

SYMPOSIUM
ON
ADAPTIVE RADIATION IN PARASITIC ACARI
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ADAPTATION TO PARASITISM IN MITES

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Mites have a remarkable power of adaptation to various conditions of life. As a matter of fact mites are found in very different habitats. Most of them are free-living but there are also very many parasitic forms, either ecto or endoparasitic. The chances of finding complete phylogenetic lines are, for this reason, greater in mites than in any other parasitic group. In most of the worms the ectoparasitic forms have disappeared or did not exist. Among the insects, ectoparasitism is practically the only form of parasitism that is encountered. For all these reasons it appears that mites constitute probably the most suitable group for the study of the various phenomena related with parasitism and more specially with adaptation to endoparasitism (FAIN, 1965a). I intend to discuss here some morphological and biological adaptations in mites, particularly those that are related to the starting of the parasitic life or that have allowed the passage from an ectoparasitic to a endoparasitic manner of life. I shall limit my discussion to the most important features relating to parasitism, and especially in the groups of mites that I have studied.

Adaptation to parasitism generally involves both the morphology and the biology of the mite.

Let us first consider the morphological adaptations.

Morphological adaptations.

From the morphological point of view, two different kinds of phenomena, completely independant of each other, are involved in the adaptation to parasitism : one is regressive, the other constructive.

The regressive or degenerative phenomena are essentially characterized by the progressive disappearing of the organs no longer in use. The final result is the extreme simplification of the different structures. Some organs may completely disappear during this processus of regression. This regression is present, in various degrees, in most of the ectoparasites but it is especially well marked in the endoparasites. All the organs may be involved in this regressive process. Among them the chaetotaxy is probably the "organ" that changes the most progressively. It is therefore by means of the chaetotaxy that one can appreciate most clearly the degree of evolution or adaptation of a parasitic mite.

In opposition to these regressive features, one may very frequently observe constructive characters consisting in the hypertrophy of existing organs or even in the appearance of some new structures. These specialized productions are secondary adaptations towards particular conditions of the parasitic manner of life. Their importance varies greatly according to the kind of the function as well as to the group or the species to which the mite belongs.

Several functions in relation to parasitic life may induce the development of new specialized organs in the parasite. Among them one of the most important seems to be the function of the attachment to the host. Let us study this function in several groups of parasitic mites.

A. CONSTRUCTIVE MODIFICATIONS PRODUCED BY THE PARASIC LIFE : ATTACHING ORGANS.

Before a free-living mite can live and develop on the body of another animal it is necessary that it begins by fixing itself firmly to the host. The attachment seems very often to be the "sine qua non" condition for the beginning of the parasitism. The problem of attachment has been solved by the mites in various ways. Attaching organs are, as a rule, more elaborate in ectoparasites than in endoparasites and in the former they are generally much more developed in permanent parasites than in the non-permanent ones. The attachment to the skin and to hairs seems to have induced the most powerful and complex structures. In some groups these organs have become so important that they have been retained as a basis for a higher classification. This is the case for the families Listrophoridae and Rhyncoptidae which are separated from other families mainly or exclusively by their organs of attachment.

Attaching organs in the skin mites parasitic on Vertebrates.

In the Ixodidae the attachment to the skin of the host is realized mainly by means of their long toothed hypostome deeply sunk in the skin. Besides, the cheliceral-digits with their recurved teeth and the tarsal suckers provide supplementary means of attaching to the skin. In some Ixodidae a cement is secreted and aids the fixation of the gnathosoma to the host.

In cuticolous Mesostigmata the fixation organs are variously developed. They

are poorly developed in most of the Dermanyssidae or in other recently-adapted parasites and they consist mainly of tarsal suckers. In some species there are also retrorse spines or hooks on the legs.

The attaching organs are more developed in the more specialized and apparently older parasitic groups such as the Ixodorhynchinae and the Omentolaelapidae¹ which are attached to the skin or under the scales of snakes, and in the Spelaeorhynchidae living on the skin of bats.

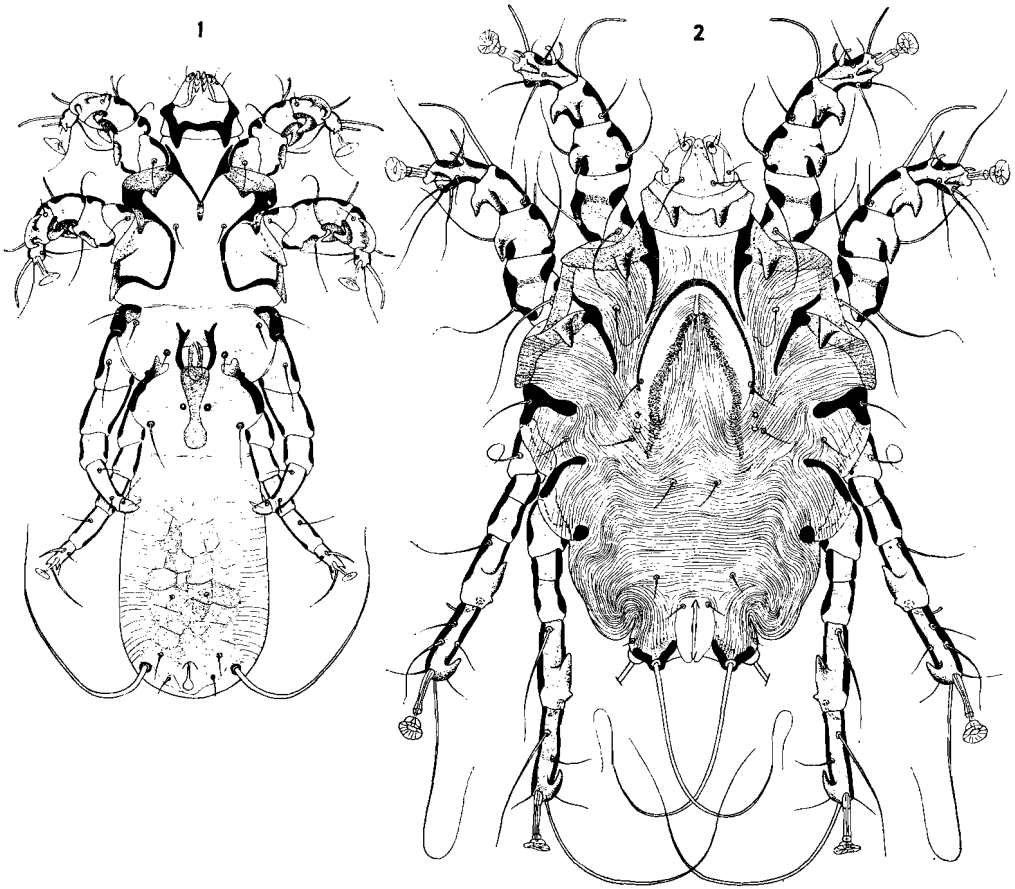


FIG. 1-2 : Examples of attaching organs on the idiosoma, the gnathosoma and the legs in the male of *Galagalges congolensis* Fain (Galalgidae) (fig. 1) and in the female of *Gaudalgies caparti* Fain (Psoroptidae) (fig. 2).

