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THE TAPEWORMS OF THE RHINOCEROSES, A STUDY BASED ON MATERIAL FROM THE BELGIAN CONGO¹

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During the course of my study on the parasitic worms collected by the Lang-Chapin expedition of the American Museum to the Belgian Congo, I have had the good fortune to examine abundant material of *Plagiotænia gigantea* (Peters). This interesting species, the first reported from the rhinoceros, has been confused with other cestodes from rhinoceros hosts, has been assigned to no less than three different genera in addition to the genus *Tænia*, to which it was originally referred, and has been the source of much discussion and difference of opinion during the past seventy years. A review of the literature on the tapeworms of rhinoceroses shows that *Plagiotænia gigantea* is very imperfectly known, that many of the descriptions are brief and indefinite, and that the whole question of the rhinoceros cestodes is clouded in uncertainty and confusion. For that reason a more complete description of the original species is especially desirable. Such information aids materially in the elucidation of the difficult problem concerning the specificity and relationships of the rhinoceros tapeworms.

The largest cestodes in the Congo Collection were those from the white rhinoceros, *Cerathotherium simum cottoni*. This material consisted of several hundred specimens which agree so completely with Peters' (1856) description of *Plagiotænia gigantea* from *Rhinoceros africanus* (*Diceros bicornis*) that I assign them to that species.

Plagiotænia gigantea (Peters)

The larger specimens measure up to 120 mm. in length, 20 mm. in width, and 3 mm. in thickness. None of these larger specimens are complete and the terminal segments detach so easily that they must be handled with extreme care. The ripe proglottids (Fig. 1) are from 1-2 mm. in length, with the genital pores on the dextral side. These large proglottids are really little more than egg capsules congested with enormous masses of embryos. In such specimens the width of the strobila increases

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more or less rapidly from the anterior end for the first 50–60 mm., after which it may continue at about the same width or sometimes become narrower. Frequently the terminal segments are sterile. Among the specimens there are a large number, the posterior segments of which (Fig. 2) are sterile, shriveled and wrinkled. Many others are completely sterile, the entire chain of proglottids consisting of these shrunk segments. In others the terminal proglottids are gravid, while those nearer the scolex are sterile, or contain a few scattered and degenerate remnants of the reproductive organs. This condition gives rise to peculiar sizes and shapes, similar to those figured by Southwell (1921) for *Anoplocephala vulgaris*.

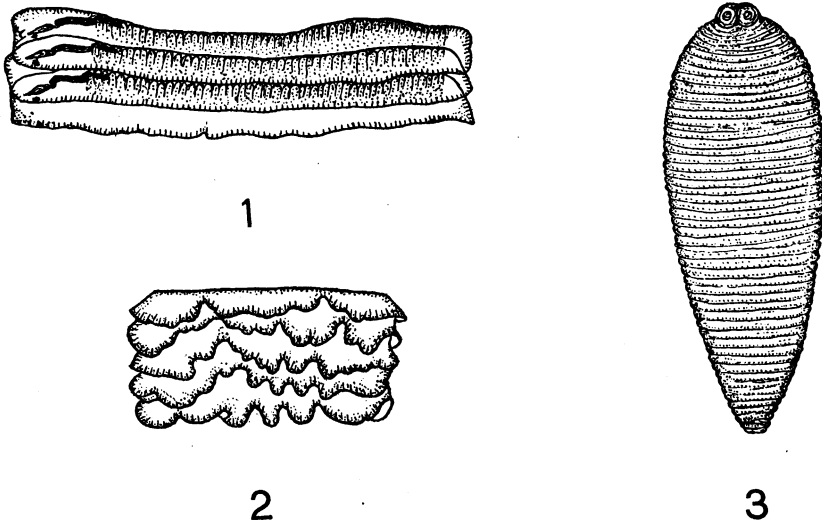


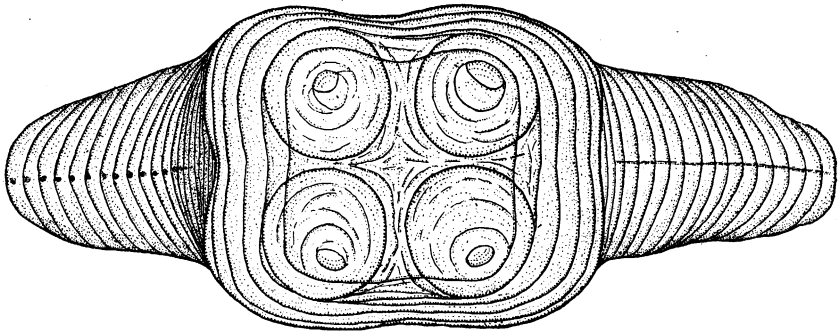
Fig. 1.—Mature gravid proglottids, $\times 3$.

" 2.—Sterile proglottids, $\times 3$.

