A REMARKABLE ORGANISM, *TELEGAMATRIX PELLONA* gen. et sp. nov. (MONOGENEA: DIPLECTANINAE) PARASITIC IN AN INDIAN HERRING

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It is seldom that an entirely novel animal is found, but *Telegamatrix* seems to be a unique example in evolution of what would appear to be an ideal copulatory arrangement for a sedentary hermaphrodite, whether animal or lower plant. Yet no parallel example comes to mind from either kingdom. Here we have hermaphrodite worms copulating at a distance by means of a tentacle containing two-way ducts (Plate XXIII, B).

The tentacle is asymmetrically placed near the hind end of the body proper, it is flexible and contractile, as are also the ducts within it; the complementary apposition of its tip to that of a neighbouring worm is nicely secured by the bent flanges of the sclerites bordering the juxtaposed male terminalia and the (distal) vaginal aperture (Fig. 3). It may, therefore, be withdrawn and used again in another direction when occasion demands. A further refinement, for steadying the tips prior to union, is a mutual twisting of the almost thread-like tentacles (Plate XXIII, A): an understandable precaution, in the face of the disturbing currents in the gill-chamber of these active fishes. The locating of the partner and the accurate accouplement is an intricate process of which we have seen only the *fait accompli*, since these monogenea were found some time after the death of the host, and on only one occasion: on the gills of *Ilisha* [*Pellona*] *indica* (Swains.), at Madras.

Biological Significance of the Copulatory Tentacle

No similar arrangement for copulation at a distance exists elsewhere in either monogenetic or digenetic trematodes, though its efficacy is obvious for the former, since it obviates the hazard of leaving the foothold and manœuvring into close proximity to a partner on a slender gill-filament. Like other Gyrodactyloidea, however, *Telegamatrix* can move looper-fashion from one feeding site to another, and secured by its posterior haptor (here, in addition to the usual marginal hooklets and two pairs of anchors, there is a dorsal and ventral lamellate friction-pad, Fig. 2); it can swing in almost a complete circle for browsing on adjacent gill-lamellæ: hence the name of the superfamily and family (Dactylogyridæ), both of which mean ' gyrating finger '.

At first sight, this novel device may recall that unique condition of permanent copulation seen in *Diplozoon*, but the morphology and biological implications there are very different : the post-larval ' diporpa ' become attached in pairs by a median genital sucker which forthwith becomes absorbed, and there is an intimate anatomical fusion of the genital atria and deep penetration of the complementary genital ducts into the appropriate lumina of the partner, also there is a complete fusion of the somatic tissues in the genital field at the region of cross-over. Thus, the pair becomes a double individual: *reducing the effective distribution of the population by half.* Therefore the only advantages to the *Diplozoon*-stock are that an effective and economical fertilization is insured, and that double the number of the rather large eggs are produced than if the worms were unisexual. *Telegamatrix*, on the other hand, reaps these advantages of hermaphroditism without having to pay the penalty of halving the effective distribution of the stock, for each member is a free individual after copulation, in the normal way. Genetically, there is also a possible advantage, for a second fertilization may take place with a different mate. Somatically, the advantages are that injury to one of the pair need not jeopardize the other (in *Diplozoon* if not killing the other, chances of subsequent fertilization would be ruined). Secondly, there is no loss of mobility or restriction of the feeding site, as there is with the two bulky Diplozoons, in which the heads point in opposite directions and in which there is no provision for co-ordinated movement—they are continually tugging at cross-purposes—the partners competing for their common sector of browsing ground, and the peripheral sector is obscured by the body of the other. In *Telegamatrix* there are no such limitations, and the full benefits of hermaphroditism are enjoyed, with the additional advantages that copulation at no time involves invasion of the feeding territory of another worm (for the tentacle reaches well beyond the feeding-site), and the hazards of a mating migration are removed.

