

STUDIES ON THE MORPHOLOGY OF THE TROMBIDIID MITE
ALLOTHROMBIUM LEROUXI MOSS (ACARI)¹

BY

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ABSTRACT

Aspects of the external and internal anatomy of the red velvet mite *Allothrombium lerouxi* Moss are reported from study of wholmounts and serial sections. The scuta and genitalia of nymph and adult are described and figured, and the utilization of these structures as valid developmental characters is discussed. The respiratory system, digestive system, circulatory system and nervous system of the adult are described and figured; attention is drawn to the tendency of some authors to confuse salivary ducts with respiratory structures.

Relatively few morphological studies of Acari have appeared in recent years; little attention has been paid the Trombidiidae since the pioneer work of PAGENSTECHER, CRONEBERG and HENKING. The problems encountered by those who have attempted to set up a workable classification for this latter group emphasize the need for renewed investigations into basic trombidiid morphology.

The present paper considers certain aspects of *Allothrombium* anatomy that were either not discussed in HENKING'S (1882) classic work or have been subsequently misinterpreted by more recent workers in acarology. The Nearctic species *A. lerouxi*, the object of the study, is on the basis of larval anatomy (Moss, 1961) very close in its affinities to the Palaearctic *A. fuliginosum* (Hermann) studied by HENKING.

MATERIALS AND METHODS.

The mite material utilized in this study was collected in the spring and fall of 1960 from dead leaves and grass in an apple orchard near Rougemont, Quebec.

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Adults and nymphs intended for preservation as wholmounts were killed and cleared in Nesbitt's solution¹ and mounted in Hoyer's modification of Berlese's mounting medium²; number one or zero coverslips were used. To prevent distortion through crushing, it was necessary to support the coverslip by means of three or more fine slivers of broken, number two coverslips. The chelicerae, pedipalps, legs, scutum and genitalia in wholmounts of nymphs and adults are normally inclined at various angles and in order to obtain an undistorted plane view of these it was found necessary to dissect and mount them separately. Slides intended for permanent preservation were ringed with Murrayite.

Spring-collected adults intended for sectioning were killed and fixed by dropping them into alcoholic Bouin's (The Brasil, 1904 or "Duboscq-Brasil" of Gray, 1954). The specimens were left in the fixative for four hours and then washed in several changes of 80 % ethyl alcohol to remove excess picric acid. After dehydration they were transferred to an absolute alcohol-benzene mixture, impregnated with Tissuemat having a melting point of 56-58° C and embedded. The mites were sectioned at ten microns in sagittal, frontal and transverse planes on a standard rotary microtome. The paraffin ribbons were attached to slides using egg albumen adhesive.

Sections were stained with Heidenhain's iron-mordant haematoxylin, Ehrlich's acid-alum-haematoxylin and Patay's triple stain. Those stained with Heidenhain's and Ehrlich's were counterstained with Orange G. The first method gave, on the whole, unsatisfactory results because of the unfortunate tendency of the albumen adhesive to dissolve away during prolonged immersion in the mordant solution. The methods of Ehrlich and Patay gave excellent results.

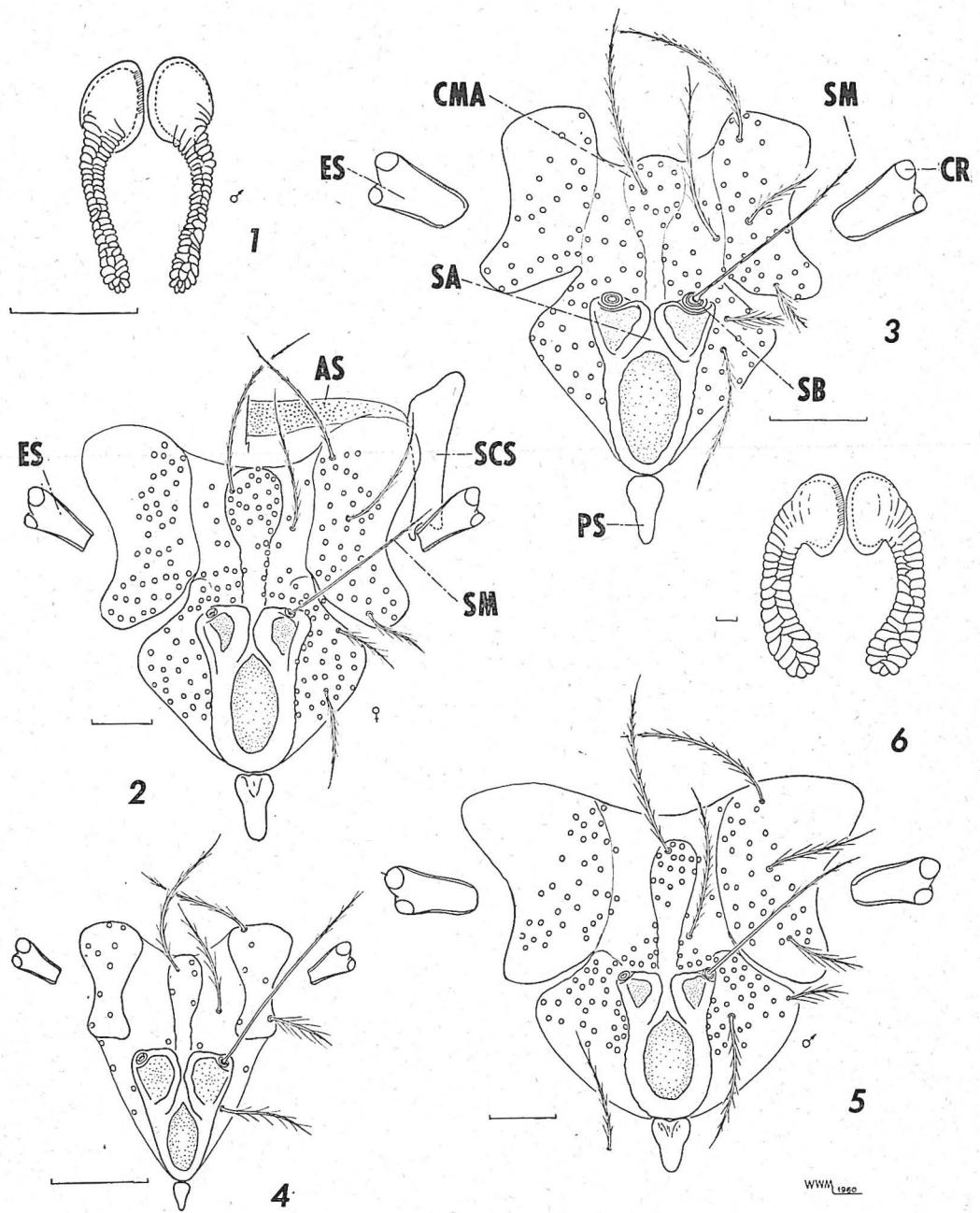
Wholmounts and sections were studied using a phase contrast microscope. Sections stained in Ehrlich's showed to best advantage using phase contrast, whereas those stained with Patay's were better observed by means of ordinary light.

Illustrations were prepared from both wholmounts and sectioned material. They were sketched freehand and with the aid of an Eddinger projection apparatus and camera lucida. Measurements given in microns were obtained by means of an ocular scale calibrated with an object micrometer.

SCUTUM.

A scutum or dorsal propodosomal shield is present in Trombidiidae exclusive of the primitive genus *Trombella* Berlese. The scutum is a sclerotized plate situated

1. 25.0 cc. water.
40.0 gm. chloral hydrate.
2.5 cc. conc. hydrochloric acid.
2. 15.0 gm. distilled water.
30.0 gm. gum arabic (clear crystals).
200.0 gm. chloral hydrate.
20.0 gm. glycerine.



Figs. 1-6. — *Allothrombium lerouxi* Moss; nymph and adult.

Fig. 1. — Peritremes of adult male, dorsal. Fig. 2. — Scutum, eyestalks and supracoxal sclerite of adult female, dorsal. Fig. 3. — Scutum and eyestalks of large nymph. Fig. 4. — Same, of small nymph. Fig. 5. — Same, of adult male. Fig. 6. — Peritremes of large nymph.

Abbreviations : AS, anterior sclerite ; CMA, crista metopica ; CR, cornea ; ES, eyestalk ; PS, posterior sclerite ; SA, sensillary area ; SB, sensillary base ; SCS, supracoxal seta ; SM, sensillum.

Note : The scale line represents 10 μ in figs. 4 and 6, 100 μ in all others. Figures 2-5 were drawn from dissected, flattened scuta; most setae are omitted but their bases are shown as circles.

on the dorsolateral walls of the propodosoma and serving as a locus for muscle attachment. Its shape and development have been utilized in generic and specific characterization. Unfortunately, since the lateral margins of the scutum are frequently indistinct and visible only in dissected material, it is rare that the complete structure is illustrated; this is especially true in the case of the genus *Allothrombium* Berlese.

BERLESE (1912) proposed a terminology for some of the component parts of the scutum; I disagree with some of his interpretations but, pending a review of the comparative morphology of the scuta of Trombidiidae, have retained most of his terms in the description below.

In the adult of *A. lerouxi* the scutum shows varying degrees of sclerotization and undergoes allometric modification during the development of the individual from nymph to adult. It is composed of four components that are distinguished from the supporting lateral areas of the scutum chiefly on the basis of sclerotization. The components of the scutum are the :

- 1) anterior sclerite (fig. 2, AS),
- 2) crista metopica (fig. 3, CMA),
- 3) sensillary area (SA) and
- 4) posterior sclerite (PS).

A *supracoxal sclerite* (fig. 2, SCS) extends from the anterodorsal margin of the first coxa upward and backward along the lateral wall of the propodosoma to embrace the base of the eyestalk. The supracoxal sclerite is not a part of the scutum. BERLESE (1912) figured it in his illustration of the scutum of a species of *Trombidium* Fabricius but did not assign it a name; ANDRÉ (1958) has shown it in his illustration of *A. athleticum*.

1) Anterior sclerite :

This structure (AS) in *A. lerouxi* stretches across the anterior border of the propodosoma as a weakly-sclerotized and faintly tuberculate transverse band. It is free for most of its length but joins the scutum at the anterolateral margins of the latter on each side.

