INSECT ANTENNAE

BY DIETRICH SCHNEIDER

Deutsche Forschungsanstalt für Psychiatrie, Max-Planck-Institut, Abt. für vergleichende Neurophysiologie, Munich, Germany

There is much more literature available on insect antennae than is possible to quote here. Earlier papers dealing with morphology and related subjects could only be cited in exceptional cases, because textbooks and monographs are available. It is hoped that the author's arbitrary selection of literature will at least lead the reader to most of the important publications in this field.

SHAPE AND FUNCTION

With the exception of members of the subclass, Protura, which have neither antennae nor eyes, all insects possess a pair of antennae. Morphologically, we find two principal types of antennae (63): (a) Segmented antennae with very similarly shaped segments and muscles in all segments except the distal segment. Postembryonic multiplication of segments is accomplished by division of the distal segment. This type is found in the apterygote subclasses, Collembola and Diplura, as well as in the class Myriapoda. (b) The flagellar antennae (annulated antennae) with two basal segments, scape and pedicel, and a flagellum sometimes composed of many similarly shaped segments. Muscles moving this type of antenna are found only in the head and in the scape. Multiplication of flagellum segments during postembryonic development is usually accomplished by division of the proximal or neighboring segments. Only rarely do all segments of the flagellum divide (46, 64). This type of antenna is present in the Thysanura among the Apterygota, and in all the Pterygota.

One of the possible adaptive reasons for increasing the antennal length might be to have more surface area available for sense organs. However, obtaining additional surface area can certainly be accomplished also by developing branches, leaflets, etc. The density of sensilla on long antennae is, in many cases, not as high as one would expect on the premise mentioned above. It seems much more probable that long antennae are long because they are literally used as feelers.

It is striking that in many or most heteronymous antennae (of butterflies, beetles, etc.) a long proximal stretch of the antennae contains only few sensilla, while some of the distal segments have many and diverse sense organs.

The large surface area of the antennae of the silkworm moth, Bombyx mori

1 The survey of the literature pertaining to this review was concluded in January 1963.

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(Linnaeus), is mainly the result of branching. Without the branches, the surface of this antenna [data from (123)] would be 4.8 mm², but the actual surface, with all the branches included, is 29 mm². A branchless antenna of the same surface area would have to be 6 times as long. An additional increase of about 8.2 mm² is provided by the surface area of the protruding sensilla, and 92 per cent of this surface comes from the sensilla trichodea. This sensilla area must not, of course, be mistaken for the receptive surface!

If insufficiency of antennal area alone was the basis for *Bombyx* to evolve a bipectinate antenna, one would expect to find a high density of sense organs over its entire surface. However, while the mean density is 1 sensillum per 1400 μ², the densest parts have 1 per 200 μ². In other insects, this value can be even higher. Sensilla basiconica on the antenna of the beetle, *Necrophorus*, are as dense as 1 per 25 μ² (6). Certainly, these ratios alone distort the actual picture. A hair is a sensillum only if it is innervated. Antennal surface can therefore only be fully utilized if the volume of the antenna is sufficient to contain the sensory and accessory cells with their blood and air supply systems. It follows that the antennae of *Bombyx* could perhaps hold on a volume basis two times the number of sensilla they actually do, but not seven times, as one might expect from the maximum density found in *Necrophorus*.

While we are far from understanding the functional meaning of all the variously shaped and sometimes very bizarre antennae, a few cases have been clarified. There is increasing evidence for the functional importance of the Johnston sense organ in the pedicel. This organ serves as a detecting instrument for mechanical oscillations or stresses (see Mechanoreception).

Although we are still lacking detailed information of a broad comparative nature, it may eventually be shown that the airspeed-meter function of the flagellar insertion into the sensitive pedicel or other related functions, are accompanied by specific morphological adaptations in different groups (26, 36, 39, 99, 100, 101, 122, 123, 139, 147, 148).

Whether antennae play a role as passive stabilizing appendages during flight is an open question. At least in slow-flying insects with long antennae, this might be the case.

