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MONOGENETIC TREMATODES

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ON THE POSITION OF AXINE BESONES IN THE SYSTEM OF
MONOGENETIC TREMATODES

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

1. Oustinoff read translation on tape.
2. Mrs. Morales transcribed translation from tape to first typescript.
3. Hargis edited typescript.
4. Typescript retyped by Mrs. Morales.

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 the author and the reader.

Certain passages were difficult to translate. Where a different English phrase seems to fit the author's 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 structures are generally given in the translation as they were in the author's 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.
U. Strelkov

ON THE POSITION OF AXINE BELONES IN THE SYSTEM OF MONOGENETIC TREMATODES

The material for the present work was collected at the Sebastopol Biological Station of Academy of Sciences, USSR for the purpose of studying this unusual asymmetrical monogenetic trematode, Axine belones, from the gills of the garfish Belone belone euxini (Gunther). The object of the study was to clarify the position of this parasite in the system of Monogenea, and for this it was necessary to determine the morphology of the attaching apparatus of the adult form and particularly of the larva of Axine, which was unknown until that time.

The analysis of the structure of the larva and of its attaching apparatus was necessary because the structure of the latter has a great and often deciding significance in the establishment of consanguinous links among monogenetic trematodes (Bychowsky, 1937). The organs of attachment of the adult form also serve for purposes of systematics. Because we wished to determine the position of Axine in the family Microcotylidae the adult attaching apparatus was studied. At the same time larvae were hatched and the details of anatomical structure of the worm were further studied.

The gills of seventy garfish were examined and from them approximately sixty trematodes of Axine belones were collected. Both the adult forms as well as the hatched larvae were examined and sketched while still alive. Moreover, adult Axine were fixed in alcohol or in Zenker-formol for whole mounts and sections. Glycerine-gelatin preparations were prepared on the site from formalin-fixed larvae.

Further study was conducted at the Zoological Institute of the Academy of Sciences USSR and the Leningrad State University by A. A. Stanov. Whole mounts of adults were made and stained in aluminous carmine. Sections were stained according to Mallory and in iron hematoxilyn of Heidenham. The present study was suggested to me by B. E. Bychowsky, who directed it. For this I am deeply thankful to him.

History of the study of the genus Axine

The genus Axine with type species A. belones from the gills of Belone acus was described by Abildgaard (Abildgaard, 1794). This was followed by a number of works in which new species of the genus were described.
Among the works describing the anatomy and morphology of *Axine belones* it is necessary to mention the research of Lorenz (1878).

In presenting the comparative anatomy and histology of monogenetic trematodes, Goto (1894), among others, also touches upon the representatives of the genus *Axine*. Nine species were described in nineteen-thirties.

In 1938 Yamaguti divided genus *Axine* into three subgenera. He attributed those worms which have clamps distributed in two symmetrical rows of unequal length on the attaching disc at the posterior end of the body, and in which the distal end of the ovary turns posteriorly instead of forward, as among *A. belones*, to the first subgenus. The varinal opening is medial on the dorsal side of the body (among *A. belones* it is located at the side). Yamaguti calls this subgenus *Heteraxine* and ascribes to it the following species: 1) *Axine* (*Heteraxine*) *heterocerca*, Goto, 1894—type species; 2) *A. (H.) triangularis* Goto, 1894; 3) *A. (H.) carangis* MacCallum, 1918; 4) *A. (H.) seriola* Ichii, 1936; 5) *A. (H.) chinensis* Yamaguti, 1937.

Yamaguti ascribed worms with the attaching clamps located in one row and having the distal end of the ovary oriented forward as in *A. belones* to the second subgenus. The vaginal aperture opens on the dorsal side. This subgenus, called *Axinoides*, contains the following species: 1) *Axine* (*Axinoides*) *tylosuri* Yamaguti, 1938—type genus; 2) *A. (A.) aberrans* Goto, 1894.