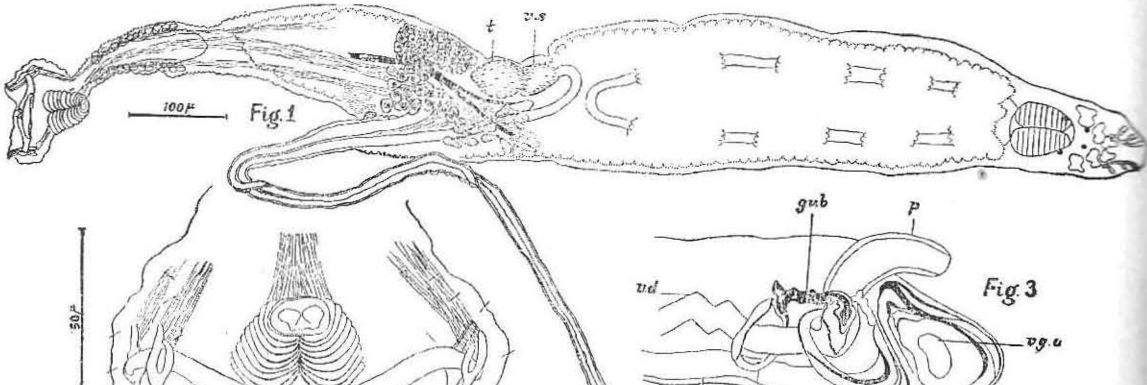
It is therefore very surprising that such a device is not common in Monogenea, also that it has not been evolved more than once in other groups of sedentary hermaphrodites, such as those exposed to strong currents or wave-action in the littoral zone. Or again, those living in more or less dense environments where movement of the whole body from the niche is laborious and hazardous, for example, commensals in sponges and the like, mud- and sand-burrowers and especially for parasitic forms in adjacent parts of soft tissues, or in turbulent internal lumina of higher animals. It would seem to be an ideal arrangement for Bryozoans.

While the male terminal organ is often greatly elongated in hermaphrodites as well as in unisexual animals, we cannot recall an instance of the female receptive organ being elongated to a comparable extent. In sedentary hermaphrodites, the siphon-like male duct is usually for discharging the sperm in jets, well away from the parent, and seldom as an intromittant organ for the economy of sperm. If they exist, cases must be very rare where the female system co-operates in securing fertilization and economy of sperm [one case is that of female *Argulus* (Branchiura), though there is, of course, no elongation of ducts in either sex—Sproston, unpublished monograph on *Argulus*—in which is described the ' apron ' of the female aiding the charging of the spermathecæ, and their controlled discharge during autofertilization]. Moreover, in Gyrodactyloidea, it is unusual for the vagina to be associated in any way with the male duct: the latter invariably opens in an anterior median ventral field, whereas the vagina is farther back and lateral: in the Diclidophoroidea it is usually dorsal; whereas in *Telegamatrix* the vas deferens and vagina, though having separate musculature, are closely associated throughout their enormously elongated distal course. In spite of the unique modifications in *Telegamatrix*, all associated with exchange of gametes at a distance, it is here placed provisionally in Gyrodactyloidea, subfamily Diplectaninæ, on the basis of the lamellate friction-pads on the haptor.

In the Archegoniatæ among the lower plants, both male and female organs can have long necks, but here, as in most animals, there is prodigious wastage of sperm; in cleistogamous flowers there is economy, but at the price of self-fertilization. In the Orchidaceæ, conservation of pollen is combined with fertilization at a distance (where the entire andrœcium is transferred on the back of a bee over relatively vast distances), we have a remote analogy with the process in *Telegamatrix*. Only one instance comes to mind among the plants where the gynœcium is extended on equal terms to meet the andrœcium: in the lower ascomycetous fungi, in Erysiphales (white leaf-mildews) there is a mutual twisting of the male and female hyphæ in the formation of the ascocarp, and though all the gametic material is utilized, the fusion is permanent, and of course only one group of spores results. Nor are the conjugation tubes of the Zygnemaceæ (such as in the well-known green alga *Spirogyra*) comparable with the device in this organism, since again the transfer is only in one direction, and the length of the conjugation tubes is relatively so short, as it is also in the " H "-pieces and clamp-connections of some of the higher fungi. The biological effect, however, is analogous to the conjugation in some Ciliata, for example, *Paramecium*, where there is a temporary union, during which there is an exchange of micronuclear material, though in no case is there an intervening siphon of any length; such might be within the scope of some of the colonial Suctoria, but in fact they utilize peritrichous motile conjugants.

THE MATERIAL AND ITS DESCRIPTION

During the extensive studies on monogenetic trematodes of the fishes of Madras (1949–52; embodied in my Thesis for M.Sc. Degree) the present anomalous forms were collected from the gills of *Ilisha* [*Pellona*] *indica* (Swains.), but set aside for subsequent examination and confirmation. Since no further material could be found from the same host, either at Madras or at Mandapam, I have been encouraged, in view of its great biological interest, to publish a preliminary account of the material in hand. There are 14 individuals, 10 of which are in couples; these are mounted in balsam on slides, and cotypes will be deposited in the collections of the Zoological Survey of India (Calcutta), and in the Department of Zoology, University of Madras.



