On the Trichobothria ("auditory hairs") in Arachnida, Myriopoda, and Insecta, with a summary of the external sensory organs in Arachnida.

By

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I. Introductory Remarks.

During the study in earlier years of various orders or families of terrestrial Arthropoda I endeavoured to discover as many external sensory organs as possible, and most of the results may be found in my papers on orders or tribes of Arachnida and Myriopoda. A treatise published by Prof. Dr. F. DAHL in 1911: *Die Hörhaare (Trichobothrien) und das System der Spinnenthiere,* which contains some curious statements on the »auditory hairs» and on the classification of the Arachnida, has induced me to take up this matter and allied topics. It is, in my opinion, a very interesting and hitherto unnoticed fact, that sensory hairs of a special kind named by DAHL »Hörhaare» or »trichobothria» and by W. WAGNER and myself in earlier publications »tactile hairs», are found not only in several orders of Arachnida, but besides in two orders of Myriopoda and in groups of lower Insects, thus in representatives of all three classes of terrestrial Arthropoda. At the same time I intend to put together an abstract of our knowledge of external sensory organs in Arachnida. It may be practical first to deal with the organs in question in each of the three classes, then to mention the main literature on the trichobothria and their probable function.

II. Arachnida.

A. The trichobothria.

The name trichobothrium is well composed, as it signifies a hair in a pit, and these sensory hairs always originate from the bottom of calicles and do not fill their inner cavity. The most convenient object to examine is a large, dark-coloured Scorpion, f. inst. *Pandinus cyaneus*. As in all Scorpions the trichobothria are only found on some joints of the palps and always on the hand and the fixed finger of their chelæ. By aid of a pocket lens one observes on this part of the chela a number of round holes; through each hole projects a long and very fine hair which is very far from filling the hole, so that the hair is freely movable. In a transverse section of the wall of the chela the hole is seen to be the opening of a very much wider cavity, on the bottom of which the hair is inserted. In *Pandinus* the inner wall of the cavity is adorned in a peculiar way as if covered with a stratum of prismatic cells much reminding one of the cells in a honeycomb (H. J. HANSEN, *a*, p. 147—48), but such adornment is of secondary interest, and is f. inst. not found in the calicles of Araneæ. It may be added that these holes with their hairs have been known during more than half a century. In *Pandinus cyaneus* I found in 1893 (l. c.) 14 such calicles on the immovable finger and 12 on the hand of the chela, thus in all 26 hairs on this joint, the fifth of the appendage, when the mouth-part itself — by W. SÖRENSEN and myself later interpreted as the mandible — is counted as first joint. On the fourth joint I found 17, and on the third joint 3 calicles, but they do not occur on the more proximal joints or on the movable finger. In smaller forms, f. inst. *Androctonus australis* L., the number of calicles is lower, and there is probably some difference in number and arrangement according to families or genera. In all Scorpions trichobothria are wanting on all other appendages and on the body.

In the *Chelonethi* (Pseudoscorpions) trichobothria are

found only on the fingers of the large chelæ. The calicles are well developed, but their opening is wide; the hairs are extremely or very long. They have been found in all main genera examined by me; they were mentioned — without description — by DAHL in 1883 (*a*, p. 270), and in 1888 CRONEBERG described them in a species of *Chernes*.

In the *Pedipalpi* the trichobothria are found only on the legs; they were discovered in this order by me in 1893 (H. J. H. *a*, p. 155 and 175). In the suborder Uropygi, both in Oxopoei and in Tartarides, they are only found at the end of the tibia on all four pairs of walking legs, two calicles on the first tibia, and a single calicle on each of the others (HANSEN & SÖRENSEN *c*, p. 21). In the Amblypygi the trichobothria are much more numerous and their arrangement very different. The patella of each of the three posterior pairs of legs has two long and very fine trichobothria protruding from well developed calicles, and a comparatively large area of the integument around the opening of each calicle is adorned in a peculiar way as if it were scaled. Furthermore the upper side of the metatarsus of the same legs has on the proximal part some calicles, and towards the distal end a number of calicles arranged in two short rows much diverging towards the end; on the upper side of the tibia is found a single calicle near the apex (H. J. H. *a*, p. 155—156). First pair of legs and the palps without trichobothria.

In the order *Palpigradi* trichobothria are only found on first pair of legs; all species examined by me have seven such hairs on each of these legs distributed on sixth, seventh, ninth and eleventh joint. They were discovered by GRASSI in *Koenenia mirabilis* GRASSI, who was inclined to interpret them as auditory organs; later they have been mentioned by HANSEN & SÖRENSEN (*a*, p. 231) and as occurring in several species by HANSEN (*b*, p. 205).

