

Contributions towards the comparative Morphology of the Mesostigmata. (Acarina) VII.

The præsternal hairs and the male genital aperture.

By

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In a previous paper »Outline of a new classification of the Mesostigmata, based on comparative morphological data» (1946, a) the author has summarized the results of his researches on the comparative morphology and phylogeny of this group. At that time I was under the impression prevalent amongst the acarologists that very few facts bearing on the natural system of the *Mesostigmata* could be gathered from the structure of the males which, at least in comparison with the bewildering display of divergent types in the females, seemed uniform to an almost monotonous degree.

The discovery of the new genus *Diarthrophallus* (comp. Trägårdh 1946 b), which possessed both a well developed, biarticulated penis and præsternal hairs, caused me, however, to revise my views on this point, the result being that in this paper an attempt has been made to investigate also the organization of the males of a number of genera belonging to different groups.

The results of this investigation will be discussed in the final chapter of this paper. But it may be stated preliminarily that the old conception of the uniformity of the male ventral shields has no foundation and that especially the anatomical study of the males doubtless will facilitate the understanding of the natural system and phylogeny of the *Mesostigmata*.

1. The præsternal hairs.

The first acarologists who noticed the præsternal hairs of the *Mesostigmata* were Kramer (1895) and Oudemans (1905). Neither of them succeeded, however, in interpreting this structure. Kramer merely delineated a pair of hairs in front of the sternal shield (fig. 9 l. c.) in

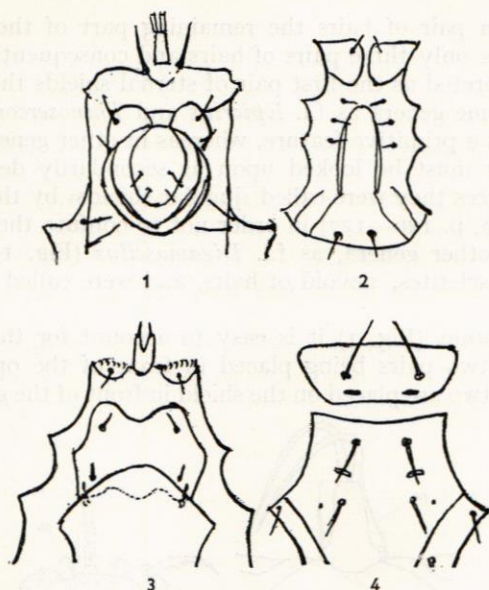


Fig. 1. Tritosternum with præsternal hairs, sternal and genital shield of *Megisthanus*. — Fig. 2. Epigynial shield and sternal shields of *Thinozercon michaeli* Halbert. — Fig. 3. Tritosternum, sternal shields and anterior part of ventral shield of *Epicrius mollis* Kr. — Fig. 4. Sternal shields of *Cercomegistus* sp.

Megisthanus obtusus from East Africa and Oudemans delineated the same hairs in *M. moaifensis* and *M. orientalis* (Figs. 25 & 41, l. c.) but considered them to be jugular hairs. The basis of the tritosternum is namely in *Megisthanus* faintly separated from the rest of the soft cuticle as a small, semicircular shield, but the cuticle of this portion is quite as soft as the rest of the præsternal area. It is this portion which is flanked by two low projections, each carrying a hair (fig. 1). This structure Oudemans describes in the following way. »Jugular shield single, median, transverse, narrow, with sharply pointed extremities, a little excavated anteriorly to receive the tritosternum, provided with two hairs.»

At this time the acarologists had, however, very hazy ideas regarding the homology of the different ventral shields of the *Mesostigmata* or, rather, they completely neglected the comparative morphological point of view. Hence Oudemans failed to perceive how very peculiar and, indeed, unique this feature was. In all other *Mesostigmata*, hitherto known, we always find four pairs of sternal hairs, corresponding to the four sternal shields and to the four leg-bearing segments. Between the base of the gnathosoma and the anterior edge of the sternal shield there are sometimes one or even two pairs of small shields. When these

shields carry a pair of hairs the remaining part of the sternal shield unvariably has only three pairs of hairs and consequently these shields must be interpreted as the first pair of sternal shields the independence of which in some genera as f.i. *Epicrotus* and *Thinozercon* (Fig. 3) must be regarded as a primitive feature, whereas in other genera as f.i. *Cercomegistus*, they must be looked upon as secondarily detached shields. In both instances they were called »jugular shields» by the author (1912, p. 20 and 1938, p. 126—127) in order not to confuse them with similar structures in other genera, as f.i. *Digamasellus* (Fig. 15), where they are accessory sclerites, devoid of hairs, and were called »præendopodal shields».

In *Megisthanus* (Fig. 1) it is easy to account for the four pairs of sternal hairs, two pairs being placed in front of the operculum while the remaining two are placed on the shield in front of the genital aperture

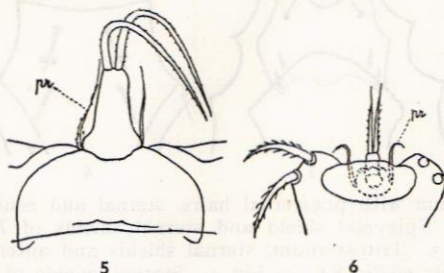


Fig. 5. Tritosternum and præsternal hairs of *Diarthrophallus quercus*. — Fig. 6. Tritosternum, præsternal hairs and anterior part of sternal shield of *Euzercon* sp.

which for this reason has been interpreted as the fused sternal shields III and IV (comp. Trägårdh 1943, Fig. 5). For this reason the author felt justified in stating (l. c. p. 8): »the presence of præsternal hairs close to the tritosternum is a quite unique character, separating *Megisthanus* from all other *Mesostigmata*. Further investigation is necessary before it is possible to say, whether these hairs or at least remnants of them exist in other genera.» Little did I guess then that within a year it would be possible to demonstrate the presence of præsternal hairs in yet three different groups, viz. the *Diarthrophallina*, the *Euzerconidae* and the *Diplogyniidae*.

