Comparative Studies on the Internal Anatomy of Three Japanese Trombidiform Acarinids[1)]

By

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(With 19 Text-figures and 1 Plate)

With regard to the internal anatomy of the Acarina, a considerable number of work have so far been published. Thanks to them, it has been recognized that various groups of the Acarina markedly differ from one another in internal organs. However, there are still so many unsolved problems, that further anatomical studies of the Acarina covering diverse groups are required not only to establish the internal anatomy *per se* but also to clarify phyletic relationships among groups within the order.

As a tentative to promote such studies, the present author has made a comparative study of the anatomy of some internal organs, using three trombidiform acarinids. In respect of the internal anatomy of trombidiform mites, Henking (1882), Michael (1895, 1896), Nalepa (1887), Thor (1903), Schmidt (1935), Bader (1938, 1954), and Blauvelt (1945) made important contributions, but further studies are needed to solve some problems, which are only partially fulfilled in the present paper.

Before going further, the author wishes to express his cordial thanks to Professor Tohru Uchida under whose direction this work has been carried out, and whose encouragement has constantly been offered to him. Thanks are also due to Dr. S.F. Sakagami, Prof. T. Imamura (Ibaraki University), and Dr. T.E. Hughes (University of London) for their valuable suggestions, and to Dr. H. Takahashi, Dr. Y. Akahira, and Mr. M. Mizutani for their extensive technical assistance. Further, he wishes to thank Prof. R. Hayashi (Toyama University) and Mr. N. Hikichi (Fukushima Prefectural Horticultural Experiment Station) for their kindness in collecting materials.

Material and method

The species herein studied and the localities of collection are as follows :

Neomolgus littoralis (Linnaeus), Bdellidae; Ranshima near Otaru City, Hokkaido

Bryobia eharai Pritchard et Keifer, Tetranychidae; Iizaka, Fukushima Pref., and Toyama City, Toyama Pref.

Hydryphantes affinis Sokolov, Hydryphantidae; Zenibako, Otaru City, Hokkaido

The descriptions are almost entirely based upon material fixed in Léonard-Pasteel's mixture or alcoholic Bouin and sectioned at 5 to 10 μ. Sections were stained mainly with

1) Contribution No. 500 from the Zoological Institute, Faculty of Science, Hokkaido University, Sapporo, Japan.

Delafield's haematoxylin and eosin, but partly with Heidenhain's azan. Besides, total stainings of body with borax-carmine were subsidiarily adopted. Excluding male reproductive organs, the descriptions are mainly based on the female specimens.

I. *Neomolgus littoralis* (Linnaeus)

(Figs. 1–10, Pl. VII, Figs. 20–25)

This mite is commonly found under sea-weeds and on rocks on the coasts of northern Japan (Thor and Uchida, 1933, Ehara, 1960). Internal anatomy of the mite under the name *Bdella Basteri* Johnston was previously studied by Michael (1896).

A. Digestive system

The alimentary canal consists of pharynx, oesophagus, and blind ventriculus. Besides, the supraoesophageal organ is described incidentally.

A–1. *Pharynx*: The pharynx is weakly chitinized in ventral part but almost membranous in dorsal part. The perpendicular muscles (Michael's "levator tecti pharyngis muscles") arising from underneath the roof of the rostrum are inserted on the dorsum of the pharynx. Each pair of bands of the perpendicular muscles and each band of the transverse pharyngeal muscles ("constrictor pharyngis muscles") are set alternately. The food is put into the pharynx and further into the oesophagus, in response to the movements of the dorsal part of the pharynx, caused by the action of these muscles. The pharynx is crescent-shaped in cross section.

A–2. *Oesophagus*: The pharynx is followed by the slender oesophagus which passes through the central nervous mass. In transverse section, the oesophagus is circular and several or more dark-staining nuclei are recognized in its epithelial layer. The oesophagus enters the medioventral portion of the anterior part of the ventriculus. So far as the author observed, the oesophageal valve, a remarkable projection of the oesophagus into the ventriculus found in most species of the Acarina, is little developed.

A–3. *Supraoesophageal organ (Michael's "receptaculum cibi")*: The supraoesophageal organ, provisionally given this name in the present paper, is a large diverticulum arising from the dorsal surface of the gut immediately behind the pharynx. This sac-like organ is proximally of narrow tube. Its anterior part runs parallel with the oesophagus ventrally located, while the posterior part is dorsad of the upper surface of the central nervous mass. The dorsal surface of the supraoesophageal organ is adjacent to the ventral surface of the azygous and the pericibal salivary glands, its lateral surfaces neighbour the latter, while the posterior end adjoins the anterior surface of the ventriculus. This organ is furnished with firm, eosinophilic wall; interior to the wall is a thin layer of irregular reticular structure, being variable in extent among different specimens. The interior of the organ is packed with a mass of granular eosinophilic substances

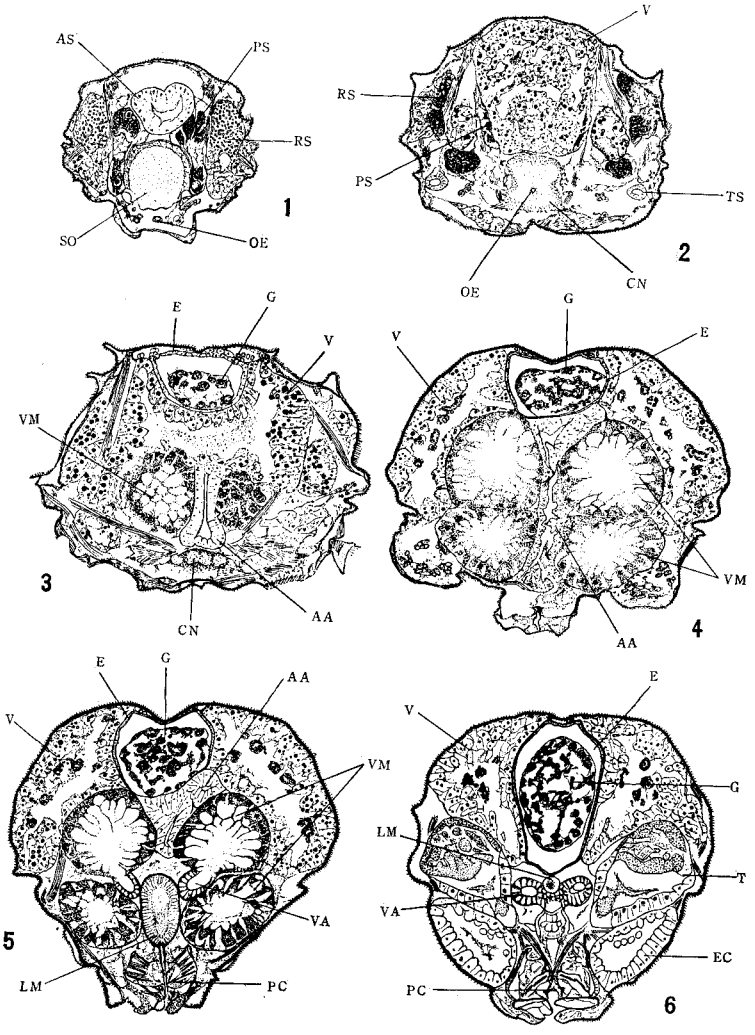
which also stain well with aniline blue. The contents frequently reach into the pharynx.

The ventral wall of the proximal end of the supraoesophageal organ is remarkably dilated; in median longitudinal section, the dilated portion is observed to be semi-circular at dorsal margin. This dilation is common to the dorsal wall of the anterior extreme of the oesophagus. The proximal end of the supraoesophageal organ is surrounded by an annular constrictor muscle arising from the dilation.