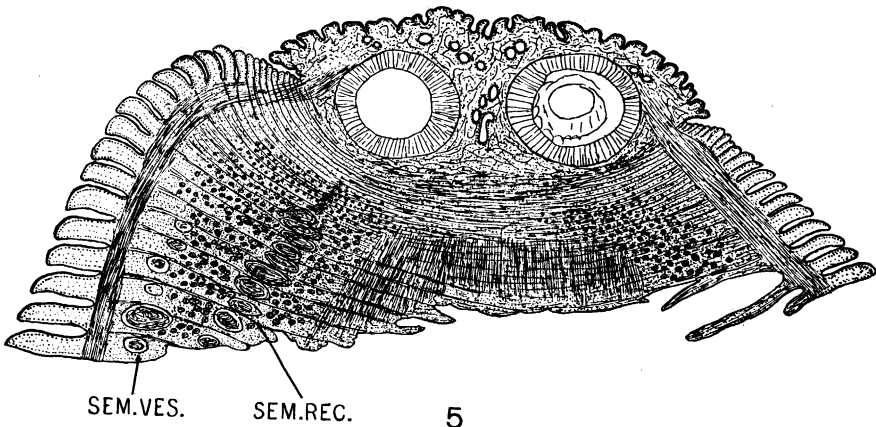
" 3.—Young specimen—entirely sterile, $\times 3$.

In the collection I found only two complete specimens of *Plagiotænia gigantea*, both small. One had 53, the other 48 proglottids. The worms widen rapidly near the head, attaining a maximum width at the level of the anterior third of the body, and taper gradually to the posterior end. They measure 20 mm. in length, 6.5 mm. in greatest width, and 2 mm. in thickness. No reproductive organs or genital pores are present in either of the specimens. One of them is shown in Fig. 3; the other was cut in longitudinal sections. In the medullary portion of the segments one can occasionally see clusters of nuclei that resemble incipient or early stages of testes, but they seem to undergo regressive changes and do not proceed to the development of functional organs. This same condition is present regularly in sterile proglottids of older and larger specimens. Since in the fertile segments the reproductive organs are in a functional condition for only a brief space of time, it has not been easy to find a complete set of stages representing the development and maturity of the male and female organs. It would appear that the first-formed segments are sterile, that after a time

fertile segments are produced, and that later the reproductive capacity is exhausted and only sterile proglottids are formed. The reproductive cycle seems to develop gradually, rising to a height during which enormous numbers of eggs are produced, and then gradually declining to complete sterility again. Maurice C. Hall (1922, Journ. Parasit., IX, p. 35) in a paper read before the Helminthological Society of



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Fig. 4.—Terminal view of scolex, $\times 10$.

" 5.—Frontal section showing genitalia, $\times 16\frac{1}{2}$.

Washington, D. C., reported two entire and one incomplete specimens of an anoplocephaline tapeworm from the goat at Antigua, British West Indies, in which the reproductive organs were either rudimentary or entirely lacking. Another anoplocephaline tapeworm, similarly agamous, he reported from the pig at Antigua. Douthitt (1915) reported that in most of his material of *Andrya translucida* from *Geomys bursarius* the terminal segments were sterile. Commenting on this condition he stated, p. 15: "To find the end proglottid, or even several of the terminal proglottids

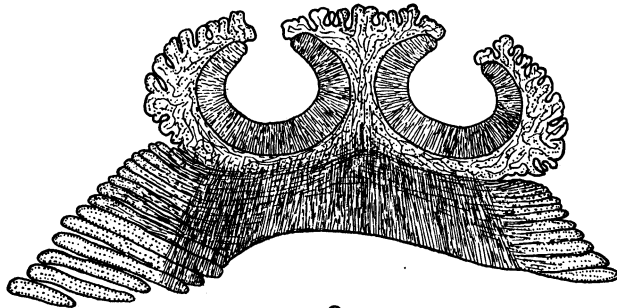
sterile would not be surprising; but to find nearly a hundred such in individuals that have already shed some of their proglottids is certainly not to be expected. Such a condition could of course arise as a mutant, . . . A more probable explanation seems to be that the gopher is not the normal host and that sterility has resulted from unnatural conditions of environment." As an explanation of the sterile specimens reported by him, Hall also would advocate development in an unusual host. Deiner (1912) in the study of tapeworms from the Indian rhinoceros observed, p. 5: "Mehrfach finden sich eingeschobene unvollständige Glieder, die nur die Hälfte oder noch weniger der gewöhnlichen Breite erreicht haben." It appears that the formation of defective and sterile segments is not an unusual or infrequent phenomenon among the anoplocephaline tapeworms. The conclusions of Douthitt and Hall are based on the examination of a very few specimens and on analogies drawn from other parasitic forms. Such an explanation seems hardly applicable to the case of the rhinoceros tapeworms. These instances are not concerned with a few isolated worms, but with a heavy infestation—hundreds of specimens in the present case and a very large number in that studied by Deiner. I am inclined, therefore, to the belief that this tapeworm is a usual parasite of the rhinoceros and the explanation presented earlier appears not only to be in entire agreement with the facts, but to fit them adequately.

A terminal view of the head end is given in Fig. 4. The scolex is large, measuring from 3–6 mm. in width, and 3–4 mm. in depth in these preserved specimens. In the living worm it is undoubtedly mobile and able to change the shape accordingly. It is short, from one-third to one-half the width, and not well set off from the strobila. In contracted specimens the scolex may be so retracted that its anterior face does not project beyond the proglottids. Fig. 5 shows the usual condition; Fig. 6 is from the most prominent and best extended scolex. No neck is present and the segmental folds extend forward covering most of the scolex (Fig. 4). The suckers usually open almost directly forward; occasionally they are directed somewhat dorsad and ventrad. They are thick-walled cups measuring from 1.2–1.5 mm. in diameter. Their walls measure from 0.2–0.3 mm. in thickness. Between the suckers and over the apical region there are many shallow grooves. There is no rostellum or apical organ. The scolex contains of course its own musculature, the coiled tubular complex of the excretory system, and the chief ganglionic center of the nervous system, but the details of these structures can be determined with certainty only by time-consuming reconstructions which so far I have not been able to make.

