

NOTES ON THE INTERNAL ANATOMY, THE FOOD REQUIREMENTS AND DEVELOPMENT IN THE FAMILY EREYNETIDAE (TROMBIDIFORMES)

BY

R. A. BAKER. *

INTRODUCTION.

Mites of the family Ereynetidae are small, whitish creatures possessing a suture between the propodosoma and hysterosoma and a body covered by a soft and finely lined integument. The family includes both free living and parasitic forms and is placed in the Trombidiform group of mites. Host parasite relationships, phylogenetic considerations and a range of forms showing increasing specialization for a parasitic mode of life have produced added interest in the group. The following account is a summary of some of the more recent work carried out on the biology of this family of mites arranged under the headings of internal anatomy, postembryonic development, nutrition and host parasite relationships.

INTERNAL ANATOMY.

The internal anatomy of the Ereynetidae is not well known and the information we have is based essentially on one species only, named *Riccardoella limacum* (Schrank) together with some brief observations on the gross anatomy of the alimentary canal in *Xenopacarus africanus* (Fain, Baker and Tinsley, 1969) and the respiratory system of *Lawrencarus eweri* (= *Riccardoella eweri* Lawrence, 1952). As far as is known no other work has been published on the internal anatomy of this or any other closely related family of mites.

The structure of the alimentary canal of *R. limacum* was briefly considered by TURK and PHILLIPS (1946) and studied more closely by BAKER (1967, 1970 b). The gut structure and nutrition of a recently described new mite, *X. africanus*, was studied by BAKER (1971). The alimentary canal of these mites consists of a powerful sclerotized muscular pharynx, a long narrow unsclerotized oesophagus, a ventriculus and associated paired blind ending caeca together with the salivary glands anteriorly and a mid dorsal duct running posteriorly which has an excretory function and may represent the hind gut in the trombidiform mites. Figure 1 is a longitudinal section roughly through the middle of the body, of *R. limacum* showing some of the main internal organ systems.

The salivary glands are complex. Both TURK and PHILLIPS (1946) and BAKER (1967) experienced difficulties in homologizing them and comparing the glands with what is known to exist in related forms of mites. The glands are widespread both paired and unpaired and their relationships and identity are uncertain as indeed is their function. However, their position, size

* Zoology. department, University of Leeds, England.

and number suggest that they may play a part in effecting entry into and in histolyzing the tissues of the host in those forms which are parasitic. TURK and PHILLIPS (1946) noted the atrophy of some of the glands and the absence of anterior and pericibal glands compared with other closely related groups of mites whereas BAKER (1967) described a large branched unpaired gland and paired anterior and posterior dorsals. The salivary glands are not well developed in *X. africanus* when compared with *R. limacum* and this may suggest a different feeding method in the former species.



FIG. 1 : Median longitudinal section through *Riccardoella limacum* to show the main organ systems of the body.
b — brain, e — excretory canal, o — ovary, ov — oviduct, s — salivary gland.

According to TURK and PHILLIPS (1946) the anterior portion of the oesophagus is the part of the alimentary canal through which absorption takes place. They based this assumption on the very thin walled cells lining this organ and on peristaltic movements of the ventriculus which appeared to drive fluid forward into the oesophagus. There appears to be little support for this idea. BAKER (1970 *b*) recognised the gut caeca as the main site for digestion and absorption. These are paired structures, highly extensible and thus variable in shape and size, and occupy a mainly dorsal position taking up most of the internal volume of the mite. BAKER (1971) recorded 6 pairs of these laterally placed caeca in *X. africanus*, clearly demarcated in this species by

the large amounts of black haematin granules contained within them. Their contents will be described more fully in the section dealing with nutrition but it is clear that they contain cells which may represent food and enucleated spherical bodies which may have arisen as a result of the continuous shedding of the gastrodermal cells lining the mid gut, a phenomenon commonly recorded by other workers in trombidiform mites and in blood sucking ticks.

Although there is now some doubt as to the homology of the excretory canal, it was thought to represent the hind gut in trombidiform mites, most authors have recorded the presence of a mid dorsal duct whose posterior portion is expanded into a "rectum" or urodaeum which TURK and PHILLIPS (1946) observed to be gradually filling up with excretory products and on occasions to be completely filled with solid white crystalline matter. Unlike most other trombidiform mites the excretory organ of *R. limacum* appears to retain its connection with the ventriculus (BAKER, 1967) and may therefore serve to remove food residues from the ventriculus in addition to its excretory function. The lumen of the excretory canal enlarges enormously in starved mites, develops lateral pouches and contains spherules which are presumed to be guanine (BAKER, 1967).

