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Contributions to the knowledge of monogenetic trematodes with primitive attaching armature

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CONTRIBUTIONS TO THE KNOWLEDGE OF MONOGENETIC TREMATODES WITH PRIMITIVE ATTACHING ARMATURE

by

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Preface

to Translation[1]

Translation of this paper was undertaken as part of a long-term research project on the systematics, host-specificity and zoogeography of monogenetic trematodes.[2] Translation and editing were accomplished in the following manner:

1. Oustinoff[3] read translation on tape.
2. Mrs. Morales transcribed translation from tape to first typescript.
3. Hargis edited typescript.
4. Typescript retyped by Mrs. Morales.
5. Hargis again edited typescript for final corrections.

A conscious effort has been made to keep this translation as near the original as possible. It is probably inevitable, however, that some of the nuances of meaning in the original have been distorted or lost. For this we apologize to Drs. Bychowsky and Gussev and the reader.

Certain passages were difficult to translate. Where a different English phrase seems to fit the authors' meaning better or serves to clarify the text, it has been inserted in brackets. Certain obvious errors or misspellings in the original text were changed, less obvious ones are noted with (sic).

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[2]Translation and editing supported by funds from Grant No. E-2389 of the National Institutes of Health.

[3]Chairman, Department of Modern Languages, College of William and Mary, Williamsburg.

For convenience in referring to the Russian text the original pagination is given in the margin of the translation opposite the place where the new page begins. Occasionally figures or tables are somewhat displaced from their original page location; however, since they, themselves, are numbered sequentially, no confusion should result.

The citation of numbers for measurements and numbered sturctures are generally given in the translation as they were in the authors' paper. This should further facilitate checking with the Russian. Unless otherwise noted, all measurements are in millimeters.

This translation is intended as a service to researchers. Though effort has been made to make it comprehensible, accurate and useful, it is likely that improvements can be made. Should literary improvements or verification appear desirable it is suggested that the researcher make his own translation. Pagination is arranged to facilitate such activity. We will appreciate constructive suggestions for improvements in this and future translations.

Thanks are due to Mrs. Patricia C. Morales of the Virginia Institute of Marine Science who transcribed, typed, and assembled the manuscript, and to Miss Evelyn Wells who assisted with final editing.

William J. Hargis, Jr.

1955 - Trudy Zool. Inst. Akad. Nauk. SSSR - XXI: 110-118

B. E. Bychowsky and A. V. Gussev

CONTRIBUTIONS TO THE KNOWLEDGE OF MONOGENETIC TREMATODES WITH PRIMITIVE ATTACHING ARMATURE

During the last fifteen years several species of monogenetic p110
trematodes which differ from others in that the primitive structure of their attaching armature consists of only 14 edge hooks have been described. These species, described from both North America and the USSR, belong to the genus Acolpenteron Fischthal and Allison, 1940. These species are characterized by a number of primitive traits; however, as will be shown later, these characteristics are undoubtedly of secondary origin. Study of the actual parasite material at our disposal and of the literary data permits us to put forth a number of interesting ideas on the questions of changes in the organization of the worms under the influence of historically new ecological conditions and also of converging similarities in the structure of parasitic worms and the significance of these similarities for phylogenetic systematics. We have been interested in this problem for a considerable period (Bychowsky, 1933, 1937; Bychowsky and Gussev, 1950; Bychowsky and Nagibina, 1954).

Before passing to the main portion of the present communication it is necessary to prefix it by a description of a new species belonging to the group under study. The study of this new species has a certain history. In 1933 B. E. Bychowsky, working on parasites of fishes off the Blagodarnenskii fish hatchery (Northern Caucasus), discovered on the fins of a carp (Cyprinus carpio L.) a single monogenetic trematode closely resembling Dactylogyrus but differing in the absence of middle hooks /anchors/ of the attaching disc /posthaptor/. This specimen was sketched but never described because it was considered to be a fortuitous abnormality of some representative of Dactylogyrus. Twenty years later in 1953, A. V. Gussev during his work in the Volga delta (Zelenga, Bylinsky Bank) found two specimens of the same worm on the gills of a carp. As a result of this second finding we must conclude that we are not dealing with an abnormality but with a special and rather widely distributed, although rarely encountered, independent species.