Yamaguti attributes the remaining species to the type genus *Axine*s. str., which is characterized by the following distinguishing characters: attaching clamps are located on the posterior end in one row; the distal end of the ovary turns forward; and, the vaginal opening is located at the side of the body.

Price (1945) separated from the family Microcotylidae the special subfamily *Axininae*, to which he ascribed worms whose bodies are shaped like narrow triangles, the short side of which bears the attaching disc with one row of attaching clamps. The ovary is U-shaped. The sex apparatus is armed.

Within the limits of this subfamily he distinguishes three genera:

1. In the genus *Axine* with vaginal aperture located laterally and armed with one horn-shaped thorn, he includes the following species: (1) *Axine belones* Abildgaard, 1794; (2) *A. triglae* Beneden and Hesse, 1863; (3) *A. cypseluri* Meserve, 1938; (4) *A. yamaguti* Meserve, 1938; (5) *A. gracilis* Linton, 1940; (6) *A. japonicum* n.n. from *A. cypseluri* of Yamaguti.
2. In the genus *Axinoides*, with a medially located vaginal aperture and one horn-shaped thorn, he includes the following species: (1) *Axinoides aberranus* Goto, 1894; (2) *A. tylosuri* Yamaguti, 1938.

3. In the genus *Neoaxine*, with a laterally located vaginal aperture around which is located an incomplete row of thorns he includes the single species *Neoaxine constricta* Yamaguti, 1938.

Finally, in 1946 Sproston’s synopsis on Monogenea appeared. In this work a full list of species of axinoid trematodes is cited. All are divided into four genera.

1. The genus *Axine* Abildgaard, 1794 with two species: (1) *A. belones* Abildgaard, 1794; (2) *A. constricta* Yamaguti, 1938; (3) *A. cypseluri* Meserve, 1938; (4) *A. inada* Ichii and Sawada, 1938; (5) *A. trilae* Beneden and Hesse, 1863.

2. The genus *Axinoides* Yamaguti, 1938 with species: (1) *A. tylosuri* Yamaguti, 1938; (2) *A. aberrans* Goto, 1894; (3) *A. gracilis* Linton, 1940; (4) *A. oligoplitis* Meserve, 1938.


Sproston did not consider Price’s work (1945) in making this list and did not separate the axinids into special subfamily.

In conclusion, one may say that as knowledge accumulated *Axine* was first divided into subgenera and then the subgenera were elevated into the rank of genera. In our opinion Yamaguti was too cautious when he separated the subgenera *Axinoides* and *Heteraxine* from the genus *Axine*. He would have been quite justified to call them separate genera as did Price in 1945. Sproston is also correct when in addition to genera *Axine*, *Axinoides* and *Heteraxine* he separates the genus *Lintaxine*, renaming the genus *Heteraxine* described by Linton (1940). One should also note all these genera were separated on the basis of purely morphological and anatomical characteristics of adult individuals without considering the structure of the larvae and consequently the position of the unusual asymmetrical trematode *Axine* in the family of Microcotyliidae was not quite clear. We shall now attempt to determine definitely the relation of genus *Axine* to the other genera of this family on the basis of the data about larval structure and the structure of the attaching apparatus of the adult form.
Anatomy of Axine

Body Shape. The body of Axine belones (Fig. 1) is flat and resembles a narrow triangle the short side of which bears the attaching disc with a number of attaching clamps. The length of the body is 4-6 mm, the width 1-1.5 mm.

Attaching Apparatus /posthaptor/. The asymmetrical attaching disc occupies the posterior end of the body of Axine belones. Attaching clamps are distributed in one row along the edge of the disc. Approximately in the middle of the row of clamps there are four small hooks—remnants of the attaching apparatus of the larva.

In structure the clamps of Axine (Fig. 2) resemble the clamps of Microcotyle and each one of them represents an invagination in the attaching disc whose thin walls are supported by a chitinous skeleton.