The genus *Diarthrophallus*, established by the author for the species *Urosejus quercus* described by Pearse & Wharton in 1936, was found on *Passalus cornutus* Fabr. in the Duke forest near Durham in North Carolina. It is so peculiar in several respects that it must be referred to a new cohors, the *Diarthrophallina*. The most important feature is that the male genital armature represents a type not hitherto met with in the *Mesostigmata* (Fig. 25). Even the female epigynial shield is of a unique type and for the time being the cohors, embracing also the

genera *Brachytremella* Trägårdh and *Passalobia* Passerini has a quite isolated position (comp. Trägårdh 1946 b).

Diarthrophallus shares with *Megisthanus* the præsternal hairs which are present both in the nymphae and the adults (Fig. 5).

This discovery of præsternal hairs in two groups which are not at all related to one another points to the possibility that there may be other genera still in which præsternal hairs exist although they have been overlooked hitherto. As a matter of fact both in the *Euzerconidae* (Fig. 6) and the *Diplogyniidae* well developed præsternal hairs exist.

In *Euzercon* (Fig. 5) and *Diplogynium* the male genital aperture, the base of the tritosternum and of the præsternal hairs are hidden underneath the protruding free edge of the sternal shield. In *Euzercon* there is a transverse, oval shield along the anterior margin of the sternal shield. It may be that this is homologous with the genital shield, which will be described subsequently in several genera.

As far as I know there are only very few exceptions to the rule that the number of sternal hairs is four pairs. Thus in the *Antennophoridae* there is a varying number of additional hairs (comp. Trägårdh 1946 a, fig. 25) and in the very peculiar genus *Varroa* described by Oudemans from Indian bees

(1904) the females, the only sex so far known, have five pairs of sternal hairs (Fig. 7). The sternal shield of *Varroa* is very remarkable, being large, transverse and semilunar in shape. It has five pairs of hairs, the anterior one of which is placed near the anterior margin of the shield while the others are lateral and fairly equidistant. It seems possible that the discovery of præsternal hairs in several other genera may throw some light on the origin of this additional hair.

In *Megisthanus* (Fig. 1) the præsternal hairs were, as a matter of fact, inserted on the strip of soft cuticle in front of the sternal shield. Assuming that this præsternal area became coalesced with the sternal shield and strongly chitinized it would not be strange if the anterior pair of hairs of *Varroa* were homologous with the præsternal hairs.

The result of this little investigation is that the presence of præsternal hairs has been demonstrated in four different genera, belonging to three different groups and that it is possible that the anterior pair of sternal hairs of *Varroa* is homologous with the præsternal hairs. The possibility of the genital hairs of some *Uropodina* being also highly modified præsternal hairs will be discussed in the next chapter of this paper.

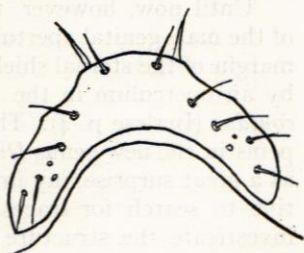


Fig. 7. *Varroa jacobsoni* Oudemans ♀. Sternal shield.

2. The male genital armature.

As is well known the *Mesostigmata* were formerly divided into only two groups, the *Gamasides* and the *Uropodina*. The first group was characterized by the male genital aperture being situated at the anterior margin of the sternal shield whereas the latter group was characterized by the genital aperture being situated in the sternal shield. In recent time, however, the whole system of the *Mesostigmata* has been remodelled on the basis of minute investigations of the female ventral shields, both the *Gamasides* and the *Uropodina* ranking as cohortes at the side of a great number of other groups (Trägårdh 1938 & 1946 a).

Until now, however, nothing more was known about the structure of the male genital aperture than that it was placed either at the anterior margin of the sternal shield or in the sternal shield and that it was closed by an operculum in the *Uropodina*, the *Antennophoridae* and the *Zerconidae* (Berlese p. 4). The discovery of a well developed, biarticulated penis in the new genus *Diarthrophallus* (Trägårdh 1946 b) came therefore as a great surprise, my immediate reaction being that it seemed imperative to search for traces of a penis also in other *Mesostigmata* and to investigate the structure of the much neglected male genital aperture and its armature.

The following genera have been investigated in order to study these structures: *Pergamasus*, *Ologamasus*, *Digamasellus*, *Liroaspis*, *Microsejus*, *Discopoma*, *Phaulodinychus*, *Cilliba*, *Oodinychus*, *Phyllodinychus*, *Megisthanus*, *Euzercon*, *Diplogynium*, *Paramegistus*, *Zercon* a. o.

It is obviously necessary that this investigation be supplemented by a study of the anatomy of the different groups. But until more collections, especially of tropical forms, suitably preserved, have been made, such an investigation cannot take place. In the meantime let us see what results may be obtained by the examination of the exoskeleton. Such an examination is, however, extremely difficult to make both on account of the minuteness of the organs concerned and because they are often withdrawn into the body. In some instances it has, however, been possible to make some dissections, which have thrown light on the minute relations of some parts to one another.

As pointed out above the starting point of the investigation was the unexpected discovery of a well developed, biarticulated penis in the new genus *Diarthrophallus* Trägårdh and doubtless also in the genera *Passalobia* Passerini and *Brachytremella* Trägårdh (comp. Trägårdh 1946 b p. 393). This organ was considered a primitive feature both on account of its great development and its position far back, in the same place as in the female. If this assumption is true it follows firstly that the forward position of the male genital aperture which occurs in some groups is a secondary one and secondly that the present simplified type of genital



Fig. 8. *Celænopsis cuspidata* Kramer ♂. Anterior part of the sternal shield. —
Fig. 9. *Pleuronectocelæno austriaca* Vitzthum ♂. Anterior part of the sternal shield.

organ is also secondary and that we may confidently look at least for traces of the segmentation present in *Diarthrophallus* in other genera.

A. Genital aperture at the anterior margin of the sternal shield.

It is generally accepted that the forward position of the male genital aperture is correlated, at least in the *Gamasides*, with their special way of copulation so admirably described by Michael (1892). In this cohort the males catch hold of the spermatophore sac, emerging through the genital aperture, with the help of their mandibles and insert it in the female genital aperture. Such a performance would obviously be impossible if the male genital aperture were situated far back between coxae III. For the purpose of grasping the females firmly during copulation the males are provided with several processes on the greatly enlarged second pair of legs.

