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Cuticular Sense Organs as Characters in phylogenetic Research

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Zusammenfassung: Kutikuläre Hautsinnesorgane von Hymenopteren als Merkmale bei phylogenetischen Untersuchungen.

In den vergangenen fünf Jahren wurden die kutikulären Sinnesorgane auf den Antennengeißeln zahlreicher ausgewählter Hymenopteren (Symphyta, Aculeata, einige wenige Terebrantes) licht- und elektronenmikroskopisch (REM und TEM) eingehend untersucht. Wie die bisherigen Ergebnisse zeigen, stehen im allgemeinen Sensillen von 6 - 8 verschiedenen Sensillentypen auf den Antennengeißeln der untersuchten Arten. Für die gesamten Sensillen aller Typen, ihre zahlenmäßige Häufigkeit und musterartige Verteilung auf den Antennengeißeln wurde der Begriff „Sensillenmuster" geprägt. Offensichtlich gibt es innerhalb der Hymenoptera systematische Gruppen, denen ein bestimmtes Sensillenmuster zu eigen ist. Wie von mir bereits 1979a dargelegt, stellen die Sensillenmuster ausgesprochen komplexe Merkmale dar, was besonders deutlich wird, wenn man daran denkt, daß die Sensillen kompliziert gebaute Kleinorgane sind, die aus einem kutikulären Apparat, Hüll- und Sinneszellen bestehen, und daß die zahlenmäßige Häufigkeit und die musterartige Verteilung der Sensillen auf den Antennengeißeln sehr unterschiedlich sein kann. Zur Analyse der phylogenetischen Beziehungen zwischen bestimmten Taxa muß, entsprechend den Regeln der phylogenetischen Systematik, in jedem einzelnen Fall nachgewiesen werden, ob das Merkmal Sensillenmuster als Ganzes, oder ein Teilmerkmal desselbigen, als Synapomorphie zu bewerten ist. Dieses macht eingehende Untersuchungen bei zahlreichen Gattungen erforderlich, insbesondere auch außerhalb derjenigen Taxa, deren Verwandschaft analysiert werden soll. Das Raster EM kann hier sehr vorteilhaft eingesetzt werden, doch sei ausdrücklich betont, daß ohne zusätzliche Untersuchungen mit dem Transmissions-EM eine Interpretation der Ergebnisse der REM-Untersuchungen nicht möglich ist.

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The importance of zoological systematics and taxonomy for other biological disciplines such as ecology, pest control and environmental conservation has been emphasized by many authors during the past ten years. MALICKY (1980) was the last author to describe the serious situation and the problems of zootaxonomy in Europe and in other parts of the world.

One fact, often used as a critical argument by those zoologists who deny the important role of taxonomy for a modern scientific conception of zoology, is the concurrent existence of different classifications of nearly any higher taxon. This divergence should be a striking proof of the unexactness of systematic methods and the small reproducibility of results in systematics.

Without wishing to enter a detailed discussion of these questions, I assume that one reason for the divergent classifications of a taxon is to be seen in the overrating of less significant characters of low complexity. During the past years, numerous attempts have been made by many taxonomists to overcome this problem. They have introduced new methods and characters from different branches of biology, such as biochemistry or ultrastructure research, into systematics and taxonomic research. Using modern methods, e.g. SEM and TEM, many new morphological and ultrastructural characters are available for systematics, as has been shown by TYLER (1976), STORCH (1979) and RIEGER et al. (1979).

In connection with my investigations concerning the morphology and fine structure of the sense organs on the flagella of *Formica rufa* L. and other ants (Formicidae) (WALTHER 1979 b, 1980, in prep.), the question arose, wether these sense organs can be used as characters for phylogenetic studies. The high complexity of the structures of the sense organs (HENNIG 1950) and some references in older publications supported this assumption.

