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The Journal of Parasitology, Vol. 5, No. 4. (Jun., 1919), pp. 176-185.

Stable URL:
http://links.jstor.org/sici?sici=0022-3395%28191906%295%3A4%3C176%3ATPNGES%3E2.0.CO%3B2-H

The Journal of Parasitology is currently published by The American Society of Parasitologists.

TETRADONEMA PLICANS NOV. GEN. ET SPEC.,

representing a new family, TETRADONEMATIDAE as now found parasitic IN LARVAE OF THE MIDGE-INSECT *SCIARA COPROPHILA LINTNER*

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HABITAT AND OCCURRENCE

Number, Location and Maturity of the Parasites.—Of this parasitic nema, both male and female are found in about equal numbers in the body cavity of the larvae of the midge insect identified by Professor H. B. Hungerford as *Sciara coprophila Lintner,* often as many as six to twelve of the parasites being found in a single larva. Adult males, about one-sixth as long as their mates, are usually found coiled about females, and both males and females are more or less entangled with the malpighian and tracheal vessels of the host, so as often to be rather difficult of extraction. These facts give rise to the specific name *plicans.* The generic name was suggested by the highly interesting four-celled organ, the tetrad, located in the anterior part of the nema. The parasites occupy a very considerable part of the body cavity of the host. In the material examined some of the nemas of each sex were surrounded by cast-off cuticula, indicating that they moult at least once after they enter the host. The fully matured females contain thousands of eggs having somewhat the form of an immature mushroom cap (Fig. 1). The shells of the eggs are smooth and of medium thickness, and contain embryos in various stages of development. The most advanced embryos seen appeared to be taking on a serpentine form and to be coiled once to twice in the egg. When, in the course of dissection of preserved material, the largest females become broken, their eggs escape in large numbers into the surrounding fluid. Preserved eggs escaping in this way are about 33μ in greatest diameter.

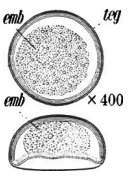
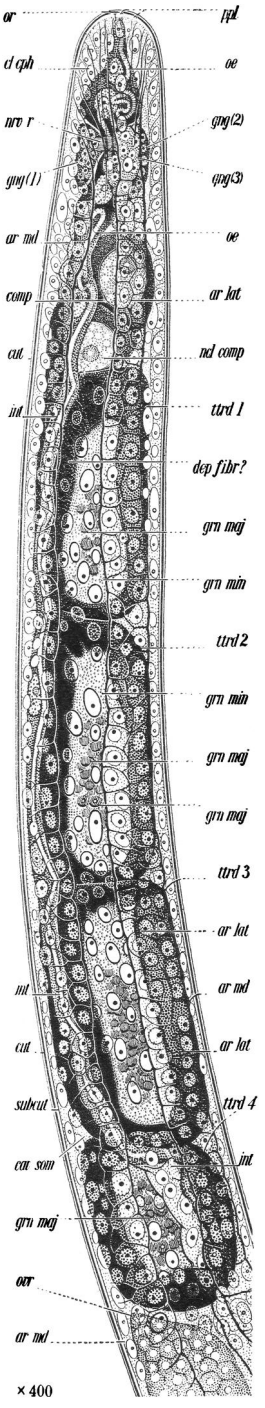


Fig. 1.—Two views of eggs from the uterus of *T. plicans. emb,* embryo; *teg,* shell of the egg.