In the Ixodorhynchinae the corniculi are strongly elongated and in some species they end in one or two small recurved and backwardly-directed barbs (fig. 3). These long and barbed corniculi curiously resemble the toothed-hypostome of the ticks and they probably have the same function (Fain, 1961b).

1. Omentolaelapidae Fain emend. nov. (= Omentolaelaptidae Fain, 1961).

In *Omentolaelaps mehelyae* Fain the fixation organ is extraordinarily elaborated. It consists of a large membranous pouch covering the ventral surface of the hysterosoma and which may act as a sucker. The posterior margin of the pouch is attached to a row of modified hairs each of which is connected to a small muscle.

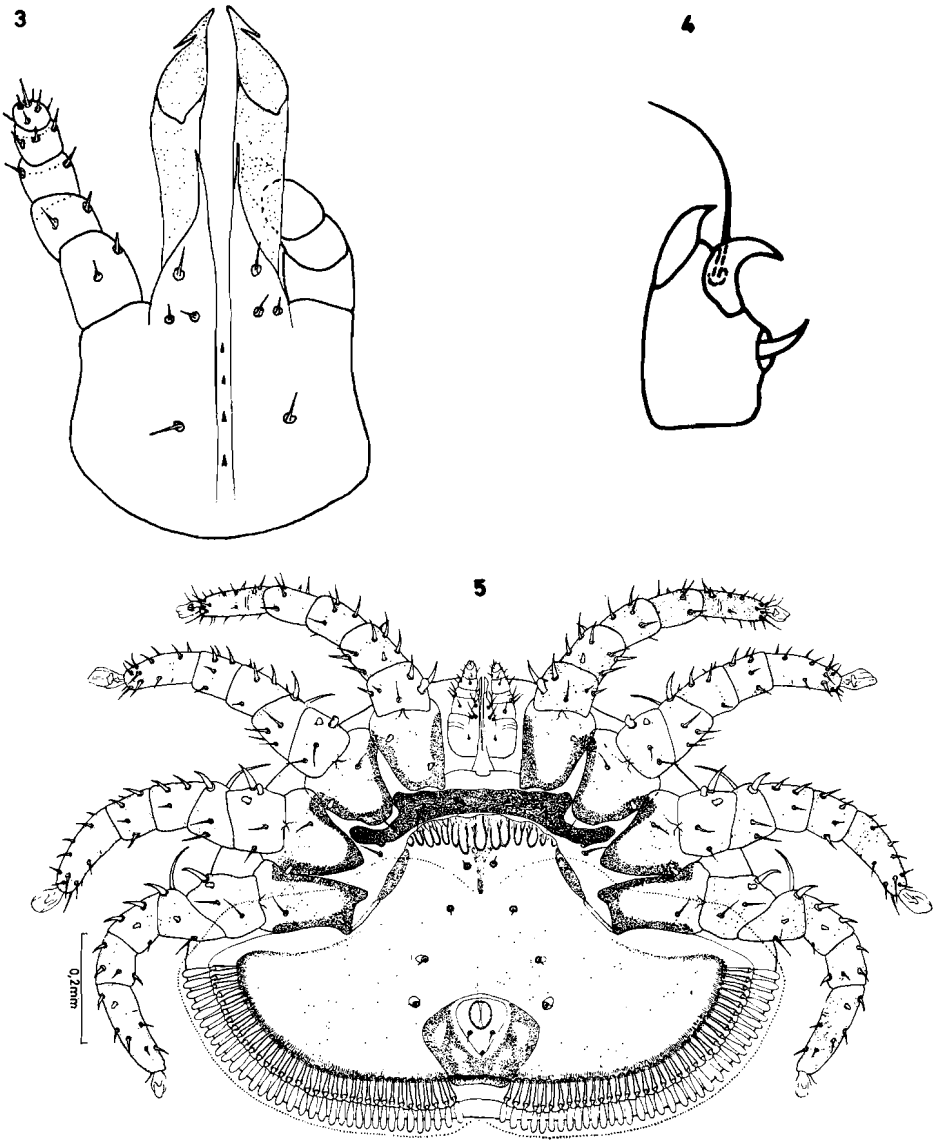


FIG. 3-5 : Strongly elongate and barbed corniculi in *Ixodorhynchus fonsecae* Fain (Ixodorhynchinae) (fig. 3). Tarsus IV in *Rodhainyssus yunkerii* Fain (Gastronyssidae) showing the small pincer-like organ (fig. 4). Transversal elongation of the body in the female of *Omentolaelaps mehelyae* Fain (Omentolaelapidae) (fig. 5).

The movements of the pouch are apparently controlled by means of the contraction of these hair-muscles (fig. 5).

It is to be noted that besides these specialized attaching organs the Mesostigmata, as well as the ticks that live on snakes, show a widening of the idiosoma which probably allows a better fixation under the scales. It is in *Omentolaelaps mehelyae*, a very evolved and specialized parasite, that this widening is the most marked. The female of this species is distinctly wider than long. This widening of the idiosoma seems to be a general phenomenon for all the mites that live under the scales of Reptiles. It is also observed in the family Pterygosomidae which constitute a very evolved group in the Trombidiformes (FAIN, 1961a). The appearance of the same specialized character (widening of the idiosoma) in three groups of mites belonging to different orders of Acarina can be explained only by the similarity of their habitats and is nothing else than convergence. It seems that convergence is not rare in parasitic Acarina. Several other cases have been observed by us in different groups of mites and for various organs.

The Spelaerhynchidae constitute another very specialized group of Mesostigmata. They are living attached to the skin of bats. The attachment to the skin is realized exclusively by means of the very powerful chelicerae which bear strong recurved hooks.

The Trombidiformes contain only few groups of skin parasites of Vertebrates. The most numerous group is that of the Trombiculidae whose larvae are permanently fixed to their hosts by means of their chelicerae.

It is in the Sarcoptiformes parasitic on the skin that the attaching organs are the most developed. In addition to the tarsal suckers which seem to be constant in these skin parasites, one may encounter very specialized fixation organs consisting generally of strong sclerotized retrorse processes that serve for their anchorage on the skin. These hooks are generally situated on the ventral surface of the gnathosomal base or on the legs, more rarely on the idiosoma. They are present also in the skin-mites of mammals (Psoroptidae and Galagalgidae) as in the skin-mites of birds (Epidermoptidae) (fig. 1-2). In most of the cases these hooks are sclerotized processes of the body, the gnathosoma or the legs and are not homologous with setae or claws (FAIN, 1963b).