Assuming this to be the true explanation of the organization of the *Gamasides* it remains to answer the question if the same explanation is valid also for other groups the male genital aperture of which is situated at the anterior margin of the sternal shield. Of special interest in this connection is the *Celaenopsidae* which occupies a very isolated systematic position. Two species, *Celaenopsis cuspidata* Kramer and *Pleuronectocelæno austriaca* Vitzthum, both found in Sweden, have been available for investigation.

In *Celaenopsis cuspidata* the male genital aperture is very large, occupying half the width of the anterior margin of the sternal shield (Fig. 8). It is protected by a short but very broad shield, the anterior edge of which is slightly thickened in the middle. This plate, which is unquestionably the counterpart of the epigynial shield of the female, I propose to call the *genital plate*. There is no trace of a ductus ejaculatorius, its walls being obviously not chitinized strongly enough to render them plainly visible through the sternal shield.

In *Pleuronectocelæno austriaca* (Fig. 9) there is also a genital plate

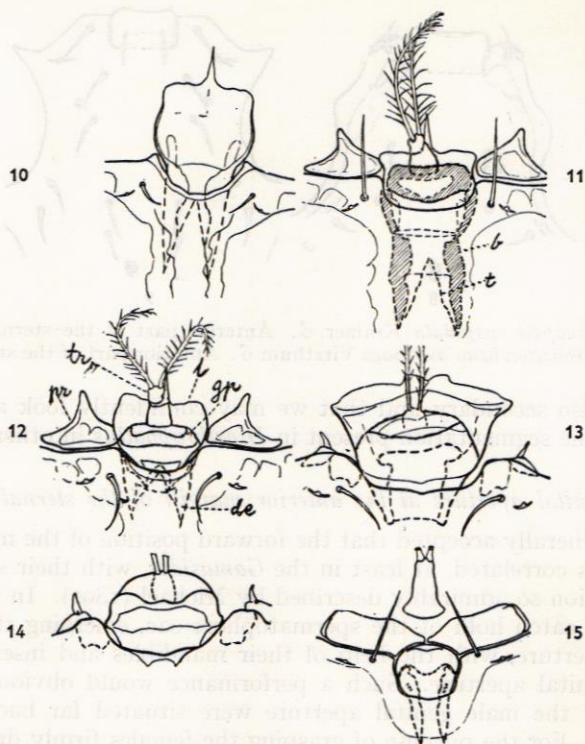


Fig. 10. *Pergamasus* sp. ♂. Genital plate, ductus ejaculatorius and anterior margin of sternal shield. — Fig. 11. *Pergamasus longicornis* ♂. Tritosternum, genital plate, ductus ejaculatorius and præendopodal shields. — Fig. 12. *P. brevicornis* ♂, same parts as in fig. 11. — Fig. 13. *Ologamasus pollicipatus* ♂, same parts as in fig. 11. — Fig. 14. *Ol. pollicipatus* ♂. Top of ductus ejaculatorius. — Fig. 15. *Digamasellus* ♂. Same parts as in fig. 11—13. *tr* tritosternum; *pr* præendopodal shield; *l* lamina; *gp* genital plate; *de*, ductus ejaculatorius; *b* the thickened walls of the ductus ejaculatorius; *t* tongue-shaped organ.

of almost the same shape as in *C. cuspidata* but smaller. Ductus ejaculatorius present, very short and wide, extending forwards to the middle of the genital plate.

In these two genera neither the second pair of legs nor the mandibles show any special adaptations such as occur in the *Gamasides*. Nothing is known about their mode of copulation but it seems certain that it cannot be performed in the same manner as in the *Gamasides*. The only conclusion that can be drawn at present is that in the *Celaenopsidae* there must be other reasons, as yet not understood, for the forward position of the male genital aperture.

If we dissect the structures surrounding the genital aperture and the ductus ejaculatorius of *Pergamasus brevicornis* or *longicornis* we notice the following features (Figg. 10—13). The anterior margin of the sternal shield has a short and broad incision flanked by the triangular præ-endopodal plates (pr). In this incision a transverse shield (gp) is attached on the dorsal side of which the tritosternum is situated (tr). This plate I unhesitatingly homologize both with the genital plate of *Celaenopsis* and with the epigynial shield of the female. Further we notice a very thin, transparent lamina (l) which I at first believed covered the genital plate. But repeated dissections disclosed the fact that this lamina is the continuation of the ventral wall of the ductus ejaculatorius (Fig. 10).

I have been unable to find this structure mentioned in the literature although Berlese has delineated it in some *Ologamasus* (1905, Fig. 13 & 14). It is not easy to recognize these organs in the description of *Parasitus kemperi* Oudemans given by Neumann (1941, p. 661, fig. 22) Neumann delineates and describes a sagittal section through a male. According to him the top of the ventral wall of the ductus ejaculatorius is claviform in shape («kolbenförmig»). This organ cannot but be the same as the lamina described above although it is of a quite different shape. N. does not figure nor mention the genital plate nor the tritosternum, but in front of what he calls «Verbindungsfalte zwischen Cuticula und Kolben» one sees a thin plate the position of which corresponds to that of the genital plate described by me. It would have been easier to understand Neumann's description if he had combined the sectioning with dissections.

The presence of the tritosternum on the genital plate is very remarkable because it means that in the male this organ is situated *behind* the genital aperture whereas in the female it is placed *in front* of it. But repeated dissections have made it quite clear that this is really the case.

If we dissect the ductus ejaculatorius, detaching it gently from the sternal shield and the genital plate, and turn it upside down so that we inspect it from the dorsal side we notice that the base of the lamina at the sides continue backwards, sending out two longitudinal, strongly chitinized, gradually tapering bars (Fig. 11 (b)) which belong to the dorsal wall of the duct. The anterior part of this structure has a distinct, transverse suture, a kind of segmentation, and on both sides of the mouth of the tube there is a fringe of very fine, hyalin appendages, directed backwards. In the wall of the tube there is a narrow, tongue-shaped appendage directed forwards (fig. 11, t).