Pseudacolpenteron pavlovskii Bychowsky and Gussev, gen. and sp. n. (Fig. 1).

Worms of medium size, 0.45 - 0.67 long and 0.16 - 0.22 wide. Body covered by a thin cuticle measuring less than 0.001 thick. Body spindle-shaped, narrowing anteriorly and toward the attaching disc. Anterior end a squared lobe. Attaching disc /posthaptor/ rather p111
sharply delineated from the body by a constriction; it is trapezoidal

in shape with its wide base oriented toward the body; the angles of the wide base are rounded; conversely the angles of the narrow side are sharpened and drawn slightly backward. Length of disc 0.09 - 0.11; width 0.13 - 0.20. Pharynx elongated, oval-shaped, length approximately 0.033, width 0.029. In front of the pharynx there are two pairs of eyes appearing like cup-shaped accumulations of pigmented seeds. A small light-refracting lens is located in each. Strongly developed vitellaria fill almost the entire body from the pharynx to the disc causing the parasites to appear very dark. The intestine extends from the pharynx and bifurcates immediately into two branches connected posteriorly.

The attaching disc is armed with only seven pairs of edge hooks, five pairs of which are located along the lateral edges of the disc; the sixth pair is on the posterior edge near the midline of the body with the seventh pair in front. The length of the hooks: of the first pair, 0.023 - 0.029; second, 0.023 - 0.030; third, 0.024 - 0.031; fourth, 0.026 - 0.033; fifth, 0.028 - 0.037; sixth, 0.028 - 0.033; and seventh, 0.025 - 0.031.

Copulatory organ consisting of a tube /cirrus/and a supporting apparatus /accessory piece/. Tube cylindrical curving smoothly so that the axes of the proximal and distal ends are almost at right angles to each other; proximal part somewhat widened; distal obliquely cut; its length along the curvature is 0.047 - 0.052, along the straight part is 0.038 - 0.043; diameter of the cylindrical portion is approximately 0.002. Supporting apparatus a thin membrane-like plate winding around the tube with a characteristic prominence, it is 0.033 - 0.038 long. p112

Vaginal armature and eggs not discovered.

Host: Cyprinus carpio L.

Location: Fins and gills (gill filaments).

Place of discovery: Northern Caucasus and the Volga Delta.

With the parasite described in the present work we know of five "Acolpenteron" which, after careful study, may be separated into two morphologically isolated groups. One consists of three species encountered in the ureters and in the urinary bladder of their hosts, the other, of two species parasitizing the gills and fins. The first three species (Acolpenteron ureteroecetes Fischthal and Allison, 1940, A. catostomi Fischthal and Allison, 1942 from North America, and A. nephriticum Gvosdev, 1945 from central Asia) show a number of common morpho-physiological characteristics. Besides the absence of middle hooks /anchors/ in the attaching armature common to both groups of "Acolpenteron", this group undoubtedly possesses the following

characteristics: 1) a special sturcture of the cuticula, 2) reduced eyes which are non-functional in the adult state, and 3) a weakly developed and almost completely inactive attaching disc /posthaptor/.

