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Studies on the Intestinal Protozoa of Termites

III. The Distribution of Glycogen in the Bodies of Intestinal Flagellates of Termites, *Leucotermes* (*Reticulitermes*) *speratus* and *Coptotermes formosanus*

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With 11 Text-figures

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Introduction

The deposit of glycogen in the body of the intestinal protozoa of the termite was detected by BUSCALIONE and COMES as early as in 1910. They believed that the intestinal protozoa of xylophagous termite can elaborate sugars and glycogen from the wood that has been taken as the food, and that this glycogen is essential to the termite in so far as it takes its nutrition from this diet. Their conclusions seem to suggest to us that the xylophagous termites and their intestinal protozoa are in a symbiotic relationship, although this has not been sufficiently proved.

Examining the intestinal protozoa of Hymalayan termite, *Archotermopsis wroughtoni*, CUTLER (1921) also has detected glycogenic deposit in the body of *Pseudotrichonympha pristina*. He reported that in this protozoa the glycogenic reaction is seen to diffuse through the whole body, contrary to the opinion of BUSCALIONE and COMES that in the body of *Trichonympha agilis* the characteristic reaction of glycogen is sharply limited to a region near the nucleus. CUTLER, however, did not discuss the physiological meanings of this glycogen.

The study of glycogen in the body of the protozoa of the termite, it is thought, will throw light on many morphological and physiological problems and thus have value for further studies.

Examining two species of Japanese termites, *Leucotermes* (*Reticulitermes*) *speratus* and *Coptotermes formosanus*, the writer was able to observe fourteen forms of intestinal protozoa, all of which showed a very conspicuous deposit of glycogen. This paper is a statement of the results of these morphological studies. The experimental studies of the same will be given in forthcoming reports. The writer is indebted to MASATADA YAMASAKI, his younger brother, for the supply of *Coptotermes formosanus*.

Materials and Methods

Colonies of *Leucotermes* (*Reticulitermes*) *speratus* are easily collected at Yoshidayama hill near the laboratory. The intestinal protozoa were observed immediately after the materials were brought from this place to the laboratory. *Coptotermes formosanus*, however, is not found in the district of Kyoto, so that this material was brought by parcel post from Kyushu. Therefore it was not so fresh as that of the former species, but when the package arrived after two or three days of travel, the termite suffered no ill effects and their intestinal menageries also were in an apparently healthy condition.

The intestinal contents of termites are diluted with 0.5% NaCl solution, smeared on the cover glass and fixed with 90% alcohol. EHRLICH's hæmatoxylin and BEST's carmine are used for staining. By this method are obtained pretty good preparations of the distribution of the glycogenic deposition in the body of the intestinal protozoa.

KOIDZUMI (1921) gave a precise morphological description of the protozoa, to which the writer has nothing to add, so that the reader is referred to KOIDZUMI in regard to the structural description.

Observation

A) Protozoa of *Leucotermes* (*Reticulitermes*) *speratus*.

This termite harbours in its hind-gut eleven forms of flagellates belonging to three families: Trichonymphidae, Holomastigotidae and Dinenymphidae. All forms show more or less conspicuous features of glycogen deposition, as will be described below.

***Trichonympha agilis* var. *japonica*.**—This is one of the most eminent forms of protozoa and has a complicated structure (text-fig. 1). The body is divided into two portions, the anterior and posterior. The anterior portion is again divided into three parts, "cap," "nipple" and "bell." The nipple contains in it a structure called "axial core." This is enveloped by a thick ectoplasmic wall which is composed of inner and outer layers. This wall is elongated posteriorly and forms the bell portion. From the posterior end of this bell a little basket-like structure hangs into the endoplasm of the posterior portion of the body. This is the so-called "corbule," in the bottom of which the nucleus is located. The posterior portion of the body is a simple mass of protoplasm with a thin ectoplasmic cortical zone.