A–4. *Ventriculus* (*mid-gut*) : The ventriculus is a large, flat, sac-like organ occupying almost the whole dorsal and lateral parts of the body cavity, except for the part occupied by the excretory organ (hind-gut). The cross sections show that the ventriculus occupies almost the entire body in the level of the posterior part of the central nervous mass. The anterior tip of the anteromedian ventricular caecum is posterior to the distal part of the azygous salivary gland; the sides of the tip neighbour the pericibal salivary gland. The ventral surface of the ventriculus is adjacent to the supraoesophageal organ anteriorly ; next, the venter adjoins the central nervous mass and tubular salivary glands, and sometimes the ventricular caeca reach the ventral part of the glands; the greater part of the ventral surface of the ventriculus presses against the reproductive organs. Most of the ventriculus is divided into two lateral parts by both reproductive and excretory organs, the latter occupying the dorsomedian region of the body cavity. The outer surface of the ventriculus is folded at intervals by dorsoventral muscles which play a rôle to promote the flow of food materials within the viscus. Thus, the ventriculus is provided with three small caeca extending anteriorly, a median and two paired lateral ones, and is furnished with two paired, much larger caeca extending posteriorly ; the posterior caeca are subdivided into three or more diverticula.

Examining the histology of the ventriculus, one finds that a single layer composed of large columnar epithelial cells is located on a fine basement membrane. The columnar cells harbour oval, deeply staining nuclei proximally; the boundaries of the cells are rather clearly recognizable. In general, the cytoplasm of the cells is reticulated proximally, and is irregularly vacuolated distally; most part of the cell is frequently occupied by vacuoles containing food spherules which generally stain with eosin but sometimes with haematoxylin. In addition, the author met with the fact that no spherules are found in the ventriculus of an individual, probably in starved condition.

The epithelial cells are often observed to project into the ventricular lumen. When these cells are exhausted, they break in their distal part, releasing the contents into the lumen until death. The food spherules released are observed in the lumen, though highly variable in number among different specimens. In a few female specimens the lumen is found to be packed with a great number of such spherules; a good number of the epithelial cells are lost there and the remainder



Figs. 1–6. Transverse sections of male of *Neomolgus littoralis* through (× 64): 1, the supraoesophageal organ ; 2, the central nervous mass ; 3, the anterior portion of azygous accessory gland ; 4, the posterior portion of azygous accessory gland ; 5, the laminated gland ; 6, the testes. Abbreviations : AA, azygous accessory gland ; AS, azygous salivary gland ; CN, central nervous mass ; E, excretory organ ; EC, embedding-sac ; G, guanine concretions ; LM, laminated gland ; OE, oesophagus ; PC, penial canal ; PS, pericibal salivary gland ; RS, reniform salivary gland ; SO, supraoesophageal organ ; T, testis ; TS, tubular salivary gland ; V, ventriculus ; VA, distal part of vas deferens ; VM, proximal part of vas deferens.

are not numerous.

Finally, it must be noted that the lumen of the ventriculus generally contains a good deal of guanine concretions, the excretory substances morphologically identical with those found in the excretory organ (hind-gut).

B. Excretory system (hind-gut)

No anatomical connection between the hind-gut and the ventriculus is recognized; namely the latter becomes blind. The hind-gut, a mediodorsal elongate sac, serves for the elimination of urinary material as the excretory organ. At the level of the posterior part of the supraoesophageal ganglia the excretory organ arises at a short distance from the dorsal integument and extends caudally; the organ in its full length is situated immediately under the dorsal integument except for the anterior tip and the posterior portion. The excretory organ lies between two large posterior caeca of the ventriculus, being about two-thirds to three-fourths as long as the ventriculus. The hinder part of the organ turns downward to form the uropore (so-called "anus"). In cross sections through the caudal portion of the body this organ occupies almost the whole area across the dorsoventral diameter of the body.

The epithelium of the organ consists of a single layer of pavement epithelial cells, which slightly and unevenly stain with eosin. The cells contain distinct nuclei of oval or elongate form. The excretory organ can expand and contract according to the quantity of its contents; when the organ is expanded in accordance with large contents, each epithelial cell becomes expanded in length and narrowed in diameter.

The lumen of the organ harbours numerous irregular concretions of urinary material, which often adhere to form more or less round masses. The urinary material is of guanine in nature, being opaque to transmitted light and white in reflected light. Besides, a good deal of secretion which stains deeply with haematoxylin or slightly with aniline blue, is very often observed in the lumen, particularly in the region adjoining the interior margin of the epithelial layer. The secretion aggregates and has a tendency to form irregularly ring-shaped masses one after another in the lumen.

In addition, the lumen of one individual (male) was observed to contain several or more food spherules near the uropore. The food spherules seem to be of strictly the same nature as those in the ventriculus.

C. Female reproductive system

The female reproductive system consists of an ovary, an oviduct, a vagina and a spermatheca.

C–1. *Ovary*: The ovary is a large sac-like organ lying in the ventral median part of body. It contains a good many germ cells, the younger ones oc-

curring anteriorly. The mature ova do not lie in the ovary but in the oviduct which is, therefore, much larger than the ovary in gravid females.

C–2. *Oviduct*: The oviduct, containing a number of mature ova (each ca. 220 μ in diameter), is not only rolled around the ovary but also extremely winding throughout the body. Accordingly, it is very difficult to determine where the oviduct issues from the ovary. According to Michael the oviduct arises from the center of the ovary. The oviduct and ventriculus fill all the available space: they press against each other; the former frequently wedges itself in the space between the exterior surfaces of the latter and the integument.

Examining the walls of the oviduct, one finds a few to several rows of irregular, columnar glandular cells on a basement membrane. These cells stain deeply with haematoxylin both in the spherical nuclei and in the granular cytoplasm; when stained with Heidenhain's azan, the nuclei become orange to reddish and the cytoplasm pale brown. The lumen of the oviduct into which some of the cells are projected, is distended in dependence upon the number of ova contained. The walls are highly variable in thickness in different parts.

C–3. *Vagina*: The vagina is a short, flexible, membranous duct following the oviduct. There is a wide lumen in the vagina. The epithelial cells, columnar in shape, do not stain deeply with haematoxylin, differing from those of the oviduct. The vagina was not distinguished from the oviduct by Michael.