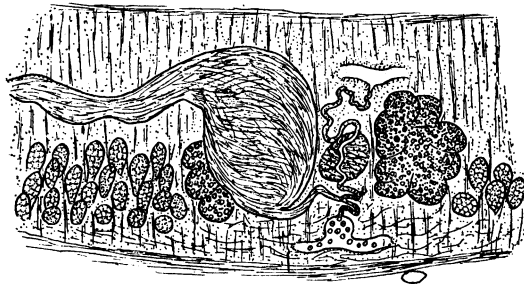
The strobila is so thick that very little can be distinguished in whole mounts and any adequate study must depend on serial sections. The first proglottids are very short and they increase slightly in length as development proceeds. The increase in length is relatively proportional to the increase in width. The posterior margin of each proglottid overlaps the succeeding one for about one-half of its length (Fig. 1), forming a tile- or shingle-like arrangement.

The musculature of the worm (Fig. 9) is strongly developed. In the proglottids there are a large number of parenchymatous fibers that extend from the dorsal to the ventral surfaces, passing through the longitudinal and transverse muscle sheets that surround the medullary zone. Similar fibers parallel the surface of the proglottid in the cortical zone passing from one side to the other. Immediately under the cuticula there is a thin sheet of longitudinal muscles and below this a layer of subcuticular matrix cells. The longitudinal muscles which form the outer portion of the sheet separating the cortical and medullary zones are frequently divided into outer and inner layers and

occasionally the outer layer may be resolved into two sheets. Fibers of the transverse muscle layers cross to the opposite side at the lateral ends of the proglottid and are inserted on the basement membrane in that region, except around the cirrus sac, where they are either inserted on the sac or, together with fibers from the sac, are reflected away from the pore, turning outward at the end of the segment to be inserted on the basement membrane of the same side. The longitudinal fibers extend through the worm and enter the scolex to form an integral part of the musculature of that organ. In the scolex there is a strong bundle of fibers near the center of the apical



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Fig. 6.—Frontal section, $\times 18$.

“ 7.—Reconstruction of female genital complex from cross sections, $\times 37\frac{1}{2}$.

side, immediately in front of the brain commissure, but it does not form a rostellar organ. It may however be the basis for the statement in Peters' description, “rostello breve rotundato conico.”

The excretory system consists of the complex of coiled tubules in the scolex and two longitudinal canals that extend posteriad from it, one on either side. In one set of sections a smaller, more lateral canal emerges from the scolex on either side but it soon disappears while the median canal extends through the strobila. It lies in the medullary zone on the median side of the large lateral nerve bundle. At the anterior

margin of the proglottid this nerve is about midway between the excretory canal and the lateral wall of the segment. On either side the excretory canal follows an undulatory course in a dorsoventral plane extending from one side of the segment to the other. On the poral side the longitudinal excretory canal lies ventral and slightly median to the inner end of the cirrus sac. These canals receive numerous secondary branches which subdivide into tertiary tubules, but whether they anastomose to form a network I am not at all certain. In each segment there is one principal lateral branch and one tubule which connects the two longitudinal lateral canals. This connecting duct lies slightly on the dorsal side of the segment, dorsal but adjacent to the primary transverse uterine tubule. Smaller excretory tubules discharge into this main transverse canal. The lateral longitudinal canals have strong walls of annular fibers and are surrounded by a large number of small nuclei. The muscular coat is lacking in the smaller ducts.

The nervous system is of the usual cestode type. The bilobed ganglion in the scolex is situated in the region between and in front of the suckers. Nerves pass from it to supply the organs of the scolex and the usual ten longitudinal nerves extend backward through the strobila. The two lateral nerves are very large, situated in the medullary layer about midway between the longitudinal excretory canals and the anterior lateral margins of the proglottids. Each of these lateral nerves is accompanied by a pair of smaller nerves, one dorsal and the other ventral and both a trifle lateral to the large trunk. They lie between the longitudinal and transverse muscles. Another pair of longitudinal nerves extends between these muscle sheets, one dorsal and the other ventral to the vitelline gland (Fig. 7). The other pair are in a corresponding position on the aporal side of the proglottid. Deiner (1912) described the commissures connecting these longitudinal nerves and the branches that supply the parts of the proglottid in the tapeworms from the Indian rhinoceros. I have not used neurological technique to demonstrate these structures and have not been able to trace them in my material. Presumably there is no important difference.

Study of the reproductive organs has proved difficult because of the agamous condition already discussed. It is not easy to tell from superficial examination whether the younger segments of a specimen are fertile or not, and I have sectioned several only to find that the proglottids are almost, if not entirely, sterile. In fertile specimens the functionally active organs are situated near the scolex in segments 12 to 50. Later the development of the uterus and its contained embryos is accompanied by a rapid reduction of the male and female organs which are soon obliterated. As previously stated, there is no neck and the earliest proglottids form at the base of the head. They may be recognized, however, by their edges, which project slightly at the lateral margins of the strobila. In these earliest proglottids the parenchyma is relatively undifferentiated, containing large numbers of small similar nuclei. In segment 10 on the right side of the median plane a transverse tubular enlargement appears which later develops into the seminal receptacle. In segment 12 its width may for a short distance equal one-half of the length of the segment but it should of course be remembered that these proglottids are very short. In segment 14 the receptacle contains spermatozoa and by segment 16 (Fig. 5) it is gorged with masses of sperm. In segment 10 certain of the nuclei begin to accumulate in small groups forming a transverse row and in segment 12 they are definitely recognizable as incipient testes. At this stage the seminal vesicle is a tubular structure and in segment 18 it begins to be filled with spermatozoa. In segment 22 the male reproductive organs are complete and functional.