In the *Araneæ* the »Hörhaare» — trichobothria — occur, according to F. DAHL (*b*, p. 2—4) on the upper side of the legs and the palps, but generally only on tibia, metatarsus, and tarsus, and sometimes they are reduced or wanting on the tarsus; in *Pachygnatha* and *Tetragnatha* trichobothria shall also occur on the femora in two rows near their base. DAHL has sev-

eral statements as to their number and occurrence on the joints mentioned in various families and some genera, showing that their number and arrangement afford characters of systematic value, but yet without carrying out the investigation of a really sufficient number of forms. — In an interesting paper (in 1888) W. WAGNER divided the trichobothria in Araneæ into two types, with a detailed account of their structure, especially as compared with that of other sensory hairs and purely protecting hairs in Araneæ; in chapter V a more detailed account of WAGNER's results is given.

In the orders *Solifugæ, Opiliones,* and *Ricinulei (Cryptostemma)* trichobothria are entirely wanting. — I am not acquainted with most of the vast literature on the *Acari*, but as far I know trichobothria are unknown in this extremely rich order.

B. Sensory Hairs not projecting from real calicles.

In Scorpions no other sensory hairs than the trichobothria are known. In the Chelonethi there exists on the lower side of the hand of the small chelæ (antennæ) a seta or generally a row of setæ, which has been named the *flagellum*. These hairs differ considerably as to serrulation or pubescence, thickness, and number in various genera (see f. inst. H. J. HANSEN *a*, pls. IV—V), but it seems to me somewhat uncertain whether they are a kind of tactile hairs, as the nerve has hitherto not been pointed out, and in no respect they are similar to real sensory hairs in other Arachnida. In 1893 (H. J. HANSEN *a*, p. 215–217) I critisized severely STECKER's fanciful description, figures and interpretation; STECKER, who later on created for himself a somewhat Herostratian celebrity in Zoology by his invention of the not-existing animal *Gibocellum*, interpreted the flagellum as an olfactory organ, and has most unfortunately been taken seriously by SIMON, GAUBERT and CRONEBERG.

In the Pedipalpi very small tactile hairs of peculiar shape are found on the distal part of first pair of legs, which always

are elongate, useless for walking and evidently serve as organs of touch. In the suborder Amblypygi (H. J. HANSEN, *a*, p. 154) these hairs are found on the distal third of the extremely elongate tarsi, and they are very numerous on the last joints. The hairs, scattered between the normal, protecting setæ, are very small, short, conspicuously clavate, and very light; their small insertions differ a little from those of usual hairs. — In the Uropygi we find the tactile hairs in both tribes. In the Tartarides (HANSEN & SÖRENSEN *c*, p. 22) they are found on the six tarsal joints and only a few on each joint; they are easily discernible from common hairs, being very much thicker and somewhat shorter than these; they are, besides, somewhat curved, with the end blunt, while their wall is thin and nearly vitreous. In the Oxopoei the tactile hairs are distributed on the joints of the tarsus, but in *Hypoctonus* some were besides found on the outer side of the distal part of the metatarsus; in this tribe the hairs are »not only proportionately many times smaller but even absolutely smaller than in Tartarides; besides they are less curved and distally more slender, but their end is yet blunt», and by their vitreous appearance they are easily distinguished from the common setæ.

The Ricinulei (HANSEN & SÖRENSEN *b*, p. 130) do not possess any other external sensory organ than six tactile hairs, each leg of the three posterior pairs having a single hair. It is inserted on the upper side of the tarsus a little before its end, is comparatively rather short, cylindrical with the terminal part thickened, and on the distal two-thirds of the length equipped with delicate branches excepting on the semiglobular apex. The hair is inserted in a small depression, and the area around this depression is peculiarly adorned and markedly different in aspect from the remaining skin of the tarsus.

