Variability of the Basal Esophageal Sheath in Belondirid Nematodes

HELEN CAROL HECHLER[1]

Abstract: The structure of the basal esophageal sheath was studied in *Axonchium amplicolle, A. chloristum, A. crassum, A. gigas, A. micans, A. rotundum, A. serpens, A. solitare, Dorylaimellus aequalis, D. parvulus, D. tenuidens, Oxydirus gangeticus, O. gigus, O. oxycephaloides,* and *Swangeria bisexualis.* In *A. gigas* the muscle bands comprising the sheath spiral dextrally, but in the other species of *Axonchium* they do not spiral but lie parallel to the esophagus. In *O. gigus* the spiral is sinistral, whereas in the other two species of *Oxydirus* it is dextral. The spiral is very slight in *Dorylaimellus aequalis,* each band passing around only about 180 degrees of the circumference of the esophagus. They completely encircle the esophagus in *D. parvulus,* and pass around about 3/4 the circumference in *D. tenuidens.* The definitions of Belondiroidea Thorne, 1964 and of *Axonchium* Cobb, 1920 are emended to recognize the variability in the structure of the sheath.

Although the sheath surrounding the base of the esophagus of *Dorylaimellus aequalis* (Cobb, 1918) Thorne, 1939 was illustrated in the original description of the species (2), it was not mentioned by Cobb in his text. The presence and taxonomic significance of the esophageal sheath in belondirid nematodes was first pointed out in 1939 by Thorne (10). In his definition of the family Belondiridae he stated: "Basal enlargement of esophagus greatly variable in size and amount of musculature, always surrounded by a sheath of spiral muscles." In this paper Thorne often illustrated the sheath by simply outlining a hyaline structure surrounding the esophageal enlargement. In other drawings the spiral arrangement of the muscle bands comprising the sheath was shown. In all illustrations showing the spiral the direction of the twisting was dextral except for *Swangeria fragilis* Thorne, 1939; in this species the spiral was sinistral.

Since 1939 the most extended papers published on belondirids, in which many species were described, are those by Williams (12), Heyns (3), Jairajpuri (6), Thorne (11), Siddiqi (8, 9), Husain and Khan (5), and Baqri and Jairajpuri (1). Jairajpuri (6) consistently illustrated the sheath in outline only, without showing the muscle band pattern. He did not mention the sheath in the description of every species, but when he did, he always stated that the muscles were spiral. Williams (12) did not mention the sheath at all in the text, and he illustrated it in outline only, without showing the spiral pattern. Heyns (3) describing four species of *Dorylaimellus,* illustrated a dextral spiral for each species and, in the descriptions, he usually stated that the basal esophageal enlargement was surrounded by "the usual spiral sheath." Siddiqi (8) illustrated *Belondira ujjanica* Siddiqi, 1966 and *Oxydirus gangeticus* Siddiqi, 1966 with a dextral spiral but did not show the pattern of the spiral for the other species described in the same paper. Thorne (11) did not mention the sheath in descriptions of the individual species, but he implied in the introductory material that a spiral sheath was present in all the belondirid species described. In this paper five species were illustrated with a dextral spiral; in the other illustrations the muscle band pattern was not shown. Baqri and Jairajpuri (1) illustrated the sheath with a dextral spiral for several species, but they did not mention it in the text. Siddiqi (9)

Received for publication 3 October 1968.

[1] Crops Protection Research Branch, Crops Research Division, Agricultural Research Service, U. S. Department of Agriculture, Beltsville, Maryland 20705.

referred to the sheath of spiral muscles several times in his text and illustrated the sheath of *Falcihasta palustris* Clark, 1964 with both a dextral and sinistral spiral. Jairajpuri (7) illustrated the sheath of *Qudsiella gracilis* Jairajpuri, 1966 with a sinistral spiral.

Hopper (4), in his description of *Swangeria bisexualis* Hopper, 1961, did not illustrate the esophagus. He wrote in the description: "Enlarged portion . . . surrounded by sheath of six conspicuous spiral muscles." The direction of the spiral was not given. In what is apparently the only report of observations on the sheath in live nematodes, he mentioned that the length of the esophageal expansion decreases and increases with contraction and relaxation of the muscle bands.

In other descriptions of belondirid species scattered through the literature, either the sheath was shown with a dextral spiral, or the muscle band pattern was not indicated.