The testicular follicles occupy almost the entire width of the proglottid, extending laterally on either side as far as the excretory canal. They lie in both anterior and posterior regions of the segment and both dorsal and ventral to the uterine cleft. In the younger segments the follicles measure 0.02 to 0.025 mm. in diameter and in older segments they increase to three times this size. They are spherical to oval to irregular in shape. Usually a space is present between the cells and the wall of the follicle, although this may be due to poor fixation. It is not easy to count the testes but frequently they number more than a hundred in each segment. The vasa deferentia are small tubules opening into a larger deeply staining vas deferens which extends transversely across the proglottid. The distribution of the follicles is somewhat irregular although frequently they are massed around the seminal vesicle and in general they are more numerous on the poral side of the proglottid. The terminal portion of the vas deferens is usually slightly coiled; about midway between the seminal receptacle and the dextral wall of the proglottid it suddenly enlarges to form the vesicula seminalis. The vesicle is coiled and its form and position vary with its development and with the protrusion and retraction of the cirrus sac. In general, after its origin from the vas deferens it expands ventrally and laterally, then turns dorsally and medially, then anteriorly, dorsad and laterad, then mediad, posteriad and ventrad to open into a thick-walled tube which follows an almost straight course to the cirrus sac. The cirrus sac is an oval structure which measures from 0.75 to 1.1 mm. in length and from 0.087 to 0.34 mm. in diameter. The seminal vesicle and cirrus sac persist in the oldest segments. The sac has strong muscular walls consisting of an outer longitudinal and an inner circular layer. Protractor and retractor muscles extend from the sac to the body wall and retractors to the transverse muscles of the proglottid. The ejaculatory duct which traverses the sac has an expanded vesicular portion for the first third or fourth of its length, then a narrow tubular portion surrounded by loose alveolar parenchyma, while the terminal third is coiled and is surrounded by cells that appear to be secretory. The duct has its own circular and longitudinal muscles. The cirrus is covered with very small spines or spicules. It has not been observed in the extruded condition and the measurements given are for the structures in the retracted state.

The vagina is on the ventral side of the cirrus sac and opens into the genital atrium immediately behind and below the opening of the cirrus sac (Fig. 8). It is obliterated after segment 24, and its former position is not easily recognized in later segments. At this level it can be traced by the rows of nuclei that lie in the parenchyma along its course. The ovary consists of a large number of clavate acini extending dorsally from a ventral transverse base. In segments 20-22 it appears as clusters of small follicles situated on the poral side near the ventral surface of the medullary portion of the proglottid. In the succeeding segments the female organs reach the height of their development and then undergo regression as the uterus develops and becomes filled with embryos. The ovarian follicles extend on the poral side to the field of the seminal vesicle but in no case do they extend mediad to the center of the proglottid. In the earlier segments they are small but in segments 40-50 they may extend almost halfway to the dorsal wall of the medullary portion of the proglottid. They are divided into two groups by the development of the vitellaria and oötype structures. The vitelline gland consists of two wings, which become confluent posteriorly. It is ventral in position, near but not touching the ventral musculature of the proglottid. Between the two wings and in front of the midportion the oviduct arises from the ovary. First

there is an expanded spherical portion, usually containing many cells (Fig. 7) from which a small funnel-shaped duct leads dorsally. It coils posteriad and ventrad and on turning antieriad and dorsad receives the short coiled sperm duct from the seminal receptacle. It then receives the short duct from the vitellaria and passes dorsally through the shell gland. After a somewhat winding course it opens into the

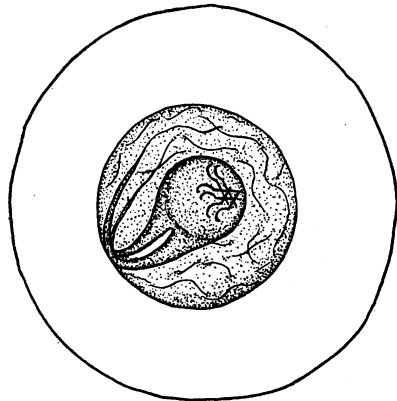
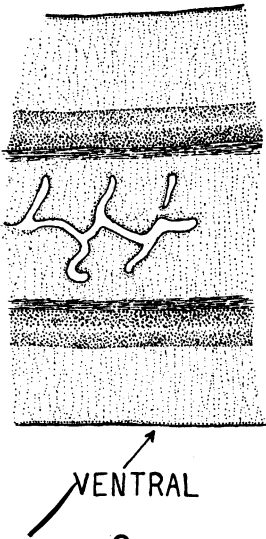
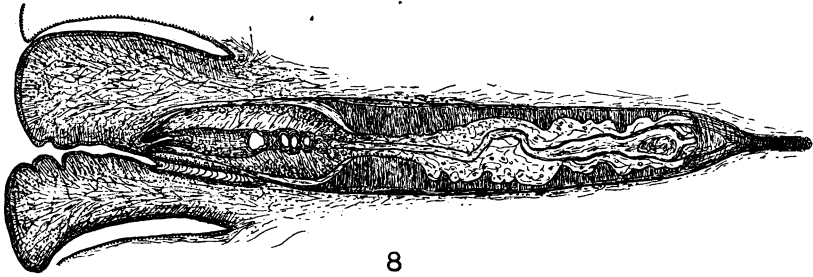


Fig. 8.—Frontal section through cirrus sac and genital pore from proglottid, No. 19, $\times 80$.