In describing their two species Fischthal and Allison (1941 and 1942) did not mention the structure of the cuticle, although they indicated "that there are some special sensitive pili located on the papillae," i.e. there are certain pecularities in the structure of the coverings of these monogenetic trematodes. The covering is not mentioned at all in the work of Gvosdev (1945) describing the third species, A. nephriticum, but a thick very wrinkled cuticle, mainly in the first half of the body, is apparent. We had at our disposal several preparations of the latter species containing a few whole mounts stained in alumcarmine (mounted in Canada balsam), as well as unstained specimens (mounted in glycerin-gelatin). Study of these preparations shows that the entire bodies of the worms, with the exception of the disc /posthaptor/ are actually covered by a thick cuticle reaching up to 0.003 in thickness and forming singular plications. These plications of the cuticle (Fig. 2) are very pronounced in the anterior part of the body up to the level of the pharynx, and often produce the impression that they actually form special papillae. In spite of very careful study we did not discover any sensitive pili on these "papillae." Furthermore, we are inclined to doubt the accuracy of the observations of the American authors. First, in their drawings of the whole mounts, the thread-shaped excretions of the cephalic glands, a common phenomenon among the lower Monogenoidea, are indicated as sensitive pili. Secondly, there is not a trace of cuticular papillae bearing bristles in the figures of the part of the body containing the sex system in the drawings made under large magnification. In addition, it is quite probable that among American species, just as among the central Asian ones, the cuticle is very much thickened throughout the entire body (the presence of the "papillae"). The cuticle is considerably thinner (approximately 0.001 thick) on the attaching disc. This unusual structure of the cuticle is undoubtedly the result of the species living under special conditions, sharply differing from the usual place of habitat of monogenetic trematodes (gaseous interchange). /It is presumed that the authors mean here that the cuticle is thickened in these worms, living in the ureters as they do, compared to those living on the gills because in the former there is less need for a thin cuticle to facilitate interchange of gases between the worm and its milieu. Another possibility is that the plication-thickened cuticle serves to hold the worm in position within the ureters where the small haptoral hooks might be partially or wholly inadequate as a holdfast. WJHJr./ It is quite understandable that at the same time the attaching disc, functional in the larva, which must first make contact with and attach to the fish, loses its physiological significance gradually with the growth of the worm but retains the initial thickness and structure of the cuticle. p113

Reduction of eyes and associated loss of their initial functional utility is sharply expressed among the three species studied. The larvae of Acolpenteron ureteroecetes and A. catostomi, hatched by Fischthal and Allison, possessed four well developed eyes equipped with small light-refracting lenses. There is reason to believe that the larvae of A. nephriticum also possess eyes, although the latter have not yet been described.

As the worms develop and the eyes lose their functional significance, in connection with the pecularities of the historically new place of habitat /the ureters/, the eyes are reduced, and their pigmented goblets disintegrate into separate pigmented seeds to varying degrees not only among different species but among the individuals of the same species (Gvosdev, 1945).

As has been indicated above, among adult individuals the attaching disc is non-functional or almost non-functional. According to E. V. Gvosdev, adult A. nephriticum lie unattached in the cavities of the ureters of its hosts. However, even after superficial examination of preparations of this species (Fig. 3) and the drawings of the two others, it is apparent that their attaching discs and the armature located thereon cannot be sufficient to attach adult worms. Undoubtedly as the worm develops the very important initial role of the attaching disc gradually diminishes. Thus, this peculiarity /of the posthaptor and its armament/ is a result of new conditions of existence which p114 influence both the morphology and the functioning of the attaching disc.

The second group of "Acolpenteron" contains only two species, the one described by us above and Acolpenteron (s.l.) ignotus Gussev, parasitizing the gills of Acanthorhodeus asmussi in the Amur Basin (Lake Khanka near the village of Astrakahnka). Both of these species differ sharply from the preceding ones not only by their place of habitat but also by differences in morphological characteristics. The cuticle of these species is the usual, rather thin one found in the majority of Dactylogyridae. Also, adults of these worms have four well developed pigmented eyes with small light-refracting lenses and a rather well developed attaching disc which serves for attachment on the body of the host. Thus, because living conditions of this group of species do not differ substantially from those of the remaining Dactylogyridae, we do not see anything peculiar in their structure, with the exception of the absence of middle hooks /anchors/ of the attaching disc. The last circumstance undoubtedly is connected with the transition to attachment on the fins. As is known, the middle hooks of Dactylogyridae are oriented with their points toward the dorsal side of the disc. Thus, in attachment of the worms to the fins the middle hooks remain practically unused because they freely protrude upward and cannot be utilized for attachment.