The skeleton of the clamps is composed of two arcs /of sclerites, i.e. anterior and posterior loop-sclerites of the clamps plus the middle piece or spring/ which in turn consist of four moving articulated parts, of a spring and of a small chitinous element located behind the arcs. Both arcs are articulated by a hinged joint. The spring is located across the clamp in the shape of an arc-shaped plate and has the form of two letters "E" connected at their bases and functions as the fastener of the clamp. The length of the clamp is 0.11 - 0.13, the height is 0.07 - 0.08.

Only two pairs of small middle hooks from the original larval attaching apparatus are retained by the adult. Generally they have the same shape and size as in the larva (see farther). Only one pair of middle hooks has a small excrescence on the handle (Fig. 3).

The number of clamps is not constant but varies considerably depending on the age of the worm. Among young individuals there are fewer of them and apparently they increase in number during the entire life of the worm as was noted by Goto (1894). According to our observations their number in six different individuals varied as follows: 28, 35, 36, 45, 51, 54.

If we arbitrarly/ take the site of larval hooks as the middle of the disc and count the number of clamps to the right and to the left from this alleged middle we find that their numbers vary considerably and without regularity. For instance; number of clamps to the right 28, 32, 18, 20, 17, number of clamps to the left 17, 18, 19, 34, 31.

The occurrence of asymmetry of the attaching apparatus in Axine belones could be represented by considering the structure /of the attaching apparatus/ among typical Microcotyle as the primitive form. In Microcotyle there are two equal symmetrical rows of attaching clamps.
located on the attaching disc which is like an isosceles triangle the apex of which is posteriorly oriented. This apex can be considered as the middle of the attaching disc as is indicated among young individuals of certain species because it is the place where the hooks of the larval attaching apparatus remain (Fig. 4).

In the genus Heteraxine the attaching disc already has developed an asymmetrical structure, which is noticeable even among certain Microcotyle: one row of attaching clamps does not develop completely and becomes shorter than the other. And here also its height must be considered as the middle of the disc (Fig. 5).

Among the genus Axine the attaching disc acquires the symmetrical form in another way than that in Heteraxine where asymmetry arose because of underdevelopment of one of the sides of the attaching disc. If the basis for asymmetry in Axine were the same then the middle of the attaching disc as designated by the larval hooks would have been at the posterior end of the row of attaching clamps. But in this case the larval hooks are located approximately in the middle of the row of the attaching clamps. Because of this we may deduce that the right side of the attaching disc of Axine pivoted around the point of rotation—the larval hooks—and fell into line with the left side (Fig. 6).

The same interpretation of the origin of asymmetry of the attaching disc could be given for genus Axinoides.

The intestine is of the usual type. The buccal opening is located at the anterior end of the body. Near it one can distinguish two small suckers. A small pharynx extends behind the buccal aperture and further along the esophagus at the level of the widening of the vaginal duct the intestine widens and gives off two branches directed toward posterior end of the body. The female sex system is illustrated in Fig. 7. The ovary is "U" shaped and is located in the middle part of the body toward the dorsal side. A short oviduct which connects the ovary with the ootype extends from the anterior end of the ovary. The pear-shaped ootype is located between the ovary and the uterus. In his paper in 1878 Lorenz insisted that this was a seminal vesical, but I clearly saw vitelline and egg cells in this organ and as a result it is undoubtedly an ootype.