FIGS. 1–3. *Telegamatrix pellona* gen. et sp. nov.—Fig. 1: Ventral view of whole worm. Fig. 2: Haptor, dorsal view. Fig. 3: Distal end of copulatory tentacle. *gub*, gubernaculum; *p*, penis; *p.c.i*, penis collar, inner; *p.c.o*, penis collar, outer; *t*, testis; *v.d*, vas deferens; *vg*, vagina; *vg.a*, vaginal aperture; *vg.c*, vaginal collar; *v.s*, vesicula seminalis.

These are small dactylogyrids, even on extension measuring only 1·074 mm., while contracted fusiform individuals are only 0·53 mm. long, the width varying from 0·15–0·183 mm. There are three pairs of head organs, unusually large cephalic gland-cells, and four eye-spots, the posterior pair being only slightly farther apart than the anterior, situated as usual just anterior dorsally to the pharyngeal field. The gently tapering posterior end, splays abruptly into the haptor; a triangular region 98 to 120 μ wide and 49 to 71 μ long, kept rigid by three relatively massive transverse bars (Fig. 2); two lateral, 47 to 51 μ long with their wider ends articulating in the middle line and at the same time curving slightly ventrally and backwards, their condyls having a curved ridge which is extended postero-ventrally into a short horn-like spine projecting through the haptoral margin (acting as an accessory marginal pair of hooklets) either side of a median distal adhesive gland; the median boat-shaped ventral bar, 51 to 62 μ long, underlies the inner parts of the laterals, but the condylar spines of the latter project just beyond its lower edge (at first sight appearing to arise from it, much as those figured by Yamaguti in *Pseudolamellodiscus sphyraenæ*; Yamaguti 1953, pl. V, fig. 19). At the two ends of the haptor are the relatively large and similar anchors, 'Y'-shaped, with equal roots and a finely tapered hook, which is bent at only a little less than a right angle to the shaft and about a third its length. The anchors do not, apparently, actually articulate with the outer ends of the lateral bars, but doubtless borrow leverage from it, situated as they are, one on either side of each extremity, the hook projecting through its respective haptoral surface; the ventral anchors are slightly external to the dorsal pair; their length (from the tip of the roots to the tangent of the hook) is within the range 30 to 49 μ. The usual seven pairs of minute, sickle-shaped, marginal hooklets are present, and they are all alike.

The lamellate friction-pads ("lamellodiscs", corresponding to the "squamodiscs" of *Diplectanum* and other genera) occupy the apical third of the haptor dorsally and ventrally. They are about 29 μ long and 33 μ wide, and consist of a pile of some 7 to 10 "B"-shaped cuticularized lamellæ, the lobes projecting beyond the surface of the haptor and their straighter edges fused to a double rib buried within it—like a series of little shelves, each smaller than the lower; the top one, only slightly lobed, being about half the diameter or less, of the basal one. There are strong longitudinal muscles attached to the lamellæ proximally, continuing forwards in the dorsal and ventral body-wall, those on the ventral side are continuous with the tentacle (Figs. 1 and 4) which also receives bundles from the lateral muscle-band from the left anchors (Fig. 1). Haptoral glands in the form of polygonal cells are present on either side of the haptoral stem; a conspicuous vesicle, median in position, is also present in between the glands and its contents are of a colloidal nature. A similar series of graded paired curved *blades* is described for *Lamellodiscus typicus* Johnst. and Tiegs, 1922 (genotype); other species, described from Celebes region by Yamaguti (1953) have lamellodiscs like nests of thin cups, or a ring of inter-locking cones, with an adhesive gland in the centre; but in *Lamellodiscus convolutus* Yamaguti (1953, pl. vi, fig. 22) the lamellodisc is shown as a pile of oval plates, probably similar to those of *Telegamatrix pellona* sp. nov., but not lobed.