SIZE AND FORM OF TETRADONEMA PLICANS

Dimensions. The Formula.—Below are measurements of male and female. The figures are averages derived from four males and two females, prepared by fixing the host in picro-aceto-sublimate and pre-

$$\frac{0.0\ \ 0.9\ \ 2.2(?)\ \ {}^{50}{}'60''^{40}\ \ 08.5}{0.0\ \ 0.8\ \ 0.8\ \ \ \ 2.4\ \ 0.9}\ 5\text{ mm.} \qquad \frac{0.0\ \ 5.7\ \ 9.3(?)\ \ {}^{71}{}'M''\ \ 87.}{0.0\ \ 3.1\ \ 3.6\ \ \ \ 5.2\ \ 4.2}\ 0.8\text{ mm.}$$



serving in 70 per cent. alcohol, and finally mounting in glycerin jelly. The tissues of the head of *T. plicans* appear susceptible of contraction, and it seems not unlikely, from the appearance of the preserved specimens here described, that the heads had become fixed in a somewhat retracted attitude, and, if so, the measurements must be interpreted accordingly; see Figure 2, in which the tortuous esophagus may indicate a retracted condition of the head. Similar retractions may occur in the heads of other nemas, e. g., *Oxyuris vermicularis,* a fact that has led some writers into a *non sequitur,* and consequent disparagement of the decimal formula. Such changeableness of form has no more to do with the method of expressing the measure-

Fig. 2.—Head end of a mature female of *Tetradonema plicans,* nearly lateral view. The entire tetrad is shown — occupying the greater part of the illustration. *ar lat,* lateral field; *ar med,* median field; *cav som,* somatic cavity; *cl cph,* nucleus of cephalic cell; *comp,* cells referred to as companion cells of the tetrad; *cut,* cuticula; *dep fibr,* semifibrous deposit between the nuclear membrane and the cell wall of one of the members of the tetrad; *gng* 1, 2 and 3, groups of nerve cells connected with the nerve-ring; *grn maj,* the major granules of the tetrad elements; *grn min,* minor granules of the tetrad elements; *int,* alimentary canal; *ncl comp,* nucleus of cell referred to as companion cell of the tetrad; *nrv r,* nerve ring; *oe,* esophagus; *or,* mouth; *ovr,* ovary; *ppl,* cephalic papillae; *subcut,* subcuticula; *ttrd* 1, 2, 3 and 4, the four elements of the tetrad; compare with Figure 3.

ments than the market value of wheat has to do with the currency in which it is expressed. The same may be said of other variabilities of form, as well as uncertainties of observation. The limits of variability may be expressed in the formula in the usual way, by using the two limiting figures. Uncertainty as to measurement may be expressed by an interrogation mark, as in the above formulae, where the location of the beginning of the intestine is indicated as questionable. Notwithstanding the uncertainty, the queried figures, $\frac{9.3}{3.6}$ and $\frac{2.2}{0.8}$, are as useful as ever in indicating the contour of the body.

STRUCTURE OF THE NEMA

Cephalic Organs and Body-Wall.—The general appearance of the tissues of the head and of the neck of Tetradonema is reminiscent

of that of some members of the Mermithidae, e. g., *Mermis nigrescens;* in both forms numerous nuclei of cells in the head are of relatively large size, and the filiform extensions by which the cells are connected with one another and with the cuticle are more or less similar in appearance in the two forms. In immature Tetradonemas the characteristic tetrad, a group of four cells, or "cysts," to be described later, is not yet fully developed; in young individuals its cells are distinguishable from other cells, for instance the larger spermatocytes lying in the testis near at hand, mainly by the fact that they are larger, and that their spherical nuclei have a more pronounced fine granulation. The head of *T. plicans* is hemispherical-conoid, then sometimes almost imperceptibly truncated at the narrow mouth opening. Occasionally one sees immediately around the lipless mouth what appear to be about six very obscure forward pointing innervations, and at other points toward the margin of the head one occasionally sees what appear to be innervations that may represent papillae (Fig. 4, *ppl*). There are no amphids or eye-spots or other pigmented tissues of any kind. The coarser, non-equidistant, transverse striations of the cuticula are indicated by fine transverse lines that break joints opposite the lateral fields, the average distance between them being about equal to one fifteenth the width of the body. Between the transverse refractive lines just mentioned there are others uniformly spaced, the true striae of the cuticula; these are barely visible with lenses of the highest power used under favorable circumstances, and are not further resolvable (Fig. 8, *str*). No definite wings have been seen. The lateral fields as seen near the middle of a male undergoing its final moult and viewed in profile appear to be about one-half to three-fifths as wide as the body. Beginning very narrow near the head, the lateral fields widen out rapidly, so that at the anterior extremity of the tetrad they are fully half as wide as the corresponding portion of the body. The fields contain large and relatively conspicuous, somewhat ellipsoidal nuclei that are more or less granular, and contain distinct nucleoli. A double row of these nuclei is the main feature of each lateral field. The median fields are of similar size and contain nuclei of a similar character (Figs. 2 and 3, *ar med, ar dsl, ar vnt*).

