

18.

**The Chaetotaxis of Tarsus I in some  
Mesostigmata.**

**With special reference to a supposed homologon  
of the tarsal organ of the genus *Spinturnix* and  
Haller's organ of the ticks.**

By  
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In an interesting paper (1942) Karl-Wilhelm Neumann investigates whether a tarsal organ homologous with Haller's organ in the ticks, is found in the Mesostigmata. Neumann thinks it possible to demonstrate that such a homology can actually be established, and on this basis he draws very far-going conclusions as to the phylogeny of the Mesostigmata.

Since, however, I did not agree with Neumann on several points of his considerations, I decided to make a supplementary investigation, in order, if possible, to come to a clearer understanding of the problems which Neumann had set himself. An account of the results of these investigations will be given below.

First I shall deal with the tarsal organ, so important for the phylogenetic considerations, in the genus *Spinturnix*.

Neumann has examined the organ in *Spinturnix vespertilionis* (Scop.). My Fig. 1 represents the same organ in a *Spinturnix* sp. from *Nyctalus noctula* Schreb.. My figure differs from that of Neumann in some few particulars.

Thus the long, narrow depression, supposed to extend from the proximal part of the tarsus and almost to the

distal part, does not exist. At the point where the depression was supposed to be, the leg is more transparent than in other parts of the tarsus (the less densely dotted area in Fig. 1) and thus gives the impression that there is a depression in the leg; however, on close inspection it will be noted that this lighter-coloured area

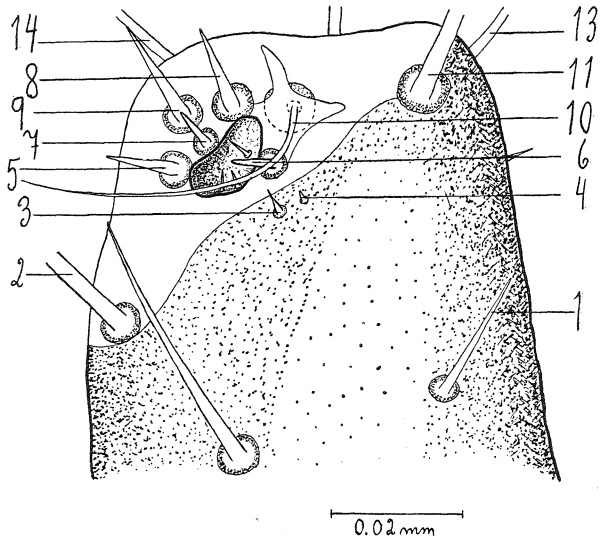


Fig. 1. *Spinturnix* sp. (On *Nyctalus noctula* Schreb., Odense, Danmark, March 9, 1939, Chr. M. Poulsen leg.). Left Tarsus I, in dorsal view. The figures in this figure do *not* correspond to the figures in the other illustrations. Ambulacral apparatus removed.

is bounded outwardly by a thin layer of skin, in which hairs are inserted, and which naturally continues the curvature of the leg. The tarsal organ itself, as shown also in Neumann's Figs. 1 and 2, is limited to the tarsal apex, where it is distinctly separated from the other part of the tarsus. Proximally to this demarcation line two small spines are situated, which are probably identical with 3 and 4 in Neumann's Fig. 2. Distally to the

line of demarcation between the tarsal organ and the remaining part of the leg the groove is the most characteristic formation. In my Fig. 1 it is broadly heart-shaped, with steep sides and three spines at the bottom. The groove is flanked on either side by a hair, which probably corresponds to 5 and 6 in Neumann's Fig. 2. Both are situated close to the groove but not united with it. Finally the small hair in front of the groove no doubt corresponds to 7, while the two large ones correspond to 8 and 9 respectively in Neumann's Fig. 2. Hair No. 10 in my *Spinturnix* is possibly a specific hair formation, which may correspond to the same figure in Neumann's Fig. 2; in its proximal part this hair pierces a peculiar two-lobed membrane which seems to arise from hairs 8 and 6 and the margin of the groove combined. Possibly, however, the membrane is merely a preparation phenomenon<sup>1</sup>); it is not inconceivable, however, that such a membrane may actually exist. Hairs 2, 11, 13, and possibly 14 are referred, though with some doubt, to the corresponding figures in Neumann's Fig. 2. Thus in the animal examined hairs 13 and 14 are not, but hair 11 is, sickle-shaped; the comparison between the hairs shown in Neumann's and my figures would have been far more reliable if Neumann had shown the structure of the hairs themselves, whether, for instance, some of them were solenidions. Hairs 2, 5—11, 13, and possibly 3—4 are all typical sensory hairs with the interior filled with plasma and with an irregular granular structure. Following the hair types erected by Grandjean (1935), I would refer hairs 5—9 and 3—4 to the acanthoides, if anything; for they cannot be solenidions owing to the swollen proximal part; hairs 2, 10, 11, and 13, however, most closely resemble the solenidions.

1) Like most of the succeeding Mesostigmata, this individual was heated in lactic acid with an ensuing washing in phenol before being examined.