The uterus connects the ootype with the genital atrium and reaches considerable length. It begins near the narrowed terminal of the ootype and extends along the medial line of the body into the anterior end, terminating at the sex atrium as an aperture surrounded by a muscular ring with thorns. Usually one egg is located in the uterus. The vitellaria are situated in two long ribbons along the entire body of the worm and extend even into the attaching disc. The vitellaria completely cover the branches of the intestine. The vitelline ducts are paired and are located at a distance of one-third
of the body from the anterior end. They emerge from each ribbon of vitellaria and having reached the midline merge into one unpaired duct which is oriented posteriorally and at the level of the anterior part of the ovary it recurves and enters the ootype. The intestinal—sex canal/emerges from the right side between the ootype and the vaginal duct. It extends forward and opens into the right branch of the intestine. The vaginal duct is rather narrow but has powerful muscular walls in the region where the genito-intestinal canal enters into it. It opens by its vaginal aperture on the right side of the body. A sac-shaped gland with chitinous sex thorn is situated near the vaginal aperture in the fold of the body (Fig. 8). This formation apparently resembles the pear-shaped organ of Turbellaria. Approximately at the mid-length of the vaginal duct one may distinguish a strong thickening of its walls. Beginning here the interior wall of the duct is covered by chitinous excrescenses which extend to the vaginal aperture.

The male sex system (Fig. 1). There are many testes which occupy the entire posterior part of the worm between the branches of the intestine. They begin at the posterior edge of the ovary and extend to the attaching disc. From the testes, as Lorenz (1878) notes, two seminal ducts, which later merge into one seminal duct, depart from the testes. The seminal duct is oriented anteriorly and curves several times along its length especially in the middle part. It terminates in the sex atrium by a copulatory organ which consists of a muscular cone-shaped sucker with chitinous hooks located at its base and by two muscular lobes /he calls them shafts/. These lobes are situated along the walls of the sex atrium (Fig. 9).

Egg and Larva

In order to obtain larvae live garfish were taken into the laboratory and Axine were carefully removed from their gills. It was found to be very important that the garfish be alive because, though it was possible to remove live trematodes from recently dead fish, we were never able to obtain eggs from these trematodes. After this one to two worms were placed in test tubes/experimental containers/ with fresh sea water and after an hour or an hour and a half one could see approximately 30 to 40 eggs at the bottom of the test tubes. These eggs were placed, in quantities varying from ten to fifteen in each, into other test tubes also with fresh sea water. The test tubes were covered and placed under a light-free hood and then into a cool place. Temperature under the hood was not constant but fluctuated depending upon temperature in the laboratory from +18 to +25°C. Under such conditions the eggs developed in 5 days and at the end of this period moving larvae were observed in them.
The egg of *Axine* (Fig. 10) is rather large, 1.0 in length and approximately 0.08 in width, and is spindle-shaped with a long little foot and filament. On one end it has an operculum which the larvae throw off by an energetic motion at the moment of hatching.

The larvae (Fig. 11) emerges from the egg and begins to swim by means of cilia, revolving around its axis. The cilia surround the body of the larva in three band-like zones. The first zone is located in the anterior end, the second in the middle and the third is at the posterior end. The first zone is located close to the end of the body and is somewhat wider than the other two. It extends approximately to the level of the eye. The second zone is somewhat narrower than the first. And the third zone, located at the posterior end of the attaching disc, is narrower than the other two. The larva swims rather rapidly so that sometimes it is difficult to keep it within the field of view of a binocular scope.

The body of the larva is elongated, and is widened toward the posterior end where the attaching disc is located. The length of the body is 0.20 - 0.30, the width is 0.08 - 0.10. Dark pigmented double eyes stand out sharply at its anterior terminal. The attaching disc occupies about one-third of the body and bears seven pairs of hooks of which two pairs are large middle hooks /anchors/ and five pairs are small lateral hooks (Fig. 12).

The large middle hooks are located on both sides of the medial line of the body and have a varying structure. The first pair resembles the middle hooks /anchors/ of *Dactylogyrus*, but it has a longer handle. The length of the hook is 0.032 - 0.034; the length of the point is 0.009 - 0.010; the length of the handle is 0.012 - 0.014. The second pair of hooks somewhat resembles the small edge hooks, but its sizes are much larger. The hooks of the second pair have a thin, long straight handle and a small point. Their overall length is 0.025 - 0.044; the length of the point is 0.008 - 0.014. In a live larva these hooks may protrude beyond the borders of the attaching disc and apparently are used to secure first attachment to the host.

