intracuticular organs that consist of:

- DTSSO: Distal Tarsal Slit Sense Organ;
 PTSSO: Proximal Tarsal Slit Sense Organ (Fig. 16.16);
 SIM: Simple Intracuticular Mechanoreceptor (Fig. 16.17);
 PSIM: Simple Intracuticular Mechanoreceptor associated with a Pore (Fig. 16.14);
 ASSO: Argasid Slit Sense Organ (Fig. 16.19);
 FTF: Foreleg Tarsal Fissure;
 GF: Genual Fissure;

(2) Composite intracuticular mechanosensitive organs consisting of:

- BFS: Basifemoral Scissure composed of one ventral (asymmetrical) and several lateral (asymmetrical) sensilla (Fig. 16.14);
 BTS: Basitarsal Scissure composed of one ventral (symmetrical) and a pair of lateral (asymmetrical) sensilla (Fig. 16.15);
 TF: The Tibial Fissure consisting of one ventral (symmetrical) and a pair of lateral (asymmetrical) sensilla.

The distribution of the mechanosensory organs on the legs of *A.*

variegatum, *I. ricinus* and *O. moubata* are represented in Figs. 16.21–16.23. The following details should be noted:

DTSSO, PTSSO, SIM and FTF are restricted to ixodids and PSIMs have been observed only in *A. variegatum*. FTFs instead of BTSs occur on ixodid foreleg tarsi. In *A. variegatum*, the SIMs are located on the anterior face and in *I. ricinus* on the posterior face of the segments. In *O. moubata* we find ASSOs instead of SIMs, but the total number of ASSOs in *O. moubata* is much higher than the number of SIMs in the ixodids. *O. moubata* females have a slightly higher number of ASSOs than males. Except for the foreleg tarsi, the homologous segments of the four pairs of legs seem to have a identical sensillar apparatus. Compared to adults, immatures possess a lower number of intracuticular mechanoreceptor organs (Figs. 16.21–23).

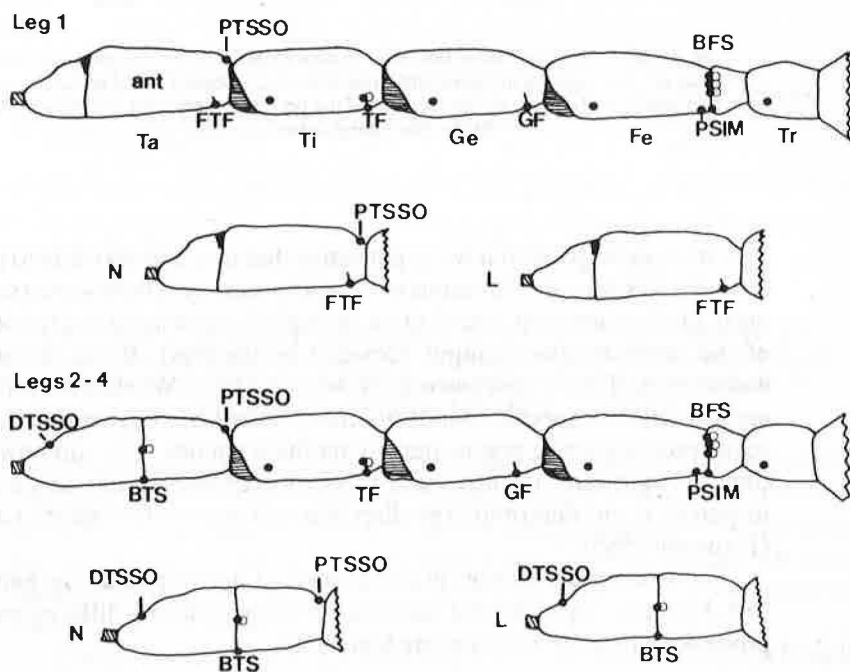


Fig. 16.21 — *A. variegatum*: Distribution of intracuticular mechanoreceptors on the four pairs of adult legs and nymphal and larval tarsi. Full circles: Lateral anterior, ventral or dorsal sensilla, open circles: Sensilla of the posterior faces. Not designated circles: SIMs. For abbreviations see text.

What is the contribution of the intracuticular mechanosensory sensilla to the total sensory input related to the legs? In *A. variegatum* it represents 324 neurons (mechanosensory units, MSU) i.e. 12% of the total population of leg MSU, in *I. ricinus* it represents 308 MSU i.e. 13%, and in *O. moubata* it represents about 1340 MSU i.e. 70% of the mechanosensory neurons of the legs. This means that ticks not only have a well developed sense of gravity