According to Neumann, this whole sensory organ should correspond to a Haller's organ at a more undifferentiated stage of development than Haller's organ in even the most primitive *Ixodidea*, where, as shown in Fig. 2, the "Kapsel und Wanne" are situated in a common depression on the upper side of Tarsus I, only slightly separated from each other. Thus, according to

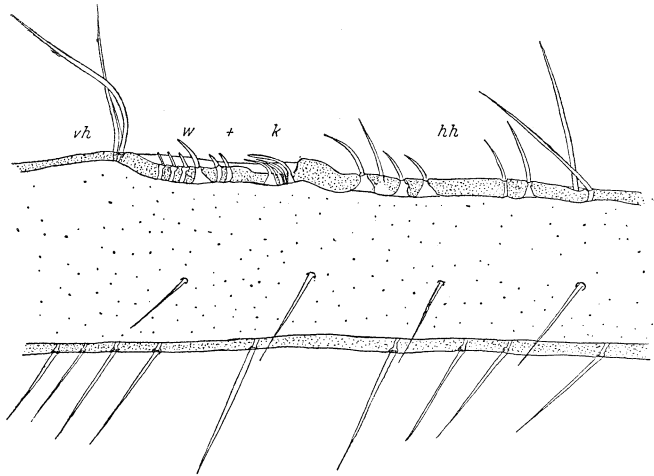


Fig. 2. *Eschatocephalus vespertilionis* (Koch) ♀. Part of Tarsus I with Haller's organ. *vh*, anterior hair group, *w+k*, the two sections of the tarsal groove corresponding to the "Wanne und Kapsel", *hh*, posterior hair group. (After Schulze).

Neumann, the groove itself in *Spinturnix* should correspond to the "Wanne und Kapsel", as he thinks he can trace slight tendencies to an incipient differentiation in the "Wanne" and the "Kapsel" respectively. He regards hairs 8, 9, and 10 as belonging to the anterior hair group, hairs 1—4 to the posterior one.

The supposition that there exists a homology between Haller's organ and the tarsal organ in *Spinturnix* hinges on the point whether or not the groove can be

interpreted as a union of the "Wanne und Kapsel". Neumann thinks that this is possible, and in this respect finds support in the observation that the groove has at the middle an incipient hourglass-shaped constriction, which thus indicates a division of the groove into two parts, as shown in Neumann's Fig. 2 and less distinctly in his Fig. 1. Since the appearance of this organ is a cardinal point in the phylogenetic considerations, we must assume that this hourglass-shaped appearance is not specific to *Spinturnix vespertilionis* alone, but is a general feature of all the species of *Spinturnix*. Besides *Spinturnix araguensis* Vitzth. perhaps (cf. Neumann 1942, pp. 54—55) not having any groove, the species shown in my Fig. 1 will be seen to have a groove of an appearance which is very unfortunate in a phylogenetic respect, as it shows no indication at all of a division into two spaces, and the bottom of the groove is quite even without any difference in level between the supposed "Kapsel und Wanne" part (cf. Fig. 2). Finally, it is very improbable that the three small spines at the bottom of the groove should develop into the many and differentiated hairs which cover the bottom of the "Wanne und Kapsel" in the ticks; hairs 7, 6, and 5 are not, as supposed by Neumann, inserted into the wall of the groove, but, as mentioned before, are free, independent hair formations, which are merely situated close to the outer margin of the groove. Finally, the position of the tarsal organ in *Spinturnix* and of Haller's organ is entirely different, for in *Spinturnix* it is situated in the tarsal apex itself, while Haller's organ lies at a fairly long distance from this. Thus according to the above considerations it seems improbable that the groove, either as regards hairiness, shape, or position, can be homologised with a still partially undifferentiated "Kapsel und Wanne".

As regards the anterior hair group, the number of

hairs composing it in *Spinturnix* differs from that found in *Prostriata*, which is the *Ixodes*-group which systematically should be most closely related to the genus *Spinturnix*; but as this figure is somewhat variable (Schulze 1941, p. 495), this point is less essential. In my opinion it is more important that the three hairs (8, 9, 10) form no morphological unit, hairs 8 and 9 being conical, short, and belonging to the acanthoidal type, while hair 10 is long and hair-shaped, belonging to the solenidionic type. As regards the position the three hairs are not well separated from the other hairs either, hairs 8 and 9 belonging to hairs 5 and 7, while hair 10 occupies a more isolated position in relation to the other hairs. Thus it would seem that neither the shape, position, nor number of hairs suggest that they may be interpreted as the anterior hair group.

As regards the posterior hair group, I think that Neumann's arguments are even more hypothetical. In the first place the fact that the hairs are only found on Tarsus I need not mean that they have any connection with a tarsal sensory organ, in this case the supposed Haller's organ; in the second place they are all situated outside the well delimited area in which the groove and the "anterior hair group" are found, and this renders it even more improbable that they should be associated with them; in the third place, in *Spinturnix vespertilionis* they lie on a line at right angles to the longitudinal axis of the tarsus, a position which I do not know from any *Ixodidea*; and in the fourth place they are present in a number not commonly found in *Prostriata* (cf. Schulze 1941, p. 495). Accordingly there are no grounds for assuming the presence of a posterior hair group either.

Altogether these considerations and Fig. 1 should show with all desirable distinctness that the tarsal organ in the genus *Spinturnix* is in no way homologous with

Haller's organ in the ticks, and that consequently no proof of a relationship between the ticks and the *Mesostigmata* can be furnished in this way. And even if a relationship had actually existed between the tarsal organ in *Spinturnix* and Haller's organ in the ticks, this, the only morphological common feature, would be too insufficient to form the basis of the far-reaching phylogenetic conclusions drawn by Neumann.

The next question Neumann sets himself is whether the tarsal organ in *Spinturnix* can be homologised with corresponding organs in the other *Mesostigmata*.