Attaching organs in the pilicolous or fur-mites.

The "pilicolous" specialization is observed mainly in the Myobiidae (Trombidiformes) and in the Listrophoridae (Sarcoptiformes).

The attaching organs are situated on the gnathosoma or on the legs. They are generally in the shape of two claspers that enclose the hair.

A similar mode of fixation is observed in the hypopi of the Labidophoridae with the difference that the attaching organs are situated on the ventral surface of the opisthosoma.

Attaching organs in mites living in the feather or the hair follicles.

In the Rhyncoptidae (Sarcoptiformes), parasitic on mammals, the attachment organs are very specialized. They consist mainly of voluminous retrorse hooks situated on the anterior legs. The palps also bear several smaller hooks. The anterior part of the body, including the first pairs of legs, is permanently embedded in the pilous follicle, while the posterior part is free. The mite is maintained with the dorsum close to the hair by means of special movable appendages situated on the anterior genua (FAIN, 1965b).

The hypopi of the genera *Rodentopus* and *Lophuromyopus* (Glycyphagidae : Sarcoptiformes) are completely sunk in the depth of the pilous follicles. All the known species are parasitic on rodents, apart from one species which lives on a *Galago*. In virtually all the cases the hypopi are embedded in the tail follicles, only in a few cases were they found in other places. The attachment organs consist of strongly modified fingered hairs that are situated on the posterior tibiae (FAIN, 1965c).

The mites of the genus *Microlichus* (Epidermoptidae) parasitic on birds live generally in the feather follicles. They attach themselves probably by means of the strong recurved sclerotized processes situated at the apex of their anterior tarsi (FAIN, 1965d).

Attaching organs in the feather mites.

The feather mites display several attaching systems. Among them the mites of the family Analgidae are probably the closest to the Epidermoptidae from the morphological as well as from the biological point of view. They live mainly on the small feathers and they come frequently in contact with the skin. It is probably therefore that their fixation organs closely resemble those of the Epidermoptidae, except that they are less sclerotized.

The true feather-mites (Pterolichidae, Freyanidae, Proctophyllodidae etc...) fix themselves on the feathers probably by means of the tarsal suckers which have a very complicated structure. In these groups the chaetotaxy of the idiosoma is generally more developed than in the Analgidae. In some of these mites (e.g. the Freyanidae) the opisthosomal hairs tend to become marginal. This migration is probably an adaptation in order to provide a better attachment of the body to the feathers.

Attaching organs in mites parasitic on the cornea and the nasal mucosa of bats.

The species belonging to the genus *Opsonyssus* (Gastronyssidae) are attached to their host by means of very delicate pincer-like organs situated on the posterior tarsi. These organs consist of two very small recurved spines. The distal spine is fixed and recurved basally while the basal one is movable and has an

opposite direction. With these very delicate pincers the mite can attach itself to very bare surfaces such as the cornea of the eye (FAIN, 1964) (fig. 4).

Attaching organs in the endoparasitic mites.

As a rule attachment organs are poorly represented in the endoparasitic mites. They probably did not become necessary because most of the parasitic niches provide sufficient protection against the danger of detachment from the host. The only exception is that of the family Turbinoptidae (Sarcoptiformes) which lives in the nares or in the anterior part of the nasal cavities of birds. These mites have strong recurved processes on some or on all of their tarsi. These fixation organs are probably necessary because in the nares the danger of detachment is greater than in other endoparasitic habitats.

The other groups of mites living more deeply in the nasal cavities or in the lungs of various hosts such as the Rhinonyssidae, the Halarachnidae, the Entonyssidae and the Ereyenetidae or those that parasitize the aerial sacs of birds as the Cytoditidae, are devoid of recurved sclerotized processes. In these groups the attachment seems to be realized only by means of the ambulacral claws or suckers, more rarely by means of the chelicerae.

In the case of the Rhinonyssidae it seems that the nasal mucus in which these mites are "embedded" contributes to retain them in the nasal cavities.

The Ereyenetidae on the contrary are quick-running and not wettable mites. They live in the posterior part of the nasal cavities and in the bone cells of the head. It is probable that their deeper situation combined with their greater agility provide them a good protection against the detachment from the host.

In the mites that live in the superficial layers of the skin or in corneous niches, for example, the Sarcoptidae and the Knemidokoptidae, the attaching organs are also very poorly developed or absent. In the genus *Sarcoptes*, however, the dorsal surface of the body is provided with backwardly-directed spines and scales which probably help to retain the mite in the skin burrows.

In the most evolved species of the Psoroptidae, especially in the Psoroptinae, there are no true attaching organs. These mites are however external skin mites and they do not burrow into the skin. The presence of these mites on the skin induces on the part of the host a strong reaction which leads to the formation of heavy crusts. As the mites are always situated at the base of these crusts one may suppose that these crusts assist in retaining the mites on the host. The strong reaction that these mites produce on the host is probably related to the strong development of sclerotized recurved processes on the apex of the tarsi.

Another mode of attachment in the endoparasitic mites is that of *Gastronyssus bakeri* Fain which lives attached, by means of its chelicerae, to the mucosa of the stomach in frugivorous bats. In this species the chelicerae are completely oriented ventrally and suspended in a strong sclerotized frame.

After this brief review of the various kinds of specialized structures in relation to the attachment on the host, I shall deal now with some regressive modifications produced by the parasitic life.

B. REGRESSIVE MODIFICATIONS PRODUCED BY THE PARASITIC LIFE.

As a rule the regression of the organs are more marked in the endoparasites than in the ectoparasites.

For instance the Rhinonyssidae (Mesostigmata) living in the respiratory tract of birds have a more reduced chaetotaxy than the Macronyssinae (Dermanyssidae) their probable ancestors, which live on the skin of the same hosts (EVANS et TILL, 1966). It is in the genus *Sternostoma*, the most evolved of the family and which includes in particular the only species that lives in the lungs, that the reduction is the most marked. This reduction involves among others the chaetotaxy, the solenidiotaxy, the peritrema, the chelicerae and the tritosternum.

The Entonyssidae, parasitic in the lungs of snakes, present also a notable reduction of the same organs especially if one compares these mites with the ectoparasitic Mesostigmata living on these same snakes. As a whole, however, the reduction is less marked than in the Rhinonyssidae.

It is in the Halarachnidae, parasitic in the respiratory tract of mammals that the reduction is the most important. It is interesting to note that in this group the regression is the most marked in a host belonging to a higher zoological group.