A widespread phenomenon is the sexual dimorphism of antennae which sometimes is associated with the occurrence of different sense organs. Mainly, the antennae of males are more complex. In some moths, the surface area of the bipectinate male antennae is several times the surface area of the thread-like female antennae [not true in *Bombyx* (123)]. This dimorphism has always been considered to be an expression of the “need” of the male to have relatively more sensilla to find his partner. Such differences are usually not present or are small in insects which live gregariously or use auditory or visual organs for sexual orientation.

A most peculiar antennal function has been reported in the water beetle family, Hydrophilidae. The antennae, together with furrows in the head capsule, form tubes through which the surfacing beetle refills its air reservoir.
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on the ventral side of the body. Here, an olfactory function of the antennae is reported to be lacking, and olfaction to be restricted to sensilla on the labial palps (102, 111, 149). A similar secondary respiratory function of the antennal flagellum is thought to be realized in other water beetle groups, the Gyrinidae (149), Dryopidae, and Leptinidae (66). Larvae of Hydrophilus even use their short antennae with cuticular teeth to capture and hold their prey (85), while the antennae of fleas (147), Collembola (47), and others, play a mechanical role during copulation.

SYSTEMS MOVING THE ANTENNAE

*Segmented antennae.*—Muscles for the control of these antennae are found in the head and in all segments except the last one. As in the first two segments of the flagellar antennae, there are several muscle groups in the head responsible for movements of the first segment, and in each segment there are two muscle groups (corresponding to those in the scape) for moving the next distal segment (63). Antennae of this type are able to achieve elaborate movements. In some Collembola, the males wind each antenna helically round the corresponding antenna of their female partner (47).

*Flagellar antennae.*—Two sets of muscles are responsible for the movements and positioning of this type of antenna (63). The situation has been analyzed in detail in the moth, *Bombyx* (122); it is similar in the honey bee (51, 136) and may not be too different in many other insects. The scape is moved by two to four muscles originating on the tentorium within the head capsule and inserting onto the base of the scape [see also (99, 101, 147, 148)].

In *Bombyx*, the articulating intersegmental membrane between head and scape is wide except at one point; at this point a sclerotized knob of the head capsule, the antennifer, and its counterpart on the scape are located. Two of the four muscles run on each side of the antennifer and are able to incline the scape as well as to exert torsions, while the two others can only incline the scape. This arrangement limits freedom of movement, but, as a whole, the system is similar to and has the advantages of a ball joint.

The two muscle groups moving the pedicel originate in the scape and insert at opposite points on the pedicel. Due to this arrangement (and the consequent freedom of movement), the connection between the first and second segment is of the simple hinge type. With these two joints nearly all possible positions of the antennae become feasible.

There are no muscles in the flagellum, but, nevertheless, it is possible to observe some movements in the flagellum and its branches. This is most obvious in the flagellar leaflets of the beetle, *Melolontha*, the complex, bipectinate flagellum of *Bombyx* and of other moths (7, 122, 144), and even in some larval antennae. These movements can only be brought about by an in- and outflow of hemolymph. The limiting factors are (a) the elastic properties of the complicated intersegmental membranes and the membranes at the bases of all the branches, and (b) the extent and possible channelling of the blood stream. While in *Bombyx* there is sufficient information available about
the membranes to explain the movements observed so far, we lack information on the pressures exerted by the blood.

CIRCULATORY AND RESPIRATORY SYSTEM

In all cases studied thoroughly, an antennal blood vessel has been found [for literature see (24, 41, 124)]. This vessel runs from the base of the antenna to the distal end and does not branch or send smaller corollaries into ramifications of the antenna. The blood is pumped into this vessel by a small "heart" in the head capsule. This accessory pulsating organ is either directly connected to the sinus at the anterior end of the main vessel of the body (as in Bombyx and the bee) or pumps blood out of the head capsule without direct tubular communication with the main heart (as in the cockroach).

The blood leaves the antennal vessel through slits in its wall as observed in some cases. From there, the blood streams back through open spaces in the antennal lumen. All tissues are separated from the blood by connective tissue membranes. The basement membrane at the inner surface of the epidermis is continuous with the membranes surrounding the nerves, smaller nerve bundles, and even the individual nerve fibres. There is also continuity with the membranes lining the septa, tracheae, and muscles.

The antenna is well supplied with tracheae. There are one or two main tracheal tubes in the middle of the antennal stem which send branches into all extensions of the system.