The nervous system of *R. limacum* consists of one large elongated 'brain' which represents a fused mass of ganglia lying in an antero-ventral position in the body. Running through the

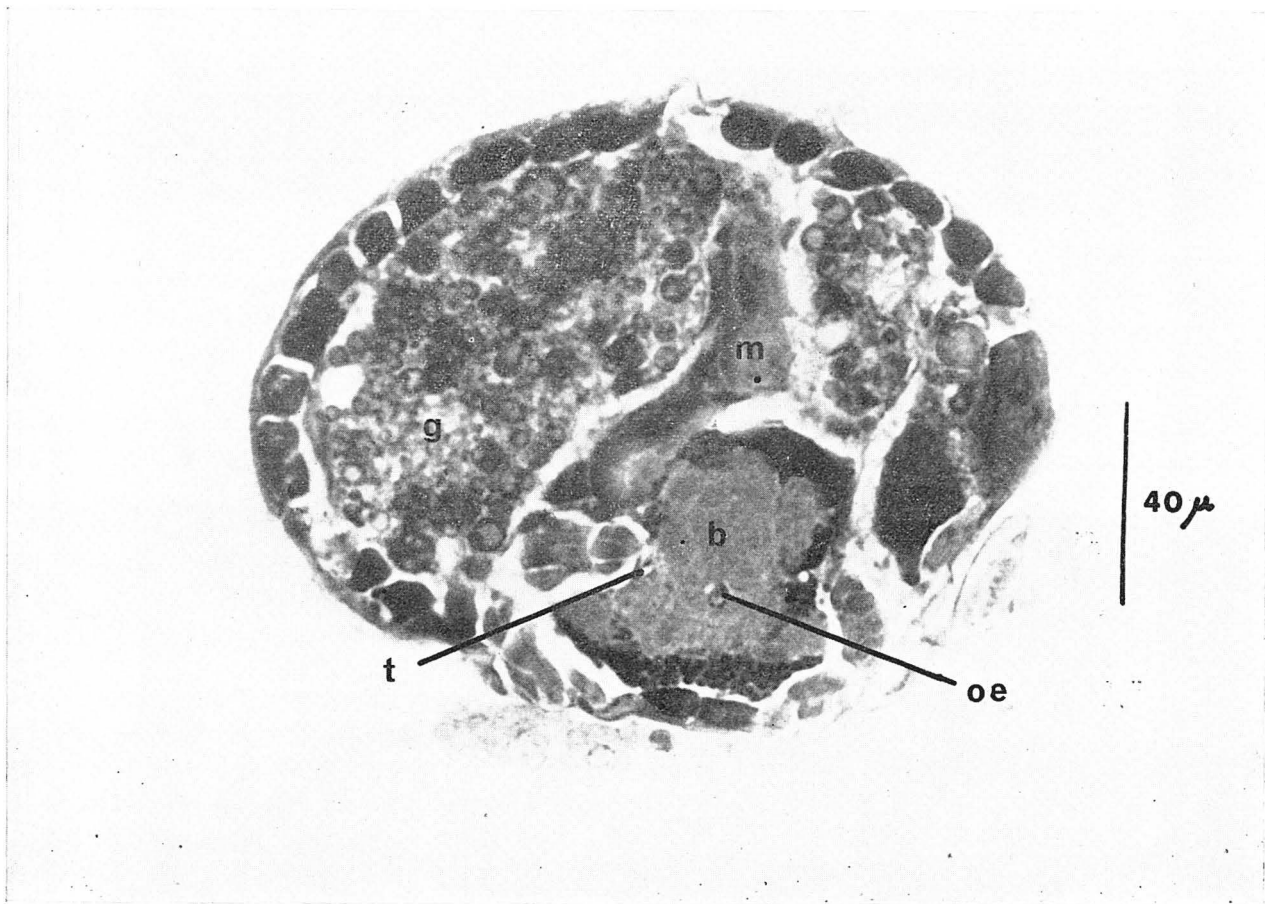


FIG. 2 : Transverse section of *Riccardoella limacum* through the region of the brain.
b — brain, g — gut caecum, m — mid gut, oe — oesophagus, t — tracheal trunk.