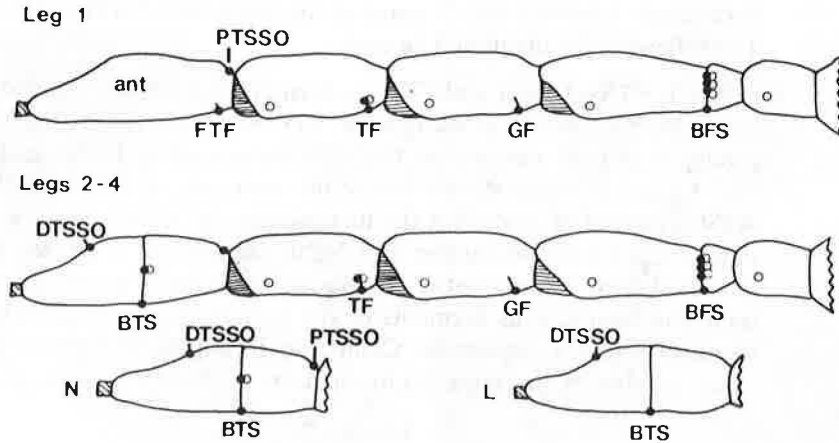


Fig. 16.22 — *I. ricinus*: Distribution of intracuticular mechanoreceptors on the four pairs of adult legs and nymphal and larval tarsi. Full circles: Lateral anterior, ventral or dorsal sensilla, open circles: Sensilla of the posterior faces. Not designated circles: SIMs. For abbreviations see text.

(orientation in space) but we hypothesize that they are also able to perceive sounds and substrate vibrations with some accuracy. These senses should be particularly important and of great biological importance in argasids (70% of the mechanosensory input provided by the legs). It has already been demonstrated in *O. concanensis* (Webb *et al.* 1977, Webb, 1979), that ticks are attracted by specific sounds of birds (*Petrochelidon pyrrhonota*), but the corresponding sense organs perceiving these sounds were unknown at the time. In scorpions, intracuticular mechanoreceptors enable this arthropod to perceive and determine the direction and origin of substrate vibrations (Brownell 1985).

The striking differences in the number of intracuticular mechanoreceptors between argasids and ixodids certainly indicate differences in the physiology of their host-seeking behaviour.

16.5 CONCLUSIONS

The foreleg tarsi of ticks are highly specialized leg segments bearing different types of mechanosensitive, thermo-hygrosensitive, gustatory, and olfactory sensilla. Characteristic differences in the number and distribution of these structure occur among metastriate, prostriate, and argasid ticks, but not among related species even if the latter differ greatly in their life cycle and ecology.

The prominent role of the foreleg tarsi in the sensory physiology of ticks is qualified somewhat by the presence of mechanosensitive and numerous thermohygro-gustatory sensory hairs on other leg segments.

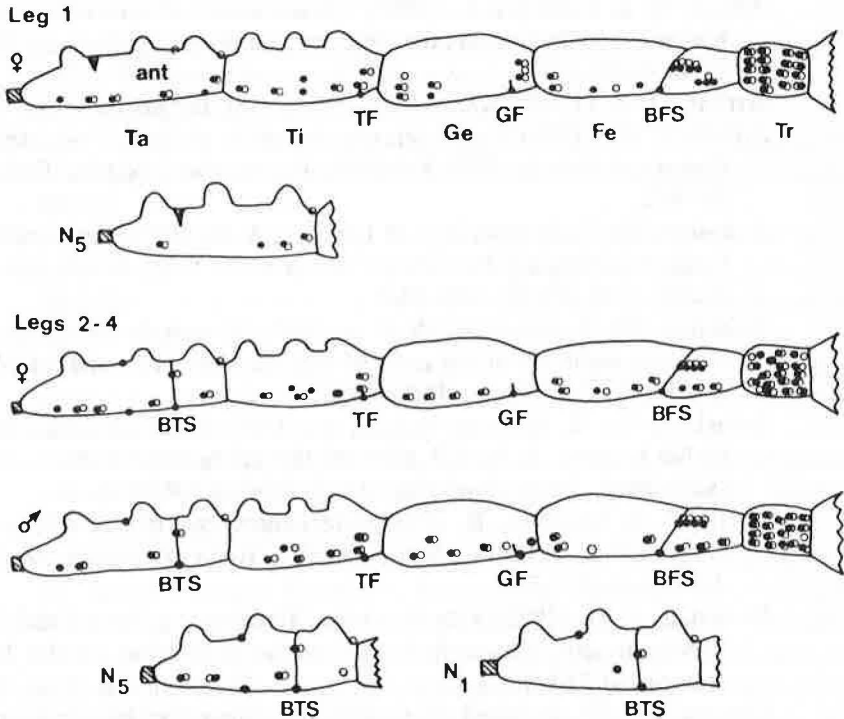


Fig. 16.23 — *O. moubata*: Distribution of intracuticular mechanoreceptors on the four pairs of adult legs and nymphal 5 and nymphal 1 tarsi. Full circles: Lateral anterior, ventral or dorsal sensilla, open circles: Sensilla of the posterior faces. Not designated circles: ASSOs. For abbreviations see text.

The presence of ten different types of intracuticular mechanosensory leg sensilla suggests that ticks most probably possess a well developed sense of gravity and the capacity to detect and to analyze substrate vibrations and sounds. This is especially true for argasids which are equipped with a great number of such sensilla which are probably used for the detection and identification of hosts.

Comparative functional chaetotaxy is a useful tool for approaching the physiology of host-seeking behaviour in ticks, but it could also be useful in studying the evolution of ticks.

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