CUTICLE

In addition to the variations in gross and fine anatomy of antennae, all kinds of cuticle differentiation have been observed. Normally, the major part of the antenna is well sclerotized with the exception of the intersegmental membranes. Here we find soft flexible cuticle (122).

Polarized light studies have revealed a complex micellar arrangement in the cuticle of antennae and some sensilla (96, 122). In the honey bee, the saturniids, and Bombyx, all antennal sensilla are sclerotized. Only the bases of some of the bristles show a soft, flexible membrane (97, 123, 138). The helical arrangement of microfibers observed in the bristles of a centipede (95) was also observed in antennal pegs of a caterpillar (28) and in hairs of moths (97).

In a number of insects, sensory pegs with presumably olfactory function, have been shown to be permeable to dyes in aqueous solution. This permeation, however, usually took place only after fixation of the antenna with protein denaturizing agents or detergents (97, 126–131, 134, 137). It later appeared that some of these pegs have pores in the cuticle where nerve dendrites penetrate all layers of the cuticle, including the epicuticle which is known to be the water barrier (133). There is direct contact of these nerve endings with the air and with applied solutions (98).

In a number of studies, it has been found that some sensilla (basiconic pegs, hairs, etc.) have a cuticular sheath which envelops the nerve fibre (62,
103, 130, 132, 133, 135). When, during moulting, the sense cell plasm retracts or is left behind (92), the sheath is lost and can be found in the exuvia (159).

Whether the disappearance of grasshopper antennal sensilla after KOH treatment really indicates that these sensilla do not contain any chitin, may be doubted (133). Such an effect could result from there being too small an amount of chitin in the socket area of the sensillum, with subsequent rupture and loss of the cuticular protuberance during treatment with strong alkaline solutions.

SENSILLA AND NERVES

A sensillum is defined as a specialized area of the integument, consisting of formative cells [tormogen and trichogen, see (95)], the sensory nerve cells and, in some cases, auxiliary cells (17, 135). All of the cells are derived from one mother cell by differential cell division (48). The trichogen cell will produce the hair only in the presence of at least one nerve cell (25).

This definition of a sensillum is strictly morphological. From the beginning of microscopic anatomy to our time, morphologists have been prone to ascribe functions to the sensilla they saw. Unless there is experimental proof, anatomy can, at most, suggest a possible sensory function. In this section we will deal only with structure, not with function. Since all sensilla are homologous formations it is no wonder that we find a number of types which can be classified only with difficulty. The first three types described below have been given very different names. All three are hairlike (trichoid or setiform). Possibly we will have a clear way to distinguish one type from another through advances in comparative fine structure analysis and physiological research. However, we also find sensilla of such bizarre shape that it is hard to place them at all (40).

Sensilla chaetica (sensory bristles or spines).—Bristles are trichoid sensilla distinguished by a specialized and flexible circular membrane at the base. This can be shown either by histological methods or mechanical deflections. This definition covers a number of different subtypes which, in some cases, have been thoroughly studied.

On the flagella of Lepidoptera and a grasshopper, bluntly ending bristles with an open tip have been found. All, or at least most of the nerve fibres end in the tip opening (7, 84, 89, 123, 132).

On the flagella of other insects, a variety of bristles of different shapes can be found. Sometimes these organs are relatively sharp and pointed [in roaches (106, 108); in bugs (154); in beetles (112)]. Sometimes they are very long and arranged in rows [in fleas (147); in male mosquitos (65, 105)].

A typical bristle is always found in areas opposite the intersegmental membrane between head and scape, as well as between scape and pedicel on the scape and pedicel, respectively. Recently, these have been named Böhm bristles after Böhm who described them in Lepidoptera in 1911 (8). They are probably present on homologous places in all insects. Sometimes, however,
the name sensillum "chaeticum" has been used for this organ. Many authors have called it sensillum "trichodeum," some also sensillum "basiconicum" (77, 89, 94, 123, 143, 147). The strategic position of these organs at articulations is analogous to that of bristle- or hair plates (76, 77, 88).