The Palpigradi have no eyes, but if *Koenenia* is compared with *Thelyphonus* we find in the former genus on places nearly answering to the eyes in the latter peculiar sensory organs which are transformed hairs. On the front end of the head is seen a small, erect, two-branched organ; each branch is seemingly lancet-shaped, in reality fusiform, gener-

ally with a number of extremely minute hairs. On the places, where the lateral eyes should be looked for, one finds either a single organ or a bundle of two to four such organs; each is oblong lancet-shaped with somewhat scarce and extremely short pubescense. These interesting organs, which had been discovered in *Koenenia mirabilis* by GRASSI, was later found in several species, described and figured (H. J. HANSEN, *b*, p. 204—5). — The Palpigradi possess other setæ which, in my opinion, probably have a sensory function. One such seta is found on the upper side of the metatarsus of the last pair of legs; another seta of different shape exists on the outer side of third metatarsal joint of first pair of legs; a more special description with figures of these setæ is found in my last-named paper (p. 206—7).

Among the Araneæ I have specially examined *Epeira diadematа* CLERCK without observing other sensory hairs than the trichobothria. But the order is extremely large, comprising many families partly rather different in various features. And W. WAGNER (1888) has mentioned hairs which have a nerve entering into their basal part and have a tactile function, but are not trichobothria, as their mode of insertion is much more simple; he pronounced that such hairs exist in all Araneæ, but unfortunately did not say anything as to their distribution on the animals. I am inclined to think that a special investigation of types of all families may yield interesting results, but for various reasons the examination will be difficult and protracted.

Of the sensory hairs or setæ in the rich and varied order Opiliones a somewhat detailed account has been given by me in 1904 (HANSEN & SÖRENSEN *b*, p. 36—40). Here a short abstract may be sufficient.

The genera belonging to the suborder Cyphophthalmi are blind excepting the genus *Stylocellus* WESTW., which has a pair of sublateral eyes. Exactly on the spot where the eye is placed in *Stylocellus*, we find in *Purcellia illustrans* H. J. H. & W. S. a seta which is many times longer and thicker than the very fine and short hairs scattered on the upper side of the cephalothorax; besides, this seta is inserted on a small hollow knot. In *Pettalus brevicauda* POCK.

a similar seta is found, and the area around its insertion is considerably raised and shows a sculpture different from that of the surrounding parts. In *Ogovia* H. J. H. & W. S., *Siro* LATR. and *Parasiro* H. J. H. & W. S. I could not find this seta, but I did not make a special præparation for that purpose. In all genera dissected, viz. *Stylocellus*, *Purcellia*, *Siro*, and *Parasiro*, I found two small sensory hairs on the upper side of the head a little from the front margin and near or rather near one another; this pair of setæ occur consequently both in forms without and in forms with eyes of this suborder, but in the two other suborders no such sensory setæ have been observed. If the Cyphophthalmi are compared with the Palpigradi, one is tempted to suppose that the two upper anterior setæ in the former group answer to the front bifid sensory organ in the last named order, consequently at least to some degree to the front pair of eyes in *Thelyphonus;* if so, the two eyes in most Opiliones answer not to the frontal eyes but to the two groups of sublateral eyes in *Thelyphonus* and other Pedipalpi, and a further result would be that the sublateral sensory seta in some blind Cyphophthalmi answers to the sublateral sensory hair or bundle of hairs in the Palpigradi.

In all three suborders of Opiliones sensory hairs or setæ are found on the legs. In the Cyphophthalmi they exist only on a shorter or longer distal part of the upper side of the tarsus of the two anterior pairs of legs; these setæ, from four to nearly a dozen on each tarsus, show generic differences, but they are always light of colour, somewhat curved, rather stout with the end obtuse, and they are easily distinguished from the other setæ. — Of the suborder Laniatores forms of three families, viz. Assamoidæ, Cosmetoidæ and Gonyleptoidæ, have been examined. The tarsus of the two anterior pairs of legs has above a few sensory setæ of the same somewhat elongate kind as in the Cyphophthalmi, and besides the tarsus and the metatarsus possess sensory setæ of another kind; in the two posterior pairs of legs the upper distal face of the metatarsus has a single stout sensory seta. In Cosmetoidæ and Gonyleptoidæ the tarsus of the two posterior pairs has on

the upper surface near the end a downwards bent process, »processus terminalis» W. S., which at least as a rule has a couple of long, slightly curved sensory hairs; in the family Assamoidæ, which has no »processus terminalis», a very short, thick sensory seta is found on the upper side of the tarsus near the end.

Among the suborder Palpatores forms of both tribes, viz. Eupnoi H. J. H. & W. S., and Dyspnoi H. J. H. & W. S., have been examined. Sensory hairs of the somewhat elongate type similar to those in the Cyphophthalmi are found on the tarsus of all pairs of legs, many more on the two anterior than on the two posterior pairs, and in genera with many tarsal joints they are only found on the more distal joints. Besides one or some conical, thick and short sensory setæ are found at least at the distal extremity of the tarsus.