In *Ologamasus* (Figg. 13—14) we notice on dissecting that the lamina is well developed, with straight lateral edges and a very thin anterior edge. As in *Pergamasus* it covers the orifice of the ductus ejaculatorius. The tritosternum is firmly attached to the genital plate.

In *Digamasellus* (Fig. 15), on the other hand, the tritosternum is

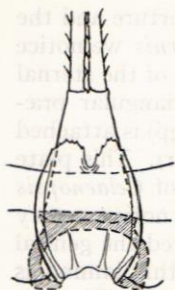


Fig. 16. *Heterozercion audax* Berlese ♂. Base of tritosternum, genital plate and lamina.

placed distinctly in front of the genital aperture. The genital plate is well developed, almost circular and fits into a deep incision at the anterior margin of the sternal shield, behind the præendopodal shields. No lamina has been found.

In *Heterozercion audax* Berlese (Fig. 16) the genital plate is very peculiar, being shaped as an oval, elongated shield which extends forwards to the middle of the tritosternum and has a deep, anterior incision; it is very thin and transparent and covers nearly the whole base of the lamina which is shaped as a kidney in outline and has its wall strengthened by a couple of radiating bars.

B. Genital aperture in the sternal shield.

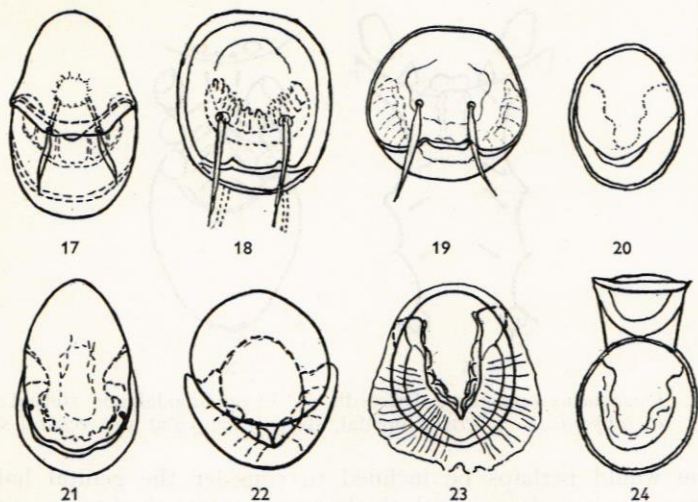
If the conception regarding the phylogeny of the *Mesostigmata* as outlined by me is valid (comp. Trägårdh 1946 b, p. 31) it follows that the position of the male genital aperture in the sternal shield distinguishes several groups which are not at all related to one another, viz. the *Agynaspida*, embracing the *Megisthanina*, the *Liroaspidina* and the *Microgyniina*, as well as the *Uropodina* and the *Fedrizziina* beside the small, isolated groups, the *Zerconina* and the *Thinozercionina* of which latter group no material of the males has been available for this investigation.

The first thing that becomes evident when one makes a comparison between the genital apertures and armatures of the forms which have it placed in the sternal shield is that Berleses' statement (1905, p. 15): »Maris foramen genitale in medio sterno apertum» is very far from the truth. As a matter of fact, the only general statement that can be made regarding these forms is that the male genital aperture is *not* situated at the anterior margin of the sternal shield.

Thus in *Liroaspis* it is situated fairly close to the anterior margin of the sternal shield, in the *Microgyniina* it is placed far backwards between coxae III and IV. In *Trachytes* it is placed on a level with the posterior side of coxae IV, in *Discopoma* between coxae IV, in *Trematura patavina* between coxae II and III and in the *Prodinychidae* a little behind a line drawn between coxae III and IV.

The minute examination of some genera of *Uropodina* reveals the fact that there are at least two different types of genital apertures.

In *Cilliba*, *Oodinychus* and *Phyllodinychus* (Figs. 20, 21 & 22) the aperture is almost completely closed by an operculum which is attached to the anterior edge of the orifice and becomes detached very easily after maceration in lactic acid. The actual opening is a semicircular slit along the posterior half of the margin. After the operculum has been removed we notice in the posterior half of the opening thus laid bare a



Male genital apertures.

Fig. 17. *Phaulodinychus* sp. — Fig. 18. *Trachyuropoda* sp. — Fig. 19. *Discopoma romana*. — Fig. 20. *Fuscouropoda* sp. with closed operculum. — Fig. 21. *Cilliba cassidea*. — Fig. 22. *Oodinychus thorianus*. — Fig. 23. *Phyllodinychus tetrphyllus* with operculum removed. — Fig. 24. *Fuscouropoda* sp. with operculum wide open.

horse-shoe-shaped bar the ventral side of which is densely clothed with small, acute projections. This feature is very conspicuous in the genera just mentioned.

In *Discopoma*, *Phaulodinychus* and *Trachyuropoda* (Figg. 17, 18 & 19), on the other hand, there is no such operculum, the aperture being a transverse slit between a larger anterior plate and a smaller posterior one. In the entrance to the ductus ejaculatorius covered by these structures we notice the horseshoe-shaped bar of *Cilliba* a. o. genera.

It is at our present, very deficient state of knowledge extremely difficult to know how to interpret these structures and one must content oneself with mere conjectures. The presence in *Discopoma* of both the two plates and the bar seems to exclude the possibility of the latter being homologous with the posterior of these plates in those genera where it has disappeared.

The operculum of *Cilliba* a. o. genera has no counterpart in the *Gamasides*. It is not astonishing that it is associated with the absence of the posterior lip which is not longer necessary for the closing of the aperture, its function being performed by the operculum alone.

The most remarkable feature of *Discopoma* and also of *Phaulodinychus* is, however, the presence of a pair of well developed hairs on the anterior plate (Figg. 17—19).