**Sensilla trichodea (sensory hairs.)**—Hairs are trichoid sensilla without any specialized basal cuticular ring serving as articulating membrane. They are distinguished from the following group by relatively greater length and are found in most insects (55, 65, 84, 89, 105, 106, 108, 113, 123, 131, 134, 158). It is typical for the sexual dimorphism of saturniid moths that only the males are supplied with these sensory hairs (7). In these animals and also in *Bombyx*, the distal third of these organs appears to be dye-permeable when treated by Slifer's methods (97, 126, 127). Between one and three nerve cells have been observed as having these sensilla.

**Sensilla basiconica (sensory pegs or cones).**—Omnipresent trichoid sensilla without any specialized basal membrane. If present together with sensilla trichodea on an antenna, they are relatively shorter and usually also have a thinner wall. From one to several nerve fibres have been observed in connection with these organs (7, 65, 89, 113, 123, 145, 151).

In grasshoppers, the honey bee, a fly, and a caterpillar, these organs have been studied with the electron microscope (33, 98, 130, 133, 134). The peg's cuticle has many pores, where packages of dendrites from sense cells are in direct contact with the air (Fig. 1). Dendrites from different cells may end side by side in a given pore (Fig. 2). Some of the pegs on the fly's antenna have this structure or innervation, others do not; the latter have a non-perforated, fluted cuticle (33).

**Sensilla coeloconica (sensory pit-pegs).**—These are thin-walled cones on the floor of depressions in the antennal cuticle. The cone's wall appears fluted in cross sections of some of these organs. In the Lepidoptera, the relatively wide pits are protected by spiny ridges of the cuticle. These organs are innervated by four or five nerve fibres forming a bundle and ending in the very tip of the cone (7, 84, 89, 123).

Dye permeation has been found at the tip of the cones on the grasshopper flagellum (103); this suggested an opening at the tip (127) and was proved by electron micrographs (133). The sensillum has four nerve cells. Similar organs have been found in Coleoptera (55) and some other orders (91, 103).

On the large, sacklike funiculus of muscids, there are pits holding several

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**Fig. 1. Sensillum basiconicum** from the antenna of a grasshopper. Distal processes (Dp) of the sensory nerve cells (Sc) are channeled into a cuticular sheath (Cs). They leave this sheath near the base of the peg, branch like dendrites of the central nervous system and end in pores of the cuticle. Here the nerve membrane is presumably in direct contact with the air (see inset, Fig. 1). Gl = gland. Tormogen and trichogen cell nuclei near the lower end of the sheath. Basis diameter of the peg: 4 to 5 μ. Drawings after a diagram of Slifer, Prestage & Beams (133). Courtesy of Dr. C. Hoffmann and *Fortschritte der Zoologie, 13* (1961).
sensory pegs (62, 75). Fine structure analysis (33) showed that these pits are supplied with three different types of pegs.

_Sensilla ampullacea (sensory flasks)._—In the Hymenoptera, there are a number of singly innervated sensory cones in deep pits of the cuticle. In cross sections the cone's cuticle appears fluted. This sensillum type varies with the species (35, 73, 96, 113, 134, 145).

If the depression is not too deep, these sensilla have also been called pit organs. The very deeply situated organs (Forel's flasks of ants) have a thin tubular part of the pit which is nearly as long as one segment of the flagellum.

_Sensilla placodea (sensory plates)._—These are elliptical or elongated plates

![Diagram of sensillum](image_url)

_Fig. 2._ Distal end of a _sensillum basiconicum_ from the antenna of a fly larva (_Calliphora_). The distal processes (NB) of the sensory nerve cells are bundled and branch into thinner endings. The endings of different nerve cells are in contact with air in pores (P) of the peg's cuticle via separate channels (C). oE = outer epicuticle; iE = inner epicuticle; Cu = endocuticle; V = vacuole. Simplified drawing (courtesy of Dr. K.-E. Kaissling) after a diagram of Richter (98).
with a thin cuticle forming the outer lining of the tormogen cell. The narrow nerve fibre bundle holds the endings of many cells, is surrounded by the trichogen cytoplasm, and ends in an eccentrically located pore from which place dendrites (do they really branch?) are reported to spread under the thin membrane ring. No direct contact of the nerve endings with the air was found (71, 96, 113, 130, 134, 145). Plate organs have also been found on the antennae of some beetles and aphids (55, 91, 110).