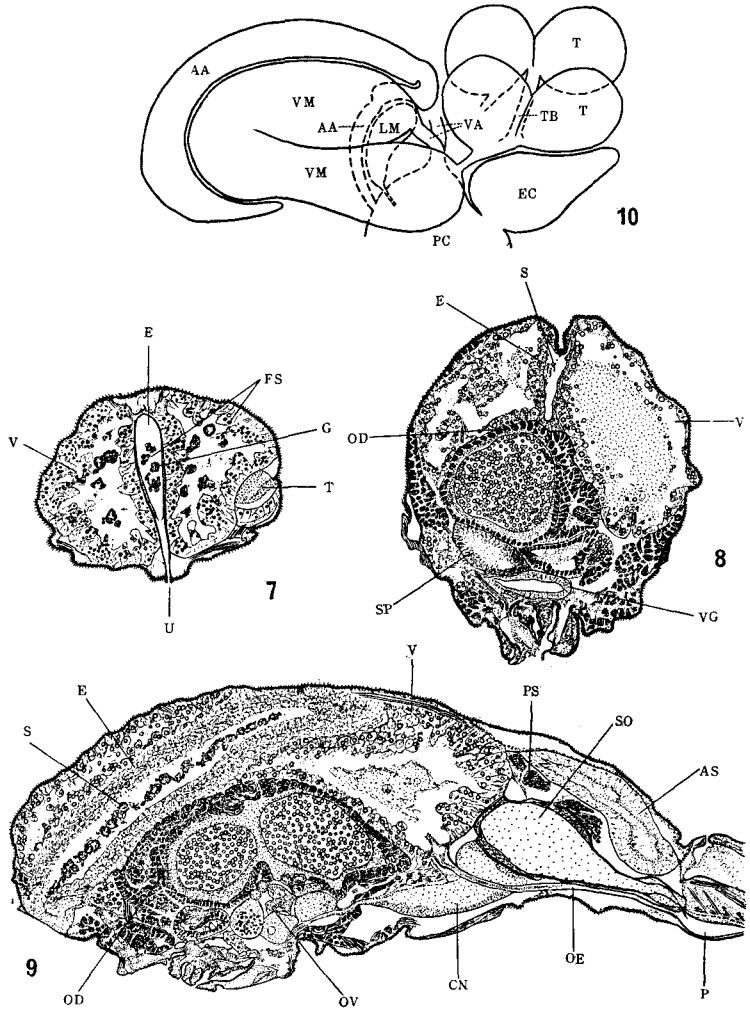
C–4. *Spermatheca*: The spermatheca is a small blind sac arising from the terminal portion of the oviduct. The cells forming the epithelium of this organ are columnar and provided with small nuclei. These cells only slightly stain with haematoxylin, differing from those of the oviduct; further, the former are slightly dyed reddish with Heidenhain's azan, while the later are dyed pale brown with the same material.

D. Male reproductive system

The male reproductive system consists of a pair of testes, a pair of vasa deferentia, two unpaired and two paired accessory glands, and a penial canal; the last-named organ is excluded from consideration in this paper. The male system is very complicated in comparison with the female one.

D–1. *Testes*; D–1–1. Testes proper: On each side of the hind part of the body, there are two testes which stain moderately with haematoxylin. Immediately above them the hind caecum of the ventriculus is located, while, immediately below them an embedding-sac is located. The ventral end of each testis terminates in a short duct which is not definitely marked off from the testis; the two ducts located on the same side unite to form a short common duct which connects with the so-called testicular bridge. Another extremity of the common duct unites into a minute passage entering the vas deferens.

The ventral and ventrolateral surfaces of the testis are composed of large,



Figs. 7–10. *Neomolgus littoralis* : 7, transverse section of male through the uropore (× 64) ; 8, t. s. of female through the vagina (× 64) ; 9, median longitudinal section of female (× 64) ; 10, reconstructive schema of male reproductive organs. Abbreviations : FS, food spherules ; OD, oviduct ; OV, ovary ; P, pharynx ; SP, spermatheca ; TB, testicular bridge ; U, uropore ; VG, vagina. For other abbreviations see Figs. 1–6 (p.413).

particular cells which contain globular, clear nuclei staining deeply with haematoxylin; the other surfaces and the interior harbour a great number of germ cells in colonies, the more mature cells occurring more ventrally. In the ventral region of the testis, there is a lumen into which the spermatozoa are discharged, though the lumen varies in extent among different specimens; a quantity of weakly eosinophilic secretion is also recognized in the lumen.

D–1–2. Testicular bridge: The so-called testicular bridge is a transverse, tubular connection joining the ventral parts of the two testes on each side of the body with those on the other side. As stated above, both extremes of the bridge each enters the testicular common duct on the same side; the bridge and the common duct are not distinctly marked off from each other. Posterior to the bridge are located embedding-sacs, anterior to it "glandular antechambers" are present, while, immediately above it, the hind caeca of the ventriculus are situated.

In transverse sections the bridge is oval in outline, its ventral end having a tendency to be slightly pointed. The wall of the bridge is composed of a basal membrane which is thicker ventrally. The bridge is provided with a thin layer of a small number of germ cells in the dorsal region. This layer is found to join the testicular, germinal tissues at both ends of the bridge. Along the whole central region of the bridge extends a layer consisting of large cells which are the same in nature as those forming the ventral and ventrolateral surfaces of the testes: these cells stain with haematoxylin, and contain clear, globular nuclei. The lumen occupying the large ventral space of the bridge contains the discharged spermatozoa.

D–2. *Vasa deferentia*: Each vas deferens consists of a proximal, extremely large part (Michael's "mucous gland"), and a much smaller distal portion (his "glandular antechamber").

D–2–1. "Mucous glands": The so-called "mucous gland," a greater part of each vas deferens, is one of the largest organs in the male. Each "gland" is U-shaped seen laterally; the region between the two bending portions stands almost perpendicularly at the level of the posterior part of the central nervous mass. The lower arm of the "gland" is connected caudally with the testes of the same side through a minute passage which is composed of three layers: a thin inner, a muscular middle, and a macronucleated outer layer. The upper arm enters the penial canal via the so-called "glandular antechamber." Both of the arms are subparallel with each other, and almost touch at their inner edges. In the anterior part, each arm is also subparallel with the corresponding arm occurring on the other side, whereas, in the posterior part, it diverges gradually from the partner. A transverse section through the greater part of the "glands" shows an appearance of four circles.

In the "gland," a single layer of large, more or less columnar glandular cells is located on a basement membrane. These cells are ca. 100 μ long in maximum and ca. 25 μ wide in maximum, provided with distinct, globular nuclei (ca. 10 μ

in diameter) which stain deeply with haematoxylin. The cytoplasm also is dyed deeply with haematoxylin, indicating the typical nature of the glandualr cells. The secretion, lightly staining with eosin or aniline blue, occurs both in the distal parts of the cells and in the "gland" lumen, the latter receiving the secretion discharged from the former.

D–2–2. "Glandular antechambers" : The so-called "glandular antechamber" is a dital, short, narrow portion of each vas deferens, joining to the partner from the opposite side posteriorly and the common region of the antechambers communicating with the penial canal. The "antechamber" is marked off from the "mucous gland" by a constriction.

The walls of the "antechamber" are thick, composed of a basement membrane and a single layer of columnar cells arranged regularly around the central lumen. These cells are similar to those of the "mucous glands," but do not stain deeply with haematoxylin. They show thick lateral lines which are regarded as their boundaries. The nuclei are very small, indistinct. A quantity of a secreted matter resembling that occurring in the "mucous glands" is found in the lumen and the epithelial cells. A horizontal section through the "antechamber" presents a honey-comb-like structure.

D–3. *Accessory glands*; D–3–1. Embedding-sacs : Each of two, paired, accessory glands, named the embedding-sacs by Michael, lies immediately under the testes on each side of the body. The glands are one of the largest organs in the male. Each gland presses against its partner in the median plane of the body. It adjoins the proximal (lower) part of the "mucous gland" of the same side anteriorly, and neighbours the integument laterally. Each gland opens into the penial canal.

The walls of the gland consists of a basal membrane, and a single layer of columnar cells which, though variable in different parts, are more or less clavate. The cells harbour large, elongate oval nuclei lying on their proximal part, and contain strongly eosinophilic cytoplasm; the boundaries of the cells are very clear. The interior parts of the cells are projected into the large lumen, their distal ends being usually convex. A small amount of a hard-to-stain secretion is found in the lumen.

D–3–2. Azygous accessory gland: The azygous accessory gland is a very long median organ which appears to be enormous in lateral view. The blind end of this gland is generally located above the posterior end of the supraoesophageal ganglia; the gland extends above the ganglia forward to curve upward along the hinder surface of the oesophagus. Next, the gland runs medially above the upper (distal) arms of the "mucous glands" backwards, each lateral edge of the former pressed by the inner edge of each arm of the latter. Further, the azygous gland bends above the top of laminated gland downwards, and, proceeds ventrally between the "mucous glands" in front of the laminated gland, to enter the anterior region of the penial canal. Since the azygous gland is thus inserted between the

"mucous glands" except for the distal blind portion, it is laterally compressed in most parts. At the region anterior to the top of the laminated gland, the azygous gland is constricted and divided into two parts: the distal larger part (called the first part below) and the proximal, short and slender one (called the second part below).