middle of this mass is the oesophagus, which divides the brain into supra- and sub-oesophageal parts. Figure 2 shows a transverse section of the body of *R. limacum*, through the region of the brain. BAKER (1967) observed a thick covering particularly over the front, dorsal and ventral parts of the brain of so called ganglion cells which have a strong affinity for haematoxylin. The fibrous part of the brain occupies the large central position. TURK and PHILLIPS (1946) observed four pairs of pedal nerves palpal (pedipalpal) and a posterior pair of nerves but no pharyngeal nerve. In addition BAKER (1967) records paired cheliceral and a single stomodael nerve as well as pharyngeal and abdominal nerves but found difficulty in tracing them.

Both TURK and PHILLIPS (1946) in *R. limacum* and Lawrence (1952) in *L. eweri* (= *R. eweri*) noted a reduced tracheal system in the adult, in fact Lawrence was unable to see any of it in the adults of *L. eweri*. Both writers, however, found a very distinct and well developed system of tracheae in the immature stages but did not discuss the reasons for this apparent deviation from the condition found in other acari.

The reproductive system of *R. limacum* is the most complex and widespread organ system within the body. TURK and PHILLIPS (1946) gave no account of the male system, believing as they did that the male was a rarity and also because of the difficulties they experienced in sectioning the material. The female system consists of a single ovary, oviduct, vagina and external valves. BAKER (1967) records oogonia, oocytes and ova at various stages of development in