MATERIALS AND METHODS

The species used in this investigation and their sources were: *Axonchium amplicolle* Cobb, 1920; *A. choristum* Thorne, 1939; *A. crassum* Thorne, 1939; *A. gigas* Thorne, 1939; *A. micans* Thorne, 1939; *A. serpens* Thorne, 1939; *A. solitare* Thorne, 1939; *Dorylaimellus aequalis; D. parvulus* Thorne, 1939; *D. tenuidens* Thorne, 1939; and *Oxydirus oxycephaloides* (de Man, 1921) Thorne, 1939 from the Gerald Thorne Collection of the USDA Nematode Collection, Beltsville, Maryland. Paratypes of *Swangeria bisexualis* were loaned by D. J. Raski; paratypes of *Axonchium rotundum* Thorne, 1964 and specimens of *A. amplicolle* were loaned by A. J. Ayala; specimens of *Oxydirus gigus* Jairajpuri, 1964 were sent from India by J. J. s'Jacob; and specimens of *Oxydirus gangeticus* were collected from turf along a roadside ditch at the USDA Plant Industry Station, Beltsville, Maryland.

Specimens of *O. gangeticus* were fixed in formalin, some of them were stained in chrome alum-gallocyanin, and they were processed to glycerine by Baker's rapid method. The other species were received in glycerine. For species of which an abundance of material was available, cross sections were cut through the esophageal region and mounted in glycerine jelly. Drawings of cross sections and of the entire esophageal expansion were made with the aid of a camera lucida.

RESULTS

The esophageal sheath in belondirid nematodes consisted of a number of muscle bands, many of which extended the entire length of the enlarged basal portion of the esophagus (Fig. 1A, J. L). Others arose at either end of the esophageal expansion and ended by tapering gradually to a point near the middle of the expansion (Fig. 1B). Many arose a short distance from either end. The bands tapered and disappeared at the anterior end of the esophageal expansion, and were not visible around the anterior part of the esophagus. Although the esophagus was surrounded by lobes of presumably nerve tissue anterior to the junction of the two portions of the esophagus, and sometimes overlapping it (Fig. 1A, B), this tissue was distinctly different from the sheath and could not be confused with it in cross sections (Fig. 1I).

In cross sections of nematodes fixed in formalin and processed to glycerine, the bundles appeared hyaline or finely granular with several round to elongate globular areas within them (Fig. 1C, D, E, F, G). These globular areas resembled the sarcoplasmic areas of the somatic muscles. In *Oxydirus gangeticus* the globular areas of the sheath and the sarcoplasmic areas of the somatic muscles stained heavily with gallocyanin, whereas the surrounding areas of both struc-

tures did not. It was not determined whether the globular areas extended the entire length of the muscle bands, although, over the distance they were traced no discontinuity was found. In some species with no spiral they could be traced for about ¼ the length of the expansion. In *O. gangeticus* (Fig. 1M) several oval bodies, which stained heavily with gallocyanin, were seen within thickenings in the sheath at the base of the esophageal expansion. They were fewer in number than the muscle bands. These were also detected in a few specimens of some of the species not stained with gallocyanin. In *O. gigus* a few were seen near the middle of the esophageal expansion. In this species it was possible to see the alternating dense and less dense myofilaments in both the somatic muscles and the sheath.

In cross sections of several species individual muscle bands in the same specimen were often quite variable in size (Fig. 1E, F, G). A few more bands were present near the middle of the esophageal expansion than at either end. In *Axonchium choristum, A. crassum, A. micans,* and *A. solitare* 9 bands were found at the cardia and at the esophageal constriction. Only one specimen of each *Axonchium* was sectioned. In *A. gigas* there were 8 bands at the constriction, 9 at the cardia, and 11 about ⅓ the length of the expansion from its anterior end (Fig. 1E). At the middle of the expansion there were 13 bands in *A. choristum,* 11 in *A. micans,* and 12 in the other species of *Axonchium.* In two specimens of *Oxydirus gigus* cut near the middle of the expansion there were 7 bands in one and 8 in the other. One specimen of *O. oxycephaloides* had 7 bands, another 9. In *O. gangeticus* one specimen had 11, the other 12 bands near the middle of the esophageal expansion. No cross sections were made of specimens of *Dorylaimellus.*

In *Axonchium gigas* the muscle bands comprising the sheath spiraled dextrally around the esophageal expansion in its posterior two-thirds; anteriorly they did not spiral but lay parallel to the longitudinal axis of the esophagus (Fig. 1B). In one specimen those bands which extended the entire length of the esophageal expansion encircled it 2½ times. In cross sections, the individual bands of the spiral portion shifted in position around the periphery of the esophagus when the microscope focus was changed; in cross sections of the anterior portion, where the muscle bands did not spiral, there was no shift in the position of the muscle bands with a change in focus. In *A. solitare* the bands did not spiral at all, but lay parallel to the esophagus throughout their length (Fig. 1A). In sections of this species cut at various levels of the esophageal expansion the position of the muscle bands did not change as the focal plane changes. In the other species of *Axonchium* examined, only straight, non-spiral muscle bands were observed in the sheath, similar to those of *A. solitare.* Thus *A. gigas* was the only species of *Axonchium* examined in which the sheath was spiral.