Of particular interest in the study of adaptation to parasitism is the family Ereynetidae (Trombidiformes) as it contains at the same time free-living species, and species that live as parasites in the respiratory tract of various animals, invertebrates and vertebrates. This group does not contain any ectoparasites. It seems therefore that all the endoparasitic forms have been derived directly from the free-living ones. The adaptation to endoparasitism is probably very old for all the parasitic species, except one, are morphologically much more evolved than the free-living ones and they belong to other sub-families. It has produced in all these species a reversion to the larval stage. The number of hairs in adults is always smaller in the parasitic species than in the free-living species while in the larvae of these groups the chaetotaxy is nearly the same (FAIN, 1963a).

The Ereynetidae are not represented in snakes but they exist in snails, in batrachians, in birds and in mammals. Curiously enough the species that parasitize the frogs and toads are more evolved, in the "regressive" sense, than those from the other hosts while on the other hand the species living in birds have generally a much more specialized chaetotaxy than those from other hosts. There is, however, an exception, it is that of the genus *Boydaia* which contains all the species living in Passeriform birds. In that genus the chaetotaxy resembles more closely that of the primitive groups.

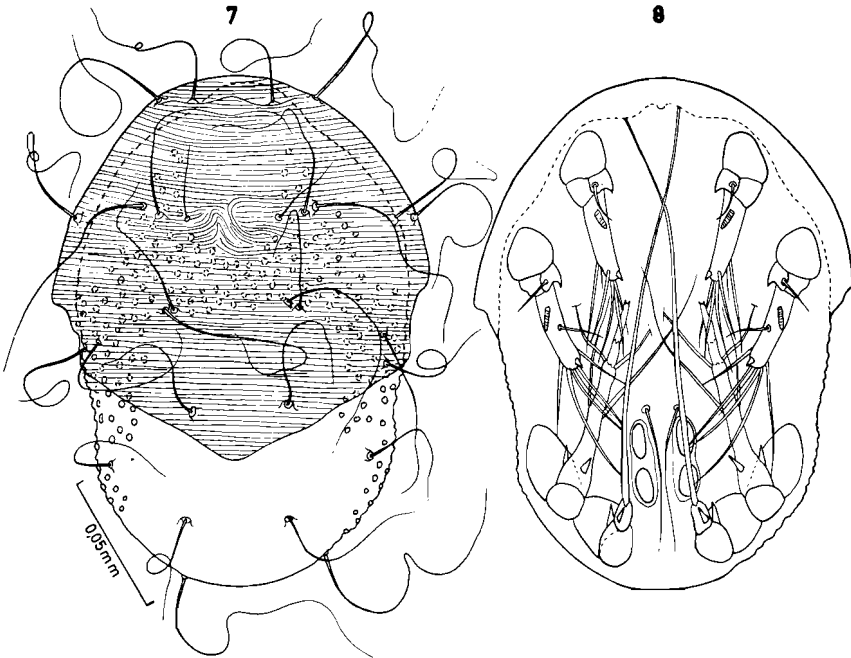
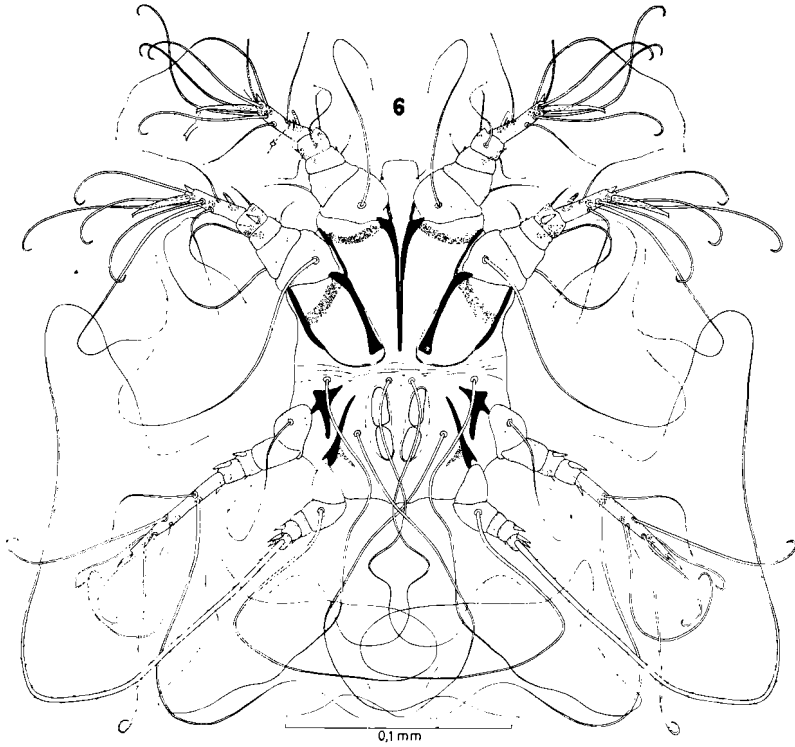


FIG. 6-8 : Small hypopus of *Hypodectes propus* (Nitzsch) found free in the nest of *Columba palumbus*, in Belgium (fig. 6). Egg found free in the same nest, the chitinous layer has disappeared, the striate-hairy membrane is the vestige of the larval stage, the verrucous membrane being the vestige of the protonymphal stage (fig. 7). The same egg showing the hypopus that it contains (fig. 8).

Biological adaptations.

I shall deal here only with the modifications of the life-cycle in relation with parasitism.

From a general point of view the parasitic life produces an acceleration of the postembryonic development.

The free-living and the ectoparasitic mites are generally oviparous. Ovivarity also exists in certain groups which are already more or less strongly engaged