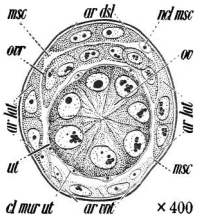


Fig. 3.—Cross section near the vulva of *T. plicans*. *Ar dsl, lat,* and *vnt,* dorsal lateral and ventral fields; *cl mur ut,* cell of uterine wall; *msc,* submedian muscular field; *ov,* ovum in uterus; *ovr,* ovary; *ut,* uterus; *ncl msc,* nucleus of muscle cell.

Longitudinal striae. Muscles.—On each side of each lateral field in the region of the neck are longitudinal striations, which either exist in the cuticula or are due to the existence of attachments of

somatic cells, presumably muscle cells. These narrow and weak longitudinal muscular fields are submedian in position, and each is represented by about four striae. The transparent tissues of the neck permit of seeing these submedian, narrow, longitudinally striated elements more clearly than they can be seen elsewhere, but they have been followed far backward, and no doubt exist throughout the length of the body (*msc,* Fig. 3). There exist in the neck, as elsewhere, not only lateral fields, but also median fields. In one of these, the ventral, the row of nuclei is more definite and the nuclei are somewhat larger than in the other.

DEGENERATE ALIMENTARY CANAL

The digestive system of the adults of both sexes is more or less degenerate or vestigial, as, it appears, is often the case with nemas inhabiting the body cavities of insects, e. g., *Allantonema, Sphaerularia, Tylenchus,* etc. It may not be an unreasonable supposition that to some extent the food of *T. plicans* is absorbed through its cuticula, since fully adequate means for imbibing it through the mouth seem to be lacking.

Alimentary Canal, Male.—There is no pharynx. From the mouth opening backward the esophageal tube is very narrow, but may present an almost imperceptible swelling just in front of the nerve-ring. This latter lies about half way to the tetrad and is nearly transverse. There are filimentous processes passing from it to the body wall, presumably nerves. Near the front of the tetrad may be dimly seen what appears to be the junction of the esophagus with the intestine. Just in front of this point the esophagus is very slightly swollen; the posterior portion of the esophagus therefore appears somewhat narrowly clavate in form, and is about one-fourth as wide as the corresponding part of the neck. In some specimens, however, this swelling was sought in vain. The succeeding part of the alimentary canal (the intestine, or the posterior part of the esophagus, as the case may be) is at first about as wide as the part of the esophagus just described, but soon diminishes in size and becomes a rather insignificant looking strand of indefinite tissue, containing a faint lumen. The alimentary canal soon passes to the ventral part of the body, and is so inconspicuous and deteriorated that one is usually unable to follow it further. In one case, at the nerve ring, which was about half way back to the first member of the tetrad, the esophagus was not more than one-fifth as wide as the corresponding part of the neck, and thence backward it diminished in size and was very difficult to follow. In the male the esophageal lumen does not seem to lead through a granular plasma as is the case in the female illustrated in figures 2 and 4. In immature males a rectum is present, and, joining it, a portion of the

intestine can be seen, extending forward a distance somewhat greater than the length of the tail, and at its widest part becoming half as wide as the body. At a point as far in front of the anus as the terminus is behind it, the intestine is smaller, and farther forward still it is difficult to follow and seems very rudimentary. This condition of things exists in those males whose testes are filled with spermatocytes about one-fifth as wide as the body; that is to say, somewhat immature males.