In *Oxydirus gigus* (Fig. 1C) the bands, as shown in transverse sections, were

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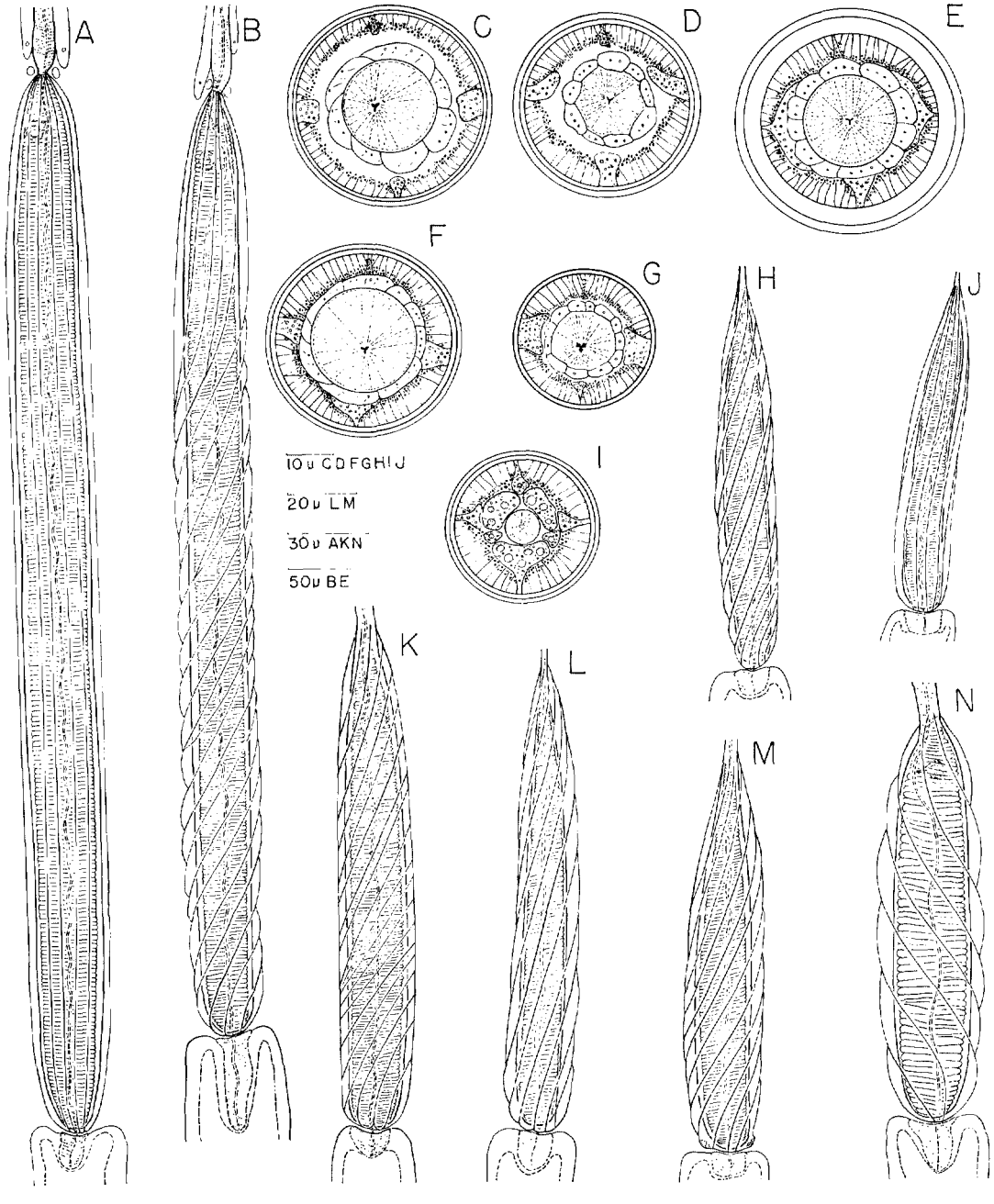
FIG. 1. A. *Axonchium solitare,* esophageal expansion; B. *Axonchium gigas,* esophageal expansion; C. *Oxydirus gigus* cross section, esophageal expansion; D. *Axonchium solitare,* cross section, esophageal expansion; E. *Axonchium gigas,* cross section, esophageal expansion; F. *Oxydirus oxycephaloides,* cross section, esophageal expansion; G. *Oxydirus gangeticus,* cross section, esophageal expansion; H. *Dorylaimellus parvulus,* esophageal expansion; I. *Axonchium solitare,* cross section just posterior to nerve ring; J. *Dorylaimellus aequalis,* esophageal expansion; K. *Oxydirus oxycephaloides,* esophageal expansion; L. *Dorylaimellus tenuidens,* esophageal expansion; M. *Oxydirus gangeticus,* esophageal expansion; N. *Oxydirus gigus,* esophageal expansion.



quite thick and slightly overlapping. The spiral pattern, which was sinistral, extended throughout the length of the esophageal expansion (Fig. 1N). In *O. oxycephaloides* and *O. gangeticus* the spiral also extended throughout the length of the esophageal expansion, but it was dextral (Fig. 1K, M). In all three species of *Oxydirus* most of the

bands appeared to encircle the esophagus at least once.