**Sensilla styloconica (terminal sensory cones).**—In moths, the distal edges of the more distal segments bear many elevations of the cuticle which end as sensory cones. The cone is innervated by three nerve fibres running to its extreme tip. With the permeation method (126, 127) the tip opening is stained and the nerve endings might be in direct contact with the air (7, 84, 97, 113, 123).

**Sensilla squamiformia (sensory scales).**—In the moth, Bombyx, these long cylindrical organs have been observed among the normal scales. The sensillum's collarlike socket is similar to that of normal scales while the sensory scale itself is more slender than a normal scale. The nerve fibre ends at the scale's base (123).

**Sensilla campaniformia (sensory cupolas).**—These are thick-walled, singly innervated, semispherical or semiellipsoidal formations of the cuticle. They have no pores or openings. While these organs are arranged in fields on insect legs and wing bases, they are in most cases solitary on the antennal flagellum (7, 55, 65, 81, 123). Only on the pedicel have these sensilla been observed in groups (26, 54).

In Bombyx, the saturniids, and Lymantria one to four of these organs are consistently found in the distal part of each flagellar segment. In these moths, the very large sense cells are in the middle of the segment and their nerve fibres run to a cavity in the thick inner part of the intersegmental membrane. The external end of the slightly sunken sensillum is the cupola which may have any of a number of different shapes (7, 123).

**Sensilla scolopalia (sensory rods).**—In the typical "chordotonal" scolopidial sensillum, the nerve cell ending is covered by a cuticular cap which extends as a filament through the tormogen cell and is fastened to the cuticle. In some types, other ligaments with auxiliary cells attach to the sense cell soma and insert at an opposite part of the cuticle, thus stretching the whole arrangement from wall to wall. Sensilla of this type are found in the Johnston sense organ in the pedicel (23, 26, 36, 39, 67, 80, 100, 123).

Solitary chordotonal sensilla have been found in the antennae of Bombyx (123) at various places. A group of chordotonal sensilla composing the antennal chordotonal organ is regularly found—but sometimes only in reduced form—in the antennal lumen of the pedicel where they are inserted at a single point on the distal rim of the segment (26, 39, 94, 143).

An excellent fine structure analysis of sensory rods was made on the insect tympanal organ (45).

**PATTERNS OF SENSILLA AND NERVES**

The distribution of sensilla on the antennae is not random. All of the
investigators who have tried to arrive at a true overall picture of the distribution of sensilla have come to this conclusion. However, studies adequately covering the pattern of sensilla and their exact localization over a part or the whole antenna are rare (7, 35, 46, 73, 84, 89, 123).

Such work is of decisive importance for the physiologist in search of the functions of sensilla. Moreover, there is no doubt that the patterns of sensilla (like the scale patterns on the wings of Lepidoptera) are the product of morphogenetic "field" effects. No research has been done on this problem so far except for one paper dealing with the cockroach antenna (46). However, on the antenna of Bombyx it was observed that the fields with sensilla coeloconica and sensilla chaetica never overlap and obviously exclude one another (123).

The antennal nerves originate in the deutocerebrum. They soon give off a motor branch or branches supplying the antennal muscles. At the antennal base in the scape, the nerves, now only afferent, divide mostly into two main trunks of about equal volume. These two can be followed to the distal end of the antenna. Because of smaller and larger branches leaving the trunks, the nerves taper and are rather small when they reach the distal region. The anatomy of the proximal nerves of insect antennae has been described in a number of species (14, 15, 99, 101, 147). In Bombyx and saturniids, the fine distribution of nerves in the whole antenna has been reported (89, 123).

In the bug, Rhodnius, it was found (153) that the terminal segment of the antenna holds between 4000 and 5000 sense cells, while only 300 axons leave this segment. The conclusion is that there occurs a fusion of nerve fibres. On the average, at least 15 fibres from individual cells merge to form one axon running to the brain. Because of the striking physiological consequences of such a possibility, this situation should be reinvestigated with the electron microscope.

In a recent electrophysiological study of the fly's antennal flagellum, it was reported that there are "many hundred-fold more cell bodies associated with the pegs than there are axons in the antennal nerve, and since synapses do not occur in the antenna, it follows that there is extensive fusion of axons. Axonal fusion is a common feature of the insect sensory system" (33).