The walls of this gland consist of a basal membrane, and a single layer of columnar cells which resemble those of the embedding-sacs. The columnar cells harbour rather proximal nuclei. The cells of the first part are uniform in shape, while those of the second part, much narrower than the former and less distinct in their boundaries, are not uniform in shape. The cytoplasm of the cells of the first part are evenly stained well with eosin, but those of the second part only slightly stained; the latter are vacuolated. In the second part, because of the irregularity of interior ends of the cells, the lumen of the gland is indented; in the first part, however, it is not so indented, though variable in diameter in different portions. The secretion of this gland is inconspicuous.

D–3–3. Laminated gland: This unpaired gland is a median, small tubular organ which enters the anterior part of the penial canal through a very narrow passage. The diameter of the gland is nearly uniform throughout, except for the convex distal end. The lumen is often provided with a secretion which is lightly dyed with eosin as well as with aniline blue.

The walls of the gland consist of a thick, strongly eosinophilic basal membrane, and of a single layer of long, lamellate cells, nearly equal in length to one another. These cells have hard-to-stain cytoplasm and wrinkled, basophilic cell boundaries; the nuclei were not definitely observed by the author.

II. *Bryobia eharai* Pritchard et Keifer

(Figs. 11–17, Pl. VII, Figs. 26, 29)

This species is known to feed on the chrysanthemums in Japan (Honshu, Shikoku and Kyushu) and in Pakistan (see Ehara, 1959). Although in the Tetranychidae the two species *Tetranychus telarius* (Linnaeus) and *Panonychus ulmi* (Koch) (=*Metatetranychus ulmi*) have been studied as to the internal organs (Claparède, 1868, Blauvelt, 1945, Gasser, 1951, Snieder-Berkenbosch, 1955), the primitive genus *Bryobia* has been little investigated.

A. Digestive system and excretory system

The alimentary canal consists of pharynx, oesophagus, ventriculus, and hind-gut. The last-mentioned organ functions also as the excretory organ.

A–1. *Pharynx*: The pharynx is a short tube, crescent-shaped in cross section, and is chitinized both in dorsal and in ventral parts. The dorso-posterior wall is greatly thickened to form a cup-shaped plunger which stains intensively with haematoxylin. The pharyngeal muscles are inserted by tendons on each side of the median region of the dorsum of the plunger; the tendons are

not concentrated at a single level but widely set. Through the movement of the plunger the food can enter the pharynx and pass further into the oesophagus. The pharynx is devoid of transverse pharyngeal muscles.

A–2. *Oesophagus*: The pharynx enters the longer and non-chitinized oesophagus. The latter runs gradually upward to enter the ventral median portion of the anterior part of the ventriculus: surrounded by a fat body in anterior half and piercing through the central nervous mass in posterior half. In transverse section, the oesophagus is oval to circular in outline, with a thin epithelial layer. The oesophageal valve, a slight projection of the oesophagus into the ventriculus is well developed; the valve is provided with some conspicuous cells that are semicircular in lateral view.

A–3. *Ventriculus*: The ventriculus occupies almost the whole dorsal and lateral parts of the interior of body. The cross sections show that, in the level of the anterior tip of the ovary, the ventriculus occupies almost the entire body; a similar situation is revealed also in the cross sections through the caudal portion of the body. The anterior portion of the ventriculus is posterior to the azygous salivary gland and the fat body. With the exception of the anterior small portion, the ventriculus is divided into two lateral parts by the reproductive organs lying ventrally and by the hind-gut extending along the dorsomedian region of the body cavity. The outer surface of the ventriculus is indented at intervals by the dorsoventral muscles, thus partitioning the organ into a number of caeca of various sizes and shapes.

The epithelium of the ventriculus consists of a single, loose layer of elongate ovoid or spindle-shaped glandular cells bearing oval nuclei. The whole epithelial cell stains deeply with haematoxylin; stained with Heidenhain's azan, the cytoplasm is dyed pale brown, and the nuclei dyed reddish. The cells are widely variable in size and shape, and are frequently vacuolated. Sometimes, the cells project into the lumen of the ventriculus to be cut off. The epithelial cells adjoining the hind-gut are characteristic in staining with eosin.

In the lumen of the ventriculus there are, in general, many food balls of irregular interior structure. These food balls are found in all caeca of the ventriculus. The colour and markings of this mite in live state are largely due to the colour and distribution of the contents of the viscus.

A–4. *Hind-gut*: The hind-gut is a long sac-like organ occupying the dorsomedian part of the body cavity, and opening out of the body through the ventrocaudal uropore which also serves as the anus as described below. The hind-gut is frequently pressed somewhat laterally by the ventral mature ova and by the lateral distended ventriculus; it varies greatly both in size and in shape regionally as well individually: in cross section through the mature ova, it takes cross-, inverse-T-, or diamond-shape and only rarely V-shape.

The epithelium of the hind-gut consists of a single layer of columnar, as if syncytial cells. These cells contain large, spherical or oval nuclei, and are

vacuolated distally. The epithelium is generally thicker than the ventricular epithelium bordering the hind-gut, and stains more lightly than that. The hind-gut epithelium appears to be formed of many lamellae arranged in a single layer. However, since the lamellae are smaller in diameter than the epithelial nuclei, it is certain that each lamella does not correspond to one cell. The distal parts of the lamellae are frequently observed to project far into the lumen of the hind-gut.

The dorsomedian walls of the hind-gut, above which the two paired lateral parts of the ventriculus meet with each other, consist of loose, vacuolated cells not easily stained with eosin. These vacuolated cells are also found to constitute the walls of the anterior tip of the hind-gut.

The large lumen of the hind-gut contains a number of very large, globular guanine concretions each of which often appears to have an outer layer formed of numerous radiating "cells." The concretions are yellowish in transmitted light and stain with aniline blue. So far as the author's observations go, food balls are occasionally recognizable in the hind-gut lumen, though a communication between the ventriculus and anterior tip of the hind-gut is not definitely found. Therefore, it seems that the hind-gut functions not only as the excretory organ but also as the digestive one, further, that the uropore also serves as the anus.