In order to solve this question it would be reasonable to examine the structure of the organ in a form as closely related to the genus *Spinturnix* as possible. I therefore chose to examine the tarsal organ in *Halarachne halichoeri* Allm. (cf. Oudemans 1925, Vitzthum 1929), even though this species differs essentially in its mode of life from the various species of *Spinturnix*. Figs. 3 and 4 show the tarsal organ in two different individuals, in Fig. 3 in the lateral view and in Fig. 4 seen more from above (owing to the perspective the same hairs differ in length in the two figures). Previously the organ has been described and figured by Oudemans (1925) and Kramer (1885), and my figures agree largely with those given by them. In this case also I will refer the short, more or less conical sensory hairs to the acanthoides, as in *Spinturnix*, while the long hair-shaped sensory hairs should probably most correctly be referred to the solenidions. The number and shape of the hairs are not entirely constant, as a comparison of the two figures, with each other and with Kramer's and Oudemans's figures, will show. The sensory field is sharply delimited from the surrounding thicker and strangely pored chitin. In the middle of the sensory organ the chitinous rings, which are found at the base of all the hairs, are fused in four of the

hairs so as to form a continuous chitinous flake, which is pierced by four holes each lying in continuation of one of the hairs.

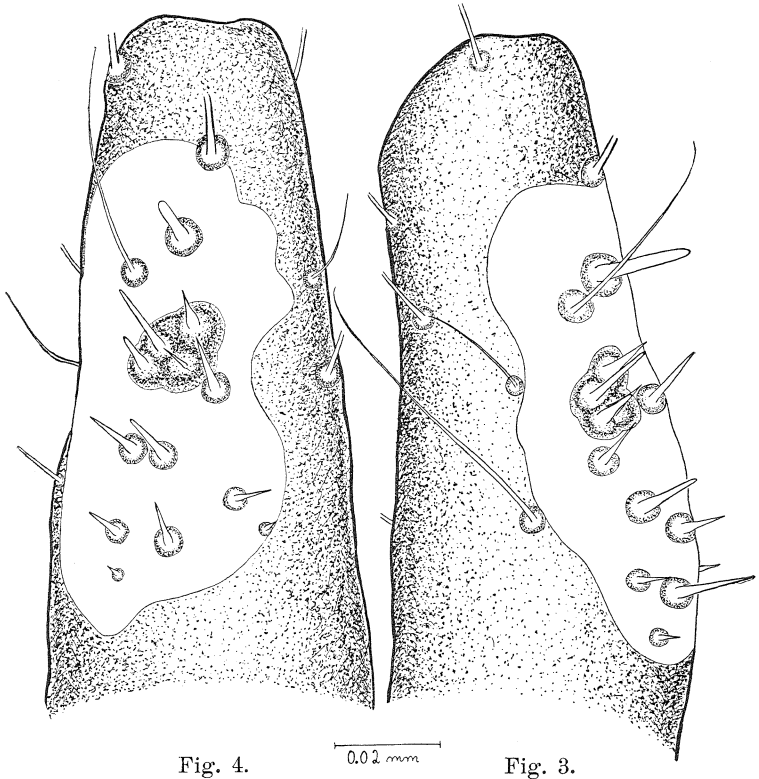


Fig. 3—4. *Halarachne halichoeri* Allm. ♀. (Bergen, Norge, March 1915. A. Brinkmann leg. et det.). Fig. 3. Left Tarsus I in lateral view. Fig. 4. Left Tarsus I in dorsal view. Ambulacral apparatus removed in both figures.

If we try to homologise the tarsal organs of *Spinturnix* and *Halarachne*, we shall soon discover that, despite a superficial resemblance at the first glance, no relationship can be demonstrated between them. The only common feature observed by me is the structure



of the hairs themselves, but this is probably a result of convergence rather than of actual relationship. The groove with the three spines at the bottom, which is characteristic of the organ in *Spinturnix*, is entirely absent in *Halarachne*, the chitinous flake in the middle cannot be parallelised with any corresponding feature in *Spinturnix*, and finally the tarsal organ in *Halarachne* has a more proximal position than in *Spinturnix*. If the tarsal organ were to be compared with any other tarsal organ, we might perhaps in this case suggest Haller's organ in the ticks. Without dealing more closely here with the systematical position of *Halarachne*, I shall merely mention that it was referred by Nehring (1884) to the *Ixodidea*, but that in Oudemans' opinion (1925) this cannot be maintained. Thus, if *Halarachne* is perhaps an original *Ixodes* type, its tarsal organ might be interpreted as a pre-Haller's organ, that is to say, a Haller's organ at such a primitive stage that neither the "Kapsel" nor the "Wanne" had yet been specialised (cf. Fig. 2). However, this is, of course, merely a hypothesis, which is of no phylogenetic interest as long as all the intermediate links are lacking.

I have been unable to ascertain any connection between the tarsal organ in *Halarachne* and the hairs at the tip of Tarsus I in other *Mesostigmata*, as for instance those figured below.

Thus, to sum up, according to our present knowledge the tarsal organ in *Halarachne* cannot be parallelised morphologically with corresponding organs in other *Mesostigmata*, and probably it has no connection either with Haller's organ in the *Ixodidea*.

While, thus, I did not succeed in parallelising the tarsal organ of *Spinturnix* with the tarsal organ even of its supposed nearest relative, Neumann thinks himself able to see the scheme for the position of the hairs on the tarsal organ of *Spinturnix* repeated in a great

number of more or less remotely related species within the *Mesostigmata*; however, in this he has not succeeded, for the simple reason that the basis for the comparison does not hold good.

In order to be able to compare the hair-covering of the tarsi of the different forms, we must, as Neumann says, have a well founded basis from which to draw our conclusions. Neumann finds this in the three spines at the bottom of the groove ("Wannenhaare"), which actually represent the only basis for his hair-topographical conclusions. However, no proof is supplied that the three spines in *Spinturnix* are actually homologous with the corresponding three hairs on Tarsus I of the different *Mesostigmata* investigated; it is not even rendered probable that a morphological connection exists between the three hairs which in the *Mesostigmata* should represent the three spines in the groove; on the contrary, their great variation both in shape and position seems to suggest that it is even very doubtful whether we are dealing with the same three hairs from one species to the other. Since, thus, the point of departure for Neumann's considerations is a mere postulate, which, moreover, is not very probable, the different patterns (Muster I—V) (pp. 55—66) and lines of development (pp. 66—72), which he erects precisely on this basis, cannot in my opinion lay claim to any great validity.