The cuticular sensilla are small and complex organs, which consists of a cuticular apparatus (plates, hairs, pegs), one or numerous sense cells and two or more sheat cells. Since the first morphological description of a cuticular sensillum was published by ERICHSON in 1847, numerous studies with the light microscope, SEM and TEM have resulted in a strong increace of our knowledge about these organs, as the reviews of SLIFER (1970), MCIVER (1975), ALTNER (1977) and ZACHARUK (1980) have shown. The numerous different structures of the cuticular apparatuses, stimulus transmitting pore systems, dendrites and sheat cells is as remarkable as the different densities, positions and arrangements of the sensilla on the antennas. Cuticular apparatuses of the sense organs can be positioned on the surface of the antennas, in pits (Sensilla coeloconica) and in chambers near the longitudinal axis of the antennas (Sensilla ampullacea).

The graet number of different sense organs and patterns of sensilla, which had already been described during the second half of the 19th century, provoked some entomologists to search for a classification of the different types of sensilla. Important investigations concerning this questions have been published by KRAEPELIN (1883) ans SCHENCK (1903). Another problem, in which many entomologists had very early been interested, was the evolutionary development of the different types of sensilla. In 1885, FOREL proposed a hypothesis as to the homology of the plate organs and their development from sense organs with vertical hairs during evolution. Another important contribution to this problem was published by WACKER (1925), who discussed FOREL's hypothesis in relation to the results of this intensive morphological study of the sense organs of many Hymenoptera. As far as I know, BÖRNER (1919) was the first entomologist to use cuticular sense organs as characters for taxonomic studies. In his classification of the Hymenoptera, he outlined some taxa corresponding to their different Sensilla placodea (plate organs) on the antennas with long, round or elliptic pore plates.

To come to a decision as to whether the antennal patterns of sensilla can be used as characters for phylogenetic reconstructions or not, I have been studying a great number of species from the Symphyta and Aculeata, as well as some Terebrantes, using the light microscope, SEM and TEM (WALTHER 1979 a, in prep.). The results of these investigations show clearly that usually 6-8 different types of sensilla are to be found on the antennas. For these different types of sensilla, their districution and arrangement, the new term "patterns of sensilla" is used.

On the antennal flagellas of the female and worker of *Formica rufa* L. for example, three olfactory, one gustatorical and mechanosensitive and two mechanosensitive sensilla are to be found. For two other types of sensilla, thermo-, hygro- and carbondioxide-sensitive function is presumed. On the male's flagellas, only two olfactory sensilla, but additionally a peg with an unknown function, belong to the pattern of sensilla.

If such patterns of sensilla are to be used as characters for phylogenetic reconstructions, first of all, it is necessary to demonstrate the homologies of the different types of sensilla (MCIVER 1980), for which the criterions of homology of REMANE (1952) could be very helpful. To support the assumption that a number of species belong to a monophyletic group, it must be determined furthermore, whether the characters are to be evaluated as plesiomorphous or apomorphous. The monophyletic descendence of a group of species is only justified if all species of this group possess the same apomorphous characters (HENNIG 1950, 1969, 1980; KÖNIGSMANN 1975; SCHLEE 1978).

The results of my previous investigations show that the antennal patterns of sensilla are characters of high complexity, which are composed of some sub-characters. The whole patterns of sensilla as well as parts of them, can be regarded as synapomorphous characters for higher taxa such as tribes, subfamilies, families and superfamilies and thereby justify or support the monophyly of these taxa concerned. As subcharacters of the patterns of sensilla, we may consider for example the density and the distribution and arrangements of the sensilla on the antennas. A very low density of sensilla is to be seen on the antennas of male and female of the woodwasp *Syntexis libocedrii* Rohwer (Syntexidae) which occurs in northern California and Oregon. In contrast, we find a high density of sensilla on the antennas of the American fossorial wasp *Myzinim maculatum* Fabricius (Myzinidae). Another sub-character is the distribution and arrangement of the sensilla on the antennas. It may be directly related to the morphology of the antennas, as is to be seen very clearly on the branched antennas of the males of *Diprion pini* (Linnaeus) (Diprionidae) as well as of both sexes of *Megalodontes cephalotes* Fabricius (Megalodontidae). In both species, we can recognize that most of the mechanosensitive sensilla are on the antennal axis, but we find the olfactory sensilla on the branches of the antennas.