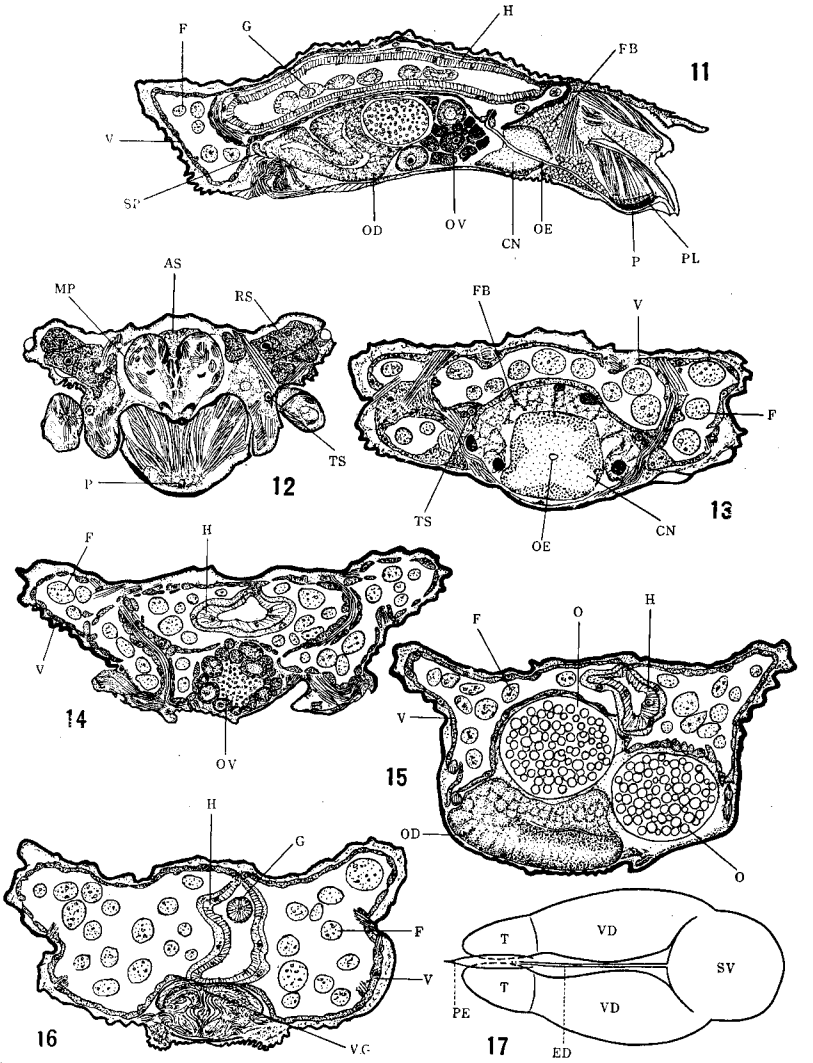
B. Female reproductive system

The female reproductive system is composed of an ovary, an oviduct, a vagina and a spermatheca ; these organs almost fill the ventral half of the interior of the hysterosoma.

B–1. *Ovary*: The ovary is a large sac pressing all neighbouring organs. The anterior tip of the ovary is located above the posterior part of the central nervous mass; its dorsolateral and lateral parts adjoin the ventriculus, while the dorsomedian portion is immediately ventrad of the hind-gut.

The ovary contains germ cells arranged in successive stages of development, with younger germ cells in the anterior part; the oogonia occur in the anterior tip and the anterior central portion, surrounded by larger oocytes. In the ovary there are usually two or three ova in advanced stages of maturity. The most mature ovum (ca. 110 μ in diameter) ready to be deposited occupies the posterior part of the ovary, the second ovum is located laterad and cephalad of the former, and the third lies laterad and cephalad of the second ovum on the opposite side. In the first and second ova the yolk mass occurs in hard-to-stain protoplasm, while, in the third ovum a less amount of yolk lies in somewhat staining protoplasm. It is occasionally observed that both the first and second ova simultaneously reach to nearly complete ripeness.

B–2. *Oviduct*: The oviduct is a large, fleshy organ, leading the posterior portion of the ovary into the anterior portion of the vagina. The epithelium of the oviduct is formed of large, glandular columnar cells. These cells stain well with haematoxylin in the proximal portions where the oval nuclei are situated;



Figs. 11–17. *Bryobia eharai* : 11, median longitudinal section of female (× 130) ; 12, transverse section of female through the reniform salivary gland (× 180) ; 13, t. s. of female through the central nervous mass (× 180) ; 14, t. s. of female through the anterior tip of ovary (× 180) ; 15, t.s. of female through the mature ova (× 180) ; 16, t. s. of female through the vagina (× 180) ; 17, reconstructive schema of male reproductive organs. Abbreviations: ED, ejaculatory duct; F, food ball; FB, fat body; H, hind-gut; MP, mandibular plate ; O, mature ovum ; PE, penis ; Pl, pharyngeal plunger ; VD, vas deferens. For other abbreviations see Figs. 1–16 (p. 413 & p. 416).

the distal parts of the cells are weakly staining and greatly vacuolated, the vacuoles frequently occupying the greater part of the cells. Since the inner surface of the epithelium is usually pressed interiorly, the central lumen appears to be almost non-existent; when a mature ovum to be next deposited is located in the oviduct, the lumen is strikingly expanded.

B–3. *Vagina*: The vagina is a short, terminal part of the genital canal, leading the posterior portion of the oviduct into the caudoventral genital opening. There is a wide lumen in the organ. The vaginal epithelium is composed of a layer of columnar cells which contain weak-eosinophilic cytoplasm and proximal elongate nuclei.

B–4. *Spermatheca*: The spermatheca is a very small, clavate blind organ entering the posterior part of the vagina via a short curved duct. The epithelium of the spermatheca consists of a single layer of columnar cells and surrounds the lumen.

C. Male reproductive system

The male reproductive system consists of a pair of testes, a pair of vasa deferentia, a seminal vesicle, and an ejaculatory duct entering the aedeagus.

C–1. *Testes*: In each side of the caudal ventral portion of body there is a testis which varies in shape among different specimens, being ovoid, spherical, or subconical. The germ cells are arranged in successive stages of development, the younger ones occurring caudally.

C–2. *Vasa deferentia*: The vasa deferentia are large and thick ducts, located cephalad of the testes. Each vas deferens leads the anterior (distal) portion of the testis on the same side, into the post-lateral portion of the median, unpaired seminal vesicles, the anteriormost organ among the male reproductive organs. The vas deferens runs almost straight with little undulation to enter the seminal vesicle via a short and narrow distal portion which is not definitely marked off from the rest. The lumen of the vas deferens is very large, containing the dark-staining spermatozoa and secretion.

The epithelium of the vas deferens consists of a single layer of glandular cells which have proximal dark-staining nuclei. These cells individually very remarkably in structure: sometimes, they are narrow in diameter and contain cytoplasm which is not uneven; occasionally, they are so distended and highly vacuolated that the glandular epithelium appears to be of honeycomb-like structure. It is possible that the epithelial cells are less active in glandular function in the former case and are active in the latter case. In accordance with the variation of the glandular activity of the epithelium the vas deferens itself also varies greatly in shape among different specimens: when the epithelium is comparatively less active, the vas deferens, in cross section, looks like a subquadrilateral in which the height is generally shorter than the width, being concave dorsally and convex ventrally; when the epithelium is active, the vas deferens is greatly enlarged and

complicated in shape.

C–3. *Seminal vesicle*: The seminal vesicle is a single, median, more or less spherical organ lying slightly behind the center of the body, occurring caudad of the central nervous mass and ventrad of the hind-gut. This vesicle is ca. 50 μ in diameter, larger than each testis. It receives one vas deferens in each of the post-lateral portions, and issues post-medially a slender ejaculatory duct entering the aedeagus which was illustrated in a previous paper by the present author (1959).

The walls of the organ bear a thin, areolate outer layer of which the cells are arranged in one stratum and are free from one another in the distal portions. Interior to this layer there is a thick, stout muscular layer which stains deeply with eosin and shows a horse-shoe arrangement in longitudinal and horizontal sections. The contraction and expansion of the muscular layer probably play an important rôle in the ejaculation of spermatozoa during coitus. The innermost layer is very thin, its cells contain elongate nuclei. The central lumen harbours the dark-staining spermatozoa.

III. *Hydryphantes affinis* Sokolov

(Figs. 18, 19, Pl. VII, Figs. 28)

This water mite is known to occur in Japan, Sakhalin, Siberia and Europe (Uchida, 1936, Imamura, 1960). In Hokkaido this species is found swimming in temporary pools during early Spring to early Autumn. The internal anatomy of *Hydryphantes* species was known mainly by Schaub (1888, published as *Hydrodroma*) and Thor (1903). Besides, a number of water mites have been studied as to the internal organs by many authors (e.g. Michael, 1895, Thor, 1903, Schmidt, 1935, Bader, 1938, 1954).

