

NOTES ON MACROCHELIDS ASSOCIATED  
WITH MANURE AND COPRID BEETLES IN ISRAEL.  
I. *MACROCHELES ROBUSTULUS* (BERLESE, 1904),  
DEVELOPMENT AND BIOLOGY.<sup>1</sup>

BY

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INTRODUCTION.

Owing to their possible function in the control of flies, and the interest taken in this by the health authorities, the Macrochelidae have received much attention in recent times. Sound taxonomic revisions of any group stimulate workers in various countries to develop their interest in this particular group. The macrochelids have been dealt with taxonomically by EVANS (1956), EVANS and BROWNING (1956) and EVANS and HYATT (1963) in the United Kingdom; by KRANTZ (1960, 1962) in the U.S.A.; by BREGETOVA and KORELOVA (1960) in the U.S.S.R. These taxonomic works form the basis of taxonomic work on the group by various workers.

FILIPPONI and his coworkers in Italy developed the system of "Experimental Taxonomy", summarized recently (FILIPPONI, 1964; further bibliography there). This school produced a large number of papers on the biology and ecology of various species as well as several taxonomic revisions of smaller groups (FILIPPONI and PEGAZZANO, 1960, 1962, 1963).

RODRIGUEZ and coworkers (RODRIGUEZ and WADE, 1962; WADE and RODRIGUEZ, 1961; RODRIGUEZ et al., 1962) were concerned mainly with nutritional requirements of *Macrocheles muscadomesticae*. AXTELL (1963 a, b) studied the role of the mites in the extermination of flies in manure.

This formidable background makes it possible to start to analyse the group geographically, and any additional information on the distribution of the species should be welcome. In a series of papers I intend to publish information concerning the macrochelids from Israel that are associated with manure and coprid beetles.

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Fam. MACROCHELIDAE.

*Macrocheles robustulus* (Berlese, 1904).

EGG : The egg is pearly white and has a smooth shiny shell. Its dimensions are  $275\ \mu$  length by  $190\ \mu$  width.

LARVA : The white larva is weakly sclerotized and no shields are discernable. The idiosoma is  $365\ \mu$  long and  $215\ \mu$  wide, it has well pronounced shoulders. The dorsum bears 14 pairs of simple setae. Ten pairs belong to the podonotal portion of the dorsum (namely i1-i5, z1, z2, s2, s5, s6) and four pairs are opisthonotal (Z2, Z3, S3, J5). Two additional pairs, S4 and S5 are ventrally inserted in the larva and move to the dorsum during ontogenetic development. The distribution and the relative lengths of the setae are shown in fig. 1. The tectum is bipartite (fig. 6).

The venter (fig. 2) bears the usual 3 pairs of sternal setae and two pairs of opisthogastric setae. The first pair of opisthogastric setae is minute. The non-functional anus is represented by a slit, the paranal setae are almost twice the length of the postanal seta. The tritosternum has an elongate base and short pilose laciniae.

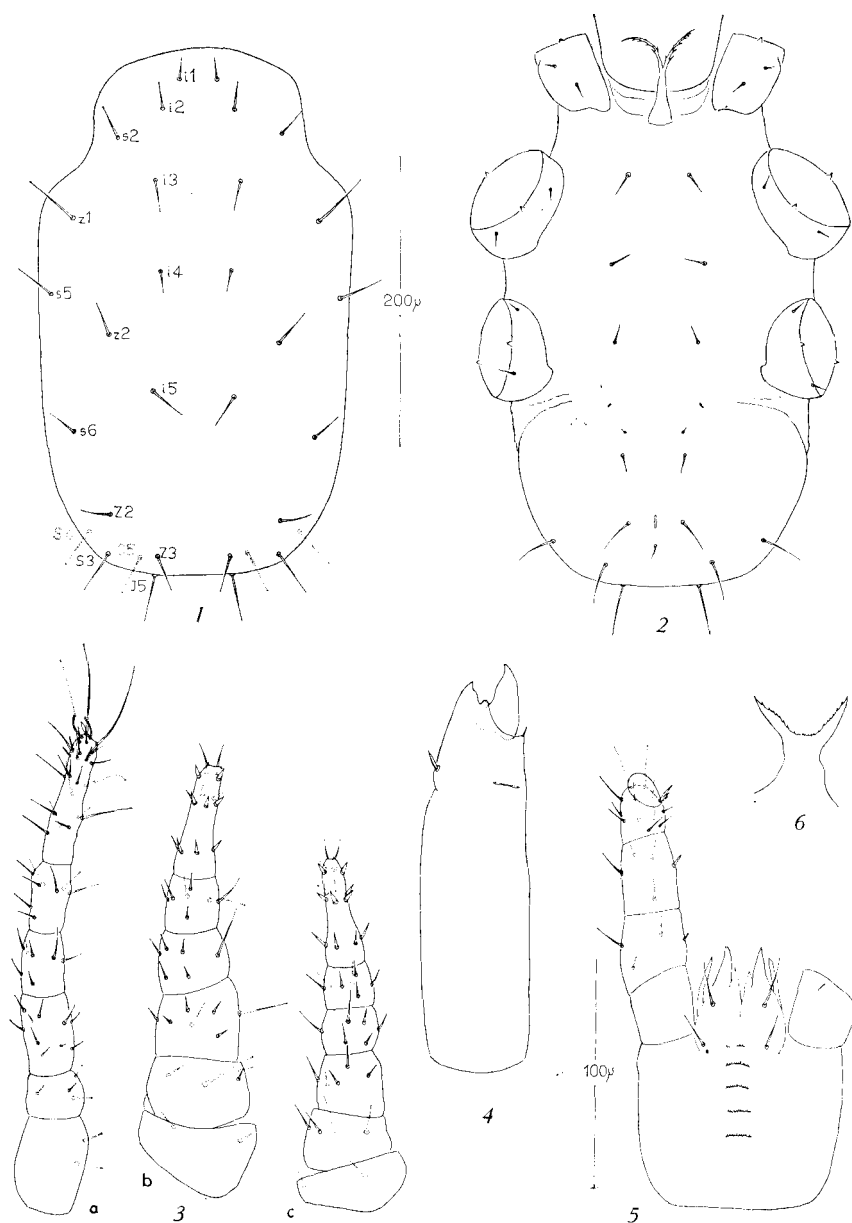
The gnathosoma (fig. 5) bears incompletely divided corniculi and internal malae, the salivary styli are rather broad and prominent. Five rows of minute deutosternal teeth are present. The chelicerae (fig. 4) are feebly sclerotized and apparently non-functional.