Alimentary Canal, Female.—An examination of the females shows that, just as in the male, the alimentary canal is much deteriorated, but the details are somewhat different (Fig. 2, *int*). Immediately behind the mouth opening the lumen of the canal becomes tubular and more or less tortuous. The diameter of the more or less corrugated lumen is about equal to the thickness of the cuticula. Surrounding the median canal is a granular tissue or "plasma" in which large nuclei are to be seen here and there. From the mouth backward this granular tissue expands so that at a distance from the anterior extremity one and one-half times as great as the diameter of the head it may become about half as wide as the corresponding part of the neck. Immediately behind this point, however, there is a constriction, and in the midst of this constriction the nerve-ring is found (Fig. 2, *nrv r*). Immediately behind the nerve-ring the intestinal canal, or esophagus, as I believe we may still term it at this point, gradually widens until it becomes one-third as wide as the body; it then again diminishes in size so that anterior to the two large cells in front of the tetrad it is only about one-fifth as wide as the corresponding portion of the body. This portion of the body seems to be what would be called the base of the neck, and if so, this constriction, for such it seems to be, corresponds with the beginning of the intestine. Behind this constriction the alimentary canal again widens and soon becomes about one-fourth as wide as the body, and then once more begins to decrease. However, even as far back as the last member of the tetrad it still appears to have a tubular lumen. At this point the tubular lumen suddenly ceases, suggesting the possibility that the esophagus really extends farther back than indicated above (Fig. 2, *int*). No trace of the alimentary canal was seen farther back than the middle of the body. As the alimentary canal, for a certain distance at least, has a distinct lumen, and there is a distinct mouth opening, small though it be, it seems likely that the intestine is still capable of taking in liquid nutriment. It is possible that the large nuclei associated with the anterior part of the alimentary canal, of which half a dozen may be counted in the esophageal portion just described, may have something to do with assimilation. It has been assumed that certain nemas parasitic in the

body cavities of insects absorb their nutriment through the cuticula, and there is good cause to suppose that in some instances this may be so. However, when the alimentary canal of the parasite contains a distinct lumen, and the mouth opening is still a distinct feature of the head, it is a fair assumption that the intestine may still function to a certain extent, especially if there are associated with it structures whose office may easily be supposed to be accessory to digestion or absorption.