A. Digestive system

The alimentary canal is formed of pharynx, oesophagus, and blind ventriculus.

A–1. *Pharynx*: The pharynx is a long tube, chitinized both in dorsal and in ventral parts. The dorsal part stains deeply and is generally larger in thickness than the ventral part which is strongly chitinized. The pharynx is crescent-shaped in transverse section. The paired, long perpendicular muscles are inserted by tendons on the median region of the dorsal part of the pharynx. Some transverse muscles are set on the dorsum of the pharynx; each band of them and each pair of the bands of the perpendicular muscles are arranged alternately.

A–2. *Oesophagus*: The pharynx is followed by the non-chitinous oesophagus which is more or less circular in cross section. It runs gradually upward in the anterior part which pierces through the central nervous mass posteriorly. After leaving the central nervous mass the oesophagus turns rapidly upward throughout its posterior part. The epithelial cells of the oesophagus are furnished with elongate nuclei and are often so projected interiorly that the lumen is indented.

The posterior end of the oesophagus enters the medioventral portion of the ventriculus caudad of the median anterior caecum. The oesophageal valve is well developed.

A–3. *Ventriculus*: The ventriculus occupies almost the greater part of the body except for the central part taken by the ovary and oviducts. Anteriorly, the ventriculus is provided with three small caeca : a median and two, paired lateral ones. Posteriorly, the ventriculus issues three large caeca : a median, dorsal and two, paired ventral ones. Laterally, a pair of small caeca arise from the ventriculus. The number and size of the ventricular caeca are variable in different specimens.

The epithelial layer is composed of light-staining columnar cells which possess round or oval nuclei. The distal parts of these epithelial cells generally harbour irregular vacuoles with eosinophilic food spherules of which a large number are found also in the ventricular lumen. The cells are often observed to project, in club-shaped form, into the lumen; when exhausted, they are cut off to release their contents in the lumen where are found a number of small guanine concretions which are morphologically identical with those occurring in the excretory organ (hind-gut).

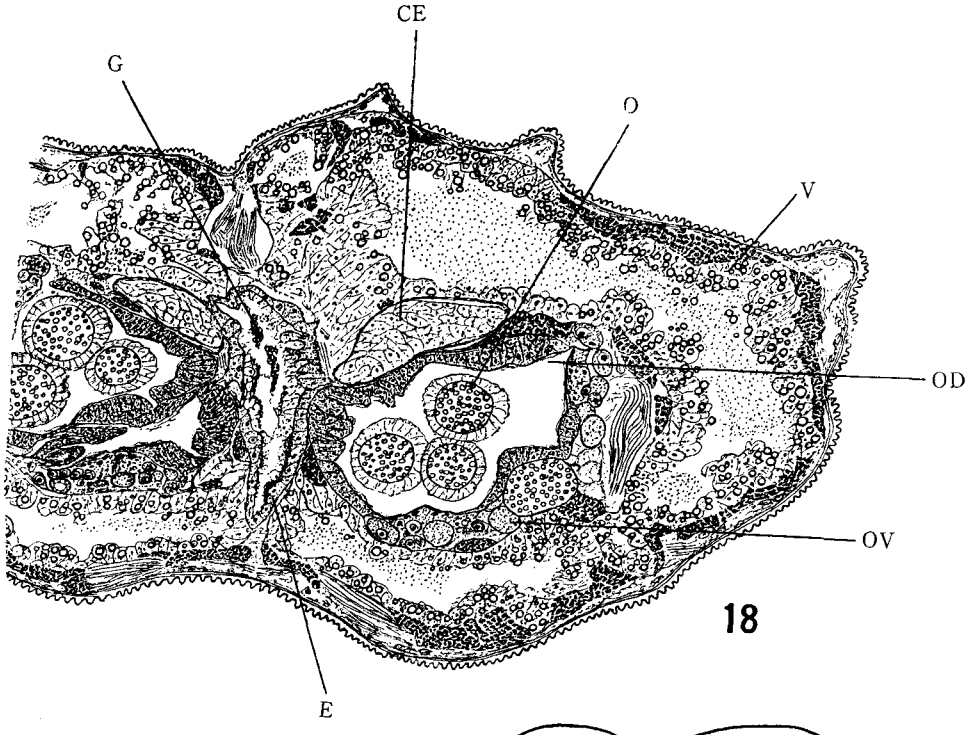
B. Excretory system (hind-gut)

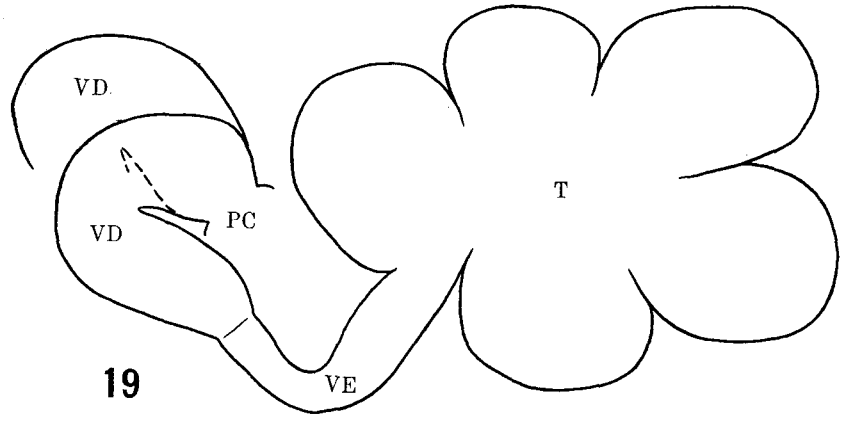
There is no anatomical connection between the hind-gut and the ventriculus; the former functions in the elimination of urates as the excretory organ. The excretory organ, a flat, sac-like viscus, is laterally bifurcate at the anterior apex; the anterior blind tips of this organ are located at the level of the posterior end of the central nervous mass. Surrounded by the ventriculus, the excretory organ extends caudally along the median axis of the body at a short distance from the dorsal integument. The posterior part of the present organ runs ventrally and caudally among the genital organs and finally opens as the uropore occurring behind the anus. The ventriculus is variable in shape among different specimens.

The epithelial cells of the excretory organ are slightly more eosinophilic than those of the ventriculus; they have clear, oval nuclei. The lumen of the organ is highly indented, and contains numerous, excretory guanine concretions of which many are also found in the epithelial cells, particularly in the cell surface. The distal part of the cells is very often vacuolated; the guanine concretions, usually very abundant in the surfaces of the vacuoles, are ochraceous by transmitted light and small in size.

C. Female reproductive system

The female reproductive system consists of a ring-shaped ovary, two paired oviducts and a vagina. These organs occupy almost all the central and ventral parts of body cavity from above the central nervous mass to the rear of the body.





Figs. 18, 19. *Hydryphantes affinis*: 18, transverse section of female through the central organ (× 340); 19, reconstructive schema of male reproductive organs. Abbreviations: CE, central organ; VE, vas efferens. For other abbreviations see Figs. 1–17 (p. 413, p 416 & p. 422).

The ovary which is considered to have originally been paired, branches out into many directions. The oviducts are paired in principle, but they ramify at intervals and are so complicated in their course that their exact structure could not be determined in the present study. Originally, the oviducts are regarded to have adjoined the ventral surface of the ovary but they often extend adjoining the other surfaces of the ovary. The walls of the oviducts are composed of very thin membrane and generally basophilic ovarian tissue; the latter narrowing near the vagina. Each gravid female harbours more than 100 mature ova in the oviduct, each of which measures ca. 45 μ in diameter excepting the outer jelly layer. The terminal portions of the ovaries are united into the short, narrow vagina leading to the genital opening which is almost centrally located in the venter of body.