The legs (fig. 3 a-c) are short. Their approximate lengths (excluding pretarsi) are : I —  $330\ \mu$  ; II —  $300\ \mu$  ; III —  $245\ \mu$ . Tarsus I bears a number of distinct, hollow (?) sensory setae. The chaetotaxy of the legs will be discussed below.

PROTONYMPH : Although the protonymph is only weakly sclerotized, its two dorsal shields are easily defined. The podonotal shield is  $220\ \mu$  long and  $210\ \mu$  wide, it bears 11 pairs of simple setae (r1 is added). Four additional pairs of podonotal setae (namely r4, r5, r7 and s7) are inserted on the lateral soft integument. The narrow opisthonotal shield is  $140\ \mu$  long and  $135\ \mu$  wide, it bears 8 pairs of setae : two pairs (S4, S5) which are ventrally inserted in the larva have moved to the dorsum and 2 pairs (Z1, J2) are added at this stage. The postero-marginal setae are pilose, except setae J5 which are short and smooth (fig. 7). Setae S1 and S2 are also added at this stage, but they are inserted on the soft integument. The tectum is shown in fig. 10.

The sternal shield (fig. 8) is irregularly shaped, it bears 3 pairs of sternal setae. Five pairs of opisthogastric setae are distinctly longer than the post-anal setae. The rudimentary peritreme is situated opposite coxa III.

The gnathosoma (fig. 9) bears well sclerotized, elongate and slightly sinuous corniculi, the transparent internal malae seem to be smooth. Five rows of deutosternal teeth are present. The chelicerae (fig. 11) are well sclerotized, both digits are bidentate. The approximate lengths of the legs (excluding pretarsi) are :



FIGS. 1-6. — *Macrocheles robustulus*, larva.

1. Dorsum. 2. Venter. 3. a-c. Legs I-III respectively, dorsal view (pretarsi omitted).  
 4. Chelicera. 5. Gnathosoma, ventral view. 6. Tectum.

I — 345  $\mu$ ; II — 290  $\mu$ ; III — 245  $\mu$ ; IV — 345  $\mu$ . The leg chaetotaxy (fig. 12 a-d) is discussed below.

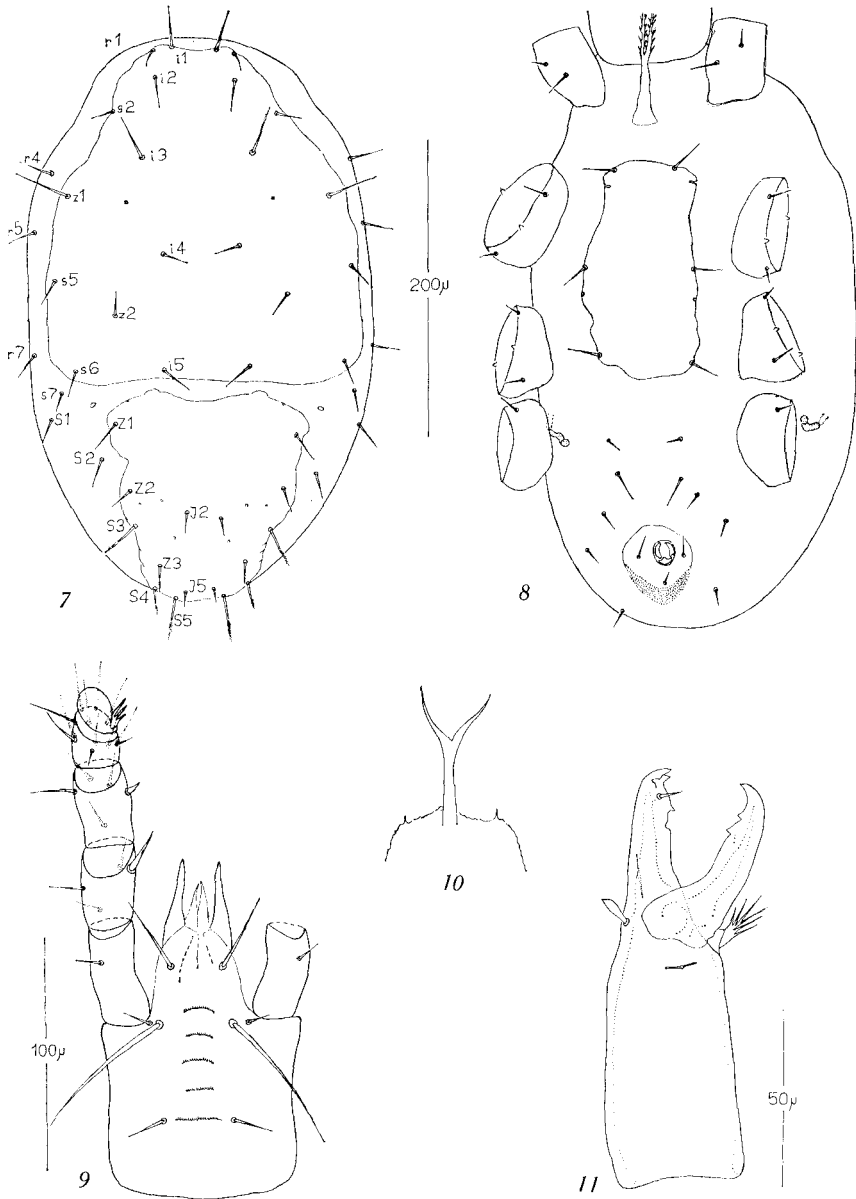
**DEUTONYMPH** : The deutonymph has a well defined, weakly sclerotized dorsal shield (fig. 14), wide incisions separate the podonotal and opisthonotal parts. The shield is 430  $\mu$  long and 245  $\mu$  wide (at the level of r5). The podonotal part of the shield bears 18 pairs of setae (r1, r3 and z3 are added at this stage and r4, r5, r7 and s7 which were inserted on the membrane in the protonymph, are now inserted on the shield). The opisthonotal part bears 10 pairs of setae, none are added at this stage, but S1 and S2 are now inserted on the shield. All the setae are simple, only S4, S5 and J5 are pilose. The tectum is shown in fig. 17.