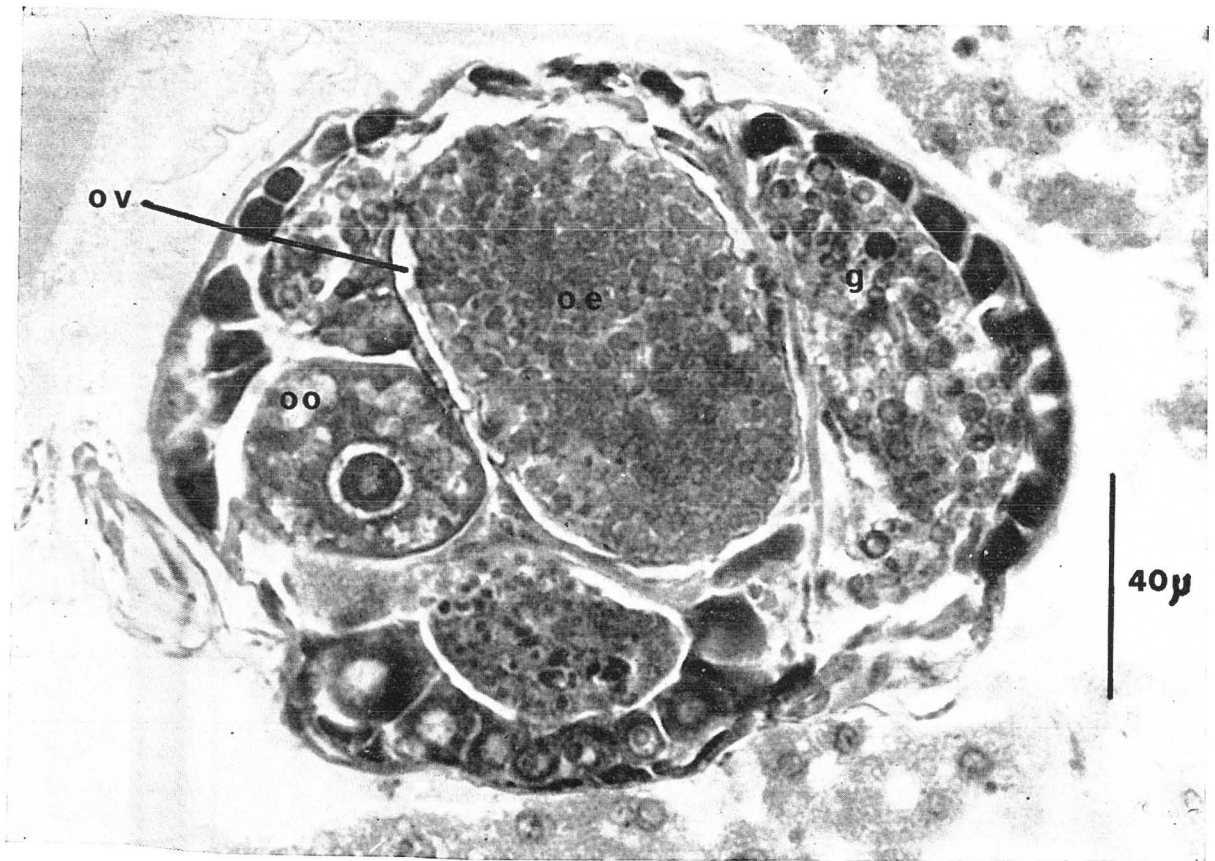


FIG. 3 : Transverse section of a female *Riccardoella limacum* through the reproductive region of the body.
g — gut caecum, oe — oviducal egg, oo — oocyte, ov — oviduct.

the ovary with ovarian eggs lying peripherally at the sides of the oviduct. According to TURK and PHILLIPS (1946) the single oviduct is rather convoluted and leads into a posterior sac into which opens the receptaculum seminis. BAKER (1967) on the other hand, recorded a straight oviduct and a short narrow vagina having a chitinous intima continuous with the external cuticle and a small pair of oval shaped glands at the posterior end of the vagina which he believed, from the point of view of position and structure, were suggestive of receptacula seminis. Figure 3 is a transverse section of the body of a female *R. limacum* through the reproductive region showing the ovary, an oviducal egg and the gut caeca.

Oviducal eggs have a shell and contain yolk spherules and are normally present in sectioned females. Histochemical tests demonstrated the presence of protein and polysaccharide within the eggs, and a strongly positive Alcain blue reaction lining the inner wall of the oviduct suggests the presence of acid mucopolysaccharide which probably lubricates and aids the passage outwards of the eggs.

The male system of *R. limacum* consists of testes containing sperms with tails, paired vasa deferentia, lined by a single layer of highly vacuolated columnar cells, which fuse posteriorly to form a large single seminal vesicle. This has an irregular outline externally, and is likewise lined by a single layer of large columnar cells which take up basic dyes and show purple metachromasia with Hoyer's thionin suggesting the presence of mucoid substances. An ejaculatory duct and at least one accessory gland is present in the hind part of the male tract where a spermatophore is often seen (BAKER, 1967). There is a well developed sclerotized penis present in some species.

POSTEMBRYONIC DEVELOPMENT.

THOR (1933) was one of the first authors to describe the life history of the family in general terms. He referred to a six legged larva and eight legged nymphal stage and stated that development was simple and direct. The female members of the family were described as oviparous and were frequently found to contain a large egg.

FAIN (1957) reclassified the family into three subfamilies, namely the Ereyetinae, Lawrencarinae and Speleognathinae. In the first subfamily postembryonic development includes three nymphal stages, in the Lawrencarinae only the proto and deutonymph are present whereas in the Speleognathinae nymphal stages are absent.

GRANDJEAN (1939) described development in certain free living species of *Ereyetes* and *Opsereyetes* which have three successive nymphal stages between the larva and adult. Nymphs can be separated from hexapod larvae by having eight legs and from the adult stage by the appearance of a genital opening in the adult stage only. BAKER (1970 a) described the life history of *R. limacum*, a form closely related to *Ereyetes*, and was in fact able to demonstrate three nymphal stages in laboratory cultures, indicating that the slug mite follows the typical pattern in the subfamily Ereyetinae, in spite of the fact that it is no longer a free living species. The only nymphal stage found on slugs in the field was the deutonymph, which may be an indication that both protonymphal and tritonymphal stages are short lived or alternatively that they spend their time in the mantle cavity of slugs and were thus unobtainable by the collecting method used. TURK and PHILLIPS (1946), however, mentioned only two nymphal stages in the life history of *R. limacum*, the proto and deutonymph, which they separated on the basis of size measurements alone, finding a gap of approximately 30 μ between each active life cycle stage.

Development is still largely unknown in the other two subfamilies. FAIN (1962) referring briefly to development in the Lawrencarinae, mentioned the fact that a completely developed

larva is sometimes observed in the body of adult females and that the species of this subfamily were viviparous or ovoviviparous and Baker (unpublished observations) has noticed differences in embryonic development between *R. limacum* and *X. africanus* which indicate that the former is oviparous and the latter viviparous or ovoviviparous.