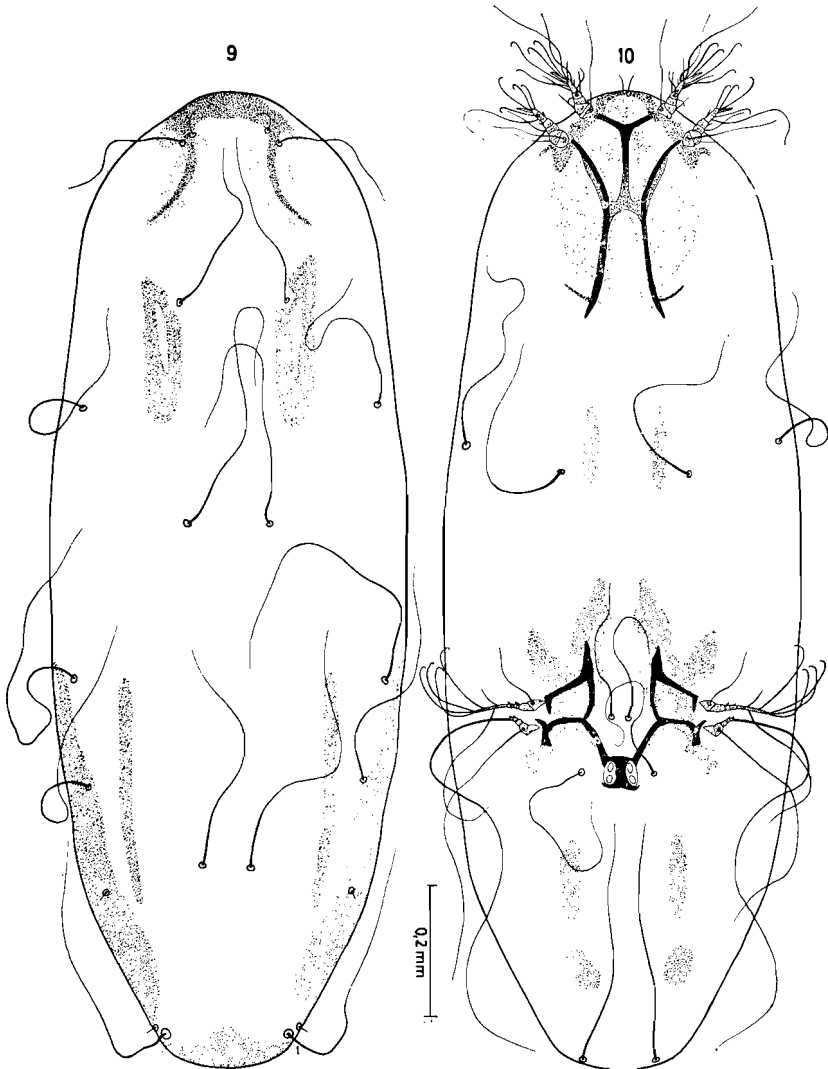


FIG. 9-10 : Large hypopus of *Hypodectes propus* (Nitzsch) found in the subcutaneous tissues of *Columba palumbus* in Belgium.

in the endoparasitic mode of life. That is the case for the Sarcoptidae that live in the corneous layers of the skin. In the true endoparasites the ovoviviparity or the viviparity is the rule. The following part of the cycle is also accelerated. Some or all the nymphal stages may disappear in the endoparasitic forms. It is to be noted, however that shortened cycles may be observed also in some ectoparasitic Trombidiformes such as the Trombiculidae or in certain very specialized nidicolous mites such as the Hypoderidae (= Hypodectidae).

The acceleration of the life-cycle in relation to parasitism is particularly well marked in the family Ereyenetidae. All the free-living species of this group as well as the single species living in the lung of Molluscs are oviparous. The life-cycle includes a larva and three successive stages of nymphs : protonymph, deutonymph and tritonymph. In the species that live in the nasal cavities of frogs and toads the development is accelerated. The female lays eggs that contain a completely developed larva. Moreover there are only two nymphal stages left, the tritonymphal stage having disappeared. The development is still much more shortened in the species living in the nasal cavities of warm-blooded animals, birds and mammals. These species are also ovoviviparous. The larva exists but there is no nymphal stage and the adult emerges directly from the larval skin. The nymphal stages however have not completely disappeared ; they are still represented by small vestigial chitinous and membranous structures (FAIN, 1963a).

In most of the ectoparasitic Mesostigmata the oviparity is the rule and ovoviviparity and viviparity are observed only in a few apparently very old groups such as the Spelaeorhynchidae, the Omentolaelapidae, the Spinturnicidae, etc.

The Mesostigmata living in the respiratory tract of Vertebrates (Entonyssidae, Rhinonyssidae, Halarachnidae) are ovoviviparous or viviparous. In two species of Rhinonyssidae e.g. *Falconyssus elani* Fain and *Ptilonyssus ploceanus* Fain, a completely developed nymph is produced by the female instead of a larva.

The ectoparasitic Sarcoptiformes are generally oviparous. This is true for the Psoroptidae and the Sarcoptidae living on the skin of mammals, for the Epidermoptidae that parasitize the skin of birds and probably for most or all the feather mites. Ovoviviparity or viviparity is met only in a few very specialized groups such as the family Teinocoptidae that lives on or in the skin of bats. In all the endoparasitic Sarcoptiformes viviparity is the rule. This is the case in the Turbinoptidae and the Cytoditidae living in the respiratory tract of birds and in the Gastronyssidae living in the respiratory passages or in the stomach of bats.

Some species that are normally oviparous may, under some circumstances, lay eggs that contain a fully developed larva. This is the case for *Dermatophagoides pteronyssinus* of which I found several ovoviviparous females in house dust in Kigali (Rwanda) and in Belgium. They were mixed with females containing non embryonated eggs. This facultative ovoviviparity is probably a general phenomenon in mites living in unstable conditions such as those that live in decaying material or in house-dust.

As an example of the extreme shortening that may occur in the life-cycle of

some Acarid mites, I shall give now a brief account of some observations that I made recently on a group of remarkable mites living in association with birds. The adults of these mites are living free in the nests, while their heteromorphic deutonymphs are parasitic under the skin of the same birds. These heteromorphic deutonymphs, also called hypopi, have been found in various birds and they are specially frequent in the pigeons, both wild and domestic ones. They are known from all the parts of the world (fig. 9 ; 10 ; 20-22).