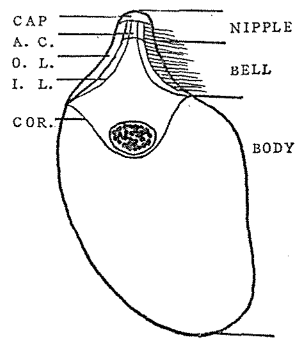

Fig. 1. An outline figure of *Trichnympha agilis* var. *japonica* to show the main structures of the body.

A. C., axial core; COR., corbule; I. L., inner layer; O. L., outer layer.

The glycogenic reaction is not diffused through the whole organism but three regions are marked in which the characteristic reactions are sharply defined. In the first portion the deposit is rarely detected. The granules of glycogen are arranged in a thin layer along the inner surface of the wall of the nipple and the bell. This distribution is identical with that in *Pseudotrichonympha* in which also the special deposit of glycogen is detected along the inner surface of the bell portion of the body.

The second centre of the glycogen deposit lies in the corbule. Here it seems as if glycogen fills up the little basket. But the quantity of glycogen in this portion is variable, and according to the variation in quantity there occur various manners and appearances of accumulation. When the quantity is very great the accumulation is so dense that it appears to be a compact mass of glycogen, and when less abundant it appears in the form of small granules. In addition to the changeable density, the reaction of glycogen is detected in various ways. Ordinarily there is a great amount of glycogen and the deposit assumes the shape of a pentagon with somewhat rounded corners, one side of which is concave along the surface of the nucleus, so that in this case it seems as if a crown of glycogen were put upon the nucleus (text fig. 2). On the contrary, if the quantity is smaller the deposit is limited in a flattened region taking the shape of a thick watch-glass and covering the upper side of the nucleus (text fig. 3), or it is compressed laterally so much that it is shaped like a candle flame. (text fig. 4).

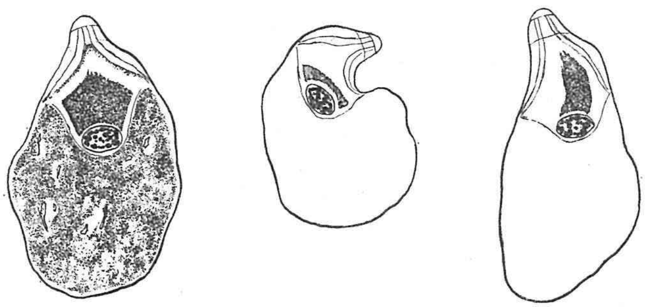

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Fig. 2. The glycogenic deposit on the inner surface of the bell-wall, crown-shaped one in the corbule and in the body part of *Trichonympha agilis* var. *japonica*.

Fig. 3. The watch glass shaped deposit in the corbule.

Fig. 4. The deposition in the shape of a candle flame.

In the third or posterior portion of the body the reaction conceivable occurs in the whole part, but there sometimes exist many food vacuoles in which no glycogen is to be seen. The amount of glycogen of this part, therefore, has a certain relation to the quantity of the food particles at that time. The organism is so voracious that it is not seldom that the region is completely occupied by food vacuoles full of food. In such a case only a small quantity of glycogen is deposited, but after the food particles are digested the larger area is offered as the space for the depositing of glycogen.

As is mentioned above, glycogen is deposited in three parts of the body separately and their density is not the same in all parts. But the quantity of glycogen in the corbule shows a more or less definite relation to that in the body; usually that of the former is greater than that of the latter. In an extreme case, the reaction is obvious only in the corbule while it is not visible at all in other portions of the body. In short the deposition in the corbule is always most conspicuous in the body. This fact seems to agree with the result recorded by BUSCALIONE and COMES as I have mentioned in the introduction.

Finally, in the nucleus or in the ectoplasmic portion of the body no trace of glycogen has ever been detected.