The anterior sclerite is attached to the anterior wall of the propodosoma and hence takes on varying conformations when viewed in wholmounts; because of the delicate construction of the sclerite it is very difficult to remove it in dissection. There appears to be little difference between the structure in nymph and adult.

BERLESE (1912) showed this sclerite in only one of his illustrations of *Allothrombium* but it appears to be well-developed in the species studied by ANDRÉ (1936 and 1958).

2) Crista metopica :

This structure (CMA) in *A. lerouxi* is present as a heavily-sclerotized median rod or plate. It originates as a narrow stalk, U-shaped in transverse section at the anteromedian margin of the sensillary area. After a short distance it expands

into a flattened, paddle-like structure that extends as far as the anterior margin of the scutum and bears numerous pectinate setae.

The crista appears to differ but little in the nymph and adult although in the male its anterior extremity frequently falls short of the anterior margin of the scutum.

The term crista metopica has been used in the past by numerous writers to designate the entire scutum. NEWELL (1958) prefers to restrict the term to the rod-like structure described above. ANDRÉ (1936) refers to the latter as the *dilatation piriforme*.

3) Sensillary area :

The sensillary area in *A. lerouxi* extends from the base of the crista backward along the midline of the scutum. Three areas of reduced sclerotization may be distinguished : these are a median oval area and two anterolateral sub-triangular areas ; the remainder of the sensillary area is heavily sclerotized and pigmented. The sensilla arise from the anterolateral margins of the lateral areas and extend outward and forward at an angle of about 60° from the horizontal.

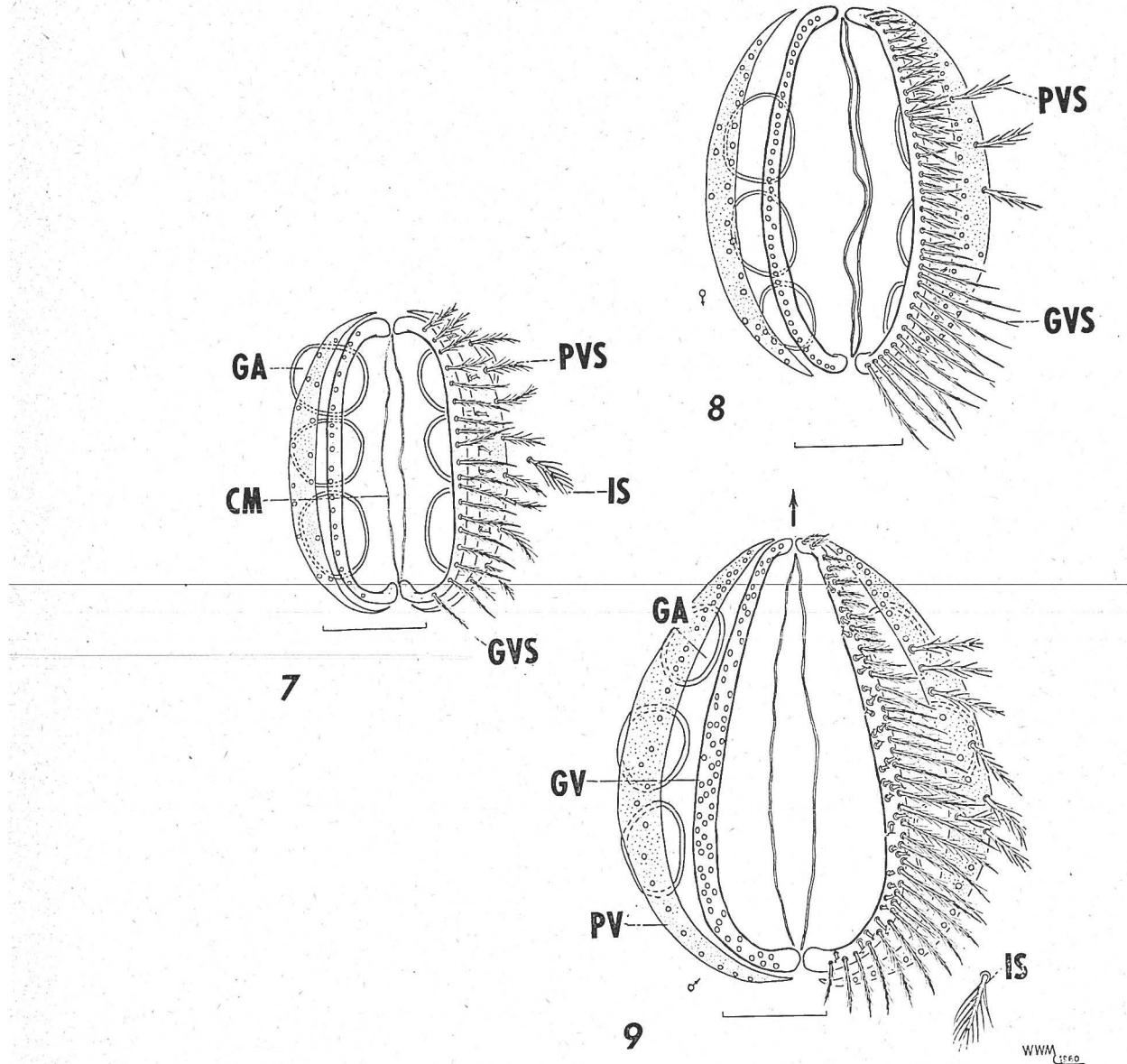
The sensillary area is the most distinctive and most frequently illustrated portion of the scutum.

4) Posterior sclerite :

The posterior sclerite in *A. lerouxi* is a small, sub-pyriform structure that extends backward from the posterior margin of the sensillary area ; its posterior pointed extremity is often at least partially hidden by the overlapping idiosomal integument.

Remarks :

Study of scutal development in postlarval stages of *A. lerouxi* has demonstrated definite evidence of allometric growth. In small nymphs (fig. 4) the entire scutum is relatively narrow and bears a small number of setae, 25 in the smallest specimen available in the present study. The anterolateral punctate portions of the sensillary area are much larger than the median area and the sensillum extends past the distal extremity of the eyestalk. In *A. lawrencei* Meyer and Ryke this latter condition is exceptionally noticeable (MEYER and RYKE, 1960). In a large nymph of *A. lerouxi* (fig. 3) the scutum is more expanded and the setae may number up to 150. The median punctate area has become larger in comparison with the anterolateral areas and the sensilla extend outward as far as the level of the corneae. In the adult stages (figs. 2 and 5) the scutum is quite distinct from that of the nymph and some sexual dimorphism is evident. The scutum is expanded in both sexes, especially in the case of the anterolateral and posterolateral scutal margins in the male. The number of scutal setae may range from 180 to 200 with a slightly larger number on the scutum of the female. The median punctate area in both sexes is greatly enlarged in comparison with the anterolateral areas and the sensilla extend but a short distance past the base of the eyestalk.



FIGS. 7-9. — *Allothrombium lerouxi* Moss; nymph and adult.

Fig. 7. — Genitalia of nymph, ventral. Fig. 8. — Same, of adult female.

Fig. 9. — Same, of adult male.

Abbreviations : CM, closing membrane ; GA, genital acetabulum ; GV, genital valve ; GVS, seta of genital valve ; IS, idiosomal seta ; PV, paragenital valve ; PVS, seta of paragenital valve.

Note : The scale line represents 100 μ in all figures.

The above findings should be utilized when a taxonomic revision of the genus is undertaken if, as is likely, allometric scutal development exists in other species. A comparison of illustrations of the scuta of *A. angulatum* Feider, *A. angustiforme* Willmann, *A. brachytrichotum* André, *A. lawrencei*, *A. subtile* Daniel and the two presumably distinct species described as *A. minutum* by FEIDER (1948) and WILLMANN (1954) shows that these forms are nymphs and possibly conspecific with other species described from the same geographic area.

GENITALIA.

The genitalia of Trombidiidae tend to exhibit little sexual dimorphism and often bear an almost unmanageable number of setae. NEWELL (1957 and 1958) found species differences in the genitalia of certain species of Johnstonianidae and Trombidiidae studied by him. Recently FEIDER (1959) described the genitalia of a large number of forms belonging to these groups.

In *A. lerouxi* (figs. 7, 8 and 9) the genitalia are located on the median ventral surface of the opisthosoma just posterad of the metapodosomal coxae. They consist of two paired structures, the

- 1) Genital valve (fig. 9, GV) and
- 2) Paragenital valve (PV).

NEWELL in 1957 referred to these as the genital and paragenital sclerites, respectively; FEIDER (1959) termed them the centrovalves and epivalves. The terminology of both authors has certain advantages: NEWELL's more adequately describes the spatial relationships of the components while FEIDER's concept of a "valve" seems preferable to the more neutral term "sclerite" utilized by NEWELL. In the present study a combination of the terminology of these two authors has therefore been adopted.

Beneath the genital and paragenital valves are located the

- 3) Genital acetabula (GA) and
- 4) "aedeagal sclerites", a series of apodermal and apophyseal processes found in association with the terminal portion of the gonoduct in the male and capable of protrusion. They are presumably utilized during spermatophore deposition.

Each of the components is described separately below with regard, where applicable, to its condition in the nymph, adult male and adult female.

1) Genital valve :

The genital valve in *A. lerouxi* is narrower than the paragenital valve. It bears a few scattered punctae in the nymph but is heavily sclerotized in the adult.

In the nymph the genital valve bears a single row of setae that number about 20. These are attenuate and bear short pectinations; the setae of the genital valve are uniform in length save for the three or four most anterior that are shorter. In the adult female the genital valve is similar in construction to that of the nymph but bears a predominantly single row of 30 to 45 setae. The first three of these,

as in the nymph, are short; the remaining setae are uniform in length except for the last ten or 15 setae. These are at least twice as long as the remaining setae and extend outward in a fan-like projection. They bear extremely fine pectinations. In the adult male the setae are borne in single to triple rows and number 65 to 70. The first few are short, the remainder of moderate length, and a posterior fan-like expansion is lacking.

2) Paragenital valve :

In all developmental stages of *A. lerouxi* the paragenital valve is present as a broad, punctate sclerite situated on each side laterad of the genital valve. The paragenital valve is weakly sclerotized and is difficult to observe, even in dissected specimens. The setae of the paragenital valve bear slightly longer pectinations than those of the genital valve.