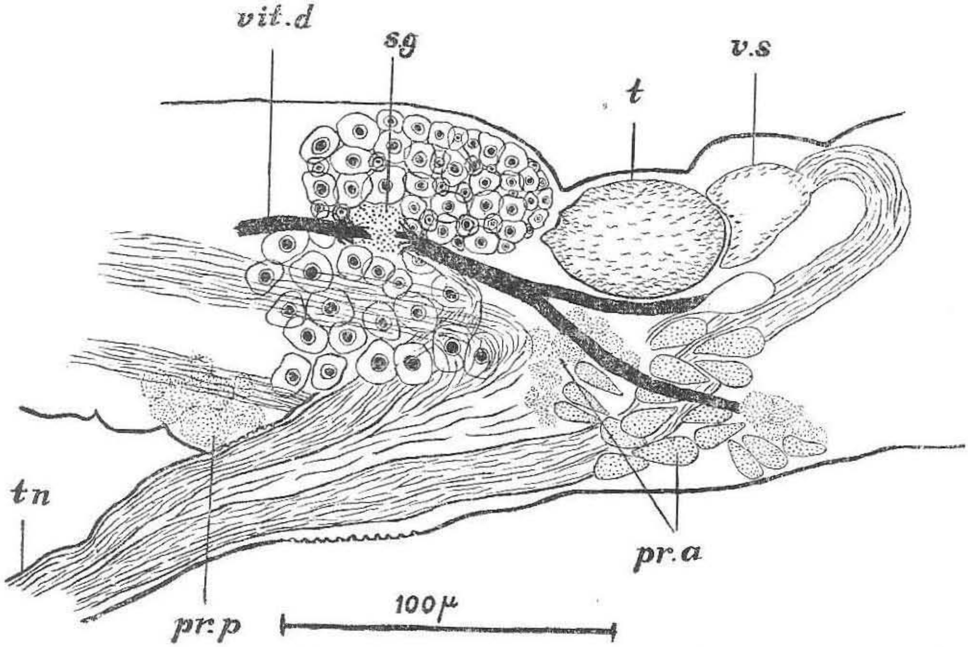


FIG. 4: *Telegamatrix pellona*, showing the gonads and the genital ducts. *pr.a*, prostatic gland-cells, anterior; *pr.p*, prostatic gland-cells, posterior; *s.g*, shell gland; *tn*, tentacle; *vit.d*, vitelline duct. (For other labels see legend to Figs. 1–3.)

The mouth is subterminal in the ventral pre-ocular zone, and after a short buccal or pre-pharyngeal canal, leads to the spheroidal muscular pharynx (54 to 68 μ by 41 to 75 μ); an œsophagus is apparently lacking, the gut branching almost immediately into simple crura which are confluent posteriorly, *in front of* the gonadal fields. The inter-crural field is completely obscured by a mass of vitelline follicles, which also overlie the crura both dorsally and ventrally, and another mass occurs between the gonadal zone and the haptoral stem.

The gonadal zone lies about three-fifths of the distance from the anterior end of the worm, and it is from the side of this zone (usually the left) near its middle, that the copulatory tentacle arises, bearing at its tip the copulatory complex of cuticularized sclerites. It is as if a normally situated group of terminal genitalia had been pulled backwards, ventrally and to the right, carrying with them the usually anteriorly placed ovary and vaginal duct, and folding them down again in the post-intestinal region. In any event, in *Telegamatrix* the testis is in a most unusually distorted position near the right margin, and the ovary and associated structures lie *behind* it; a unique orientation in Gyrodactyloidea, but for the partial exception of *Thaparocleidus* Jain, 1952.

The compact ovoid *testis* (49 μ by 39 μ) lies on the extreme edge of the body, usually on the right side, slightly anterior to the origin of the tentacle which is on the opposite side of the body (usually left, subventral); the *vas deferens* is short and leads to a similar sized vesicula seminalis immediately anterior and dorsal to the testis; thence arises the thick muscular *ductus ejaculatorius*, receiving, as it takes its forwards and backwards turn across the body, ducts from the anterior *prostatic gland-mass*, which is situated in the median field alongside the testis and slightly behind it (where the gland-cells are pyriform and larger); the ductus ejaculatorius arches backwards as a conspicuous band of longitudinal muscle fibres, following the body margin of the left side till it reaches the base of the tentacle, which it enters along with the vaginal duct just behind it. In the anterior angle of the base of the tentacle is the main part of the posterior prostate gland, though some of its larger cells, and vesicle, appear to be consistently just at the side of and behind the origin of the tentacle (Fig. 4, *pr.p*).