In his final chapter, Neumann further deals with the tarsal organ in *Trombidiformes* and in this connection mentions the Sig Thor organ<sup>1)</sup>; here, I think, he is guilty of a couple of minor misunderstandings. According to Willmann's and others' descriptions and figures, the scale is not attached to the sides of the groove, but to its bottom by means of a chitinous knob and more-

1) Cf. Haarløv (1942, pp. 29—32) where it is proposed to call this organ, which was previously called the Rhagidia organ, the Sig Thor organ, because the Rhagidia organ has now been ascertained in other genera than *Rhagidia* and the name accordingly is misleading, and because Sig Thor was one of the first to study this organ more thoroughly.

over there is only apparently a hole at the bottom of the groove, the chitinous knob, owing to its refraction, appearing as a hole.

As will appear, I hope, from the preceding pages, no bridge can be built between the *Mesostigmata* and the ticks on the basis of the hair-covering of Tarsus I. Another point is whether any features common to the different *Mesostigmata* can be ascertained as regards the topography and shape of the hairs on Tarsus I. Neumann's treatment of this question has been mentioned above. Since, as stated above, I did not regard this as entirely satisfactory, I made up my mind to investigate the question myself, trying to pay as great attention as possible to both the mutual position of the hairs and to the morphology of the individual hairs. All the specimens examined are found in the Zoological Museum of København. During this investigation the agreement between the topography of the hairs on Tarsus I of the different species, with the exception of *Antennophorus pubescens*, proved to be so great that I think I am justified in homologising with each other the hair-coverings of Tarsus I of the different *Mesostigmata* examined. In Figs. 5—11, but *not* in Fig. 1, the hairs which in my opinion correspond to each other are marked with the same figures. 1 a, 1 b, 2 a, and 2 b are four long sensory hairs with a characteristic large insertion situated close to each other in the distal part of the tarsus; a and b indicate their symmetrical position in relation to each other. Hairs 3—9 are all solenidions; they are constricted at the base, have partially parallel sides and an irregular internal construction, in which, however, I failed to detect any spiral structure. Their mutual position is fairly constant, but their shape differs somewhat within the different species. On the other legs there are no solenidions. Hair-shaped solenidions, if any, are not referred to solenidions, but to ordinary hairs. Hair 10 is always inserted in the same place and has a charac-

teristic sword-like shape, sometimes with a swelling at one end (cf. however Fig. 6). It somewhat resembles the hair which Grandjean (1935, Fig. 1 a and p. 28) supposes may perhaps be a famulus. Hairs 1—10 are pre-

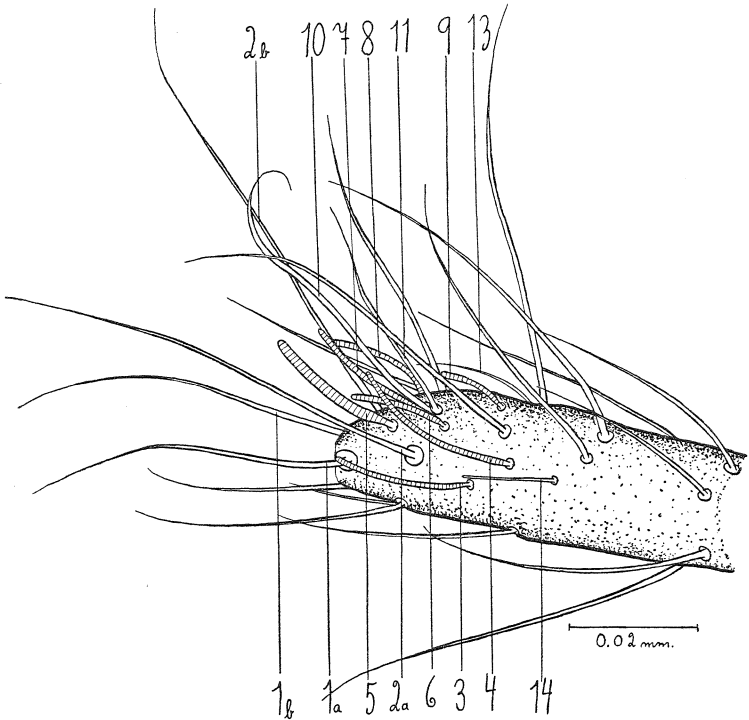


Fig. 5. *Pergamasus* sp. (*robustus* Oud.?) ♂. (Eremitagesletten, Danmark, Aug. 13, 1942, Sample 109, Haarløv leg.). Left Tarsus I. Ambulacral apparatus removed.

sent in nearly all the figures, whereas hairs 11—14 are of somewhat more irregular occurrence. Hairs 11 and 12 are inserted close to the root of hair 10, and hair 13 is short and sickle-shaped. In Fig. 7 hair 13 is possibly replaced by a thick hair which resembles a solenidion in shape, but which, in contrast to this, is massive.

When present, hair 14 is always inserted in the same place, obliquely behind hair 4; it is thin, has nearly parallel sides and no distinct structure.