The sternal shield (fig. 15) is well defined, it is widest just in front of the 2nd pair of sternal pores. The anal shield (fig. 16) is octagonal to sub-circular.

The gnathosoma is shown in fig. 19, the well sclerotized chelicerae (fig. 18) are practically identical with those of the protonymph. The approximate lengths of the legs (excluding pretarsi) are : I — 380  $\mu$ ; II — 325  $\mu$ ; III — 280  $\mu$ ; IV — 425  $\mu$ . Leg I bears mainly short setae whereas the setae of the distal segments of leg IV are rather long and pilose (fig. 13 a-d). The leg chaetotaxy is discussed below.

**FEMALE** : The female has been described and figured recently several times (EVANS & BROWNING, 1956 — under the name *Macrocheles rothamstedensis*; BREGTOVA & KOROLEVA, 1959 — under the name *Macrocheles punctillatus* Willmann; AXTELL, 1963) and the Israeli material agrees with these descriptions. The dimensions of the dorsal shield in our specimens are 710-770  $\mu$  length and 380-400  $\mu$  width. Setae i3, z1, r4 and Z3, S5 are distally pilose (fig. 20).

The “*sacculus foemineus*” : In well cleared specimens (cleared in Vitzthum's fluid), the sacculus foemineus and associated structures are clearly defined (figs. 21a, b). As the functions of these organs are still disputed (vide below), I shall retain the nomenclature coined by MICHAEL (1892), used in the excellent and detailed papers by WARREN (1940, 1941) and more recently by EVANS ((1963b). In *Macrocheles robustulus* the sacculus consists of two globe-like structures which are connected by a wide passage from which the *cornu sacculus* originates. The proximal part of the cornu is thick-walled (it is very similar to the “cervix” of the Phyto-seiidae) and from its apex arises a narrow duct which ends in a not clearly defined mass. Into each of the globes of the sacculus enters a *tubulus annulatus* which opens externally at the base of coxa III. At the junction with the sacculus the tubulus is slightly expanded and forms a small *ramus sacculus*. The tubuli annulati are much better defined than the narrow duct of the cornu, ring-like thickenings of the walls, however, could not be discerned. The sacculus foemineus is dorsally situated and during dissection of the cleared mite (separation of the dorsal shield from the venter) it is usually lifted with the dorsal shield. The natural orientation of the structure is with the cornu pointing to the venter. A schematic representation of the various structures (generally applying to gamasina possessing them) is shown in fig. 30.



FIGS. 7-11. — *Macrocheles robustulus*, protonymph.  
 7. Dorsum. 8. Venter. 9. Gnathosoma, ventral view. 10. Tectum. 11. Chelicera.

MALE : The male of *M. robustulus* has been described shortly but not figured, by EVANS and BROWNING (1956) under the name of *Macrocheles rothamstedensis*. The dorsal shield (fig. 23) is 610  $\mu$  long and 355  $\mu$  wide. All the setae are simple and needle-like, setae i3, z1, r4 and s6 are distinctly longer than the remaining dorsal setae.

The venter is covered by a holovertral shield (fig. 24) which bears 10 pairs of setae in addition to the anal setae. The shield is well ornamented with pores, similar to the ornamentation of the sternal shield in the female.

Five rows of deutosternal teeth are present on the gnathosoma (fig. 26). The corniculi are long and well sclerotized, the inner malae are membranous. The salivary styli are narrow. The chelicerae (fig. 25) has a tri-dentate fixed digit. The spermatophoral process tapers strongly, its length about equals that of the digit.