D. Male reproductive system

The male reproductive system is composed of a pair of testes, a pair of vasa efferentia, a pair of vasa deferentia, and a penial canal.

D–1. *Testes and vasa efferentia*: On each side of the hind part of the body, there is a testis which is divided into several lobes distally. The testis and the ventriculus which surrounds the former press against each other. The interior of the testis is packed with numerous spermatids and spermatozoa, leaving a small quantity of spermatogonia and spermatocytes in the periphery. There are a good many, light- to dark-staining spheres of the secretion in the testis; these spheres vary in size and shape. The testis discharges ventrally a broad vas efferens.

The walls of the vas efferens are formed of a thick, loose outer layer of deeply eosinophilic, fibrous cells, and of a thin, indistinct inner layer. The vas efferens which harbours the spermatozoa and secretion as in the testes, runs anteriorly and ventrally, and proceeds inward to enter the glandular vas deferens.

D–2. *Vasa deferentia*: Each vas deferens is a large, glandular duct, connecting the vas efferens with the penial canal. The vas deferens is not so much developed as that of *Neomolgus littoralis* which is somewhat similar to this mite as regards the male genital organs. The proximal end of the vas deferens communicates with the vas efferens ventrally. The vas deferens proceeds forward in proximal half to turn back dorsally at a short distance behind the central nervous mass. The dorsal part (the distal half) of the vas deferens runs caudally and interiorly to join the corresponding part of another vas deferens on the opposite side of the body. The common portion of the vasa deferentia enters the penial canal occurring medioventrally.

The histology of the vasa deferentia is almost constant throughout the organs. The epithelial layer is composed of light-staining columnar cells which have clear, oval nuclei proximally. The lumen of the vasa deferentia contains numerous spermatozoa and many, light- to dark-staining spheres of the secretion;

the spheres are variable in size and shape (seemingly similar in nature to the spheres found in the testes and the vasa efferentia). The junction between a vas efferens and vas deferens is slightly constricted externally but greatly constricted internally. Around the lumen of this region, there are a number of tall and narrow, particular epithelial cells which contain small nuclei and deeply eosinophilic cytoplasm.

Discussion

The data described above are generally in accordance with results of observations published by previous authors, but among them occur some new findings and a few problems to be considered herewith.

The supraoesophageal organ of *Neomolgus littoralis* was assumed by Michael (1896) to be a food-storing organ (his "receptaculum cibi") analogous to the so-called sucking stomach in some insects of the Lepidoptera, Diptera and Hymenoptera. According to him, the body fluid of the prey sucked out by the action of the pharynx, is provisionally stored in this organ. On the other hand, Grandjean (1938) asserted that the supraoesophageal organ produces a mucous fluid used in grasping prey, hence, does not contain the body fluid of the prey, but some granular mucous mass. However, he did not present any histological evidence to confirm his assertion. So far as the present author observed, though the organ does harbour a mass of granular eosinophilic substance staining also with aniline blue, it does not show clear glandular structure. Apart from its ambiguous function, the supraoesophageal organ of the Bdellidae is a peculiar organ found in no other groups of the Acarina.

The ventriculi of the three species studied are not essentially different either in general form or in histological structure, showing the type characteristic of the suborder Trombidiformes. However, a few interesting differences were found: the epithelium of the ventriculus is thin in *Bryobia* but is thick in the other two species; further, the epithelial cells of *Bryobia* stain dark with haematoxylin and contain no distinct food spherules, while those of the latter stain lightly and bear irregular vacuoles having many eosinophilic food spherules which also occur freely in the lumen; furthermore, the phenomenon that these cells are constricted off and fall into the lumen to release their contents, happens, in the former, apparently far less frequently than in the latter. Moreover, it must be mentioned that in *Bryobia*, in contrast with the other two species, the ventricular epithelium in the parts bordering the hind-gut has a different structure from the remainder. The author is now inclined to think that these differences between *Bryobia* and the others are largely due to their different food-habits.

As regards the internal anatomy of Tetranychidae a few recent studies have been published by Blauvelt (1945) and Gasser (1951) on *Tetranychus telarius*[1], and Snieder-

1) *Tetranychus* and *Panonychus* (= *Metatetranychus*) belong to the subfamily Tetranychinae, while *Bryobia* pertains to the subfamily Bryobiinae.

Berkenbosch (1955) on *Panonychus ulmi*. Judging from their observations, there are some differences between *Bryobia eharai* and the two previously studied tetranychids in the structure of the ventriculus. The epithelial cells of the ventriculus of *Bryobia* are similar to those of *Panonychus* but somewhat different from those of *Tetranychus* : they are much elongated to form a thin epithelium in *Bryobia* and *Panonychus*, but round or oval in *Tetranychus*. Blauvelt stated that food balls are often present only in the anterior one or two pairs of the lateral caeca in *Tetranychus*. In *Bryobia*, however, the food balls are found in all parts of the ventriculus. Further, as regards the pharyngeal plunger, there is a difference in these species : in *Tetranychus* the pharyngeal muscles are inserted on the plunger at a single level, while in *Bryobia* they are not concentrated at a single level but widely attached. Referring to Snieder-Berkenbosch's illustration, one sees that the plunger of *Panonychus* is of the *Tetranychus*-type. Thus, the pharyngeal muscles of *Bryobia* bear a resemblance to those of trombidiform mites other than tetranychids : namely, the plunger, having an adaptive significance for the suction of plant sap in the Tetranychidae, is still not so differentiated in *Bryobia*, a primitive representative in this family.

The excretory organ homologous to the hind-gut in the mites other than the Trombidiformes is different in histological structure in the three mites here studied : this organ is provided with a lamellate epithelial layer in *Bryobia* but with normal epithelium in *Neomolgus* and *Hydryphantes*. The organ contains a great deal of excretory guanine concretions in the lumen, in accordance with previous author's data that excretion is active in mites of the Trombidiformes. The guanine concretions are different in shape in these mites : in *Neomolgus* they are small, showing a tendency to adhere to form irregular, more or less round masses; in *Bryobia*[1] they are globular, large in size but small in number; and finally in *Hydryphantes* they are very small and scattered. It is interesting that in *Neomolgus* a good deal of the excretory concretions are always found also in the lumen of the ventriculus. In addition, the ventriculus of *Hydryphantes* was seen to contain fewer excretory concretions in the lumen than is found in *Neomolgus*.

Until recently, it has been the popular view in acarology that the gut of mites of the Trombidiformes has no anal opening, and that their hind-gut, separated from the gut, functions exclusively as an excretory organ, with a caudal uropore (homologous to the anus in mites of the remaining suborders). Blauvelt demonstrated in *Tetranychus* communication between the hind-gut and ventriculus, and asserted that the hind-gut functions both in the evacuation of food residues from the ventriculus and in the elimination of urates as the excretory organ. With respect to the closely related form *Panonychus*, Snieder-Berkenbosch also reported the same finding, without stating whether he could actually confirm or not communication between the hind-gut and ventriculus. In *Bryobia eharai* of the same family as the above two species, the author observed occasionally several food balls in the lumen of the excretory organ (hind-gut). No communication between this organ and the ventriculus was definitely detected, though the anterior tip of

1) The concretions of *Bryobia borealis* Oudemans were illustrated in photomicrograph by Thor (1930).

the former is provided with unique, hard-to-stain, vacuolated cells which may be a valve normally closed, opening only when permitting the entrance of food balls from the ventriculus; the dorsal median portion of the hind-gut is formed of the cells which are the same in nature as those forming its anterior tip. At any rate, also in *Bryobia*, a primitive genus of the Tetranychidae, it is certain that the hind-gut which has a true anus serves for the removal of food residues as well as for the elimination of excretory matter, because of the occurrence of the food balls in the organ in question. Incidentally, the hind-gut of *Tetranychus* is an organ of V-shaped cross section, while that of *Bryobia* does not show such a constant cross section but varies from part to part and with individuals.