While Figs. 5—10 show a distinct common character, Fig. 11 seems at first glance to differ considerably

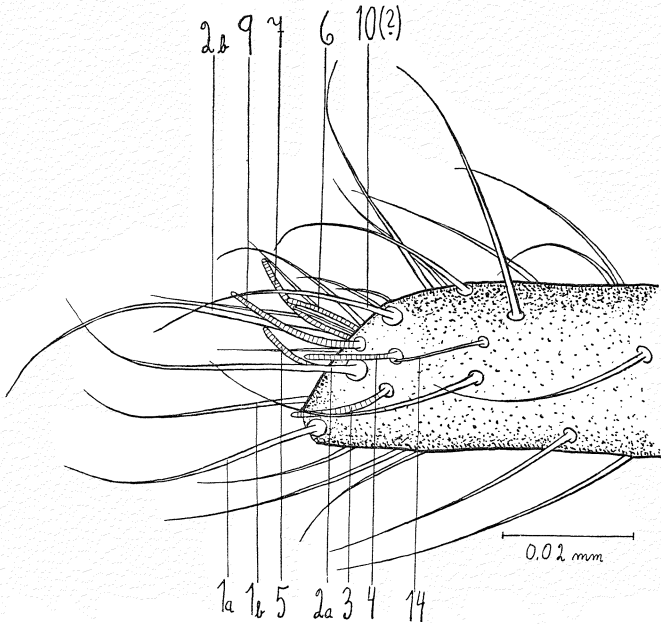


Fig. 6. *Ololaelaps hemisphaericus* (C. L. Koch) ♀. (Mælifell, Skagafjörður, Island, June 22, 1933, Sample 32 p, S. L. Tuxen leg.). Left Tarsus I. Ambulacral apparatus removed.

from this. The genus *Macrocheles*, as is well known, has no ambulacral apparatus on Tarsus I. However, in a phylogenetic respect the ambulacral apparatus, according to Vitzthum (1940), consists of transformed hairs, and since on the under side of Tarsus I of the figured *Macrocheles* sp. an especially long and vigorous hair (termed A in Fig. 11) is found in the place whence the ambulacral apparatus usually issues, it is natural to con-

clude that this hair is homologous with the ambulacral apparatus in the sense that the amount of chitin which should otherwise have formed the ambulacral apparatus, has instead been used for the formation of the long undifferentiated hair. On this basis I think that the other hairs can be naturally correlated with the hairs repre-

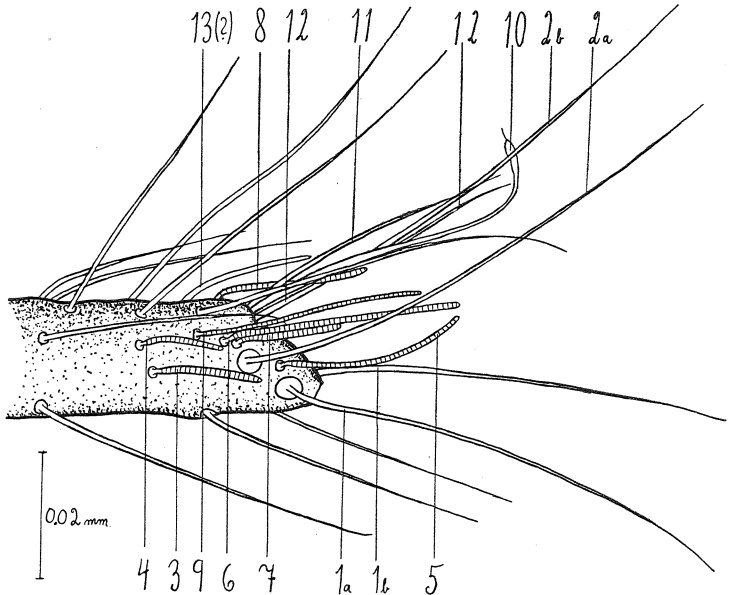


Fig. 7. *Cyrtolaelaps* sp. (*kochii* Trgdh.?) ♀. (Eremitagesletten, Danmark, Aug. 1, 1942, Sample 103, Haarløv leg.). Right Tarsus I. Ambulacral apparatus removed.

sented in the other figures, as shown in Fig. 11; however, the insertions for hairs 1 and 2 are not essentially larger than the insertions of the other hairs on the tarsal tip. I am unable to correlate naturally Fig. 12 with the other figures. There are three solenidions, and off each of them there is a hair of the same appearance as hair 14 in the other figures.

Fig. 9 represents Tarsus I of *Zercon solenites* Haarløv described by me (1942) as full-grown. According to