The disappearance of the middle hooks is not a special peculiarity of "Acolpenteron". Although it would be tempting to consider the forms with attaching discs but without middle hooks as primitive or primary, the lack of the middle hooks is, without doubt, a secondary phenomenon encountered convergently in different groups. Thus, Isancistrum loligans Beauchamp parasitizing the gills of Alloteuthis subulata (Cephalopoda) has only 16 edge hooks on the attaching disc, although it undoubtedly originates from ancestors resembling Gyrodactylus, the disc /posthaptor/of which is equipped with two middle hooks /anchors/in addition to the edge hooks. Converging similarities between Gyrodactylus and Dactylogyrus were reported earlier (Bychowsky, 1933). It is probable that the absence of middle hooks among Anonchohaptor Mueller is also a secondary phenomenon. This genus contains only one species, A. anomalum Mueller, 1938 which is encountered in North America on several species of Catostomidae and has only 14 small edge hooks on its attaching disc. On the same hosts from the same region, Mueller also discovered Murraytrema copulata Mueller, 1938, which has four middle hooks and resembles Anonchohaptor anomalum closely in the structure of the armature of the copulatory organ and the vaginal duct (Fig. 4). It seems to us that both of these species are undoubtedly genetically related and descend from common ancestors.

From the point of view of the question being considered, it is not without interest to note the structure of the attaching apparatus in Dactylogyrus singularis Gussev (1955), the middle hooks /anchors/ of which are rather small in relation to the edge hooks and apparently lose their function. This case indicates one of the possible routes leading to the disappearance of middle hooks of the attaching apparatus.

We can conclude, for various reasons, that the disappearance of middle hooks is a phenomenon which is not very rare among the lower Monogenoidea and that it takes place among different groups independently, creating more or less considerable convergent similarity among the species which are evolving. p115

Questions arise in this connection as to what is the origin of all "Acolpenteron" and what are their phylogenetic interrelations and their position in the system of Monogenoidea.

This analysis and also personal familiarity with the internal structure of the worms makes us confident that, in the first place, all five species of "Acolpenteron" indicated above descend from ancestors similar to Dactylogyrus and, in the second place, that the two groups mentioned differ enough from each other to make recent common origin unlikely. /In other words, their recent ancestors may have been similar but not the same./ The geographical distribution of the first three species and the adaptation to endoparasitism as

adults, which has been reflected in a number of morphological characteristics, indicates the considerable antiquity of this group. The interrupted distribution of this group, with two of the species encountered in North America and one in central Asia--that is, the presence of the so-called North Atlantic break in the range of the group resembling that in Lucioperca and a number of other fishes and freshwater invertebrates--points to the probability that all three parasitic species under consideration represent relics of an ancient fauna common to Eurasia and North America. The fact that these three species are encountered in fishes far removed from each other phylogenetically (Catostomidae, Cobitidae and Centrarchidae) substantiates this indirectly, and, considering the well known high specificity of Monogenoidea, this also attests to the antiquity of separation of parasites.

The second group contains two ectoparasitic species en- p116
countered on carp fishes in the Punto-Caspian and Amur basins, i.e., it also has a considerable disruption in range but in the European-Far Eastern area. This /disruptive distribution/ occurs widely among freshwater animals and in particular among carp, the hosts of the species just described. It is not unlikely that in future studies the latter will be discovered also in the Amur basin where, in spite of the studies of A. K. Achmerov and A. V. Gussev, one may still expect a great deal that is new to the faunistic record. One must indicate that, just as Anonchochaptor anomalum is connected with Murraytrema copulata, Acolpenteron (s.l.) ignotus Gussev without doubt is genetically close to Dactylogyrus triaxonis Achmerov (Fig. 5). An extraordinary similarity in the structure of their copulatory organs as well as the fact that they are encountered on the same host, Acanthorhodeus asmussi, serves as a basis for this /hypothesis/. It is very likely that both species have a common ancestor very close to D. triaxonis or even that Acolpenteron (s.l.) ignotus descends directly from D. triaxonis. Another extremely interesting theoretical question arises in this connection. One can hardly suppose that the species described above from carp descends from Acolpenteron (s.l.) ignotus. It is more likely that its ancestor was some Dactylogyrus or a form similar to it. Thus, two species of one new genus apparently descend from two different species of one old genus. Is it possible to allow such an interpretation using the principle of the monophyletic origin of systematic categories as a basis? This question cannot be answered here as this digression would take us far from the theme under consideration. But in our opinion this question is timely and we hope to return to it in the near future.