" 9.—Portion of a cross section showing musculature and formation of uterus, $\times 22\frac{1}{2}$.

" 10.—Egg with contained embryo, $\times 720$.

uterus. The oötype structures are slightly more than one-fourth of the width of the proglottid from the poral margin. They lie between the dorsal and ventral submedian nerve trunks of that side. The seminal receptacle consists of two portions. Medially there is a large oval sac which extends dorsoventrally. From its ventral end the spermatic duct leads to the oötype. Dorsally it is continuous with a large saccate

duct that passes toward the pore side, dorsal to the seminal vesicle. Here it disappears but in earlier segments it can be traced ventrally behind the cirrus sac where it is continuous with the vagina. The uterus first appears in proglottids 12-14 as a line of cells extending horizontally across the segment near its center. By segment 50 the lumen is conspicuous and is a tube with an undulating course extending from one nerve trunk to the other. At each dorsal and ventral angle in its course a short dorso-ventral evagination (Fig. 9) is formed and frequently between the regular outpocketings others appear. As the segments grow older the uterus becomes more and more filled with embryos until finally the proglottid is little more than an egg capsule. Anteriorly there are sac-like pockets separated by fibrous parenchymatous partitions but posteriorly these structures open into and are continuous with the main transverse canal. The cells are massed in the ovarian follicles and consequently are irregular in shape. They are not properly fixed for cytological study. The ova in the expanded portion of the oviduct at its origin from the transverse ovarian canal are slightly larger than those in the follicles and measure from 0.017 to 0.02 mm. in diameter. They have a clear cortical zone and contain masses of deeply staining material. In early stages in the uterus they are similar except that the clear cortical area has disappeared. In ripe proglottids the eggs are 0.067 to 0.075 mm. in diameter. The embryo measures from 0.015 to 0.016 mm. in diameter and is provided with a well-developed pyriform apparatus (Fig. 10.)

DISCUSSION

Cestodes have been known from the rhinoceros for a long time, yet the number of species, the details of their structure, their relationships and systematic position remain uncertain. The first record is that of Peters (1856), who found the worms in the intestine of an African rhinoceros which died in the zoölogical gardens of Berlin. His description is as follows:

Tænia gigantea n. sp. Caput magnum, latum, globosum, quadrilobum, rostello brevi rotundato conico, bothridiis crassis, margine postico libero; collum subnullum; corpus crassum lanceolatum; articuli brevissimi et latissimi, marginibus postice excisis, angulis obtusis; aperturæ genitales marginales secundæ; penes filiformes, limbo globoso cincti. Long. tota 0.12 m.; art. max. 0.003; lat. max. 0.027-0.029; lat. cap. 0.006; colli, 0.005. Hab: *Rhinoceros africanus*, Camper; in intestino tenui. —(Mossambique).

Murie (1870) described as belonging to a new species certain proglottids from an Indian rhinoceros that died in the zoölogical gardens of London. His description reads:

Tænia magna n. sp. Segments of body pale colored, unequal in size and large; flat, relatively thick, broader than long, and transversely ribbed or banded. The larger segments measure fully $1\frac{1}{2}$ inches broad and 1 inch long; the smaller segments have a diameter of an inch lengthwise and across; the latter with lateral convex margins, and concave attached surfaces; other pieces are cubical in outline, some parallelopiped, but the larger chiefly subquadrate. The free borders of the bands are wavy, at some points verging toward subcrenation. Here and there a band presents a

partial fold on itself; the outer recurved margins of the one band partially overlap that behind, giving a somewhat lateral serrate character to each segment. Genital outlet apparently on each band, and opening at the lateral border (?). Head and neck not known. Body supposed to increase from before backward to the middle, or beyond, and thence to diminish. Habitat: Intestines of *Rhinoceros indicus*.

Peters (1871) repeated his earlier description and gave figures of the scolex and anterior end of the worm. He commented on the obvious error of Murie in regarding portions of the strobila as single proglottids and concluded that the segments described by Murie belonged to the species he had described from the African rhinoceros. That species, described as *Tænia gigantea*, he named type of a new genus, *Plagiotænia*.

Garrod (1877) described a cestode from the Javanese rhinoceros, *Rhinoceros sondaicus*, which he regarded the same as those described by Peters and Murie and which he called *Plagiotænia gigantea*.

Blanchard (1891) considered the cestodes from the different rhinoceroses as representatives of a single species. He suppressed the generic name *Plagiotænia* and transferred the species *gigantea* to the genus *Anoplocephala*.