On the antennal flagella of the wood wasps from the families Siricidae, Xiphydriidae and Orussidae, the chemosensitive sense organs are concentrated on one half and the mechano-sensitive tactile hairs on the other. This distribution may be also considered as a special sub-character.

Many hymenoptera from Aculeata, which show noumerous sexual dimorphisms, possess also a great number of sex-specific differences between the antennal patterns of sensilla of female and male. In both sexes, we may find different types of sensilla or different numbers of types. The densities and the distributions of the sensilla in male and female may also show great differences.

The genus *Thynnoides* and some other genera of the aculeate family Thynnidae, which is distributed over the

Australian and parts of the South American continent, may be used as example to explaine the sex specific differences described above.

The pattern of sensilla of the male shows on each segment of the antennal flagella about 50 - 70 olfactory Sensilla trichoidea T1, concentrated in one elliptic patch. They are surrounded by numerous Sensilla placodea T1 with long pore plates and many mechanosensitive tactile hairs between them (Fig. 1).

On the lateral parts of the antennal flagella of the female, we find numerous olfactory sensilla placodea T2 with round or elliptic pore plates (Fig. 2). A great number of the olfactory Sensilla basiconica T1 are distributed in the dorsal region, whereas the mechanosensitive tactile hairs are to be seen on the whole surface of the flagella between the other sensilla. Some Sensilla placodea T3 with a smaller elliptic pore plate are only located between the Sensilla placodea T2 and the Sensilla basiconica T1.

It seems to be obvious that these differences between the pattern of sensilla of female and male, each of which must be regarded as a sub-character, always require the investigation of both sexes.

The different morphological structures of the cuticular apparatuses (hair, pegs, plates), which can be investigated by SEM, may also be used as sub-characters, comparing for example the pore plates of the sensilla placodea of *Anoplius viaticus* Linnaeus (Pompilidae), *Monodontomerus obsoletus* Fabricius (Chalcididae), *Ophion luteus* (Linnaeus) (Ichneumonidae), and *Scolia flavifrons* Fabricius (Scoliidae), we can observe the great variation ot these structures. The same variation can be found between the pegs of the different olfactory Sensilla basiconica of *Pseudogonales hahni* (Spinola) (Trigonalidae), *Bembex rostrata* Linnaeus (Sphecidae), *Formica rufa Linnaeus* (Formicidae), and *Anoplius viaticus* L.

The SEM method can be very useful for morphological studies of the outer surface of such cuticula structures as these hairs, pegs and plates. However, the results of these investigations alone does not permit a functional interpretation of these structures. Additional investigations by TEM are necessary to explain the function of these structures of the sense organs. Only such a functional morphological interpretation of these results of the study of such sense organs justifies the important significance which we attribute to the sense organs as characters in phylogenetic reconstructions.

The TEM studies supply additionally numerous new characters from the fine structure. We can use the pore structures of the chemical sense organs, which show a great variation, as the studies of MEINECKE (1975) have demonstrated, as one subcharacter. The varying innervations of the different types of sensilla which we have found in different taxa of the Hymenoptera (WALTHER, in prep.) are also sub-characters of the pattern of sensilla, which can be used only after TEM studies. Investigations of other Arthropod taxa in the future will show whether this complex character can be also helpful in phylogenetic studies of these groups.