In the species of *Dorylaimellus* examined a dextral spiral pattern occurred, extending throughout the length of the esophageal expansion. The amount of twisting is variable: in *D. parvulus* each band appeared to encircle the esophagus once (Fig. 1H); in *D. tenuidens* there was less twisting, each band passing around ½ to ¾ the circumference (Fig. 1L); and in *D. aequalis* the twisting was 180 degrees or less (Fig. 1J).

In paratypes of *Swangeria bisexualis* the spiral was sinistral.

Discussion

Most authors have assumed that the belondirid esophageal sheath is composed of muscular tissue. The observations of Hopper (4) support this assumption. It is also supported by the similar staining characteristics of the sheath and the somatic musculature and by the presence of myofilaments in the sheath. Possibly each band comprises a single muscle cell, and the dark staining ovals at the base of the esophageal expansion in *O. gangeticus* may be nuclei.

Yeates (13) expressed doubt of the existence of the esophageal sheath in any nematode species after he failed to find a sheath in cross sections of the esophageal expansion of *Dorylaimellus tahatikus* Yeates, 1967. He suggested that the spiral appearance was the result of the twisting of the anterior part of the body, a characteristic which is common to many belondirid species. Siddiqi (9) has shown the existence of the belondirid sheath in cross sections and has transferred Yeates' species to *Tylencholaimus* De Man, 1876. In several specimens studied here, part of the body was twisted in such a way that the vulva appeared in lateral view and the amphids were seen in dorso-ventral view. This resulted from, at most, a 90-degree twist. However, in *Axonchium gigas* some of the muscle bands of the sheath encircled the esophagus two and one half times, ten times the quarter turn produced by the twisting of the body. The sheath spiral, therefore, could not result from twisting of the body alone, offering additional evidence that the sheath is not an artifact.

Among the species studied here the arrangement of the muscle bands which comprise the sheath varies from species to species, both in the direction and the extent of the spiral. *Axonchium gigas,* with a spiral sheath, differs from the other species of *Axonchium* in which the muscle bands are straight. *Oxydirus gigus* differs from the other two species of *Oxydirus* in having a sinistrally spiral sheath. In the three species of *Dorylaimellus* the amount of twisting was different. Perhaps the very small amount of twisting in *D. aequalis* was the result of the extremely short esophageal expansion. In contrast, in *Swangeria gracilis, S. bisexualis,* and *Qudsiella gracilis,* all placed in the same family by Siddiqi (9), the sheath is sinistral in all three species.

The variability in the sheath shown here for the genera *Axonchium, Oxydirus,* and *Dorylaimellus* may occur in other belondirid genera. This variability may be useful for the taxonomic separation of species, and it is unfortunate that this detail has been disregarded in many descriptions of belondirids. Siddiqi (9) gave two drawings of the sheath of *Falcihasta palustris,* one with a dextral and one with a sinistral spiral. This is the only indication noted from the literature that the structure of the sheath is not consistent for all specimens within a species. Careful observation of large numbers of specimens may expose other examples of variability within a species. Perhaps many belondirids in other genera than *Axonchium* have a sheath similar to that of *A. solitare,* with the

muscle bands parallel to the esophagus; in drawings of many of those species in which the sheath was illustrated in outline only, it is possible that the spiral may not have been indicated because there was none present. In specimens with a non-spiral sheath, it is difficult to distinguish between the sheath muscle bands and the somatic muscles. The details of the sheath show best under the lateral chord. The non-spiral nature of the sheath is best demonstrated in cross sections; the shifting position of the muscle bands around the esophagus with a change in focus will not occur if the sheath is not spiral.

BELONDIROIDEA THORNE, 1964 AND *AXONCHIUM* COBB, 1920 EMENDED

The definition of the superfamily Belondiroidea Thorne, 1964 includes the statement: "Basal portion of esophagus surrounded by a thick sheath of spiral muscles" (11). On the basis of information given here it is appropriate to emend this statement to read: Esophageal expansion surrounded by a sheath of muscle bands which may lie parallel to the esophagus, spiral completely around it in a dextral or sinistral direction, or spiral slightly without completely encircling the esophagus.

The definition of *Axonchium* Cobb, 1920 should be emended to include species with both a spiral and a non-spiral sheath.

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