Deiner (1912) reproduced the figures of Murie, Peters, and Garrod, and called attention to the disagreement between the tapeworms from the three different species of rhinoceros. He made a careful study of the cestode from the Indian form, first described by Murie 1870, and, since the specific name *magna* proposed by Murie was preoccupied by *Anoplocephala magna* Abildgaard 1789, Deiner renamed the species *Anoplocephala latissima*.

MacCallum and MacCallum (1912) described segments of the cestode from the Javanese rhinoceros (*Rhinoceros sondaicus*), which they ascribed to the species *Tænia gigantea* Peters. The worm was about 20 feet in length and apparently all the segments so mature that the vagina was not visible. These authors did not have the head of the specimen. Their description is consequently incomplete and in certain particulars it is incorrect, as they evidently confused the ovary with the vitellaria and the cirrus sac with the seminal vesicle.

Douthitt (1915) recognized the specific distinctness of *Tænia gigantea* Peters and *Anoplocephala latissima*, but the description of *Tænia gigantea* used by Douthitt in this determination was that of MacCallum and MacCallum (1912) of the cestode from the Javanese rhinoceros and not that of Peters based upon the African form. Both of these species he transferred to the genus *Schizotænia*.

Southwell (1921) described a cestode from the African rhinoceros, *Rhinoceros bicornis* (*Diceros bicornis*) as a new species, *Anoplocephala*

vulgaris. He made no adequate comparison of his material with the description of Peters but accepted and used the description of MacCallum and MacCallum as valid for *Tænia gigantea*. In an attempt to justify this procedure he stated: "To avoid confusion, it appears to be best to associate the name *Anoplocephala gigantea* with the worms described in detail by the MacCallums." The description and measurements given clearly distinguish his specimens from the Javanese species described by MacCallum and MacCallum. Consequently he designated his material as belonging to a new species, although he said, p. 363: "It should be noted that the worm with which we are dealing conforms, as regards size, much more closely to Peters' worm than to the MacCallums." In a subsequent paper (1922) Southwell reported a single specimen from *Rhinoceros sondaicus* in the collection of the Indian Museum. Date and locality were not available. Concerning the specimen he said: "From a superficial examination of this worm in 1916, I was led to the opinion that it probably belonged to the genus *Thysanosoma*. A more careful examination of the anatomy has, however, left no doubt that it is an *Anoplocephala*, identical with the species *vulgaris*."

A critical survey of this literature will do much to elucidate the problems relative to the cestodes of the rhinoceros. Deiner (1912) clearly distinguished between the previously known cestodes of the Indian and African rhinoceroses and established *Anoplocephala latissima* from the Indian host as a distinct species. He pointed out also that the scolex of the cestode described by Garrod from the Javanese rhinoceros differs markedly both in form and size of suckers from that of either the Indian or African species. It seems very probable that MacCallum and MacCallum were dealing with the same species as Garrod, since both were from the same host and manifest much morphological similarity. Garrod noted the difference between the scolices of his specimens and those of the African form figured by Peters which led him to publish figures of his material. He reports that detached groups of proglottids were quite indistinguishable from those of the Indian species figured by Dr. Murie, but this is not surprising as in various regions of the strobila one would find proglottids of corresponding sizes, and differences in shape would naturally not be distinguishable. One very important observation appears to have been overlooked by later writers. According to Garrod, ten centimeters from the scolex the proglottids are 1.42 cm. in breadth, and in the previous sentence he reports segments more than twice as broad. Therefore, the strobila must have been very much longer than

10 cm. and probably many times as long. In the description of *Tænia gigantea*, Peters gives 12 cm. as the greatest length and in that of *Anoplocephala latissima* Deiner gives 10 cm. as the greatest length. In both of these species the tendency for the proglottids to separate as they grow older is so marked that it would be practically impossible for them to reach the length of Garrod's specimens. Only in the specimen described by MacCallum and MacCallum from the same host, *Rhinoceros sondaicus*, do we find a strobila of such great length and this agreement constitutes strong evidence that MacCallum and MacCallum were dealing with the same species as Garrod. At any rate, it appears quite certain that the MacCallums did not have *Tænia gigantea* Peters. Not only was their specimen from a different host and different continent, but comparison of the length of their worm and the size of the separate proglottids with the description of Peters is sufficient to demonstrate that the two do not belong in the same species. It is equally certain that their material does not belong to the Indian species described by Deiner as *Anoplocephala latissima*. In my opinion it is more than probable that the specimens from *Rhinoceros sondaicus* described by Garrod and by MacCallum and MacCallum belong to the same and as yet unnamed species. Its distinctness from *Plagiotænia gigantea* (Peters) and *Anoplocephala latissima* Deiner has been demonstrated by Deiner and other authors. For it I propose the name *Plagiotænia longa* adopting a specific diagnosis based on the descriptions of Garrod (1877) and MacCallum and MacCallum (1912).

***Plagiotænia longa*, new species**

Scolex 4 mm. broad, 3 mm. thick, 3 mm. long. Suckers large, contiguous. Strobila narrows behind the scolex which causes it to be set out squarely in conspicuous manner. Ten cm. from scolex proglottids approximately 1.42 cm. in breadth; greatest breadth 6.5–7.5 cm. Length up to 600 cm. (twenty feet).

Genital organs functionally active in segments 2.5 cm. in width. These proglottids are approximately 2 mm. in length. Testes numerous, mostly anterior, mostly on the pore side. Cirrus armed. Ovary posterior, oötype one-third of width of proglottid from poral margin.