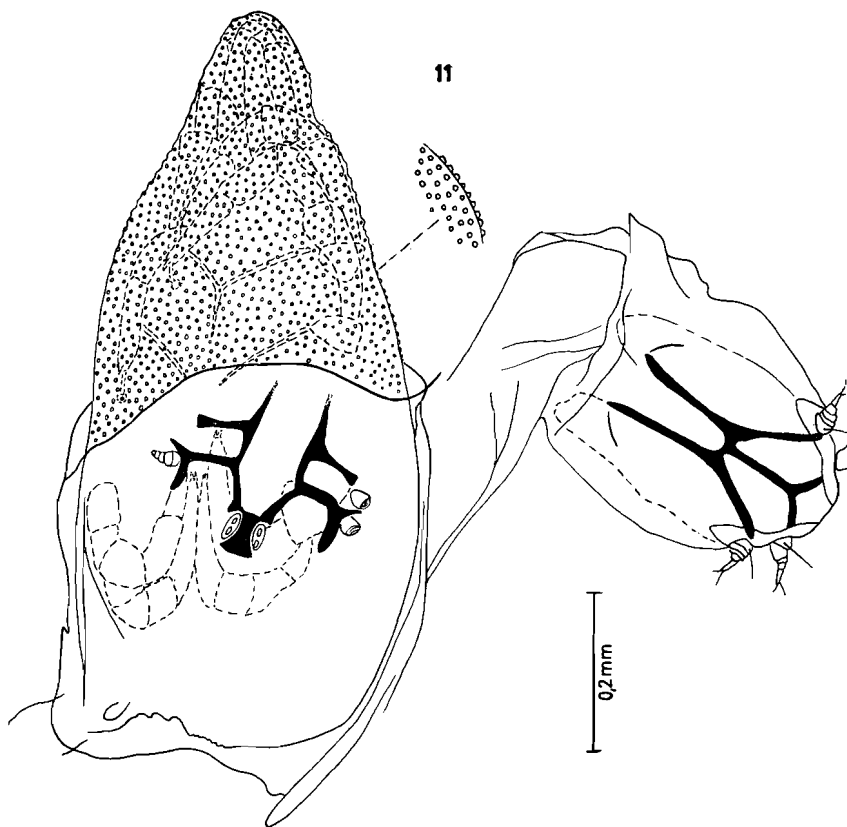


FIG. 11 : Large hypopus of *Hypodectes propus* (Nitzsch), in the molting stage, found in the nest of a *Columba palumbus* in Belgium. This hypopus contains an adult male of *H. propus*. (N.B. : 1) The hypopus has been accidentally broken when it was mounted ; 2) The verrucous sac between the hypopial skin and the adult mite is a vestige of the tritonymphal stage).

So far it was thought that these hypopi represented heteromorphic deutonymphs of the feather mite *Falculifer rostratus*. This belief is based on the writings of Robin and Megnin in 1877, and it has been accepted by all acarologists until now.

In examining the nests of the pigeon *Columba palumbus*, in Belgium, I dis-

covered a remarkable and undescribed acarid mite that I could not classify in any known family. The *female* of that species was sacciform in shape and it was filled with about 40 eggs. The chelicerae were strongly reduced and had very short and apparently non-functional digits, the palps had only one long and narrow article. The *male* was also very curious and contrary to the female had very

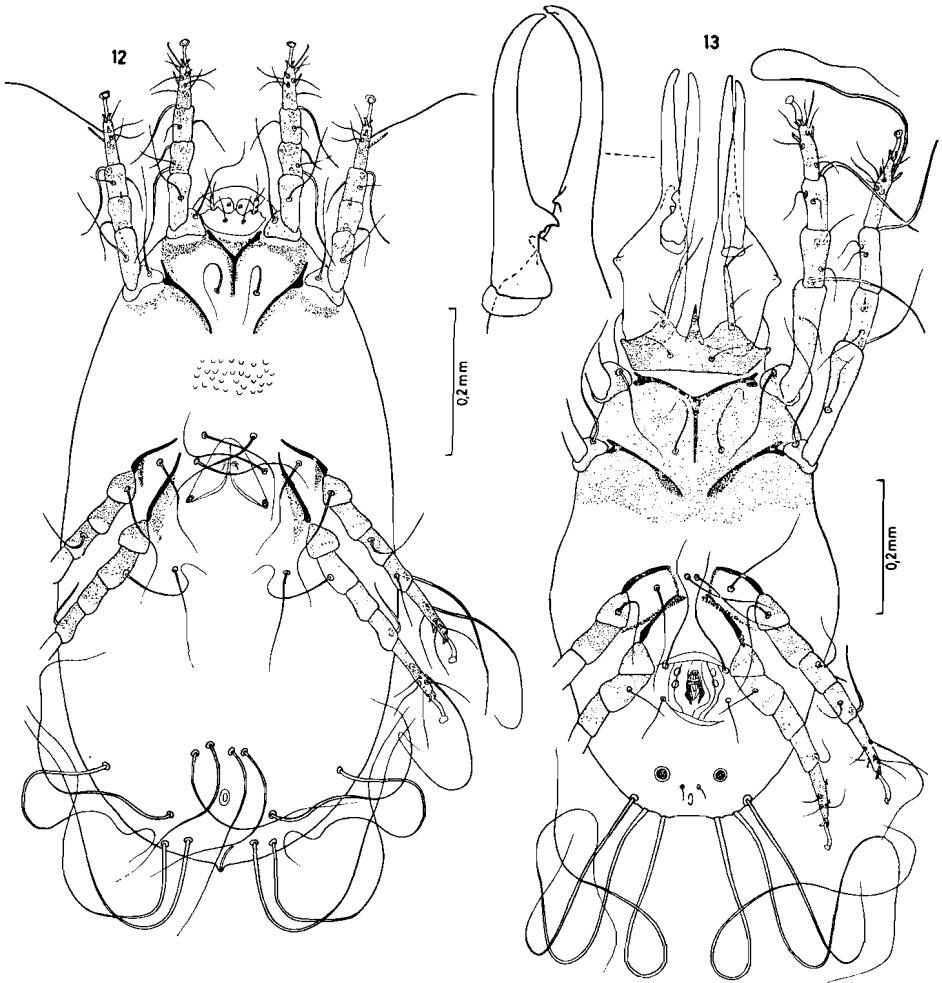


FIG. 12-13 : *Hypodectes propus* (Nitzsch) : Adult female (fig. 12) and male (fig. 13) found free in the nest of *Columba palumbus*, in Belgium.

strong chelicerae ending into two very long digits (fig. 12-15). At first aspect this male resembled the heteromorphic male of *Falculifer rostratus*. However, this mite could not belong to this species nor to any family of the parasitic Acaridiae owing to the structure of the leg chaetotaxy which was typically that of a free-living mite. For instance the tarsi I and II bore respectively 11 and 10 setae

and the anterior tibiae 2 setae. There was also one seta on genu III and one on femur IV (fig. 16-19). In all the parasitic Acaridiae, without any exception, the anterior tarsi bear never more than 8 setae, the anterior tibiae only one seta and there are no setae on the posterior genua or femora.

These mites were, without any doubt, free living-mites. Another curious feature was the fact that the mature eggs enclosed in the female showed two successive layers : an external one chitinous and smooth and an internal one striated and covered by long hairs.