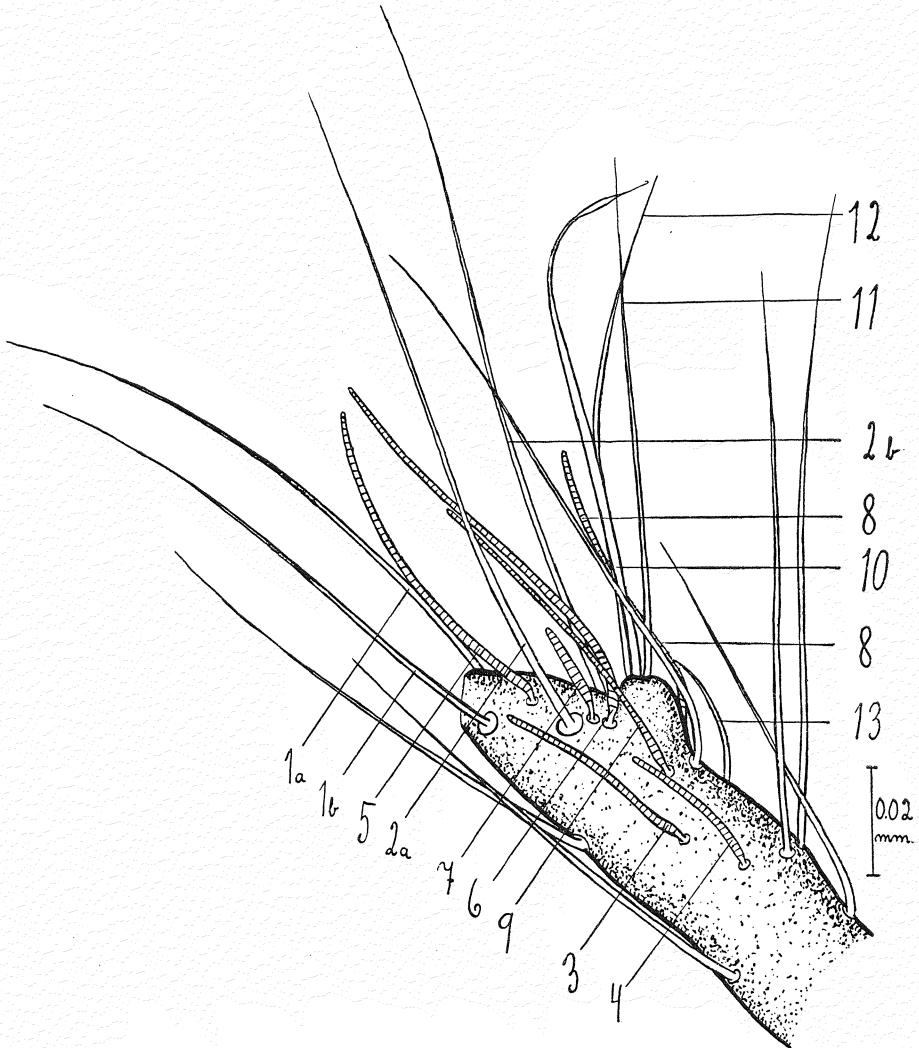


Fig. 8. *Veigaia herculeanus* (Berl.) ♀. (Eremitagesletten, Danmark, Oct. 24, 1942, Sample 133, Haarløv leg.). Left Tarsus I. Ambulacral apparatus removed.

kind information by Dr. Max Sellnick, Königsberg, it is no full-grown specimen, but a deuto-nymph of this species. I here take the opportunity to thank Dr. Sellnick for this correction.

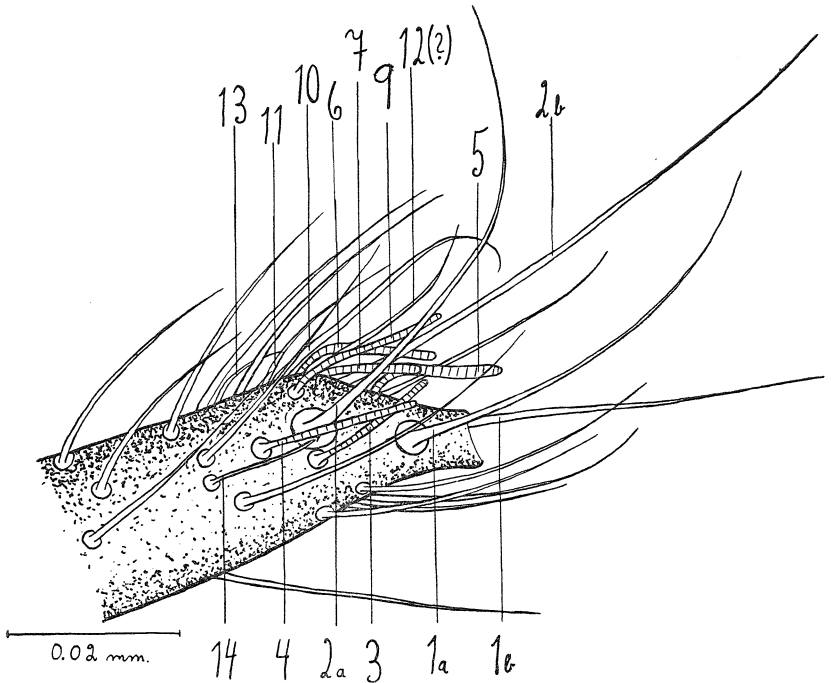


Fig. 9. *Zercon solenites* Haarløv. Deutonymph. (Mørkefjord, Northeast Grønland, 1940, Sample 110, Haarløv leg.). Right Tarsus I. Ambulacral apparatus removed.

It is impossible to draw any conclusions regarding the systematical position of the *Mesostigmata* figured in this paper; this would require a far greater material than the eight species examined here, and at the same time other structural features than the hairiness of the tarsal tip should naturally also be taken into consideration. I merely wish to point out the remarkable fact that *Zercon solenites* resembles Figs. 6—8 and 10—11 far



more closely than Fig. 12, with which it has systematically greater affinities than the other species; Tarsus I of an adult specimen of *Zercon curiosus* Trgdh. corresponded, as far as I could make out, to Fig. 9.