SENSORY FUNCTION AND ITS LOCALIZATION

Mechanoreception.—Many classical observations indicate that the insect antenna bears mechanoreceptors (17). In the cases of the Johnston organ (105) and the Böh m bristles (51, 77) it has been possible to identify the sensilla responsible for these functions. Nerve impulse recordings from the whole antennal flagellum during mechanical stimulation produced additional evidence that such receptors are present here (9, 10, 12, 22, 58, 115, 116). In one of these papers (116) it is suggested that the response of two or three isolated units observed in some cases possibly came from the campaniform sensilla in the intersegmental membrane. The mechanoreceptive function of these sensilla is highly probable because of the results obtained by Pringle (86, 87).

Subsequently, it was found that the bluntly ending sensilla chaetica of
the moth antenna are supplied by one mechanoreceptive fibre (in addition to other fibres of unknown functions), giving a receptor potential and phasic spike responses to deflections (117). This corresponds to the observation made on tactile and taste bristles of the fly (156, 157).

Also, the Böhm-type sensilla chaetica at the two proximal joints of the honey bee antenna could electrophysiologically be shown to be phasic-tonic mechanoreceptors (74). Presumably they function as proprioceptors [see also (88, 138)], perceiving the antennal position.

The mechanoreceptive Johnston sense organ in the pedicel did and does attract the interest of many investigators. In the highly specialized pedicel of male mosquitoes, the organ is tuned to the flight sound of the female (3, 4, 67, 68, 69, 105, 139, 140). In the gyrinid beetles (37, 38, 155), the organ is a detector for oscillations of the water surface. The most general purpose of this organ in flying insects appears to be that of an airspeed control receptor. In the fly, Calliphora, it was observed that the more its antennal flagelli are deflected to the sides, the slower it flies (18, 19, 20, 61).

The whole functional network is probably very complex, and not yet fully understood. In the fly (18, 19), as in the honey bee (51), there are phasically working Johnston receptors and tonically working Böhm bristles acting together. The regulatory input of the bee’s wingbeat comes from the Johnston organ which is maximally sensitive to frequencies between 200 and 350 cps. Here it is the phasic oscillating stimulus which depends upon the airspeed and which is the control stimulus. The tonically working Böhm bristle fields report the antennal position as proprioceptors. The angle of spread of the antennae indicates the airspeed (49, 50, 51). A comparable function might be present in the aquatic dragonfly larvae (141).

The fly’s Johnston organ responds also to sonic waves. In this insect, the maximal response was found to be between 120 and 180 cps (150). In a field of standing sonic waves, the antenna responds to the airspeed but not to the air pressure, as predicted for receptors of this type (1).

Electrophysiological experiments have also been made with the Johnston organ of the migratory locust and some moths, to demonstrate its mechanoreceptive properties (117, 142). However, we do not yet know in these cases about the biological meaning of this function.

A possible criticism in all of the investigations on the Johnston sensilla function is that we find in the pedicel one or more other chordotonal organs as well as campaniform sensilla. As long as the Johnston organ is so enormously developed as in the mosquito and the bee, it seems correct to identify the electrical mass recordings as coming from these sensilla. If, however, the Johnston organ consists of only a few sensilla, fine electrode recording might be necessary to make sure with which organ one is dealing.

Gravity reception was for some time also expected to be localized in the Johnston organ. That this is not generally the case has recently been shown, because, in a number of insects, bristle (or hair) sensilla at different body joints serve this function (16, 34, 76, 77). In some studies, however, the authors claim that the Johnston organ is at least involved in the gravity response (3, 4, 5, 90, 93, 146). A very clear study of ants and other Hyme-
noptera proves that the bristle fields of the Böhm-type sensilla chaetica at many body joints are the receptors responsible for gravity reactions (77). Each of the two groups of bristle fields on the antenna (the head-scape fields and the scape-pedicel fields) is able to guarantee the gravity reaction when all other body joints are mechanically fixed (it should be noted here that these bristles are identical with the ones thought to control the speed-dependent antennal position).

Unidentified flagellar mechanoreceptors of the honey bee induce reactions of the antennal muscles with a response delay time of 7 msec (52).