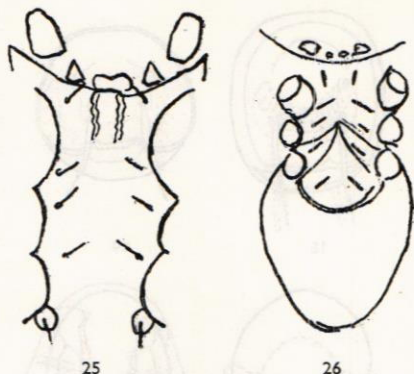


Fig. 25. *Pergamasus lapponicus* Trägårdh ♂. Præendopodal and sternal shield.
 Fig. 26. *P. lapponicus* ♀. Præendopodal, sternal, epigynial and ventral shields.

One would perhaps be inclined to consider the genital hairs of *Discopoma* as homologous with the hairs present on the female epigynial shields of so many *Gamasides*. But two arguments may be brought forwards against such an assumption. One is that in the males the hairs occur on the plate *in front* of the aperture whereas the female epigynial shield with its hairs is situated *behind* the genital aperture. The other argument is that if we count the number of hairs present in the intercoxal portion of a male and female of the *Gamasides* we find in both sexes five pairs of hairs, viz. the four sternal hairs and the genital hair. This is f.i. easily demonstrated in *Pergamasus lapponicus* (Figs. 25—26) where in the male the last pair of hairs, inserted near the posterior margin of coxae IV on a small, semidetached shield, is without the slightest doubt homologous with the genital hairs of the female.

For these two reasons the two hairs of the male of *Discopoma* cannot be homologous with the genital hairs of the *Gamasides*.

It may of course be argued that the hairs are a new departure, a structure *sui generis* and that it is waste of time to try to trace their origin. But the recent minute investigations regarding the origin and phylogeny of the different types of organisation of the female ventral shields have been based on the assumption that there is nothing fortuitous about the hairs which, on the contrary, show a very remarkable persistence on the shields to which they belong, even when the shields themselves have become almost or quite obliterated through a retrogressive development. The fact that this way of reasoning — that the primitive type of organization was four pairs of sternal shields, each with one pair of hairs — led to the discovery of the fate of the metasternal shields in the

Uropodina may be considered to have conclusively clenched this argument (comp. Trägårdh 1942).

This being the case the question arises whence these hairs come. The following facts may be marshalled in order to throw light on this very intricate problem. The original position of the tritosternum and of the præsternal hairs is in front of the sternal shield from which they are often separated by a strip of soft cuticle. And as the original position of the male genital aperture is somewhere between coxae III and IV both organs were originally removed very far from one another. But in those forms where the male genital aperture has secondarily moved forwards to the anterior edge of the sternal shield the tritosternum became, at least in some genera, topographically so intimately associated with the sclerites surrounding the genital aperture that on dissecting it remains attached to the genital plate (comp. figg. 11—14).

It seems conceivable that in this way the præsternal hairs became associated with the genital aperture as the genital hairs of the *Uropodina*. Granted this we are, however, forced to draw a very sweeping conclusion which the facts so far known admittedly do not seem to permit, viz. that in the *Uropodina* the present position of the male genital aperture in the sternal shield is not a primitive feature but that the *Uropodina* are descendants from ancestors which had the genital aperture at the anterior margin of the sternal shield. This assumption is, moreover, quite in accordance with the fact that the *Uropodina* through forms such as the *Trachytidae*, the *Polyaspidae* and the *Polyaspinidae* — as regards the metasternal shields — have descended from some primitive *Gamasides* with distinct metasternal shields in which possibly the male genital aperture was præsternal. Hence we are forced to assume that the genital aperture has altered position twice, the first time forwards, the second time backwards to its original place, which admittedly is highly conjectural. It is, however, the only hypothesis which can explain the presence of a pair of hairs on the genital plate in *Discopoma* and other *Uropodina*.

It may of course be argued that such a development is contrary to Dollos' law of the irreversibility of development. But this law only states that if an organ, having a certain function, becomes rudimentary it can never develop again but, if need arises for such an organ, it develops from some other part of the body. Hence Dollos' law does not apply in this instance because there is no question of any retrogressive development of an organ, the only change having taken place being the moving of the aperture from somewhere in the middle of the sternum to its anterior margin. And the fact that this change has taken place once may evidently be used in favour of its having taken place once more albeit in an opposite direction.

Genital hairs having been discovered in *Discopoma*, *Phaulodinychus* and *Trachyuropoda* it was natural that they were looked for also in

other genera. So far they have only been discovered in *Cilliba* where they are very small (Fig. 20) and in *Épicrius* (Fig. 29). In *Phyllodinychus* and *Oodinychus* they have not been found, being either quite reduced or too small to be seen.

The remaining genera investigated belong to five different groups, viz. the *Megisthanina*, *Liroaspina*, *Microgyniina*, *Fedrizziina* and *Diarthrophallina*.

Of these the genus *Diarthrophallus* (Fig. 27) has a very isolated position both on account of the presence of præsternal hairs and its large, biarticulated penis which is directed backwards and not separated from the surrounding cuticle by any suture at the base. Moreover it has a pair of elongated acute appendages on both sides of the terminal joint, the function of which is probably to fix the penis within its groove.

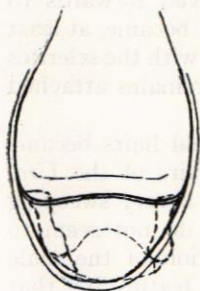


Fig. 27. *Diarthrophallus quercus* Pearse & Wharton. Penis.

The structure of the other genera is rather difficult to understand without sectioning them, because the organs are too small to be dissected. Hence it is sometimes very difficult to tell whether the aperture, is situated between the two plates or if the structure is a biarticulated plate, attached to the anterior side of the opening in which case the opening is a semicircular slit along the posterior margin of the posterior plate.

Hitherto we have made the acquaintance of four types of genital apertures and surrounding structures.

1. In the *Gamasides* the orifice is protected both by a plate which was interpreted as the genital plate, homologous with the epigynial plate of the female, and by a thin lamina which is a projection from the ventral edge of the ductus ejaculatorius. This type is highly specialized and differs profoundly from the other types.