Teratonympha mirabilis.—This is a protozoa found in Japanese termites only. It has a very complicated structure and a queer appearance. Its body is differentiated into anterior and posterior regions, of which the anterior is more complicated than the posterior. The anterior end consists of a barrel-shaped axial column or the cylinder and a peripheral layer surrounding this; the latter is a thick ectoplasmic layer traversed by numerous flagella. Behind this is a part in which a nuclear apparatus is enclosed. The nuclear sac, in which the nucleus is held, is a flask-shaped body hanging by its slender neck below the base of the cylinder. The nucleus is held in the spherical portion of the body. This body is not suspended freely but supported by the flange-like horizontal extension that connects the body with the posterior end of the peripheral layer. Bordered by the peripheral layer and the nuclear sac there is a narrow endoplasmic region. The posterior portion of the organism shows no remarkable internal construction but has a very conspicuous structure on the body wall. There are many transverse ridges encircling the body and the flagella are set on from the top of these ridges (text figs. 5 and 6).

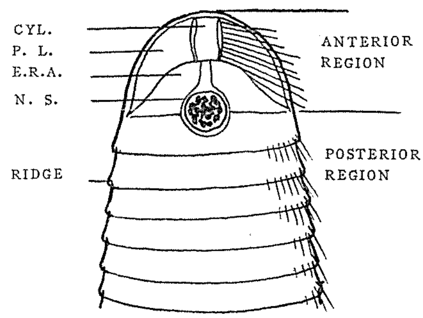

Fig. 5. An outline figure of *Teratonympha mirabilis* to show the structure of the head region.

CYL., cylinder; E. R. A., endoplasmic region of the anterior portion of the body; N. S., nuclear sac; P. L., peripheral layer.

Being thus constructed the body is separated into five portions in each of which glycogen is deposited separately, namely, the peripheral layer, the nuclear sac, the endoplasmic part of the anterior portion of the body, the endoplasmic part and the body wall of the posterior region of the body.

The peripheral layer is closely traversed by numerous flagella and the protoplasmic intervals between two neighbouring flagella is occupied by the glycogen deposit, and this is dense in the postero-peripheral region of the layer while in the antero-internal region the deposit is lacking. Glycogen is found in the nuclear sac at the neck of the flask. Its quantity is small but the reaction can be clearly observed. The deposit has the shape of a tall cone lying above the nucleus (text fig. 6). In the endoplasmic region of the anterior portion of the body glycogen is deposited ordinarily in moderate quantity and no such remarkable variation is observed as has been described in the corbule of *Trichonympha*. But it is not yet certain whether this endoplasmic portion is to be included in the nuclear apparatus or not, though this is more or less separated from the endoplasm of the posterior body part and no wood particles are taken into it.

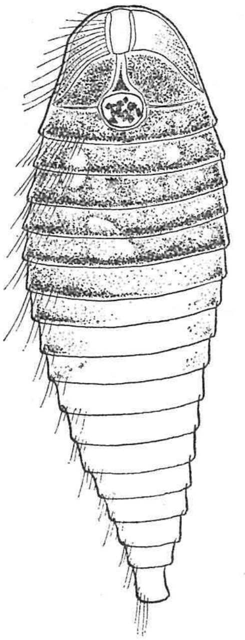

Fig. 6. *Teratonympha mirabilis.* The dots represent the granules of glycogen.

The endoplasmic portion of the posterior part of the body is a region into which the food particles are taken and where many vacuoles are observed. As in the case of *Trichonympha*, the quantity of glycogen is inversely proportional to that of the food particles. In the peripheral region of the body glycogen accumulates most densely in the ridges, and the density here is usually greater than in the central portion. Therefore, the main region of the glycogen deposit is easily discriminated from the central portion. The flagella are set on from the ridge so that it can be said that glycogen is deposited surrounding the basal granules of the flagella.

As in *Trichonympha*, in the present protozoa glycogen is not detected in the nucleus, but is found in remarkable quantities in the peripheral layer of the body.

Holomastigotes elongatum.—This is a small species and the number of individuals is also less than that of the other protozoa. The body is fusiform and on its surface exist many dextro-spiral ridges. The flagella are set on from this ridge. There are no complicated internal structures as in the previous forms. The nucleus is situated near the anterior tip of the body.