What systematic deductions are possible from what has been p117
expressed above? In our opinion they are quite clear. We think that it is necessary to include only the three first species in the genus Acolpenteron and to establish a new genus for remaining two. The diagnoses of these genera and their scope are given below. However, preliminary words are necessary about the position of the

two genera in the system of Monogenoidea. On the basis of the opinion of Price, Fischthal and Allison attributed the genus they described to the family Calceostomatidae (Parona and Perugia, 1890) Price, 1937. This, of course, is completely incorrect. Unfortunately, the error of Fischthal and Allison is repeated in a number of works and in Sproston's synopsis (1946) without critical analysis. Were one acquainted even cursorily with any species of Calceostomatidae one would indubitably see that the latter do not have a single sufficiently important characteristic in common with Acolpenteron, beginning with the structure of the cephalic end and the attaching disc /posthaptor/ and ending with the structure of the intestine and the sex system. Actually Acolpenteron, just as the genus established herein, undoubtedly must be attributed to the family Dactylogyridae, with representatives of which its species are closely related as has been shown above.

ACOLPENTERON (FISCHTHAL and ALLISON, 1940) BYCHOWSKY and GUSSEV, emend.

Dactylogyridae with weakly developed attaching disc armed with only 14 edge hooks. Cuticle of the body of considerable thickness. Eyes reduced in adult state. Intestine with branches merging at the posterior end. Sex system of the usual type with a vagina present.

Parasitizes ureters and urinary bladder of fishes.

The genus contains: 1) A. ureteroecetes Fischthal and Allison, 1940 (type); 2) A. catostomi Fischthal and Allison, 1942; 3) A. nephriticum Gvosdev, 1945.

PSEUDACOLPENTERON BYCHOWSKY and GUSSEV, gen. n.

Dactylogyridae with a well developed attaching disc armed with only 14 edge hooks. Cuticle of the body not significantly thickened. Two pairs of well developed eyes in adult. Intestine with branches merging at the posterior end. Sex system is of the usual type, with vagina present.

Parasitizes gills and fins of fishes.

The genus contains: 1) P. pavlovskii Bychowsky and Gussev sp. n. (type); 2) P. ignotus (Gussev, 1954) Bychowsky and Gussev comb. nov. (Syn. Acolpenteron (s.l.) ignotus Gussev, 1954).

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FIG. 1. Pseudacolpenteron pavlovskii Bychowsky and Gussev, gen. and sp.n.
1--Overall view of the specimen from Cyprinus carpio from the Volga;
2--From carp of northern Caucasus;
3--Attaching disc from the same individual;
4--Edge hook;
5--Copulatory organ from an individual from the northern Caucasus;
6--The same from an individual from the Volga.

FIG. 2. Cuticles of (1) Pseudacolpenteron pavlovskii and (2) Acolpenteron nephriticum.

FIG. 3. Attaching disc /posthaptor/ of Acolpenteron nephriticum.