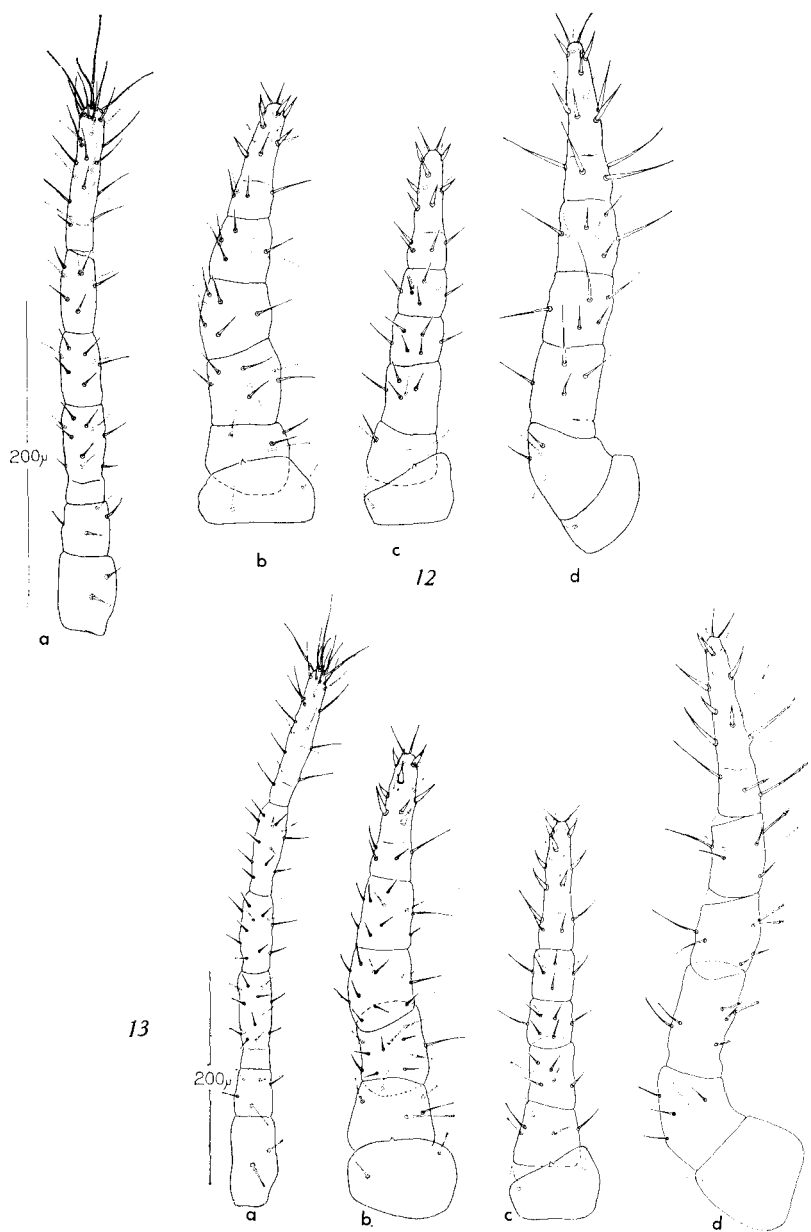
Leg II (fig. 28) bears a femoral thumb-like protuberance, short processes are borne by the genu and tibia respectively. Femur IV bears one lateral and one ventral spur (fig. 27).

#### BIOLOGY.

This species has been redescribed as *Macrocheles punctillatus* by WILLMANN (1939) who has collected it from cultures of *Enchytraeus albidus* (a soil annelid that is cultured in moist soil). This habitat is also mentioned by BREGETOVA and KOROLEVA (1959), who add *Onthophagus* sp. as host. EVANS & BROWNING (1956) have collected both males and females from bullock manure. AXTELL (1961) has collected it from cow and horse manure in the United States. I have collected *M. robustulus* from *Copris hispanus* (COSTA, 1963), and many specimens were collected from this beetle in laboratory cultures. I was keeping single beetles in culture jars with fresh manure and moist soil. These were checked monthly, when they were cleaned from mites and after that fresh manure was added. In one case as many as 104 females of *M. robustulus* were collected off a single beetle after one month. It seems that moist soil (which may be rich in nematodes and enchytraeids) is one of the factors needed for massive development of this mite.

In the laboratory I have reared the mites in plaster cells as described in an earlier paper (COSTA, 1966), they feed readily on nematodes of the genus *Panagrellus*.

COPULATION : Copulation has been observed frequently in the rearing cells. The male starts to chase the female deutonymph prior to its moult. Immediately after the female emerges, while she is still whitish and soft, the copulation starts. Up to a point, my observations agree with those of OLIVER & KRANTZ (1963) on *M. rodriguezi*, they state : " The male does not line up parallel to the female but is off to one side and tends to line up with the long axis of her body at approximately 45° angle ". The authors then assume that in this position the spermatophore is



FIGS. 12-13. — *Macrocheles robustulus*.

12. a-d. Legs I-IV respectively of the protonymph.

13. a-d. Legs I-IV respectively of the deutonymph. Dorsal view (pretarsi omitted).

placed into the genital opening of the female, pointing out "although this has not actually been observed". In cases observed by me the male stayed during the whole time of copulation aligned at an angle of 45° degrees to the long axis of the female. This embrace continued in several cases after my turning the female on her back with a soft brush. During the embrace leg IV of the female is firmly grasped by the front legs (legs I and II) of one side of the male. The chelicerae of the male are strongly pressed to the area of the external openings of the tubuli annulati between coxae III and IV. I have never seen a male trying to reach the female genital opening, moreover, I doubt if he could reach the female genital aperture from his position. A spermatophore has not been seen by me, nor has a spermatophore been described from any macrochelid to the best of my knowledge. I believe therefore, without being yet able to state this unequivocally, that non-vaginal insemination via the tubuli annulati is possible. The spermatophoral process of the male macrochelids seems nicely adapted to it. Copulation has been observed only between males and newly emerged females, I have never seen a male paying the slightest attention to a well hardened and sclerotized female.