In the Speleognathinae a free living nymphal stage is absent but a recent detailed study by FAIN (1972) has demonstrated the existence of three vestigial nymphal phases within the larval skin. They take the form of membranous sacs without any sclerotized structure apart from the pharynx and appear to be completely inactive and immobile. All the development from the protonymph to the adult takes place within the larva and up to four sclerotized pharynges, of different sizes, can be seen in the cast larval skin. Such acceleration of the evolutionary cycle within this subfamily is thought to be an adaptive character related to parasitism.

A complex deutovial membrane occurs within the egg. On this develops a chitinous dehiscient organ which is thought to help in the hatching of the larva. In the same way the larva itself has its own dehiscient organ (FAIN, 1972).

Sexual dimorphism is more marked in the free living species and in those forms living in invertebrates than in those forms parasitizing the vertebrates (Speleognathinae). In free living forms such as *Ereynetes* or *Opsereynetes* males are distinguished from females by the very sclerotized armature of the genital region and by the presence of specialised hairs in this region of the males (GRANDJEAN 1939, FAIN 1964). BAKER (1970 a) working on *R. limacum* distinguished males from females by the shape of the genital opening and the presence or absence of barbed setae. The female opening is long and narrow, whereas the male has an oval shaped aperture which is broader and shorter than that of the female. In addition the male has a more strongly sclerotized lining to this opening and possesses three pairs of barbed setae in the genital vestibule. In the Speleognathinae, although sexual differences are less marked they still occur, for example (FAIN 1963 a) the large hairs on the front surface of legs I of the females in *Paraspeleognathopsis strandtmanni* Fain and the network of chitinous lines on coxae III and IV in the males of *Boydaia sinensis* Fain and Bafort (1963).

Perhaps the most interesting feature of the life cycles so far described in this family is the case of apparent neoteny recorded by TURK and PHILLIPS (1946) in *R. limacum* and by FAIN (1963 b, 1964) in parasitic species such as *Boydaia trochila* Fain. BAKER (1970 a), however, could find no evidence for a neotenuous deutonymph in *R. limacum* or that the adult stage was disappearing from the life cycle as TURK and PHILLIPS believed. He found adult females normally containing eggs and both adult males and females were by far the most commonly occurring active stages taken from slugs at different times of the year.

The life cycles found within the family Ereynetidae can best be summarized as follows. The free living forms have the following life cycle : egg — larva — protonymph — deutonymph — tritonymph — adult. This pattern is maintained in *R. limacum* and is characteristic of the subfamily Ereynetinae. In those forms parasitic in toads and frogs, the Lawrencarinae, there is a reduction in the number of active nymphal stages to two and the life cycle becomes egg — larva — protonymph — deutonymph — adult. In the Speleognathinae, parasitic in birds and mammals the active nymphal stages are absent and their life cycle is : egg — larva — adult. Since reduction in the number of active life cycle stages and ovoviviparity/viviparity are often associated with a parasitic mode of life the features described may well indicate a steadily increasing parasitism through the three subfamilies.

NUTRITION AND HOST PARASITE RELATIONSHIPS.

The majority of trombidiform mites are fluid feeders on the juices of plants and animals. Nothing is known about feeding in the free living forms of the Ereyneidae and it can only be assumed that they are predacious or feed on plant juices like the closely related tydeid mites. THOR (1933) was cautious when, referring to the family, he stated that 'It is probable that these mites suck in different fluids but no one knows with certainty what the food is'.

Published work on the nutrition is confined to those forms associated with invertebrates and vertebrates. Not until the food and method of feeding has been established can any real attempt be made to examine the exact relationship existing between a particular Ereyneid and its 'host'. The 'hosts' of Ereyneids include slugs, snails, insects, frogs, toads, birds and mammals and in most cases the mites live associated with the respiratory passages of these animals. The features of a respiratory apparatus normally include a good blood supply and an epidermal lining of cells producing a layer of mucus over the surface. Perhaps because parasitic Ereyneids live associated with this system it has previously been assumed by authors that mucus forms the diet of this group of mites. In the case of *R. limacum*, TURK and PHILLIPS (1946) believed the food to be the mucus of slugs or snails but felt it may be supplemented by the role of intracellular symbiotic Haplosporidia present in the gut of the mite supplying vitamins of the B group.