The *vaginal duct* is also highly muscular, the outer layer, at least, being longitudinal; within the tentacle it is about the same diameter as the ductus ejaculatorius, though it may be constricted at intervals and granular material (? foreign sperms) seen in the lumen, suggesting an inner layer of circular muscle fibres. The ductus ejaculatorius, on the other hand, seems to depend mostly on its longitudinal fibres, for at least near its distal end it is frequently thrown into zig-zag bends. The tentacular sheath has an outer layer of circular muscles which are conspicuous at its base, but in the extended state the longitudinal fibres are more obvious along its length.

The *copulatory complex* at the tip of the tentacle (Fig. 3 and Pl. XXIII, C) consists of two flanged collars which are more or less spirally ridged internally, the distal *vaginal collar* narrows to the reniform aperture of the vaginal canal (Fig. 3, *vg.a*); the proximal is double, the outer part (*outer penis collar*) similar in outline to the vaginal collar (since in copulation it must interlock with it), but the lower collar (*inner penis collar*, and probably a spiral continuation of the outer) is buried obliquely below, and through both projects the fleshy penis, or end of the ductus ejaculatorius. There is an ' accessory piece ', which could more aptly be called the *gubernaculum*, since it acts as a governor, regulating the sperm-flow into the *penis* (not a cirrus since it is apparently not eversible); the gubernaculum is double hammer-headed and somewhat twisted, highly cuticularized (brightly refractile with a zig-zag closed cavity) and placed so that one head overlaps the outer collar, and one the inner (Fig. 3, *gub*), the " knee"-bends in its axis articulating with the rims of the collars, as fulcra, so that it may rock alternately, proximal or distal end downwards. For instance, in the first action when the distal head is drawn downwards, the lifting of the proximal head releases stricture on the duct within the inner collar, permitting seminal fluid to pass as far as the now depressed distal head; in the second part of the action, the gubernaculum would rock backwards and the proximal head would engage on the ductus, preventing further release of the main stream, and at the same time permitting the escape of the " pinched-off " column of fluid into the penis itself. This is an ingenious mechanism for producing jets of seminal fluid and conserving the supply, probably forthcoming at considerable pressure in the muscular ductus ejaculatorius. The mechanism, though complex, is obvious in *Telegamatrix*, and it would be interesting to deduce the action of the accessory-piece or gubernaculum in other Dactylogyridæ, which show a great variety of structure in the sclerites of the male terminalia, but which are seldom as unobscured as in the present case.

The *ovary* is considerably larger than the testis which it immediately follows: the dense rounded proximal portion appears spheroidal in less mature worms than that of Fig. 4, thence it widens and curves dorsally twisting to the right and then sharply to the left, where the shell-gland is situated and the confluent *vitelline ducts* from the anterior body meet the posterior single vitelline duct, and the vaginal canal originates. The length of the ovary varies from 84 to 155 μ, and its width from 38 to 43 μ. The *uterus* limits cannot be made out clearly, but to the left of the shell-gland complex a number of large ovules with clear nucleus can be seen scattered anteriorly and laterally, opposite to and behind the origin of the tentacle, so the uterus may follow this course, along which immature eggs have been forced by pressure in mounting; indeed, in two specimens, ovules are seen emerging from an aperture in a cuticular fold some little way behind the base of the tentacle; this is taken to be the uterine pore, but unfortunately in no specimen is there a vestige of an egg-shell; the largest uterine ovules are 14 μ in diameter.

SYSTEMATIC DISCUSSION

Apart from the reversed orientation of the gonads, and the removal of the copulatory complex from the usual anterior position near the intestinal bifurcation to the end of the long muscular tentacle, *Telegamatrix* agrees with *Lamellodiscus*, in the Dactylogyrid subfamily Diplectaninæ, where the friction-pads are lamellodiscs, and not squamodiscs (concentric rows of scales or rods placed end to end, or more or less continuous concentric lamellæ) as they are in the five other genera (Sproston, 1946, & Yamaguti '53). The possession of the copulatory tentacle and reversed gonads may be qualifications for the erection of a higher taxonomic category than genus, since there is no parallel to this in the entire class, but for the present, the creation of a new genus will suffice, though this will imply appropriate emendation of all the existing higher taxonomic categories to allow for these anomalies.