In the nymph the paragenital valve bears a double row of about 15 setae (fig. 7, PVS) that are uniform in length. In the adult female they are in a double row and number about 25. In the adult male the paragenital valve setae are present in a single or double row and number about 30.

3) Genital acetabula :

The genital acetabula, discs, or "suckers" are three pairs of ovoid or round sensory structures located beneath the valves. Occasionally an extra acetabulum may be present; a similar abnormality was reported by MICHENNER (1946) in the case of *Manriquia bequaerti* Boshell and Kerr, and *Microtrombidium maculatum* Michener.

4) Aedeagal Sclerites :

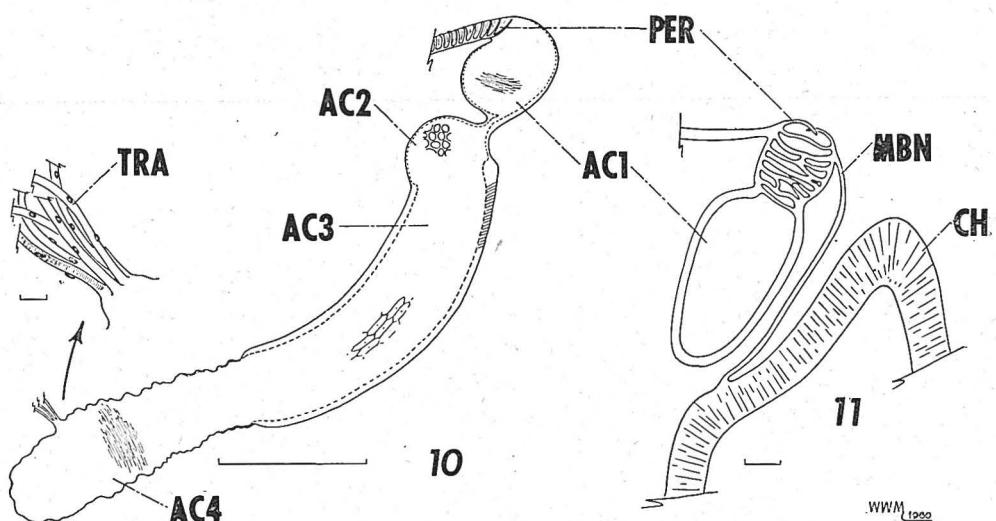
FEIDER (1959) figured the aedeagal sclerites of *A. fuliginosum* and proposed a terminology for the component parts. Similar structures are present in *A. lerouxi* but the apparatus seems somewhat more complicated than in the species studied by FEIDER. A description of the aedeagal sclerites of *A. lerouxi* is not given in the present paper.

Remarks : FEIDER (1959) stated that the sexes of Allothrombiinae may not be differentiated on the basis of the structure of the genitalia. The above findings demonstrate that valid differences do exist in the genitalia of nymph and both sexes in *A. lerouxi*.

The genera *Allothrombium* and *Manriquia* Boshell and Kerr normally possess three pairs of genital acetabula in the nymphal stage, rather than the two pairs found in most other genera of Trombidiidae. This has led to confusion in the past, several species of *Allothrombium* having been described from nymphs doubtless mistaken for adults because of the possession of this otherwise "adult" characteristic.

An exception to the rule has lately come to light : *A. lawrencei* is figured with two pairs of acetabula by MEYER and RYKE (1960). The number of acetabula

would appear to be a significant character and the appearance of two pairs in this species is therefore noteworthy. The length of the idiosoma in *A. lawrencei* is given as 787 μ , while the same measurement in the smallest specimen of *A. lerouxi* available to me was 1120 μ : the latter had three pairs of acetabula. If it can be assumed that *A. lawrencei* is at least as large a mite as *A. lerouxi* (and since the largest species of *Allothrombium* are tropical this seems a logical assumption), we might infer that in *Allothrombium* the earliest nymphs possess two pairs of acetabula, adding an extra pair subsequent to further growth and, presumably, after one or more moults.



FIGS. 10-11. — *Allothrombium lerouxi* Moss; adult.

Fig. 10. — Respiratory apparatus, lateral. Fig. 11. — Peritreme, first air chamber and mediodorsal wall of chelicera. Transverse section.

Abbreviations : AC₁, first air chamber ; AC₂, second air chamber ; AC₃, third air chamber ; AC₄, fourth air chamber ; CH, incised mediodorsal wall of chelicera ; MBN, membrane supporting peritreme ; PER, peritreme ; TRA, trachea.

Note : The scale line represents 5 μ in the magnified portion of fig. 10, 10 μ in fig. 11 and 100 μ in fig. 10.

Against the above hypothesis stands Terzi's illustration in HIRST (1926) showing a freshly-emerged nymph of *A. fuliginosum* with three pairs of genital acetabula. Rearing or collections of more mature nymphs of the South African species should clarify the problem.

RESPIRATORY SYSTEM.

The respiratory system of many of the higher Trombidiformes is composed of a paired tubular apparatus that runs internally on each side downward and backward into the propodosoma from its origin above the chelicera. Numerous tracheae arise from the respiratory apparatus. These pass in tracts forward to

the gnathosoma and its appendages and backward to supply the propodosomal and metapodosomal appendages, as well as the various organs of the idiosoma. The tracheae may bear faintly visible taenidia and because of this are occasionally confused with the similarly reinforced ducts of the salivary glands:

Literature :

Several writers have studied the respiratory system of the group. PAGENSTECHER (1860) and CRONEBERG (1879) figured the respiratory apparatus of two species of *Trombidium*; HENKING (1882) illustrated and thoroughly described that of *A. fuliginosum*, while MICHAEL (1895 a) did the same for the much simpler apparatus of the water mite *Thyas petrophilus* Michael.

OUDEMANS (1916) figured portions of the respiratory apparatus of five species of *Allothrombium*: *A. fuliginosum*, *A. adustum* Oudemans, *A. fuligineum* Oudemans, *A. incarnatum* Oudemans and *A. molliculum* (Koch); later (1928) he described in more detail that of *A. aequinoctiale* Oudemans. VITZTHUM (1930 and 1933) studied and described the respiratory apparatus of *A. meridionale* Berlese and *Microtrombidium fasciatum* (= *demeijerei*) (Koch), respectively.

More recently BLAUVELT (1945) has studied the complete respiratory system of the two-spotted spider mite *Tetranychus telarius* Linnaeus. WHARTON (1950) reviewed recent reports of tube-like structures that open on the gnathosoma in several genera of larval chiggers and discussed the possible function of these tubes. BROWN (1952) reported the complete absence of a tracheate respiratory system in the adult of the common North American chigger *Trombicula alfreddugesi* (Oudemans).

FEIDER (1955) summarized his earlier work (1950) on the respiratory apparatus of several species of trombidiids. He found five categories of apparatus that he defined principally according to the presence or absence of peritremes: his first three categories have the stigmata exposed while the remaining two are provided with peritremes. Those of the first category, as in *Rhinothrombium nemoricola* (Berlese), lack cheliceral sclerites and the respiratory trunks dichotomize freely posterad of the stigmata. His second and third categories include those forms that have cheliceral sclerites: through these structures on each side runs the penultimate section of the respiratory apparatus. In *Georgia pulcherrima* (= *ramosa*) (Haller), a representative of Feider's second category, the respiratory trunks branch arborescently posterad of the cheliceral sclerites whereas in the third category, as exemplified by *Eutrombidium odorheiense* Feider, each trunk expands posterad of the sclerite into a chamber that gives rise to numerous groups of tracheae.

The apparatus of categories four and five have the stigmata covered by peritremes and in both cases cheliceral sclerites are present. In the fourth category, as in *Podothrombium agicense* Feider, each respiratory trunk branches arborescently posterad of the cheliceral sclerite. In the fifth category the respiratory apparatus expands posterad of the cheliceral sclerite into a chamber that gives rise to numerous

groups of tracheae. The respiratory apparatus of *A. lerouxi* is an example of the last category.

The Romanian author, FEIDER, includes as an intrinsic part or the respiratory system in all cases mentioned above a "lateral tracheal trunk" that is in reality the common salivary duct. This point is discussed later in this paper under "Digestive system".

HUGHES (1958) redescribed the respiratory apparatus of *A. fuliginosum* and compared it with that of the trombidiid *Dinothrombium tinctorium* (Linnaeus) and the cheyletid *Cheyletus eruditus* (Schrank). NEWELL and TEVIS (1960) provide an illustration of the respiratory apparatus of the trombidiid *Angelothrombium pandorae* Newell and Tevis.

Description :

The respiratory system of *A. lerouxi* is quite similar to that described to date for most other species of the genus. The system is divided basically into three parts : the peritremes, the respiratory apparatus and the tracheal tracts that arise posteriorly from the tracheal apparatus as it emerges on each side from the cheliceral sclerite.

PERITREMES.

The respiratory apparatus originates in a pair of characteristic and distinctive peritremes (figs. 1, 6, 10, 11 and 12). These are supported by a thickened membrane that arches dorsally over the incised posterior bases of the chelicerae and joins them laterally as shown by figure 11. When viewed from above the peritremes bear a vague resemblance to a horse-shoe open posteriorly. The hollow arms of the horseshoe appear to be covered by a series of overlapping scales, in reality fine ridges of sclerotized chitin that serve to strengthen and support the otherwise membranous peritremes. The ridges gradually become fewer and disappear as the peritremes enlarge anteriorly to join the first air chamber of the respiratory apparatus.

Diffusion of air presumably takes place across the membranous, unsclerotized portions of the peritremes. PAGENSTECHER (1860) believed, according to HENKING (1882), that air entered through slits on either side of each peritreme in *Trombidium*; HENKING (1882) and VITZTHUM (1930) claimed that the peritremes in the two species of *Allothrombium* studied by them were provided with a dorsal longitudinal slit to permit entry of air. HUGHES (1958) could find no trace of a dorsal opening in *A. fuliginosum* and the same condition appears to hold true for *A. lerouxi*. OUDEMANS (1916 and 1928), FEIDER (1955) and HUGHES (1958) show a median longitudinal ridge or thickening running dorsally along the length of each peritreme; I can find no such structure in *A. lerouxi*.

RESPIRATORY APPARATUS.