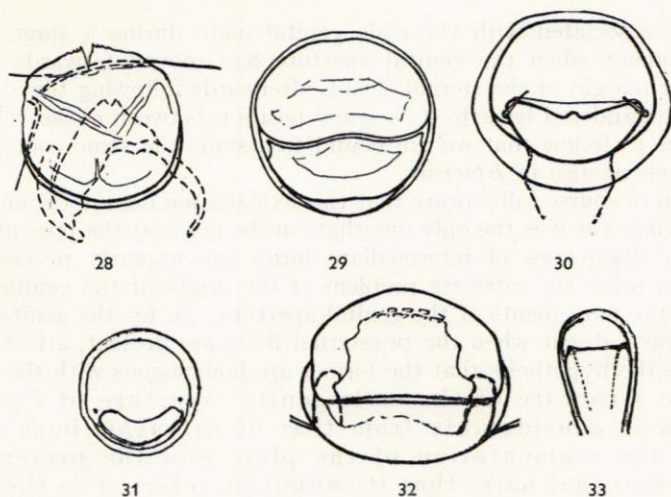
2. In the more primitive *Uropodina*, such as *Discopoma* and *Trachy-uropoda*, the aperture is a transverse slit between two plates which have no counterparts in the *Gamasides*.

3. In the more specialized *Uropodina* the anterior plate has developed into an operculum, closing the whole aperture, the posterior plate being correspondingly reduced.

4. In *Diarthrophallus* there is an biarticulated penis, directed backwards and fitted into a groove.

Let us now see whether the remaining genera may be referred to any of these types or represent other types.

In *Liroaspis togatus* (Fig. 28), one of the genera unanimously considered to be one of the most primitive forms, we notice an almost circular opening surrounded at the anterior side by a very low, collar-shaped fold of the surrounding cuticle and closed by a plate which is attached to



Male genital plates.

Fig. 28. *Liroaspis togatus* K. — Fig. 29. *Megisthanus* sp. — Fig. 30. *Epicrius mollis* Kr. — Fig. 31. *Zercon* sp. — Fig. 32. *Paramegistus confrater* Trägårdh. — Fig. 33. *Microgynium rectangulatum* Trägårdh.

the margin in the anterior half, leaving open a narrow, semicircular slit along the posterior margin. Below the surface the outline of a chitinous structure, resembling an half-open forceps, is visible. It may be argued that this structure resembles the operculum of the *Uropodina* but the resemblance is only superficial because in *Liroaspis* the plate is firmly coalesced along the anterior half of the margin of the aperture which must make the plate very rigid except at the posterior edge which may be bent slightly downwards owing to the elasticity of the thin plate.

In *Microgynium* (Fig. 33) we notice the following features. There is undoubtedly a kind of penis although much smaller than in *Diarthrophallus* and pointing forwards instead of backwards. But it is not articulated and is cut off transversally at the top; in front of the penis there is a small, semicircular plate, completely coalesced with the margin of the aperture.

In *Epicrius mollis* (Fig. 30) the genital aperture is closed by a biarticulated plate. The anterior plate is much larger than the posterior one, the base of which it embraces with its projecting angles which have a pair of small but very distinct hairs pointing obliquely forwards and towards the median line. The slit is thus situated along the posterior margin of the opening.

The presence of genital hairs in *Epicrius* is very puzzling. Because if the hypothesis set forth above is true that these hairs are homologous with the præsternal hairs of *Megisthanus* and other genera and that they

became associated with the male genital plate during a stage in the development when the genital aperture had moved forwards to the anterior margin of the sternal shield, afterwards following the aperture when it wandered back to its original position between coxae III, then it seems to follow that we are bound to assume the same complicated development also in *Epicrius*.

I am of course fully aware that this explanation does not sound very convincing, yet it is the only one that can be made at the present time. Further discoveries of intermediate forms are urgently necessary in order to solve the intricate problem of the origin of the genital hairs and of the movements of the genital aperture. So far the genital hairs are always absent when the præsternal hairs are present, a fact which favours the hypothesis that the former are homologous with the latter.

The structure of the male genital aperture of *Epicrius* differs so considerably from that of *Liroaspis* both as regards the segmentation of the plate and the presence of the præsternal hairs that it cannot be referred to the same systematic unit.

Megisthanus (Fig. 29), representing the cohors *Megisthanina*, is of very great interest because the presumably primitive feature, the well developed præsternal hairs, are very conspicuous in this genus for which reason it was first noticed here by the older acarologists who, however, failed to understand the significance of the feature. The structure closing the genital aperture seems to be built after the pattern of the more primitive *Uropodina* with the exception that there are obviously no genital hairs since, if my assumption is true, these persist as præsternal hairs on both sides of the tritosternum. We notice two plates, one larger, anterior and one smaller posterior, the genital aperture being a narrow, transverse slit between the two plates.

In *Paramegistus* (Fig. 32) it is easy to discern the joint between the two plates, the aperture being a semicircular slit along the posterior margin.

In the *Zerconina* (Fig. 31) the aperture resembles very much that of *Epicrius* (Fig. 28). It is closed by a large plate which is fused with the margin at the base and the sides and has a small, transverse, semilunar plate hinged to its posterior margin. In the posterior angles of the basal plate we notice two small points which may be the greatly reduced genital hairs.

In *Thinozercon* Halbert (1915, p. 82—83, pl. VII, Fig. 26 b) describes the aperture in the following way: »the genital foramen is a small, circular aperture between the third legs; it is protected by two minute, semicircular plates with thickened outer margins; the first of these carries a pair of stout bristles.» Hence the aperture resembles very much that of *Discopoma* and other *Uropodina*. This is a very important fact, linking the genus to that group.

3. Summary of the results.

The investigations have yielded the following results.

The præsternal hairs.

Præsternal hairs, situated on both sides of the tritosterum, are presumably a primitive feature. Previously they were only known in the *Megisthanina*. Now they have been found both in the *Diarthrophallina*, the *Euzerconidae* and the *Diplogyniidae*.

The male genital aperture and its structures.

The hitherto prevalent opinion of the acarologists that the structure of the male genital aperture was very simple is quite unfounded. The truth is that even this short investigation has disclosed several new structures some of which are very puzzling. Further extensive researches combined with anatomical investigations are necessary before it will be possible to arrive at a satisfactory solution of these problems.

Genital aperture præsternal.