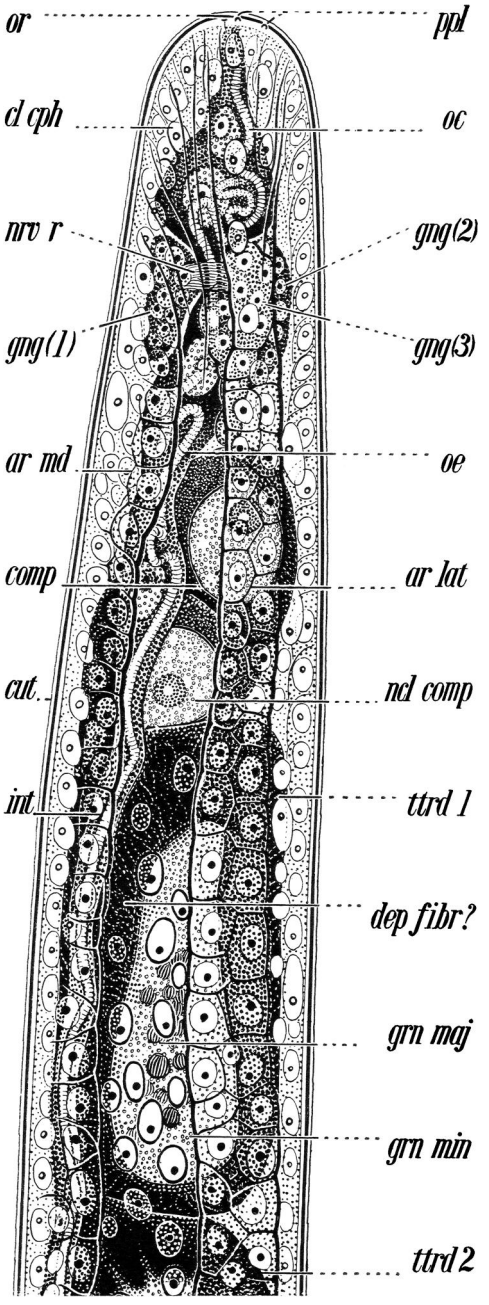


Fig. 4.—Head end of a mature female of *Tetradonema plicans;* nearly lateral view. Compare with Figure 2. *ar lat,* lateral field; *ar med,* median field; *cl cph,* nucleus of cephalic cell; *comp.* cells referred to as companion cells of the tetrad; *cut,* cuticula; *dep fibr ?,* semifibrous deposit between the nuclear membrane and the cell wall of the front member of the tetrad; *gng* 1, 2 and 3, groups of nerve cells connected with the nerve ring; *grn maj,* major granules of the tetrad; *grn min,* minor granules of the tetrad; *int,* alimentary canal; *ncl comp,* nuclei of one of the cells referred to as companion cells of the tetrad; *nrv r,* nerve ring; *oe,* esophagus; *or,* mouth; *ppl,* cephalic papillae; *ttrd,* one of the elements of the tetrad.

THE TETRAD

Structure of the Tetrad.—A very striking feature of the anatomy is the occurrence, toward the head end, of four large unicellular organs, arranged tandem, and occupying in this region the greater portion of the body cavity (Fig. 2, *ttrd,* 1, 2, 3 and 4). It is this quartet of bodies, the tetrad, that gives rise to the generic name *Tetradonema.*

That each of the four elements of the tetrad is unicellular is shown by the fact that in the younger nemas, where the tetrad is smaller, it is

quite clear that each of its elements is a single cell containing a large spherical nucleus having a distinct nucleolus. In the full grown female the tetrad is much more strongly developed, and the entire space between the cell wall and the nuclear membrane of each element is completely filled with a semi-fibrous, semi-granular deposit (Figs. 2 and 4, *dep fibr?*). Under these circumstances the form of the cells is no longer spherical, but more or less cylindrical, owing to very great increase in size and consequent pressure from surrounding organs. In the males, also, the tetrad cells may become so large that the nuclei are no longer spherical, though this seems less commonly the case than in the females. The nuclei of the tetrad may become half as wide as the body, the deposit surrounding them then becoming thicker and more opaque, and seeming to be more "fibrous" the older it becomes. The tetrad in the male may be of such a size as to be twice as long as the distance between its anterior extremity and the mouth opening. Accompanying the tetrad, and in front of it, are to be seen two smaller more or less spheroidal cells that seem to be larger in the female than in the male (Figs. 2 and 4, *comp*). Occasionally each of this pair of cells is so large as to suggest that they are "companions" of the cells comprising the tetrad.

Function of the Tetrad.—Such a striking organ as the tetrad of *Tetradonema* cannot but give rise to the question, "What is it for?" I have been unable in the examination of the small amount of preserved material available to make out the histological connections of the tetrad, but the following facts are clear as a result of the examination made.

1. The organ is found in both sexes in the same form and consists of four unicellular, apparently equivalent, components, which develop from comparatively normal cells lying near the base of the neck, the usual location of the renette, and seem to grow with the age of the organism rather than with its size.

2. As the nema ages these elements not only increase in size, but also change in structure, one of the principal changes being a bulky, apparently semi-fibrous deposit just inside the cell wall. Meanwhile the nucleolus becomes a locus rather than a cell organ, and finally there are deposited in the very much enlarged nucleus, relatively large, spherical, more or less structureless granules (Figs. 2 and 4, *grn maj*). Sometimes these major granules have a distinctly refractive element. As these larger granules appear only in the larger tetrads, the possibility is suggested that they are a degeneration phenomenon, but I am more inclined to regard them as excretory in nature, along with the semi-fibrous matter outside the nucleus. The nucleus maintains its membrane to near the close of the history of the tetrad.