The respiratory apparatus posterad of the peritremes is divided on each side into four chambers :

- 1) First air chamber or atrium (figs. 10, 11 and 12, AC₁).
- 2) Second air chamber (AC₂).
- 3) Third air chamber (AC₃) and
- 4) Fourth air chamber (AC₄).

Each of these is described separately below. Mention is made of the shape, location, connections and appearance of each chamber. Measurements were taken from two gravid females, approximately equal in size, sectioned sagittally and transversely, respectively.

1) First air chamber :

This portion of the respiratory apparatus (AC₁) is a hollow chamber subspherical in sagittal section and oval in transverse section. It is broadly continuous dorsally with the peritreme and connects with the second air chamber through a short, strongly sclerotized tube. A small chitinous flap overhangs the opening of the tube, where the latter connects with the first air chamber. This flap might act as a closing mechanism. The first air chamber bears a few faint striations. Diameter of the chamber in sagittal section was 60 μ , in transverse section 35 μ .

HENKING (1882) referred to this portion of the respiratory apparatus as the first air chamber and HUGHES (1958) termed it the atrium.

2) Second air chamber :

The tube leading downward from the first air chamber opens into an expanded second chamber (AC₂) that is rounded dorsally and sub-circular in sagittal and transverse section. It is broadly continuous with the third air chamber. The smooth walls of the second air chamber are strengthened by a network of sclerotized ridges in this and other species of *Allothrombium* except for *A. meridionale* where the walls appear to be thrown into a series of folds. Diameter in sagittal section was 60 μ , in transverse section 25 μ .

HENKING (1882) referred to this portion of the respiratory apparatus in *A. fuliginosum* as the "weakly chitinized tube section". He believed that a closing mechanism for the system might be located in this area, although it is difficult to explain how such a mechanism would operate. OUDEMANS (1916) and HUGHES (1958) do not show this chamber in their illustrations of the respiratory apparatus of what was presumably the same species.

3) Third air chamber :

The third air chamber (AC₃) is the largest of the chambers of the respiratory apparatus. From its broad connection with the second chamber it runs ventrad

and backward within the cheliceral sclerite; posterad of the sclerite it narrows very slightly and joins the fourth air chamber. The third chamber is mildly boomerang-shaped in sagittal section and oval in transverse section. The walls are provided with fine striae arranged in a predominantly hexagonal pattern in this and all other species of *Allothrombium* described to date. The length of the chamber in sagittal section was 250 μ , width in transverse section 35 μ .

It was difficult to determine in my material whether the third chamber actually ran as a tube within the length of the hollow cheliceral sclerite as WHARTON (1950) suggested for *A. fuliginosum* or whether the chamber and sclerite are one and the same. The first alternative is more likely the correct one although the presence of a distinct tube within the hollow sclerite is difficult to demonstrate.

Cheliceral levator and other muscles are attached along the exterior surface of the sclerite but it is unlikely that their contraction results in distension of the chamber, as HUGHES (1958) has noted in the case of *A. fuliginosum*.

4) Fourth air chamber :

The terminal chamber of the respiratory apparatus (AC4) is a blindly-ending sac that extends posterad of its junction with the third air chamber to a point just anterad of the brain in the prodosoma. The fourth air chamber is weakly sclerotized and its walls are thrown into numerous folds. At intervals toward the posterior end of the chamber small tubercles arise and from each of these approximately ten tracheae take their origin. The length of the fourth chamber in sagittal section was 65 μ , width in transverse section 35 μ .

TRACHEAL TRACTS.

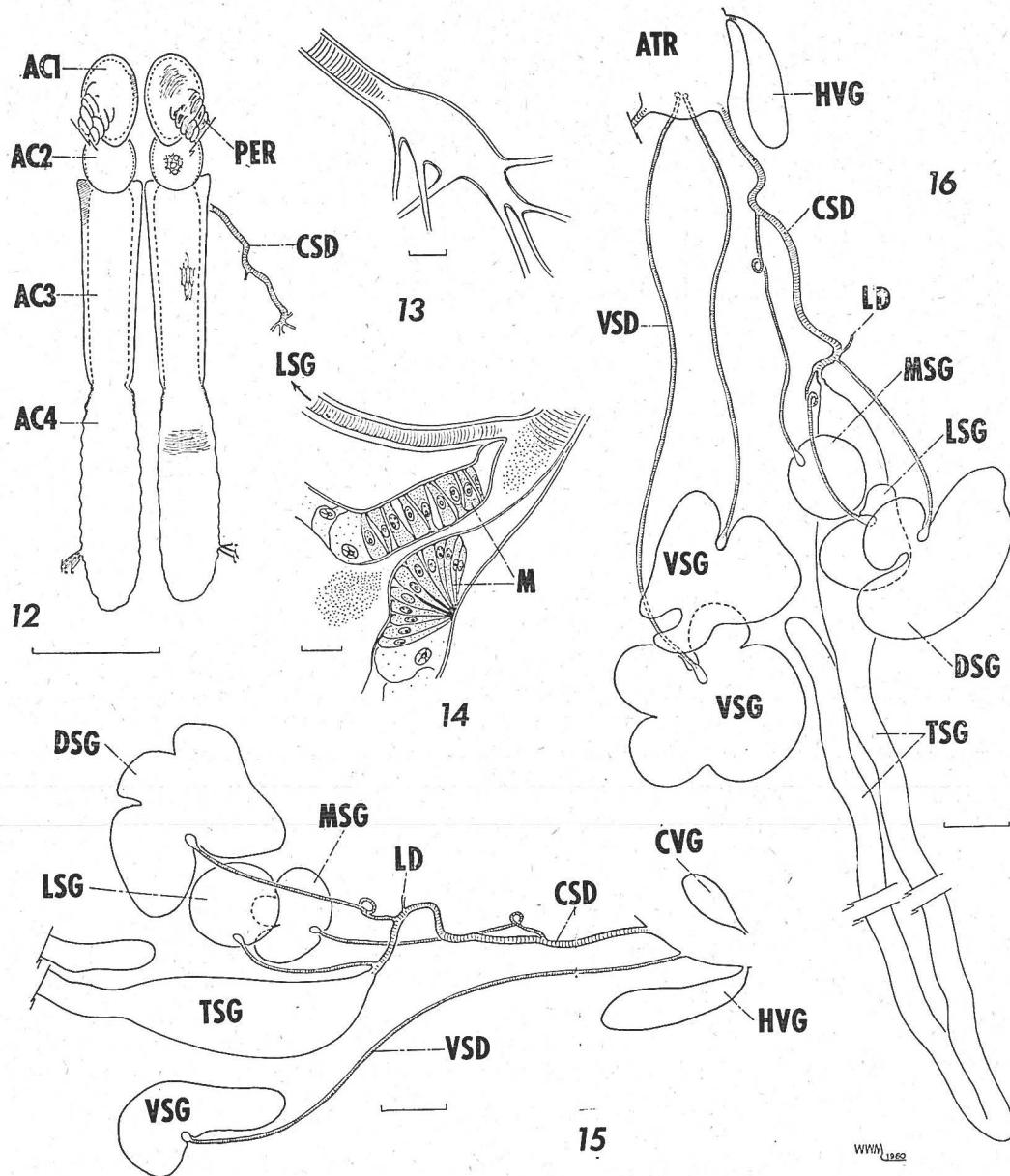
Large tracts of tracheae pass from their origin in the terminal chamber of the respiratory apparatus forward into the gnathosoma, laterally in the propodosoma and backward into the metapodosoma and opisthosoma. Those passing forward supply the pharyngeal muscles, chelicerae and pedipalps, while lateral tracts pass to the first and second legs. Of those passing backward, small tracts follow the oesophagus upward through the brain while others, larger, supply the third and fourth legs, gonads, body musculature and midgut.

In opposition to HUGHES' (1959) statement that the walls of the tracheae in *Allothrombium* lack spiral thickening, I have found that those of *A. lerouxi* bear faintly visible taenidia.

DIGESTIVE SYSTEM.

The morphology of the gnathosomal components of the digestive system of Acari was elucidated by SNODGRASS (1948) and in 1952 BROWN thoroughly described the feeding apparatus of the adult chigger *Trombicula alfreddugesi*.

The mouthparts, pharynx, oesophagus, stomach or midgut and excretory organ



FIGS. 12-16. — *Allothrombium lerouxi* Moss ; adult.

Fig. 12. — Respiratory apparatus and common salivary duct, dorsal. Fig. 13. — Ampulla of anterior ventral salivary gland. Fig. 14. — Dilator muscle of tubular gland, sagittal section. Fig. 15. — Diagrammatic representation of salivary glands and ducts, lateral. Fig. 16. — Same, dorsal.

Abbreviations : ATR, atrial trough or atrium ; CSD, common salivary duct ; CVG, cheliceral venom gland ; DSG, dorsolateral salivary gland ; HVG, hypostomal venom gland ; LD, lateral duct ; LSG, lateral salivary gland ; M, dilator muscle ; MSG, median salivary gland ; TSG, tubular salivary gland ; VSD, ventral salivary duct ; VSG, ventral salivary gland.

Note : The scale line represents 10 μ in figs. 13 and 14, and 100 μ in figs. 12, 15 and 16.

or hindgut of *A. lerouxi* differ fundamentally in no respect from HENKING's 1882 description of these structures in *A. fuliginosum*. The last-mentioned author could not locate a communication between midgut and hindgut in his species, nor could CRONEBERG (1879) in the species of *Trombidium* studied by him. MACLEOD (1884) claimed to have found a small pair of openings located at the anterodorsal extremity of the hindgut in a species of what was probably *Trombidium* or *Allothrombium*. BLAUVELT (1945) reported that the hindgut and midgut of the spider mite *Tetranychus telarius* were joined and WHARTON (1946) suggested that a similar situation might exist in the case of the adult chigger *Ascischongastia indica* (Hirst). I have been unable to demonstrate the presence of such a communication between the two components of the gut in *A. lerouxi*. The thin membrane of the hindgut is applied closely against that of the lobate midgut and the former structure contains, uniformly throughout its lumen the white, granular excretory matter described by HENKING (1882) in *A. fuliginosum*. I can entertain no reason why waste products in the haemolymph and those arising from the liquid food material contained in the midgut could not pass by direct diffusion across the thin membranes separating midgut from hindgut in the latter two species.