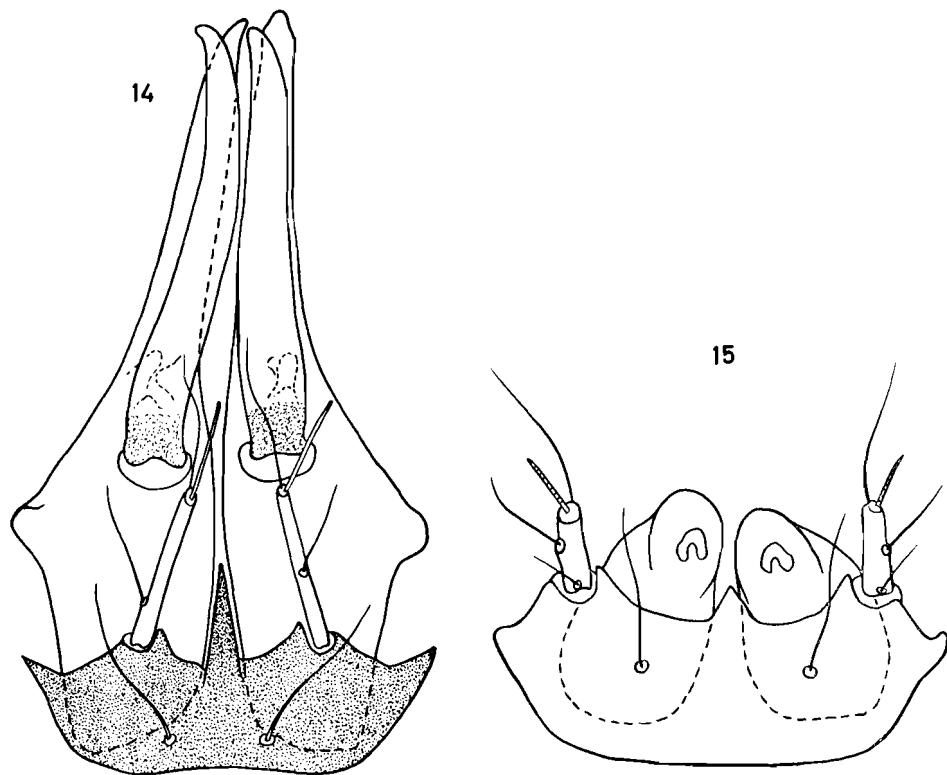


FIG. 14-15 : Gnathosoma and chelicerae of the male (fig. 14) and the female (fig. 15) of *Hypodectus propus* (Nitzsch) (ventral view).

In another nest I found free eggs similar in structure to those enclosed in the female but more developed and containing hypopi. Between the striated-hairy layer and the hypopus there was another layer verrucose in structure. This verrucose layer is probably a protonymphal membrane and the striated-hairy layer a larval membrane. These hypopi were similar in all their characters to the hypopi found in the cellular tissues of the pigeons except that they were much smaller and less sclerotized (fig. 6-8).

I also found free in these nests numerous small hypopi that I could not distin-

guish from those in the eggs, and also 8 large hypopi identical in structure to the hypopi found in the tissue of pigeons. All these large hypopi were in the molting stage and they contained a voluminous verrucous sac. In all of these hypopi this sac was broken and empty except in one where it still contained an adult mite, which was a male identical to the free-living males that I found in the nests. The verrucous sac found in the hypopus is probably the vestige of the tritonymphal stage.

So it became clear that the hypopi found under the skin of the pigeons were not the deutonymphs of a feather mite but those of a mite living free in the nest¹. We created for this mite the new family Hypodectidae (FAIN and BAFORT, 1966) but this name however must fall in synonymy with the name Hypoderidae proposed by Murray in 1877.

It is now possible to trace the life-cycle of this very curious mite. The adult mites are present in the nest only during the breeding period of the bird. As soon as the bird is incubating its eggs, the large hypopi that infiltrate the subcutaneous tissues of the abdomen begin to migrate. They pass actively through the skin and drop in the nest. This migration is probably induced by the lactation hormone that impregnate the bird at that moment. After its dropping in the nest the hypopi molt into adults. Owing to the strong reduction of its cheliceras the female is probably not able to feed. It seems that the male with its monstrous chelicerae does not feed either. This suggests that the adults have only a very short life.

The female produces numerous eggs which all develop directly into hypopi. These hypopi are very small but they have the same structure as the large tissue hypopi. They penetrate through the skin of the young pigeons as soon as the pigeons hatch from their eggs. I have found many of these small hypopi under the skin of pigeons of only a few days old. The infestation of the birds continues as long as they are in the nest. Under the skin of the bird the hypopi absorb food by osmosis and they develop finally into the large forms. The complete development probably takes several months.

As soon as the young birds have left the nest the adult mites die and disappear. It seems therefore that the role of the adult mites is only to produce rapidly a great number of hypopi during the short time that the young birds are in the nest.

One of the most strange aspects of this mite is probably the fact that the adult mites, although they have mouth parts, do not feed, whereas the hypopus which has no mouth at all is the only feeding stage. Actually it is a very active feeder. When the hypopus invades the young bird it is only 150 microns long. When it leaves the adult pigeon after having completed its growth, it reaches about 1500 μ in length.

1. For the description of these adults see FAIN and BAFORT 1966 and 1967. The hypopi have been figured by FAIN 1967.



FIG. 16-22 : *Hypodectes propus* (Nitzsch). Adults : Leg I of the homeomorphic male (fig. 16) ; legs I (fig. 17) and IV (fig. 18) of the heteromorphic male ; leg I of the female (fig. 19). Hypopus : legs I (fig. 20), III (fig. 21) and IV (fig. 22).

After this brief review of the morphological and biological modifications in relation with the adaptation to parasitic life I should like to discuss now shortly the important question of the origin of the endoparasitic mites. These mites could have evolved either from the ectoparasitic forms living on the same host or directly from some free forms living in close contact with the hosts.

The first eventuality is probably true when the host harbours both ectoparasitic and endoparasitic forms closely related to each other. The transformation from ecto to endoparasitic form is probably very old and must have happened at a time when the ectoparasites were still undifferentiated and devoid of any specialized character. It is possible that even in these cases the endoparasites might have been derived directly from more primitive and probably free-living or semi-parasitic forms like those encountered in the nests of birds and in the burrows of mammal.

This direct evolution has probably taken place in all the groups where ectoparasitic forms are absent as is the case in the family Ereyneidae which comprises only free living and endoparasitic mites (FAIN, 1965a).

New studies of the fauna of the nests would probably throw more light on this important problem and bring an answer to some of these questions.