Chemoreception.—This topic was reviewed some years ago (29–32, 56, 57), the reviews covering practically all of the earlier important literature, and more recently (17, 60) dealing also extensively with the later electrophysiological approach.

Gustation (contact chemoreception).—While recent electrophysiological investigations of insect taste sensilla (bristles or hairs) from the legs, the proboscis, and other parts of the body have made these organs the best known chemical sense organs in animals, not much is known of contact chemoreceptors on the antenna. In behavior experiments, it was shown that such receptors are located on the antennal flagellum of some butterflies, moths, bees, and ants (42, 43, 72, 79, 82, 114). To date, no identification of the sensilla involved has been possible. Using the wide electrode method in which the electrode fluid is in direct contact with the bristle's tip (58, 59), attempts were made to test the blunt ending sensilla chaetica of butterflies and moths with the expectation of finding functions analogous to those of the well-known taste bristles (117). While such sensilla gave good responses to mechanical deflections, no clearcut answer to taste stimuli was observed.

Olfaction.—While authors of the eighteenth and nineteenth centuries suggested that the antennae are the principal site of insect olfactory receptors (29), it was von Frisch in 1921 (44), who unequivocally demonstrated that the honey bee's reactions to odor are lost when the distal eight segments of the flagellum are amputated. Similar experiments with other insects corroborated this observation. The olfactory power of insects is fully or partly lost with the loss of the antennal flagellum [see (78)]. Additional evidence for the flagellum as site of the olfactory sense organs was obtained by electrophysiological experiments (9–12, 58, 109, 115, 116, 118, 119, 121).

These studies, as well as the behavioral investigations, could not identify the sensillum type involved in the reaction. Most authors discuss this problem and sometimes decide in favor of one or several sensillum types. Abundance, thinness of the cuticle, dye permeability after proper treatment, and the appearance of a peculiar sensillum which is specific for one sex or a species known to be specialized, are the main points in favor of some sensillar types. There is much evidence of this kind ascribing olfactory properties to the sensilla basiconica. In the bee, it is still undecided whether the pore-plates are olfactory organs because there are also pegs on the flagellum of the worker bee (but not many on the drone's flagellum!). Very often, an argument such as the following is presented: “The antennaless insect lost its olfactory power. There are three morphological types of antennal sensilla in
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question. Since two of these are also found elsewhere on the animal, the third one is the receptor in question." This may be true, but it is necessary to be cautious. In Bombyx, both sexes have microscopically identical sets of sensilla on the antenna (123), but only the male's sensilla react to the female's attracting substances (116). This demonstrates that microscopic identity does not prove functional identity!

However, in three cases, using a refined amputation or sealing method, it was possible to identify olfactory sensilla basiconica on antennae with only few sensilla (13, 27, 151).

If an antenna is supplied with many sensilla, only localized electrical recordings from the outside with optical control or otherwise exact knowledge of the distribution of the sensilla will lead to an identification of the function. In the beetle, Necrophorus, and a sphingid moth, sensilla basiconica have been found to react to olfactory stimuli (6, 119, 120). In this situation it seems possible to approach a far-reaching physiological analysis of such systems because receptor (generator) potentials and nerve impulses have been recorded simultaneously.

It is obvious, from all experiments, that some of the olfaction generalists among the insects also have olfactory organs on the palps, and perhaps widely distributed over their bodies. The highly specialized sensilla for perceiving the sexual attracting substances, however, are restricted to the flagellum of the antenna, as far as we know.

A suitable method to work out details of the olfactory function during the perception of the female moth's sexual attracting substance, was the recording of the overall electrical response. If an odorous air current hits the antenna, the peripheral part of the flagellum becomes electrically negative in relation to the basal part. This response was called the "electroantennogram" (EAG) (115, 116, 121). Its amplitude varies with the intensity of the stimulus and within limits also with the airspeed. Subsequently, it was demonstrated that the EAG is the sum of a probably large number of receptor (generator) potentials of individual receptor units properly timed by the steep stimulus rise (119, 120).