Before leaving the Opiliones it may be mentioned that most peculiar hairs of very compound structure and unknown function are found on the more distal joints of the palps of *Nemastoma lugubre* O. F. MÜLL. and in some other species of the same genus. They have been described in 1893 (H. J. HANSEN, *a*, p. 197), and on the same page I described some remarkable bundles of hairs found in the male of *Phalangium parietinum* DE GEER on the lower side of the metatarsus and some of the more proximal tarsal joints in the three anterior pairs of legs.

In the Solifugæ I have not been able to discover sensory setæ of any kind, but the clothing makes the investigation of these animals difficult, and therefore I do not venture absolutely to deny the possibility of the existence of a few sensory hairs in these curious animals. On the Acari I can say very little. In the suborder Notostigmata WITH in 1904 found small and very thin, strongly curved hairs »placed in deep and large articulation cavities» and he considered them to be sensory hairs; they were found »along the dorsal side of the metatarsus of the second, third and fourth pair of legs and ot the outer side of the fourth pair of femurs». — The Oribatidæ possess a pair of organs named by MICHAEL (1884) »pseudostigmata». He described them as »usual

cylindrical externally, and more or less projecting, with a large external opening, but funnel-shaped and twisted within»; each has an organ projecting from it, viz. a hair, which varies in shape, being clavate or broadly flabellate, etc., most frequently having a long and thin stalk and the terminal part expanded, while sometimes the organ is nearly globular with a very short stalk. The organs are placed dorsally on the body rather far in front and more or less near the lateral margins. MICHAEL said that »it seems most natural to suppose hearing or smell (I incline the former) to be resident in these organs», but I am more inclined to compare them with the organs substituting the eyes in the Palpigradi. — On other sensory hairs in Oribatidæ MICHAEL says: »At the distal end of the tibia of the first leg there is almost always a very long setiform hair arising from the upper median line... it evidently has a tactile office, and I call it the tactile hair. A similar hair, smaller in size, is frequently found on the tibia of the second leg, and sometimes on those of the two hinder pairs». — According to MICHAEL (1901) the Tyroglyphidæ have a tactile hair on the tibia of the two anterior, frequently also on the two posterior pairs of legs. — In *Trombidium fuliginosum* HENKING (1882) found a very complex sensory organ placed dorsally and far in front in the median line of the body; what he says on »Tastborsten» on the legs is very explicit, but the setæ mentioned are uncommonly simple.

C. **Other external sensory Organs.**

It may be justifiable to enumerate here the other kinds of sensory organs hitherto observed in Arachnids. The only feature they have in common is that no hair is observed.

Let us begin with the so-called *lyriform organs*. Seen by transmitted light they seem to be fissures in the chitine with a very or extremely small round dilatation at the middle or towards one of the ends of each fissure. The fissures are either single and scattered or collected in groups; in these the fissures are either rather irregularly distributed or so regularly shaped and arranged that the name

»lyriform organ» has been given by GAUBERT, and this name has been extended so as to apply both to single, isolated fissures and to groups. BERTKAU is the first author who (in 1878) found and briefly mentioned a part of the fissures and groups in Araneæ. In 1885 F. DAHL (*b*, p 9—10) found and described a single compound organ near the distal end of the upper side of metatarsus of all legs in Araneæ; that he found only this organ proves that his investigation of the legs has been very superficial, and the sentence »Ob dieses Organ vielleicht auch bei der Herstellung des Gewebes dient?» is very unfortunate. In 1892 GAUBERT undertook a more special study of the lyriform organs, and as to their histological structure I refer to his paper. In *Epeira diadematа* he found thirteen compound organs and some single fissures on each leg, and besides groups or isolated fissures on the palps, the antennæ and the sternum. In 1893 I (H. J. H. *a*, p. 237— 239) added a considerable supplement to GAUBERT on such organs in *Epeira diadematа*, pointing out some more fissures on the legs and other appendages, and besides on the cephalothoracic shield, labium sternale, the stalk, the lower side of the abdomen, and the mammillæ. GAUBERT found also a portion af the fissures existing on the legs and palps in both suborders of the Pedipalpi, in Chelonethi and Opiliones; in 1893 and in later papers I showed that in these orders single fissures exist more or less regularly distributed on all parts of the body, and single fissures or groups of fissures on some or most of the joints of all appendages, in the family Phalangioidæ fissures even on the two branches of the ovipositor.