LAWRENCE (1952) working on *R. eweri*, now redescribed as *Lawrencarus eweri* (FAIN, 1957) observed that these parasites appeared to live in the mucus of the host's nasal cavities but was not certain that this species fed on mucus, because the alimentary canal was filled with a black opaque substance resembling the stomachs of typical blood sucking mites. It was thought possible also that they may feed on small solid particles embedded in the mucus of the host. BAKER (1970 b) examined the food and feeding of *R. limacum* and came to the conclusion that this species was not a mucus feeder. Histochemical tests carried out on transverse sections failed to demonstrate mucus in the gut caeca of the mites. The caeca contained large numbers of cells and cellular fragments some of which closely resembled the amoebocytes found in the tissues of their slug hosts. He came to the conclusion that *R. limacum* fed on the blood of its host. BAKER (1971) working on *X. africanus*, which lives in the nasal passages of the African clawed toad *Xenopus laevis* Daudin, demonstrated the presence of blood in the gut of the mite using histochemical tests, but could find no intact *Xenopus* erythrocytes. Large amounts of haematin were found arising as a result of the degradation of haemoglobin by the mite. Haematin marks the end product of haemoglobin digestion in this species. A parasite of passerines, *Boydala nigra*, presents a black opaque appearance due to its gut contents and there seems little doubt that this Ereyneid also is a blood feeder.

It should not be assumed that all parasitic Ereyneids feed on blood. Only a few species have so far been examined and no work has been carried out on the food and feeding of the Speleognathinae. If, however, mucus were the food source in some species the mites would have to deal with large quantities of a highly viscous material which would produce difficulties in transfer to the mouth and swallowing.

The chelicerae of *X. africanus* consist of a fixed basal digit and a pointed, serrated movable digit as described and illustrated in FAIN, BAKER and TINSLEY (1969). The chelicerae in this case appear capable of achieving entry into host tissue. On the other hand, the digitus mobilis of *R. limacum* is long, slender and needle-like and in the view of TURK and PHILLIPS (1946) the mouthparts appear to be inadequate for piercing the skin of their host. However, one must take into account the role of the salivary glands when considering the possibility of entry into