The deposit of glycogen is observed in every part of the body except in the nucleus and the very thin ectoplasmic cortical zone. Usually the reaction is given in a granular state and it is more or less dense in the portion along the longitudinal axis of the body where the nucleus is situated. When the quantity of glycogen is small the reaction is restricted to this axial portion, while the other portion of the body is destitute of the deposit and the nearer the portion to the nucleus the denser the reaction. Furthermore, when the quantity is extremely reduced the reaction is visible only in a narrow region surrounding the nucleus. When, in other words, the nucleus is apparently surrounded by a ring of glycogen the other parts of the body are completely lacking in the deposit. In this protozoa, therefore, the occurrence of the deposit of glycogen must be related very closely to the nucleus.

PROTOZOA OF DINENYMPHIDAE. This family includes two genera and eight species of protozoa.

Pyrsonympha.—The organisms belonging to this genus are variable in size and changeable in shape. Usually the body is long and slender, the anterior tip being sharp and the posterior round. But the posterior part may be thickened in several ways so that its shape becomes irregular. The body is twisted and the flagellar cords wind around it. The cords are eight in number, starting at the anterior tip of the body and running backwards on the surface of the body towards the posterior end of the body until they become free at this place. A well-developed axial filament is to be observed. It arises at the anterior tip of the body and hangs freely in the endoplasmic mass. The nucleus occupies the anterior end of the body and has connections with both the flagellar cords and the axial filament. Two species are included in this genus: *P. grandis* and *P. modesta.* The former is larger in size and occurs in a greater number of individual than the latter, and a great majority are living attached to the wall of the intestine of the host.

In both species, the quantity of glycogen is remarkable owing to the large size of the body, but as the structure of the body is simple no complicated distribution takes place inside the body. The greater quantity of glycogen is accumulated in the thick posterior half of the body where the metabolism is more active. When the quantity is very great, the whole body becomes full of glycogen and no differentiated distribution is observed, but when the quantity becomes smaller a deposit is found separated into the portion surrounding the nucleus and the posterior thickened part of the body. When the quantity of glycogen is further reduced, the reaction is detectable only at either the former or the latter portion.

Dinenympha.—This genus embodies six species: *D. exilis, D. rugosa, D. leidyi, D. nobilis, D. parva* and *D. porteri.*

The body is long and slender, tapered sharply both in the anterior and posterior ends. The axial filament is more or less well developed, it is attached to the anterior tip of the body and is stretched along the longitudinal axis of the body. The distal end of the axial filament does not lie freely in the endoplasm as in the former genus but is fixed to the posterior end of the body. The flagellar cords arise from the anterior tip of the body and run backwards as in *Pyrsonympha.* The nucleus is situated at the anterior tip of the body excepting *D. rugosa* whose nucleus is placed in the middle portion of the body.

Glycogen is usually deposited diffusely in the whole body. But in some special cases, the reaction is most conspicuous in a portion surrounding the nucleus. This phenomenon becomes more striking when the quantity of glycogen in the body decreases, and in an extreme case, fine granules of glycogen are seen scattered very coarsely or no reaction is given in the body part at all, while in the narrow region surrounding the nucleus the dense reaction of glycogen remains distinct. But the motor apparatus, or the flagellum, shows no trace of the glycogen deposit, with the single exceptional case, that of *D. rugosa*. This protozoa has a more or less conspicuous ridge construction on the body wall and the flagellar cords run along the top of the ridges. By this organism sometimes the dimension of the granules of glycogen becomes large and in such a case these granules are arranged in a line along the course of the ridges or along the flagellar cords.

Generally speaking, in every species the body is filled by the compact mass of glycogen when its quantity is considerably great. When the quantity diminishes large granules appear coarsely scattered in the body. And when the quantity is further reduced the reaction comes to be restricted in the region surrounding the nucleus only. The flagellar cords seem to have no distinct relations with the deposit of glycogen.

B) Protozoa of *Coptotermes formosanus.*

The termite, *Coptotermes formosanus*, has three species of protozoa in its hind-gut: *Pseudotrichonympha grassi*, *Holomastigotoides hartmanni* and *Spirotrichonympha leidyi*, belonging to families Trichonymphidae, Holomastigotidae and Spirotrichonymphidae respectively. These parasites, especially the former two, have a large size and posess a complicated structure and show a very conspicuous tendency to deposit glycogen.