GAUBERT denied their existence in Scorpions and Solifugæ, but in Scorpions I found (*a*, p. 142—145) a number of fissures, many of them arranged in groups, on second to sixth joint of the walking legs and on second and third joint of the palps, but none on the antennæ or the whole body. In Solifugæ I found (*a*, p. 178—180) two groups of fissures on the lower side of first and second joint of the antennæ, but none on any other appendage or on the body. Among the Acari single fissures have been found by WITH in the Notostigmata and by me in Oribatidæ. In the

Palpigradi and, what is more curious, in the Ricinulei no fissure could be detected. — Among the hypotheses on the function of the lyriform organs two (proposed respectively by DAHL and by CARL VOGT & YUNG) are nonsense; GAUBERT has attempted to show that they permit »aux araignées de percevoir les sensations de chaleur», but his experiment is not convincing; «il est en outre probable que ces organes perçoivent des sensations du même ordre, telles que l'humidité et peut-être toutes les sensations generales». BERTKAU, W. WAGNER, and SCHIMKEWITSCH suppose that they are auditory organs; the last-named author compared them with the chordotonal organs in Insects, which probably are auditory.

In Scorpions still two other kinds of sensory organs are known. One of these is the combs (pectines), which have been well elucidated by GAUBERT (op. cit. p. 91—96). The second kind of organs has been discovered by me (H. J. H. *a*, p. 148—149); they are placed on the upper side of the last tarsal joint of all walking legs, and here I may only refer to the description quoted, though it contains too little of histological particulars.

On the fingers of the large chelæ in species of *Chernes* (of the order Chelonethi) and on the movable finger in a species of *Chelifer* I found in 1893 (H. J. H. *a*, p. 218) organs which as to structure are similar to those on the upper side of the tarsus in Scorpions, excepting that in the Chelonethi the organs are simple, in Scorpions collected in a single group or in two groups. — In Solifugæ two kinds of peculiar organs have been found. The «raquettes coxales» or »malleoli», which are found on the three proximal joints of the last pair of legs, are very conspicuous; they have been well examined by GAUBERT (op. cit. p. 96–98). The same author discovered and described (op. cit. p. 98—100) a very peculiar sensory organ at the end of the palps and of the first pair of legs, and he said that these four organs perhaps have an auditory function.

In Araneæ F. DAHL (*b*, p. 6—9) found in the mandibles (maxillæ auct.) an organ, which he believed to be olfactory, but later in the same year (1884) BERTKAU studied the same

thing, would not accept DAHL's interpretation, and did not believe it to be a sensory organ. In the same paper BERTKAU mentioned a very different organ found by him in two genera of Araneæ in the mandibles, and he supposed it to be an organ of taste.

In the orders Pedipalpi, Palpigradi, Ricinulei and Opiliones no organ not mentioned above has been discovered.

Before concluding this chapter it may be emphasized, that a bewildering number of different external sensory organs are known in the Arachnida taken together, that »lyriform organs» are known in most orders, trichobothria in more than half of the orders, other sensory hairs or setæ in several orders, while each of the remaining organs are found only in a single order or at most in two orders. The occurrence, distribution, or absence of the organs afford fine characters for the orders, and sometimes (Pedipalpi, Opiliones), though in much lower degree, for the suborders.

III. **Myriopoda.**

Tactile setæ in the two orders *Pauropoda* and *Symphyla* have been mentioned by several authors, but I am not aware of that such setæ have been found in Chilopoda or Chilognatha. In the Pauropoda the body has five pairs of lateral tactile setæ projecting beneath the lateral margins of second to sixth dorsal plate. *The setæ must be named trichobothria*, as each projects from a calicle; each seta has »a bulbous base connected internally with a oval mass of ganglionic cells» (Kenyon, in 1895), and the seta does not fill the opening of the calicle. In my paper on the order (1902) I added various particulars on the setæ, their pubescence, etc., and pointed out that in the same animal they can be referred to three varieties; it may be mentioned here that the setæ of third pair in certain forms are thickened either at the middle or at the distal end.

As is well known the Symphyla possess a single very conspicuous pair of trichobothria inserted on the body near the base of the cerci. The setæ are very long, and their basal part within the calicle is strongly bulbous. In the

genus *Scolopendrella* the calicles are regularly shaped, the opening is very large though scarcely as wide as the calicle, and the margin is naked. In *Scutigerella* the calicles are very irregular, the anterior and lateral parts of the wall being vertical and its posterior part very oblique, besides a large portion of the margin has numerous hairs (comp. my monograph in Quart. Journ. Micr. Sc. Vol. 47, 1904).