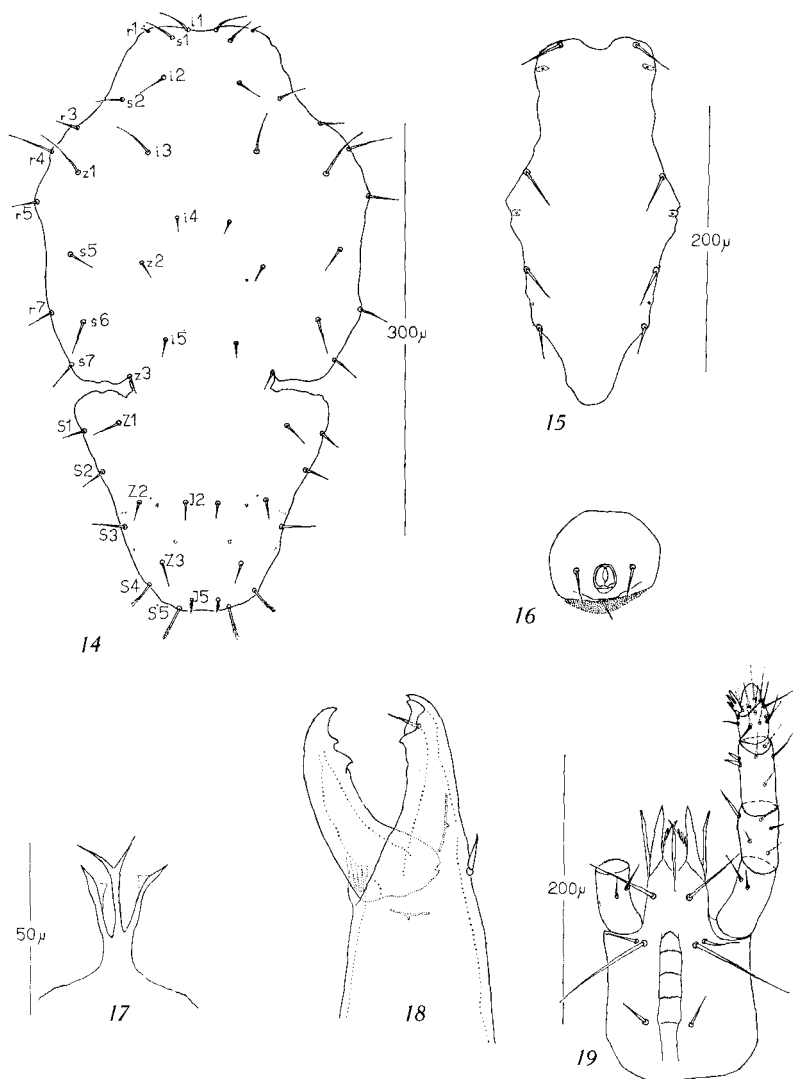
For rearing purposes, six females of unknown age were taken off *Copris hispanus* in the laboratory. Each mite was reared individually in a rearing cell, at room temperature. The results of the F<sub>1</sub> generation obtained thus is summarized in table 1. All the cultures were kept until the natural or the accidental death of the females.

TABLE I — The F<sub>1</sub> progeny of 6 females of *M. robustulus*  
(started at the 25th March).

Date of death	No. of days of observation	progeny		adults obtained	
		eggs	larvae	♂	♀
1. 18th April	24	4	2	3	1
2. 7th May	44	9	7	1	5
3. 19th April	25		2		1
4. 26th April	32	3	6	6	1
5. 8 th April	14	—	—	—	—
6 20th May	57	4	1	1	2

An inspection of the table shows that the females of *M. robustulus* have a longevity of at least 2 months, probably longer (during April the average room temperature is still rather low). A more interesting point is that although *M. robustulus* is arrhenotokous (FILIPPONI, 1964), females taken in nature produced males as well as females. My impression is that males became more abundant towards the end of the reproductive period of each female.





FIGS. 14-19. — *Macrocheles robustulus*, deutonymph.

14. Dorsal shield. 15. Sternal shield. 16. Anal shield. 17. Tectum. 18. Chelicera.  
19. Gnathosoma, ventral view.

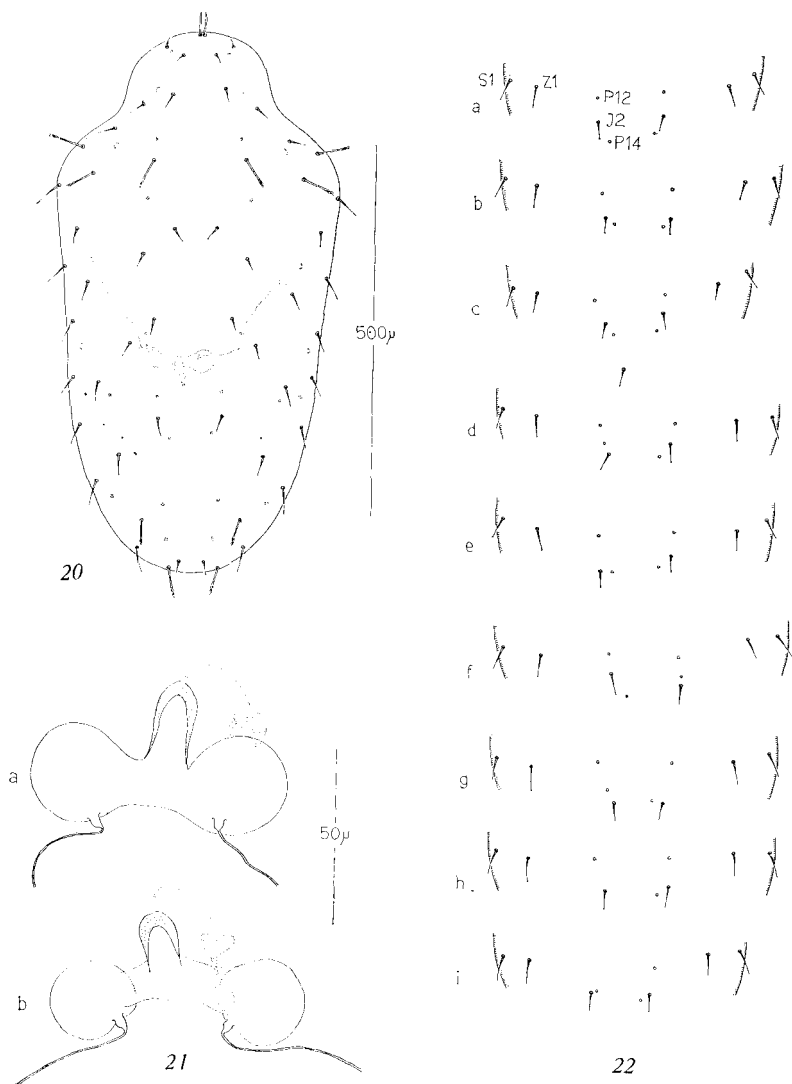
An  $F^2$  generation has been reared only once, two virgin females (reared in one cell) produced during 56 days (12th April to 7th June) 29 offspring from which 27 males were obtained, two nymphs having died during development.