The structures described as fat bodies by HENKING (1882) in *A. fuliginosum* were correctly reinterpreted by THOR (1904) as immature eggs. The latter are found in *A. lerouxi* in association with the wall of the midgut between this structure and the integument. A definitive fat body as described by BLAUVELT (1945) for the spider mite *T. telarius* appears to be lacking in *A. lerouxi*.

SALIVARY GLANDS.

The earliest Trombidiformes were doubtless predacious, but because of the anatomical construction of their mouth parts were restricted to a liquid diet, and presumably fed solely upon the haemolymph of their small arthropod prey. With the evolution of a salivary or digestive gland complex, they were able to more fully utilize other sources of food. A mechanism evolved whereby these glandular secretions were carried by ducts to the preoral cavity to be forcibly injected into the body of the prey, resulting in extensive histolysis and predigestion of muscle and other solid tissue. The liquified mixture of saliva and prey tissue that was produced was then drawn up into the stomach through the action of the suctorial pharynx. Finally, in the advanced state of salivary gland development exemplified by *A. lerouxi*, little is left of the prey after feeding but a collapsed and brittle ectoskeleton.

Literature :

The glands of the higher Trombidiformes have been described in varying detail by previous workers. The earliest of these was PAGENSTECHER (1860) who studied a species of *Trombidium* and described paired reniform and tubular glands. CRONEBERG (1879), in a study of what was probably a different species of the same genus,

referred briefly to the glands and described the common salivary duct, as well as the blindly-ending distal extremity of the tubular gland. HENKING (1882) mentioned the tubular gland and figured sections of the hypostomal and ventral glands, and a portion of the common salivary duct in the adult of *A. fuliginosum*. He described and figured for the larva of the same species two paired glands, oval and tubular. Von SCHAUB (1888 and 1889) found three pairs of glands in the water mites *Hydrodroma* Koch and *Midea* Bruzel.

MICHAEL (1895 a) reported five pairs of glands and a possible sixth pair in the water mite *Thyas petrophilus*. The tubular gland in this species was interpreted by the English acarologist as having the function of a reservoir and it is interesting to note that the ducts of the reniform and quadrate glands are described as double, a condition not subsequently reported from other Trombidiformes.

In a thorough anatomical study of *Neomolgus litoralis* (Linnaeus) (= *Badella basteri* Johnston), MICHAEL (1896) found one unpaired and four paired salivary glands. These were the azygous gland, the anterior glands, which he homologized with the quadrate glands of *Th. petrophilus*, and the reniform and tubular glands which he compared to those of the same name in the latter species. In *N. litoralis* the tubular gland is much reduced and does not appear to function as a reservoir. His "pericibal" glands are difficult to homologize.

BADER (1938) found one unpaired and six paired glands in the water mites *Limnesia koenikei* Piers. and *Piona coccinea* (Koch) but only six pairs in *Hygrobates longipalpus* (Hermann).

BLAUVELT (1945) recognized three glands, two paired and one unpaired, in the spider mite *Tetranychus telarius*. The two paired glands (of which one pair is tubular) have lost their salivary function and produce silk, while the unpaired gland apparently retains its primitive enzyme-producing function.

JONES (1950) described the salivary glands of the larva of the British harvest mite or chigger, *Trombicula autumnalis* (Shaw). He found two pairs of glands, including an oval and a "large" gland. The oval gland he homologized with the gland of the same name in the larva of *A. fuliginosum* but believed the large gland to be homologous with the pericibal gland of the adult *Neomolgus* studied by MICHAEL (1896).

BROWN (1952) studied the gnathosomal anatomy of the adult of a common North American chigger, *Trombicula alfreddugesi*. In this species he found five paired glands and was able to trace their ducts and figure the complete gland complex.

THOR (1904) listed the one unpaired and six paired salivary glands that may be present in the higher Trombidiformes. As recent authors (VITZTHUM, 1943; BLAUVELT, 1945; JONES, 1950 and HUGHES 1959) have cited this list it would seem superfluous to reproduce it at this point. THOR provides in his paper many illustrations of isolated glands and their ducts but does not show the complete, interconnected salivary gland complex of any species studied by him. In the present study BROWN's 1952 system of terminology has been utilized. Although compa-

rison have been made with the glands of the trombiculid studied by BROWN, I make no formal attempt to homologize the glands of *A. lerouxi* with those enumerated by THOR. Probable homologies do include the tubular gland of *A. lerouxi* with Thor's *glande tubulaire*, the median gland with his *glande réniforme*, the lateral gland with his *petite glande dorsale antérieure* and the dorsolateral gland with his *glande dorsale postérieure*. I agree with BROWN, however, that the homologies of salivary glands should be inferred only after a comparative study of the mites concerned and not, as has been the wont of various writers in the past, solely from the evidence furnished by the literature.

Description :

The glands concerned with extra-oral digestion in the adult of *A. lerouxi* lie within the gnathosoma and the anterior portion of the idiosoma. The location, probable homology with a comparable gland in the adult chigger *Trombicula alfred-dugesi*, the course of the duct and the shape of each gland are reported below. The reader should note that the salivary glands, although constant in their position relative to each other, show a certain amount of individual variation in shape. Measurements were taken at the greatest dimensions of each gland, from two gravid females approximately equal in size, sectioned sagittally and frontally respectively. Figures 15 and 16 are composites constructed from observations of the ducts of cleared wholermounts as well as frontal and sagittal sections.

The glands of the gnathosoma include two pairs, the

- 1) hypostomal (HVG) and
- 2) cheliceral (CVG) glands.

These bear a certain histological similarity to each other and differ markedly from the remaining glands. The hypostomal and cheliceral glands may be the producers of toxins and such an interpretation is tentatively assigned them in this study.

The glands of the idiosoma consist of five paired structures situated dorsad, ventrad and laterad of the brain. Four pairs of these latter, the

- 3) dorsolateral (DSG),
- 5) median (MSG) and
- 6) ventral (VSG) salivary glands

possess a characteristic histological structure which differs slightly in each pair but is quite distinct from the condition exhibited by the hypostomal and cheliceral glands. The last four pairs of glands mentioned above are distributed in dorsal and ventral groups. The dorsal group includes the dorsolateral, lateral and median glands while the ventral group comprises the ventral glands separated from the dorsal group by the brain. The remaining paired idiosomal gland, the

- 7) tubular (TSG) gland

exhibits yet another type of histological structure and, as discussed below, may have become modified in this species to serve as a reservoir for the secretions of this and perhaps two other glands of the dorsal group.

The ducts of the dorsolateral, lateral and median salivary glands on each side

discharge their contents into a common salivary duct (CSD) that begins at the anterior extremity of the tubular gland and runs forward to the atrial trough. The ventral glands convey their contents to the atrium via independent ventral salivary ducts (VSD).

1) Hypostomal venom gland :

This gland (HVG) is located in the gnathosoma and runs from a point slightly anterad of the epistome backward on either side along the lateral wall of the basis capituli. A comparable gland is lacking in *Tr. alfreddugesi* but was described by HENKING (1882) for *A. fuliginosum*. Sac-like, the hypostomal gland measures 265 μ in length by 70 μ in diameter.

2) Cheliceral venom gland :

The cheliceral gland (CVG) is located within the chelicera and extends from the base of the digitus mobilis a short distance back into the basal joint of the chelicera. A comparable gland is lacking in *Tr. alfreddugesi*. Sac-like, but relatively broader than the hypostomal gland, the cheliceral gland measures 135 μ in length by 50 μ in diameter.

3) Dorsolateral salivary gland :

This is the largest (DSG) of the dorsal group of glands and is located in the most anterior portion of the idiosoma slightly above the level of the scutum and just below the integument. It overlies the other glands both dorsally and laterally and thus, although probably homologous with the dorsal gland described by BROWN (1952) for *Tr. alfreddugesi*, is assigned the name dorsolateral salivary gland in *A. lerouxi*. Its duct departs anteromedially and may or may not describe a complete loop before it joins the common salivary duct (CSD) as the latter nears the top of its curve dorsad. With two lobes when viewed in frontal section and four in sagittal section, the dorsolateral gland measures 285 μ in length by 250 μ in width by 315 μ in height.

4) Lateral salivary gland :

The lateral salivary gland (LSG) is a smaller body situated below and mediad of the dorsolateral gland, and partially overlain by the anteromedial portion of the latter. The lateral gland is most likely homologous with the gland of the same name in *Tr. alfreddugesi* and for this reason the name lateral gland is retained although, strictly speaking, the term is somewhat of a misnomer when applied to *A. lerouxi* since the lateral gland of this species is medial to a portion of the overlying dorsolateral gland. The duct of the lateral gland leaves the anteromedial margin of the gland and runs forward to join the common salivary duct just anterad of the origin of the latter at the anterior extremity of the tubular gland. Rounded, with a short blunt lateral lobe when viewed in frontal section and subcircular in sagittal section, the lateral gland measures 160 μ in length by 150 μ in width by 145 μ in height.

5) Median salivary glands :

The smallest of the dorsal group of glands, the median salivary gland (MSG) is located anterad and mediad of the lateral salivary gland and in the same horizontal plane as the latter. It appears to be homologous with the median gland of *Tr. alfreddugesi*. Its duct, which may loop once, leaves the anteromedial margin to pass far forward and join the common salivary duct at the level of the anterior margin of the first coxa. Rounded in frontal section but with three posterior lobes in sagittal section, the gland measures 135 μ in length by 115 μ in width by 165 μ in height.

6) Ventral salivary glands :

The ventral salivary glands (VSG) make up the ventral group of glands in this species. Situated in the midline, the ventral glands overlie the fused bases of the propodosomal coxae and in turn form a cushion on which the brain rests. In *A. lerouxi* the ventral salivary glands are in tandem, the more anterior slightly overlapping the second; in *Tr. alfreddugesi* the ventral glands are situated opposite each other. The anterior and posterior ventral glands of *A. lerouxi* are described separately below. Diameter of the independent ventral ducts is 7 μ .

Anterior ventral salivary gland :

The duct (VSD) of this gland leaves the anterolateral margin of the latter and runs forward into the right side of the gnathosoma where it empties into the atrium ventrad and somewhat mesad of the entrance of the dorsal duct. The anterior ventral gland when viewed in frontal section has four lobes and in sagittal section is -shaped. It measures 265 μ in length by 250 μ in width by 175 μ in height.