The trichobothria in the two orders of Myriopoda differ from those in the Arachnida in being inserted on the body, besides they are proportionately longer and stronger with the basal part within the calicle strongly swollen, and the opening of the calicle at most a little narrowed, sometimes (in *Scutigerella*) very wide.

IV. **Insecta.**

Especially in a paper published in 1905 (Zool. Jahrb. Suppl. VI) F. SILVESTRI has mentioned sensory hairs on some joints of the antennæ in *Japyx*, *Campodea* and *Eutrichocampa*, and nearly similar hairs on the cerci of forms belonging to the family Lepismatidæ. He named this kind of hairs on the antennæ »sensilli uditivi», auditory hairs, and those on the cerci only »sensilli». I had discovered these sensory hairs respectively on the antennæ and the cerci in representatives of the families in question before SILVESTRI had published anything on the matter, but I never wrote about it before now. SILVESTRI said on these hairs in the antennæ of *Campodea:* »10 sensilli uditivi costituti da una fossetta circolare dal fondo della quale sorge una lunga e sottilissima setola», and he found them on third to sixth article. *These hairs are therefore real trichobothria*, but SILVESTRI does not seem to have known that such hairs long time before had been found in Arachnida. The sensory hairs on the cerci in Lepismatidæ are also trichobothria and in the main similar to those on the antennæ, though their calicles are perhaps somewhat smaller; SILVESTRI named them »sensilli», without supposing them to be auditory organs, but if the trichobothria on the antennæ of the

Thysanura entotropha shall be interpreted as auditory organs, there is scarcely any reason for not interpreting those on the cerci of the Lepismatidæ in the same way. As to more special information on the occurrence of the trichobothria on the appendages mentioned in various forms the reader is referred to SILVESTRI's above named paper and to some other papers published from 1904 to 1912 by the same author.

Outside the Thysanura trichobothria have not, as far as I know, been discovered in any other order of Insects. But many years ago, while arranging the collection of Forficulidæ in the Copenhagen Museum, I found sensory hairs rather similar to trichobothria on the forceps of a single fine form, *Chelisoches superbus* DOHRN. On the outer third of the upper side near the base of each ramus of the forceps is seen about six somewhat deep but only moderately well limited impressions, and from the middle of each impression projects an extremely fine, moderately long hair. That we here have a kind of trichobothria with the calicle only moderately developed is, in my opinion, quite certain. — I was unable to find trichobothria on any other species of Forficulidæ in the Copenhagen Museum, but our collection of this group is somewhat imperfect, and it is probable that trichobothria can be found in some other tropical forms. — In the Blattidæ and Mantidæ I have examined the cerci in vain.

V. The trichobothria, their function, and systematic value.

In 1883 F. DAHL *a*, p. 267—270 discovered the trichobothria on the legs and palps of Araneæ, and added that he had also found them on the two joints of the large chelæ in Scorpions and Chelonethi. He did not name them trichobothria but »Hörhaare», and two years after he (*b*) published further observations on the occurrence of these auditory hairs in families and genera of Araneæ, with some new figures of their structure. In order to prove that the hairs have

an auditory function he took a leg of a living animal, laid it instantly under a microscope arranged for enlarging about 600 times, and when he then produced a somewhat deep tone on a violin, he saw that the distal part of such a hair vibrated; a few minutes after the leg had been torn off the blood was coagulated, and then the sound of the violin could not produce any vibration.

In 1888 W. WAGNER published an interesting paper: *Des Poils nommés auditifs chez les Araignées.* He critisized DAHL's first paper, but seems to have overlooked the second. He gave a very detailed account of the differences found by him in the modes of insertion, etc., between the types of sensory hairs compared with each other and with normal protecting hairs. The zoologist interested in the matter must read his paper, but some main points may be briefly mentioned here. He discerned between »simple tactile hairs» and the »hairs called auditory». The hairs of the first-named kind do not project from a calicle, but their base, »radix», is much thickened, so that the surrounding, somewhat elevated part of the skin becomes removed from the subbasal part of the hair. The hair named auditory projects through the constricted opening of a large calicle, on the bottom of which is found (in Araneæ) a flat calicle or cup, and in the middle of this cup the hair is inserted. Furthermore WAGNER described two forms of such hairs differing from one another in thickness, length and other minor particulars, and he named them respectively «poils à chapelets» and «poils tactils fins». On the tarsus of a species of *Mygale* he found a third type, viz. a very short hair consisting af a short stalk and an oblong-oval plate, while the stalk protrudes from a calicle which is lower with a comparatively wider opening than in the «poils à chapelets». Unfortunately WAGNER said next to nothing on the occurrence of the types in genera or families. He has made an experiment as to the vibration of the so-called auditory hairs, but with a negative result, and he could not accept DAHL's interpretation of their function, but he considered all types of sensory hairs on the legs of Araneæ as tactile organs, suggesting the possibility that the

so-called auditory hairs might serve as a kind of organs for possible alterations in the weather.