HABITAT.—Intestine of *Rhinoceros sondaicus*. Garrod states that the three specimens discovered by him were found in the commencement of the colon. The worms probably inhabit the small intestine and had passed into the colon after the death of the host.

In my opinion there is still some doubt whether *Anoplocephala vulgaris* Southwell may not prove to be identical with *Plagiotænia gigantea* (Peters) from the same host. The morphological differences noted in the original description are chiefly in the size of the scolex and in the length of the proglottids. It should be noted that, although Peters mentioned

a rostellum and neck in the species, such structures are not shown in the figures. Important differences between Southwell's description and the specimens that form the basis for the present study are found in the size of the scolex and of the suckers, in the development of the musculature, in the position and extent of the ovary, in size of cirrus sac, and size of eggs. The differences in size of scolex and of the suckers are considerable and it seems almost certain that the two forms can not be members of the same species. It is unfortunate that Southwell did not make a comparison of his specimens with Peters' description. He apparently was satisfied to demonstrate that his material was specifically distinct from that described by MacCallum and MacCallum. He says, p. 363: "Whether the MacCallums were correct in their inference that the worm found by them in *Rhinoceros sondaicus* is identical with those found by Peters and Murie in the African rhinoceros and Indian rhinoceros respectively, seems to be a matter of some doubt, having consideration to the enormous difference in size, but as neither Peters or Murie give any detailed account of the internal anatomy of these worms, it is impossible to form any definite judgment."

I am unable to agree with Southwell that it is impossible to form any definite judgment regarding the specific identity of the worms described by Peters, Murie, and Garrod. While the descriptions are brief, they do contain important data, and with the figures provide sufficient information to enable the observer to recognize the forms and consequently to establish the species. The original descriptions of many well known and generally accepted species are no more complete than the ones in question. Deiner's work has placed the Indian species of Murie on a firm basis. Southwell's conclusion that *Tænia gigantea* Peters could be disregarded because the description was brief and did not treat of internal anatomy is far from correct. Anyone familiar with the literature knows how few descriptions of that date, or for that matter of more recent periods, contain descriptions of the internal anatomy. The species is certainly valid and requires only the collection of additional material from the type host and type locality to complete the description. Such information is supplied in the present paper. Southwell's further conclusion that the name *Tænia gigantea* could be transferred to the Javanese species described by MacCallum and MacCallum is equally incorrect. His attempt to avoid confusion by associating the name *Anoplocephala gigantea* with the worm described by the MacCallums has quite the opposite effect. Since *Plagiotænia gigantea* is the name given by Peters to the African species described by him it must so remain, quite in-

dependently of either MacCallum and MacCallum's error in determination, or Southwell's good intentions. The fact that the specimens of Southwell are demonstrably different from the worm described by MacCallum and MacCallum does not establish the validity of *Anoplocephala vulgaris* or distinguish that species from *Plagiotænia gigantea* (Peters). The probability is that the two species are distinct, but the later account of Southwell (1922) in referring a specimen from *Rhinoceros sondaicus* to *Anoplocephala vulgaris* indicates that the species is not well established. Of course, it is always possible that museum specimens have been misplaced and incorrectly labelled and that the specimen referred to in 1922 was from an African source. If the record is correct and *Anoplocephala vulgaris* proves to be specifically distinct from *Plagiotænia gigantea*, the former species must occur both in Africa and India.

The idea presented itself that perhaps the white and black rhinoceroses of Africa, *Ceratotherium simum* and *Diceros bicornis* respectively, harbored different and distinct species of tapeworms. This appeared more probable in view of their particular food habits, the former species subsisting on grass, while the latter browses on shrubs and small trees. Such a conclusion would have been tenable, however, only if the original description of *Plagiotænia gigantea* had recorded the species from *Ceratotherium*. Peter's monograph on the mammals of Mozambique shows that he was familiar with both rhinoceros species and that both were present in the Mozambique area in the middle of the last century. His statement that *Plagiotænia gigantea* was from *Rhinoceros africanus* (*Diceros bicornis*) is clear and definite. Both *Plagiotænia gigantea* and *Plagiotænia vulgaris* are from the same host and the present paper is the first record of a cestode from *Ceratotherium*. There seems to be no doubt that this latter worm is the same as that described by Peters (1856) and that *Plagiotænia gigantea* occurs in both the black and white rhinoceroses of Africa.

In transferring *Anoplocephala latissima* Deiner and *Tænia gigantea* of MacCallum and MacCallum to the genus *Schizotænia*, Douthitt (1915) was admittedly treading on very uncertain ground. Consideration of the anatomical features of *Anoplocephala latissima* convinced Douthitt that the species does not belong in the genus *Anoplocephala*. He says, p. 41: "In one character only does this cestode resemble *Anoplocephala*; the genital pores are all dextral." In certain respects *Anoplocephala latissima* and the *Tænia gigantea* of MacCallum and MacCallum resemble *Schizotænia* and Douthitt expanded that genus to receive them. He emended the diagnosis of von Janicki to include the cestodes of the rhinoc-

erose, various species from rodents, and *Schizotænia decrescens* (Diesing), 1856, from *Dicotyles*. He then characterized the genus as follows:

Anoplocephalinæ, with segments broader than long. Genital pores regularly alternate or dextral, and in one doubtful species irregularly alternate. Dorsal excretory duct lateral of ventral. Genital canals pass usually dorsal of longitudinal excretory vessels and nerve, though the reverse condition has been observed. Testes confined to the median field, either distal in position or proximal, and mostly on the pore side. Cirrus pouch very large and muscular, cirrus spiny. External vesicula seminalis present. Vagina and vaginal pore anterior to the cirrus pouch. Female glands placed toward the pore side of the median field. Oviduct joins the ovary directly in front of the middle of the vitelline gland. Uterus not a simple transverse tube, usually perhaps always a degenerate reticulum; confined to the median field in anlage, and in its fully developed stage either there or crossing the excretory ducts mostly on the dorsal side. No pyriform apparatus. Adults in mammals.