Pseudotrichonympha grassi.—This is the largest known protozoa from Japanese termites. In general, the shape of the body resembles *Trichonympha* and is divided into the anterior region, or the head, and the posterior region, or the body. The head is again divided into two portions, the nipple and the bell, as in *Trichonympha.* These two portions have a common outer ectoplasmic layer, under which the axial column in the nipple part and the inner layer in the bell part are found. The outer layer is traversed by numerous flagella. They are set on from the inner surface of the layer where the basal granules are arranged. The body has no distinct morphological structures and the entire surface is densely covered by the numerous flagella. These are arranged very closely in numerous fine rows, giving to the body surface the beautiful spiral striations. Three layers can be distinguished in the posterior region of the body. The outermost region is a thin but distinct ectoplasmic cortical layer and is traversed by closely arranged flagella. The middle layer of the body is the subcortical layer or the peripheral zone of the endoplasmic region. This is hardly distinguishable morphologically, but it becomes conspicuous if the material is treated with BEST's carmine for the glycogen examination. The central portion of the body is distinguished from the middle layer by the difference in the manner of the depositing of glycogen and this is the portion where wood particles are taken in and digestion may take place. The nucleus is situated freely in the endoplasm. In this respect it is remarkably different from *Trichonympha*.

Glycogen is deposited in two portions in the head region, one of which is the border line between outer and inner layers. In this place the granules of glycogen are arranged along the row of the basal granules of the flagella. This deposit is limited to the bell part of the head (text fig. 7). The other portion of the head region in which glycogen deposits appear is the central endoplasmic region. Usually glycogen is granular here (text fig. 7), but when it is great in quantity the dimension of these granules becomes greater, and in that state drops of glycogen are seen filling the portion.

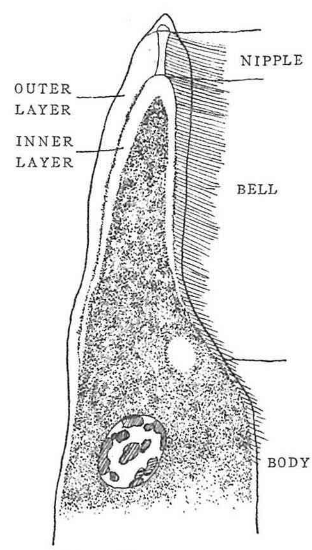

Fig. 7. Figure of *Pseudotrichonympha grassi* showing the structure of the head region and the deposit of glycogen. Dots show the granules of glycogen.

In the posterior region of the body the deposit of glycogen shows a zonal differentiation. In the outer layer glycogen deposit seems to begin at the portions near the basal ends of the flagella; then as this becomes greater in quantity, the area spreads out along the course of the flagellar cords until the head of the deposit reaches the surface of the body. In this state it is visible from the surface that glycogen is deposited in numerous rows arranged closely and run spirally in the body wall. But when the quantity of glycogen is small the rows of basal granules of flagella which are stained dark by hæmatoxylin are more distinct than the deposit of glycogen. By means of a section preparation it can also be recognized that glycogen deposits surrounding the flagella and the head of the deposit reach the surface of the body (text fig. 8).

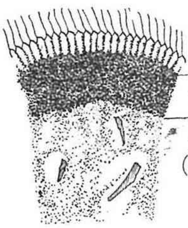

Fig. 8. A cross section of the body part of *Pseudotrichonympha grassi* showing the zonal differentiation of the protoplasm. Dots are the granules of glycogen.

The middle layer usually occupies a narrow space between the outer and inner layers. Ordinarily a dense accumulation of glycogen is detected here. It is often the case that a very intense reaction is found in this layer only, while in the other part merely a moderate quantity of glycogen is found. This fact makes the middle layer distinguishable from the central one, though there exists no distinct morphological border line between them (text fig. 8). The thickness of the middle layer is determined by the quantity of glycogen contained. Usually it is a comparatively narrow one, but when the quantity is very great it spreads inwards so deeply that the central portion becomes very narrow. In the central portion of the body the quantity of glycogen is usually moderate, for, here the wood particles are taken in and, as in the case of many other protozoa, the diet is kept in the vacuole where no reaction of glycogen is to be proved. But as the wood particles are digested and no large amount of food remains, the central portion becomes very narrow. In other words, this is a state in which the middle layer spread very much inwards. The thickness of the central portion is determined by the quantity of food particles it contains.