BIBLIOGRAPHY

- EVANS (G. O.) & TILL (W. M.), 1966. — Studies on the British Dermanyssidae (Acari : Mesostigmata). Part II. Classification. — Bull. Br. Mus. nat. Hist. zool., **14** (5) : 109-370.
- FAIN (A.), 1961. — Une nouvelle famille d'acariens, parasites de serpents du genre *Mehelya* au Congo : Omentolaelaptidae Fam. nov. (Mesostigmata). — Revue Zool. Bot. afr., **64** (3-4) : 283-296.
- FAIN (A.), 1962. — Les Acariens mésostigmatiques ectoparasites des serpents. — Bull. Inst. r. Sci. nat. Belg., **38** (18) : 1-149.
- FAIN (A.), 1963a. — Chaetotaxie et classification des Speleognathinae. — Bull. Inst. r. Sci. nat. Belg., **39** (9) : 1-80.
- FAIN (A.), 1963b. — Les Acariens producteurs de gale chez les Lémuriens et les singes avec une étude des Psoroptidae (Sarcoptiformes). — Bull. Inst. r. Sci. nat. Belg., **39** (32) : 1-125.
- FAIN (A.), 1964. — Chaetotaxie et classification des Gastronyssidae avec description d'un nouveau genre parasite nasicole d'un Écureuil sudafricain (Acarina : Sarcoptiformes). — Revue Zool. Bot. afr., **70** (1-2) : 40-52.
- FAIN (A.), 1965a. — Quelques aspects de l'endoparasitisme par les acariens. — Ann. Parasitol., **40** (3) : 317-327.
- FAIN (A.), 1965b. — Un nouveau type d'hypope, parasite cuticole de Rongeurs Africains (Acari : Sarcoptiformes). — Z. Parasitkde, **26** (1) : 82-90.
- FAIN (A.), 1965c. — A review of the family Epidermoptidae Trouessart parasitic on the skin of birds (Acarina : Sarcoptiformes). — Verh. Konink. Vl. Acad. Wetensch. Let. schone Kunst. België, N° 84, Part I : 1-176 ; Part II : 1-144.

- FAIN (A.), 1967. — Les Hypopes parasites des tissus cellulaires des oiseaux (Hypodectidae : Sarcoptiformes). — Bull. Inst. r. Sci. nat. Belg., **43** (4) : 1-139.
- FAIN (A.) & BAFORT (J.), 1966. — Les Hypopes parasitant les tissus cellulaires des pigeons sont les deutonymphes d'un acarien libre et pas celles d'un acarien plumicole (Note préliminaire). — Revue Zool. Bot. afr., **74** (3-4) : 313-316.
- FAIN (A.) & BAFORT (J.), 1967. — Cycle évolutif et morphologie de *Hypodectes* (*Hypodectoïdes*) *propus* (Nitzsch) acarien nidicole à deutonymphe parasite tissulaire des pigeons. — Bull. Acad. r. Belg. Cl. Sci. : sous presse.

DISCUSSION.

F. RADOVSKY (U.S.).

What do you consider the "hypopal" stage to represent in *Falculifer*? Is this the deutonymph?

FAIN (Belgium).

Yes. It appears directly in the eggs, but when you examine the egg containing a hypopus you find two membranes, the larval membrane and the protonymphal membrane.

J. BRADY (U.K.).

By what means does this new species of tissue parasite (hypopus) digest and ingest the host tissues? Is there any sign that the cuticle of the mite is modified to this end as, for example, in parasitic nematodes?

FAIN.

Food probably passes directly through the cuticle because there is only one small orifice in these hypopi and this is the anal orifice. It is a very small orifice and it seems unlikely that the hypopi would feed through the anal orifice.

EVANS (U.K.).

We have recently sectioned these hypopi. The material was not in an very good state of fixation and the only internal structures that one could make out definitely were the muscles to the appendages, which are important, of course, for the animal's movement; a very well developed nervous system and large oral or salivary glands with ducts running towards the anterior end of the body. It seems highly probable that these hypopi produce large quantities of digestive enzymes to break down the surrounding tissues, but how the digested food enters the animal is problematic. The cuticle seems to be well sclerotized except possibly for certain regions between the legs.

FAIN.

It seems that it has no digestive tract.

EVANS.

No, there does not appear to be a well-defined digestive tract.

FAIN.

When the hypopi have grown to about one millimeter in length you can see in the posterior part of these hypopi many granules. I don't know whether they are fat globules or other material but they appear in the posterior regions of the parasites body : maybe it is nutriment absorbed from the bird. These hypopi always lie in the fat of the bird and very often they are impregnated with fat ; when mounted fat granules escape from the specimen. I don't know if they absorb fat but it would be a very interesting question to know whether they are able to absorb fat directly.

AMERSON (U.S.).

If the hypopi have no mouthparts, how do they get in or out of the host ?

FAIN.

They have salivary glands and very large and strong legs. It would not be difficult for them to break open the skin with the claws of these legs. Actually, I have found them beneath the skin of small pigeons only three or four days old. The skin of these birds is very delicate and breaks very easily. There is also the problem of hypopi coming out of the bird. They do so by way of special incubator plates which are present on the abdomen of the birds.

AMERSON.

But some birds don't have these plates.

FAIN.

They probably have no hypopi.

HUGHES, A. M. (U.K.).

Have you seen any signs of breakdown of the tissues of the pigeon ?

FAIN.

Hypopi are so small, about 150 microns, that it is not possible to follow them under the microscope. But I have found them around the anus of very small pigeons. There were several under the skin. I have never seen them crossing the skin but probably they are very fast and you would be lucky to see them.

VERCAMMEN-GRANDJEAN (U.S.A.).

Did you observe the relative proportions of adult and larvae.

FAIN.

The larvae are always very small.

VERCAMMEN-GRANDJEAN.

How would you explain the fact that a hypopus can give rise to an adult which is bigger than itself ?

FAIN.

Probably the egg was very rich in yolk.

TREAT (U.S.A.).

I understand that the hypopi, when engorged, contained considerable fat. Is that so ?

FAIN.

It seems so but it is not proved. I have no idea what kind of material they contain but it is a granular material.

VERCAMMEN-GRANDJEAN.

You have no idea what causes this increase in size ? Might it result from the absorption of water ?

FAIN.

I can't explain why one hypopus can give rise to a female with 30 or 40 eggs. They must absorb very rich food. I don't think they absorb water. During the transformation from small hypopi to very large hypopi there are some morphological modifications. The epimera disappear completely and are replaced by other epimera. These particular epimera are much longer than the primary epimera and are required for the insertion of new muscles. The large hypopi need very large amount of muscles to cross the skin of the big pigeons and so it is necessary that they have food for the construction of new tissues.

TREAT (U.S.).

If the hypopi absorb food rather than water only, it seems inappropriate to refer to the process as "osmosis".

FAIN.

There is a rapid and active crossing of the food.

EVANS.

There was no evidence of fat in the hypopi I sectioned. They were over 1,000 μ in length.

FAIN.

In order to exclude fat you have to examine small hypopi during the stage of feeding.

EVANS.

I think another very interesting feature of the life cycle of this mite is the synchronisation of the life cycle of parasite with the reproductive cycle of the host. This phenomenon is probably widespread in many groups of parasitic mites.