Posterior ventral salivary gland :

The duct (VSD) of this gland leaves the anterolateral margin of the latter and runs forward into the left side of the gnathosoma where it empties into the atrium on the same level as, but independently of, the duct from the anterior ventral gland. The posterior ventral gland when viewed in frontal section has four lobes and in sagittal section is more or less dumb-bell shaped. It measures 315 μ in length by 300 μ in width by 160 μ in height. This gland is not shown in Figure 15.

7) Tubular salivary gland :

This gland (TSG) is located ventrad of the lateral and median glands and in the same vertical plane. It extends as an expanded, hollow chamber from a point just anterad of the median gland backward alongside the brain to about the level of the posterior margin of the dorsolateral gland. Here it narrows and proceeds into the idiosoma as a tube of uniform external diameter and narrow lumen that slopes gradually toward the dorsum. At a point from one-third to two-thirds of the way from the anterior margin of the idiosoma the tube doubles back upon itself and eventually ends blindly on a level with the posteroventral margin of the

dorsolateral gland. The tubular gland in *A. lerouxi* is clearly homologous with the structure of the same name in *Tr. alfreddugesi*.

The common salivary duct originates at the anterior extremity of this gland. The ampulla-like structure (fig. 13) that serves to drain the remaining salivary glands is replaced in the tubular gland by the dilator apparatus illustrated in figure 14. Dimensions of the tubular gland are as follows : expanded chamber 400 μ in length by 135 μ in diameter ; tubular portion 2400 μ in length by 55 μ in diameter. This gives a total length for the tubular gland of 2800 μ which agrees well with THOR's 1904 observation of 2600 μ for the same structure in *A. fuliginosum*.

COMMON SALIVARY DUCT.

The tubular, lateral, dorsolateral and median glands are drained by a large tube, the common salivary duct (CSD). The tortuous course of the latter, from its origin at the anterior margin of the expanded portion of the tubular gland to its ultimate termination at the atrial trough, is as follows. Curving dorsad and slightly laterad from the tubular gland, the common duct almost immediately receives the duct of the lateral salivary gland (LSG). Continuing upward and outward, it is joined slightly below the base of the eyestalk by the duct of the dorsolateral salivary gland (DSG) and, at the same level, by a small lateral duct (LD) which passes dorsolaterally ; I was unable to trace the destination of the latter, which narrows slightly and disappears shortly after its junction with the dorsal duct. In wholermounts an ovoid body, unaffected by clearing agents, was occasionally visible in the lumen of the lateral duct a short distance from the junction. MICHAEL (1895 a) found a similar duct in *Thyas petrophilus* and was similarly unable to trace it. He believed the duct to end in a small gland located in that region ; a comparable gland appears to be lacking in *A. lerouxi*.

The common salivary duct continues its upward curve until it reaches the level of the eyestalk base when it turns, continues anterad for a short distance and then loops ventrad and mesad. It now passes forward, and at about the level of the anterior margin of the first coxa receives the duct from the median salivary gland (MSG). At this point the dorsal duct once again proceeds laterad, then anterad and mediad and eventually, following the epistomal apodeme, enters the postero-lateral angle of the atrial trough.

Diameter of the dorsal duct is about 15 μ .

Remarks :

a) Salivary ducts.

It is at times a difficult task to trace the salivary ducts of higher trombidiids such as the species under study, as myriads of true tracheae take their origin from the main tracheal trunks in the same region of the body. Whereas the ducts of the hypostomal and cheliceral glands are quite short, those of the salivary glands

in the restricted sense are longer and bear strengthening taenidia, apparently of an annular nature. Because of these characteristics, the ducts of the salivary glands may easily be mistaken for tracheae. The same condition is found in the ducts of the labial glands of Insecta (IMMS, 1957). Tracheae and salivary ducts in the species under study differ as shown by table I.

TABLE I.
Distinctions between Adult Tracheae and Salivary Ducts of *A. lerouxi*.

	<i>Trachea</i>	<i>Salivary Duct</i>
Diameter	3.5 — 4.5 μ	7 — 15 μ
Walls thickened.....	—	+
Tube accompanied by nuclei....	+	—
Tube may branch.....	—	+
Tube ends in expanded ampulla.	—	+

MICHAEL (1896) commented that a tube strengthened by taenidia in Acari is more likely to be a salivary duct than a trachea. Subsequent workers, however, have consistently misinterpreted these structures. ANDRÉ (1930) described the salivary ducts of *Trombicula autumnalis* as respiratory structures; HUGHES (1959) noted that even OUDEMANS (1932) was not above this error.

WHARTON (1950), writing on the respiratory organs of trombiculids, reported that there was more than one type of tube supported by taenidia in these mites and he suspected that some might be glandular in origin. BROWN's (1952) work confirmed this suspicion. Misinterpretations continue to be made for Trombidiidae, however, and two recent examples are herewith brought to the attention of the reader.

FEIDER's (1955) contribution to the series *Fauna Republicii Populare Romîne* treats of the systematics of the trombidiid mites of Romania and includes an extensive introduction to the anatomy of the group. On page 47 of this work, FEIDER reviews his previous study (1950) of the respiratory system of Trombidiidae. I did not have access to this earlier publication but it appears from the text and illustrations of the later (1955) work that the Romanian acarologist has mistaken the common salivary duct of the species he studied for a portion of the respiratory system. Below is included a translation of the passage in question. The translation and italics are mine, as are those portions in square brackets.

"Respiratory apparatus. — The respiratory apparatus of *Trombid[i]oidea* is composed of a pair of stigmata, exposed or covered by a peritreme. The stigmata are continuous with an anterior tracheal trunk. This trunk bifurcates into an upper lateral branch or *lateral tracheal trunk* and an interior branch or *median*

tracheal trunk. The latter includes two regions : a) an anterior expanded prism-shaped portion with chitinous walls, limited by a chitinous sheath [= cheliceral sclerite] and b) a posterior unchitinized portion. The latter branches arborescently in some species and in others gives origin to a tuft of tracheae."

Figure 12 of the present paper shows the respiratory system and the adjacent common salivary duct of *A. lerouxi*. A comparison of this figure with FEIDER's (1955) illustrations will show that whereas the Romanian writer's "median tracheal trunk" does represent a portion of the true respiratory system as currently understood, his "lateral tracheal trunk" is in point of fact the common salivary duct of his species. The common duct gives origin to medial and distal branches, which in turn undoubtedly pass to salivary glands.

LELIÈVRE-FARJON (1960) figures a *grosse trachée spiralee* for the trombidiid *Podothrombium gallicum* Lelièvre-Farjon. This structure originates in the same area as the "lateral tracheal trunk" illustrated by FEIDER (1955) for *P. agicense* Feider. There are, however, certain important differences evident in the findings of the two workers. The "lateral tracheal trunk" of *P. agicense* has four branches of which the terminations are not shown. The main trunk of the species studied by the French author has five branches, of which four subsequently bifurcate : three of these give rise to terminal thread-like structures which radiate outward from their common origin at the end of the branch.

It is difficult to explain, on the basis of the salivary duct hypothesis outlined above, the modifications of the main trunk as described by LELIÈVRE-FARJON. I suspect that his "large, spirally-thickened trachea" is in reality the common salivary duct. MICHAEL (1895 a) found that certain of the salivary glands in *Thyas petrophilus* are drained by paired ducts which enter the common salivary duct independently. Fusion of originally distinct ducts just before junction with the main duct might explain the situation in *P. gallicum* although one of the branches illustrated by LELIÈVRE-FARJON dichotomizes twice. The filaments which arise from the ends of several branches in the latter species might represent the fine tubular structures which extend throughout some glands in *A. lerouxi* (fig. 13) ; these ductules originate in *A. lerouxi* from an expanded ampulla-like chamber that is not figured for *P. gallicum*. On the other hand, true tracheae pass in profusion over and under the salivary ducts of *A. lerouxi* and close observation is necessary to demonstrate the fact that the two do not join. It is obvious that a study of the internal structure of *P. gallicum* would aid greatly in clarification of the problem, as difficulties may arise when cleared wholemounts are the sole object of study.

The common salivary duct and its modification in various groups has been the subject of several excellent studies by GRANDJEAN (1938, 1944 a, 1944 b and 1947) who found that this structure may be entirely internal as in *Allothrombium* and in the genera *Cunaxa* von Heyden, *Cheyletus* Latreille, *Odontoscirius* Thor, *Trombicula* Berlese and *Smaris* Latreille. Alternately, the common duct may be internal for a portion of its posterior course and subsequently turn to the exterior to run for

a distance as an open or partially open trough along the lateral propodosomal wall. After a time the duct again turns inward to open at the base of the chelicerae. The latter condition was found by GRANDJEAN in certain lower Prostigmata such as the genera *Anystis* von Heyden, *Caeculus* Dufour, *Linopodes* Koch, *Lordalychus* Grandjean, *Pachygnathus* Dugès and *Penthalodes* Murray (= *Penthaleus* Berlese). In most of the above cases the common duct runs forward on each side and receives the ducts of at least two salivary glands during its course. In the genus *Cheyletus*, according to HUGHES (1959), only a single gland and hence a single duct exists.

Although the common salivary duct had been previously recognized and described by CRONEBERG (1879) and MICHAEL (1895 a and 1896), who called it the "main excretory duct" and "main common duct", respectively, GRANDJEAN (1938) coined the term *canal podocéphalique* or podocephalic canal¹ for this structure and subsequent writers (e.g. NEWELL, 1958; and HUGHES, 1959) have followed GRANDJEAN's example. This is unfortunate, not only because the earlier workers' more correct terminology has priority, but also because the French author's term is imprecise and misleading. It is only in some of the lower Prostigmata that the common salivary duct might be considered to resemble for a portion of its length a canal, i.e. an open trough. Secondly, since the primitive protocephalon of Acari has become insensibly incorporated with the cheliceral and pedipalpal segments to form a discrete and compact capitulum or gnathosoma, the implied denotation of a cephalic tagma inherent in GRANDJEAN's term is inappropriate and unacceptable.