Holomastigotoides hartmanni.—This is a medium-sized protozoa harboured by *Coptotermes formosanus*. The body is oval in form. The endoplasmic portion has no remarkable construction except that the nucleus is embedded in a mass of a special protoplasm near the anterior end of the body. The body wall is a thin but well defined ectoplasmic layer excepting the posterior end of the body where the ectoplasmic layer is especially thin and covered by long, coarse flagella. The surface of its body is not smooth but provided with numerous ridges running around the body. They start at the anterior tip of the body, run downwards and fade away at the posterior portion. The basal granules of flagella are arranged along the bottom of the grooves between two neighbouring ridges, and the flagella are set on from this place.

The main deposits of glycogen are found in the endoplasm posterior to the nucleus and in the region near the body wall. It is peculiar to this protozoa that there is at the anterior portion of the nucleus a region where no glycogen is deposited and remains clear (text fig. 9). The area posterior to the nucleus is rich in glycogen. But this organism is so voracious that usually the portion is highly vacuolated; therefore, the density of glycogen is not so great in this place. In spite of a thin body wall the reaction of glycogen in it is very remarkable. Glycogen is detected always near the basal granules of the flagella, namely, in the region close beneath the bottom of the groove of the body wall. But when the quantity of this glycogen becomes greater the area of the visible reaction spread towards the surface until it reaches the bottom of the groove. This glycogen deposit is most prominent at the anterior part of the body where the cortical layer is thicker than that of the posterior part and the ridge construction is most conspicuous (text figs. 9 and 10). This deposit is the same with that on the body wall of *Pseudotrichonympha*, but in the case of this protozoa this deposit of glycogen does not extend inwards so that the area corresponding to the middle layer of *Pseudotrichonympha* does not develop.

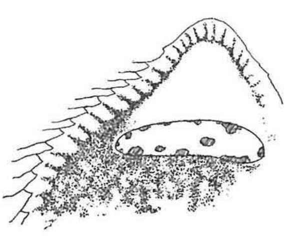

Fig. 9. (Left) A longitudinal section of *Holomastigotoides hartmanni* showing the ridge construction of the body wall and the deposit of glycogen in the anterior part of the body.

Fig. 10. (Right) The anterior region of *Holomastigotoides hartmanni* stained with Best's carmin; dots represent the granules of glycogen.

Spirotrichonympha leidyi.—This is the smallest protozoa of *Coptotermes formosanus*, and the number of individuals is not so large as in the other protozoa. The body is in the shape of a tall cone. A spiral ridge construction is observed on the body wall. It starts at the anterior tip of the body and runs posteriorly, winding around the body. The flagella are set on from this ridge. The nucleus is situated near the anterior end of the body and is surrounded by protoplasm of unusual appearance.

Although the glycogen deposit is detected in all parts of the body, the most distinct reactions are visible at the anterior portion of the nucleus and in the ridge of the body wall. In the former place the deposit is distinctly detected to be in the shape of a cone. The reaction in this region is remarkably more intense than in the surrounding portions and is as sharply differentiated as was observed in the case of the corbule of *Trichonympha* (text fig. 11). This is an interesting fact, compared with *Holomastigotoides* which also has a special protoplasmic region around the nucleus. Such regions around the nuclei must be identical morphologically in both protozoa, but when they are treated for the detection of glycogen they show the distinct contrast described above. In the ridge of the body wall a distinct reaction is also given, so that if the granules of glycogen be stained by carmin the organism seems to be covered by a scarlet band running around the body (text fig. 11).

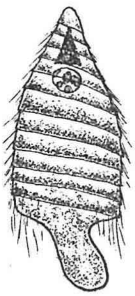

Fig. 11. *Spirotrichonympha leidyi*, the general appearance and the distribution of glycogen. Glycogen is shown by dots.