The three groups characterized by the præsternal position of the male genital aperture, viz. the *Gamasides*, the *Celaenopsidae* and the *Euzerconidae* (with the closely related *Diplogyniidae*) are not related to one another. In the *Gamasides* this feature is undoubtedly correlated with the secondary adaptation of the mandibles and the second pair of legs for the purpose of copulation. In the other groups there are no such adaptations and although it cannot be doubted that also in these groups the præsternal position of the genital aperture is a secondarily acquired character yet this development must have been quite independent and caused by other factors, as yet quite obscure, than in the *Gamasides*.

The failure to find any præsternal hairs in the *Celaenopsidae*, while they are very conspicuous in the *Euzerconidae* and the *Diplogyniidae*, and the presence of a genital plate, homologous with that of the *Gamasides* makes it doubtful whether the *Celaenopsidae* are related to the *Euzerconidae*.

Genital aperture in the sternal shield.

In a previous paper (1946 a) the author has endeavoured to draw the outlines of a new classification of the *Mesostigmata* based on the organization of the ventral shields of the females. The group was divided into two main groups, the *Agynaspida* with no epigynial shield yet developed and the *Eugynaspida* with an epigynial shield. To the *Agynaspida*, which was considered as the more primitive group, was referred the *Liroaspina* with the two families *Liroaspidae* and *Epicriidae*, the

Microgyniina with the two families *Microgyniidae* and *Microsejidae* and the *Megisthanina*. To the *Eugynaspida* the following groups were referred: *Thinozerconina*, *Zerconina*, *Gamasides*, *Trachytina*, *Uropodina*, *Celænopsina*, and *Fedrizziina*.

It would of course be very fortunate for the systematist if the examination of the exoskeleton of the males would yield results which permitted the same division. Surveying the different types of genital apertures of the males one is, however, very forcibly struck by the impression that the development in different directions has at least sometimes been quite independent of the relationship manifested in other organs.

Thus the *Liroaspina* and the *Microgyniina* agree completely in several fundamental respects, such as the presence of several dorsal shields, traces of segmentation of the sternal shield and the entire absence of secondary sexual adaptations of the mandibles and of the second pair of legs of the males. But the male genital apertures are of quite different types in the two groups, viz. in the *Microgyniina* closed by a tongue-shaped plate directed forwards and not separated from the surrounding cuticle at its base, whereas in the *Liroaspina* the orifice is a semicircular fissure along the posterior edge of the genital plate which is else completely soldered to the margin of the aperture.

The only conclusion that can be drawn at the present time from these facts is that this organ must possess a great adaptability, presumably connected with the different ways of copulation. But as, unfortunately, for the time being, nothing is known of this part of the biology the very foundation is missing on which an understanding of these adaptations must necessarily be based.

For this reason it is most prudent not to expect much guidance into an understanding of the phylogenetic development of the group from the study of the male genital apertures. Because an organ which is prone to secondary adaptation is obviously ill fitted to act as a beacon in such matters. For the same reason it is not always possible to know for certain which forms of closing the aperture are more primitive and which are more specialized.

Very extensive researches embracing a great number of different genera, the anatomy and the mode of copulation of which must also be investigated, are necessary before it will be possible to substitute inferences by solid facts.

In the light of the fact that not less than four different types of male genital apertures occur in the *Agynaspida* one is sorely tempted to doubt whether this group is as «natural» as one could wish. Two results have, however, been the fruits of the present investigation. One is that the establishing of a distinct cohort for the two families *Microgyniidae* and *Microsejidae* was well founded. The other is that the genus *Epicrius* with its bisegmented genital plate and its one pair of hairs on the

basal joint cannot be referred to the *Liroaspina* but must be considered the representative of a special cohors, the *Epicriina*.

If we assume that in the ancestral *Mesostigmata* the mechanism of closing the male genital aperture was the same as that of the females viz. by a projection from the ventral shield, not separated from the ventral shield by a suture at the base, then this stage may be said to exist in principle in the *Microgyniina* (Fig. 31). But in this group there is also an anterior plate, albeit is completely fused with the walls of the aperture, and in my opinion this structure is not primitive.

In *Discomegistus* (Fig. 34) a plate exists which is articulated at the base and actually resembles a small female epigynial shield. This feature is probably primitive and is the more extraordinary as the genus, living on large *Julidae* in Trinidad, is in other respects highly specialized and adapted to this peculiar mode of living (Trägårdh 1911).

Such a genital plate has also been found in several *Gamasides* f.i. *Pergamasus* (Fig. 11) *Ologamasus* (Fig. 14) and in the *Celaenopsidae* (Figg. 8 & 9). It has not been possible to ascertain its presence in the *Euzerconidae* and *Diplogyniidae*, these structures being completely hidden by the protruding edge of the sternal shield and hence difficult to examine.

In *Pergamasus* and *Ologamaus* the projecting ventral edge of the ductus ejaculatorius is shaped as a thin lamina which apparently is a special structure to which no counterpart has hitherto been found in other genera.

Such a genital plate, more or less articulated at the base and fitted into an incision at the anterior margin of the sternal shield has not been found in any other groups. At least it seems very doubtful whether the posterior plate sometimes present in those forms which have the genital aperture in the sternal shield is homologous to this plate because in the genera mentioned above the plate is attached *behind* the aperture while in the others it is an integrating part of the very wall of the orifice.

As emphasized above it is not safe to draw any conclusions regarding the more or less primitive nature of the genital aperture from the organization in other respects. If it were as simple as that we might content ourselves with saying that *Liroaspis*, being admittedly the most primitive genus amongst the *Mesostigmata*, must also have the male genital aperture of the most primitive type. On the contrary I am fully convinced that such a way of reasoning is quite wrong. How deplorable this state of things may appear we must face the facts and restrict our-

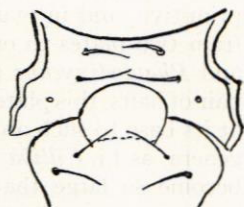


Fig. 34. *Discomegistus pectinatus* Trägårdh ♂. Sternal and genital shield (after Trägårdh).

selves to some conjectures regarding the possible lines of divergent evolution.