It might be considered an unwise or premature step, considering our as yet fragmentary knowledge of the salivary gland complexes of Acari, to propose a terminology alternative to podocephalic canal that will in the future prove adequate for all groups. Nevertheless, the term common salivary duct is to date applicable to certain members of the Hydrachnella, Anystidae, Bdellidae, Cunaxidae, Pentalodidae, Smaridiidae, Trombidiidae etc., and it is quite probable that its homologue will be found to exist in most of the Trombidiformes. The writer therefore urges adoption of the more explicit term "common salivary duct" in preference to the alternative now in use.

b) The interrelations of the salivary glands.

The following comments are of necessity speculative in nature and result purely from a consideration of the morphological findings. Complementary evidence of an experimental nature is not available at this time.

It is not known with certainty whether the salivary glands of Trombidiformes produce and expel their secretions only upon the initiation of feeding or whether this production takes place continuously. It is possible that both alternatives may occur, according to the individual gland and the interconnections of its ducts.

In *A. lerouxi* the ventral glands are drained by individual ducts. In this case

1. So termed because it originates in the vicinity of coxae I and passes forward to empty its contents in the "cephalic" region.

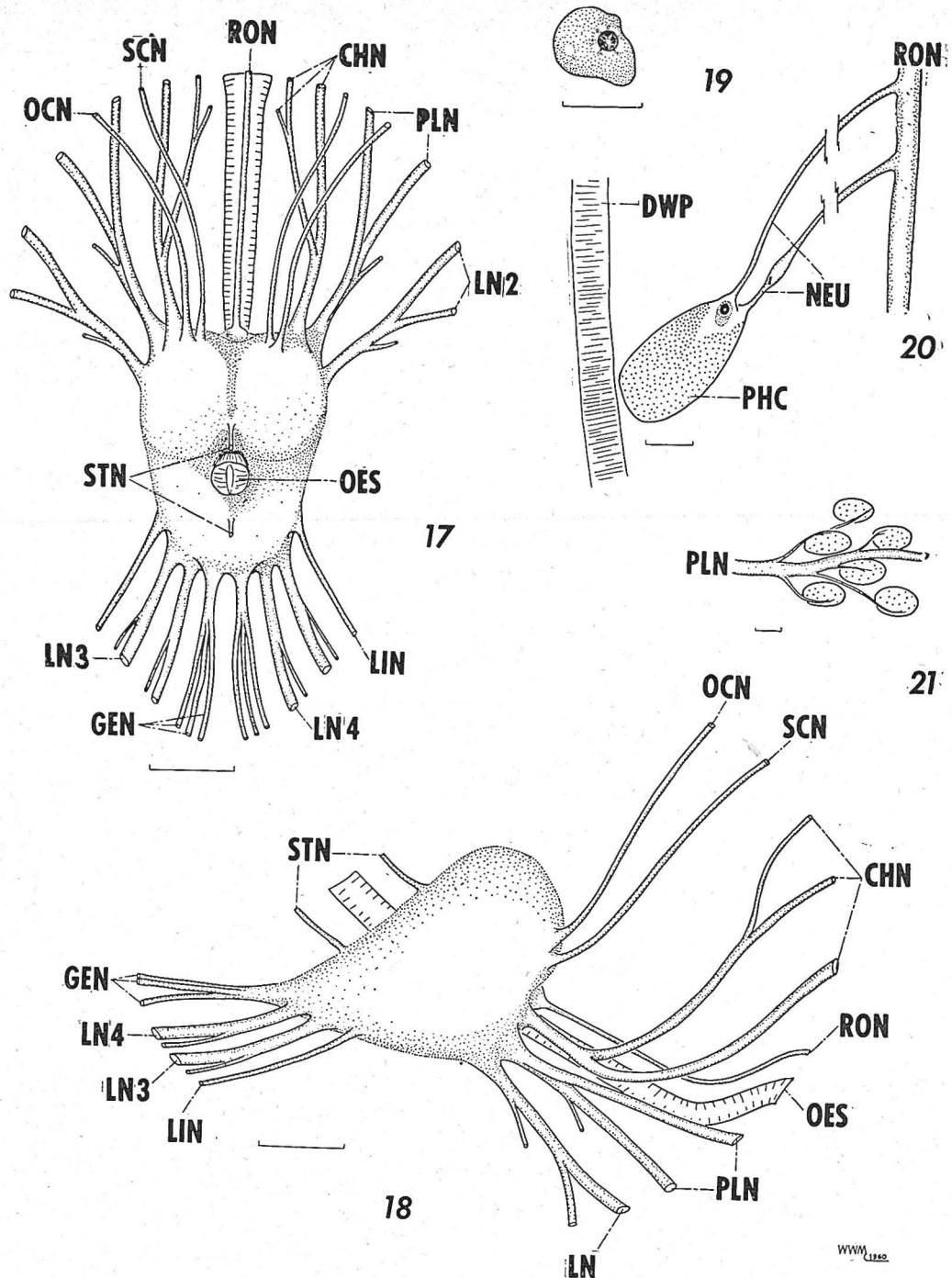
little storage of excreted products could take place and hence it seems likely that active secretion and expulsion of products occurs only when feeding.

For the remaining glands the second alternative may in part hold true. It appears that the tubular salivary gland secretes continuously, its products being formed in the distal narrow-lumened portion and stored in the reservoir provided by its expanded, thin-walled anterior chamber. The presence of a dilator muscle at the junction of the latter with the common salivary duct would tend to support this hypothesis. Contraction of the dilator presumably occurs when feeding takes place, allowing the contents of the reservoir to pass into the common salivary duct and thence forward to the mouth. The elastic properties of the chitinous walls in the vicinity of the junction would serve to prevent premature discharge.

The reservoir of the tubular salivary gland may contain only the product or products of this gland. However, a consideration of the location of the ducts of the lateral and dorsolateral salivary glands shows that the secretions of the latter might, as well, find their way to the reservoir. The ducts draining these glands join the common salivary duct immediately above its origin and just before it reaches the top of its dorsal curve, respectively. If these glands were to secrete continuously, their products could pass down their individual ducts to the common duct and thence to the origin of the latter at the anterior extremity of the tubular gland. Contraction of the dilator muscle at this point would allow entry and mingling of the latter secretions with those of the tubular gland.

A different situation exists in the case of the median salivary gland, the duct of which joins the common salivary duct far anterad of the ducts from the dorsal and dorsolateral glands. In order to enter the tubular gland reservoir the products of the median gland would have to pass back, up and over the prominent dorsal loop of the common duct. The effect of gravity would argue against such an occurrence. Capillarity might be sufficient to bring the products of the median gland back to the reservoir but this would also draw them forward to the mouth opening, resulting in a constant slow discharge of saliva, an unlikely state of affairs. It thus appears that the median gland operates in the same fashion as the ventral gland, discharging only during the act of feeding. The dorsal loop of the common duct might have evolved as a result of the forward migration of segments posterad, resulting in a dorsad buckling of the tube. The loop so formed would subsequently act as a mechanical barrier to prevent premature mingling of digestive enzymes from the median gland with the enzymes of those more posterior. In *Tr. alfred-dugesi* a similar loop occurs in the common salivary duct but the ducts of all glands enter posterad of the loop.

In conclusion, although the secretions of the ventral and median glands remain separate until the act of feeding, those of the tubular, lateral and dorsolateral glands may be stored together in a common reservoir. An alternative to this conclusion is to assume that the secretions of all glands remain separate and the large expanded chamber of the tubular gland serves solely to store its own secretions. Because of the dimensions of its storage chamber, the tubular salivary gland may



Figs. 17-21. — *Allothrombium lercuxi* Moss; adult.

Fig. 17. — Central nervous system, dorsal. Fig. 18. — Same, lateral. Fig. 19. — Amoebocyte.

Fig. 20. — Innervation of pharyngeal constrictor muscle by rostral nerve. Fig. 21. — Innervation of coxal muscles by nerve to first leg.

Abbreviations : CHN, cheliceral nerve ; DWP, dorsal wall of pharynx ; GEN, genital nerve ; LIN, lateral idiosomal nerve ; LN₂, nerve to second leg ; LN₃, nerve to third leg ; LN₄, nerve to fourth leg ; NEU, neuron ; OCN, ocellar nerve ; OES, oesophagus ; PHC, pharyngeal constrictor muscle ; PLN, combined nerve to pedipalp and first leg ; RON, rostral nerve ; SCN, scutal nerve ; STN, stomatogastric or stomodaeal nerve.

Note : The scale line represents 10 μ in figs. 19-21 and 100 μ in figs. 17 and 18.

secrete a fluid, the primary function of which is to act as a carrier for the less copious enzymatic products of the remaining dorsal group of glands served by the common duct. Before qualitative analysis of the secretions of all the glands, opinions must remain speculative. It is hoped that the above findings and speculations will promote further research in this line.

CIRCULATORY SYSTEM.

The blood circulatory system of *A. lerouxi* is lacunar. A heart is lacking but numerous amoebocytes (fig. 19) are present in the haemocoel. HENKING (1882) thoroughly described the amoebocytes of *A. fuliginosum* and THOR (1904) reported their presence in a number of the higher Trombidiformes.

NERVOUS SYSTEM.

Central Nervous System :

The central nervous system in the Trombidiformes is represented by a circumoesophageal body composed of the migrated and subsequently fused segmental ganglia. The brain lies in the region of the propodosoma except in the Tetrapodili, where it is displaced backward into the opisthosoma (HUGHES, 1959). It gives rise to the nerves passing to the appendages and various organs of the body as well as to the sensilla and ocelli when these latter are present. The central nervous mass is pierced medially by the tubular oesophagus, and, frequently, by the tracheae which accompany the latter.

The boundaries of the original ganglionic components of the central nervous mass are indistinct, at least externally. If discrete supra-and suboesophageal ganglia did at one time exist, their limits are in most species obscured by the thickness of their circumoesophageal commissures and by the intimate fusion of these with the remainder of the central nervous mass. For this reason, use of the term central nervous mass or simply "brain" seems preferable to the retention of terms such as supra- and suboesophageal ganglia which, when applied to the Acari, may be somewhat misleading or ambiguous.