Conclusion and Discussion

The distribution of reserve glycogen deposits in fourteen forms of flagellates harboured in *Leucotermes* (*Reticulitermes*) *speratus* and *Coptotermes formosanus* has been examined. Glycogen is found everywhere in the endoplasmic portion of the body. But whenever the body shows distinct structures, the deposit of glycogen is also divided into those regions determined by those structures. This is especially true in the forms that have the complicated structures such as *Trichonympha, Teratonympha, Pseudotrichonympha* or *Holomastigotoides*. Even in the smaller forms provided with comparatively simple constructions of the body the deposit is not diffuse throughout the whole body, but follows certain modes of distribution.

Owing to the fact that the body of the protozoa is divided into sections, the regions belonging to the nucleus, the motor apparatus and the remaining endoplasmic parts respectively, the deposits of glycogen are also separated into these three regions. In almost all species of protozoa there are some regions near the nucleus that show a distinct reaction of glycogen or are well-defined from the surrounding portion by a sharp border. This is most conspicuous in the case of the protozoa which have distinct structures of the nuclear apparatus such as the *Trichonympha* and *Teratonympha.* Although the other protozoa have no morphologically defined nuclear structures they seem to have physiologically specialized regions near the nuclei in which the characteristic reaction of glycogen is given. While *Holomastigotoides* and *Pseudotrichonympha* afford two exceptions on this point, the former has a distinct region immediately anterior to the nucleus in which no glycogen is deposited and in the latter the situation of the nucleus is indefinite and specially deposited glycogen is not visible near the nucleus.

The distinct reaction of glycogen is also detected near the basal ends of flagella. This is most remarkable in the case of the protozoa that have definite structures bearing the flagella. In the *Trichonympha* and *Pseudotrichonympha,* though the quantity is small, a special and distinct deposit is found on the inner surface of the bell-wall of the head region at the point where the long flagella are set on. In the organisms, as *Teratonympha, Holomastigotoides* and *Spirotrichonympha* etc., which have a distinct ridge construction on the body surface, a conspicuous deposit of glycogen is always observed in this ridge. In the protozoa of Dinenymphidae, no special construction is developed that bears the flagella, so they are set on from the anterior tip of the body and usually the nucleus is situated near it. A distinctly dense deposit of glycogen is often observed here. This glycogen is perhaps related to the nucleus and the motor apparatus at the same time.

In the endoplasmic portions other than in the above two portions, glycogen is also observed. This is the portion into which the wood particles are taken. These particles are kept in the vacuoles in which no glycogen is deposited. Glycogen is reserved in the protoplasm surrounding the vacuoles. According to this, when a large quantity of food matters are injected, the area in which glycogen is deposited becomes so narrow that the quantity of glycogen is comparatively small, and *vice versa.* This phenomenon is very distinct in the large and voracious forms such as *Trichonympha, Teratonympha, Pseudotrichonympha* and *Holomastigotoides.* In

Pseudotrichonympha it is especially remarkable, the endoplasm of the body being differentiated into the central and the middle layers, of which the former chiefly sustains wood particles while the latter reserves glycogen. The exact physiological significance of the glycogen deposit is not yet clear but it is highly probable that the located deposit in a special region is due to the location of the physiological activity in that part of the organism. It is not clear whether glycogen in the nuclear region is produced by the activity of the nucleus or is prepared for the use of the nucleus, but, in any case, there must be some connection with the activity of the nucleus. Concerning the deposit in the motor apparatus, it seems that glycogen in this portion is an energy source of the flagellar movement. On the other hand, glycogen in the remaining endoplasmic portions seems to be a reserve material. In the *Pseudotrichonympha*, the endoplasmic portion is differentiated into two parts: one is for the digestion of wood or the elaboration of glycogen and the other for the storage of glycogen.

Glycogen may not be the only material reserved but it does play an important role in the physiological processes of the protozoa, such as in the flagellar movement or in the respiration of the organism. It may be true, furthermore, that the body of the protozoa, especially of larger forms, is separated into several portions for different physiological functions. These problems can only be solved after further experiments in this field.

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