In almost all cases larvae as well as eggs were produced although the conditions were identical during the whole time. I could not find any relation between larviparity or oviparity and external conditions (FILIPPONI & FRANCAVIGLIA, 1964).

The incubation time for the eggs was 5-6 days during February-March and 1-2

days during May-June. The whole cycle from larva to female took 14 days in April and only 9-11 days for the male. During July the whole cycle was as short as 5-6 days.

The larva seems to be non-feeding, all the other stages fed readily on nematodes.



FIGS. 20-22. — *Macrocheles robustulus*, female.

20. Dorsal shield. 21. a-b. Sacculus foemineus, two views. 22. a-i. Variations in the position of setae J2 and the pores P12, P14.

## DISCUSSION.

### *The development of the dorsal chaetotactic pattern.*

LARVA : The unsclerotized podonotal region of the larva bears 10 pairs of setae (and not 9 pairs, as stated by EVANS & HYATT, 1963). The setae are 11-15, Z1, Z2, S2, S5, S6. The opisthonotal region bears 4 pairs of setae : Z1, Z3, S3, J5 and two additional pairs of future dorsal setae (S4, S5) are ventrally inserted.

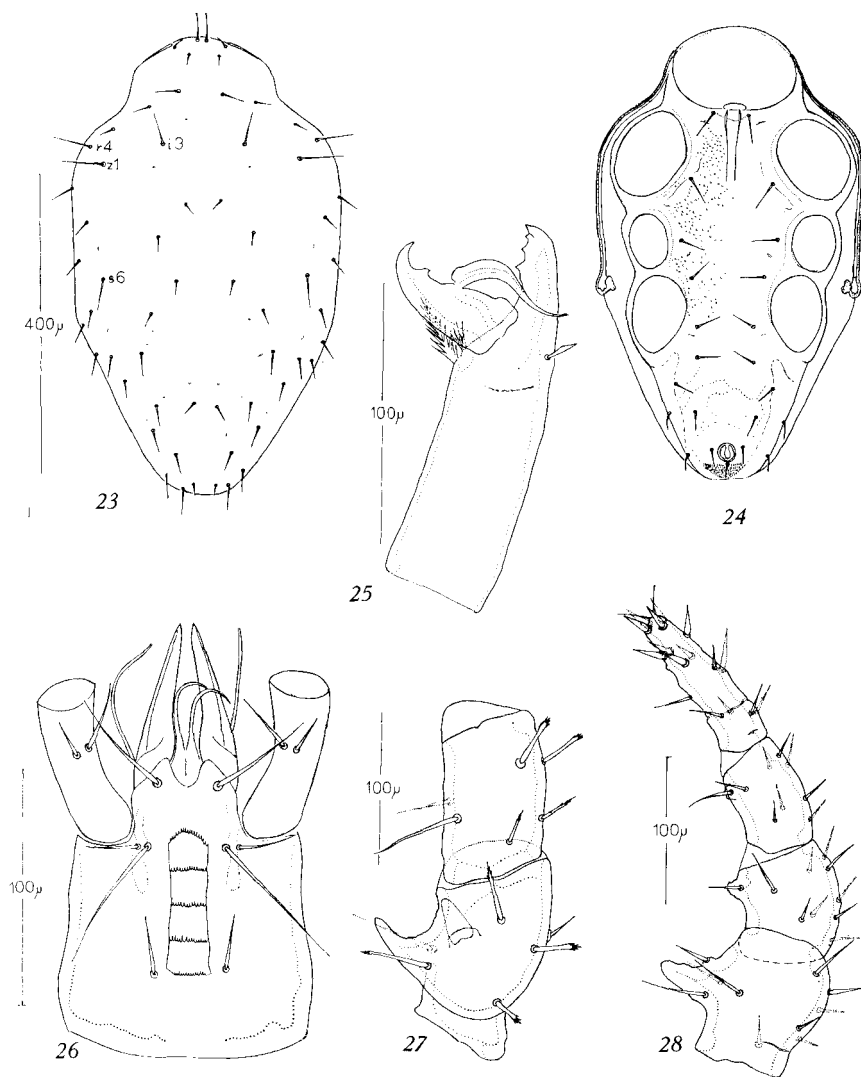
PROTONYMPH : Eleven pairs of setae are inserted on the podonotal shield : r1 is added at this stage. Four additional pairs of podonotal setae, namely r4, r5, r7 and s7 are also added at this stage but they are inserted on the soft membrane. Eight pairs of setae are inserted on the opisthonotal shield (J2 and Z1 are added) and two additional pairs (also added at this stage — S1 and S2) are inserted on the membrane.

DEUTONYMPH : The deutonymph has already the full adult complement of 18 pairs of setae on the podonotal shield (s1, r3 and z3 are added at this stage) and 10 pairs on the opisthonotal region of the shield. The development of the dorsal chaetotactic pattern is summarized schematically in fig. 29.