The male genital aperture must obviously be build so as to serve two different purposes, on one hand to let through the sexual discharge and on the other hand to lock the aperture firmly when it is not functioning. The simplest way to solve this problem seems to be a transverse fissure between an anterior and a posterior lip, both either articulated at their base and movable through special muscles or fused to the walls of the orifice, the lips being opened slightly owing to the elasticity of the thin cuticle.

This type of genital aperture occurs in the *Megisthanina*, a cohors which as regards the well developed præsternal hairs must be considered primitive, and in many *Uropodina*. Within that cohors a development from two plates to one has taken place. In *Discopoma*, *Trachyuropoda* and *Phaulodinychus* (Figg. 17 & 19), in which the anterior plate has a pair of hairs, this plate has increased in size considerably and is articulated at its base to such an extent that it can be opened 90° degrees. In other genera, as f.i. *Cilliba* (Fig. 21) and *Fuscouropoda* (Fig. 24), the plate has become so large that it closes the whole opening, the posterior plate being correlatingly reduced or even quite abortive.

If, on the other hand, the anterior plate increases in size but coalesces with the wall of the orifice except along the posterior margin this is the type represented by *Liroaspis*.

Finally the anterior plate develops to such an extent that it covers completely the genital aperture. But at the same time the posterior part of it has become detached as a special plate through a transverse joint. This type has so far been found in the *Fedrizzina*, the *Epicriina* and the *Zerconina*.

From the types described above, which are all ringshaped, the *Microgyniina* and *Diarthrophallina* differ profoundly in not being ringshaped but formed as an open loop. This common feature does not, however, indicate any close relationship between the two groups because the *Diarthrophallina* have undoubtedly a real, biarticulated penis directed backwards while in the *Microgyniina* the opening is closed by a thin, unsegmented plate directed forwards.

The main result of the investigations regarding the structure of the male genital aperture is that not less than eleven different types have been found which is as many as the main groups recognized by me. Further discoveries of new genera and groups will presumably also increase the number of different types and will undoubtedly reveal the existence of intermediate types which may facilitate the understanding of the different trends of evolution.

As emphasized above (57) it is essential not only that the different modes of copulation be studied but also anatomical researches carried out.

One feature is, however, so conspicuous that at least a tentative conclusion may be drawn from it. In most of the genera in which the aperture is situated in the sternal shield the fissure is placed along the *posterior* margin of the structure. This feature seems to be correlated with the fact that the female genital aperture is at the anterior and either of the epigynial shield or of the other shields, functioning as such. These two facts seem to permit only one conclusion, that the sexes when copulating are turned in opposite direction with head to tail.

4 Synopsis of the different types of genital apertures.

A. Aperture in the sternal shield.

I. Aperture ring-shaped.

a. Aperture closed by a single plate.

x. Plate hinged to ventral shield along its posterior margin

Discomegistus.

xx. Plate completely fused with the wall of the orifice in the anterior half, leaving open a semicircular fissure along the posterior margin.....

Liroaspis.

xxx. Plate articulated along its anterior margin

Uropodina.

b. Aperture closed by two plates between which there is a transverse fissure.....

Megisthanus, some *Uropodina*.

c. Aperture closed by a biarticulated plate, attached at the anterior margin

Thinozerconina, *Zerconina*, *Epicriina*, *Fedrizzina*.

II. Aperture not ring-shaped.

y. Plate biarticulated, directed backwards

Diarthrophallina.

yy. Plate not segmented, directed forwards...

Microgyniina.

B. Aperture præsternal.

I. Genital aperture protected both by a genital plate and a lamina. Mandibles and legs II with special adaptations for copulation purpose. No præsternal hairs.....

Pergamasus, *Ologamasus*.

II. Aperture protected only by genital plate. No adaptations of legs II or mandibles. No præsternal hairs.....

Celaenopsidae.

III. Aperture situated above protruding edge of sternal shield.

Præsternal hairs present.....

Euzerconidae, *Diplogyniidae*.

Bibliography.

- Berlese, A. Acari, Myriopoda et Scorpiones hucusque in Italia reperta. Ordo Mesostigmata. — Padua 1882—1892.
- Monografia del' Genere Gamasus Latr.-Redia, vol. I, fasc. 2. 1904.
- Kramer, P. Ueber zwei von Herrn Dr. F. Stuhlmann in Ostafrika gesammelte Gamasiden. — Beiheft z. Jahrb. d. Hamb. wiss. Institut, XII.
- Michael, A. D. On the variations in the internal anatomy of the Gamasinae, especially in that of the genital organs, and on their mode of coition. — Trans. Linne. Soc. of London, vol. 5. 1892.
- Neumann, K. H. Beiträge z. Anatomie und Histologie von Parasitus Kempersi Odms. — Zeitschr. f. Morphologie und Ökologie d. Tiere, Bd. 37, H. 4. 1941.
- Oudemans, A. C. On a new genus and species of parasitic Acari. — Notes from the Leyden Mus. vol. XXIV, no. VIII. 1905.
- Acari of New Guinea.
- Trägårdh, I. Discomegistus, a new genus of myriopodophilous Parasitidae from Trinidad. — Ark. f. zool. Bd. 7, N:o 12. Stockholm 1911.
- Further contributions towards the comparative morphology and classification of the Mesostigmata. Ent. tidskr. 1938.
- Further contributions towards the comparative morphology of the Mesostigmata. Where are the metasternal shields of the Uropodina? — Ark. f. zool. Bd. 34 A, N:o 3. 1942.
- Microgyniina, a new group of Mesostigmata. — Ent. Tidskr., Årg. 63, h. 4—5. 1942.
- Further contributions towards the comparative Morphology of the Mesostigmata, VI. The Antennophoridae and the Mesostig Megisthanidae. — Ark. f. zool., Bd 34 A, N:o 20. 1943.
- Outline of a new classification of the Mesostigmata, based on comparative morphological data. — K. Fysiogr. Sällsk. Handl. N. F. Bd. 57. Nr. 4. Lund 1946 a.
- Diarthrophallina, a new group of Mesostigmata, found on Passalid beetles. — Ent. Medd. Bd. 30. 1946 b.