Literature :

The brain and its principal nerves in the higher Trombidiformes have been described by previous workers. PAGENSTECHER (1860) and CRONEBERG (1879) studied a species of *Trombidium* and both reported 12 pairs of nerves; the latter also described a median unpaired rostral nerve that has been found in all species subsequently studied. An examination of CRONEBERG's illustration reveals that he found in reality only nine paired nerves, since some of those that he described as separate entities arise quite obviously from the same main trunk. Previously he had published (1878) a study of the water mite *Eylais extendens* (Müller) that included a description of the central nervous system.

HENKING (1882) mentions only briefly the brain and its nerves in the adult of *A. fuliginosum*, but figures and describes the central nervous system of the larva. He found a rostral nerve and seven paired nerves but admits that one or two nerve trunks might have been omitted from his illustration since he had no sectioned larval specimens. Later, in 1888, Von SCHAUB studied the central nervous system of the water mite *Hydrodroma* Koch.

MICHAEL (1895 a) reported a rostral nerve, a triple stomatogastric nerve and nine paired nerves in *Thyas petrophilus*. In a subsequent study (1895 b) he found a rostral nerve and nine paired nerves in the adult of *A. fuliginosum* and later (1896) distinguished a rostral and ten paired nerves in the bdellid *N. litoralis*. HILTON (1933) cites the work of HANSTRÖM (1919) who studied the nervous system of a species of *Trombidium*.

More recently BLAUVELT (1945) found three unpaired and seven paired trunks in the two-spotted spider mite *Tetranychus telarius*.

Description :

The central nervous mass or brain in the adult of *A. lerouxi* is a compact structure somewhat longer than wide, with a height approximately equal to its length. It rests upon a "cushion" formed by the ventral salivary glands that in turn overlie the sclerotized coxal bases of the propodosoma. The brain when viewed from above (fig. 17) is roughly rectangular, with its principal nerves arising from each of the four corners of the rectangle. From the side (fig. 18) the brain resembles a right-angled triangle with the hypotenuse bearing a single pair of nerves, the stomatogastric; the remaining nerves originate from the other sides. In *Th. petrophilus* the brain assumes an almost spherical shape. The brain of *A. lerouxi* is traversed by the oesophagus (OES) which passes upward and backward at an angle of about 45° to the horizontal. It narrows slightly as it pierces the central nervous mass and is accompanied in its course by tracheae. Immediately above the papilla-like prominence from which the rostral nerve (RON) originates, lies a cavity left when the rostral ganglion failed to fuse completely with the rest of the brain. This cavity or fissure extends inward to communicate with the passage containing the oesophagus. Tracheae enter by it and pass backward closely appressed against the dorsal wall of the oesophagus. Other tracheae pass through the brain in association with the ventral wall of the oesophagus.

In the adult of *A. lerouxi* one unpaired and ten paired nerve trunks have their origin in the central nervous mass. The unpaired nerve is the

- 1) rostral (RON) nerve.

The remaining trunks include ten pairs which pass on each side to the

- 2) ocelli (OCN),
- 3) scutum (SCN),
- 4) chelicerae (CHN),
- 5) pedipalp and first leg (PLN),
- 6) second leg (LN2),

- 7) third leg (LN₃) and
- 8) fourth leg (LN₄).

In addition to these, there exist paired

- 9) lateral idiosomal (LIN),
- 10) genital (GEN) and
- 11) stomatogastric or stomodaeal (STN) nerves.

The first five pairs of nerves mentioned above arise from the anterior surface of the brain, the first four dorsad, the fifth ventrad of the entrance of the oesophagus. The next four pairs take their origin along the ventrolateral margin of the brain, while the genital nerves depart posteriorly. The stomatogastric nerves arise from the posterior surface above and below the exit of the oesophagus.

Each nerve trunk is described separately below and comparisons are made with the condition in related species. Since an outline of the musculature was not attempted, only the more proximal ramifications of the nerves are discussed in this study.

1) Rostral nerve :

The median unpaired rostral nerve (RON) arises from the anterior surface of the brain where its ganglion extends outward as a papillalike projection. As described above, a cavity passing back into the brain immediately above the rostral ganglion facilitates the entry of tracheae accompanying the oesophagus during passage of the latter through the central nervous mass. The rostral nerve from its origin runs forward above and roughly parallel to the oesophagus, turning upward with the latter just before the oesophago-pharyngeal junction and passing forward horizontally to lie above the pharynx. Here branches of the rostral nerve ramify to supply the pharyngeal musculature. Figure 20 shows two neurons (NEU) from a twig of the rostral nerve passing down to innervate a pharyngeal constrictor muscle (PHC).

A branch of the rostral nerve of *N. litoralis* passes to the sphincter muscle of the crop or *receptaculum cibi*; a comparable modification of the digestive system is lacking in *A. lerouxi*.

In *T. telarius* the rostral nerve trifurcates into two lateral nerves passing downward on either side of the oesophagus and a median nerve that continues forward to the tip of the gnathosoma.

In one specimen of *A. lerouxi* a single lateral branch appeared in sagittal section to arise from the main rostral trunk about halfway between the brain and oesophago-pharyngeal junction; a second lateral branch was not visible. I have been unable to demonstrate the presence of a similar lateral nerve in the remainder of my sectioned material and have thus figured the rostral nerve as an unpaired trunk.

2) Ocellar nerve :

The slender paired ocellar nerve (OCN) is the most dorsal of the trunks arising from the anterior surface of the brain. Each trunk runs upward and outward to

enter an ocellar peduncle where it splits to innervate the individual ocelli. Similar nerves have been reported from other trombidiforme mites studied to date.

3) Scutal nerve :

The scutal nerve (SCN) on each side is approximately the same diameter as the ocellar nerve and leaves the central nerve mass ventrad and slightly mediad of the latter, passing upward to supply certain of the muscles arising from the scutum, and possibly the sensilla as well.

A similar nerve is present in *Th. petrophilus* and *N. litoralis*.

4) Cheliceral nerve :

The stout nerve to the chelicera (CHN) originates on each side ventrad and later of the rostral nerve and runs forward above and more or less parallel to the oesophagus. A short distance from its origin the main trunk bifurcates and both branches pass upward. The more anterior continues to the cheliceral muscles while the more posterior divides distally to give a stout anterior nerve that supplies cheliceral muscles and a slender posterior branch innervating the muscles extending from the scutum to the cheliceral sclerite.

A common origin was described for the cheliceral and pedipalpal nerves in *Hydrodroma*. In all other forms studied to date the cheliceral nerve departs independently.

5) Combined nerve to pedipalp and leg I :

Ventrad and somewhat laterad of the cheliceral nerve on each side arises a stout trunk (PLN) which passes forward, below and at an angle of about 45° to the horizontal. This trunk immediately bifurcates into two branches, an anterior one which continues forward parallel to the oesophagus, subsequently to enter the pedipalp, and a posterior branch which continues outward to the first propodosomal appendage. Almost at its point of origin the nerve to leg I gives off a small posterior twig. Figure 21 illustrates ramification of the first leg nerve among the muscles of this appendage.

The common origin, in this species, of the nerves serving pedipalp and leg I is most unusual. Illustrations of the brain of *Trombidium*, *Th. petrophilus*, *N. litoralis* and *T. telarius* show distinct pedipalpal and leg nerves arising from the central nervous mass. In dissected and sectioned material of *A. lerouxi* the nerves in question appeared to have a common origin and I have so figured them in my illustrations.

In *Thyas petrophilus* the pedipalpal nerve serves both pedipalp and hypostome.

6) Nerve to leg II :

This stout nerve (LN₂) supplying the second appendage of the propodosoma arises at the same level and posterad of the combined nerve to the pedipalps and leg I. Two branches are given off. The first, smaller, emerges shortly after the origin of the main trunk and the second, larger, just as the latter enters the second leg.

7) Nerve to leg III :

The stout nerve trunk to leg III (LN₃) arises from the posterolateral margin of the central nervous mass posterad and slightly ventrad of the origin of the lateral nerve on each side. A small lateral branch is given off a short distance from the brain.

8) Nerve to leg IV :

The second appendage of the metapodosoma is supplied by a stout nerve (LN₄) originating at the same level as the nerve to leg III but slightly posterad of the latter. A small lateral branch is given off a short distance from the brain. This branch, as well as comparable nerves arising from legs I, II and III, appears to be identical with the "accessory" leg nerve figured by earlier writers.

9) Lateral idiosomal nerve :

A slender idiosomal nerve (LIN) departs from each side slightly dorsad and anterad of the nerves supplying the metapodosomal appendages. I was unable to demonstrate with certainty the destination of this nerve although it most likely supplies the dorsoventral muscles as does a similar nerve in *N. litoralis*. A lateral idiosomal nerve is present in *Trombidium* and *A. fuliginosum* but is lacking in *Th. petrophilus*.

10) Genital nerve :

The genital nerve (GEN) or "splanchnic" nerve on each side arises as a stout trunk from the posterior surface of the brain somewhat dorsad of the bases of the nerves to legs III and IV. Almost immediately the main trunk of the nerve trifurcates, the resulting branches continuing backward to the reproductive system. Three branches are present in *Trombidium* although *A. fuliginosum* and *Th. petrophilus* appear to have but two. The genital nerve of *N. litoralis* passes back on each side as a single large trunk that gives off small ventral twigs at intervals. In *T. telarius* the genital nerve is unpaired.

11) Stomatogastric or stomodaeal nerve :

Slender median nerves (STN) arise from the dorsal posterior wall of the central nervous mass above and below the exit of the oesophagus. Both nerves run backward and parallel to the latter and could be traced but a short distance posterad of the brain. They are extremely tenuous and are best demonstrated in sectioned material. Stomatogastric nerves were not figured for *A. fuliginosum* and are lacking in *N. litoralis*. In *Th. petrophilus* they are triple : one stem arises below the oesophagus and the remaining two depart from the posterior surface of the brain above and on each side of the oesophagus. *T. telarius* has a single unpaired stomatogastric nerve that passes back above the oesophagus to supply the midgut.

Peripheral nervous system :

HENKING in 1882 described in detail the peripheral ganglia located in the tarsi of leg and pedipalp in *A. fuliginosum*. Similar ganglia are found in *A. lerouxi* and from these nervous connections proceed through passages in the integument to the setae. The peripheral network is most concentrated in the tarsi of leg and pedipalp where the majority of specialized sensory setae are located. The hypostome as well is richly supplied, in keeping with the localization of eupathidia in this area.

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