In my paper from 1893 I discarded DAHL'S view of the trichobothria which I named tactile hairs, and pointed out the main features of their occurrence in various orders of Arachnids; in the papers on Palpigradi (H. J. H., *b*) and Tartarides (H. J. H., & W. S., *c*) additional observations are given.

Such was the state of things when F. DAHL in 1911 published his treatise: *Die Hörhaare (Trichobothrien) und das System der Spinnenthiere* (DAHL, *c*). The name »trichobothria» is very good, but I do not know if it is used by DAHL in 1911 for the first time or perhaps invented before, possibly by another author. DAHL critisized WAGNER'S paper in a way which is very far from convincing, and maintained his opinion on the auditory function. He mentioned my discovery in 1893 of very small clavate tactile hairs on the tarsi in the Amblypygi, but his critical remarks show only that he had looked on my description (in English) in the most superficial way. He enumerated six reasons which should make it necessary to adopt his opinion on the function of the trichobothria; among these reasons only three need quotation, as the three others are absolutely insignificant. The first is that tones from an instrument make them vibrate. The second is that Araneæ really can hear — a fact also mentioned by WAGNER — and that in Araneæ no other organ has been found which can be interpreted as having an auditory function. (This question shall be dealt with later on.) The third reason (the sixth of DAHL) is the fact that the trichobothria can be sharply distinguished from hairs which certainly are tactile. DAHL does not seem to have known that trichobothria quite similar to those in Arachnida had been found respectively on the antennæ or on the cerci in various Thysanura, and that trichobothria of a somewhat aberrant type were known in two orders of Myriopoda. But evidently he laid much stress on their occurrence or absence in the orders of Arachnida, as he gives an analytical key of the classification of this class, and in that key uses the »auditory hairs» as one of the main characters, one may almost say as the most important character. Though the

occurrence and distribution or absence of the trichobothria afford fine characters for the orders, it seems to me that DAHL overrates their value very considerably; the above-named occurrence of typical trichobothria on the antennæ of the Thysanura entotropha, on the cerci in one of the two families of Thysanura ectotropha, and of a little modified trichobothria in a very low percentage of the Forficulidæ induce me, together with other considerations, to suppose that the systematic value of the trichobothria is of less high degree. For the rest, DAHL referred the Cryptostemmatoidæ to the order »Phalangida» and removed the Cyphophthalmi to the Acarida, an anomalous classification which scarcely will be accepted by any contemporaneous or future Zoologist, who possesses some knowledge of the whole class. Prof. J. C. SCHIÖDTE more than once pronounced to me the most correct dicton: »classification is fine tact» — and in the history of Zoology many classifications proposed show the opposite of »fine tact» in their makers.

Finally the question: are the trichobothria auditory or specially developed tactile organs? Their occurrence in some Insects speaks strongly against the interpretation, that they have an auditory function; that the Insects with trichobothria should be able to hear and all other Insects be deaf is certainly wrong; that the trichobothria in the Insects mentioned or at least in the Thysanura entotropha are auditory organs, while other Insects which can hear have quite different auditory organs, is highly improbable. And that at least some Insects which do not possess trichobothria, can hear is certain. The best proof has, as far as I know, been published by J. C. SCHIÖDTE, and as it seems to be nearly unknown among Zoologists, I will translate the most important part of his text (Naturh. Tidsskr. 3. R., Vol. VIII, 1870, p. 188). SCHIÖDTE experimented with specimens of *Necrophorus,* especially *N. vespillo.* »When listening to a flower-pot in which several specimens of *Necrophorus* are about letting down a carcass [a small mammal or bird], one hears distinctly that they during the work underground communicate mutually by the language of stridulation. The sound is now higher and hasty, now deeper and smoothered, and on the whole modulated in the most

manifold way. Sometimes a pause is suddenly interrupted by a single sharp tone instantly answered by a similar one from another specimen or simultaneously from several specimens, and one gets the impression of the different moods agitating the animals during the pains of the work: eagerness, impatience, fretfulness, weariness, exultation: and sometimes the whole company mades a kind of chorus-cry for the measured regulation of the work». — I think that at least all stridulating Insects and larvæ, and probably many other Insects, can hear. And the so-called chordotonal organs, which have been found in various Insects, are most probably the auditory organs in this class.