EVANS and HYATT (*op. cit.*) use as a key character the presence of 28 or 29 pairs of dorsal setae, stating that this is caused by the presence or absence of J2 (following HIRSCHMANN, 1957). In my opinion J2 is always present and the difference in number is caused by the presence or absence of J3. Setae J2 are characterized extremely well by being normally in a field delimited by two pairs of pores (P12 and P14 in the notation of VAN DER HAMMEN, 1964). While checking this pair of setae, it turned out that the whole area is rather variable (figs. 22 a-i). Although in the majority (« normal ») of specimens the setae are within the field described by the pores, they may be inserted below the field, the situation may be assymetric, one of the pores may be missing and in one case an additional seta (?J3) was present. Even more remarkable is the movement of the pores (P12 and P14) and the seta (J2) relative to the other setae (e.g. Z2) during ontogenetic development. In the protonymph the J2 setae are posterior to the line connecting the bases of Z2, in the deutonymph they are at the same level with the bases of Z2 and in the adult they are much anterior to this line. The two pairs of pores are present at all these stages.

### *Leg chaetotaxy.*

The leg chaetotaxy of the larva and the protonymph agree in the main with the formulae given by EVANS (1963a) for *Pergamasus* sp., the only exception being genu I which in both stages of *M. robustulus* has only 7 setae, namely  $1 - \frac{2}{0}; \frac{2}{1} - 1$ , the anterior ventral seta being absent. The formulae for the deutonymph and the adult as stated by EVANS for the Macrochelidae.



FIGS. 23-28. — *Macrocheles robustulus*, male.

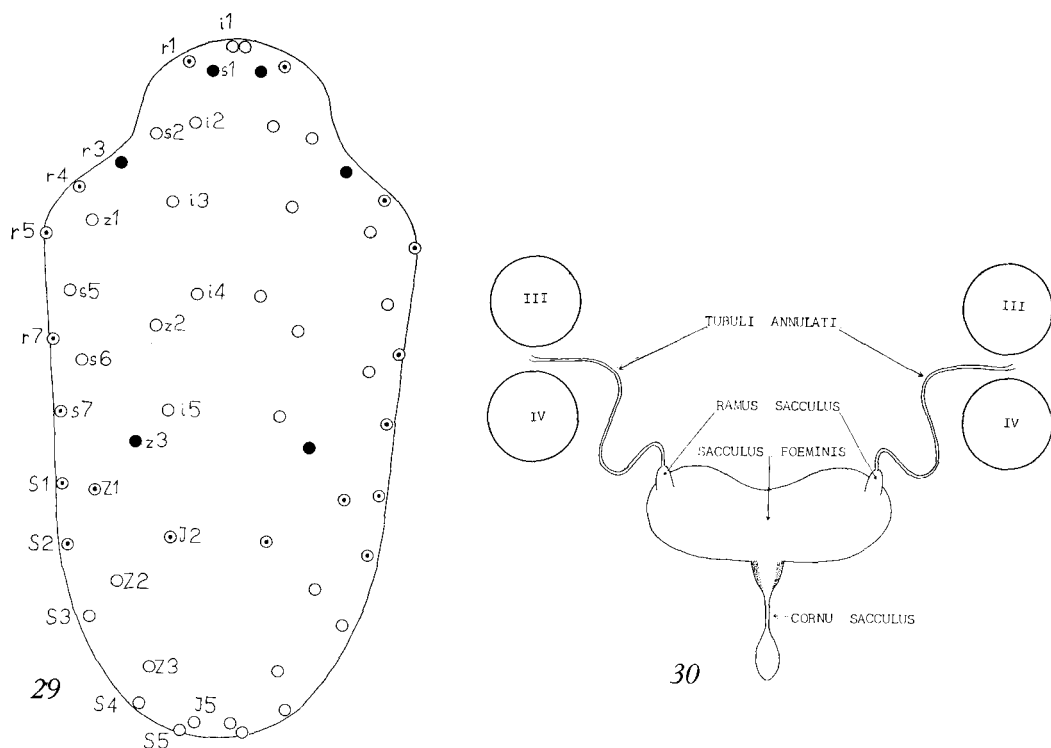
23. Dorsum. 24. Venter. 25. Chelicera. 26. Gnathosoma, ventral view.  
27. Femur and genu IV. 28. Leg II (femur to tarsus, pretarsus omitted).

### *The sacculus foemineus and associated structures.*

For taxonomic purposes the sacculus has been used extensively only in the Phytoseiidae (named spermatheca there). Recently it has been used by EVANS (1963b) in his study of the genus *Neocypholaelaps* Berlese. FAIN (1963) has described and figured in detail these female structures in several species of the families Halarachnidae, Rhinonyssidae and Entonyssidae, he reviews also most of the avai-

lable information on the structures and their function. BREGETOVA & KOROLEVA (1964) use the "spermathecae" for the separation of species of the genus *Ololaelaps* Berlese. The sacculus and associated structures are clearly defined in the genus *Macrocheles*, and I intend to introduce their structure as a taxonomic criterion in this group.

Information concerning the structure and function of the sacculus and associated structures is both scanty and contradictory. The first detailed description of the organ was given by MICHAEL (1892) who also coined the various terms used.



FIGS. 29-30. — *Macrocheles robustulus*.

29. The ontogenetic development of the dorsal chaetotactic pattern in the female (schematic). o = setae appearing in the larva ; ◐ = setae appearing in the protonymph ; ● = setae appearing in the deutonymph. 30. A schematic representation of the sacculus foemineus and associated structures in the gamasids.

WARREN (1940) gives an excellent account of these organs in the female of *Dermapnyssus gallinae*, and in an additional paper (WARREN, 1941) he surveys several other gamasids.