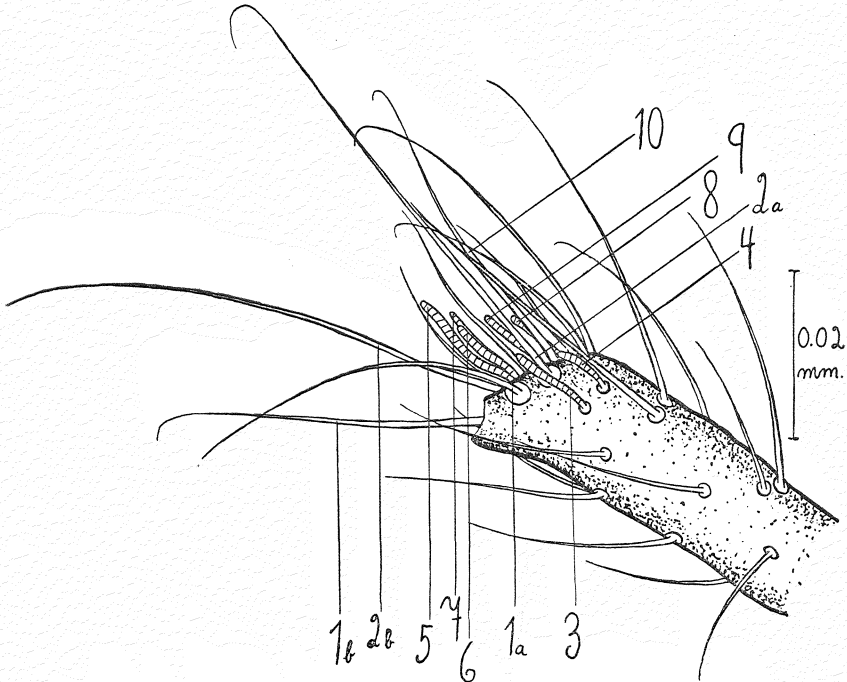


Fig. 10. *Episeius* sp. (*glaber* Berl.?) ♀. (Eremitagesletten, Danmark, Aug. 1, 1942, Sample 102, Haarløv leg.). Left Tarsus I. Ambulacral apparatus removed.

Thus, although no great or comprehensive result of Neumann's and my investigations on the hairiness of the tarsal apex is arrived at, they tend to show that on a more comprehensive and detailed investigation of the position and morphology of the individual hairs on Tarsus I of a great number of species highly interesting morphological and systematical results may be gained.

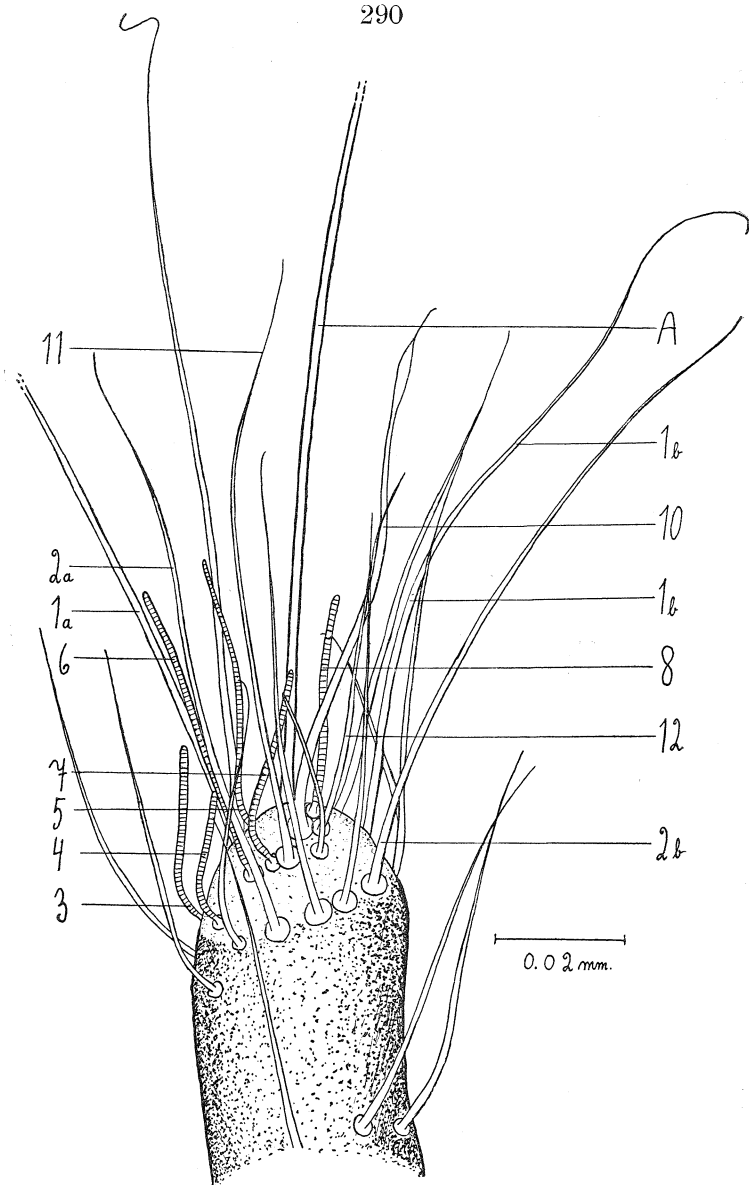


Fig. 11. *Macrocheles* sp. (*penicilliger* Berl.?) ♀. (Reykjarhóll, Skagafjörður, Island, June 18, 1933, Sample 42 b, S. L. Tuxen leg.). Left Tarsus I, seen from above. A: hair homologous with the ambulacral apparatus.