3. It is noticeable that no trace of the usual excretory pore and renette has been seen in any of the specimens.

Is it possible that the cells of the tetrad are storehouses for excreta? The food of this nema may be predigested, but the catabolism must give rise to waste matter. Now there is no true anus; nor has any excretory pore been seen. To this statement of the entire absence of the main channels through which excreta are usually voided, may be added the suggestion that should the parasite pour its excreta into the body fluid of the host, presumably the effect on the host would be injurious, and this in turn would be inimical to the parasite. If such a thing were possible, it would seem advantageous to the nema under the circumstances to store up within its body the wastes of its own metabolism, the excreta due to its growth and reproduction. The data thus far disclosed leave it possible to suppose the tetrad to have some such function. On the other hand, no such organ is known in any other parasitic nema, though of course it is conceivable that organs having the function here imagined but more obscure or of smaller size, might hitherto have escaped notice. It is desirable that the tetrad be studied in living specimens, and be submitted to chemical tests.

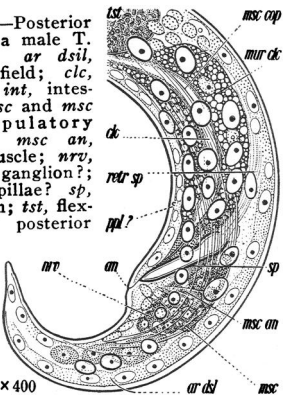


Fig. 5.—Posterior end of a male T. plicans. *ar dsil*, dorsal field; *clc*, cloaca; *int*, intestine; *msc* and *msc cop*, copulatory muscle; *msc an*, anal muscle; *nrv*, anal ganglion?; *ppl*, papillae? *sp*, spiculum; *tst*, flexure of posterior testis.

Sexual Organs of the Male. — The single spiculum is median in position, and without accessories. There is no bursa and there are no ventral supplementary organs, and no distinct caudal papillae. Oblique copulatory muscles are to be seen for some distance in front of the anus. The ejaculatory duct is about one-half as wide as the body. In somewhat immature males the main portion of the two testes already nearly fill the body cavity, and contain many thousands of spermatocytes, whose average diameter is about one-fifth to one-sixth that of the body. Immediately behind the tetrad a flexure is to be seen in the anterior testis. At this point the testis suddenly diminishes considerably in size and extends thence backward and ends; this blind end of the anterior testis seems to lie toward the middle of the nema, and is nearly one third as wide as the corresponding portion of the body. Toward the posterior end of the nema, as far in front of the anus as the terminus is behind it, there is a definite

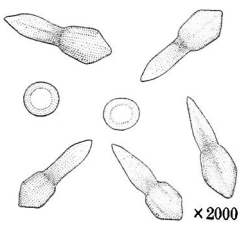


Fig. 6.—Sketches of the sperm cells of *Tetradonema plicans*. From various points of view.

broad contour line indicating the presence of a flexure of a similar character in the posterior testis. The two testes meet near the middle of the body where their junction with the vas deferens is more or less plainly visible. The fully mature spermatozoa found in the *vas deferens* of the male and in the uterus of the female are somewhat asymmetrically elongated-fusiform bodies about one-sixth as long as the body is wide, and about one-third as wide as long. Packed together with them in the proximal portion of each testis are more or less finely granular, spheroidal, apparently non-nucleated bodies of various sizes, the largest being one-fourth as wide as the body of the nema, and the smaller having not more than half this diameter. As these spheroidal bodies are most numerous and most apparent near the proximal ends of the testes, it is assumed that in the ripening of the sperm these bodies are formed. The ripened spermatozoa occur in thousands and are reminiscent of those of *Mononchus, Dorylaimus* and *Anticoma*. In the uteri of the female they have more or less the contour of tadpoles (Fig. 6). The sperm cells appear to be produced in groups, possibly in groups of four. It was found difficult to make an accurate count, so closely were they packed in the testes, but the number of individuals in a group is certainly small.