But to return to the Arachnida. That most or probably all Araneæ can hear has been stated by W. WAGNER, who has performed fine biological work on many animals of that order. And it seems to me very improbable that all Opiliones are deaf, but trichobothria are unknown in this order. Most of the Solifugæ have well developed stridulating organs on the antennæ in both sexes (H. J. H. *a*, p. 184—186), but trichobothria could not be discovered on any part of the animals, and it is extremely improbable that the sensory organs at the end of the palps and first pair of legs are auditory, while in Araneæ the same function has been taken over by the trichobothria. Besides one is inclined to consider the trichobothria on the fingers of the large chelæ in the Chelonethi and on the chelæ and more distal joints of the palps in Scorpions as tactile organs, especially when the movements of the palps with the chelæ in walking animals are taken into account. And is the statement of DAHL really correct that in the Arachnida no other organ than the trichobothria is known which can be supposed to have an auditory function?

If the chordotonal organs in Insecta are to be considered as auditory, it is very probable that the above-mentioned lyriform organs in Arachnida have the same function, an opinion favoured by BERTKAU, SCHIMKEWITSCH and W. WAGNER. The assumption at least removes various difficulties, but it will be difficult to prove it; I suppose that the Solifugæ may perhaps be the best objects for experiments, as the lyriform organs in this order are found only on the

lower side of the antennæ and therefore can be covered or damaged without considerably hurting the animal. It is a well-known fact that it is very difficult and frequently impossible to ascertain the function of sensory organs in Arthropoda, because we have only our own senses as starting-point, and, excepting to a certain degree the eyes, the structure of the external sensory organs in Arthropoda and in higher Vertebrata is extremely different. But I think to have shown with tolerable certainty that the trichobothria in terrestrial Arthropoda are scarcely auditory organs but tactile hairs of special structure, perhaps also of somewhat special functions. As partly mentioned above the trichobothria show, for the rest, considerable differences as to the hair itself, which generally is long or extremely long, most frequently very thin but sometimes (Myriopoda) more robust, often glabrous but not infrequently with short or very short pubescence at least on its distal part; the part of the hair inside the calicle is most frequently cylindrical but sometimes (Myriopoda) much swollen; the inner surface of the calicles differs considerably, being sometimes smooth, sometimes striated or sculptured, and on the bottom of the calicle is frequently found a cup bearing the hair, frequently no such thing. Further studies with high magnifying power of sections of these and other of the above-named sensory organs in different Arthropoda will certainly reveal numerous fine modifications, and large numbers of experiments with living animals of various orders will be needed before a deeper insight in the functions of the trichobothria, other kinds of sensory hairs, lyriform organs, etc., can be gained.

V. List of main papers quoted.

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1883. *a.* Dahl, Fr.: Über die Hörhaare bei den Arachnoiden. (Zool. Anzeiger, vol. 6, p. 267—270.)

1885. *b.* Dahl, Fr.: Das Gehör- und Geruchsorgan der Spinnen (Archiv f. Mikrosk. Anatomie, vol. 24, p. 1—10.)

1911. *c.* Dahl, Fr.: Die Hörhaare (Trichobothrien) und das System der Spinnentiere. (Zool. Anzeiger, vol. 37, p. 522—532.)

1892. GAUBERT, P.: Recherches sur les Organes des Sens et sur les Systèmes tégumentaire, glandulaire et musculaire des appendices des Arachnides. (Ann. Sc. Natur., Zool., ser. VIII, vol. 13, p. 31—184.)

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1901. *b.* HANSEN, H. J.: On six Species of Koenenia, with remarks on the Order Palpigradi. (Entom. Tidskrift utg. af Entom. Fören. i Stockholm, vol. 22, p. 193—240.)

1897. *a.* HANSEN, H. J., and SÖRENSEN, WILLIAM: The order Palpigradi THOR. (*Koenenia mirabilis* GRASSI) and its relationship to the other Arachnida. (Entom. Tidskrift utg. af Entom. Fören. i Stockholm, vol. 18, p. 223—240.)

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