A number of questions were answered with this method. Did perhaps females not react to their own perfume because they were "switched off" in the central nervous system? This is not the case, because their antennae do not respond to their own substances while other odors elicit an EAG. None of the females reacted to any lure substance of any species tested so far. It was, furthermore, possible to determine the intensity reaction curve, which, in Bombyx, covered a range of 12 decadic concentration steps or more. It was also possible to compare quantitatively the effect of compounds related to the sexual attracting substances, such as the isomers which are less effective. Another question of considerable interest was the specificity of the sexual attracting substances. It was shown that among the subfamily Saturniinae there seems to be little specificity; while Lymantria (Porthetria) and Bombyx attracting substances are inactive beyond the limits of their family. Much more work is needed before we will have a full picture, but all of the earlier data as well as the recent EAG recordings show a lack of specificity between
related species and genera while different families are not attractive to one another (118, 119).

After completion of the manuscript, the function of the following antennal sensilla was clarified in the author’s laboratory using microelectrode recording: sensilla basiconica of the blow fly Calliphora, as well as sensilla placodea of the worker honey bee and the drone, are organs serving the general olfactory sense. The olfactory units of these sensilla respond to a number of odorous substances either with a phasic-tonic increase or a depression of their spontaneous impulse frequency. The qualitative reaction spectra of all the units (cells) so far registered are different from one another but show considerable overlapping (Boeckh, J. Z. Vergleich. Physiol., 1963/64, in preparation; Lacher, V., and Schneider, D. Z. Vergleich. Physiol., 1963, in press). In the male saturniid moth, Antheraea, antennal sensilla basiconica responded like the ones described above. However, these sensilla never reacted to the sexual attracting substance produced by the female of this species. It was concluded that they serve only the general olfactory sense. Sensilla trichodea of this moth (which are found only in the saturniid males) gave a phasic impulse response to the female lure scent. These hairs, which are very abundant on the male saturniid antenna and are lacking on the female antenna, are, therefore, the specialized pheromone receptors (Schneider, D., & Lacher, V. Z. Vergleich. Physiol., 1963/64, in preparation).

Hygroreception.—In many insects it has been clearly shown that the antennae bear humidity receptors (2, 17, 21, 65, 70, 73, 107, 152). In some cases, it was possible to identify the flagellum segment where the organs are located (107). The majority of authors suggest that basiconic, placoid, or pit-peg sensilla are involved in these reactions.

In the human louse, the humidity sense organ was found to be a tuft organ on the antenna (151). This sensillum is similar to a small sensillum basiconicum with four tiny hairs.

Thermoreception.—It is an established fact that many, if not all, insects possess thermoreceptors on their antennae (17, 21, 53, 152). There has been much speculation on the sensilla which may be involved in this reaction.

ORIENTATION

Receptors located on the antennae play an important role as instruments necessary for orientation. Some authors claim that the possibly close arrangement of tactile and olfactory receptors on the antennae must be very important and deduce that insects such as honey bees [see (44)] may have a complex sensation where these two modalities work together. The work of the antennae is impressively demonstrated when, e.g., a parasitic wasp is locating its prey through wood several millimeters thick. It “stridulates” the wood with its antennae for a considerable time before it finally begins to “drill” the tube for the ovipositor.

Without doubt, many antennal receptors work simultaneously when in-
sects orient towards their partner, host, prey, etc. This is especially well established in the mosquito (2, 65, 104, 105, 106).

It should be noted here that olfactory receptors (on different antennae) can probably serve to localize the stimulus source only in a steep intensity gradient and with strong absolute stimulus intensity. Normally, the odor is only a signal telling the animal to move upwind [for a discussion see (116, 119, 125)]. In flying insects, other sense organs—probably the eyes—serve to find the upwind direction. In walking insects, however, the antenna may very well help to locate the air's movement. It has been observed in the field that gypsy moth males found their females when one antenna had been amputated (125).

Many insects show, during orientation, vibratory movements of the antennae. This was interpreted as "sniffing," or as the production of relative movement between olfactory surfaces and air (83, 125). In Bombyx, the frequency of these movements of the flagella in the "resting" situation was about 1 per sec but increased in the excited animal (116).

A close-range mechanism of olfactory orientation in winged insects was recently described (116). The flightless moth, Bombyx, produces a strong air current with its wings. Since the direction of this current is parallel to the body's longitudinal axis, the animal is able to trace the position of a nearby odor source simply by testing the air it is drawing through its antennae successively from different directions. Such a mechanism might very well be of importance for other insects as well.

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