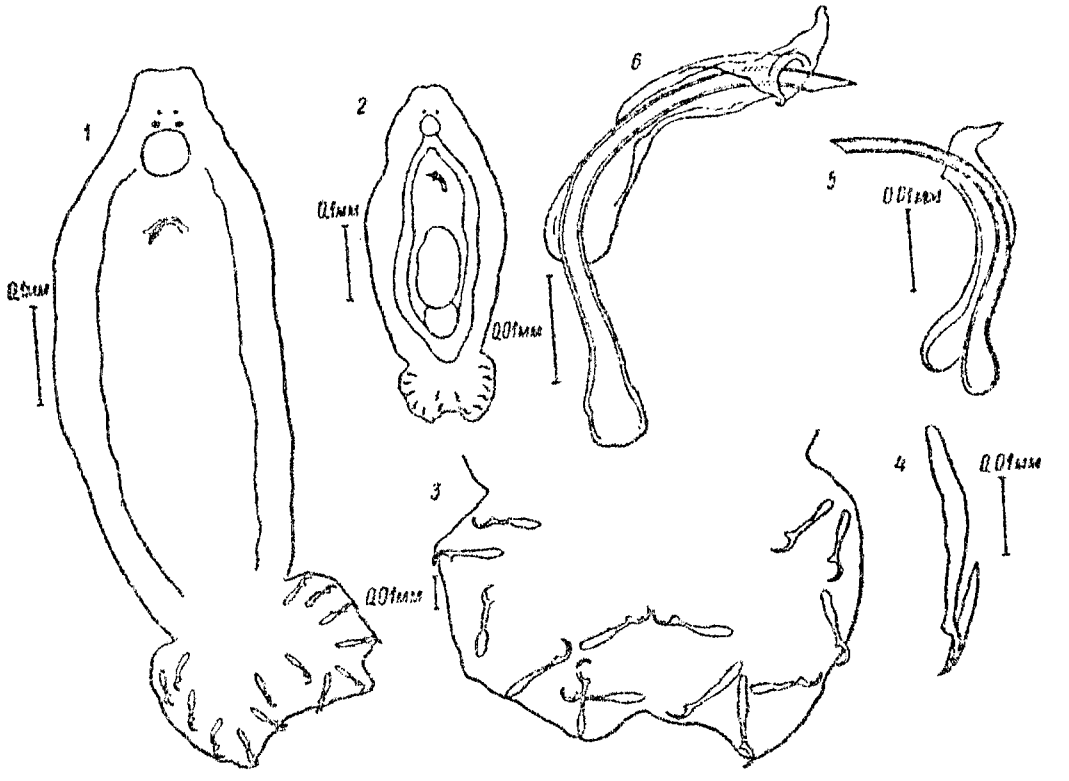

FIG. 1

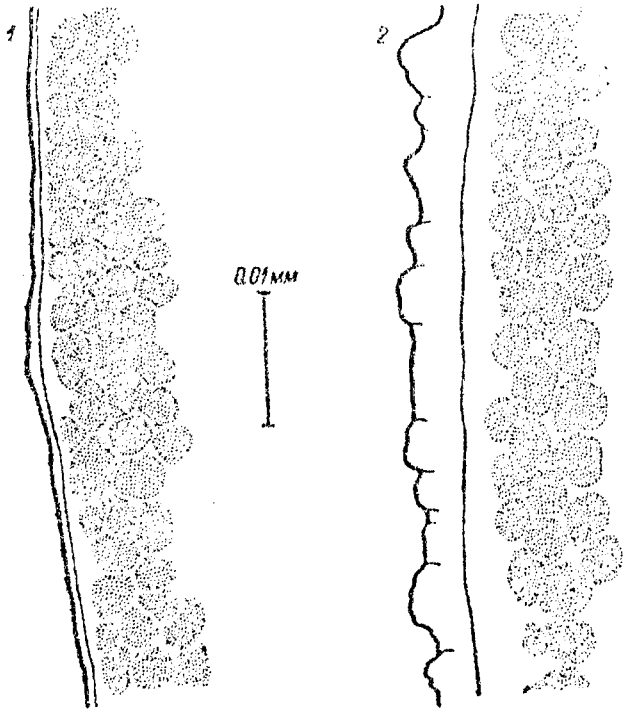

FIG. 2

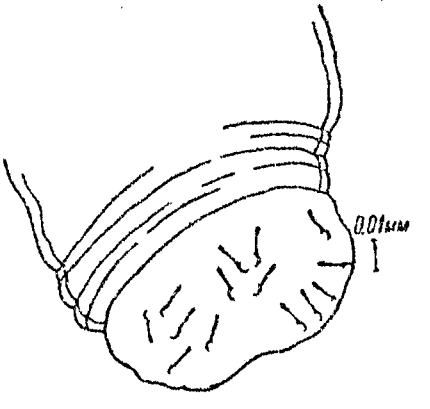

FIG. 3

FIG. 4. Attaching armature and copulatory organ of (1) Murraytrema copulata, and (2) Anonchohaptor anomalum (Mueller, 1938).