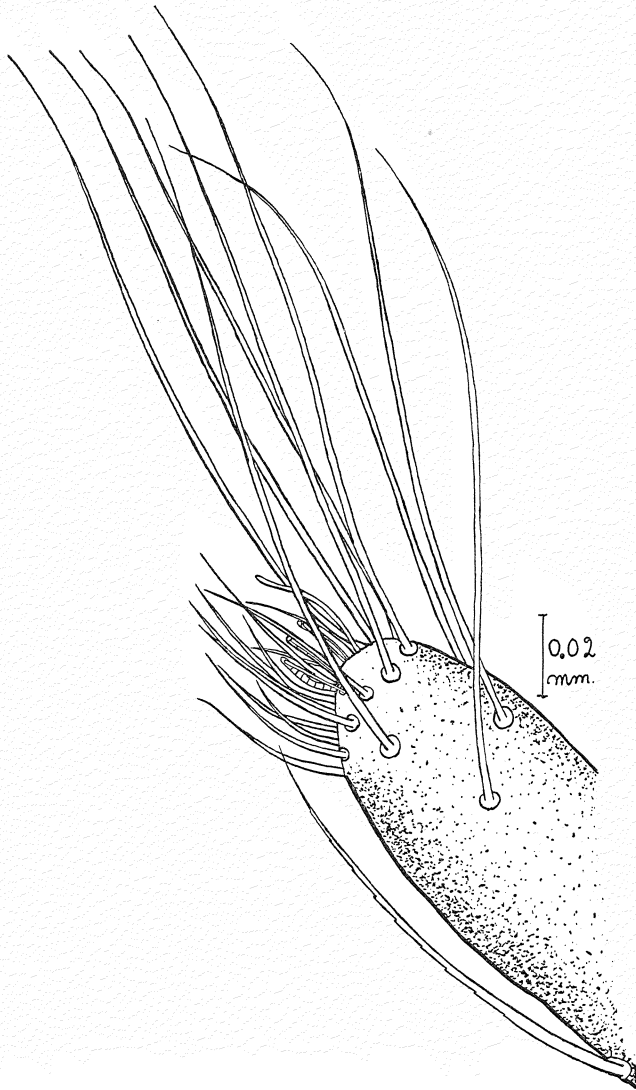


Fig. 12. *Antennophorus pubescens* Wasm. ♀. (Eremitagesletten, Danmark, May 21, 1942, Sample 39, Haarløv leg.). Right Tarsus I in ventral view.

In conclusion I wish to thank the chief of the Zoological Museum of København, Professor R. Spärck, Ph. D., for working facilities at the Museum and for the permission to use the collections of the Museum. I also wish to tender my cordial thanks to mag. sc. S. L. Tuxen for the support and interest extended to me during the preparation of the present paper.

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### Summary.

1) Description of the tarsal organ in *Spinturnix* on the basis of Neumann's investigations (1942), and a demonstration that a homology between the tarsal organ in the genus *Spinturnix* and Haller's organ in the ticks is not possible.

2) Description of the tarsal organ in *Halarachne halichoeri* Allm. as compared with earlier descriptions of it, and discussion of a possible relationship between this and other known tarsal organs. Such a relationship could not be established, unless it should be interpreted as a pre-Haller's organ.

3) Discussion of the possibility of comparing the tarsal organ in the genus *Spinturnix* with the hairs on Tarsus I of a number of *Mesostigmata*. In the author's opinion, however, this is impossible.

4) Brief mention of the *Sig Thor organ*.

5) Discussion of Figs. 5—12. Figs. 5—11 showed such a marked common character that the hairs on Tarsus I of the different species could be naturally homologised; homologous hairs are marked with the same figures; hairs 3—9 are solenidions. In *Macrocheles* the ambulacral apparatus is replaced by a very vigorous hair (A). Fig. 12 occupies a special position compared with the other hairs. Systematical conclusions on the basis of Figs. 5—12 are not drawn; only the remarkable feature is pointed out that *Zercon solenites* shows more agreement with Figs. 5—8 and 10—11 than with Fig. 12.

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### Dansk Oversigt.

1. Benpar hos Miderne har samme Funktion som Følehornene hos Insekterne. Det er derfor udstyret med særlige Sansorganer. Hos *Ixodiderne* ("Tægerne") findes saaledes det Haller'ske Organ (jfr. Fig. 2), og inden for en anden stor Midegruppe, *Mesostigmaterne*, findes, f. Eks. hos Slægten *Spinturnix*, der snylter paa Flagermus, et lignende Organ (jfr. Fig. 1). K.-W. Neumann (1942) mener, at Organet hos *Spinturnix* forestiller et primitivt Haller'sk Organ og slutter heraf, at *Ixodiderne* er nært beslægtet med *Mesostigmaterne* og afledet af disse. Jeg mener herimod at kunne paavise, at Organet hos *Spinturnix* i sin Opbygning intet har til fælles med det Haller'ske Organ; det formodede nære Slægtskab mellem de to Midegrupper bortfalder derved automatisk.

Sanseorganet paa Tarsus I af *Halarachne halichoeri* Allm., som lever i Næsehulen af Graasæler og er nært beslægtet med *Spinturnix*, undersøges og tegnes (jfr. Fig. 3 og 4). Noget Slægtskab med Organet hos *Spinturnix* kan ikke paavises.

Neumann mener i Behaaringen af Tarsus I paa en lang Række Arter inden for *Mesostigmaterne* at kunne genfinde Skemaet for Haarenes Placering i Sansorganet hos *Spinturnix*. Disse sammenlignende Betragtninger mener jeg dog er ganske uholdbare,

idet han hverken tager tilstrækkeligt Hensyn til de forskellige Haars Udseende eller har noget fast Udgangspunkt for de enkelte Haars indbyrdes Beliggenhed; hermed falder ogsaa de Klasser han inddeler de undersøgte *Mesostigmater* i og den kunstige Udviklingsrække han opstiller fra den mest „primitive“ *Mesostigmat* via *Spinturnix* til *Icodiderne*.

Selv har jeg med indtil 800 Ganges Forstørrelse undersøgt Haarenes Udseende og Placering paa Tarsus I af nogle tilfældigt valgte *Mesostigmater* (jfr. Fig. 5—12). Paa nær hos en enkelt Art (Fig. 12) viste der sig en saa tydelig Sammenhæng mellem Haarenes Placering og Udseende inden for de undersøgte Former, at jeg mente mig i Stand til at genfinde de samme Haar paa de forskellige Tarser; disse er benævnt med samme Tal; om der kan drages systematiske og fylogenetiske Slutninger her ud af, er det endnu for tidligt at udtale sig om; det vilde have krævet Gennemgang af et langt større Materiale end det foreliggende.

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