Concerning the function of the sacculus MICHAEL states that it may "safely be said that the contents of the sacculus are the products of the male genital organs". WARREN (*op. cit.*) found that "the semen which is found in the sacculus is copious and the naked spermatozoa or the sperm chambers are embedded in a bulky secre-

tion which nearly fills the large sacculus''. More recently JAKEMAN (1961) stated : " This chamber was observed only when filled with elements which take the same stain as the material in the testes of the male, and which may well be the sperm mother cells described by MICHAEL in the sacculus of his specimens ".

The main difficulty is the way by which the male genital products reach the organ as there is no direct connection between the vagina and the sacculus (MICHAEL, WARREN, *op. cit.*). Quoting MICHAEL again : " The other possible method is that the products of the male organs are ejected from the narrow mouth of the capsule into the more or less trumpet-shaped mouth of the ringed tubes in the cuticle joining the coxa of the third leg to the more chitinized part of its acetabulum, and pass directly up the ringed tubes into the sacculus ; this is a sufficiently simple method ". And further on : " The only objection which I see to this is the fact that spermatocysts found in the sacculus undoubtedly appear considerably too large to have passed through the ringed tubes ; this is a serious difficulty, but it is possible, and even probable, that the ringed tubes may be capable of distension, and that the spermatocysts, which are soft bodies, are capable of compression, and can be forced through very small apertures, just as the eggs are forced through even hard, not distensible, openings which seem quite incapable of allowing them to pass ».

WARREN (1940) finding himself in the same dilemma offers the following explanation : " it is just possible that in copulation the male places its genital aperture tightly against the dorsal surface of the female over the site of the sacculus, and by muscular contraction of the ejaculatory apparatus the bulky semen is actually forced through the thin cuticle into the sacculus ; and if copulation takes place just after the ecdysis of the female the slight mechanical injury would be healed at once. Some of the sections are not unfavourable to this suggestion, but I have failed to obtain definite confirmation ". WARREN's suggestion seems unacceptable to me, it would also be very hard to explain the function of the male spermatophoral process in this connection.

On the other hand, WARREN's observation that copulation seems to take place just after ecdysis of the female is very pertinent. On p. 431 he states : " The female receives semen from the male before the general growth of the body has ceased. In fact copulation would seem to occur when the female is not much larger than a mature male ". In *Macrocheles* species I have observed copulation only in recently hatched females, in which all the organs were still capable of distension. Moreover, males introduced into a cell with a female three days after her ecdysis, failed to fertilize her and she remained male producing. MICHAEL concludes : " Taking all these matters into consideration, I incline to think, although I should not like to state it as a fixed opinion, that in what I may call the sacculus species, the sperm elements enter the body of the female by the ringed tubes and not by the vagina ".

It seems to me that in mesostigmatic mites both ways of insemination exist : via the vagina as in the Parasitidae and the Otopheidomenidae (vide TREAT, 1965) or via the ringed tubes as in the Macrochelidae, Phytoseiidae and probably also in the Ascidae, Laelapidae, Halarachnidae, Rhinonyssidae and Entonyssidae. Most

interesting is DOSSE's (1959) contradictory account of the copulation of *Typhlodromus*. DOSSE describes and figures clearly and unequivocally what amounts to insemination via the *tubuli annulati* and then, surprisingly, concludes that the spermatophore is introduced into the genital opening of the female.

If, as I do believe, the spermatheca of the phytoseiids is homologous to the *sacculus foemineus*, than the *major duct* is homologous to the *tubuli annulati*; the *minor duct* to the *cornu sacculi*; the *cervix* to the proximal, thickened, part of the *cornu sacculi* and the atrium would be the remenant of the *ramus sacculus* which has moved to the apex of the *cervix*. The *vesicle* is of course homologous to the *sacculus foemineus* (phytoseiid terms after SCHUSTER & PRITCHARD, 1963). In the Phytoseiidae the organ is paired, seemingly without any connection between the two parts. FAIN (*op. cit.*) suggests the possibility that the two minor ducts meet in an unpaired spermatheca near the ovarium. This author also suggests that the *sacculus foemineus* serves as a maturation chamber of the spermatozoa and that the distal part of the *cornu sacculus* is the real spermatheca.

The *sacculus* and its associated structures are chitinous (remaining intact also after hot maceration of the mite) and clearly of ectodermal origin, in this respect they are similar to the spermathecae of other arthropods. From DOSSE's (*op. cit.*) account it seems probable that a chitinous wall is secreted by the *sacculus* around the sperm material injected by the male, forming the pear-shaped spermatophore which can often be observed inside the spermathecae of phytoseiids. WARREN's (1940) observations on the development of the *sacculus* are pertinent to this and quoted therefore: "The wall has been differentiated out of an originally solid structure, and consequently in the young female it is often irregular and rough on the inner surface, which at first has no cuticular lining." And further on: "Finally the epithelium of the *sacculus* and also of the anterior part of the *cornu* disappear, and the *sacculus* persists as a very thinwalled cuticular sac and the *cornu* as a thick-walled chitinous tube which in the fertilized female contains a mass of closely packed spermatozoa".

The whole problem will be finally solved only after careful histological studies.

#### SUMMARY.

The various stages and the biology of *Macrocheles robustulus* (Berlese, 1904) are described. The function of the *sacculus foemineus* and associated structures and the mode of copulation in the gamasids are discussed.

#### ACKNOWLEDGMENTS.

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#### ADDENDUM

The following has escaped my knowledge while writing the manuscript : the male of *M. robustulus* has been shortly described and figured by BALOGH (J.), 1958 (Macrocheliden aus Bulgarien (Acari, Mesostigmata). *Acta Ent. Mus. Nat. Pragae*, 32 : 247-256).

The *sacculus* and associated structures of several macrochelids have been described and figured by PETROVA (A. D.), 1960 (Materialien über den Bau des inneren Säckchens des Receptaculum seminis der gamasoiden Macrochelidae Vitzth. *Zool. Anz.*, 165 : 393-400).