FIG. 5. Attaching armature and copulatory organ of (1) Dactylogyrus triaxonis and (2) Pseudacolpenteron ignotus.

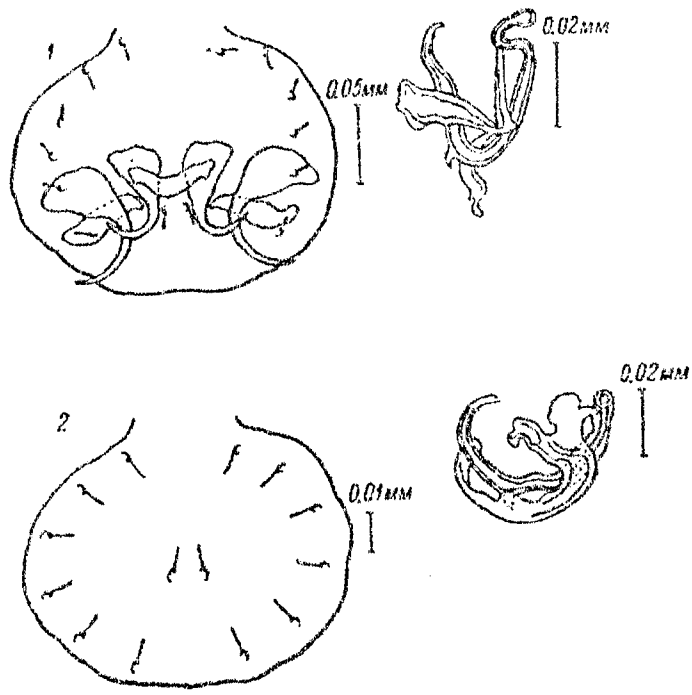

FIG. 4

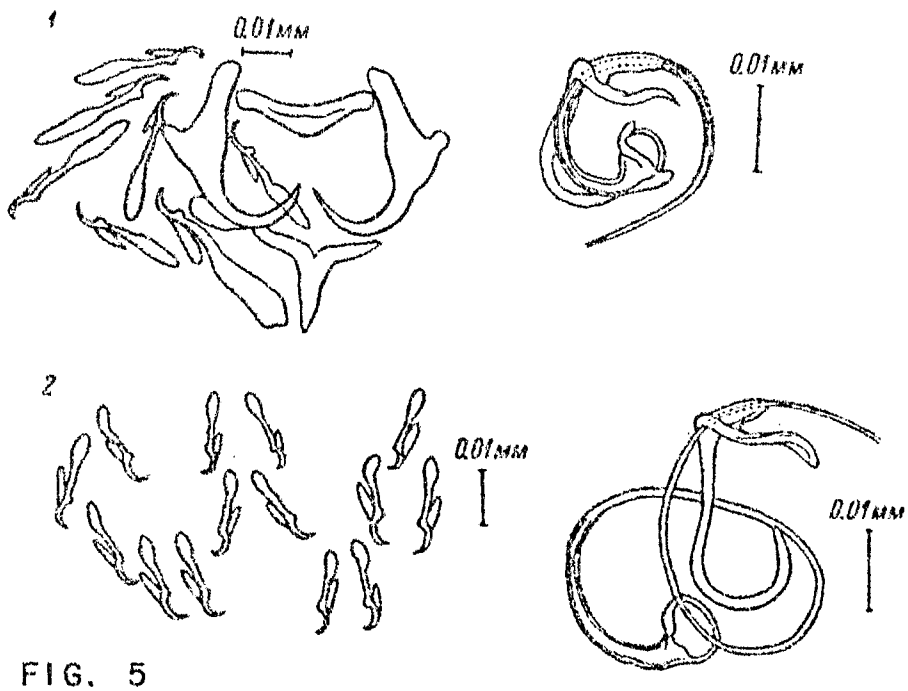

FIG. 5