Generic Diagnosis.—Diplectaninæ with an elongated copulatory tentacle and post-testicular ovary. Three pairs of head organs and copious gland cells in pharyngeal zone; intestinal crura simple and confluent in pre-gonadal zone. Haptor shape typical of family, with dorsal and ventral lamellodiscs and three haptoral bars; a similar dorsal and ventral pair of anchors, and seven pairs of marginal hooklets of uniform type. Gonads in posterior third of body proper and behind the intestinal zone; single testis with immediately anterior vesicula seminalis; two not very compact areas of prostatic gland-cells, and an enormously elongated ductus ejaculatorius running through the muscular tentacle, opening in a penis just behind its tip which is guarded by two cuticularized collars, the proximal one obliquely imbedded and weaker, their rims support a gubernaculum for regulating the flow of seminal fluid. Muscular vaginal duct accompanies the male duct in the tentacle and opens at the tip under a flanged cuticularized collar which interlocks with the similar male (outer) collar of a partner worm when the tentacle tips are apposed. Ovary large, in post-testicular field, coiled towards tentacle base; oviduct indeterminate and the shell-gland complex more or less imbedded in distal expanded part of ovary; uterus probably a single coil up to near testicular field and back, to open on left side just posterior to tentacle-base. Vitellaria completely filling intercrural field and obscuring intestine from its bifurcation to confluence, and serving the shell-gland by Y-shaped collecting ducts anteriorly, and posteriorly a single duct from the mass of vitellaria in post-gonadal and prehaptoral zone. No shelled eggs seen. Worms united by tentacle tips over distances usually greater than half the length of the worm; tentacles of all worms *in copula* show a mutual twist in their distal half, but union apparently only temporary. Parasites on the gills of marine fishes.

A monotypic genus typified by *Telegamatrix pellona* gen. et sp. nova, from the gills of *Ilisha indica* (Swains.) from Madras.

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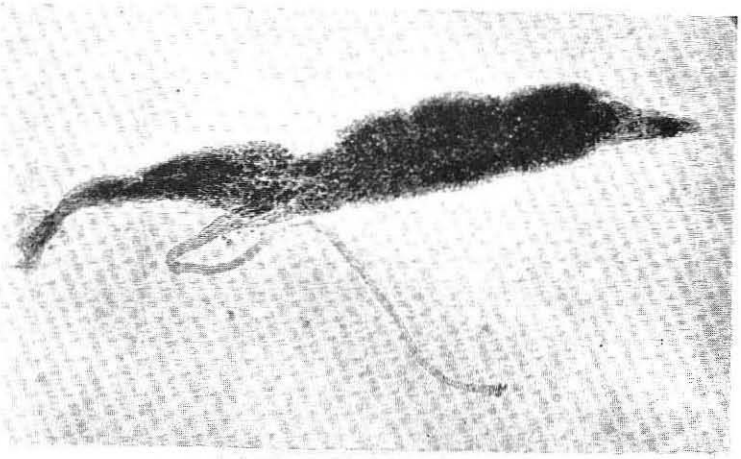
EXPLANATION OF PLATE

Telegamatrix pellona gen. et sp. nov.

A. Single worm, entire (see Text-Fig. 1).

B. Two worms *in copula*.

C. Distal end of copulatory tentacle (see Text-Fig. 3).



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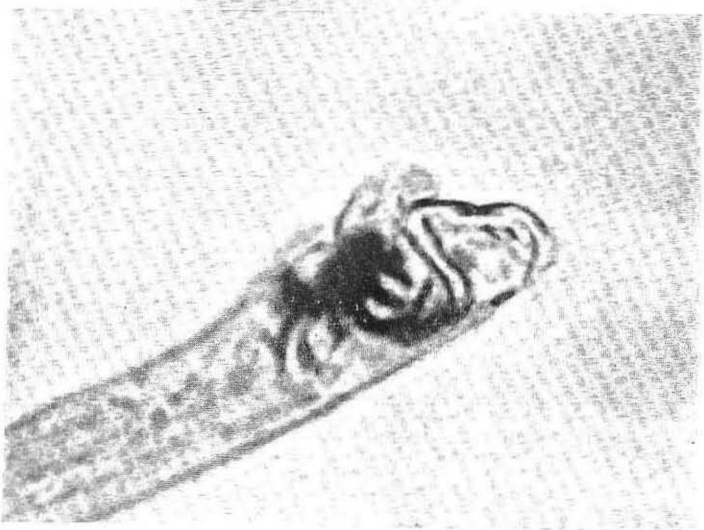

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