The small edge hooks are located along the edges of the attaching disc and are so small that they are often difficult to see. These hooks consist of a curved handle and of a small point. Their overall length is 0.014 - 0.016; the length of the point is 0.005 - 0.006. It is possible to distinguish the beginning of the intestine in the middle part of the larva.

Position of the genus *Axine* in the family Mycrocotylidae

Examination of the details of the structure of *Axine belones* and the study of its larva enables us to place it in the family Mycrocotylidae in close proximity to the genus *Microcotyle*. 
The criterion in establishing this close relationship is the great similarity of their larvae. Specifically, both the larva of Axine and those of Microcotyle belong to the larval type two which is characteristic of Microcotyliidae and Octocotyliidae (according to classification of Bychowsky, 1937). The presence of two pairs of large middle hooks/anchors/ and five pairs of small edge hooks is characteristic for this category. Moreover as several authors note, the structure of adult worms confirms the close relationship between Axine and Microcotyle. For instance, Vogt, (1879) writes that difference between Axine and Microcotyle consists only in the asymmetrical position of the attaching disc. Goto (1894), underscoring the proximity of these two genera, indicates that these genera should be retained as separate only for the convenience of classification.

However, it is difficult to agree with the latter. There are good reasons to separate Axine into an independent genus. Nevertheless it is anatomically very close to the genus Microcotyle. This proximity is expressed in the similar arrangement of the sex system (the description above can also serve as a general plan of the structure of the sex system for Microcotyle) and of the attaching clamps.

Proceeding from this it is impossible to agree with Price (1945) who separates Axine belones into the special subfamily Axininae. In determining the limits of the subfamily he supports his decision by the following:

1. Price presents the asymmetrical structure of the attaching disc as the first characteristic distinguishing the subfamily Axininae. However, one must note that the asymmetrical structure of the attaching disc already appears among certain species of Microcotyle (M. seriola Yamaguti, 1940 and M. reticulata Goto, 1894.

2. Price considers the presence of larval hooks in the attaching apparatus of adult individuals to be the second distinguishing characteristic of the subfamily Axininae. But these hooks exist also among the young individuals of M. donavini Beneden and Hesse, 1863.

3. Price considers that the presence of the copulatory organ is the third distinguishing characteristic of the subfamily Axininae. However, the copulatory organ also exists in M. eriensis Bangham and Hunter, 1936.

4. Finally, Price considers that the presence of the armature of the vaginal aperture is characteristic for Axininae; however, this armature exists also in Microcotyle/, for instance in M. chizi Goto, 1894 and M. elegans Goto, 1894. In other words, the similarity between the genera Axine and Microcotyle is so great that there is no basis to create as does Price a special subfamily Axininae within the limits of Microcotyliidae.
LITERATURE


FIG. 1. *Axine belones*.

1. buccal suckers;
2. copulatory organ;
3. vaginal duct;
4. ootype;
5. seminal duct;
6. ovary;
7. testes;
8. attaching clamps.
FIG. 2. Skeleton of the attaching clamp of Axine belones.

FIG. 3. Larval hooks /anchors/ of an adult Axine belones.

FIG. 4. Distribution of the attaching clamps in Microcotyle.

FIG. 5. Distribution of attaching clamps in Heteraxine.

FIG. 6. Distribution of attaching clamps in Axine.
FIG. 7. Female sex system of *Axine belones*.

1--yolk duct;
2--uterus;
3--vaginal duct;
4--intestinal sex canal;
5--ootype;
6--ovary.

FIG. 8. Armature of the vaginal aperture of *Axine belones*.

1--vaginal aperture;
2--gland;
3--muscular lobe;
4--chitinous sex thorn (longitudinal cross section).

FIG. 9. Copulatory organ of *Axine belones*.

FIG. 10. Egg of *Axine belones*. 
FIG. 11. Larva of Axine belones.

FIG. 12. Attaching hooks /anchors and hooks/ of a larva of Axine belones.