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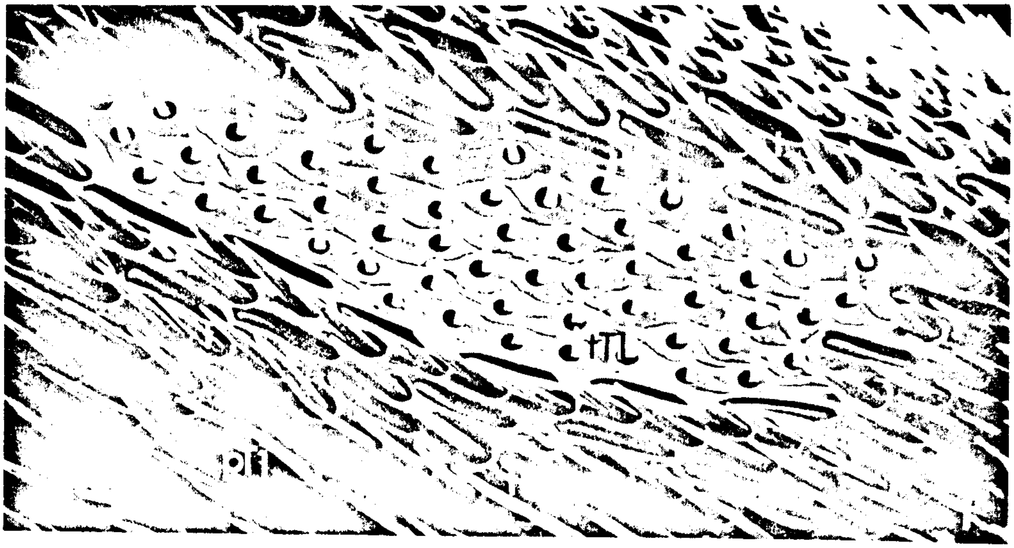

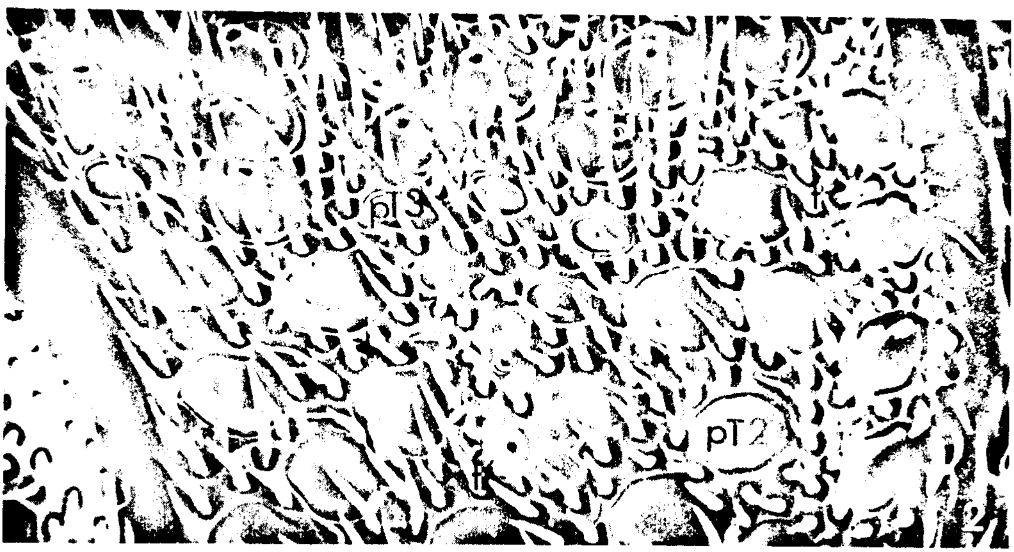

Fig. 1:
The concentration of 50 - 70 olfactory Sensilla trichoidea T1 (pT1) in an elliptic patch on each segment of the flagellum of male wasps from the genus Thynnoides is a special sub-character. A great number of olfactory Sensilla placodea T1 (pT1) and many tactile hairs (t) cover the surrounding region. x 1400.

Fig. 2:
In the dorsal region of each segment of the flagellum of female wasps from the genus Thynnoides we can recognize many olfactory Sensilla basiconica T1 (bT1). Lateraly, many olfactory Sensilla placodea T2 and T3 are to be seen. Between them, we can identify some Sensilla coeloconica (c). Tactile hairs are spread over the whole surface of the segments. x 1400.

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