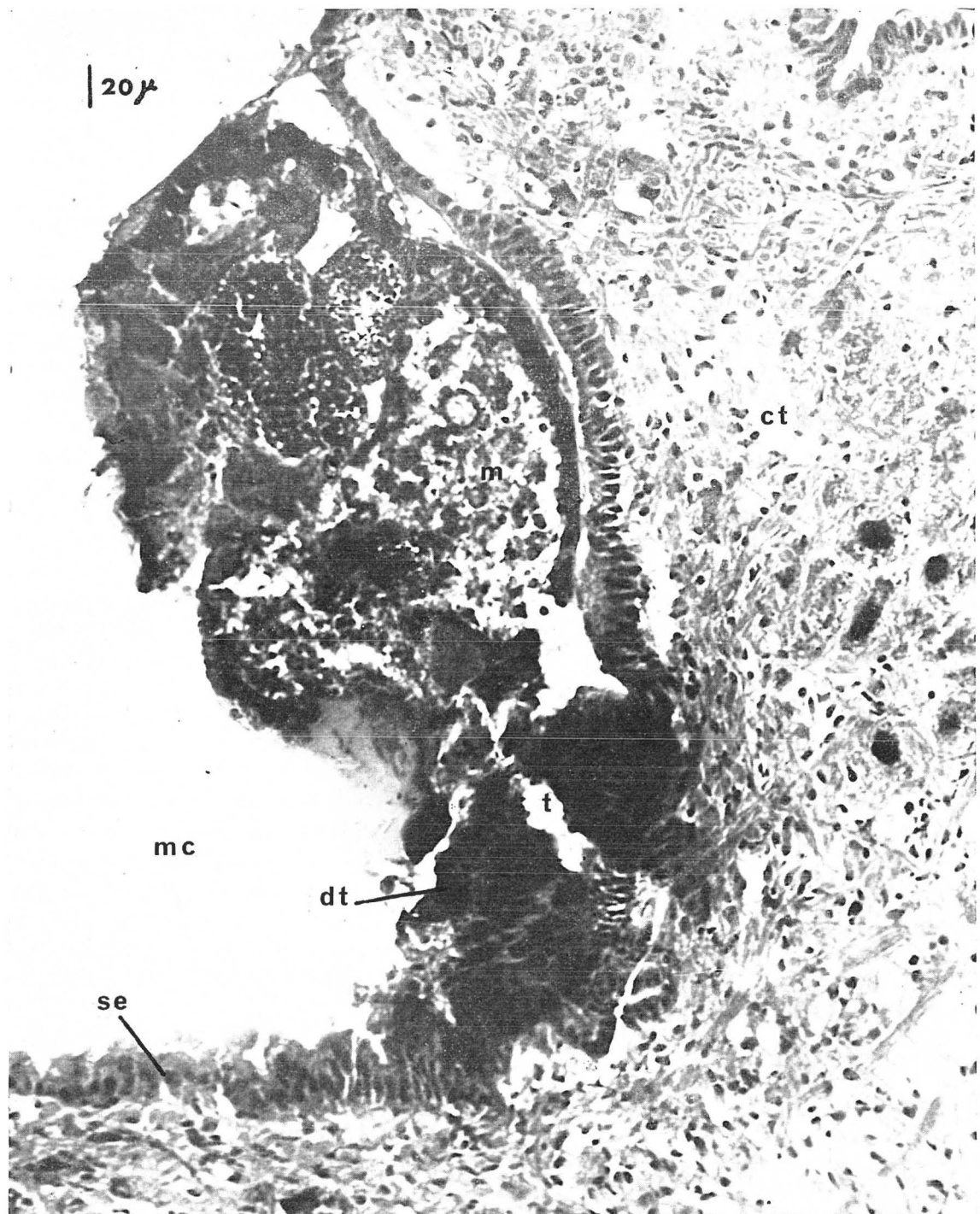


FIG. 4 : Section through the mantle cavity and connective tissue of a slug showing a frontal section of *Riccardella limacum* in situ within the mantle cavity and attached to the body of the slug. The formation of a tissue canal can be seen surrounded by the displaced and disorganized epithelial tissue of the slug. ct — connective tissue of slug, dt — disorganised slug tissue, mc — mantle cavity, se — epithelial lining of mantle cavity, t — tissue canal.

host tissue. The very extensive and well supplied array of glands at the anterior end of this animal, to which a salivary function has been assigned, would be sufficient to effect penetration of host tissue once initial attachment had been made. The ejection of an active salivary secretion which dissolves host tissue by pre-oral digestion leads to the establishment of a tissue canal (cytostome, stylostome or histiosiphon) in the tissues of the host. A large number of workers including ANDRÉ 1927, JONES 1950, HOEPPLI and SCHUMACHER 1962, SCHUMACHER and HOEPPLI 1963 and WHARTON and FULLER 1952 have studied this organ produced by trombidiform mites but there is still disagreement as to its exact formation and function. The tissue canal of *R. limacum* has been described briefly by BAKER (1970 *b*), and an early stage in its establishment is illustrated here in Figure 4. The epidermal lining of the mantle cavity of a slug and a section of the mite in situ within this cavity is shown. Alteration and multiplication of host epidermal cells has occurred leading to the production of two masses of disorganized host tissue in the centre of which the tissue canal has been produced. When fully developed it can have a length far in excess of that of the mite and has a strong affinity for Heidenhains Iron Haematoxylin. The general consensus of opinion is that it arises as a result of the salivary activities of mites but may also be the result of a reaction on the part of the host. Once established the tube serves to provide a single passage in host tissue for the ejection of saliva and for the suction of food. In the case of *R. limacum* mites are found embedded in slug connective tissue and have presumably reached this position by destruction of host tissue and gradual migration inwards as a result of their feeding process.

The feeding of ereynetid mites, involving the production of a stylostome, appears to be basically similar to that already described in such trombiculid mites as *Neotrombicula zachvatkini* Schluger and *Trombicula autumnalis* Shaw. However, SCHUMACHER and HOEPPLI (1963) were of the opinion that in the case of *N. zachvatkini*, the salivary secretions produced little histolysis of host tissue, believing that histolytic activities could be dispensed with if a connection with the intercellular spaces of the host was maintained via the tissue canal.

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