Designated as type: *Schizotænia decrescens* Diesing, 1856.

The well-defined species he arranged in two groups:

I. *Magna* group. Genital pores dextral; testes mostly anterior and mostly on the pore side; size of known species enormous.

Schizotænia latissima (Deiner) and *Schizotænia gigantea* (Peters).

II. *Hagmanni* group. Genital pores alternate; testes posterior; known species small.

Schizotænia hagmanni von Janicki

Schizotænia variabilis Douthitt

Schizotænia americana Stiles

Schizotænia anoplocephaloides Douthitt

Concerning *Schizotænia decrescens* he says that this species "which von Janicki unfortunately designated as type of the genus seems to belong to the group and should be treated as such until better known." In defining the genus he stated that "the poorly known *Schizotænia decrescens* should not be given serious consideration. Its position in the genus is not assured and the statements concerning it are not clear cut and dependable." Notwithstanding the possibly unfortunate selection of von Janicki, *Schizotænia decrescens* is type of the genus *Schizotænia*, and, if other species differ from it in generic features, they can not be included in the genus. The genus as conceived by Douthitt is an unnatural assemblage and the inclusion of such different forms violates the morphological unity of a natural genus.

Meggitt (1924) followed the arrangement of Douthitt and included the rhinoceros cestodes in the genus *Schizotænia* which he characterized as follows:

Anoplocephalinæ: A single set of reproductive organs in each proglottis. Genital pores alternate. Genital ducts pass dorsally to longitudinal excretory vessels. Vaginal pore anterior to cirrus sac. Testes posterior, mostly poral. Female glands slightly poral. Extreme lateral portions of the uterus become functional early as sac-like enlargements; remainder of uterus develops as a complicated system of irregular lacunæ. Eggs with pyriform apparatus. Adults in mammals.

Type species. *Schizotænia decrescens*, Diesing, 1856.

Synonymy. *Plagiotænia* Peters, 1871.

Neither of the diagnoses are adequate or satisfactory and in regard to important features they do not agree with each other. Douthitt was in error in quoting Deiner regarding the position of the vagina and the vaginal pore. According to Deiner, in the species studied by him the vagina parallels the cirrus sac in the same dorsoventral plane and the opening of the vagina is immediately above that of the cirrus sac. I am inclined to suspect that in this instance the author confused dorsal and ventral sides. Douthitt was correct in removing the rhinoceros tapeworms from the genus *Anoplocephala* but their inclusion in the genus *Schizotænia* was not a happy solution of the difficulty. The *magna* group of Douthitt's genus *Schizotænia* (to which should be added also the species from the Javanese rhinoceros described by Garrod and the MacCallums and for which I have proposed the name *longa*, and also *Anoplocephala vulgaris* Southwell) are actually members of a distinct genus. Peters (1871) gave to it the name *Plagiotænia* and designated *Plagiotænia gigantea* as type. In my opinion *Plagiotænia* is not a synonym of either *Anoplocephala* or *Schizotænia* and should be accepted as a valid genus. It may be characterized as follows:

PLAGIOTÆNIA Peters, 1871

Anoplocephalinæ: Single set of reproductive organs in each segment, genital pores dextral, genital ducts passing dorsal to the longitudinal excretory vessel. Testes mostly poral, mostly anterior, mostly dorsal, extending from the longitudinal excretory canal of one side to that of the other. Cirrus spiny. Prostate gland reduced or absent, vagina ventral and somewhat posterior to the cirrus sac. Female organs on the poral side, posterior, ventral. Uterus at first tubular, branched and finally saccate. Eggs with pyriform apparatus. Type by designation, *Plagiotænia gigantea* Peters.

Contains the following species:

I.—*Plagiotænia gigantea* (Peters), 1856.

Tænia gigantea Peters, 1856.

Plagiotænia gigantea Peters, 1871 (in part).

Anoplocephala gigantea (Peters), 1856; Blanchard 1891 (in part).

Schizotænia gigantea (Peters), 1856; Douthitt, 1915.

Plagiotænia gigantea (Peters), 1856; Stunkard, the present paper.

II.—*Plagiotænia latissima* (Deiner), 1912. Stunkard, the present paper.

Tænia magna Murie, 1870 (name *magna* preoccupied).

Plagiotænia gigantea Peters, 1871 (in part).

Anoplocephala gigantea (Peters), 1856; Blanchard, 1891 (in part).

Anoplocephala latissima Deiner, 1912 (*magna* renamed).

Schizotænia latissima (Deiner), 1912; Douthitt, 1915.

III.—*Plagiotænia vulgaris* (Southwell), 1921; Stunkard, the present paper.

IV.—*Plagiotænia longa*, new species; Stunkard, the present paper.

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