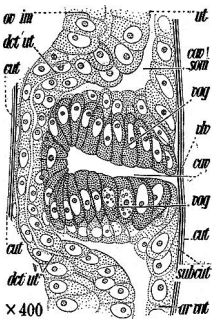


Fig. 7.—Optical section vulvar region of *T. plicans*. *ar vnt*, ventral field; *cav som*, somatic cavity; *cav*, cavity of the vagina; *cut*, cuticula; *dct ut*, uterine duct; *ov im*, oocyte; *subcut*, subcuticula; *ut*, uterus; *vag*, wall of the vagina; *vlv*, location of the vulva.

Sexual Organs of the Female.—From the rather inconspicuous vulva, the very strongly developed vagina passes inward at right angles to the ventral surface three-fourths the distance across the body. It is composed of a bulky mass of cellular tissue three-fourths as wide as the nema, and is one of the main features of the middle of the body (Fig. 6). Its distinct cavity appears rather narrow, and is lined with a layer consisting of scores of closely packed, relatively large, elongated cells. This more or less columnar "epithelial" lining is the main feature of the developing vagina. Outside it, however, there is a layer of smaller cells placed somewhat irregularly. From the proximal part of the vagina, toward the dorsal side of the body, two comparatively narrow tubes lead in opposite directions to the two uteri, one in front, the other behind. Each uterus is about three to four times as long as the body is wide, and in young females appears to be about half as wide as the body. Where the uterus joins

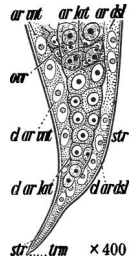


Fig. 8.—Tail end of female. *ar dsl, lat* and *vnt*, the dorsal, lateral and ventral fields; *cl ar lat, vnt* and *dsl*, cells of the fields; *ovr*, posterior flexure of the ovary; *str*, striae.

the ovary there is a faint constriction, and the contour of the organs is here so definite as to make it evident that the ovaries are reflexed (although I usually found it impossible to clearly identify the reflexed portion throughout its length), for a longitudinal optical section at this portion of the body discloses ovarian tissue other than that comprised in the portion of the ovarian tube that joins the uterus. This ovarian tissue extends to near the vagina, from which it is evident that the reflexed portions of the ovaries reach back to near the vulva. These details were made out from the study of nearly mature but unfertilized females. The flexure in the anterior ovary is at the back end of the tetrad; the flexure in the posterior ovary is only a short distance from the end of the tail (Figs. 2 and 8 *ovr*).

Tail.—The female has no anus, nor is there any vestige of such an opening. However, its former location may be estimated from consideration of the position of the anus on the male, whose tail end has a similar form. With this estimate in mind it becomes evident that the tail of the female begins to taper some distance in front of the position of the theoretical anus. The tail of the female is rather like that of the male in form, being at first conoid, but ending in a subcylindroid or somewhat convex-conoid terminus, about one fifteenth as wide as the body, and about two to three times as long as wide, and having a more or less acute tip. Considering the tail to comprise that portion of the posterior end extending from the flexure of the posterior ovary to the terminus, this final narrow portion of the tail occupies about one-third of its length. On this portion of the tail the transverse striae of the cuticle can be seen more plainly than on almost any other part of the body. There are, of course, no caudal glands.

New Family of Nemas.—I consider Tetradonema, of which the type species is *Tetradonema plicans,* to be the type genus of a new family, the Tetradonematidae.

TETRADONEMATIDAE fam. nov.

TETRADONEMA gen. nov.

Small naked insect-parasites with minute males; cuticula wingless, minutely transversely striated; head rounded, tail acute; mouth minute, lipless, oral papillae minute, anus none; esophagus simple, with lumen, intestine vestigial; male and female gonads double, symmetrically reflexed; vulva central, uterine eggs numerous, asymmetrical, containing embryos; spiculum single without accessories, supplements and bursa none.