Furthermore, it is of interest that, in a single individual of *Neomolgus*, the excretory hind-gut was observed to harbour several or more food spherules in the lumen near the uropore. This suggests the possibility that this mite, remotely related to tetranychids, may have also communication between the hind-gut and ventriculus.

It was revealed that each female harbours only one mature ovum in *Bryobia*, but more than 100 in *Hydryphantes*. However, occasionally, *Bryobia* bears two mature ova nearly completely ripe. Each female of *Neomolgus* is found to harbour a number of mature ova. On the other hand, it has been reported that tetranychid mites usually deposit one or two eggs per day, whilst water mites lay a number of eggs in a batch. Therefore, the present anatomical observations accord with these biological data on the reproductive potentials. Gasser illustrated the "Speicher-organ" in his note on the internal organs of *Tetranychus telarius*. But the present author is inclined to identify this organ with a part of the oviduct.

Regarding the testicular bridge of *Neomolgus*, Michael mentioned : "There is never any sign of the cells of the bridge becoming sperm-mother cells, or of their giving rise to spermatozoa." However, it is certain that the bridge is provided with a number of charged germ cells in the dorsal region along its whole length ; the layer of these cells was observed to join the testicular, germinal tissues at the both extremes of the bridge. On the other hand, it has been considered by acarologists that the bridge of *Neomolgus* is perhaps homologous to the short junction between the two testicular masses in *Lundbladia petrophilus* (Michael), to the curved region of the almost horseshoe-shaped testicular mass of *Allothrombium fuliginosum* (Hermann), and to various testicular junctions in many trombidiform mites. This hypothesis seems to be supported by the author's observation mentioned above.

Concerning the distal part of the vasa deferentia (Michael's "glandular antechambers") of *Neomolgus*, Michael spoke of very irregular arrangements of columnar cells of its walls. But, regular arrangements of these cells were recognized in the author's examinations. According to Michael, the male azygous accessory gland of *Neomolgus* is known to be composed of two parts which are morphologically distinctive from each other. This fact is accepted by the present author, too. The two parts are possibly differentiated in their functions.

So far as the present author is aware, no vasa deferentia have been reported

in the Tetranychidae. However, in *Bryobia* the author found tow paired, well developed glandular vasa deferentia which vary strikingly in structure and of course in glandular activity. Each vas deferens of this species may be homologous to the junction between the seminal vesicle and a testis in *Tetranychus*. According to Michael, the seminal vesicle of *Tetranychus* is composed of a single layer of columnar cells surrounding the lumen which is lined with a heavy clear wall, possibly of chitinous nature. In *Bryobia*, the walls of the seminal vesicle were observed to be formed of three layers : a thin, non-chitinous inner, a thick, muscular middle, and a thin, areolate outer layer. It seems that the contraction and expansion of the muscular layer play an important rôle in the ejaculation of semen during copulation.

With respect to the taxonomic position of the Tetrapodili, some discussions have been presented : Vitzthum (1940–1943) regarded this group as a separate suborder, though he accepted the close systematic relationship between the group and the Tetranychidae. Baker and Wharton (1952) recognized the Tetrapodili as a group within the suborder Trombidiformes. The latter opinion is maintained by a few items of evidence : Ewing (1922) asserted that the Tetrapodili are closely related to the phytophagous families of the suborder Trombidiformes : Tetranychidae and Tenuipalpidae, on the basis of comparative studies on the mouth parts, tarsal armature and form of the body among these groups. Baker (1948) described a new tenuipalpid mite indicating a phylogenetic relationship between the Tetranychidae and the Tetrapodili.

Judging from the observations by Blauvelt, Snieder-Berkenbosch, and the present author, it has become almost certain that most of the Tetranychidae are not provided with a usual trombidiform blind gut, but with an anus-bearing gut. Such structure of the alimentary canal is seen also in the Tetrapodili in question (Nalepa, 1887, Hassan, 1928). This fact seems to support the settlement of Baker and Wharton on the taxonomic position of the Tetrapodili, which is based upon their life mode tending probably to a parasitic wormlike mite. In conclusion, it can be said, in disagreement with Vitzthum, that the Tetrapodili are only an offshoot of the tetranychid stem within the suborder Trombidiformes, although recent European authors have as yet followed Vitzthum's ranking of this group.

With regard to the anatomical and histological structures of the ventriculus and the excretory organ (hind-gut), the Tetranychidae differ from many other families of the suborder Trombidiformes. The present author is inclined to consider that, as lightly touched upon by Hughes (1959), this difference does not mean two remote phyletic origins, but is merely due to the adaptive divergence caused by the different food-habits : the former are phytophagous while the latter predatory.

Summary

1. The internal anatomy of digestive, excretory, and reproductive organs of both sexes was described for *Neomolgus littoralis* (Linnaeus), *Bryobia eharai*

Pritchared et Keifer, and *Hydryphantes affinis* Sokolov. For the first time detailed internal anatomy of species of *Bryobia* was presented in this paper.

2. The hind-gut of *Bryobia* bears a true anus and functions both in the removal of food residues and in the elimination of excretory matter. The anatomical similarity of the alimentary canal of the Tetranychidae to that of the Tetrapodili, that it opens into the exterior through an anus, would support the assertion of Baker and Wharton that the Tetrapodili should not be ranked as a separate suborder but are only an offshoot of the tetranychid stem within the suborder Trombidiformes.

3. The remarkable differences in the anatomical and histological structures of the ventriculus and hind-gut between the Tetranychidae and many other families of the suborder Trombidiformes are possibly due to the divergence in their food-habits : the former are phytophagous while the latter predatory.

4. Further, some particularly interesting data obtained were : 1) the discovery of charged germ cells in the testicular bridge of *Neomolgus*, by means of which this bridge is homologized to the junction between two testicular masses in many trombidiform species, 2) the primitive nature of the pharyngeal plunger in *Bryobia*, 3) the occurrence of large, glandular vasa deferentia in *Bryobia*, and 4) the possession of a stout muscular layer by the seminal vesicle of *Bryobia*.

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Explanation of Plate VII

Fig. 26 was stained with Heidenhain's azan and all others with Delafield's haematoxylin.

Fig. 20. Longitudinal section of male of *Neomolgus littoralis* through the nearly median line, showing secretion found in the excretory organ, × 32.

Fig. 21. Showing the secretion found in the excretory organ of male of *Neomolgus littoralis*, horizontal section, × 260.

Fig. 22. Showing the non-distended excretory organ of male of *Neomolgus littoralis*, transverse section, × 260.

Fig. 23. Showing the distended excretory organ of male of *Neomolgus littoralis*, transverse section, × 260.

Fig. 24. Showing the food spherules found in the excretory organ of male of *Neomolgus littoralis*, transverse section, × 260.

Fig. 25. Showing the testicular bridge of *Neomolgus littoralis*, longitudinal section of body, × 510.

Fig. 26. Horizontal section of female of *Bryobia eharai* through the hind-gut, showing a food ball, × 64.

Fig. 27. Horizontal section of male of *Bryobia eharai* through the reproductive organs, × 260.

Fig. 28. Showing the guanine concretions in the excretory organ of female of *Hydryphantes affinis*, transverse section, × 260.

Abbreviations : CG, charged germ cells ; DS, discharged spermatozoa. For other abbreviations see Text-figures. 1–19.

S. Ehara: Internal Anatomy of Trombidiform Acarinids